NEURAL PLASTICITY AND THE LIMITS OF SCIENTIFIC KNOWLEDGE

Volume 1

Pasha Parpia

(Dawood Yusuf Parpia)

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This work is dedicated to the memory of my parents

Zohra and Yusuf

and my brother

Sulaiman.

I hereby declare that this thesis has not been and will not be submitted in whole or part to another university for the award of any other degree.

Signature:

UNIVERSITY OF SUSSEX

Pasha Parpia
(Dawood Yusuf Parpia)

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Summary

Western science claims to provide unique, objective information about the world. This is supported by the observation that peoples across cultures will agree upon a common description of the physical world. Further, the use of scientific instruments and mathematics is claimed to enable the objectification of science.

In this work, carried out by reviewing the scientific literature, the above claims are disputed systematically by evaluating the definition of physical reality and the scientific method, showing that empiricism relies ultimately upon the human senses for the evaluation of scientific theories and that measuring instruments cannot replace the human sensory system.

Nativist and constructivist theories of human sensory development are reviewed, and it is shown that nativist claims of core conceptual knowledge cannot be supported by the findings in the literature, which shows that perception does not simply arise from a process of maturation. Instead, sensory function requires a long process of learning through interactions with the environment.

To more rigorously define physical reality and systematically evaluate the stability of perception, and thus the basis of empiricism, the development of the method of dimension analysis is reviewed. It is shown that this methodology, relied upon for the mathematical analysis of physical quantities, is itself based upon empiricism, and that all of physical reality can be described in terms of the three fundamental dimensions of mass, length and time.

Hereafter the sensory modalities that inform us about these three dimensions are systematically evaluated. The following careful analysis of neuronal plasticity in these modalities shows that all the relevant senses acquire from the environment the capacity to apprehend physical reality. It is concluded that physical reality is acquired rather than given innately, and leads to the position that science cannot provide unique results. Rather, those it can provide are sufficient for a particular environmental setting.

Contents

VOLUME 1

VOLUME 2

Preface

In a fully scientific view of the world, only material things are real. Materialism sees the universe as a physical system. Everything that exists in it must be some sort of matter or something that emerges from matter. Indeed, the reductionist or mechanistic stance extends also to the life sciences for modelling brain function, through the assumption of a brain-mind equivalence, and, indeed, the materialist stance is applied widely in the realms of medicine.

Furthermore, there are many who question the notion of the brain-mind equivalence, and there have been moves to eliminate the notion of the *mind* by seeking to account for it in mechanistic terms by suggesting how it may be created in a computational device (For a history of approaches to this end see Boden (2006)). In this view, science is a project of exorcism that aims to rid scientific discourse of anything that cannot be understood in terms of physical laws. However, to date, there has been no satisfactory demonstration of mental functions such as attention, the capacity for phenomenal experience and free will in any computational device.

Be that as it may, none has sought to enquire in the present age, when significant advances have been made in neuroscience, how it is that the notion of *matter* arises in the human mind, and how the human organism becomes competent in functioning in the physical world?

In the present work *the key issue addressed is our capacity to perceive the material world*, and to evaluate the extent to which it arises simply through a process of maturation, as opposed to its coming into being through learning from our interactions with the developmental environment.

This issue has significant consequences for the status of matter given that there is extensive plasticity in the human sensory and cognitive systems. I will show that this issue is germane also to determining the status of science as a methodology for discovering absolute truths, as is generally claimed for it by the scientific community.

In the present work, a strictly scientific approach is taken to address the above-mentioned key issue using experimental results obtained from the broad domains of developmental neuroscience and diverse other areas pertaining to sensory function and deprivation in humans and other species.

Jean Piaget's work on child development in the early part of the last century provided a clue to the possibility that learning through exploration is a prerequisite for competence in dealing with the physical world. Namely, that our capacity to deal with physical reality was not given innately; it had to be acquired through learning.

The significant advances in the neurosciences and related disciplines over the past hundred years enable us to use the results accumulated to revisit some fundamental philosophical issues. In particular, we may now reassess the nature of physical reality through an examination of the physiological processes that allow us access to what we deem to be the physical world. It will be shown how this examination has consequences also for the status of science.

Our ability to perceive the physical world of objects appears to be stable across human populations, and a diversity of motivations, particularly over the past 500 years, have led to the development of the methods of Western science to describe and utilize what appears to be commonly manifest physical phenomena. That we generally agree about the properties of any given object has been attributed, tacitly, to the view that ‘core’ perceptual and cognitive capabilities are given innately, and therefore render the apprehended properties of objects fixed across individuals.

However, studies of sensory development and deprivation in humans and laboratory animals, sometimes in controlled environments, have led to the discovery of extensive plasticity in the nervous system that now suggests that we need to *learn to perceive*. Further, it is proposed that the reason that the world of objects appears to be the same across populations is because the environmental settings have, in general, common affordances for the configuration of the individual nervous systems enabling perception.

Plasticity in the nervous system has fundamental consequences for the status we may attribute to physical reality and indeed the status of science. This is because science relies upon empiricism, and thus on perception for the generation and evaluation of its theories. So sensory development in radically different environments might, in principle, result in significantly differing senses. Such findings also bring to the fore the issue of the status of what we perceive; of whether we may, with any degree of confidence, entertain a notion of a unique, universal reality or science.

The traditional developmental psychological view, that a set of 'core' concepts and perceptual capacities are given innately, which ensure a common stable world of objects, has been challenged by contemporary models of brain development, and resist also what has been previously meant by the notion of innateness. Instead, these contemporary models emphasize that the process of brain development engages both inherited and environmental factors, and relies on their dynamic interactions. It would appear that neuronal plasticity not only participates in the generation of memory but extends also to the configuration of our senses through whose agency memories form.

In this view, the temporally early structuring of the sensory and cognitive systems occur during appropriate 'critical' periods for the different sensory and cognitive functions, during which time the relevant nervous tissue is particularly plastic. Following this 'window' period, the underlying nervous fibres and connections remain relatively stable, and enable the interactive construction of higher order structures, although conceptual and motor learning can, clearly, occur at all stages of life.

It would seem from the work to be presented here that we learn to see, hear and touch etc. in much the same way as we learn, for example, our first language, relying on input to our senses for the process of sensory and cognitive configuration to take place. Support for this proposal allows us to question whether what we apprehend as the real objective world may be not unique but contingent particularly on the input to the senses during early life. If so, it may require a re-assessment of the nature of physical reality and indeed the status of empirical science.

The work presented here has been carried out principally by meta-analysis of published literature, in the same manner as that employed for the author's recent paper on the role of neural plasticity in the origins of the discontinuities in the somatosensory homunculus (Parpia, 2011).

In the present work, the role of empiricism in the scientific method is initially outlined, and the sensory modalities through which physical reality is apprehended are delineated. The neuroscience underlying learning is explored along with studies, for instance, of sensory deprivation and critical periods in the various stages of human development. In addition, literature from diverse subject areas including physics, computational neuroscience and anthropology are accessed.

The analyses presented use the conventional 'bottom-up' approach of neuronal activity-driven learning; it is a reductionist, activity-dependent account of neuronal processing that is considered to lead to lasting changes in the stimulus-response relations between the neurons. The approach is directed at analysing the development of the human sensory and cognitive systems in respect of the capacity to perceive the physical quantities generally used by physicists to construct and evaluate their theories.

More specifically, it is proposed that the sensory systems learn to recognize repeated sensory primitives present in the input data stream, in a particular environmental setting in much the same way as a child learns to recognize the phonemic primitives present in any particular linguistic setting and thence the meaning of words. And indeed, that the human motor repertoire used for perception through tactile manipulations is composed of motor primitives learned from activities afforded in a particular environmental setting.

A validation of this suggestion would imply that what the subject apprehends as a material object is not a fixed entity, because different environments will cause the senses to be configured differently, and two individuals raised in radically different settings would apprehend the physical world in their own separate ways. Underlying the scientific method, by contrast, is the view that material objects have shared characteristics irrespective of who describes them.

Such separate perceptions of the physical world would challenge the status of science, because proper use of the scientific method requires that its theories be evaluated through a final arbitrator: experiment, with physical events interpreted through human perception. The existence of plasticity in the realms of sensory perception, as suggested above, brings into question the existence of a universal objective reality.

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1

INTRODUCTION

Perhaps the most important legacy in the formalism of science is that left by Newton in his composition of classical mechanics (in *Philosophae Naturalis Principia Mathematica* – Mathematical Principles of Natural Philosophy, published in 1687), where he established for the first time a close mapping between a formal system and the behaviour of real physical objects (Rynasiewicz, *Stanford Encyclopaedia of Philosophy*). A formal system is an abstract, usually mathematical, structure consisting of definitions and axioms from which theorems or proofs may be derived. In themselves, formal systems tell us nothing, since we can construct them with whatever properties we desire. A formal system only relates its assumptions to its conclusions via its inference rules, and in general we are free to choose these rules arbitrarily. However, scientific theories are crafted to derive their worth through their capacity to relate abstract thought to the physical world. Euclid of

Alexandria’s work on plane geometry (*Elements, ~ 300 BC*) is held to be the first formal system.

The issues raised bring to the fore the following two points:

1) What is the status of a formal system
2) What is the status of physical reality

Newton’s theory was supported by extensive terrestrial experiments carried out in diverse areas of mechanics and by minutely detailed astronomical observations that together provided a fit between theory and experiment so close that the Newtonian theory of mechanics was taken by many for the literal truth.

These ‘truths’ about the behaviour of physical objects remained largely unchallenged among natural philosophers (physicists) for more than two hundred years until the early part of the twentieth century when Newton’s view of absolute space, absolute time and simultaneity of events were supplanted by notions derived in Einstein’s Special Theory of Relativity (Einstein, 1905; see, for instance, Smith, 1965).

Newton conceived of both space and time as being absolute: space existed independently of the presence of bodies within it, and time ‘… from its own nature passes equably without relation to anything external.’

In Newton's view, a pair of observers in relative motion, each estimating the rate of passage of time for the other would find that time passed at the same rate for the other as it did for himself irrespective of their relative speed. Also, all mutual measures of length and mass by such observers would be in accord.

The formal system that comprised Einstein's Special Theory of Relativity was based on two axioms in addition to those employed by Newton in his mechanics. These are Einstein's two 'postulates':

1) That the laws of Newtonian mechanics apply in what Einstein referred to as 'inertial frames of reference', and that in all frames of reference moving uniformly relative to an inertial frame, the same laws of physics hold.
2) That the speed of light is independent of the speed of its source.

Using just these two postulates, in addition to Newtonian mechanics, and much thoughtful algebra Einstein charted out his Special Theory. His work challenged Newtonian notions of absolute space and time. According to Einstein's theory, time would be estimated to pass more slowly for a relatively moving observer (time dilation), and that length measures, as determined by the relatively moving observer, would be shorter (relativistic length contraction). Such measurements in relation to mass would show them to be greater in the relatively moving frame of reference. Results obtained for the values of mass, length and time, in the case of the Special Theory, would vary depending on the relative speed of the two observers. Einstein’s formal system, or theory, has been amply substantiated, once again, by empirical observation.

Einstein’s finding challenged the very core of the basis of physical reality because mass, length and time are the three ‘fundamental dimensions’ used for the description of all physical phenomena by use of algebra (see chapter 4), and yet empiricism deemed Einstein’s theory to be valid. It is little wonder that Einstein asked the participants gathered at the first international course of lectures in Davos (among them Jean Piaget), over which he presided, to evaluate: ‘Is our intuitive grasp of time primitive or derived?’ (Piaget, 1969; see also chapter 10).

The common theme in the advance of physics has been its methodology: of having a specified formal system, with its definitions, axioms and proofs, and of having a mapping process whereby events in the world are related to the formal system. In other words, the methodology consists of having a mathematical theory for the description of the behaviour of physical phenomena and empiricism as a means of evaluating the theory.

It is worth emphasizing the fact that having the algebraic expression of a theory within a formal system does not in itself give the theory any greater validity, as was witnessed by the supplanting of Newtonian mechanics by Einstein’s Special Theory. It is empiricism that is the final arbitrator.

Newton's classical mechanics and Einstein's Special Theory are but two examples of the general schema of the scientific approach. Many areas of academic enquiry have aspired to emulate this scheme, and have met with varying degrees of success according to the complexity of the problem-domain and, indeed, the competence of the participants. In the present age the mechanistic or reductionist approach also dominates the Life Sciences and Medicine.

Even though a well-defined formal system may not be always feasible, what the scientific approach in the different disciplines relies upon in common is empiricism; science is dependent on human perception to make measurements to evaluate the results of experiments. Scientific instruments, as will be elaborated in chapter 2, cannot ontologically substitute for the human senses.

Apart from phenomena such as illusions, our perception of the physical world is considered to be stable and uniform across populations, and is not generally questioned. In this respect, there seems to be little doubt that our perception may be thought to be reliable informants of our settings. They allow us to establish what is real, and it is with respect to this reality, in essence, that scientific theories are formulated and evaluated.

The worth of science, then, depends on human senses in respect of their being a source of reliable (temporally stable and culturally and environmentally universal) information. However, the facts as they are perceived cannot transcend their human origins. This view provides the orientation that will be adopted in regard to Einstein's question posed at Davos and the 2 points mentioned earlier.

Accordingly, the current work seeks to address the processes underlying the ontogeny of human perception and cognition, relevant to empiricism, in the nervous system in order to addresses the status of science. Such an enquiry seems apt in that for several decades the central debate within developmental psychology has focussed upon the question whether and to what degree is the neonate innately equipped to interpret and act upon the world as it matures, and to what extent does his sensory and cognitive development rely on learning?

It will become clear in the course of the present enquiry, as Boden (2006, p. 275) notes, epigenetic development does not fit the nature versus nurture dichotomy, because what happens at any moment during its course depends on both the genetic constituents and the environment, and indeed, the prior history of the organism.

Traditional nativist developmental psychologists accounted for the finding that our organs of perception conveyed, apparently, a common physical reality on the grounds that our nervous systems are innately endowed with rudimentary 'core' concepts. It is claimed that the items of core knowledge relate to language, mathematics, mapmaking, tool-use, reasoning about the physical and social world and so on (see, for instance, Stiles, 2008, 2009). These 'component cognitive systems' are built upon in subsequent lifelong learning, and are '… mechanisms for representing and reasoning about particular kinds of ecologically important entities and events – including inanimate, manipulable objects and their motion, persons and their actions, places in their continuous spatial layout and their Euclidean geometric relations, numerosities [sic.] and numerical relationships.' (Spelke, 2000). Under this view, a stable, reliable common perception might result across human populations.

However, Jean Piaget's work on child development suggested, by contrast, that learning through exploration is a prerequisite for competence in dealing with the physical world (see chapters 2 and 3). This work provided a clue to the possibility that our very organs of perception (and cognitive systems) might have to acquire their capacity to apprehend the physical world; that perceptual competence does not result simply as part of a natural process of maturation. Rather, the organs of perception become functional only by learning through interacting with the input from the environment.

Following Piaget's lead in his studies of development in infant and child behaviour, the position of the nativist psychologists has been vigorously challenged through the substantial progress made by David Hubel and Torsten Wiesel on plasticity in the visual cortex (see, for instance, Hubel et al., 1977 and chapter 3), Donald Hebb's contribution to the theory of learning in the nervous system (Hebb, 1949; see also Schott (2011) for citations of other workers' input to the neurophysiology of learning) and the advent of the constructivist approach to brain development and function in recent decades (Quartz and Sejnowski, 1997; Quartz, 1999; Westermann et al., 2007; Stiles 2008, 2009). Computational modelling of brain function too has provided 'existence proof' for the constructivist stance (see, for instance, Rumelhart and McClelland, 1986; McClelland and Rumelhart, 1986; Kohonen, 1987; Anderson and Rosenfeld, 1988. For a historical account see Boden, 2006).

The current work seeks to address the processes underlying the ontogeny of perception and cognition relevant to empiricism. An example is provided below to illustrate the effects of visual deprivation on the development of visual perception.

1.1 Visual Plasticity and Sensory Configuration – An Example

Blakemore and Cooper's seminal work on visual development in kittens demonstrates the effect of the early environment on subsequent visual competence (Blakemore and Cooper, 1970). The kittens in the experiments were housed in a completely dark room for the first two weeks after birth.

They were subsequently kept for about 5 hours a day in an apparatus (see Fig. 1.1 (left)), where the kittens sat or stood on a clear glass platform inside a tall cylinder, the entire inner surface of which was covered with high-contrast black-and-white stripes, either horizontal or vertical. The routine of being either in the apparatus or in the dark room lasted till the kittens were 5 months old, until after the end of the 'critical period' (see chapter 3, §3.2.3, footnote 4), during which time visual deprivation is known to cause severe sensory deficits (Hubel and Wiesel, 1970). From a qualitative evaluation of their behaviour the authors noted that the kittens were found to be virtually blind for contours perpendicular to orientations they had been exposed to; they could see only edges of orientations they had previously experienced.

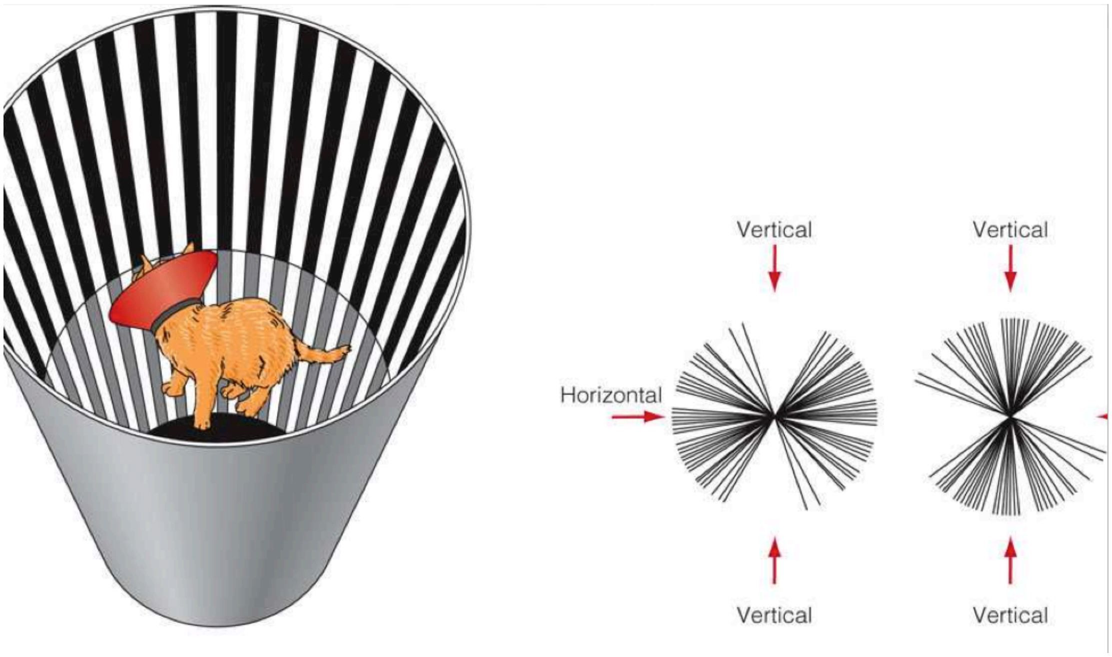

Fig. 1.1 Left: the apparatus (vertical stripes) used, with the kitten wearing a ruff to mask sight of its body. Right: polar histograms of single cell recordings from striate cortex showing the optimal orientations from a horizontally experienced cat on the left and a vertically experienced cat on the right (Blakemore and Cooper, 1970).

On examining the responses of neurons in the kittens' visual cortex, that were selective for lines and edges in the visual field, when the cats were 7.5 months old, it was found that the orientation of edges to which these cells would respond was highly abnormal. The cells, whose orientation preference would normally be distributed 'around the clock', were found to be skewed. The orientation preference of the neurons was found to be centred around the orientation of the black-and-white stripes they had previously experienced in the enclosure (either vertical or horizontal), see Fig. 1 (right).

Blakemore and Cooper’s experiment is but one of the many such that elaborate upon plasticity in the mammalian sensory and cognitive systems. A large number of studies have been carried out on plasticity over the intervening 40 years. These will be elaborated upon in chapter 3 and elsewhere in the thesis.

2

PHYSICAL REALITY

2.0 Introduction

The conventional scientific view of reality is that it is ultimately constituted or determined by entities – objects, events, properties and so on – that are physical. Physical objects have shared characteristics irrespective of who describes them. They are thought to exist regardless of any knowledge or perception there may be of them. As the classical physicist would have defined them, they have mass, spatial extent, and at any time have a location in space, independent of human conception or consciousness of them.

Further, it is assumed that any two people can agree, after an opportunity to clarify terminology, about the nature and state of a classical object regardless of any separate cultural backgrounds. Such a view is consistent with the conception of a veridical nature of the human perceptual system, in that it is a faithful informant of the state of the environmental setting, and is in accord with the nativist psychologist's view of the existence of a universal 'core' knowledge about the world that enables a genetically moderated association between 'reality' and the way in which the sensory system works (Stiles, 2008, p. 1; Stiles, 2009).

In his work, the experimental physicist takes the physical environment and the objects of his interest to be so convincingly present physically, that he feels he has little doubt of the reality of what he perceives. Such an 'objective' stance is assumed by anyone attempting to take the scientific approach to the study of any problem.

In the nineteenth century the branches of physics were classified according to the sensory modality that most aptly corresponded to the physical phenomenon under investigation: optics, acoustics, heat, mechanics etc. With a greater understanding of the underlying processes at the atomic and molecular levels, a common substrate emerged so, for instance, radiant heat became unified with optics through being understood as infrared radiation and heat conduction allied with the mechanics of molecular motion and so on.

Thus, instruments began to be used that measured these underlying mechanisms and came to be substituted for the human senses, and along with them 'human frailties' were increasingly removed from the process of scientific measurement. This progression made for greater objectification, and ultimately a more precise expression of physical behaviour in the language of mathematics.

However, it is crucial to realize that the substitution of the senses with scientific instruments does not eliminate the ontology of the observer from the process of making measurements. The human being designs the instruments so that they function in a way that informs his notion of physicality. This relationship ensures that the output of the measuring or recording device is meaningful.

For instance, if a microscope, designed to replicate and extend the effect of moving one's eyes closer to the object of study, should also progressively rotate the image as the magnification is increased, one would say that the instrument is not functioning correctly. This is because such a rotation of the image is not a part of the human experience in the unaided situation.

In respect of the elaboration of human experience by scientific instruments, Smetacek and Mechsner (2004), and Raymond Tallis (1991), respectively, observe:

> Just as tools are extensions of the body, so basic scientific instruments – the balance, pendulum and measuring rod – are extensions of the body sense.
>
> Smetacek and Mechsner (2004)

> Scientific measurements may 'correct', 'reform' or at least question individual unaided observations but there cannot be a systematic, universal discrepancy. The truth of

> scientific observations in this context must therefore be based ultimately upon subjective experience and cannot transcend it.
>
> Tallis (1991, p. 52)

Thus, it seems clear that the functioning of science proceeds through the final arbitrator: experiment, with physical events interpreted ultimately in the human domain. That is, through the gross human perceptions at the end of the causal chain of any measuring devices, which are themselves contrived to be in accord with human perceptual expectations. And even though Karl Popper would insist that a key feature of a well-formulated scientific theory is that it should be structured in a form so that it is capable of being falsified (Popper, 1959), it is ultimately through human observation that the process of falsification may be carried out. This is not to deny freedom to the physicist in the formulation of theories that might predict results that might be unexpected to human anticipations, as in the case of relativistic length contraction mentioned in the *Preface*. Popper would, however, require that theories be open to falsification through experiments – that might be interpreted in the human realm.

Two major crises occurred in physics at the beginning of the twentieth century, with the proposals of the theories of Quantum Mechanics and Special Relativity (Herbert, 1985). In the Copenhagen interpretation of Quantum Mechanics, the classical notion of the permanence of dynamic objects was called into question. The location, at any time during its flight, of what manifests as an individual particle, could not be enquired about. Objects, whose quantum behaviours are readily demonstrable, like an electron or a photon, could show their presence only when a measurement takes place. It was inappropriate, according to this interpretation, to expect to have one's classical notions satisfied about the physical location of the particle between measurements. Quantum Mechanics also challenged the notion of direct causal relations between interacting objects.

Any deeper theory, that might contain this information, compounded in classical terms, was unavailable within the scope of Quantum Theory. It is for this reason Einstein considered the theory as being incomplete. He felt that a deeper theory should be sought, which would be in accord with our everyday sense of physicality.

Einstein's Special Theory of Relativity altered our notion of mass and energy and showed that space and time could not be regarded as separate entities but were interrelated as a result of his formalism.

Be that as it may, the evaluation of both the theories of Special Relativity and Quantum Mechanics have rested upon empirical evidence, and to date, these theories have withstood diverse experimental tests.

Many of those who participated in the development of Quantum Theory wrote about the challenge that the theory posed to our notion of physical reality (Bohm, 1980, Bohm and Hiley,1984; Bohr, 1963; Einstein, 1950, 1954; Heisenberg, 1958; Planck, 1963; Schroedinger, 1965 and Von Neumann, 1955, amongst others). Although some of these authors acknowledged that there was a need to enquire into our mode of knowing the external world, they could not directly address the issue because an appropriate depth of understanding of the workings of human perception and cognition was, at that time, still in its infancy.

It is worth reiterating at this juncture that the present enquiry is not concerned specifically with quantum phenomena or particles moving at close to relativistic speeds. Rather, the work is directed at examining the physiology underlying the perception of macroscopic objects.

2.1 Einstein on Science and Epistemology

Albert Einstein's legacy to physics and science extends to the philosophy of science, cognition and epistemology, and due credit is given here to his contributions. In his later years Einstein reflected about science thus:

> Science is the attempt to make the chaotic diversity of our sense-experience correspond to a logically uniform system of thought. In this system single experiences must be correlated with the theoretic structure in such a way that the resulting coordination is unique and convincing.
>
> The sense-experiences are the given subject-matter. But the theory that shall interpret them is man-made. It is the result of an extremely laborious process of adaptation: hypothetical, never completely final. Always subject to question and doubt.
>
> Einstein (1950, p. 95)

Both Einstein's and Newton's methodologies accepted that mapping sense experiences with the theory was the correct means for assessing the worth of the theory in seeking fundamental truths. And, despite the fact that Einstein's Special Relativity altered our notion of time and space, as not being in accord with common experience, the evaluation of the theory relied on empiricism. That is, theory evaluation took place through the use of ordinary human observations or by use of instruments that complied with a human comprehension of what was being measured. This exemplifies the level of the present enquiry. The current work is directed at ordinary or Classical human perceptual capacities: common experience. Although perceptual processes might be analysed at the quantum level, the current work dwells neither in quantum phenomena within the human sensory system nor on illusions or hallucinations to form the substance of its narrative.

Einstein goes on to elaborate upon the status of sense-experience and whether or not it has the capacity to provide any essential reality.

> The belief in an external world independent of the perceiving subject is the basis of all natural science. Since, however, sense perception only gives information of this external world or of ‘physical reality’ indirectly, we can only grasp the latter by speculative means. It follows from this that our notions of physical reality can never be final. We must always be ready to change these notions – that is to say, the axiomatic basis of physics – in order to do justice to perceived facts in the most perfect way logically. Actually, a glance at the development of physics shows that it has undergone far-reaching changes in the course of time.
>
> Einstein (1931)

Margineau observes that Einstein, in common with practically all scientists, assumes the existence of an external objective world (Margineau, 1977), but Einstein clearly had the wit to leave unanswered the basic metaphysical problem underlying all science: the meaning of externality. That is, he gives credence to the position that the ‘perceived facts’ are dependent on the human system (see §2.4); the issue of the external world independent of the observer must be left open.

Albert Einstein regarded the generation of reality in physics as being a two-step process. The first is generated by the repeated presentations of sense experiences that give rise to the notion of different bodily objects. The resulting sense impression of bodily objects he takes as given. The second step is the one of analysis and theorizing. It is out of this theory that the *notion* of a reality or 'a real existence' is generated. It is worth noting Einstein's reflections upon physical reality and comparing them to those elaborated upon above. It is, further, plain to see the accord between Einstein's ideas of the construction of images out of primitives familiar to contemporary neuroscience. (see §3.6.8 and, particularly in regard to the generation of meaning, see chapter 9, §9.1.1.

> I believe that the first step in the setting of a 'real external world' is the formation of the concept of bodily objects and of bodily objects of various kinds. Out of the multitude of our sense experiences we take, mentally and arbitrarily, certain repeatedly occurring complexes of sense impression (partly in conjunction with sense impressions which are interpreted as signs for sense experiences of others), and we attribute to them a meaning – the meaning of the bodily object. Considered logically this concept is not identical with the totality of sense impressions referred to: but it is an arbitrary creation of the human (or animal) mind. On the other hand the concept owes its meaning and its justification exclusively to the totality of the sense experience we associate with it.
>
> The second step is to be found in the fact that, in our thinking (which determines our expectations), we attribute to this concept of the bodily object a significance, which is to a high degree independent of the sense impression which originally gave rise to it. This is what we mean when we attribute to the bodily object 'a real existence.' The justification of such a setting rests exclusively on the fact that, by means of such concepts and mental relations between them, we are able to orient ourselves in the labyrinth of sense impressions. These notions and relations, although free statements of our thoughts, appear to us as stronger and more unalterable than the individual sense experience itself, the character of which as anything other than the result of an illusion of hallucination is never completely guaranteed. On the other hand, these concepts and relations, and indeed the setting of real objects and, generally speaking, the existence of the 'the real world,' have justification only in so far as they are connected with sense impressions between which they form a mental connection.
>
> Einstein (1950, pp. 59-60)

As mentioned earlier, Einstein's interest in matters epistemological manifested amply when he presided over the first International Course of Lectures on Philosophy and Psychology at

Davos in 1928 (Holton, 1982), which Jean Piaget attended. Einstein urged the participants to work towards determining whether the notions of space and time, which his work on the Special Theory had radically altered, were primitive or derived.

Piaget acknowledges his being prompted thereby to investigate these questions in the foreword of *The Child's Conception of Time* (Piaget, 1969). Indeed, Piaget directed much of his work, within the sphere of child development, to addressing the fundamental concepts like space, time, and causality, salient both to Relativity Theory and Quantum Mechanics.

2.2 Sensation, Perception and the Objective Stance

On the subjective level, all sensory experience is accessible to cognitive analysis, and indeed to being restricted and processed selectively through the agency of attention. An objective stance entails a choice in a disciplined manner to remove the wider ramifications associated with sensory input so as to be left to consider only those aspects of the sensory process pertinent to the scientific enquiry: what happened, what was apprehended by the senses?

Given that the subject matter of the current enquiry is the apprehension of physical reality, it seems appropriate to address the issue of perception. There exists discussion in the literature about the distinction between 'sensing' and 'perceiving'. For instance, Nicholas Humphrey (1993, pp. 116-126) holds that sensing is personally directed and requires the specification of the modality through which the sensation was derived. For instance, in the somatosensory realm, the body part – the locus of where it was felt – too, would need to be indicated.

Perception, by contrast, he maintains, is ‘out there’ and is potentially, universally accessible. Perceptions are concerned with what they signify in the external world, and according to Humphrey, are essentially amodal.

In respect of perception, the philosopher Ned Block makes the distinction between ‘Representationism’, ‘Mental Paint’ and ‘Direct Realism’ (Block, 2010). By Representationism he indicates the philosophical position that the world we see in conscious experience is not the real world itself but a replica of the world in an internal representation. By ‘mental paint’ he suggests that perception can extend beyond a direct awareness, and representational content to include the many mental features that the input can prime. For instance, the smell of burning toast can prime the scene of smoke in the kitchen and the anxiety provoked by the prospect of the activation of the smoke-alarm. Mental paint, then, consists in the sensory elaborations upon the initial perception of burning toast.

Humphrey (1993) quotes Thomas Reid (1785) on the distinction between sensation and perception thus:

> The external senses have a double province – to make us feel, and to make us perceive. They furnish us with a variety of sensations, some pleasant, others painful, and others indifferent; at the same time they give us a conception of an invincible belief in external objects. This conception and belief which nature produces by way of

> perception we call *sensation* [itals in original] …. When I smell a rose, there is in this operation both sensation and perception. The agreeable odour I feel, considered by itself, without relation to any external object is merely a sensation …. Perception [by contrast] has an external object; and the object of my perception, in this case, is that quality in the rose which I discern by the sense of smell.
>
> Humphrey (1993, pp. 24-25)

However, Humphrey elaborates upon a state where sensation and perception may be separable, at least for the sake of argument, quoting Schachtel (1963), who makes the distinction between the ‘autocentric’ and ‘allocentric’ modes of experiencing the world. In the autocentric, there is no objectification of the source of input. Rather, there is an assessment only of degrees of aesthetic appreciation, as in the assessment of the effects of different types of music, for instance. In the allocentric mode, the nature of the object is dwelt upon. There is thus the sensation (autocentric) – perception (allocentric) distinction.

Humphrey goes on to elaborate, citing Reid (1785) that it is ultimately impossible to distinguish between sensation and perception. However, with the rise of science, there has been an increasing objectification of the world. There is hope of a resolution, through clarifications provided by E.D. Starbuck (1921), of the distinction between the same sensory input from objects in the world that may be interpreted in two different ways. Humphrey (1993, p.26) cites him thus:

> There has been a double line of development and evolution [both] equally important: the one moving fast and far in the direction of description, scientific analysis, practical manipulation, logical construction, and system-building. The other line has achieved equal success in interpreting its objects and their meanings in subtle and skilful ways and in holding the individual in right relationship to his world of experience….
>
> Starbuck (1921)

A similar distinction is sought between perception and cognition to limit, and so, simplify the domain that needs addressing in respect of the issue of the environmental configuring of the human sensory and cognitive systems that behold physical reality.

In this respect it would be useful to eliminate from the present scientific enquiry cognitive aspects that have ‘linguistic and cultural, higher-level’ sources of input because they enlarge the task domain and reduce the scope of the conclusions the current limited enquiry might deliver. However, such an aspiration cannot be entirely fulfilled, as will have to be conceded while considering the status of time as used in algebra (see chapter 10).

Jesse Prinz, in his philosophical work *Furnishing the Mind* (Prinz, 2002), sought to uphold the view that ‘Nothing is in the intellect that is not first in the senses’. This view implies that the higher order concepts derive their constituents from the lower orders of sensory processing. Perception thus corresponds to a lower order of analysis, while the term cognition represents the higher. Such a distinction is manifest in the visual system, for instance, where the primary visual cortex is sensitive to local features of objects such as the orientation of contours at specific retinal location, whereas neurons in V2 respond to ‘virtual’ contours; IT neurons respond to overall object features such as shapes. Such segmentations enable the process of visual object recognition (see, for instance, Desimone et al., 1990).

Admittedly, this model is a simplification of what is essentially a *heterarchical* rather than a hierarchical organization in the human brain, as will be briefly dealt with in chapter 3, with re-entrant feedback projections from the higher regions substantially influencing processing in the primary and lower sensory regions. Nevertheless, these feedback projections are reliant on the bottom-up pass for the initial segmentation processes, and so an attempt to restrict the definition of what constitutes the physical seems apt.

With the objective of containing the problem while addressing low-level reality (rather than all of the intellect), I seek to make a distinction between the terms ‘physical reality’ and ‘the *apprehension* of physical reality’.

‘Physical reality’ as used here is intended to convey the wider phenomenon, and aspects of a naïve physics are included in the term so that it incorporates the behaviour of objects, in having mass, for instance, and so a propensity to fall under gravity, and, under the pervasive influence of Newton’s mechanics in the present age, to obey in outline his laws of mechanics and motion. Clearly, what might be thought of as ‘physical reality’ will vary in any community according to whether they adhere to, metaphorically, for instance, the ‘phlogiston’ or atomic theory of heat. However, both will apprehend physical reality as being the same in that a short metal rod held in a flame will be apprehended to get hotter according to the period for which the heat source is applied.

It is Ned Block’s third meaning, Direct Realism, which refers to the perceptual experience constituted by the direct experience of the properties or objects in the world, that comes closest to that intended in using the term ‘apprehension of physical reality’ in the present work. Thus, the term ‘physical reality’ includes theoretical properties of bodily objects in addition to those required for their bald perception, whereas ‘the apprehension of physical reality’ is intended to mean being perceptible to the senses without necessarily singling out any particular sensory modality, and leaves out, in so far as it is possible, the theoretical aspects of the behaviour of objects, and only requires an ability for their minimal perception. In this sense, the word ‘apprehend’ is used in its multimodal sense: ‘know’ or ‘understand’, and unlike the terms ‘grasp’ or ‘see’, that have modal connotations. ‘Apprehend’ is not intended to mean ‘seize’ or ‘arrest’.

After all, before about the year 1500, people in the West generally understood events in the natural world in terms of organic relationships within the teleology provided by the Christian scriptures. These relationships were interpreted by Thomas Aquinas (1225-1274) by incorporating the views on theology and ethics held by the Christian Church, and the legacy of Aristotle (384-322 BC), as comprising a comprehensive system of nature. It was based on both reason and faith, with the objective of understanding the meaning and significance of things as they abutted people’s lives, rather than seeking to predict and control them in the way the Enlightenment has influenced our thinking. Theological questions and those relating to the human soul and ethics were considered to be of the highest significance (see, for instance, Capra, 1983).

In the example provided earlier by Starbuck, there is a common starting point in the apprehension of objects. However, their interpretations are separate. The point of interpretative divergence provides the demarcation between what is referred to as ‘the apprehension of physical reality’ and ‘physical reality’ in the current work. The ‘double line' is common to the objectives of (1) 'scientific analysis', 'system building' etc. and (2) interpreting objects in respect of obtaining the 'right relationship' for the individual with regard to his world.

Current neurophysiology, as discussed earlier, is in accord with the view that the 'raw' afferent pass of activity from the sensory receptors into the higher cortical regions is generally followed by an efferent feedback projection that carries information from higher-order memory stores. These stores in any age would contain information compounded in a manner determined by the prevailing paradigm of analysis. In the present age in the West, this efferent pass would be, in general, tempered by reductionism, materialism and the other features imbued in us by the Enlightenment, as mentioned, in the interpretations that would be made of the signals from the sensory receptors. Pre circa 1500, the analyses would be tempered by the medieval mindset, as mentioned earlier. It would be, however, hasty to assume that apprehension of physical reality for both the pre and post 1500 AD cohort will be identical.

The separation of sensation and perception, dwelt upon by Reid, provides an interesting dichotomy but is not realizable unless one is considering a fetus or infant in a sufficiently early stage of development, where the notion of bodily objects have yet to develop – a state that this thesis suggests exists.

Nicholas Humphrey, Thomas Reid, Ernst Schachtel, E.D. Starbuck and Ned Block's intuitions about sense perception provide examples of the degree of elaboration that can be engaged in within a philosophical treatise. The present thesis, although indebted to such work, does not seek to apply the philosophers' methodology, of analysing the finer distinction between the meaning of words and the coining of new terms, in order to evaluate the status of science. Instead, the present work is intended to be a scientific enquiry, with the analysis of empirical results providing the substance of the labour. Furthermore, the present work seeks to initially define scientific reality in terms used by physicists to mathematize science, i.e., in terms of the three fundamental dimensions: of mass, length and time. The work will then examine, using the scientific method, to show that the capacity for the apprehension of each of these fundamental dimensions is acquired. This is due to the plasticity inherent in neural tissue. In this manner, the application of science will be used to assess the limitations of scientific knowledge.

In sum, by the term 'apprehension of physical reality' I mean perception of material objects or phenomena with the barest minimum of theoretical accompaniment in respect of the nature of matter. Essentially, it is concerned with the gross perception of classical objects such as 'buttons and bows'. 'Physical reality' in accord with Einstein's position mentioned earlier, by contrast, is open to as much theoretical elaboration as is appropriate for the context in which it is being used.

Postscript: It is reassuring to find that what is referred to as 'apprehension' herein is what most experimental studies that will be cited do, indeed, measure and refer to as perception. Words and expressions used in the present work are intended to have their standard English dictionary meanings, and the meanings of technical terms used may be found in volumes such as *The Oxford Dictionary of Psychology* (2006); *The Oxford Companion to the Mind* (1987); *A Student's Dictionary of Psychology* (1999); *The Penguin Dictionary of Biology* (2004) and the glossaries provided in texts such as *Neuroscience* (1997) and *The Fundamentals of Brain Development* (Stiles, 2008).

2.3 A Sketch of the Argument

If the functioning of the human perceptual system were regarded as primitive, our capacity to apprehend the physical world would develop simply through a process of maturation. These basic perceptual capacities would be universally manifested, and occur independently of the environment in which the subject developed. Under this assumption, the basic notions of physicality will be stable through many thousands of years, given that change in human genetics associated with sensory perception has occurred only slowly, and what was perceived to be a physical entity would be common to all cultures[1].

Human perception of the physical world can then form a reliable and universal bench-mark against which one might formulate and evaluate scientific theories. Whether or not the practice of science, under these conditions, gives us access to any ultimate truths is not at issue. It is just that a situation where a common human capacity to perceive is genetically determined provides for a given, stable platform from which we may construct (and evaluate) our theories of physical reality.

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[1] The human gene pool can be radically altered or entirely annihilated in the event of a cosmic disaster. However, such an event is not countenanced in the present consideration.

Alternatively, the human perceptual systems may be partly or wholly configured in the self-same nervous system by environmental factors. In this case, a stable human-based definition of physical reality, and in consequence, the notion of a universal, stable science, becomes problematic. The situation being considered here is of the likelihood that the human sensory systems become configured through their interactions with the environment *within a single lifetime*, or substantially before the ends of their respective critical periods.

Prompted by Einstein's question, about whether or not the concept of time is primitive or derived (see *Introduction*), the present study is directed at considering the extent to which our capacity to apprehend physical reality in its relation to evaluating scientific theories is (1) innate, that is, genetically pre-determined, and therefore fixed and constant across cultures. This is assuming that the manifest genetic variations that do exist between individuals and the different races do not affect their respective perceptual and cognitive systems; as indeed, it is generally assumed that the genetic variation between males and females do not affect the perceptual systems in respect of their basic apprehension of the physical world.

Alternatively, (2) is the capacity to apprehend physical reality wholly acquired, through our interactions with our environments, and consequently what we apprehend as the physical world is susceptible to being sensed differently according to the nurture provided by different environments. There is, of course, the third option (3) that it is partially determined genetically and partly configured through experience. In this case, physical reality still could not be regarded as being invariant under environmental changes, and science would produce results that would hold only for the appropriate sub-set of individuals raised in a particular setting.

There is a further issue. Even if there is sufficient commonality in all terrestrial environments to permit a commonality in our apprehension of physical reality, that leads to universal stable science, this does not ensure the possibility that what we take to be physical reality might not be acquired through our interactions with it rather than our being imbued with it genetically.

Such a situation would leave open the possibility of artificially altering our capacity to apprehend physical reality through, for instance, not raising the embryo and fetus *in utero* but *in vitro*, with subsequent development also contrived to occur in a radically altered nurturing environment. The demonstration that what was apprehended as physical reality might thus be altered, albeit through radical means, would also change the status of what we regard as reality. This is because reality would then be shown to be defined in a circular manner rather than absolutely, as it is thought to be by present convention. We would then have a scientific account to support the philosophy of Plato, Locke and the Empiricists, and indeed have support for Einstein's conjecture cited earlier that our notion of physical reality can never be final but, in this case, environmentally contingent.

It is worth reflecting that with altered perceptions, the cognitive system would be accordingly changed. In time, this scenario opens the possibility of the compilation of a radically different science, which we might insist was 'the' science. So, rather than have the computational devices and telemetry we have in the present age, we might have instead equally sophisticated but ‘other’ technological innovations.

Should the conclusion of this piece indicate that our capacity for the apprehension of physical reality is plastic to environmental factors, this would mark a point of departure from the current scientific paradigm of proportions greater than those posed by Relativity Theory and Quantum Mechanics. This is because the latter two were theories that were elaborations on the foundation provided by Newton and his predecessors. In the present investigation what is being called in to question is the stability of the ontological status of empiricism. This possibility is something Einstein was prepared to anticipate but has remained a topic that could not be investigated until the present age.

2.4 The Nature–Nurture Debate

As should be clear from the previous sections, the current scientific paradigm relies on empiricism for the furtherance of scientific enquiry, while adherents to the results of such an enquiry are led to treat scientific findings as somehow ‘cast in stone’ because truth is tacitly assumed from the dictum ‘seeing is believing’. Questioning this view brings forth the issues associated with the status of knowledge gained from perception. If the organs of perception are configured to enable function by their input, then this leads to a circularity in the definition of physical reality. If, instead, there is innately given ‘core’ knowledge, as is held by Nativist Psychologists, that leads to the establishment of physical reality, then a universally accepted and stable science might result.

To elaborate briefly, there is no doubt that the human genome participates in determining human anatomy and physiology, and that their development is contingent on a nurturing environment. The issue in question is concerned with the human sensory system and the neurophysiology that supports its mode of function. The enquiry is, thus, concerned with the neural plasticity thought to be innately incorporated into the nervous system, and the degree to which the interaction between the human genome and the environment participate in shaping sensory system functions. In this regard, attention will be confined to sensory capabilities relevant for the evaluation of scientific theories.

It is not the intention to provide any detailed account of the nature–nurture debate (the term was coined by Francis Galton (1822-1911) (Ridley, 2003, p. 70)). Suffice to say that the recent literature adequately covers the broader aspects of the issues (see, for instance, Elman et al., 1996; Prinz, 2002; Ridley, 2003 and Stiles, 2008).

Stiles summarizes the issue thus:

> The central debate in the field of developmental psychology has centred for decades on the very old and somewhat fluidly defined dichotomy between nature and nurture. The unifying questions of the psychological debate concern the origins of knowledge and action. To what extent are humans innately prepared to interpret the world, and to what extent do they rely on learning.
>
> Stiles, 2008, p.1

Indeed, the aspects of this debate that are relevant to the current work are restricted to those that deal with the acquisition of knowledge through ordinary perception of the physical world. Issues concerned with the inherited component of psychological issues such as personality traits and so-called talents and sporting function do not fall within the scope of the present work. After all, a practitioner of science endeavours to make his observations regardless of whether he be tall, short, crooked in his gait, irrespective of whether or not the colour of the walls of the laboratory pleases him.

Furthermore, it is not intended to provide anything that may be even remotely considered to be a comprehensive survey of the philosophical literature on the status of knowledge and how it comes to be in the mind. Instead, the current work is intended to be a contemporary scientific account about how we come to perceive the material world that the physicist deals with.

As should be clear by now the approach to be taken is that of conceding that the laws of science that we might formulate are only those that are discoverable by beings constituted as we are. The present work dwells on the particular features of our perceptual and cognitive systems that allow us to apprehend the physical world as we do, and thus enable us to practise the scientific method as we conceive of it.

It is worth mentioning that there have been significant advances in neuroscience over the past century beginning with the pioneering neuroscientists Santiago Ramón y Cajal (b. 1852); Richard Caton and Hans Berger's work (Caton, 1875; Berger, 1929) in electrical emanations from nervous tissue (later substantiated by Adrian and Mathews, 1934). These and the single-cell recordings from the optic nerve of a toad by Adrian (1928) have greatly transformed the subject (see chapter 3).

In parallel, over the past several decades significant advances have been made in our understanding of the basic stages and mechanisms of mammalian brain development. Studies elucidating the neurobiology of brain development span the levels of neural organization and function from the macroanatomic and cellular to the molecular. This large body of work provides a picture of brain development as the product of a complex series of dynamic and adaptive processes operating within highly constrained but constantly changing biological and environmental contexts (Morange, 2001; Waddington, 1939).

Joan Stiles notes that the process of development is dynamic, and from its inception involves a continuous interaction of genetic, epigenetic and environmental factors. These findings challenge nativist psychologists' claims about innate behaviours in the brain. Such behaviours are thought to be largely outdated as is the foundational construct of the nature versus nurture debate. Instead, present models of development emphasize that the processes of brain development engage both inherited and environmental factors, and rely on their continuous interaction, interdependence and reciprocity (Stiles, 2009). These issues will be elaborated on in chapter 3.

Aspects that will be cited from the philosophical literature are those that have been of interest to the author, and can be appraised in relation to findings in the recent neuroscience and experimental psychological literature. These choices are, in that sense idiosyncratic, and are included, at best, as a tribute to the insights of the selected authors, or at worst, perhaps to their sheer good luck. However, ideas emanating from the nativist psychologists are at variance with the prevailing constructivist approach, and warrant addressing in the light of modern findings.

2.5 The Empiricist Philosophers

There is an extensive literature in Western philosophy that addresses the origins of knowledge dating back to Aristotle (384-322 BC), who first wrote about the *tabula rasa* or un-scribed tablet in his *De Anima* or ‘On the Soul’.

> … the intellect is the object of thought, but nothing in actuality before it thinks, and the potentiality is like that of the tablet on which there is nothing actually written.
>
> Aristotle, *De Anima* (Book III.4, 430a)

It is surmised here that by ‘intellect’ Aristotle means the mind, that is being likened to a blank slate (‘mind’ is used in accord with the sense employed by Baars (1988) and Humphrey (1993)).

The Aristotle scholar Jonathan Barnes (1987) states that Aristotle regards thoughts as being on the level of perception, and that they lead to a change in the perceiver’s cognitive system in that ‘… it receives the form of the object without its matter’, and leaves a physical trace (referred to by Aristotle as ‘phantasms’; they constitute the objects of *phantasia,* or the faculty of imagination) in the body (this view is in accord with current neurophysiological thought, see Baars 1988, p. 215).

Aristotle holds that thought is dependent on imagination, and hence on perception, in that thought is not possible without *phantasms*. In other words, we cannot think without having first perceived, and the scope of our thought is determined by the extent of our perceptual experience.

In respect of Aristotle's notion of thought, and, if its effect leads to memory formation, then Aristotle's account is remarkably close to current findings in neuroscience, in that Stiles (2009) holds that there are no behaviours that do not require gene expression and activity (see chapter 3, §3.6.2).

The view that the mind may be regarded as a blank slate did not progress much for more than a millennium. It was later developed more clearly by the Persian philosopher Ibn Sina (known as Avicenna in the Western world), who held that the 'human intellect at birth is rather like a *tabula rasa*, a pure potentiality that is actualized through education and comes to know', and that knowledge is attained through 'empirical familiarity with objects in the world from which one abstracts universal concepts' (Rizvi, 2006). The process of gaining further knowledge occurred through an iteration of reasoning and observations which when compounded lead to further abstract concepts.

Our modern idea of the theory concerning *tabula rasa* is mostly attributed to John Locke, whose expression of that notion is contained in his seventeenth-century work *An Essay Concerning Human Understanding* (Locke, 1690).

Locke was unequivocal about his stance with regard to the contents of the human mind when he stated:

> How comes [the mind] to be furnished? Whence comes it by that vast store which the busy and boundless fancy of man has painted on it with an almost endless variety? Whence has it all the materials of reason and knowledge? To this I answer, in one word, from EXPERIENCE.
>
> Locke (1690, II.i.2)

According to Locke, the human mind at birth was largely empty, and it was through the sensory experience that knowledge was gained. In this view Locke neglects the fact that the human mind is creative and makes inferences and deductions to create new knowledge. As such, the contents of the intellect are not restricted to knowledge that has entered through the portals of the senses. Further historical accounts of empiricist and nativist philosophers and psychologists may be found in the article by Hochberg (1962).

As a concluding remark, it has to be conceded that even though the notion of science as a unique enterprise is being questioned, what is currently known from the conventional scientific standpoint will be used in the present work; there appears to be no other option. We are thus in the curious situation where results that have been obtained using the scientific method will be used to evaluate the status of science.

3

PLASTICITY IN THE NERVOUS SYSTEM

3.0 Introduction

The present chapter is directed at an exploration of current thought in the realm of brain development in regard to the underlying principles that govern the establishment of perception and cognition. The objective is to address the broader issues of the genesis of our capacity to apprehend physical reality and their effects on the status of science.

Developments in neuroscience, particularly since the middle of the twentieth century have indicated that perception does not arise exclusively from a natural process of maturation. Instead, according to Donald Hebb's suggestion:

> … 'simple' perceptions are in fact complex: that they are additive, that they depend partly on motor activity, and that their apparent simplicity is only the end result of a long *learning* process [italics added].
>
> Hebb (1949, p. 17)

In regard to Hebb's proposal that the sensory system needs to learn to perceive, it is perhaps worth summarising the plan of this chapter while highlighting some of its key proposals. The present work sets out to provide a constructivist account of the development of sensory function (Quartz and Sejnowski, 1997; Quartz, 1999, 2003; Schultz et al., 2007) and how its course might be altered by changes in the significant parameters this account of development relies upon. The questions addressed are: what are the relative contributions of genetic, anatomical, physiological, environmental and experiential factors that participate in the development of perception? And, crucially, might changes in these elements nevertheless lead to a singular outcome whereby a unique and universal capacity for the apprehension of 'sense data' might result?

This approach will be contrasted with the nativist viewpoint of, for instance, Descartes (see, for instance, Hochberg, 1962) and his followers in the present age (reviewed by Stiles, 2009), who proposed that the human being is imbued with innate *categories* such as form, position, space, time and so on, into which our perceptions are organized. In these nativist accounts the capacity for perception was tacitly assumed to be given.

In the prevailing constructivist and developmental neurobiological approaches, it is proposed, instead, that the capacities for the apprehension of such categories arise hierarchically from the primitives of perception usually coupled with linguistic input from the environmental setting, both of which are learned through experience (see chapters 3 and 9).

It is evident that the synthesis of the nervous tissue that supports the development of perception is generated through the transcription of the information contained in the nucleotides of the DNA molecule (Stiles, 2008). It will be shown that the resulting brain growth during early development is guided by intrinsic spatially specific signalling of neural progenitor cells in the proliferative zone that generate the basic intra-areal organization and connectivity in the brain. This tissue is refined initially by endogenously generated activity (for instance, in the cochlea: Tritsch and Bergles, 2010; and retina: Wong, 1999).

Later, after the onset of rudimentary perceptual function, further growth of nervous tissue is promoted by environmentally derived activity originating in the sensory epithelia (Kats and Shatz, 1996; Stiles, 2009). The degree to which endogenous and exogenous processes contribute to perceptual function will be addressed in the present chapter, particularly in regard to the development of vision. The role of environmental input in generating function in the other senses will be elaborated upon in the subsequent chapters that deal with the other sensory modalities. It will be shown through citing results of sensory deprivation studies, that environmentally induced activity in the nervous system is, indeed, needed to ‘configure’ the sensory system to enable perceptual function. Furthermore, the nature of the environment, and therefore the type of input it generates, results in the type of sensory function that is generally appropriate for that input. Furthermore, there is also need for the subject to actively engage with the input in order to *learn to perceive*. In this regard Hebb elaborates upon what learning entails:

> … no learning is possible without intention to learn, no memory of a sensory event unless it was 'attended to' at the time of its occurrence.
>
> Hebb (1949, p. 151)

Indeed, of interest is the manner in which such mandatory learning, prior to the onset of full function, can determine physical reality, and how alterations in that input might change the subject's sense of reality. Blakemore and Cooper (1970) demonstrated such effects in their study of the visual development of kittens in enclosures composed exclusively of either vertical or horizontal edges (see Fig. 1.1). Their results are generally interpreted to show that environmental manipulations can systematically alter the kittens' sense of reality (see Introduction and § 3.4.6).

It has been shown that a lack of sensory input results in substantial sensory deficits for the deprived sense. Furthermore, sensory deprivation in a particular modality generally leads to a 'recruitment', or redeployment, by other senses of the nervous tissue that might otherwise have supported that function (see, for instance, Sur, 2005 and §5.2).

It will be shown in this chapter (and elsewhere in this thesis) that the processes of brain development (as mentioned above) engage both inherited and environmental factors, and rely on their continuous interaction also *during* sensory and cognitive function (Stiles, 2009). In this regard, it is proposed that the nature-nurture debate be replaced by the view that development consists of an environmentally dependent process that involves the construction and alteration of nervous tissue using cellular machinery inherited from the first cell and used to transcribe information contained in the genome.

As discussed earlier, it has been tacitly assumed by the scientific community hitherto that the careful practice of science can yield unique and universal knowledge because of the veridical nature of human 'sense data'. It is proposed that this view has prevailed largely unchallenged because there has been little reason to question it, and because until recently there has been insufficient theoretically evaluated experimental information about the development of sensory function to challenge the view that scientific knowledge is universal and unique.

However, these issues can now be addressed with some confidence. This situation has arisen particularly through the work, in the middle of the twentieth century, by Wilder Penfield and colleagues[2] in charting the overall hierarchical nature of brain function in the sensory and associational areas through eliciting patients' responses to electrical stimulation of their exposed cortex prior to surgical intervention for epilepsy. See, for instance, Penfield and Jasper (1954).

Donald Hebb, too, has made substantial contributions, particularly towards the establishment of a theoretical foundation for learning in the nervous system through suggesting the role of coincident neuronal activity in the pre- and post-synaptic neurones in

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[2] For details of the other workers who participated in the early charting of the different functional regions in cerebral cortex see Parpia (2011).

the modification of mutual synaptic connections and in the formation of cell assemblies (Hebb, 1949).

This has been followed by careful analyses of the results of single-cell studies in the striate cortex of cats and monkeys by David Hubel and Torsten Wiesel and colleagues to demonstrate the existence of an explicit hierarchical organization in the visual system (Hubel, 1982; Wiesel, 1982; Hubel, 1988). Furthermore, the effects of monocular suture on the development of the visual system in these animals described by Hubel and Wiesel clearly delineate the separate contributions at the cellular level of natural maturation and (b) exogenously derived activity in the development of vision, and reinforces the view that the capacity to see requires learning (see chapter 3).

Hebb's theoretical contributions and the experimental results mentioned above continue to provide the basis for experiments on memory formation in the Life Sciences and also enable computational modelling of brain function, which can generate 'existence proofs' for theories about perceptual and cognitive function and their development (see below). Such modelling work provide support for Jean Piaget's view that perceptual abilities arise from a process of construction in nervous tissue, and set out the basis for constructivism (Quartz and Sejnowski, 1997; Quartz, 1999; Quartz, 2003), neuroconstructivism (Westermann et al., 2007) and the current neurobiological position on brain development (Stiles, 2008; 2009).

Hebb acknowledged that his insight that sensory function is based on learning was inspired by work previously reported by von Senden (1932/1960[3]) of findings in the congenitally blind who were 'given sight' by surgical operations. Hebb states that his position was reinforced by the results reported by Riesen (1947) that visual competence did not fully develop in chimpanzees that had been subject to periods of dark-rearing in their infancy (Hebb, 1949, p. 18).

A review is provided below of the early literature that indicated the existence of plasticity in the nervous system, where plasticity is the general term applied to an alteration in structure or function of the nervous tissue brought about by development, learning and experience (Loring, 1999). Such plastic changes are also known to occur as a result of sensory deprivation or injury to the nervous system. In the present context, it is the change in architecture and the synaptic weights of the connections between the neurons, paralleling learning, which are of primary interest.

3.1 Comparison Between the Information in the Brain and in the Human Genome

Before going much further into the enquiry about the origins of knowledge in the nervous system, it would be judicious to make an order of magnitude calculation of the amount of information there is in the human genome as compared to that contained in the adult brain. This is with a view to trying to assess whether there is any indication that the genome

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[3] Von Senden's original German text was published in 1932. Its English translation was published in 1960. This work will be referred to henceforth as 'von Senden' (1960).

could, at least in principle, be capable of providing innately all the information contained in the brain.

3.1.1 Information in the Human Genome

The concept of information in biology has been discussed by Maynard Smith (2000), and a number of workers have previously made estimates of the amount of information contained in the genome. Among them are Gierer (1988), Singer (1990), von der Malsburg (1990) and Tweed (2003). A calculation similar to theirs is provided below directed at making a comparison between the information contained in the human genome and that contained in the adult brain.

The DNA in the genome carries its information as a sequence of base pairs. In a genetic message there are four alternative base pairs: adenine-thymine, thymine-adenine, cytosine-guanine and guanine-cytosine. Thus, the DNA message can be written with four distinguishable symbols. For a given string of n symbols, each of which can be in any one of 4 equally likely states, and if each was independent of all other symbols, Shannon's measure (Shannon, 1948) assigns the string $2n$ bits of information (Maynard Smith, 2000). As such, the quantity of information in the four base pairs would be 8 bits, and there would be 8 bits of information in the 4 symbols, giving 2 bits per base pair.

However, Maynard Smith (2000) notes that the bases are not equally likely and there are correlations between neighbours in the genome, so this reduces the amount of information, but it is not very great, and is usually ignored. A greater reduction occurs as a result of the redundancy in the genetic code, mentioned above. Thus, a measure of two bits per base pair may be taken as a conservative upper limit.

The size of the human genome has been revised in recent years and is thought to contain approximately 3.5×10^9 base pairs (Baltimore, 2001). Of these, only about 1% are able to sequence proteins, and over half of the DNA consists of repeats of just a few bases. As such, the genome is composed of approximately 16×10^6 base pairs specifying some 39,000 protein-encoding genes in the human genome. This is about the same amount of information as that contained in a single JPEG image.

3.1.2 Information in the Human Brain

The architecture of the interconnections between the neurons in conjunction with the plastic synaptic strengths is generally thought to contribute to the representational functions that can be performed by the assembly of interconnected neurons. This view has gained support through the pioneering theoretical analyses by McCulloch and Pitts (1943) who showed that arrays of neuron-like processing units were capable of performing logical operations. However, Hebb's seminal work (Hebb, 1949) provided major conceptual insights into the dynamics of such assemblies and the possible cognitive functions that may be achieved by collections of neurons. Indeed, Hebb's focus on the dynamics of the system has found validation through, among others, the work of Singer and co-workers in the domain of the physiology of vision (Rauschecker and Singer, 1979, 1981; Castelo-Branco et al., 2000).

For a review of some of the earlier developments in computational neuromodelling see Rumelhardt et al. (1986) and Anderson and Rosenfield (1988). Boden (2006) provides a history of its development. The calculation given below is made on the basis of current neural network theory.

There are of the order of 10^{11} neurons in the human brain that are mostly provided at birth. Bullock (1977) estimates that a single cortical pyramidal neuron has about 30,000 afferents. Thus there are approximately $3x10^{15}$ synapses in the adult brain.

If each synaptic weight were specified to have, for example, 16 strengths, i.e., 4 bits were allocated to it, 2 base pairs would suffice to contain the information in each synaptic weight, so the $3x10^{15}$ synapses in the human brain would require $6x10^{15}$ bases. This rough calculation shows that there is a deficit of approximately $5x10^{15}$ bases in the genome were it to code for every synapse in the brain.

The above calculation represents a conservative estimate of the information in the brain, given that the following additional considerations have been neglected because of the difficulty in quantifying them.

i) The variable geometry of the connective fibres and their dynamic properties, with regard to the information contained in these structures. Dendrites, for instance, are not passive fibres. Rather, they too are capable of producing action potentials that back-propagate towards the synapses (Yuste and Tank, 1996). Thus activities within them may be regarded as sources of further information.

ii) The effects of hormonal release into the cerebrospinal fluid and the local production of active chemical agents (e.g. nitrous oxide) on parts of the brain, thereby increasing the information content of the brain when these variables are included.

iii) Nervous tissue is not confined to the brain but pervades the entire body, with significant amounts of both grey and white matter being contained, for instance, in the spinal cord.

iv) There are two types of synapses: electrical and chemical. Electrical synapses permit direct, passive flow of electrical current carried by ions from one neuron to another in amounts that are, in principle, as small as a single unit of charge, thus enabling fine variations in synaptic weights. Chemical synapses enable communication via the secretion of neurotransmitters. These are contained in vesicles with about 10,000 molecules each, depending on the sizes of the transmitter molecules and the vesicles. They are released in units of vesicles, and several thousand units may be released in each releasing event (*Neuroscience*, 1997, p. 107). Multiple transmitters can be released by any one neuron at chemical synapses, in a process involving co-transmitters (*Neuroscience*, 1997, p. 104). In these cases, if the different transmitters are contained in separate vesicles, the transmitters need not be released simultaneously. As such, different combinations of neurotransmitters may be released at different times and at different synapses by the same neuron. Such co-transmitter releases appear to be governed by the frequency of the pre-synaptic activity. Given that there are over a hundred types of neurotransmitters, such an assembly has vast combinatorial information content ascribable to the individual synapse and the individual neuron. This further increases the potential information that may be contained in the chemo-dynamics of the nervous system. The electrical and chemical synapses thus provide a single neuron with the capacity to operate on a scale where the information transfer may be regulated with microscopic gradations. Instead, a full-scale of only 16 levels has been used in the result presented above.

v) Although neuron numbers had been previously thought to remain constant postnatally, evidence has emerged since the early sixties for neurogenesis in the olfactory bulb as well as in the granule cells in the dentate gyrus (Altman, 1962). As such, the information content in the adult is likely to be an increasing quantity with age. This factor has been left out.

Von Neumann (1979) made an estimate of the amount of information that might be transferred to the human brain during a lifetime, and suggested that the lower bound of this capacity is about 2.8×10^{20} bits, suggesting that any prospect of its innate pre-specification must be ruled out.

Gierer (1988) has suggested several strategies that the biological system may utilize to economize on its use of genetic information for the organization of brain architecture. However, he concedes that the large number of synapses that would nevertheless need specification makes the notion of a genetic predetermination of human brain function untenable. Some of these strategies in the form of self-organization and learning in the nervous system are explored later in this chapter.

3.2 Early Indications of Plasticity in the Nervous System

3.2.1 The Molyneux Question and the Nature-Nurture Debate

In 1688 Mr William Molyneux, the Irish philosopher, posed a question in a letter to John Locke that concerned a hypothetical case of an adult who had been blind from birth (Locke, 1690, p. 100). This person could distinguish by touch the difference between a sphere and a cube. Molyneux's question was that if the blind person were spontaneously given sight, might he be able to distinguish between the two objects using sight alone?

Molyneux's question served to activate debate for three centuries over the role of experience in the development of perception and the existence of innate or acquired cross-modal relationships between the senses. This issue raises a host of related questions: what would it take to restore sight to a blind person? This would, clearly, depend on the reason for the blindness. If it were a case of congenital cataract or infection of the cornea, lens removal/replacement or the transplantation of the affected corneal tissue might enable the patient to be 'spontaneously given' sight. Indeed, it begs the question about the genesis of vision. Furthermore, does having haptic[4] perception alone ensure the presence of visual-haptic intermodal links capable of providing the repaired visual system with sufficient

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[4] The term haptic refers to perception through active touch and exploration, usually by the hands, allowing, for instance, object recognition to occur.

information to distinguish between the two objects using sight alone? Could it be that such visual-haptic intermodal links develop in concert only when both sensory modalities coexist, or might it be the case that such links might develop as part of an innate endowment irrespective of a lack of prior visual experience? Would the outcome of surgical intervention depend on the point in time during development when the damage occurred and the period of sensory deprivation?

In addition, what of the parts of the brain that would otherwise support the processing of vision during the period of blindness? Will these still remain available or might they have been recruited by other sensory modalities in the absence of visual input, or will they have atrophied from a lack of use? Indeed, how might it be distinguished between development as maturation, which might occur irrespective of sensory input, and development that arises from experience and learning in a particular developmental setting?

William James (James, 1890) argued that the perception of space in different sensory modalities has intrinsically different properties that make it *impossible* for cross-modal information to be relayed between sight and touch without experience. He noted, for example, that visual space is projective and non-Euclidean, whereas tactile space is Euclidean, implying that he considered the occurrences of mappings between Euclidean and non-Euclidean spaces unlikely without the participation of experience.

As mentioned earlier, Hochberg (1962) has charted the philosophical debates between the nativist and empiricist philosophers, for whom the issue of how we come to gain knowledge about the world was important, because such questions affected all fields of knowledge and underpinned our tests of truth and certainty.

For instance, the nativist position maintained that the categories into which we organize our sensations must themselves be determined by the [given] nature of our minds, not by the world itself, and therefore the concepts of time and space must be innate. Descartes, as mentioned earlier, held that we are born with certain innate and valid ideas, *viz.* size, form, position, motion etc.

The Empiricists proposed, instead, that all our ideas of the world came through our senses, and that we could not perceive such properties as the distance and size of objects directly, simply through a process of maturation; we had to learn to do so. For further details of the development of the early debates and the related issues that have been addressed by researchers in diverse disciplines between the posing of the Molyneux question in the late-seventeenth century and the present age, see Hochberg (1962).

It is interesting that von Senden (1960, p. 108) described the very experiment proposed by Mr Molyneux, which was conducted on a four-year-old girl following the removal of her congenital cataracts. When she was shown in turn a sphere and a cube, both of which she had often held in her hands and could perceive by touch to be different, she was found not to be able to distinguish between the two objects using her ‘restored’ sight. It has been demonstrated more recently that intermodal perception is learned (see §5.1).

3.2.2 Early Work on Visual Deprivation in Humans and Chimpanzees

The two most common causes of blindness are cataract and corneal scarring. Cataract operations have been documented in Sanskrit texts of 2000 years ago, which suggest that 'navigational' vision may be given to a blind person by the dislocation of an opalescent lens by use of a sharp instrument (Rostron, 2003). Congenital cataracts occur in approximately 2.2 to 2.5 of 10,000 live births and can be either unilateral or bilateral (Francis and Moore, 2004). Effective treatment of corneal scarring has been more elusive because the complete removal of a diseased cornea requires its transplantation with similar transparent tissue if the integrity of the globe is to be preserved.

Corneal transplantation has become feasible on a routine basis only in the mid-twentieth century. Such transplantations have successfully restored the sight of those blinded later in life. However, for the *congenitally* blind, who have had their opalescent cataracts replaced by prosthesis, or diseased or damaged corneas transplanted, the prognosis for the restoration of vision has been dependent significantly on how soon after birth the operation is carried out.

Von Senden (1960), Gregory and Wallace (1963) and Dolezal (1982) have reviewed issues that such cases raise. Gregory and Wallace (1963) observe that operable cases of blindness are of two kinds: cataract of the lenses and opacity of the corneas. For such cases to be suitable for surgery, the retina must be functional. They note that in cases where the retina shows no sensitivity to light there are no instances of recovery from blindness.

The ophthalmic surgeon M. von Senden reported 66 cases of individuals born blind whom he had operated on to attempt to restore their vision (Von Senden, 1960). Despite the removal of the opalescent tissue of either the infected cornea or a cataract, it was found that their impression of the outer world immediately after surgery consisted mostly of a vague grey mass with changing intensity and sometimes of different colours, and without cues to depth perception. The patients failed to recognize form or space, and the same shape in a different colour was not recognized as having the same form, i.e., there was no form perception irrespective of its colour.

Work of a similar nature was carried out on chimpanzees by Riesen (1950), where instead of attempting to restore vision by using surgery, the animals were deprived of normal vision by being raised in complete darkness, except for brief periods of light each day for care and feeding. Tested at the age of 16 months, it was found that they were sensitive to light, in that they showed pupil constriction but, as in the case of the human subjects, they showed no signs of being able to discern complex visual patterns. They were found not to visually track approaching objects and did not react to objects looming towards their faces by showing a blink response until contact, when they showed a startle response.

In the case of an animal that had been previously raised in normal lighting for 8 months, and then in darkness till the age of 24 months, when returned to an illuminated setting, it was found that the chimpanzee had lost the capacity to use vision. His recovery in normal lighting conditions was slow and still only partial. These findings were taken to suggest that the capacity for vision was not given innately, and that the capacity to retain visual competence required on-going visual experience.

More recently, Gregory and Wallace (1963) followed the case of the subject SB (Sidney Bradford, born in 1906) who had lost sight in both eyes at the age of about 10 months, and after 50 years as a blind person, had received corneal grafts to attempt to restore his sight. Immediately following the operation, he was unable to recognize humans or the many items he had previously perceived only by touch. However, it is clear that SB's sight improved with time, and has been interpreted as resulting from a process of learning. It is interesting to note that he was struck by how objects changed their shape when he walked around them, and wondered at the fact that they looked different and yet remained the same as gauged by sensory means other than sight.

Indeed, Hebb, too, had made this observation. He noted that a patient having received a corneal graft must still count corners to distinguish a square from a triangle despite weeks of practice. When the patient gets to the point of naming the object promptly, the recognition is destroyed by putting the object into a new setting or by changing its colour; the capacity to generalize over settings and colours occurs only after a prolonged and arduous training process. He went on to observe that there was no support for the idea that when the object was recognized from one viewpoint that it will be also recognized from another (Hebb, 1949, p. 50).

Gregory and Wallace (1963) take care to remark that cases of ‘restored’ vision in adulthood differ from the process of vision acquisition during normal development. For instance, the acquisition process occurs more rapidly during infancy. Nevertheless, they acknowledged that the capacity to see is acquired through learning, even though this process is a long and difficult one in adulthood, and that the capacity for depth perception is never acquired.

This finding is reported also in the more recent case of Michael May (born in 1954), who lost his sight in both eyes at the age of 3, and had his vision restored by corneal transplants at the age of 40. His vision did also improve with practice, but as in the case of Sidney Bradford, he has never acquired depth perception and has difficulty distinguishing between males and females even 9 years after transplantation (Sendero Group Library, 2003).

In his correspondence with Richard Gregory about the subject SB that Gregory and Wallace had studied, von Senden remarked, in regard to the Molyneux question, that a person born blind, having had his vision ‘restored’ in adulthood by corneal transplantation, is incapable of properly learning visual shape-perception, so that a percept gained through haptics (active touch) may not be readily integrated multimodally with a visually obtained image.

This view is affirmed in the more recent work documented in the review by Merabet and Pascual-Leone (2010), who notes that in the cases of patients with treatable early-onset blindness (by cataract removal or corneal transplantation), restoring vision in adulthood leads to profound difficulties in visual tasks, particularly those requiring the visual recognition of objects. These outcomes have largely been attributed to the idea that early visual deprivation has striking effects on the development of the visual cortex and its ability to process complex visual information.

However, more comprehensive behavioural and neuroimaging studies have revealed a different potential explanation. Specifically, results from adults with early-onset blindness, whose sight had been surgically restored, suggested that visual areas that process different visual attributes might vary in their susceptibility to deprivation and in their recovery rates. Furthermore, although patients might not show a striking improvement in measured visual acuity following surgery, other aspects of their visual perception can improve, disproving the assumption that if acuity does not progress then neither will other aspects of visual function.

These studies also reveal that after years of blindness from an early age, the brain retains an impressive capacity for visual learning. Furthermore, these observations might lead to new strategies of visual rehabilitation that take advantage of the cross-modal transfer of sensory information (for example, registering the direction of motion signalled through touch with what is perceived through vision) or using one visual attribute to ‘bootstrap’ and enhance the development of another (for example, learning to perceive object form as defined by its motion).

Regardless of the diverse prognoses for sight restoration following transplantation, visual experience seems to be an essential component in the acquisition of visual competence.

Indeed, the answer to the Molyneux question remains ‘No’, in that any cross-modal transfer in the newly vision-restored individual would not occur spontaneously and would, nevertheless, need a period of learning.

3.2.3 Early Work on Visual and Motor Deprivation in Kittens

Riesen (1975) and Ganz (1975) have reviewed a series of experiments on the effects of visual deprivation on both visual competence and visual-motor coordination. Some of the experiments that were performed on kittens are presented here. They provided early indications that visual perception was learned rather than endowed as a part of maturation.

When the normal cat is held by the torso with forelimbs free, and is brought slowly towards a horizontal surface, it will extend its paws in the direction of that surface in a manner appropriate for an impending landing. This is known as a visual placing response. Eye-opening occurs in kittens between 3-15 days after birth. However, they do not display the visual placing response until 22-28 days, showing evidence that normal visual-motor development has been attained. Visually guided motor responses continue to develop and become more accurate in kittens, with the ‘sensitive’, or critical period[5] extending to about 12 weeks of age. However, the most susceptible period for inducing deprivation-induced visual deficits comprise the first four weeks after birth (Riesen, 1975).

Dark-rearing kittens for 4 weeks from birth abolishes the development of the visual placing

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[5] Hubel and Wiesel coined the term ‘critical period’ (Wiesel, 1982) to describe a period in a kitten’s early life during which the cortex remained labile (plastic) enough to be affected by sensory deprivation due to monocular suture. See §3.5.6.0.

response. The imposition of diffused-light filters over their eyes to prevent the input of structured images does not affect this response. It would seem that motion parallax due to gross cues of looming through the filters is sufficient for the development of the response. It would appear that the sensitization of visual motion detectors to the low spatial frequencies involved in the detection of looming might be transmitted through the light filters.

However, if the kitten is lowered onto a serrated edge, where accurate placing is necessary so as not to miss the prongs, it cannot position its paw to land onto a specific prong, indicating that structured visual input is necessary for the development of visual perception of finer detail.

It was found that kittens deprived of the sight of the movement of their limbs suffered deficiencies in visually mediated guidance of those limbs. Furthermore, the visually guided paw-placing learned for one forelimb was found not to transfer to the other limb; animals that had seen a binocular view of one limb during the learning period were able to guide that limb to the prongs on the serrated edge when being placed there, but when tested with a limb not viewed prior to testing, they performed only at chance levels. These results suggest that the role of correlated visual feedback is highly specific, and that such coordination is developed through learning.

Such experiments led to the proposal of the empiricist theory of visual-motor coordination of Held and his colleagues (Hein and Held, 1962; Held and Freedman, 1963), which can be described as follows: when an observer moves with respect to the various objects in his everyday world, his view of them changes. Their images move on his retinas in a manner highly correlated with his movements. Thus, any one of his movements tends to cause a characteristic sensory feedback. The central nervous system retains information about the correlation between the output motor signals, which generated the movements, and the sensory input dependent, in part, on that movement (referred to by the authors as 'reafferent stimulation'). The learning and retention of this correlational information is thought to be essential for maintaining accurate sensory-motor control.

Further evidence in support of this view comes in part from studies on adaption to wearing visually displacing prisms. These studies show that full adaptation is achieved only where the subject is actively moving his limbs while wearing the prisms. It is an essential aspect of the theory that each limb movement in each direction of visual space for every position of the eyes, and, separately, for each position of the head, entails a specific set of values that the nervous system must keep track of to enable eye-limb coordination (Held and Freedman, 1963). See § 3.3.

Ganz (1975, p. 201) also noted that for accurate visual-motor coordination, an animal must match every position of the head and eyes with some visual feedback of where the hand was after a particular movement. Therefore thousands of correlations are required for each limb separately. Held and Hein (1962) have extended this theory to apply, equally, to the development of visual-motor coordination through a process of learning. They do not believe that a kitten is born with correlated information about the position of its limb in its visual field, after a particular efferent pattern is sent downstream, for every position of the head and eyes. Thus, many correlations must be gradually built up through the experience of seeing the limb while it is moved. They surmise that every part of the visual field must be separately calibrated for every direction of the head and eyes.

It is interesting to observe that over a decade earlier Hebb (1949) noted that multiple presentations were required on all parts of the retina for learning the transformations required for apprehending Euclidean distances and orientations of lines presented to the retina.

> … during the continuous, intensive, and prolonged visual training of infancy and childhood, we learn to recognize the direction of line and distance between points, separately for each grossly separate part of the visual field.
>
> The eyes are constantly moving when the subject is awake. Every waking moment then provides the necessary conditions for reinforcing the perception of lines, in every part of the retina.
>
> Hebb (1949, pp. 47-48)

O'Regan and Noë (2001) provided an illustration (see Fig. 3.1) of the transformations that would be required for retaining the perceived identity of a horizontal line when the eye shifts its gaze from having the centre of that line on the optic axis to looking at a point directly above it. They proposed, following Hebb's suggestion, that such transformations would need to be learned in nervous tissue for all retinal locations during the critical period, when the early primitives of visual perception are acquired (see also § 3.5).

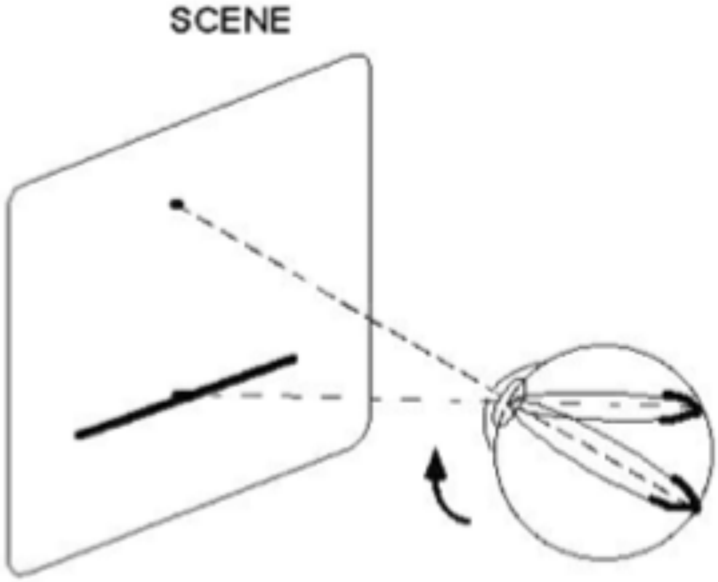

Fig. 3.1 The eye initially fixates the middle of a straight line at eye-level, and then moves to a point above the line. The resulting retinal stimulation caused by the line moves from a great arc on the equator of the eye to a different smaller great arc above it. Sensorimotor transformations need to be learned in order that both lines of retinal stimulation can be perceived to arise from the same straight line. (Source: O'Regan and Noë, 2001, Fig. 1).

It is interesting to observe that systematic distortions imposed to such mappings at the level of the whole visual field, by wearing visually distorting goggles (or spectacles), are demonstrated to be adapted to even during adulthood. Such work displaying plasticity in the visual system is described below.

3.3 Adaptation to Visual Inversions and Displacements

Simple visual transforms such as those required for the reliable use of a motor vehicle rear-view mirror, or in the perhaps more exacting task of the use of mirror vision while performing dental surgery (Walsh et al., 2010) are readily mastered during adulthood. The acquisition of competence in the use of such devices requires the learning of the new sensorimotor coordinations for mirror inversion that apply to the part of the visual field comprising the mirror. This process takes place while the subject is fully situated in the reality conveyed by the remainder of the visual field and the inputs from the other sensory modalities.

During normal visual function, as Fig. 3.1 shows, appropriate image formation generally requires making transformations between the input to the *entire* sensory epithelium and cortical tissue. Any changes to visual input by use of image-distorting goggles pits the entire visual field against its existing multimodal integration within the other senses. And indeed, Leonardo da Vinci (1452-1519) appears to have given consideration to such matters when he was the first Western thinker to raise the issue of whether there was an inverted image of the visual field projected onto the retina. He erroneously conjectured that the lens re-inverted the image to present an upright one upon the retina. However it was known long before by the Arabian scholar Ibu al Haytham (965- ~1040 AD) that the optics of the eye resembled that of the camera obscura, which had been in widespread use in eleventh-century Arabia for observing solar eclipses, and that the retina did, in fact, receive an inverted image of the visual field. For further details of the early work on this issue see Dolezal (1982, Chapter 1).

It was not until the nineteenth-century pioneers Herman von Helmholtz and George Stratton performed their classic experiments on visual displacement and inversion that a more scientific approach was brought to bear on the issue of visually induced re-mapping of visual-motor transforms.

It was generally assumed that underlying the re-mapping process was a single mechanism that removed or minimized the artificially created disturbance to the global visual field created by distorting spectacles. Indeed, the same mechanism was thought to bring about normal visual function, with the suggestion that there might be an environmental component in the development of normal vision. This view was guided by the empiricists' suggestion that an exploration of the way the brain processes sensory data, and *constructs* an effective image of the outside world might shed light on the supposed unconscious learning processes involved in the establishment of sensory function (Kohler 1962, pp. 63-64).

Helmholtz's initial studies were on the accuracy of pointing at an object during and after gazing briefly through laterally displacing prisms (see, for instance Dolezal, 1982). He found that vision was a guide to proprioception[6], and during the process of adaptation to the goggles, those parts missing from the visual field of the inverting goggles (e.g. head and shoulders) remained inverted in the estimation of the haptic, somatosensory and proprioceptive senses.

Stratton (1896), following the historical interest in the inverted retinal image, explored more rigorously the subjective experience of the effects of projecting an upright image of the visual field onto the retina, and analysed the initial disorientation in his visual and

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[6] For details about proprioception: see §5.2.

motor experiences. The inverting device consisted of a pair of lenses, and was applied to only one eye, whilst the other eye was covered with a patch. The philosophical thrust of the present work was anticipated, interestingly, by Stratton when he observed that:

> If no previous experience had been stored up to stand in opposition to the new perceptions, it would be absurd to suppose that the visual perceptions in such a case would seem inverted.
>
> Stratton (1896, p. 618)

A diversity of such optical devices have been constructed that displace, invert, reverse or tilt the normal visual field and induce a discrepancy between the actual and apparent visual fields. Wearing the devices creates a spatial discord between the normal maps coordinating vision and the other senses (including haptics) and the new spatial mapping that wearing such devices would require for appropriate sensory motor function. Thus, displacing prisms might render looking at the scene ahead into seeing the same image originating from 15 degrees to the left. Equally, while wearing right-left inverting glasses, shifting one's gaze to the left would have the effect of looking to the right (Degenaar, 2012). Image inversion lead to the situation where shifting one's gaze upwards results in the expansion of the visual field in the downwards direction. A review of experiments on the adaptation to distortions in the visual input have been presented by, among others, Kohler (1962); Dolezal (1982); O'Regan and Noë (2001) and Degenaar (2012).

Kohler (1962) observes that the mapping between the retina and the visual cortex can adapt to a number of such distortions and also to others that are inherent to the eye. For instance, the lens in the eye is not corrected for either spherical or chromatic aberration.

Nevertheless, the mapping processes involved in visual perception compensates for these deficits affecting the whole visual field. It would appear that similar processes of remapping cater for distortions that can result from the repositioning of the sensory epithelium itself in cases of surgical repair for detached retinae. Despite the distortions imposed by surgery, the visual system adapts to provide normal vision in due course.

The donning of distorting goggles initially leads to a sense of confusion about the subject's actions and the apparent relationships of body parts to one another and to the environment. Dolezal observes that the difficulties experienced by adults shortly after putting on transforming glasses are strikingly similar to the bumbling and groping confusion of the 16-22-month-old infant, implying that both adult and infant behaviours exhibit in common the early discordant activities involved in the process of *learning* sensory motor coordination (Dolezal, 1982, footnote, p.15).

Degenaar (2012) reports in some detail the diverse eye and head movements that he had to relearn whilst wearing a pair of left-right inverting prisms in front of each eye over a period of 43 days. These were worn for on average 4 hours a day. It took him 15 days of practice before he was able to walk out of doors with confidence, having attained visual stability[7] quite abruptly on the thirteenth day. The experience of visual stability, he felt, could not be captured in terms of visual images. It was, rather, a matter of having a firm visual grasp on the scene, or having the right exploratory skills in place.

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[7] The effect of wearing left-right inverting glasses results in head movements giving rise to an apparent movement of the scene. This results from an alteration in the relation between retinal stimulation and the movement of the subject's head, and generates a sense of instability of the visual field (Degenaar, 2012, p. 153).

Kohler (1962) reports that after a few weeks of wearing of left-right reversing goggles Erismann’s subject (mentioned in Kohler (1962)) was able to adapt sufficiently to the visual distortions to ride a motorbike through Innsbruck whilst wearing the goggles. It emerges from these studies that after wearing prism glasses for several weeks, the subject adapts to a range of complex distortions created partly by the movement of the head and goggles and by the movement of the eyes relative to the prisms contained therein. It would appear that in adapting ‘… somehow the visual system has learned a general rule …’ (Kohler 1962, p. 67).

In this regard, the process of re-mapping to restore normal vision whilst wearing the optical apparatus might be considered to be the sensory analogue of concept learning in the prefrontal cortex (Klob et al., 2012; also see §10.4.1.5). This position was taken by O’Regan and Noë (2001) who remarked on the fact that higher-level contextual input aids the process of adaptation to image distortions. They observe that during adaptation to wearing inverting glasses, an inverted candle flips to being in the upright position when it is lit, because flames must flow upwards; a cup flips from being inverted into being upright when coffee is poured into it, because a fluid must pour downwards. These appear to be cognitively driven adaptations in visual perception.

The view of the role of the need for cognitive input is supported by the observation that large proportions of the entire visual field engage in the transformation required for adjustment to goggle-induced distortions. Thus, adaptations might occur in neurons that have large receptive fields, and, indeed, visual receptive field-sizes become larger and capable of greater abstraction the higher they are in the visual hierarchy (Desimone et al., 1990), supporting the view that such adaptations occur higher in the visual hierarchy. In any case, as will be elaborated upon below, neurons in, for instance, striate cortex are unlikely to be engaged in such adjustment processes since their ‘effective stimuli’[8] are determined and fixed during a critical period early in development (see § 3.2.2; § 3.3). In regard to the physiological processes involved in adaptation to the altered visual input, it is suggested that studies of plasticity in the space maps in the intraparietal cortex would provide details about the processes involved (see § 5.3.7)

These experiments have shown that on wearing distorting spectacles the subject is initially quite incapacitated, but his sensorimotor systems adapt to the imposed visual transforms over a period of about a month and a half. These results provide information at the subjective and behavioural levels about the learning process in the sensorimotor adaptation to distorting spectacles and suggest that these transformations were learned in the first place. The common rules referred to by Kohler (1962) that apply to the creation of mappings between the visual field and the inner structures of the nervous system will be addressed more explicitly in § 3.6.

3.4 Development of Visual Depth Perception in Kittens

Early work on the visual system of kittens was carried out by Gibson and Walk (1960),

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[8] ‘Effective’ or ‘enabling’ stimuli are those to which a cell responds when it is present in the cell’s receptive field. For details see Moran and Desimone (1985).

where they dark-reared kittens up till the age of 27 days, sufficient to inhibit the early stages of visual learning. Their visual capacity in general, and in particular their ability to gauge distance visually was assessed by use of a 'visual cliff'. This consists of a sheet of glass that overlies a sheet of checkerboard-patterned cloth (see Fig. 3.2). On the 'shallow side', the patterned cloth is placed immediately beneath the glass. On the other 'deep side' the surface of the same patterned cloth is lower by about 4 feet. As such, in being placed upon the shallow side of the glass beside the visual cliff, the kitten sees what appears to be a drop of 4 feet while being safe from a fall should he venture over the apparent visual cliff.

On being allowed to roam on the floor, the dark-reared kittens were observed to bump into obstacles, lack normal eye movements and appeared to stare straight ahead. When these kittens were placed on the shallow side of the visual cliff they did not back off in a circle in the manner displayed by normal light-reared kittens. Instead, they strayed over the edge as often as they moved towards the safe side.

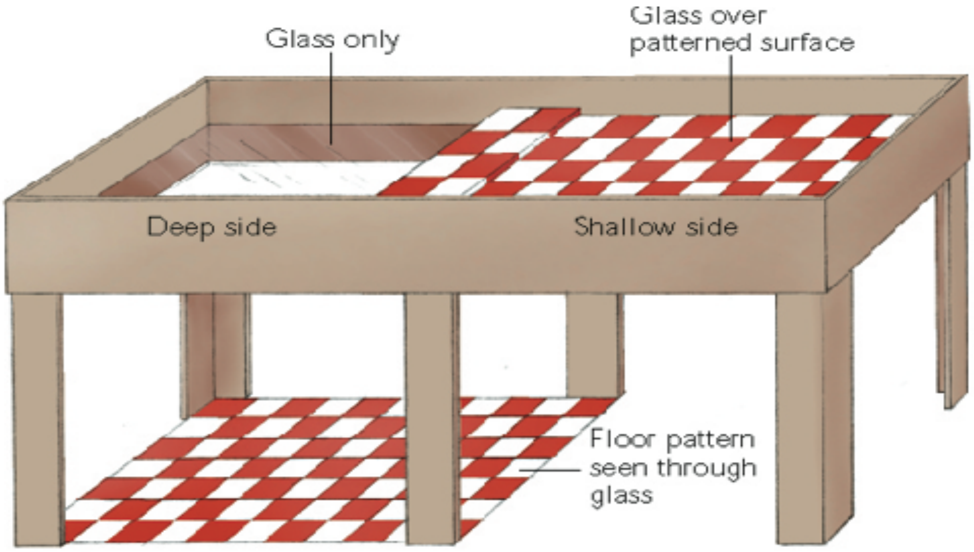

Fig.3.2 The Visual Cliff. Source: www.hartnell.edu

However, after a week of living in normal lighting conditions, their behaviour gradually resembled those of normally raised kittens. These results were taken to indicate that normal visual depth perception did not develop initially in these kittens because dark-rearing had delayed their process of visual learning.

3.5.0 Single Cell Studies in Primary Visual Cortex by Hubel and Wiesel

Knowledge of cortical function at the level of single cell processing in the visual system was relatively limited until the late 1950s. However, clues from the study of the behaviour of visually deprived humans and animals (described above) and the theoretical insights provided by Hebb (1949), led to the strategically designed experiments by David Hubel and Torsten Wiesel beginning in the late 1950s. They sought to investigate how the highly specific response properties of cortical cells emerged during postnatal development. They were also interested in examining the role of visual experience in normal development.

Their recordings from single cells found in the early part of the visual tracts, initially in cats and then in macaques, provide insights into the finer structure of the neural mechanisms underlying development and the effects of visual deprivation observed by the previous workers mentioned above. Perhaps the most accessible descriptions of their work are to be found in their Nobel Lectures (Hubel, 1982; Wiesel, 1982).

The insights of Hebb coupled with the experiments and careful analysis of the results obtained by Hubel and Wiesel have laid the foundations for the description of development in nervous tissue. The plethora of results from subsequent experiments on the effects of sensory deprivation on development, many of which will be described herein, can be seen to generally reinforce the view that sensory development in the cortex depends initially on endogenously driven neural activity, and thereafter upon activity thought to be driven by intention and attention. The rules that are generally found to govern the growth and pruning of the microstructure of the underlying tissue across the range of sensory modalities are essentially those proposed by Hebb (see below).

Barlow (1953) and separately Kuffler (1953) probed the electrical responses of retinal ganglion cells (see, for instance, *Neuroscience*, 1997, Fig. 10.4) respectively in the frog and the cat with a small circular light source directed at the retina. Tracking small movements

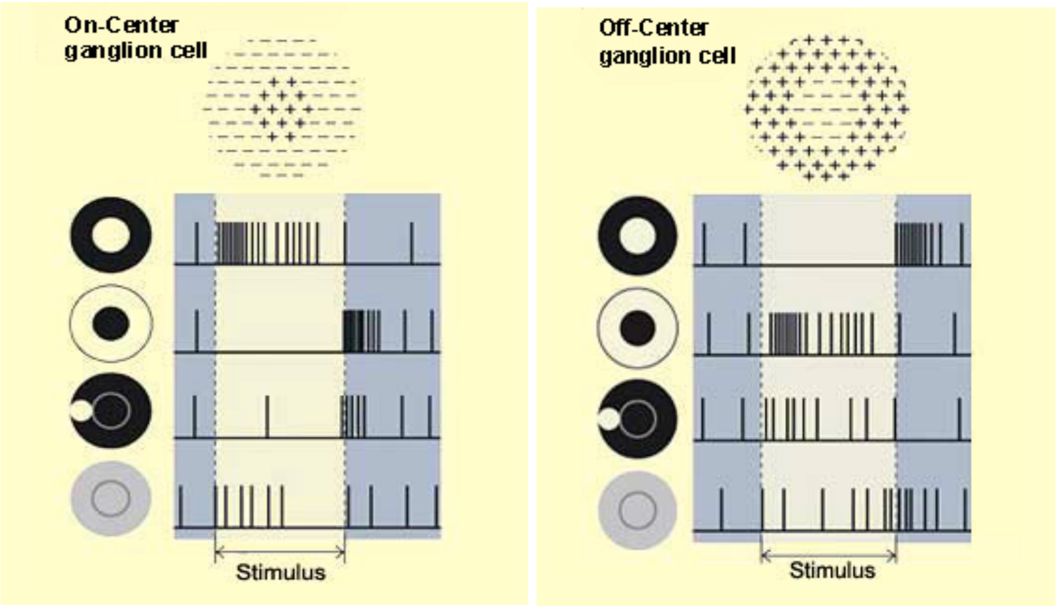

Fig. 3.3 Temporal plot of the response of On and Off-Center ganglion cells to retinal stimulation by a disc of light positioned, successively, from top to bottom, (a) light spot in center; (b) dark spot in center; (c) light spot in surround and (d) diffuse light covering both center and surround. Source: *Neuroscience*, 1997, Fig. 10.13).

of the light probe whilst monitoring the cell's output showed that the retinal ganglion cells had an antagonistic concentric 'on' and 'off' center-surround organization, with each ganglion cell generating an above or below threshold firing rate, depending on whether the light-probe was illuminating, respectively, the 'on' or 'off' part of the ganglion cell's antagonistic receptive field (see Fig. 3.3 and Hubel 1988; *Neuroscience*, 1997, Fig. 10.13). Such 'on' and 'off' centered retinal ganglion cells have an overlapping receptive field distribution over the entire area of the retina, with there being roughly equal numbers of 'on' and 'off' center ganglion cells distributed across the retinal surface. In this way several 'on' and 'off' center ganglion cells analyse the illumination of each point on the retina.

Stone (2012) has presented a theoretical analysis and computer simulations of the transform of a black and white portrait by such an array of overlapping receptive fields of simulated 'on' and 'off'-center retinal ganglion cells. The transform of the portrait by such an array can be interpreted to show that the ganglion cells convert the spatial variation in the intensity in the portrait into one where there is intensity enhancement in the output at locations of *changes* in intensity in the image (See Stone, 2012, Fig. 3.23).

Within the broad but apparently sound assumptions made in the model, the retinal ganglion cells do not behave as simple photo detectors. Instead, they can be seen to be sensitive to small spatial differences between the levels of light incident on the retina in a center-symmetric manner. The retinal ganglion cell can be seen to behave like a pattern or feature detector. The outputs of these 'center-surround' ganglions are now understood to form the first stage in the visual processing hierarchy, which is consistent with the orientation tuning for line segments that is apparent in cortical cells at higher levels (see below).

It is observed in *Neuroscience* (1997, p. 193) that having two separate luminance channels, in the form of the ‘on’ and ‘off’ center ganglion cell, means that changes in light intensity are always conveyed to the brain by an excitatory process, rather than relying on decreases in activity below some set resting level to signal diminished luminance. As a result of this mode of information coding, and the ganglion cell’s response characteristics of generating a rapid set of action potentials when the cell is activated, a more rapid and robust response to absolute changes in illumination is provided.

3.5.1.0 Anatomical Development of the Visual System

The million or so axons of the retinal ganglion cells from each of the two eyes form the two branches of the optic nerve carrying visual information for further processing into the brain. These fiber systems, originating in the two eyes, target some 20 or more structures in the brain involved in visual processing (see, for instance, Desimone et al., 1990). The pathways that innervate the lateral geniculate nucleus (LGN) of the thalamus, in six eye-specific layers, and then target the primary visual cortex are generally considered to be the ones that give rise to conscious visual perception. The cells in the LGN also have center-surround receptive fields. The outputs from the LGN (the geniculocortical afferents) are organized in a retinotopic manner, so that corresponding points in the retina of each eye innervate the same small region in layer IV of the primary visual cortex[9].

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[9] Primary visual cortex is also referred to as V1; striate cortex and Brodmann’s area 17.

In carnivores and primates the outputs from these eye-specific layers in the LGN initially innervate overlapping regions of layer IV in the striate cortex into a series of alternating stripes. Thus, the input from each eye is distributed into a series of branching bands that are about 0.5 mm wide and alternate with similar bands serving the other eye. See Fig. 3.5. These bands span all the cortical layers across the depth of the striate cortex. By the addition of large numbers of branches and synapses within appropriate regions and the elimination of the sparse collaterals initially present within inappropriate regions, LGN arbours gradually form dense, eye-specific patches in the striate cortex. This forms the anatomical basis for ocular-dominance columns.

The process of development and the response properties of individual cortical cells in the cat, macaque and spider monkey striate cortices were studied by Stephen Kuffler's doctoral students David Hubel and Torsten Wiesel, and has led to the discovery of further visual 'feature detectors'. These have been described by Hubel (1982; 1988) and Wiesel (1982). A summary of their findings is given below.

3.5.1.1 'Simple' Cells

Once again, probing the retina with diverse patterns of illumination whilst monitoring the output of cells in the LGN showed that their responses were not dissimilar to those of retinal ganglion cells, in having an antagonistic concentric center-surround organization, with perhaps a greater power of the receptive field surround to cancel the input from the center more exactly.

In the cat, cells in the striate cortex were found whose receptive fields were more complex than those of geniculate cells. Among them were cells that responded to highly specific patterns of light presented to the retina. These were termed ‘simple’ cells. For these cells, the receptive field was divided into adjacent antagonistic regions. Background activity was enhanced or depressed according to which of the two regions the enabling (or effective) stimulus illuminated.

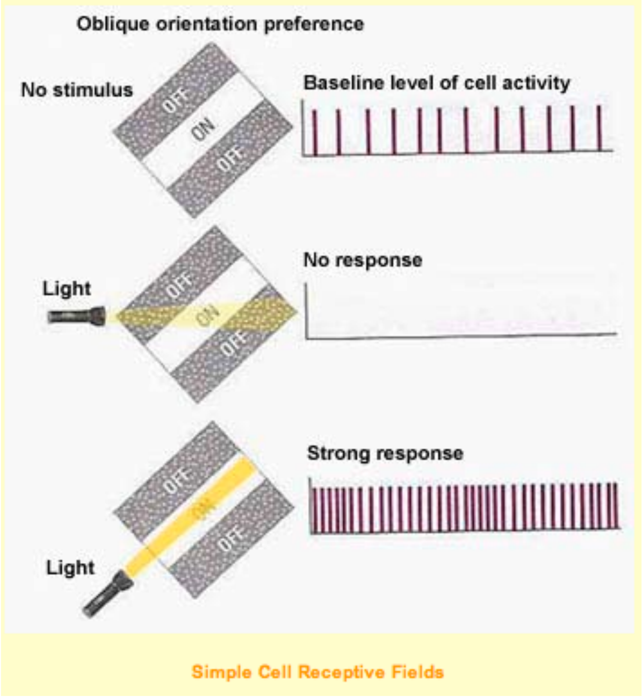

Fig. 3.4 ‘Simple’ cell receptive field responses, successively from top to bottom, to (a) no stimulation; (b) illumination at an angle that is oblique to the receptive field’s orientation tuning and (c) illumination parallel to the tuning direction. (Source: http://thebrain.mcgill.ca/flash/d/d_02/d_02_cl/d_02_cl_vis/d_02_cl_vis.html)

The antagonistic sub-divisions of the receptive field were separated by straight lines whose orientation was one of its salient properties. The optimum stimulus was, thus, a stationary slit, dark bar or edge of a specific orientation, so that a stationary line stimulus worked optimally in activating the ‘simple’ cell when its boundary coincided with the boundaries of the subdivisions of the receptive field (see Fig. 3.4). Displacing the line to a new position led to a sharp decline in the response. Diffused light produced no response.

To recapitulate, ‘simple’ cells had effective stimuli that were features like small line segments, with different such cells responding to line segments of only (a) the right orientation and (b) in the right location in the receptive field of the particular cell in the striate cortex. These ‘simple’ cells were also referred to as bar or edge detectors (Hubel and Wiesel, 1959). In the cat, these cells are found mostly in layer IV. In the macaque and spider monkeys they were found deep in layer III and in IVA, and IVB, where they form a large proportion of the population (Hubel and Wiesel, 1968).

Any line oriented at 90 degrees to the optimal orientation produced no alteration in the threshold firing-rate of the cell; the response was as though the excitatory and inhibitory effects were mutually cancelled. This was regardless of its position along the receptive field, suggesting that the subpopulation of receptors so stimulated in the retina also had precisely mutually cancelling effects.

A brief mention will be made of the previous suggestions about how the receptive fields for the effective stimuli for ‘simple’ cells might develop from the center-surround transformation performed by the retinal ganglion cells and that carried out in the LGN. Hubel (1982, Fig. 3) presents a simplistic sketch of how an assembly of center-surround receptive fields might be assembled along a straight line to show the receptive field properties of a ‘simple’ cell in layer IV.

A more considered account of how such receptive fields might be generated through a process of self-organization (see for instance Kohonen, 1987) was presented by Barrow (1987). A similar account was provided previously by von der Malsburg (1973) of the development of orientation columns by a process of self-organization (see below) that did not, however, address the sequence of transforms performed in the retina, LGN and striate cortex. Instead, he used simple artificial stimuli (bars) directly applied to the cortical model.

Barrow (1987) shows results similar to those presented by Stone (2012) for the output of retinal ganglion cells, and that such a self-organizing process could account for the formation of ‘simple’ cell receptive fields without need for their innate pre-specification. It is worth noting, however, that the origins of orientation tuning continues to be debated (Jin et al., 2011; Ringach, 2011)

3.5.1.2 ‘Complex’ Cells

Hubel and Wiesel (1962) studied the receptive field properties of other cells also found in the striate cortex, that they referred to as ‘complex’ cells, which were sensitive to line-segment stimuli of a specific orientation anywhere in their receptive field. Such cells also responded to edges moving in a particular direction (Hubel and Wiesel, 1962). They were called ‘complex’ cells because their receptive field properties could not be easily derived from those of the behaviour of the center-surround characteristics of the retinal ganglion or LGN cells, nor in any obvious way from those of the ‘simple’ cells.

‘Complex’ cells had larger receptive fields, and they responded to edges in a range of retinal locations within their receptive fields. Each ‘complex’ cell, nevertheless, had its own orientation preference in respect of the effective stimulus it responded to. Furthermore, the cells were sensitive to the direction of motion of the stimulus, with some cells not responding to motion in the opposite direction.

Hubel (1982) notes that subtypes of ‘complex’ cells exist. For instance, those in layer II and III, typically, have small receptive fields, low spontaneous activity and may not be highly orientation selective, but are sensitive to different optical wavelengths, apparently responding to red but not white lines, and they vary in their sensitivity to the length of the stimulus. They are ‘end-stopped’ cells – see below. Cells in layer V and VI have larger receptive fields. Those in layer V have high spontaneous activity, and respond equally well to long and short moving lines. Many cells in layer VI respond best to very long lines. *Others respond best to lines of a specific length: when the line is extended in one or both directions, the response declines*. These cells were initially referred to as ‘hypercomplex’ but are also known as ‘end-stopped’ cells.

The sensitivity to stimulus length was accompanied by selectivity for a specific stimulus orientation and direction of motion. *‘Hypercomplex’ cells might respond, for instance, only to a line oriented at 45 degrees that travels upwards, or detect corners or the ends of a given stimulus.*

The hierarchical development of ‘hypercomplex’ cells that enable the establishment of stimulus length is of particular significance for the present thesis. This is because the development of cells that have acquired this capability permit the claim that visual length perception, while regarding length as a vector, is an acquired characteristic. The significance of this issue is elaborated upon in chapters 4 and 5.

Hubel (1982) conceded that it was not possible to explain by any elementary projection how ‘complex’ cells might arise from the collective inputs of LGN cells. It is worth noting that the cell classification scheme of Hubel and Wiesel (1965) has been superseded in the light of further work (Hubel, 1982).

In sum, a ‘complex’ cell responds to, for instance, a black rectangle of a specific orientation anywhere in its receptive field, whether it is stationary or moving, and evokes a sequence of rapid action potentials by the cell while the stimulus is moving in a specific direction, but not when it is moving in the opposite direction. As mentioned, Hubel conceded (in 1982) that it was not possible to explain how orientation specificity might arise from the collective inputs of LGN cells. He suggested, however, that cells that had the same orientation tuning and had receptive fields in the same part of the visual field were likely to be interconnected.

3.5.2 Receptive Fields and Functional Hierarchy in Monkey Striate Cortex

Hubel and Wiesel (1968) showed that the different cell types they classified according to complexity of response are systematically distributed in a hierarchical manner in the different layers of the striate cortex. It was found that the cells respond to features of increasing complexity with their distance away from layer IV, where the visual cortex receives inputs from the LGN. This was seen to be true for distances both towards the cortical surface and downwards towards the white matter.

The input layers IVA and IVB in the macaque monkey mostly contained ‘simple’ cells. The upper layers (II and the upper two-thirds of III) contained ‘complex’ and ‘hypercomplex’ cells, but ‘simple’ cells are virtually absent here. However, the deeper third of layer III contains ‘simple’ cells. The pattern broadly repeats itself moving downwards from the input layers into layers V and VI, which are occupied mostly by ‘complex’ and ‘hypercomplex’ cells. Hubel (1982) notes that the different layers of the striate cortex project to different destinations: the upper layers mainly to other cortical regions; layer V to the superior colliculus, pons and pulvinar, and layer VI form corticothalamic projections back to the LGN and the claustrum. What is clear is that a hierarchical organization exists even within the striate cortex. It is evident that many other types of feature detectors exist at higher levels in the visual cortex that respond only when particular combinations of lower-level features are presented to the eye (see § 3.6.8).

Hubel (1982) observed that knowledge of the selectivity of cortical cells to stimuli in the visual field provides a means for the analysis of visual image formation and the generation of percepts such as lines and curves. He provided the example of the effect of the movement of the outline of an egg between two stationary locations in the visual field. Such a linear displacement would cause a completely new set of ‘simple’ cells to be activated, because these cells are position sensitive.

However, it would cause a much smaller change in the number of ‘complex’ cells that would remain activated after the displacement because ‘complex’ cells are translation invariant, and have larger receptive fields. He cautioned, however, that the line segments that ‘simple’ and ‘complex’ cells are responsive to are generally rather short, and collections of such cells may be better thought of as curve detectors at a higher level in the cortical hierarchy.

The above results suggest that visual analysis for perception takes place through a hierarchical segmentation of the input data into its separate repeated primitives. As mentioned earlier, of particular interest in regard to the proposal that visual length perception is acquired through learning, are the characteristics of ‘hypercomplex’ cells that are specialized for the detection of corners and ends of stimuli, as are the orientation sensitive ‘simple’ and ‘complex’ cells, or orientation detectors, that respond to line segments or edges delineating regions in the visual image that showed a rapid change in visual intensity to enable object recognition and length determination. Further studies of cells such as orientation detectors and cells that respond only to moving spots are described in § 3.5.7. The latter study shows that visual primitives need not be linear segments.

Within the context of the computational representation of visual information processing, these findings may be thought of as comprising the elements of the tool-kit from which David Marr's proposed 'primal sketch' might be constructed (Marr, 1982).

3.5.3 Orientation Columns

On charting the nature of the effective stimuli for cells in the striate cortex, Hubel and Wiesel found that the cells that may be thought of as orientation detectors were arranged in columns perpendicular to the cortical surface, and that cells responding to similar edge orientations were clustered around one another in such columns, or more specifically, slabs with walls separating them stacked adjacent to one another (see Fig. 3.5). There was a

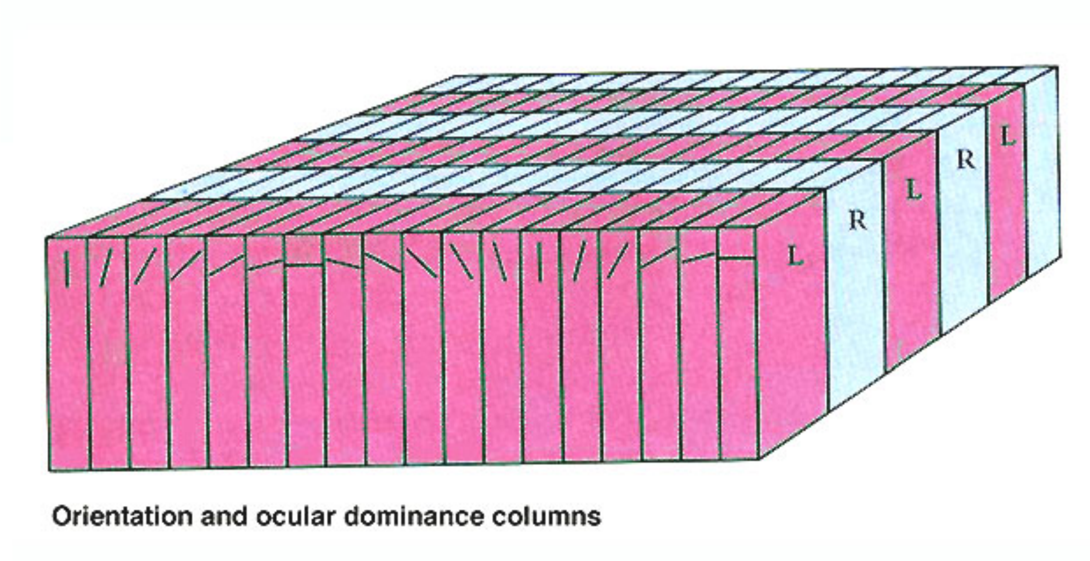

Fig. 3.5 The cortical surface is above and white matter below. Tangential (left-right) electrode penetrations at different depths from the surface reveal columns in which cells have effective stimuli that have edges of the same orientation. Penetrations in the back-front direction reveal ocular dominance columns: regions with cells responding, predominantly in layer IV, preferentially to input separately from the left or the right eye. Source: Schmolesky (2007).

systematic variation in the direction sensitivity of the cells in the individual columns with distance, measured tangential to the cortical surface in the left-right direction as shown in the figure.

3.5.4 Ocular Dominance Columns

As indicated earlier, during development, cells in layer IVC of the striate cortex in the macaque monkey receive separate sets of inputs from the left and right eye-specific cells in the LGN. These initially overlapping inputs to layer IVC from the two eyes are refined, and segregate into ocular dominance columns by the age of 4-6 weeks, such that the cortical cells in layer IVC are strictly monocular. However, cells in the upper and lower layers contain binocular cells, where the degree of binocularity increases with distance away from layer IVC.

The overall organization of the spatial layout of the retinal cells in the eye is preserved in the regions of the striate cortex targeted by the eye-specific cells in the LGN, so that there is a ‘topographic’ mapping between the receptors in the retina and the cells in the striate cortex. Thus, adjacency is preserved between the spatial layout of the retinal cells and those in the visual cortex, which perform the analysis of the retinal input from any one location. However, cortical processing for each patch of retina occurs within a block of cortex referred to by Hubel (1982) as a ‘hypercolumn’ (see below).

The cells in layers above and below layer IVC in the striate cortex receive horizontal and diagonal inputs from monocular afferents that traverse adjacent eye-specific column boundaries. See Hubel (1982, Fig.10). This is in addition to the major intra-columnar vertical connections that are confined to each column, with each unit being about 0.5 mm wide. The cells above and below layer IV are the first to receive convergent input from the two eyes. The receptive fields of the cells where binocular fusion occurs are similar in size, complexity, orientation and position in the visual field. There is, thus, a duplicate set of connections containing common information to these cells from each eye. Although these cells, receiving convergent afferent fibers from the two eyes, are binocular, they nevertheless retain an ocular dominance that is aligned to the eye providing input to the layer IVC cells.

As observed earlier, the cells in the orientation columns are interconnected, so that the hierarchy of ‘simple’, ‘complex’ and ‘hypercomplex’ cells form a little ‘machine’ that gives the locale of the column an identity within which analysis takes place of the visual input for a particular edge orientation in any particular part of the visual field.

Within each column, the connections tend to be mostly in the up-down direction, connecting the hierarchically organized cells that take part in visual processing within each cortical column, while the lateral and oblique connections are short and less dense and act to promote binocular fusion.

Hubel (1982) observed that what emerged from their work, and that by other workers in the field, was the view that the visual cortex could be seen to have a clear modular function: the transformation of information from the circularly symmetric form, generated in the retinal ganglion cells and the LGN, into an orientation-specific form, with the stepwise increase in complexity within the different cortical layers of enclosed cortical columns.

3.5.5 Variation with Depth of Cortical Receptive Field Size

It could be seen that the cortical analysis by both eyes of a small patch of retinal input that incorporated all orientations of edges would require the full depth of cortex having a surface area of ~ 1 mm x 2 mm. This was the volume incorporating a 180-degree range of orientation columns and a pair of ocular dominance columns. Hubel and Wiesel called this volume of material a ‘hypercolumn’ since it incorporated all the tissue required for the binocular analysis of all orientations of edges at any location in the visual field.

The question arose of how might a fine-grained retinotopic mapping be maintained in the cortex when the cortical material required for the analysis of all orientations of edges at one site in the visual field had a relatively coarse cortical tiling pattern of 1-2 mm square? Hubel and Wiesel addressed this apparent anomaly by making an electrode penetration normal to the cortical surface to chart the receptive field sizes and their locations in the visual field for that point in the striate cortex.

This revealed that (a) the receptive field sizes for the cells encountered varied with depth and (b) that the position of the center of their receptive fields relative to visual field also varied, so that the cells encountered showed a scattering of locations of their receptive field centers in the visual field. Point (a) above may be accounted for on grounds that receptive field sizes would increase with the complexity of the effective stimuli they analysed. Point (b) was the key finding, in that it demonstrated that there was not a one-to-one mapping between a location in the cortex and points in the visual field. Instead, there was a one to *many* mapping from the striate cortex onto the visual field, with a scatter over the same area as that of the cross section of the 'hypercolumn'.

On making successive vertical penetrations that were laterally displaced across the cortical surface, it was found that there was a corresponding gradual drift in visual field positions being processed by cells at that cortical location superimposed on the random scatter mentioned in (a). It turned out that a movement of about 2 mm across the cortex was sufficient to produce a retinotopic displacement in the visual field into an entirely new region. This systematic drift was found to hold across the whole of the striate cortex.

It can be seen, with reference to Fig. 3.6, that a lateral shift to the right across cortex by 1-2 mm is accompanied by an angular shift in effective stimulus orientation by 180 degrees (one full complement of orientations), and a displacement at right angles (to the left in Fig.3.6) by around 1 mm results in traversing ocular dominance change between the two eyes. As mentioned above, Hubel and Wiesel referred to this 1-2 mm x 1-2 mm cross-sectioned block of cortex as a 'hypercolumn', which contains all the cellular material in the striate cortex that is required for the analysis of a small region of the visual field. Fig. 3.6 shows the layout of 4 pairs of ocular dominance columns and 4 *sets* of orientation columns. Together the block displayed in Fig. 3.6 comprise 4 'hypercolumns'.

3.5.6.0 Visual Deprivation and Single Cell Responses

Hubel and Wiesel's further work provided information at the cellular level also about the processes underlying the visual impairments that persist in humans despite the removal of congenital cataracts or the transplantation of congenitally scarred corneas later in life, and for the visual deficits found in animals raised in the dark or in environments devoid of contours. Their work on the monocular deprivation of structured visual input in monkeys shows that the innately generated connectivity is sufficient for determining the initial layout of the geniculocortical fibers into layer IVC in the striate cortex, but that the detailed organization of the connections in the cortex require simultaneous coordinated input from both eyes for the establishment of binocular function. These findings indicate that the detailed structuring of the striate cortex is guided by learning from environmentally derived input and also shed light on the possibility of altering normal function by alterations to the environment.

Torsten Wiesel's Nobel Lecture (Wiesel, 1982) is a significant source for the account given below on the effects at the cellular level of monocular eyelid suture in macaque monkeys. In their experiments, rather than dark-rear their animals to study the effects of visual deprivation, they applied monocular eyelid suture for the first 3 months from birth. This created a condition similar to that imposed by a cataract in one eye, so that there was a minor (3-fold) decrease in the light level reaching the retina and, significantly, it obscured the fine structure in the forms of objects in the visual field. Monocular suture had the virtue of providing in the same animal the effects of visual deprivation to one eye while having the other act as a control.

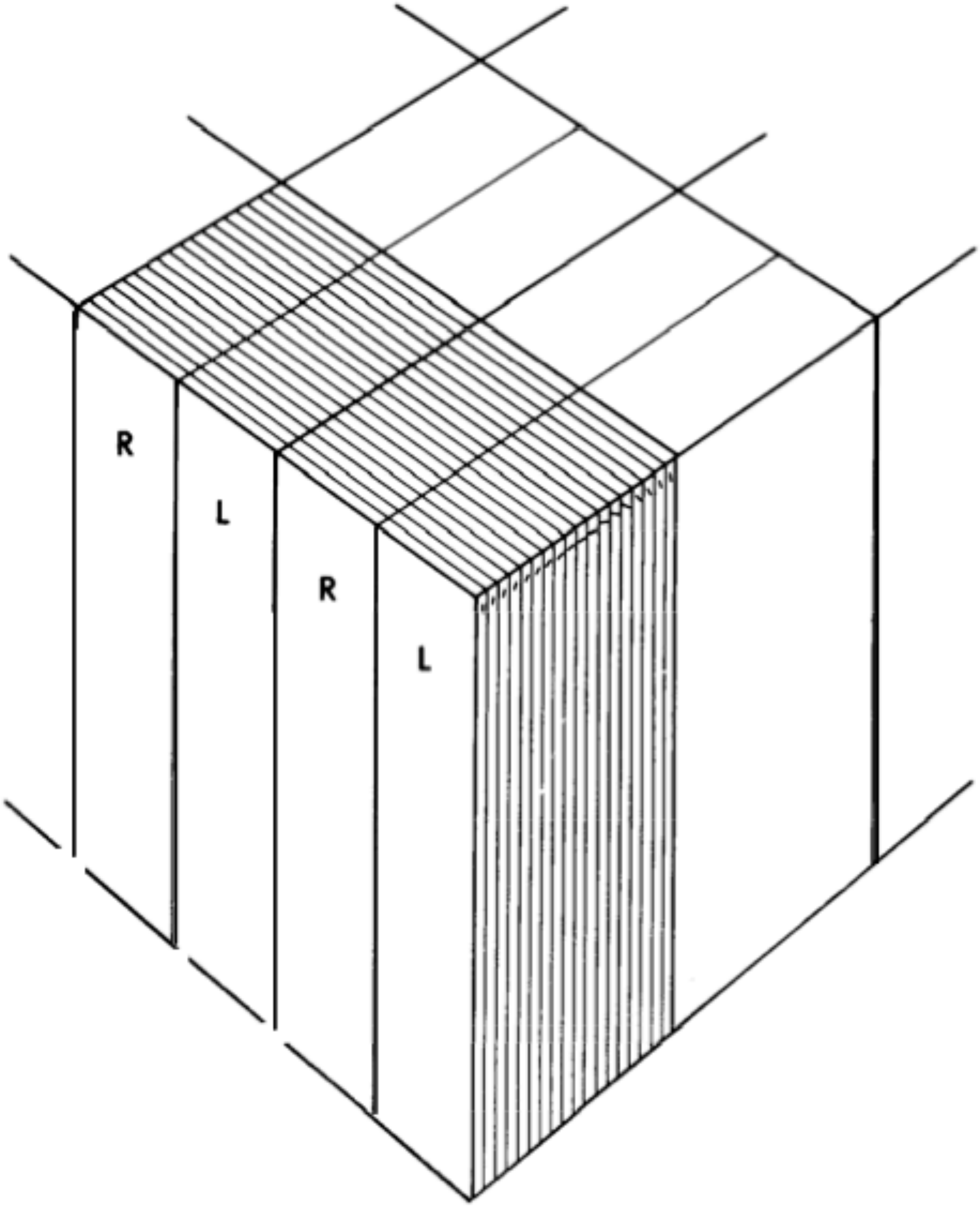

Fig.3.6 A model of striate cortex showing the ocular dominance columns (marked L-R) and the orientation columns running at right angles to them, with the direction of orientation preference indicated by the small lines on the top-right edge of the block. The top surface of the block represents the cortical surface. The entire block shown comprises four ‘hypercolumns’. Source: Hubel (1982, Fig. 15).

Consistent with previous work, it was found that when the deprived eye was opened after 3 months the animal was unable to see with it. However, there were no obvious changes in the ocular media or the retina that could explain the deficit; instead, marked changes were found at the level of the primary visual cortex, which suggested that this region was involved in performing analyses on the fine structure in the visual input.

Hubel and Wiesel sought to document the changes induced in cortical function by recording from cells in the striate cortex to determine their ocular preference. As mentioned earlier, in the monkey there is normally an even balance between cells driven preferentially by one eye and those driven preferentially by the other eye, and that in the input layer IVC most cells are strictly monocular, and outside layer IVC they are binocular by varying degrees.

Under conditions of monocular deprivation the majority of the cortical cells were found to respond to input exclusively from the non-deprived eye. It is interesting to observe that even though the cells in the LGN received unstructured input from the deprived eye they were found to be present in normal numbers and respond briskly to stimulation of the deprived eye, and had normal receptive fields. However, the deprived LGN cells were smaller than those in the non-deprived layers. As such, monocular deprivation does not substantially alter the LGN. However, substantial changes were seen in the striate cortex.

In the normal monkey, the afferents from the LGN remain segregated in an eye-specific manner when they reach layer IVC of the cortex. However, the afferents invading the cortex initially overlap completely, and studies in the fetal monkey show that not until a few days before birth do the afferent fibers begin to sort into ocular dominance columns. Only by the age of 4-6 weeks is the process of segregation completed, when the input from each eye is distributed into a series of branching bands, which are about 0.5 mm wide, and alternate with similar bands from the other eye, forming the anatomical basis for the ocular dominance columns mentioned earlier. This process appears not to require experience since it occurs also in animals raised in the dark.

Hubel and Wiesel studied the process of cortical innervation in some detail also in kittens, where it was found that each geniculate afferent gives off numerous branches that innervate without interruption an area covering several future ocular-dominance columns. As the axon matures, there is a selective loss of branches so that the afferent terminals innervate cells in ocular dominance columns serving only one eye and leave gaps for the column serving the other eye.

However, in an animal that had undergone monocular deprivation, the geniculate terminals from the non-deprived eye continue to occupy the region of initial non-segregated spread, which they would otherwise have relinquished, and take over much of the space that would normally have been occupied by the inputs from the deprived eye (which, nevertheless, transmits light and low spatial frequency variations in intensity patterns through the sutured eyelids). Meanwhile, the inputs from the deprived eye are severely trimmed to leave a small trace of shrivelled strips lying between the inputs from the non-deprived eye. Cells in these strips are either unresponsive or driven by the non-deprived eye.

The expansion of the input from the non-deprived eye occurs at the level of single geniculate afferents. Wiesel (1982) suggested that one reason that the deprived cells in the LGN are smaller than normal (mentioned earlier) is because their shrunken cortical arbours may require a smaller soma to maintain them. Autoradiographs labelling of the afferents in layer IVC showed that the greater proportion of the cells in this layer receive inputs from the un-deprived eye, and that the cells ‘higher’ in the hierarchy from the input layer had shifted their allegiance from the deprived to the non-deprived eye. This work provided the first detailed account of a competitive invasion of cortical territory that would have supported a deprived sensory source by one that continues to function. It also marked the interface between endogenously driven wiring of the segregated inputs into layer IVC and the initiation of analysis of the fine structure in the environmental input within the cortical columns of the striate cortex.

3.5.6.1 The Critical Period

Hubel and Wiesel sought to determine if there was a period over which the cortex retained its plasticity, and found that there was a definite interval of time early in life when the striate cortex remained labile, after which alterations in sensory input did not change cortical connectivity. They called this interval of heightened plasticity the ‘critical period’. This early susceptibility to alterations in fundamental visual function would account for the earlier finding of the poor results for the restoration of vision in the congenitally blind that had received surgical treatment late in life to restore their vision. It also accounts for the finding that adults suffering from late onset cataracts will have normal vision when the cataracts are removed.

Wiesel (1982) observed that the effects on ocular-dominance distribution of the cells in the striate cortex resulting from eye closure at different ages in the monkey showed that the most profound deficits were seen in the period from birth till around 6 weeks. There were no cortical changes when the closure was done in the adult, with plasticity to deprivation remaining until the age of 1-2 years. From clinical observations in humans, it is shown that the critical period may extend to 5-10 years, although it is most pronounced in the first year. Wiesel (1982) observes that critical periods vary in onset and duration between different brain regions (as will be shown elsewhere in the present work) and even between layers of a given cortical area.

Eye closure in the monkey during the entire critical period leads to permanent blindness because the subsequent pattern of geniculate innervation of cortex and the eye preference of cortical cells can no longer be modified. This would presumably apply also to the pattern of innervations in the whole extent of the cortical column.

The application of early ‘reverse suture’ in both cats and monkeys provides an example of the degree of early plasticity in the visual system. In this case, a previously sutured eye is opened and the other eye is sutured. This procedure can lead to a complete switch in eye preference if it is done in the early part of the critical period at 5 weeks in kittens (Blakemore and Van Sluyters, 1974). Geniculate innervations of layer IVC was also reversed, so that the shrunken regions connected to the initially closed eye expanded at the expense of the other eye, and consequently the cortical cells switched eye preference in favour of the eye that had been closed before.

Binocular fusion is clearly important for depth perception, and relies upon the solution to the correspondence problem, in which a one-to-one mapping needs to be established between a light source in the visual field of one eye with the same source in the visual field of the other, laterally displaced eye. Given that the visual acuity of the eye is about 30 arc seconds, a correspondence between the ocular inputs need to be established at this level if the maximum depth perception ability is to be attained.

A strong indication that binocular fusion is acquired by learning is shown by the fact that there has to be an overlap between the visual fields of the two eyes and both eyes need to work together to create the mapping. Situations that disrupt these requirements are those of strabismus (or crossed eyes) and amblyopia (lazy eye). The former can arise congenitally or may be induced surgically. Cortical effect of strabismus can be effected in the normal animal by alternately patching each eye, one at a time, so that visual input from both eyes are not experienced simultaneously.

Wiesel (1982) reports that the striate cortex of animals in which strabismus had been induced between the ages of 3-5 weeks, and examined about a year later, showed a striking absence of binocular cells. This was found to be the case also for animals that had been subjected to alternate patching. Although these animals had normal visual acuity in each eye, they were unable to learn to fuse the images in the two eyes because they had not been provided with synchronous foveal input from overlapping visual fields of the two eyes. Monocular cells were found to be grouped in the usual columnar fashion, but with a marked deficiency in binocular cells and an absence in the binocular function required for depth perception.

In summing up, Wiesel (1982) observes that while innate mechanisms endow the visual system with highly specific connections from the retina to layer IVC of the striate cortex, visual experience is important for the development of and maintenance of normal visual function. The deprivation experiments showed that the neural connections could be radically altered by environmental influences during a critical period of postnatal development, leading to a loss of otherwise learned functions such as binocular fusion. He concluded that the sensitivity of the nervous system to the effects of experience might represent a fundamental mechanism by which the organism adapts to its environment during a critical period of growth and development.

3.5.7 Further Early Recordings from the Striate Cortex

The seminal work by Blakemore and Cooper (1970) was described in the Introduction, and showed that the development of visual sensitivity to contours does not develop without their presence in the early environment. However, it should be emphasized that rectilinear receptive field boundaries and the rectilinear nature of the effective stimuli found in the kittens and monkeys by Hubel and Wiesel were obtained from animals that were raised in ‘normal’ laboratory environments.

These would have, presumably, comprised cages, other man-made objects and overall containments for human habitation incorporating rectilinear edges. The effect of visual input from such an environment can be expected to bias the development of receptive field characteristics and the effective stimuli, to which the cortical cells respond, into being linear segments. Such a developmental bias carries the risk that it may be taken that the cortical cells are furnished innately with a propensity to respond to rectilinear segments. Wiesel (1982) noted that although it was unclear if cortical cells can develop fully through innate mechanisms, it was found that animals raised in the dark or with binocular lid closures seem to have a certain fraction of unresponsive or ‘unoriented’ cortical cells.

Seeking to address the issue of whether linear-segmented effective stimuli were given innately, Pettigrew and Freeman (1973) dark-raised kittens until 28 days after birth. Then for 13 days the kittens spent 3 hours daily in a planetarium-like sphere of 90 cm diameter that admitted a random array of point sources of light through the upper hemisphere with a random array of spot-sources of light, none of which were closer than 3 degrees in visual angle. A detailed study of single cell responses in the striate cortex of 2 of these kittens revealed that a majority of cells that responded to the test stimuli were optimally activated by moving spots of light, and only two cells out of a total of 69 units were found to be edge detectors.

The finding that the cortical neurons were more sensitive to spots of light than to straight lines was in marked contrast to that obtained from normally raised cats. Examination of the cells in the striate cortex of a control cat, that was raised in the dark, showed neurons with no clear preference for lines or spots, although there was a weak directional preference for a stimulus sweep. Consequently, it would appear that the findings by Hubel and Wiesel that the effective stimuli are line contours appears to be a feature of the developmental environment, and that line segments are not innately specified as effective stimuli in kittens. The finding by Pettigrew and Freeman (1973) shows that the primitives of vision are perhaps more labile to the early environmental setting than the previous work might suggest, and that the center-surround response of the retinal ganglion and LGN cells can be modified in the processing hierarchy into responding to moving spots as effective stimuli.

It is interesting to note that some cells in the striate cortex in the kittens studied by Blakemore and Cooper (1970) showed circles as effective stimuli. These may have developed in response to the visible circular edges of their containing enclosure of black and white stripes and those of the conical collars that were attached around their necks to obscure sight of their bodies. The above findings would suggest that the visual cortex is more susceptible to experience-driven plasticity than was previously thought.

3.5.8 Summary of Findings Using Single Cell Recordings

- Work on macaques suggests that the pathways from the retinal receptors to the point of segregation of the geniculate afferents into the ocular dominance columns in layer IVC of striate cortex occurs without the participation of visual learning or experience. This appears to mark the nature-nurture divide. Configuration of the striate cortex occurs thereafter by the nurturing effects of environmental input.

- Deprivation experiments demonstrate that visual function cannot arise without experience during the critical period for development.
- During this critical period, environmental input influences the sensitization of ‘simple’, ‘complex’ and ‘hypercomplex’ cells to respond to hierarchically more complex visual primitives.
- Binocular fusion and function require synchronous structured overlapping input from the two eyes, and is thought to be learned.
- The above findings account for the inability of individuals with vision ‘restored’ late in life having poor object recognition and not being able to acquire depth perception by stereopsis.
- The visual system is not confined innately to learning only primitives in the form of line segments of different orientations. The system can also become sensitized to, for instance, other primitive forms like moving spots.
- Given that visual length perception relies (a) on visual function and (b) on the capacity to apprehend the end points of length segments in the visual field, and that edge detection is learned, visual length perception must be acquired.
- As indicated above, visual depth perception by stereopsis is not given innately because binocular fusion relies on the capacity for structured vision through the acquisition of visual primitives prior to being able to solve the correspondence problem upon which stereopsis relies.

Visual depth perception can be sensed also by optic flow and motion parallax (see, for instance, Stone, 2012, p. 122). Both these functions rely on visual motion detectors. It is explained in §10.7 that there is a columnar organization in cortical region V5 that has been linked to the higher order processing of visual motion, and that the development of the capacity to apprehend visual motion depends on experience during the critical period for visual motion sensitization. In sum, it would appear that visual length perception is not given innately but depends on learning from the environment. The issue of whether the capacity for visual length perception is native or derived is elaborated upon in §5.7.

3.6.0 Constructivism

Following the early work carried out on laboratory animals that led to a basic understanding of cortical processes (some of which has been described above), much subsequent work has resulted in the emergence of a consensus among workers in the domain of neurophysiology and those in computational neuroscience about how the representations underlying cognitive skills emerge. This issue has been addressed by Quartz (1999) by integrating neurophysiological, cognitive and computational perspectives. The results are in accord with Piaget's constructivist themes, and form the constructivist approach to development. For details of the publications referred to herein please consult Quartz (1999).

Quartz (1999) observed that the results obtained from studies of developmental plasticity makes nativist proposals increasingly untenable. Instead, cortical development appears to involve the progressive elaboration of neural circuits in which experience-dependent neural growth mechanisms act alongside intrinsic developmental processes. This view is in accord with Piaget's themes of progressive constructive growth of cognitive and motor competence, and supports the view of human cortical development as a protracted period of hierarchical construction that involves a cascade of increasingly complex representations.

Plato's insight was that learning needed a rich stock of prior knowledge. As such, Locke's proposal of *tabula rasa* is unfeasible if one considers learning to be a rearrangement of pre-given elements that only get reconfigured. For this reason the nativists (e.g., Chomsky and Fordor) presented influential arguments for why significant amounts of conceptual knowledge must be encoded *a priori* in cortical structures. This nativist model is the cornerstone of evolutionary psychology's proposals about how evolutionary pressures might have shaped the human mind as a collection of domain-specific mental modules.

However, evidence from developmental neurobiology makes it increasingly problematic to suppose that complex conceptual knowledge is somehow encoded in the cortex prior to experience. For instance, in subjects who were blind from an early age, tactile processing during Braille reading, which is generally supported by secondary somatosensory cortex, is re-routed in blind subjects to ventral occipital cortical regions that are normally employed for visual shape discrimination. While these results do not preclude domain-specific biases in various cortical regions, the capacity of cortical regions to become functional within a novel sensory domain makes it problematic to posit native complex sensory encodings in them.

Nevertheless, the results obtained by Hubel and Wiesel and co-workers presented above, combined with behavioural work show that visual primitives are assimilated from the environment during early development, as are the auditory primitives associated with speech perception (See chapter 9). In this regard, the nativists have neglected the cortical capacity to bootstrap representational structures by the creation of Hebbian cell assemblies. Although Piaget's developmental themes were dismissed by nativists as theoretically confused, the emerging constructivist view of development supports his original proposals about the hierarchical, activity-mediated construction of mental representations.

3.6.1 Selectionist Development

According to the neural selectionist, or epigenetic theory of Changeaux (and colleagues) and Edelman (both cited in Quartz, 1999), development involves two stages. The first phase consists of an initial activity-independent overproduction of cortical structures that might contain pre-formed modules containing innate knowledge. This is followed by a second phase of activity-dependent selection of a subset of those structures that contains information useful to the organism. Thus, there is a combination of both genetic and extrinsically generated signals that result in a diversity of representations. This produces the background knowledge against which learning can proceed. Cognitive development may be then regarded as a competitive search through these representations, with those poorly matched being eliminated. Experience does not play a role in the construction of these representations, but only in their elimination.

3.6.2 Constructivist Neural Development

Constructivism belongs to the tradition that began with Jean Piaget, and was developed by Hebb (1949), who provided many insights mentioned earlier (in § 3.2) that enabled the establishment of a parallel between behavioural development and the ordering of neural tissue. In this view, constructivism is endemically hierarchical. If cognitive and neural processes really do interact, then learning can alter what can be subsequently learned because learning causes major changes in the underlying hardware; essentially, that learning guides brain development.

In this view, the nature-nurture debate breaks down as a dichotomy for both epigenetic development and for constructivism. Selectionist development relies on genetic endowment to provide the range of neural structures from which environmental factors select what is to be pruned and what is to be retained. The constructivist approach relies upon the genetic endowment to provide the instructions for the construction of new nervous tissue as structures in which environmentally driven learning gets represented in a hierarchical manner (see Kandel, 2006, p. 276). Indeed, Stiles (2009) proposes that there are no behaviours that do not require gene expression and activity.

Quartz and Sejnowski (1997) observe that the brain structures underlying development undergo large-scale changes during cognitive skill acquisition; that these changes depend on the interactions between the sensory and motor systems of the organism with the environment. The constructivist account of learning does not rely on a rearrangement of prior knowledge so that learning might take place.

It is based, instead, upon a bootstrapping procedure reliant on Hebb's proposal of the construction of cell assemblies, and thence of neural circuits generated from patterned activity in the sensory input. In essence, the process of construction depends on Hebb's rule, that suggested that the co-firing of neurons leads to the formation and appropriate adjustment of connections between neurons. As mentioned in Quartz and Sejnowski (1997), dendritic growth is an active process where growth and connections form under the influence of patterned activity generated in both the dendrites and the axonal arbours.

3.6.3 Spontaneously Generated and Experience-Dependent Construction

Essentially, Hebb proposed that patterned neural activity could participate in the construction of neural circuits. Evidence has accumulated in recent years to support Hebb's stance that (i) spontaneously generated activity, for instance, in the form of retinal waves (Wong, 1999; Fox and Wong, 2005) and those in cochlear spiral ganglion cells (Jones et al., 2007; Köppl, 2007) and (ii) experience-dependent activity both play a role in constructing and refining cortical circuits. This view is consistently found to be the case rather than the selectionist one that views development as consisting of a selection from among innately given pre-existing cell assemblies. Spontaneously generated activity may be considered to represent a part of neural maturation and ordering prior to the later phase of experience-dependent circuit construction. It would appear that Hubel and Wiesel's finding of the segregation of the geniculocortical afferents into separate cortical columns according to their eye of origin is regulated by the endogenously generated retinal waves.

This view supports the stance that the later development of cortical circuits is a constructivist one of progressive elaboration rather than one of selective elimination. In this regard, Purves et al. (1996) conclude: '… we consider a Darwinian [selectionist] framework to be particularly misleading.' Both Purves et al. (1996) and Quartz and Sejnowski (1997), who examined the developmental time-course of synaptic numbers, axonal processes and dendritic arbours, concluded that the bulk of the evidence favours a progressive and constructive form of neural development.

In this regard, more recent work has focussed on the participation of brain derived nerve growth factors in promoting the growth of dendrites. Quartz (1999) cites results that suggest that the combined effect of activity and the release of neurotrophins provide a mechanism for enhancing the growth and connectivity of active neurons in developing cortex.

There is, thus, evidence that cortical development is not characterized by an early overproduction followed by selective elimination. Instead of the cortex containing specialized innately-given modules, the constructivist view supports the notion of a 'protocortex' proposed by O'Leary (1989). In this view, the cortex may be generally regarded as having, initially, a generic architecture, sharing common circuitry and basic repetitive arrays of cell types that are then configured by the modality of thalamic input, to enable its specific function.

It is, thus, the different patterns of activity, reflective of the different sensory modalities that confer area-specific properties to the cortex, and not innate predispositions that are somehow embedded in the recipient cortical structure. In this regard, neural constructivism considers modularization not as the starting point of development, but is the end point of hierarchical development, and this process of construction may be regarded as one of learning.

Such a view is supported by findings reported by Sur and colleagues (see Sur and Rubenstein, 2005) who succeeded in diverting visual input via the medial geniculate nucleus into the auditory cortex to form visual receptive fields in the auditory cortices of ferret kits. A system in which the cortex is ‘enslaved’ by the periphery has a number of useful features in terms of being able to respond flexibly to varying environmental pressures and changes in body size. Such a system is also able to respond to being re-deployed in the event of early damage to the peripheral sensory organs or, indeed, the afferent sensory pathways.

This description of the activity-dependent organization of representations in cortical material does not account for the general architecture of the cortex, or indeed for the layout of the brain as a whole. The development of this organization is attributed to the spatially specific molecular signalling of neural progenitor cells in the proliferative zone, which is thought to establish the overall layout of the brain and the pathways separating the primary divisions of the cortex. The extent to which such molecular signalling, rather than activity-driven factors, determine topographic maps in the cortex is the subject of continuing debate between those who hold with the protocortex or the protomap view. The protomap view holds that molecular signalling cues determine both the location and function of the neurons in the primary subdivisions of cortex, whereas, as mentioned, the protocortex position holds that cortical material has its identity determined by the nature of the activity generated ultimately in the sensory receptors (Killackey et al., 1995; Wong, 1999; Sur and Rubenstein, 2005; Stiles, 2008). It is likely that both purely genetic and constructivist factors contribute to the development of the overall layout of the cerebral cortex.

It is worth emphasizing, however, that principles set out in the constructivist account of the genesis of neural circuits within the separate cortical regions is not in any way undermined by the suggestion that the overall cortical layout is reliant on genetic factors. Constructivist learning is consistent with Piaget’s central theme that learning plays a central role in constructing mental representations.

Singer (1990) observes that later brain development differs radically from the development of other organs because electrical activity is added to the biochemical messengers as a further signalling system in the self-organization dialogue between the genes and the environment. These electrical signals influence gene expression and posttranslational modifications. Electrical signals are transported by neuronal processes over appreciable distances, and with high topographical selectivity. This enlarges dramatically the range and the complexity of the environment that is available to the self-organization process within the organism. From the onset of the critical period, the brain possesses functioning sense organs that convert signals from extra-corporal space into electrical signals. Thus, the environment relevant for brain self-organization includes all domains with which it is capable of interacting. The action potentials that convey sensory input are used by the brain for the construction of internal representations. As the complexity of the brain increases, the complexity of its interactions with the environment increases as well. Because of this spiral of reciprocal interactions between the genome and its environment, a relatively small amount of genetic information suffices to promote the development of the highly differentiated structures in the human brain. Singer (1990) suggests that the processes that support experience-dependent self-organization during development are closely related to the more general processes that serve to adapt the mature brain to its environment and can be considered to be a process of learning.

3.6.4 Neural Network Modelling of Constructive Development

Computational neuroscience demonstrates the intimate connection between the morphological aspects of structures in the nervous system and their computational properties. Two modifiable morphological properties of neural structures are (1) the number of processing nodes (or units) and the number of levels in which they are arranged and (2) the synaptic weights. Other factors such as neurotransmitter release have also been considered (see Quartz, 2003).

Much of neural networks research has employed networks with fixed architectures. However, a growing body of more recent research focuses on ‘constructive’ neural networks in which the architecture itself can be altered as a part of learning (Quinlan, 1998; Schultz et al., 2007). Given that the representational properties of neural networks are derived from their structural properties (see, for instance, Rumelhart and McClelland, 1986; McClelland and Rumelhart, 1986; Kohonen, 1987; Anderson and Rosenfeld, 1988; White, 1990; Gerstner and Kistler, 2002; for a historical account see Boden, 2006), activity-dependent change in their architecture, whether by the addition of new processing units or connections, amounts to a process of the construction of new representations.

White (1990) has deduced that networks that add units at an appropriate rate relative to their ‘experience’ are able to ‘learn’, essentially, any arbitrary mapping between the input and its internal representation. Schultz et al. (2007) have demonstrated an example of this property by employing a ‘cascade-correlation’ algorithm that uses activity-dependent architectural plasticity by adding hidden units or by forming new connections. In this way new information is built upon previous information. Among the tasks addressed by the modellers was the reorganization of the inferior colliculus of juvenile barn owls fitted with optical prisms that shift the visual field across the azimuth, so that the sound source direction and its visual location no longer coincided. This network was shown to successfully model the neuronal plasticity involved in the recalibration process in the juvenile owl’s inferior colliculus.

3.6.5 Hierarchical Constructive Development

Quartz (1999) observes that Piaget's central view of development remains sound with respect to the constructivist paradigm, in that it involves the expansion of hierarchically organized sequential construction of competence. In this view, development begins with perceptual and sensorimotor functions, and becomes more complex as development proceeds. The question arises whether this process of hierarchical construction occurs regionally or if development occurs simultaneously across regions.

This distinction is important because according to the selectionist model of neural Darwinism, there is an exuberant proliferation of synapses *simultaneously* across the cortex. Instead, in the constructivist view, development occurs as a cascade of increasingly complex representational structures, in which construction in a particular region would depend on the prior development of another. Such a progression would add substantially to the complexity of representational structures that can be constructed through the interaction of intrinsic developmental programmes and activity-mediated growth algorithms.

The former neural Darwinist (selectionist) view would rule out also the finding that in somatosensory development, ordering occurs from the sensory periphery to the higher associational areas (Killackey et al., 1995; Scott and Atkinson, 1999; Rubel, 2004), and that myelination and dendritic arborization develop regionally.

Furthermore, Quartz (1999) cites work by Huttenlocher and Dabholkar (1997) who reported that human synaptogenesis occurs regionally, which is in accord with the hierarchical developmental schedule observed for axonal growth, dendritic growth and myelination of the subcortical white matter. The view of hierarchical development, where construction in certain regions is dependent on the prior development of others is manifested both behaviourally and physiologically in the acquisition of infant sound perception. Indeed, hierarchical structures are documented in the auditory cortex along which the complexity of preferred stimuli increase from tones and noise bursts to words and sentences (see §9.5). In accord with these findings, Fuster (1997) observes that the general cortical substrate for memory and knowledge can be viewed as an upward expansion of a hierarchy of neural structures.

It is worth noting that although there are extensive *efferent* connections leading from the higher cortical regions to the lower ones and, indeed, to subcortical structures, the spatial organization in the brain is such that the regions closer to the sensory periphery encode lower-order, or elementary, i.e., less complex representations than do areas further removed from the sensory epithelia (as observed also by Hubel and Wiesel in §3.5.0). In vision, touch and audition there appears to be a hierarchical stacking of perceptual memory categories in progressively higher and more widely distributed networks (Fuster, 1997).

Furthermore, in support of an overall hierarchical ordering of the brain is the finding that the temporal order of activity in the visual pathway, recorded by Hillyard et al. (2004), showed that sensory input creates a feed-forward activity in the brain that proceeds up the hierarchy of the different visual processing regions (the bottom-up pass). In the cortex, V1 is thought to be the initial region that is configured by visual input (Lee and Mumford, 2003; Deco and Lee, 2004). The feed-forward pass is then followed by ‘top-down’ re-entrant feedback projections that augment the processing in the lower regions.

Quartz (1999) also concluded that converging lines of evidence suggest that human cortical development results from an environmentally induced construction of neural circuits. This process is not concurrent across cortical regions, but proceeds regionally from those closest to the sensory epithelia in a hierarchical manner to the higher regions, so that the development involves experience-dependent neural growth mechanisms acting alongside intrinsic developmental processes to construct the representations underlying mature perceptual and motor skills.

3.6.6.0 Measures of Variation in Complexity with Development

In order to support their constructivist stance for the development of perception and cognition Quartz and Sejnowski (1997) provided an analysis whose conclusion was that absolute synaptic numbers alone are an inadequate measure of representational complexity. They observed that in connectionist models there is a direct relation between the number of connections and a network’s complexity. However, in many real neurons, the spatial arrangement of pre- and postsynaptic elements is thought to be crucial to their response properties. One reason for this is the presence of active conductance properties in the cell’s membrane. These amplify or otherwise change the incoming signal in non-linear ways and shift the emphasis from the importance of absolute synaptic numbers to their spatial arrangements. In this regard, Quartz and Sejnowski (1997) consider axonal and dendritic arborization to be more central to determining circuit complexity.

3.6.6.1 Axonal Arborization and Dendritic Development

Quartz and Sejnowski (1997) show, in their Table 2, evidence to support the view that retinogeniculocortical pathways increase in their complexity throughout development, and that the elimination of action potentials generally blocks structural development. However, there is also some retraction of early axonal structures, so development involves both selective elimination and considerable growth and elaboration.

It is widely known that there is a general increase in the arborization and length of dendrites (see, for instance, Quartz and Sejnowski, 1997, Fig. 7) during ontogenesis. The dendrites are actively growing neuronal formations that accommodate to changing functional demands. In enucleated animals, dendrites re-direct their growth towards active afferents. These response properties are not predetermined but depend on interacting with the information modality latent in the pattern of incoming activity. The dendrites shape their responses to adapt to that activity as was manifested in the development of ocular dominance columns, with the borders of the columns representing changes in correlated activity. This provides an example of how self-organization through the degree of correlated activity, rather than activity *per se,* might overcome the need for pre-specification of dendritic targets by use of intrinsic molecular cues. Other such examples of activity sensitivity in dendrites may be found in Quartz and Sejnowski (1997) and elsewhere. It is interesting to observe that these findings are in accord with Hebb's original proposal that in the context of neural development, cell assemblies and new synapses were constructed on the basis of correlated activity (Hebb, 1949).

In support of the constructivist stance that growth of neuropil supports in part the representational structure for perceptual and cognitive competence, Quartz and Sejnowski (1997) observe that at birth the human brain is about 25% of its mature weight. Dendrites in the striate cortex are between 30-50% of their adult length at birth. By contrast, cells in the frontal cortex, being higher up in the hierarchy, are far slower to develop, with the majority of their growth occurring after 2 years of age. By adulthood they grow by more than 30 times their length at birth. This reflects the prolonged period in which the environmental inputs shape the brain. In accord with a the existence of a hierarchical structure, as observed earlier, the higher cortical areas being further away from the periphery, develop later. As development proceeds, the different areas of the brain become increasingly specialized for particular functions, reflecting a cascade of environmental shaping. Quartz and Sejnowski (1997) observe that the brain is not a hodgepodge of specialized circuits, each chosen by evolutionary pressure. Rather, the hallmark of cortical evolution is an increasing representational flexibility that allows environmental factors to shape the human brain's structure and function.

3.6.7 Critical Periods, Hierarchies and Primitives

The constructivist approach proposes the means for the development of the neural substructure for perception and cognition. These are considered to be continuous with one another, in that the neural substrate that supports both is organized hierarchically in their development and function and there is no easily discernible line of demarcation between the parts of the neural substrate that support perception and cognition. In line with Hebb (1949, p. 109), the constructivist approach supports the hierarchical view that all learning tends to utilize and build on any existing structure instead of replacing it, so that much early learning tends to be permanent. In this respect, there is a distinction between the more permanent earlier learning, during which, for instance, visual primitives are learned, which has associated critical periods mentioned earlier, and later learning, which can be 'one shot', as in the capacity to remember for instance, a train departure time. It is the permanence of the early learning that leads to a stable perceptual reality.

In general the learning of primitives have associated critical periods, after which they become fixed to provide a stable base upon which subsequent structures may be constructed. In the early stages, it is only these early structures that may be recognized and manipulated.

For example, during early stages of learning speech recognition, and later, in respect to the learning of motor primitives in regard to speech production, it is only the set of phonemes which have been learned that may be recognized and uttered at will. In later stages, larger collections of sounds may be recognized and produced: words and sentences that are composed of the phonemic primitives. However, the recognition and production of new phonemes become difficult after their appropriate critical periods (see Chapter 9).

3.6.8 Hierarchical Processing and Gnostic Neurons

The pioneering work of Hubel and Wiesel described in §3.5.0 showed that there was a hierarchy of visual mechanisms that extended from the retina through the geniculostriate system, in which lines of specific orientations but non-specific length were effective stimuli for the excitation of 'simple' cells. As mentioned earlier, the term effective stimulus refers to stimuli that give rise to a maximal change of discharge rate when that stimulus is introduced into the receptive field of a neuron. In this view, neurons are 'tuned' to respond to particular features in sensory input. Visual processing was thus thought to proceed through a series of hierarchically arranged set of 'filters'.

Moving up the hierarchy of visual processing, the receptive fields of the neurons become larger and they become more specific to the stimuli they respond to. For example, the orientation of a slit presented to the retina is not material to the firing pattern of retinal or lateral genicular cells, but is of significance for cortical cells. The length of a slit is critical for a 'hypercomplex' cells but not for a 'simple' or 'complex' cell in V1.

Following this early work, Gross (1972) found that there were units in the inferotemporal cortex (IT) of macaque monkeys, whose response was specific to the silhouette of a macaque hand, oriented with the fingers pointing in an upward direction. Further, that there were units that had effective stimuli, which were three-dimensional objects rather than two-dimensional patterns. These results were obtained from paralysed, adult macaque monkeys that had been anaesthetized with nitrous oxide and oxygen. IT is now known to be a region that participates in visual pattern recognition and lies beyond and above the circumstriate belt in the visual processing hierarchy.

These findings supported Konorski's hypothesis of 'gnostic units' (Konorski, 1967), which proposed that for each unit in a given afferent field of a given analyser, there is a stimulus or a set of stimuli which produces its optimal response. The higher the level of the given afferent system, the more complex and refined is the effective stimulus to which the units of this level will react.

This hypothesis has now found validation in that some neurons have as effective stimuli highly complex natural images, such as faces, snakes, hands and flowers (Desimone et al., 1984), and parts of faces like eyebrows and noses (Rolls, 2007). Other neurons respond to 'synthetic' objects such as desks and motor vehicles, although it is held that there is nothing unique about faces *per se*, and the synthetic-natural distinction is invalid (Nelson, 2001). However, some neurons respond only to faces and show both position and rotation invariance for the input images.

There seems little doubt that the units that have as their effective stimuli synthetic objects and specific faces will have acquired their response properties through learning (Gauthier et al., 1999). A similar argument is used in the present work during the course of analysing the auditory system, which also exhibits a hierarchical organization, to make the claim that the sounds made by synthetic objects are acquired (see chapters 8 and 9). As elaborated above, this learning process had been previously thought to have occurred through a bottom-up flow of activity, beginning with external stimuli impinging upon the sensory epithelia, and thence up the processing hierarchy.

3.7.0 Topographic Maps and Learning

Thus far this chapter has dealt with the correlations between visual behaviour and the formation of visual primitives at the cellular level. In what follows, the conventional ‘bottom-up’ view of activity-dependent learning, as it manifests on a larger scale in diverse regions of the cortex, will be recounted. By bottom-up theories I refer to the view that the neuronal activity that derives from the sensory epithelia is regarded as being sufficient to account for the learning observed. Such a view ignores all top-down factors that may be associated with any autonomously directed attentional component. Any considered elaboration upon this topic would require addressing the term ‘attention’ as a mental phenomenon within what is proposed as an objective evaluation of the status of science, and so lies beyond the scope of the present work. The term ‘attention’ as used herein may be taken to conform to the Hebbian definition: ‘… a central facilitation of a perceptual activity.’ (Hebb, 1949, p. 102).

Learning within the neural substrate at large is most robustly evaluated through the changes in the activities of groups of neurons associated with particular behavioural tasks. As mentioned earlier, the total number of neurons in the nervous system remains roughly constant after the early stages of ontogeny. However, as skill acquisition proceeds the neurons that participate in the execution of the skill become more finely tuned to the accomplishment of their tasks.

There is also a recruitment of other, often adjacently located neurons into participating in the activity. This can often increase the numbers of neurons seen to be involved in a particular task. In these cases there is a concomitant growth of new connective tissue (neuropil) as well as alterations of the synaptic weights between the different cells. These changes provide perhaps the most robust neural correlates of learning.

The neurons, be they associated with sensory, motor or abstract mental processes, tend to be contained within two-dimensional ‘topographic’ maps in which spatially adjacent neurons are found to perform similar tasks. These maps are ubiquitous in the mammalian nervous system and are associated with virtually all functions performed by nervous tissue (for a popular account see Blakeslee and Blakeslee, 2007).

Since alterations in the functional characteristics of topographic maps will be used as a major method for the assessment of skill acquisition in §3.7.1, a brief account will be provided below of the genesis of topographic maps and their plasticity during what is regarded as bottom-up learning.

For a review of the molecular theories of memory formation, which elaborate upon the processes that give rise to the growth of neuropil, see, for instance, Kandel and Squire (2000); Martin et al. (2000); Kandel (2006).

3.7.1 Topographic Maps

It was Cajal who first remarked upon the precision of the connectivity among the diversity of neuron types that he had charted in the brain (Cajal, 1894). This near ubiquitous feature of brain organization is manifested in ordered two-dimensional topographies, where the physical layout of the projections from the primary receptors in the majority of sensory epithelia is maintained in the various nuclei in the central nervous system. For instance, the retinotopic arrangement of the light receptors in the eye is retained in the retinofugal projections to the various retinoreceptive nuclei. In this arrangement, neighbouring retinal ganglion cells project their axons to neighbouring positions in the optic tectum (or superior colliculus in mammals) and the other visual processing centres mentioned earlier, thereby retaining a quasi-continuous neural representation of visual space.

The tonotopic adjacency relations present in the basilar membrane are maintained in the cochlear nucleus and the subsequent acoustic processing stages (see Robertson and Irvine, 1989, for details). Topographic projections from receptors in the skin, and indeed from the vibrissae, that form the major haptic sense organs of rodents (Mitchinson et al., 2007), maintain a precise mapping of their overall layout also in layer IV of the somatosensory cortex. This is despite the fact that the map in the barrel cortex, for instance, is a third-order projection from intervening processing stages (Nord, 1967; Arvidsson, 1982).

The corpus callosum has over 200 million axons passing through it, and along with the anterior commissure, it provides the only direct link between the cortices of the right and left hemispheres. The corpus callosum is also topographic in its organization. Anterior fibers connect frontal regions of the two hemispheres, and pass through the rostral portion of the corpus callosum, including the genu. Posterior fibers connect posterior cortical structures, and these fibers from regions such as the superior parietal lobule and the occipital cortex pass exclusively through the splenium. This anterior to posterior organization results in modality specific regions of the corpus callosum. Motor related information is transferred from one hemisphere to the other via fibers in the anterior midbody of the corpus callosum, somatosensory information via the posterior midbody, auditory information via fibers in the isthmus, and visual information via splenial fibers. The functional architecture derived from anatomical studies has been supported by behavioural studies on patients who have had incomplete sections of the corpus callosum (Stalin and Bullier, 1995; Funnell et al., 2000).

More recently, Thivierge and Marcus (2007) (who provide a useful review) have conjectured that topographic maps may be involved also in the regions that support higher cognitive functions such as reasoning and analogy.

Electrical stimulation studies by Penfield and Boldrey (1937), in awake human patients, and by Woolsey (1958) in animals, demonstrated that there is a systematic map of the body's musculature in the primary motor cortex (M1), which is the locus of the long-term acquired representation of specific motor skills. A variety of motor tasks can be thought of as consisting of a sequence of simple components. The acquisition of a motor skill can be, accordingly, thought of as learning the correct components in the proper order, and determining the time at which each component movement is initiated, and ensuring the smooth continuity from one component to the next. See also chapter 6.

It has been found more recently that rather than have each motor neuron control an individual muscle, which was the traditional view of motor cortex, there is a more complex relationship between the motor neurons and individual muscles in the body. It appears that each point in the cortex connects to several muscles, and likewise each muscle is connected to several different neurons in the motor cortex. For a more recent account of cortical hand representations in primates see Blake et al. (2002).

Graziano and co-workers (Graziano et al., 2002) reviewed the discovery of complex topographic motor maps in monkeys, in which electrical stimulation of specific sites generated movements of the hand to particular destinations. These movements corresponded to stereotypical actions a monkey may perform that are of behavioural relevance to the animal, such as motion of the hand to the mouth or to defensive positions in cases of attack. It is found that the map for arm postures is embedded in a larger, coarse map of the monkey's body.

Topographic maps that retain a spatial metric have been studied also in the superficial layers of the superior colliculus, where separate auditory, visual and somatosensory maps are in close alignment. In this arrangement, each location in the three-layered structure represents the same spatial position obtained through vision, touch and audition. Such a scheme is thought to facilitate rapid cross-modal information transfer by use of the common spatial metric. Topographic maps have been found in virtually all species examined: cat, mouse, opossum, hamster, monkey, rabbit, rat, guinea pig etc. (Stein and Meredith, 1994, p. 87). In rattlesnakes, the infrared organ's view of the world is represented in map-like form in the optic tectum, and is in spatial register with visual representation (Stein and Meredith, 1994, p. 97).

In any brain area, a large amount of the information processing occurs in the local circuits. For instance in V1, afferent inputs form only 5-10 % of the inputs in that area (Peters and Payne, 1993). The rest of the synapses are inputs from other modulatory areas or from local feed-forward and feedback circuits. The recurrent activity generated by local circuitry serves a number of functions, including facilitating the generation of oscillatory activity in large groups of neurons (Haider et al., 2006).

Chklovskii and Koulakov (2004) have used the example of the retinotectal system to argue that the organization of sensory maps represent solutions that minimize resources needed for wiring for intracortical connectivity. Laughlin and Sejnowski (2003) provide a wider analysis of communication in neural networks to reach similar conclusions. The latter work suggests that the manifest design of neurons, circuits and neural codes reflect a conservation of space, materials, time and energy.

In both cortex and in sub-cortical nuclei, neurons are arranged in two-dimensional sheets. However, the functions performed by neurons in the hierarchically early parts of sensory processing vary according to the sensory modality of the particular set of neurons. As mentioned earlier, in the visual and somatosensory systems the topographic maps preserve the spatial metric from the retina and skin through to the superior colliculus (the tectum in amphibians), and their respective early cortical regions.

However, in the auditory system, cortical maps are found to be arranged tonotopically. This corresponds to a Fourier transform of the frequencies present in the auditory input; the transform performed initially in the basilar membrane in the cochlea. In the superior colliculus, there exists a map of sound source location derived from intensity and time difference between the sound source's reception at the two ears. Although a spatial metric is maintained in topographic maps, the functions that can be mapped spatially are found to be almost arbitrary.

This cross-functional nature of the adjacency relations manifested in biological topographic maps was systematized in Kohonen Nets (Kohonen, 1987). The computational model, inspired by the early work on self-organization in the visual system by von der Malsburg (1973), demonstrated a self-organization process whereby a spatial adjacency relation could be achieved in two-dimensional arrays of artificial neurons through the application of simple rules to the appropriately processed input data stream.

On the completion of the bottom-up-driven organization process, a spatial adjacency relation was achieved that manifested the similarity relations of the weight vectors that the artificial neurons represented. Such a computational model went some way to convincing neuroscientists of the worth of the bottom-up position, and its appeal still manifests in the current literature. It must be emphasized that the results obtained from such models rely significantly on the need for the normalization of the stimuli and synaptic weights in such competitive learning networks. Parkinson and Parpia (1998) have suggested a novel method by which this may be achieved in a simple way.

3.7.2 Development of Topographic Maps

The process by which this faithful mapping is generated in biological tissue has been the major focus of developmental biologists over the past 60 years. The emerging view is that chemoaffinity cues, initially proposed by Sperry (1944), establish a coarse organization of the projections, and activity-dependent mechanisms fine-tune the maps (Udin and Fawcett, 1988; Ruthazer and Cline, 2004; Price et al., 2006).

It is thought that the coarse organization is achieved in the early stages of development by molecular gradients, so that chemoaffinity expression levels change systematically with distance in both the input and target structures. Price et al. (2006) suggest that in thalamocortical networks, guidance molecules including Eph receptors and ephrin ligands may be involved. Signalling molecules and transcription factors, expressed with graded concentrations across the cortex, are thought to be important in establishing cortical maps of the topography of sensory surfaces.

The most prevalent hypothesis of the source of similarity in function between neurons in the output structure is that there exist lateral connections between them, with an efficacy that declines with distance. An alternative suggestion is that neurons in the output structure release molecules in an activity-dependent manner, and it is the diffusion of these molecules that provides locality information in the target (Goodhill, 2007). However, as mentioned, recent studies have indicated that spontaneous endogenous activity might also be required at the early stages of axonal targeting.

It is known that oxygen deprivation can cause severe defects in human brain development, although the precise cellular and molecular consequences of changes in the oxygen level on nervous system development is not known. A further complicating factor, identified by Pocock and Hobert (2008), is that oxygen deprivation during the early stages of development can affect axonal pathfinding in *Caenorhabditis elegans*. Thus, it appears that map development is a highly complex process, and a conservative conclusion would be that all these processes participate by varying degrees during the early stages of topographic map formation, and that further work needs to be done before the processes involved in early development are identified.

As mentioned earlier, once the targets are reached by the outgrowing sensory axons, a process of activity-dependent selection is thought to take place. Adjacently targeted axon terminals that are co-active are supported by the release of trophic molecules through processes described by Purves (1988), and the terminals that do not co-fire atrophy. The rationale given for this system of selection is that signals emanating from the natural environment are generally spatially continuous. Adjacent sensory receptors would accordingly be processing signals that co-occur. A stray axon from an inappropriate projection would reflect input from a part of the sensory epithelium that would, in general, have a different firing signature, and this would be manifested in its lack of synchrony with the other terminals in its vicinity (Katz and Shatz, 1996).

Price et al. (2006) note that the process of early overproduction of projections followed by selection after contact with the target is a strategy that is often used in the development of cortico-cortical and cortico-callosal connections. This position, too, needs careful consideration in the light of a recent report where individual retinal ganglion cells (RGC) from wild-type zebrafish were transplanted into a mutant without any RGCs. The experiment showed that the distal tips of the axonal arbours were located in retinotopically appropriate positions, ruling out an essential role for competition in the innervation of the posterior tectum (Gosse et al., 2008).

The complexity of the axonal guidance process is exhibited by the work of Nishiyama et al. (2008) on *Xenopus laevis* spinal neuron growth cones. They report that diffusible axon guidance molecules can modulate membrane potential shifts in the growth cone, producing either attraction or repulsion. The membrane potential is regulated by many external stimuli, which transduce their signals by regulating calcium entry into the neuron.

Specifically, they found that diffusible guidance molecules cause membrane potential shifts that determine the growth-cone turning direction.

Wong (1999) has reviewed the role of endogenous activity of the retinal ganglion cells in the form of ‘retinal waves’, as mentioned earlier, that create action potentials in the afferent fibers. Retinal waves have been detected in the immature retina even before the onset of vision. This mechanism has been proposed as the source of activity involved in refining visual connectivity in the immature optic tract.

Immature ganglion cells are found to fire patterned synchronized bursts of action potentials, and a Hebb-type rule is suggested, whereby correlations in presynaptic and postsynaptic activity patterns strengthen and retain correct synapses, and eliminate inappropriate ones, as outlined above. Computer simulations have been performed to model the resulting refinement process (see Goodhill, 2007, for a review). Subsequent stimulus-evoked activity, after the onset of sensory function, is thought to facilitate further topographic map refinement and development.

It is interesting to note that up to the present time, precise topographic map alignment of receptive field properties in binocular and indeed multimodal areas are thought to arise from an initial period that involve molecularly defined mechanisms. Thereafter, experience is considered to be critical for their refinement and maintenance (Ramdya and Engert, 2008).

3.7.3 Plasticity and Topographic Maps

In his review of the literature, Kass (1991) considered specific questions about the reorganization of adult mammalian sensory and motor maps in the event of sensory deprivation and direct damage to the supporting nervous tissue. He was also concerned with the plasticity of these maps in the way that they might reflect recovery. It was already known that map reorganization occurred, and he addressed issues about the stages in the sensory hierarchy where reorganization might occur, and whether all sensory maps were capable of being modified and their extent and time-scale.

His general conclusion was that topographic maps would reorganize following changes in neural activity patterns induced by impediments to the flow of feed-forward activity, regardless of whether the change was due to a lesion or sensory deprivation. He observed that ablation of parts of the sensory epithelium can be followed by partial or complete recovery of the silenced neural substrate supporting the ablated receptors. However, ordered topographic patterns need not necessarily follow.

Sensory maps are known to change in a variety of mammalian species, and in some cases these changes can occur very rapidly even in adults. These rapid changes have been documented in the somatosensory (Kaas, 1991), the visual (Gilbert and Wiesel, 1992) and the auditory systems (Robertson and Irvine, 1989). More recent work supports this view and suggests that changes in sensory maps can occur on a real-time basis in the early visual and auditory cortices (Murray (S.O.) et al., 2006; Fritz et al., 2003).

Gilbert and Wiesel (1992) used a laser to make focal lesions (or scotomas) on the retinas of adult cats and monkeys, and investigated the resulting changes in the receptive fields of V1 neurons. They found that the neurons that previously supported the central part of focal vision were initially silenced, but recovered activity that supported vision after a few months. They found immediate enlargements and shifts of the receptive fields of the tissue in V1 that previously supported vision at the edges of the scotoma. The affected neurons now supported input from the undamaged part of the retina.

A more recent elaboration on this early work has been carried out using two-photon imaging to monitor functional and structural alterations in the visual cortex of adult mice following a retinal lesion (Keck et al., 2008). The report documents the almost complete replacement of the intracortical dendritic spines in the two months following the retinal lesion, and a recovery of visual responses. Significantly, the authors attribute the recovery process to the activity-dependent establishment of new cortical circuits that served the recovery process.

Physiological evidence for the view that neural activity is associated with the organization of immature circuits, and their reorganization during learning in the mature phase, has been presented also by Katz and Shatz (1996). They dwelt largely on the visual system, and also elaborated upon the role of neurotrophins in activity-dependent synaptic remodelling.

Benedetti (1995) investigated the effects of coincident electrical activity of nerve cells on the reorganization of topographical maps in newborn mice. In his novel experiments, an artificial bridge of pig hair was used to connect two locations: (1) the ear with the nose and (2) the ear with the shoulder. In these arrangements, there was simultaneous tactile activity at two locations whenever the hair or either of the two skin locations was stimulated. The mice could also see the bridge. As such, in addition to alterations in the somatosensory maps, changes in the visual topography could also be expected in the 'bridged' mice, compared to normal mice.

On examining the differences in the topographical maps between 'normal' and 'bridged' mice in both the somatosensory cortex and the superior colliculus, Benedetti (1995) concluded that evoking coincident electrical activity accounted satisfactorily for the altered maps in the bridged mice.

It is known that transection of a sensory nerve in adult vertebrates results in profound abnormalities in sensory perception. Florence et al. (1996) withdrew an arm of a foetal monkey from the womb and transected the median nerve to the hand midway between the wrist and elbow. The nerve was reconnected without attempting to match the fibers and returned to the womb. After birth, the primary somatosensory cortex was found to be essentially orderly. The authors conjectured that despite the disorderly conjunction of the median nerve fibers at their joins, the ordered topography in the cortex resulted from the coordinated patterns of sensory stimulation that occurred within the womb and after birth. This activity-induced reorganization was taken to be the essential cue to the establishment of ordered topography in the brain. It would appear that there is a critical period during which such an ordering process is possible. It is unknown whether the equivalent of retinal waves emanate from the skin receptor cells during foetal development.

3.8.0 Plasticity and the Discontinuities in the Somatosensory Homunculus

A similar conjecture to that proposed by Florence et al. (1996) has been expressed by Farah (1998) who made proposals about the origins of the two major discontinuities that are generally believed to exist in the 'homuncular' map in the primary somatosensory cortex (S1). See Fig. 3.7. Adjacent regions of skin are found to map onto adjacent neurons in S1.

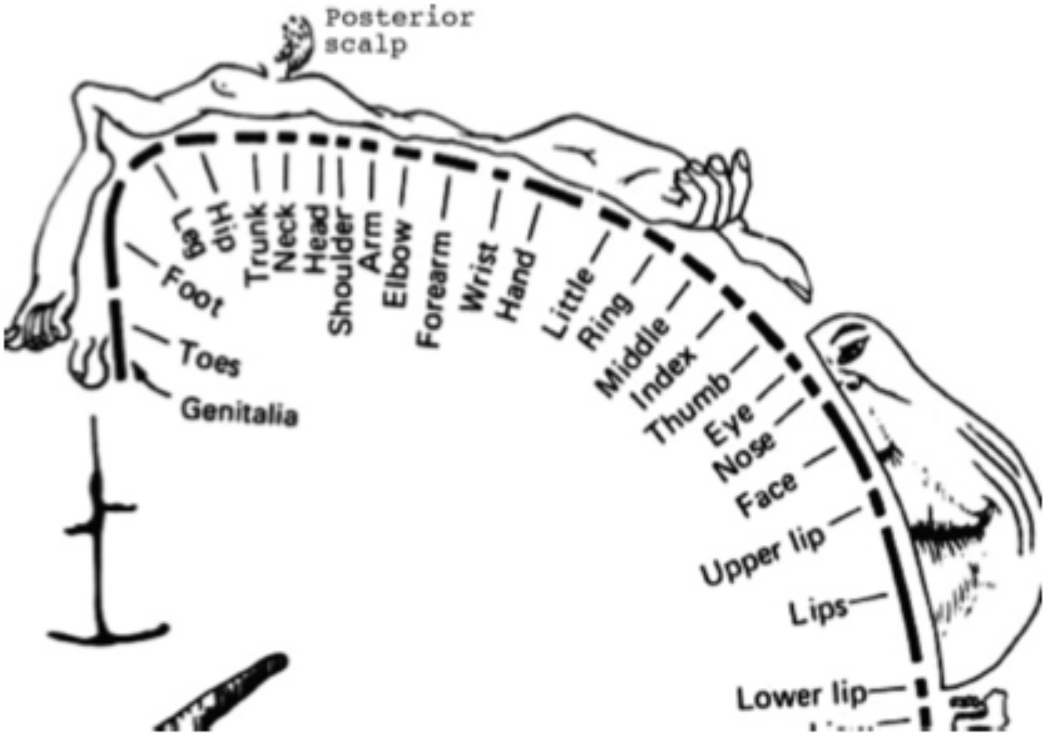

Fig. 3.7 The Penfield homunculus depicting the representation of cutaneous sensation in primary somatosensory cortex. According to Penfield and Rasmussen (1950) the penile representation is located inferior to that of the foot. The face representation is inverted and displaced as a whole from that of the neck and posterior scalp. (Source: Modified from Penfield and Rasmussen, 1950.)

In each cerebral hemisphere, this general pattern is thought to be violated at two locations: between the hand and the apex of the head, and the foot and the genitalia. Farah (1998) proposed that the statistics of prenatal sensory experience, resulting from the curled-up posture of the fetus in the womb, where the hands abut the face and the feet the genitalia (Fig. 3.8), is the predominant factor in the genesis of the somatosensory homunculus and the apparent discontinuities. Computer modelling using a Hebbian variant of the self-organizing Kohonen Net was found to support Farah's proposal. Parpia (2011) carried out an extensive analysis of the literature to evaluate Farah's hypothesis. He discovered that the genital representation in S1 for cutaneous sensations (as opposed to tumescence) had been revaluated recently and reported to be continuous with the lower trunk and thighs. Further analysis led him to propose that the somatosensory homunculus, in fact, comprised just two distinct regions: the face representation and that of the rest of the body. These findings show that there was an error in the homuncular map worked out by Wilder Penfield and his colleagues, where tumescence was mistaken for cutaneous sensations. The principles of self-organization did not account satisfactorily, in this case, for the overall homuncular map, and confirmed that computational models can provide only an 'existence proof' and need not reflect biological development. A copy of his report (Parpia, 2011) is presented in the Appendix.

Buonomano and Merzenich (1998) reviewed the bottom-up approaches to account for plastic changes in somatosensory, barrel, visual and auditory cortices. They also pointed out that the changes in cortical representations, thought to arise from task learning, could be accounted for by using the Hebbian organizing principle. Molecular mechanisms and results of computational studies based on the organizing principle were also elaborated upon.

Zhou and Black (2000) point out that topographic maps are also found in the limbic circuits that mediate learning, memory and emotions; that the hippocampus is connected to the subcortical target, the septum, in a highly organized manner. The similarity in organizing principles between the limbic circuits and sensory systems suggests that learning and memory are governed by the same spatial constraints as sensory information processing.

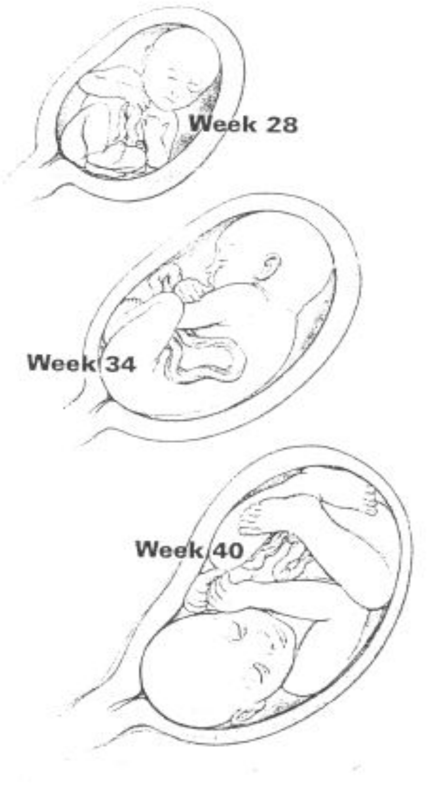

Fig. 3.8 In the womb, the fetus has its hands frequently in contact with its face and its feet touching its groin. It was proposed that these conjunctions might account for the adjacent representation of these body parts in the cortex. Source: Farah (1998).

They too considered the refinement process to be guided by activity, and provided evidence to support this view also in the retinotectal system, evoking the findings of Purves (1988) (mentioned above) that trophic factors support overlapping activities and prune inappropriate connections. Further elaborations on the activity-dependent release of neurotrophins, and their effects on facilitating plasticity in synapses, were provided by Levine and Black (1997).

In reports by Roe et al. (1990) and Sharma et al. (2000), where ferret kits had visual receptive fields induced into the auditory cortex, activity-driven plasticity has been postulated to account for this novel demonstration of cross-modal cortical adaptation. These ‘re-wired’ animals were found to behave as if they were ‘seeing’ by use of their auditory cortices (von Melcher et al., 2000). The re-wiring manifested raises difficult and as yet unresolved issues with regard to the previously proposed innately governed processes that guide the establishment of the network of afferent and efferent pathways in the brain (see §3.7.2).

Baseler et al. (1999) investigated the extent to which topographical maps in human extrastriate areas reorganize after damage to a portion of primary visual cortex. They showed that the higher visual regions were reorganized by activity-driven recruitment of nearby unaffected cortex in much the same way as V1 became reorganized to redeploy the healthy neurons made redundant by the scotoma induced and described by Gilbert and Wiesel (1992).

A similar rewiring process to the one reported by Roe et al. (1990) and Sharma et al. (2000), mentioned earlier, was repeated in mice that were using their auditory cortex for vision (Newton, 2004). This experiment was directed at evaluating reaction times for fear signals. The responses generally take longer for fearful visual stimuli than for similar auditory ones. However, with fearful visual signals being processed in the auditory cortex, the response times were found to be shorter than if they had been processed in the visual cortex. The rewiring process and their consequences were attributed to activity-dependent plasticity (Newton et al., 2004). Sur (2004) presents a review of some of this work.

Recent work shows that some blind people are able to locate objects by producing mouth clicks and listening to the returning echoes (Thaler et al., 2011). Click-echo processing recruits brain regions typically devoted to vision rather than audition in both early and late-blind echolocating experts. Similar findings in the blind are reported by Collignon et al. (2011), where spatial properties of sounds were found to be processed in the occipital cortex that would otherwise serve vision.

Also, the auditory field of the anterior ectosylvian sulcus (FAES), associated with an orienting response, serves a visual orientation response in early-deafened cats (Meredith et al., 2011). Furthermore, there exists a visual-word-form reading area, which is a part of the ventral visual stream that processes visual reading. In the congenitally blind, this area shows activity during Braille reading (Reich and Szwed, 2011).

Elbert et al. (1995) used magnetoencephalograpic recording to study the representations of the digits of players of stringed instruments in the primary somatosensory cortex. They reported that there were a greater number of neurons devoted to the fingers of the left hand in string players than in non-musical controls, and that the amount of cortical reorganization in the players correlated with the age at which practice had commenced. The effect was smallest in the thumb; no differences were found in the representations of the digits in the right hand. They attributed the changes to an adaptation to current environmental demands.

Lendval et al. (2000) investigated neuronal structure-based plasticity of spines and filopodia in rat barrel cortex. These protrusions, which are related to plasticity, were generally highly motile. Their sensory deprivation studies, which reduced neuronal activity, had the effect of reducing protrusive motility. The authors concluded that sensory experience drives structural plasticity in dendrites.

Kahn and Krubitzer (2002) reported that blindness induced by early eye removal in opossums resulted in an invasion of the visual cortical areas by the auditory and somatosensory systems. Once again this effect was attributed to activity-induced plasticity.

Blake et al. (2002) have presented an extensive review on the representation of hand use in cerebral cortex. In mammals, hand movements and their sensory inputs are represented respectively in the primary motor cortex and the anterior parietal strip. The main rule underlying their organization is that the representational area and columnar structure in the cortex is determined by their degree of innervations. This in turn was shaped by behaviour and other input manipulations, i.e., by activity. A review of similar reports with a focus on early development, associating neuronal plasticity with activity, has been presented by King and Schnupp (2000). The above reports attributing neural plasticity to bottom-up processes are a subset of the many that support this view.

3.8.1.0 Perceptual Learning in the Early Sensory Regions

It was commonly thought that the neuronal circuits in the different primary areas of sensory cortex became fixed by the end of their critical periods of development, and that the learning that took place after these early stages was more complex and occurred only in the higher sensory and associational cortical regions. However, there is much evidence to show that neural plasticity in primary sensory cortex is present also during adulthood (see reviews by Gilbert (1994) and Recanzone (2000)).

Many of the experiments that demonstrate learning during adulthood have also shown that there is a correlation between the improvements in skills and the changes in corresponding topographic maps. Since these results provide robust links between brain activity and learning, some of the well-known ones will be summarized below.

3.8.1.1 Topographical Map Changes Correlate with Learning

While much of the work cited in the previous section indicates that specific cortical areas are involved in the processing of particular functions, studies of changes in both the overall structure of cortical maps and the function of individual neurons provide more convincing evidence of the relation between memory acquisition and behavioural skills.

Bakin and Weinberger (1990) stressed the above point. In their study of the change in the acoustic receptive fields in guinea pig cortices, they found highly specific receptive field plasticity corresponding to the frequency of the tone used as the conditioning stimulus in their fear conditioning experiments. Sensitization training produced a general increase in responses of all the neurons examined. The distinction between the specificity of the change in response to the particular auditory frequency used in the classical conditioning case and the overall increase in responsiveness of the neurons induced by sensitization would have been missed without investigating the responses at an individual neuron level.

Among such single neuron studies are the ones by Xerri et al. (1994) that show that the cortical representation of the ventral body surface in nursing rat mothers is larger than the corresponding one in non-nursing female rats. The surgical fusion of two digits in primates results in a region in the somatosensory cortex in which the receptive fields of neurons cross the suture line (Allard et al., 1991; Merzenich et al., 1987). This is not found to be in the case for hand representations in normal animals.

Studies of the primary motor cortex of monkeys show that the dominant hand has a larger representation than the non-dominant hand (Nudo et al., 1996). Also, blind individuals who read Braille have larger representations of their Braille-reading finger pads than non-Braille-reading sighted or blind controls. These results were obtained using both evoked potentials measured on the scalp and by transcranial magnetic stimulation of the sensorimotor cortex (Pascual-Leone and Torres, 1993; Pascual-Leone et al., 1993). It was also revealed that Braille reading by the blind evoked activity in their visual cortex. Such activity was not observed while sighted subjects read Braille, suggesting that visual cortex had been co-opted to participate in the process.

In follow-up experiments to the ones described by Florence et al. (1996), concerning the transection and reconnection of the median nerve in macaques, Florence et al. (2001) evaluated the topographic organization of the hand in primary somatosensory cortex (region 3b) according to the amount of hand use during the recovery process. The conditions that followed surgery were varied for the different animals, between being restrained from using the hand, and 'enriched' because hand use for food foraging that required fine haptic and tactile discrimination was encouraged. The results obtained by Florence et al. (2001), that it was cortical receptive field organization that was restored rather than that in the thalamus, is consistent with Hubel and Wiesel's findings mentioned in §3.5.6.0 that experience-dependent effects do not affect the visual pathway in the LGN.

Electrophysiology revealed that the monkeys who had been subjected to the enriched environment had more ordered somatosensory maps than controls or those whose sensory input had been restricted. The maps of the 'enriched' monkeys were more discrete, in that the cortical neurons had smaller receptive fields, and there were fewer disordered regions that disrupted the functional organization of the cutaneous receptive fields than in controls or deprived subjects. The authors conjectured that both correlated synaptic inputs, and attention to the task (as suggested also by Burton et al., 1999 and Jabaley et al., 1976) were the reasons for better topography after rehabilitation of the ‘enriched’ environment monkeys. Two further experiments will be described in greater detail below to illustrate similar findings.

3.8.1.2 Tactile Vibratory and Acoustic Frequency Discrimination

Recanzone et al. (1992) trained adult owl monkeys to focus on the frequency of a vibratory stimulator applied to a patch of skin on one finger. The training required them to remove their hand from the stimulation source for reward in an operant conditioning task when the vibration frequency rose above 20 Hz. After several weeks training, their acuity for tactile frequency discrimination improved from an initial response value of 25 Hz down to 21–22 Hz as the threshold frequencies.

The regions in the topographic map in their primary somatosensory cortex (S1), corresponding to the skin region of the trained finger and the non-trained finger of the opposite hands, were charted and compared using electrophysiological methods. It was found that there was a progressive increase in area of representation of the trained skin compared to similar untrained skin surfaces. This increased area corresponded to the larger number of neurons that responded to the target stimulation frequency on the selected skin area of the trained finger.

A similar result was found by Recanzone et al. (1993) in the primary auditory cortex (A1) in monkeys trained to perform an operant conditioning acoustic frequency discrimination task. The monkeys had to make a response when a tone at the target frequency was presented. Following training, the cortical area in primary auditory cortex, corresponding to the target frequency, was found to be enlarged compared to controls. The increased neuronal representation (area) of the trained frequency was closely correlated with the improvement in performance in frequency discrimination acuity.

3.9 Summary

Following a description of the early work, suggesting that learning was required for the development of perception, a detailed account was presented of the work carried out at the cellular level in kittens and macaque monkeys by Hubel and Wiesel. A summary of their findings and their relevance to the present thesis was provided in §3.4.7. In particular, it was deduced from the work by Hubel and Wiesel that the capacity for visual length perception, by use of stereopsis, must be acquired through learning. It was explained also that depth perception by optic flow and motion parallax was not given innately but acquired by learning. Thus, it can be stated that the visual apprehension of length by these means is acquired. This is elaborated upon in chapter 5.

The constructivist approach was reviewed and it was shown that this was consistent with the work by Hubel and Wiesel, and presents a mechanism for the development of the neural structure in the brain for the establishment of the capacity for perception and cognition.

Further, that this scheme was sufficiently flexible to enable an arbitrary mapping between the nervous system and sensory input.

The approach proposed that the representational structures arise from the environmentally induced activity generated in the sensory receptors. This activity in neural tissue leads to the construction of structures from material in the cytoplasm using information obtained by second messengers from the genome of the neurons (Kandel, 2006). The basic cortical substrate given endogenously is common to the different sensory modalities. However, the pattern of the input generated in the receptors of the different sensory modalities determines the specific representational structures generated.

A comparison was also presented between (a) the nativist, or selectionist, approach and (b) the constructivist stance on the development of perception and cognition. Both the nativists and the constructivists generally acknowledge that learning occurs in the nervous system. However, the nativist position appears not to address the genesis of perception. Instead, it tacitly assumes the presence of perceptual categories and insists that these must be given innately because it regards learning as a rearrangement of these pre-existing percepts. The pre-specification of such percepts was considered to be highly unlikely for a number of reasons delineated later in the chapter, not least because there is a large deficit in the information contained in the genome to enable the provision of such information in the brain.

The description of the seminal work by Hubel and Wiesel and the constructivist manifesto provided a detailed account of the plasticity in the nervous system. The former also showed the existence of the *learned* hierarchical organization of the visual primitives that enable the capacity for edge detection. This ability is central for visual length perception (the capacity for the perception of length is fundamental in enabling the description of physical phenomena using algebra: see chapter 4). Work was cited that showed that a hierarchical organization existed also in the associational cortex where cells, referred to as gnostic neurons, responded to larger features such as hands and faces and parts of faces.

The findings by Pettigrew and Freeman (1973) were described, which emphasized that the capacity for edge detection is not given innately, and need not develop if edges are not present in the developmental environment. As such, it would not be possible to measure a static length if the visual system had developed in an environment that rendered it capable of perceiving only moving spots.

It was found that no general distinction is made in the constructionist approach between the establishment of perception and cognition in regard to the constructive processes involved; the neural substrate that supports both is organized hierarchically in their development and function, and there is no easily discernible line of demarcation between the parts of the neural substrate that support the two. It was shown that this generally holds true except that there exist diverse critical periods for the establishment of early primitives for the different representational functions in the different sensory modalities. Cognitive processes generally remain plastic throughout adulthood but are, nevertheless, confined to operating within the range made available by the sensory primitives established during early life. The greater permanency of the earlier learning, when the primitives of perception are formed, accounts for both the visual deficits that result from early deprivation and for a stable perceptual world.

A diversity of experimental results were then presented in this chapter to support the constructivist approach which applied to many different sensory modalities within the context of plasticity in the topographic organization of brain representations. The protocortex versus protomap issue, regarding the genetic and environmental contributions to the layout of cortical representation of neural function, was elaborated upon. Although the initial layout of the nervous system appears to be pre-defined by chemoaffinity cues, for the greater part, topographic adjaciencies occur from environmentally driven activity.

n the course of examining the degree of plasticity existing in the somatosensory system, work by Parpia (2011) on his detailed analysis of the origins of the homuncular discontinuities was recounted. It had been previously suggested by Farah (1998), that the adjacency between (a) the face representation and that of the hand and (b) the foot representation and that of the genitalia in primary somatosensory cortex, arose from coincident sources of stimulation in the fetal position.

During the course of this literature-based investigation, Parpia (2011) charted the development of the cutaneous receptors in the face, the genitalia and the rest of the body, and showed that the homuncular discontinuities could not be accounted for by the effects of neuronal plasticity as proposed by Farah (1998). Instead, that separate face representation in the cortex appeared to be genetically pre-specified. This analysis also served to emphasize that neural network modelling, which supported Farah's proposal, has only the status of an 'existence proof'.

The overall findings in the evaluation of the visual system, which was the focus of work presented in this chapter, showed that images are analysed hierarchically by cells in the visual system according to the presence of primitive elements of increasing complexity. These elements appear not to be pre-defined. Rather, the experiments cited showed that they are extracted from the statistics of the patterns present in the environment. As such, the analytical apparatus of the visual system is constructed by the information contained in the environment.

The findings to be presented in the later chapters, where other sensory modalities are examined in greater detail, also confirm, as indicated in the present chapter, that the neural substrate is plastic and the rules of neural plasticity that apply to vision apply also to the other modalities. Results cited that show correlations in the change in the representation in topographic maps of sensory function with perceptual learning confirm this finding. Further examples are cited in the ensuing chapters.

The next chapter provides an account of the development of the methods of dimensional analysis. The results of this analysis show that *all* physical phenomena may be represented in algebraic form using the three 'fundamental dimensions' of mass, length and time. The application of such a methodology will enable a rigorous evaluation of whether or not the plasticity manifested in the nervous system undermines the stability of empiricism, which science relies upon for evaluating its theories, and, indeed, if plasticity undermines the uniqueness claimed for scientific findings.

4

DIMENSIONAL ANALYSIS

4.0 Introduction

In order to address the issue of whether or not our sensory capacities for the apprehension of physical reality are primitive or derived, it would be useful to identify and address individually the different human sensory modalities (vision, audition etc.) that are employed in the empirical process. To this end, the method of dimensional analysis will be used to unequivocally link the human sensory systems with the physical parameters used to mathematically define physical reality in science.

In discussing the historical development of dimensional analysis and its mode of application in the realm of physics, this chapter demonstrates the long and difficult process whereby algebra has been crafted for the mathematizing of physical phenomena. Significantly, this shows that the description of the physical world in algebraic expressions does not confer to it any privileged or absolutist status over phenomena described in a natural language. Algebra provides only a more economical language than a natural language for the expression and manipulation of physical quantities. I hope to demonstrate that the internal consistencies imposed by the syntax of dimensional analysis are inventions in much the same way as are the proposed inventions of the syntaxes of the diverse natural languages, in that they help to disambiguate meaning and help to prevent the making of category errors.

This section will show that the development of applied mathematics and the growth of the scientific realm occurred in parallel, and that the two areas influenced one another. This clarification is important because many psychologists and scientists alike are under the false impression that expressing physical laws in mathematical terms gives the laws a neutral, context-independent vehicle for the discovery of the 'truth about the world'; as if the application of the language of mathematics carries with it some inherent reality.

It will be shown, rather, that our ability to apply the language of mathematics to the physical realm is founded on an axiomatic base that has been developed over the millennia, and is subject to further elaborations, as was illustrated by Einstein's development of the mathematical basis used by Newton to modify Newtonian mechanics.

Dimensional analysis is often introduced in sixth-form school physics as a method for reducing algebraic expressions describing physical quantities into their 'fundamental' dimensional components (see §4.2). The methodology is central to algebraic formalism in the physical sciences, and often used for checking for inadvertent errors in algebraic manipulations. Given that *all* physical quantities can be expressed in terms of these fundamental dimensions, the same set of dimensions will be used herein as a means of both defining and identifying sensory capacities that participate in apprehending reality in the physical sciences.

Needless to say that whenever algebra is used to formally represent human sensory and motor functions, be it in the analysis of visual accommodation (for instance, Schor, 2009) or the dynamics of the basilar membrane in the inner ear (for example, Goldstein, 1990), the methods applied make use of the very same mathematical formalisms as those involved in the present quest. Only, in the present exercise the sensory modalities that inform us about the fundamental dimensions, and so physical reality, are themselves to be identified.

4.1 Background to Formal Representations in Physics

Physicists generally seek to describe the behaviour of the physical world through laws expressed in algebraic equations. The rationale behind this practice will be briefly explored below since the method of dimensional analysis is embedded within, and is consequently a subset of, the algebraic representation of the physical world.

The roots of algebra can be traced to the mathematics of ancient and medieval Mesopotamian, Chinese, Hindu, ancient Egyptian, and medieval Muslim scholars (Cooke, 2008). And, although our current use of algebra for the representation and manipulation of physical quantities was not known to Galileo (1564-1642) (who died in the year Newton was born), its current level of sophistication owes much to these aforementioned scholars.

The abstract assignment of measure to physical quantities has developed only slowly since the medieval period. The formulation of analytical (or algebraic) geometry by Descartes (1596-1650) provided an example of the representational capacity of algebra in the realms of geometry. It is contested, however, that Descartes' work led directly to our current capacity to use algebra to represent and manipulate physical quantities other than those pertinent to geometry (i.e., pertinent to the fundamental dimension of length – see below) (Macagno, 1971).

During the development of geometry it was noticed that areas were proportional to the product of two line lengths, and volumes to the product of three line lengths (or one length and an area). From this geometrical property, an analogy was drawn that enabled an abstraction in the use of numbers to represent geometrical quantities. Any number that could be expressed as a product of two natural numbers was called a 'rectangular' number, and one that could be expressed as the product of three lengths (or an area and a length) was referred to as a 'solid' number. The terms 'squared' and 'cubed', as applied to numbers, are vestiges of this analogy. Exponents can thus be associated with a geometrical interpretation to signify the dimension of the quantity being measured (Martins, 1981).

Accordingly, it made sense that areas could be added to and subtracted from one another, with the same rule applying to lengths and volumes. However, it would be meaningless to add a 'rectangular' number to a 'solid' number. Out of this realization arose the mathematical concept of geometrical dimensions and its relation to the concept of homogeneity.

Lengths have dimension 1, areas 2 and volumes 3. Only magnitudes of the same kind (homogeneous quantities, that have the same dimensions) can be meaningfully added, subtracted or equated, and only these homogeneous quantities of the same dimensions have a meaningful ratio. The symbol L is used to indicate the physical dimension length. Thus, line-lengths have dimension L^1 (to the power one), areas L^2 (L squared) and volumes L^3.

The above series of conceptual transformations and the notion of homogeneity of dimension enabled Descartes to reduce to algebraic form the spatial realm of geometry. This process of algebraic reduction relied on the fact that the spatial dimension could be shown to share the property of 'closure'.

Closure is a property of a formal system whereby a mathematical operation performed on an algebraic object generates another object belonging to the same formal system. Thus, Cartesian geometry being closed to the four arithmetic operations of addition, subtraction, multiplication and division allowed Descartes to describe physical space using algebra.

A historical account charting the progression of the algebraic representation of all physical quantities can be found in Macagno (1971), with useful elaborations by Martins (1981). Additional material may be found in the texts by Ipsen, 1960; Palacios, 1964; Pankhurst, 1964; Roche, 1998 and Gibbings, 2011.

It is evident from these accounts that progress has been a slow one spanning millennia, with many notable mathematicians, natural philosophers, physicists and engineers involved in the work. Among them were Euclid (300 BC), Pappus, de Muris, Galileo, Newton, Leibniz, Euler, Lagrange, Laplace, Fourier, James Clerk Maxwell, Rayleigh, Bertrand, Lucas, Carvallo, Clavenad, Vaschy, Mercadier and Vogt. In 1911 the Russian Riabouchinsky went over ground covered previously by Carvallo and Vaschy, and more recently Bridgeman, Birkhoff, Buckingham, Brand and Saint-Guilhem have done further work on the subject of dimensional analysis, now enabling the algebraic representation of all physical phenomena. Many consider the work by Joseph Fourier (1768-1830) as pivotal in formalizing the current form of the method of dimensional analysis.

It seems inappropriate to dwell further upon the development of algebra for the representation of physical quantities. Instead, a brief account is given below of the method of dimensional analysis, whose results will be used to associate specific sensory modalities and motor functions with individual ‘fundamental’ dimensions.

4.2 Dimensional Analysis

Work carried out over the millennia has resulted in the identification of three physical dimensions that may be used to express in algebraic form the properties of all physical entities and processes. The fundamental dimension of length (L) was elaborated upon earlier. To this dimension have been added those of mass (M) and time (T), and together they comprise the ‘fundamental’ dimensions.

We may thus obtain the set of sensory capacities that will suffice to define the ability to apprehend *all* of physical reality relevant to the scientific realm. These sensory competences can be then evaluated with respect to the task in hand: to assess whether these sensory capabilities are primitive or derived.

Mathematics is concerned with the study of numbers and the rules and relationships that govern them. In physics these numbers have ‘units’ associated with them. For instance, distance is measured in units such as metres, miles and inches. An interval of time is measured in seconds, minutes and hours. Mass is generally manifested in two ways: by (1) the force due to a body’s weight resulting from the earth’s gravitational field and (2) the force required to change its state of motion. It is a happy coincidence that inertial mass and gravitational mass behave identically in terms of their physics, and both are generally expressed in units of grams, pounds, kilograms and so on.

Although physical quantities can be measured in different units, the interpretation of the quantity being measured does not change. Metres, miles and inches are measures of distance, and have dimension length (L). Seconds, minutes and days are measures of time intervals, and are referred to as having dimensions of time (T). Grams, pounds, kilograms etc. are measures of the dimension mass (M).

Speed is measured, for example, in feet per second, miles per hour, kilometres per hour, and is always represented as a length divided by a time. Unlike measures of time, length or mass, which are each composed of only one fundamental dimension, speed is a multivariate or ‘derived’ quantity, in that it has dimensions L/T. Acceleration, a, another derived quantity, is measured in units of, for instance, metres per second per second, or

$$a = \mathrm{L}/\mathrm{T}^2.$$

According to Newton’s second law of motion, force, f, is related to acceleration by the expression f = mass (m) x acceleration (a) ($f = ma$). The dimensions of force may be stated as follows:

$$f = \mathrm{ML}/\mathrm{T}^2.$$

These equations enable the expression of the dimensions of any quantity involving force in terms of M, L and T. For instance, pressure, p, which is force per unit area, may be expressed as

$$p = \mathrm{F}/\mathrm{L}^2$$

(where F is the dimension of force),

$$= ML^{-1}T^{-2},$$

and work, w, which is defined as the product of force and the distance through which the force was applied, may be expressed as

$$w = FL,$$

$$= ML^{2}T^{-2}.$$

Alternatively, the dimensions of any quantity involving mass may be expressed in terms of F, L and T. For example density, d, which is the mass per unit volume, can be expressed as:

$$d = ML^{-3}$$

$$= FL^{-4}T^{2}.$$

The important point here is that of the four dimensions, M, F, L and T, we do not need to retain both F and M. Just three suffice because they may be expressed in terms of one another. The dimensions of all physical quantities can be expressed in terms of the three fundamental dimensions M, L and T (or in terms of F, L and T).

To recap, expressions for quantities like those given above, *viz*., speed, acceleration, force, pressure and so on, that are composed of several fundamental dimensions, are referred to as 'derived' dimensions, whereas M, L and T are 'fundamental' dimensions.

In some specialized applications two additional dimensions that may be used are the absolute temperature (ϑ) and electrical current (I). As in the case of force above, there is redundancy in these dimensions, and they are not all necessary in the description of any particular physical phenomenon. Depending on the application, certain dimensions are found to be more convenient to use, which is the only criterion for use of any particular set of fundamental dimensions.

For instance, in the case of thermodynamics, temperature is a convenient measure of the state of a system of molecules, obviating the need to refer to their masses and velocities. These can, of course, be obtained if required, since the absolute temperature can be related to the kinetic energy of the molecules (and thus M, L and T) through the Boltzmann probability distribution (see, for instance, Eisberg, 1964).

The same applies to the dimension current (I), which is a convenient measure for the analyses of electrical circuits. However, the current can be, in principle, substituted by a measure of force, since the magnetic force field generated by a current is linearly related to the current. Needless to say the decomposition of an electric circuit into its resultant forces would be an awkward means for its analysis, even though it is, in principle, sound. After all, the function of an ammeter is based on the relation between electrical currents and the forces they generate.

It is interesting to note that it is essential for equations that represent physical relationships to remain homogeneous regardless of the level of sophistication of a theory in modern physics. For instance, although the classical definition of momentum would have to be modified to comply with Einstein's Special Theory of Relativity for precision at relativistic speeds, the dimensionality of the expression obtained after making the modification is the same as in the classical case. This is shown below.

The relativistic momentum, p, of a mass, m, moving at a speed uc, where u is a dimensionless constant expressed as a fraction of the speed of light, c, is derived to be

$$p = m\mathrm{uc}/\sqrt{(1\text{-}\mathrm{u}^2)},$$

has the same dimensionality, MLT^{-1}, as in the Newtonian case.

Well-formed equations can be constructed which include constants that are not dimensionless. For instance Planck's constant, h, which defines the quantum of energy, E, of a photon of frequency v, through the equation

$$E = hv,$$

where h has dimensions L^2MT^{-1}.

It is interesting to note that the well-known relativistic expression for mass-energy equivalence for a particle of rest-mass m ($E = mc^2$) might have been derived solely through the use of dimensional analysis. And, indeed, E has the dimension L^2MT^{-2}, which is common to classical and quantum mechanics, and relativity theory.

The same requirement that equations in geometry need to be homogeneous applies also in the general case for equations containing all the fundamental dimensions. That is, each of the terms of such general equations needs to be homogeneous in each of the fundamental dimensions.

This process of homogenizing an equation may be likened to ensuring that a category error is not being made when formulating a logical argument expressed in natural language. For example, the relativistic energy, E, associated with a body of rest-mass m and a momentum p is given by the expression

$$E^2 = m^2 c^4 + p^2 c^2.$$

Each of the terms in this equation has the same dimensional composition: $(L^2MT^{-2})^2$. The equation is therefore found to be homogeneous, as required.

Homogeneous equations express relations between the different physical quantities that can be considered to hold true irrespective of the units used to measure them. The dimension of each physical quantity indicates its physical nature. The units used for its measurement are, however, determined by mutual consent, and institutions such as the UK National Physical Laboratory and the *Bureau International des Poids et Mesures*, in Paris, provide exemplars of such standards in physical form for common reference and coordination. There are thus, standardized definitions for units of length, mass and time. The ones generally used are the metre, kilogram and second (the 'absolute' MKS) or International System of Units (SI system) and the centimetre, gram and second (CGS system).

Perhaps the simplest application of dimensional analysis, as mentioned earlier, is to provide a means for checking the dimensional correctness of the mathematical analysis of a problem, because, as explained, an essential feature of a physically meaningful algebraic expression, or equation, is that the dimensions of all its terms must have the same components in M, L and T. The deviation of a mathematical expression for a physical quantity from homogeneity of all its terms would indicate that there was an error in its derivation.

The current interest in dimensional analysis stems from the fact that in general the three fundamental dimensions of mass (M), length (L) and time (T) are sufficient to formally describe all physical quantities. As such, we need consider only those perceptual abilities that inform the mind about mass, length and time in order to encompass the description of all of physical reality used in the scientific realm. This provides a simple criterion for the elimination of factors such as ‘mental paint’, referred to in § 2.2, from the present work on the status of physical reality. Work to be cited herein as dealt with in the scientific literature is largely free of ‘mental paint’, and may be considered to generally address the ‘apprehension of physical reality’.

Typically, physicists carry out experiments whose results can be interpreted using algebraic formulae. Parameters in these formulae can be manipulated to obtain new results that can then be evaluated experimentally. As mentioned in chapter 2, the success of physics in establishing fundamental ‘truths’ about physical reality derives from the methodology of formal description and empirical evaluation that unify individual observations into laws or theories.

It is worth mentioning, however, that the way in which an algebraic system bears on the outcome of experiments is not by virtue of any reality inherent in the algebraic parameters and hypothetical operations invented to allow algebraic closure. Instead the success of the methodology results from the similarities between the operations of algebra, its axiomatic basis and the physical characteristics assigned to them, which have been achieved through a refining process over the millennia. And, importantly, at every stage in the refinement process the theoretical aspects of the algebraic representation of the physical quantities have been subject to empirical evaluation. For further details supporting this view see Hattiangadi (http://www.bu.edu/wcp/Papers/Scie/ScieHatt.htm).

That said, the use of algebra and the assignment of physical quantities to algebraic variables and operations allow a convenient method for associating formal physical reality with the individual sensory modalities used for its apprehension, as will be elaborated upon in chapters 5: *Multimodal Integration, Proprioception and Visual Length Perception* and 10: *Apprehension of Time*. Mass and time being scalar quantities can be fully represented by their magnitudes. However, length being a vector, requires also its direction to be specified.

5

MULTIMODAL INTEGRATION, PROPRIOCEPTIVE AND VISUAL LENGTH PERCEPTION

An Overview of the Chapter

The results of the previous chapter on dimensional analysis showed that the notion of physical reality can be represented by the fundamental dimensions of mass, length and time. As such, the capacity for the apprehension of physical reality can be addressed by evaluating whether the capacity to perceive these fundamental dimensions are native or derived. The dimension of time, which is thought to be a concept rather than being one that has specific sensory modalities associated with it, is addressed separately in chapter 10.

In regard to addressing the dimensions of mass and length, it would appear that this would require identification and addressing of the many separate sensory modalities that contribute to their apprehension. The perception of these dimensions, clearly, occurs in a multisensory way. However, the onerous task of identifying these separate modalities is mitigated by the fact that much progress has been made in our understanding of the processes underlying multimodal integration, and indeed, as elaborated upon in chapter 3: *Plasticity in the Nervous System*, that the learning rules underlying neuronal plasticity and, indeed, multimodal integration, appear to be common across the sensory modalities (see §5.1).

The present chapter provides support for the existence of common learning rules in the nervous system through a review of the literature on multimodal integration, particularly in respect of the findings relevant to developmental plasticity. A brief account is provided of the infrequently referred to sense of proprioception, which is pertinent to the apprehension of length and mass. This sense derives its function from across several conventional boundaries separating the different sensory modalities. The ubiquity of cortex for the support of different sensory functions and the common learning rules that appear to apply in it, are manifested in a number of experiments that will be described. These demonstrate the existence of plasticity in the process of multimodal integration, and show that this capacity is learned. A resumé will be provided of the literature on space maps in intraparietal cortex that support the dynamically changing sense of body schema and multimodal integration.

The capacity for length apprehension by use of vision will be elaborated upon, using the findings cited previously in chapter 3, to show that this capacity is learned. Finally, experimental results from the domain of haptics will be cited to support the view that the capacity for haptic length apprehension is also learned. A detailed analysis of the genesis of the capacity for mass apprehension, significantly within the domain of motor development, is provided separately in chapter 6: *Apprehension of Mass*. Issues associated with the auditory sense are addressed in chapters 7, 8 and 9.

5.0 Introduction

Perception has been viewed historically as a modular function with the different sensory modalities being treated as functioning independently of one another. This is reminiscent of the division of the study of physics, as mentioned in chapter 2: *Physical Reality*, into heat, light, mechanics etc., prior to the formulation of the kinetic theory of matter. The separate areas of physics were more united once the underlying processes were better understood, so that the separate topics could be interpreted increasingly to arise from a common substrate.

The state of development in neurophysiology at around the middle of the twentieth century was not dissimilar to that of physics at the end of the nineteenth century, where the different sensory modalities were addressed separately according to their respective primary cortical areas. The separate modalities were thought to be integrated to form multimodal percepts only in the higher associational regions of cortex.

However, with the seminal work by Donald Hebb and other theoreticians (see chapter 3: *Plasticity in the Nervous System*; Boden, 2006, Vol. 2, Chapter 12), there has been much success in the domain of computational modelling of brain function, which has demonstrated that there exist rules of neurodynamics that apply in common across the different sensory modalities. These rules have been used extensively by computational neuromodellers to investigate a diversity of sensory and cognitive abilities (see also McClelland et al., 1986; Rumelhart et al., 1986; Anderson and Rosenfield, 1988).

As such, not only have common processing rules been revealed but it has been discovered that regions that were previously treated as being dedicated to individual modalities are to some degree multimodal, in that cross-modal processing is found to take place even in the primary regions of sensory cortex, with afferents from different sensory modalities terminating in diverse early sensory areas.

The existence of a diffuse presence of such multimodal projections into regions otherwise containing only unimodal neurons provide for a mixing of the senses early in the processing hierarchy, as will be elaborated upon later. Furthermore, re-entrant feedback projections from higher cortical regions and the extensive multimodal cortico-cortical (or intra-cortical) connections lead to a general mixing of sensory information (Gilbert and Sigman, 2007; Rauschecker and Scott, 2009; Gilbert and Li, 2013). Despite this, through reflection, it is generally possible for an individual to distinguish between the different sensory modalities that participate in the construction of any percept, which renders the senses separable one from another on a subjective level. This is, clearly, dependent on knowledge of the functions provided by the different sensory modalities. A summary is provided below on current findings in multisensory integration.

5.1 Multisensory Integration – An Overview

The natural environment provides a flux of concurrent stimulation to all our senses, and the integration of the degenerate cues from the distinct sensory modalities is a fundamental feature of perception and cognition. We do not generally dwell upon disparate streams of sensations from the separate modalities, particularly when engaged in some purposeful activity, like playing a game of tennis. Instead, proprioception, vision, the vestibular senses, audition etc. provide an integrated set of degenerate inputs that work in concert to create a sense of engaging in the overall activity.

The process by which the perceptual features carried by distinct sensory modalities are bound together both in the temporal and spatial dimensions, in order to get a common, coherent, representation of space and physical objects, forms the subject of multisensory or multimodal integration. This process of integration has many functional advantages including an increase in salience, resolution of ambiguities and greater ease and speed for the recognition of objects, surroundings or processes (see, for instance, Stein and Stanford, 2008).

The study of multisensory integration has advanced much in the past decade, and although vision, audition, olfaction, proprioception (including active touch, or haptics – see below) all contribute to creating the unified percept, the present work on the apprehension of physical reality will not address olfaction and other chemical senses. This is in keeping, historically, with their neglect in favour of vision, proprioception and audition that have been considered formally to be more objective.

The current literature on multimodal integration is extensive. For instance, use of the *Web of Science* (in July 2012) to identify publications citing Daphne Bavelier and Helen Neville's 2002 comprehensive review *Cross-Modal Plasticity: Where and How* (Bavelier and Neville, 2002) returned 267 diverse citations, many pertinent to the current investigation. Given that the present overview is intended to provide only a brief introduction to the subject, much of this material will be left out. More space will be devoted instead to the topic of plasticity and the development of multisensory integration, with the view of demonstrating that integration is learned rather than given innately.

Approximately a quarter of the brain was previously considered to carry out sensory processing in a hierarchical manner, with the early regions believed to be unimodal. Multisensory convergence of the output of unisensory processing was thought to occur primarily in the associational regions that occupy the remaining three-quarters of the brain. These areas consisted of the frontal, temporal and parietal cortical lobes (the last, the parietal cortex, providing loci also for maps that support the multimodally compounded body image and schema (Maravita et al., 2003; Price, 2006)), and the mid-brain nuclei, the superior colliculus, and the three nuclei contained in the thalamus (*Neuroscience*, 1997, p. 467).

More recent findings indicate that there exist multisensory neurons[10] in many locations that were previously thought to be unisensory, including primary sensory cortices. As such, multisensory convergence and integration effects are now believed to occur early in the hierarchy. Furthermore, there is evidence for direct connections between the primary visual and auditory cortices (Foxe and Schroeder, 2005). Falchier et al. (2002) also give anatomical evidence that regions of the striate cortex supporting peripheral vision receive projections from the auditory cortex as well as from the superior temporal polysensory area (STP) of the temporal lobe, involved in movement and orientation.

There appear to be multisensory feed-forward pathways in the brain corresponding to the dorsal and ventral visual pathways, processing, respectively, object properties (the ‘what’ pathway) and their spatial attributes (the ‘where’ pathway). See, for instance: http://en.wikipedia.org/wiki/Multimodal_integration.

These pathways have the virtue that damage to the higher-order integrative regions in humans nevertheless spares the ability to integrate across sensory modalities.

Collignon et al. (2008) report that extrastriate occipital areas contribute to the spatial processing of sounds in both humans and other animals. They note that studies have

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[10] The term ‘multisensory neuron’ refers to a sensory neuron that has axonal terminals from other neurons processing sensory modalities that differ one from another. The neuron is tuned to ‘synthesize’ multisensory inputs so that it optimises its outputs on receipt of such inputs. That is, its output is greater on the coordinated receipt of multisensory inputs than the sum of the individual inputs received one at a time. Stein and Meredith (1994) note that maximal multisensory interactions are not dependent on matching the onset of two different sensory stimuli, or their latencies, but on how the activity patterns resulting from the two inputs overlap. Stein and Meredith’s example takes account of the different conduction times for visual and auditory stimuli.

demonstrated the contribution of the posterior parietal cortex (PPC) to spatial hearing. These findings have led to the conclusion that the PPC is part of an auditory ‘where’ stream, projecting from the caudal superior temporal cortex to the dorsolateral prefrontal cortex. Other brain areas, which are traditionally regarded as exclusively involved in visual information processing, seem to also play a role in auditory spatial processing.

Taken together, these results challenge the classical view that the extrastriate occipital cortex (OC) is exclusively dedicated to vision, and suggest close interconnections between the neural representations of auditory and visual spaces. It seems that the OC represents a preliminary step in the remapping process, and thus exerts a ‘feedforward’ influence on the PPC in the production of a multisensory spatial percept for action.

Multisensory neurons have been discovered in clusters at the borders between the major cerebral lobes, such as the occipito-parietal space and the occipito-temporal space, suggesting a parcellation scheme in which modality-specific cortical domains are separated from one another by transitional multisensory zones (Wallace et al., 2004). The existence of multisensory neurons, often incorporated among unimodal neurons (with whom there is generally a high density of short-range connections), would provide ‘nuclei’ for the ‘invasion’ of these cortical regions in the event of sensory deprivation. Indeed, there is the suggestion that neocortical operations are essentially multisensory (Ghazanfar and Schroeder, 2006). However, the major afferent sensory pathways are essentially unimodal, and dedicated to the projection of output from the various sensory epithelia, and target neuron populations that are largely unimodal for the respective processing regions[11].

5.1.1 Development of Multisensory Integration

The traditional view of sensory development in general and the development of multisensory integration in particular have been significantly influenced by Jean Piaget, who suggested that the capacity to perceive the physical world was acquired through the experience gained by an infant through its interactions with its environmental setting.

In this view, which held sway until almost the end of the twentieth century, it was proposed that the separate senses developed separately, followed by a period of mutual coordination and integration. This integration was thought to be brought about by the infant interacting with objects, experiencing concurrent feedback from different senses, leading to a mutual calibration of one sense with another, and their subsequent mutual integration.

Piaget (1952; 1954) proposed that it was not until the age of about 6 months that vision and touch began to be integrated. Prior to this time the sensory integration process was aided by visually guided reaching whilst acting upon objects, and was thought to lead to the conversion of the two-dimensional visual percept into a three dimensional one promoted by the merging of vision with tactile and proprioceptive input. Until the gradual achievement

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[11] That said, the major sensory pathways each comprise input from a diversity of receptor types. For instance, sensations of cutaneous touch in glabrous skin, for the perception of mechanical pressure, are generated by no fewer than 4 main receptor types (see, for instance, Purves et al. (1997), Table 8.1, p. 149). For further discussions see §5.5.

of sensory integration, infants were thought to perceive only unimodal patterns of visual, acoustic and tactile stimulation.

Infant-based research over the last few decades, inspired by work by the perceptual psychologists J.J. Gibson and E. Gibson, has challenged the traditional view. It is now known that senses function in concert from early infancy. For instance, Bahrick et al. (1981) demonstrated that by the age of 4 months infants presented with 2 superimposed films, and a soundtrack that corresponds to only one of them, will attend to the appropriate film track. In addition, in the full-term newborn, auditory stimulation, typically, results in an orienting response: a turning of the eyes in the direction of the sound source (Lickliter, 2011).

5.1.2 Principles for Cross-modal Feature Binding

The process of sensory integration, according to the Gibsons, arises from the capacity of the subject's perceptual system to work together in order to pick up invariant aspects of stimulation across the senses. For example, the sight, sound and proprioceptive aspects of hands clapping share temporal synchrony in having a common tempo and rhythm, the unity of which is both perceived during the active process of clapping by the subject, and also when the subject observes others performing such activities. This, according to the Gibsons, precedes any dwelling upon the separate sensory components (Lickliter, 2011; Lickliter and Bahrick, 2012).

Stein and Meredith (1994) note that during the early stages of sensory development the infant (or fetus) must be able to sense commonality in the information processed by the different sensory modalities without reliance on details of the structured subjective experiences that each of the senses is capable of producing. This 'raw' partially-resolved sensory information, collected from the individual modalities early during ontogeny, may be thought to be 'amodal', or interchangeable among modalities.

The consistencies among these amodal stimulus-features like intensity, form, number, and duration are believed to be transferred readily across modalities, and provide a basis for perceptual cohesiveness when cues from multiple sensory modalities are coincident, thereby facilitating a rapid integration of the information they carry.

Context rather than specific stimulus features now becomes a dominant behavioural determinant, since often even the simplest behaviours require the integration of combinations of environmental stimuli for their elicitation.

Stein and Meredith (1994) state that multisensory integration itself is ubiquitous across animals, including unicellular organisms and flatworms. They observe that they know of no organism studied having a nervous system that did not integrate information from different sensory modalities. This view extends also to insects (see, for instance, Wessnitzer and Webb, 2006).

More recently, Lickliter and Bahrick (2012) have also elaborated upon the issue of features in multisensory stimuli that facilitate their binding across sensory modalities. In their proposed framework, referred to as the Intersensory Redundancy Hypothesis, they reiterate that amodal information such as temporal synchrony, rhythm, tempo, and intensity are cornerstones of early perceptual development. By attending to amodal information, there is no need to resolve in depth the contents of the separate streams of information in order to integrate stimulation across the senses to perceive unified objects and events. Such a view was proposed also in the constructivist accounts of early perceptual and cognitive development (Piaget, 1952; 1954).

Lickliter and Bahrick (2012) cite evidence that confirms that intersensory redundancy (or ‘homology’) enhances perceptual learning during development in non-human embryos, and in infants. The capabilities cited are face discrimination, numerical discrimination, sequence detection, abstract rule learning, word comprehension and segmentation.

However, selective attention, which is initially more stimulus-driven during early development, becomes increasingly endogenous and modulated by top-down processes including the individual’s goals, plans and expectations. Thus, for experienced perceivers, prior knowledge, categories, plans and so on guide selective attention to gather specific information.

The process of sensory integration seems to rely on the following general principles for subjects raised in natural settings.

1) Integration is more likely when the constituent unisensory stimuli arise from the same location[12].
2) Integration is more likely when stimuli arise at approximately the same time.
3) Integration is stronger when unisensory stimuli evoke weak response when presented in isolation.
4) Of the senses that contribute to object identification, it is the modality that has the greater sensory acuity that dominates percept or process identification in the event of discord between the senses.

In this respect, vision is generally dominant over auditory or tactile senses for spatial identification, and audition is better than vision or touch for temporal tasks. However, for fine-grain texture determination or for the detection of vibrations, haptics dominates the other senses. Needless to say that prior knowledge, in the form of contextual and semantic congruence, and indeed expectations also play an important part, particularly in the more experienced subject.

5.1.3 Prenatal Multisensory Integration

It is now thought that the infant's capacity to integrate information across the senses arises from prenatal experience in the womb, where the fetus experiences a variety of tactile,

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[12] Deprivation studies have demonstrated, interestingly, that spatial binding can be induced across different sensory modlities between temporally coincident events occurring at different locations (see, for instance, in the owl: Knudsen et al., 1982; Knudsen, 1999 and in the cat: Wallace and Stein, 2007).

proprioceptive, vestibular, visual and auditory stimulation. These experiences are considered to form the basis for subsequent learning to integrate sensory information.

Following the initial differences in their onset of function (see below), the sensory pathways develop in parallel, so it seems reasonable to assume that the perceptual function they provide would be witnessed as an ongoing process, without any significant reference other than antecedent perceptual states. Perception would be holistic, with co-variances of changes in perception across modalities being apprehended as events of significance.

Lickliter (2011) points out that such stimulation in the fetus can arise from the sounds of the mother's speech, laughter, heartbeat, or breathing that may simultaneously create tactile stimulation that share the temporal patterning of the sounds as a result of changes in the musculature involved in producing them. Equally, when the mother walks, dances, engages in physical work or partakes in conversation, there will be movements that have tactile and/or vestibular correlates that share intensity and temporal patterning with the sounds.

Fetuses also engage in spontaneous and volitional motor activity. Such movements generate coordinated proprioceptive and tactile stimulation, which would aid learning and the process of sensory integration. Evidence for such prenatal learning comes, for instance, from work that shows a preference in the neonate for its mother's voice, whose input to the fetus would be multimodal (auditory/somesthetic) at its inception (DeCasper and Fifer, 1980). See also chapter 9, §9.2.2.

In their natural setting, the sensory systems of birds and mammals (including humans) become functional in a predefined sequence: tactile > vestibular > chemical > auditory > visual. The alteration of this sequence by artificial means has been used to provide evidence in quail chicks to support the view that the environment participates in embryonic development, in that such alterations can lead to developmental deficits (see §5.1.4). The study of such effects has relevance also for the provision of a suitable setting for the development of preterm infants in neonatal intensive care units. The sensory environment of such units, Lickliter (2011) points out, are far from being womb-like, and need further study to assess if they might be improved to prevent developmental defects in preterm infants.

5.1.4 Animal Experiments

Animal-based research provides an opportunity to artificially alter the developmental environment, and has provided most of the advances in the study of the emergence of multisensory integration. Lickliter (2011) points out that such experiments demonstrate the importance of the temporal stage at which sensory experience occurs during prenatal development, the strong intermodal linkages of the sensory modalities during prenatal development and the critical role of intersensory redundancy in guiding the shaping of perception, learning and memory.

Lickliter (1990) found that the introduction of unusually early prenatal visual experience in bobwhite quails interfered with species-typical auditory responsiveness in the chicks after hatching; birds that experienced patterned light before hatching did not exhibit a naïve preference for their species-specific maternal call. As such, early visual experience altered auditory behaviour. Related research demonstrated that increasing the amount of tactile and vestibular stimulation in quail chicks altered their postnatal auditory and visual responsiveness. Furthermore, when the augmented tactile and vestibular stimulation coincided with the onset of auditory function, embryos subsequently failed to learn a species-typical maternal call before hatching. Markham et al. (2008) demonstrated that embryos receiving auditory stimulation during the middle or late stages of prenatal development showed altered postnatal visual responsiveness when compared to controls. Prenatally stimulated birds also showed a higher neuronal density in deep optic tectum (the bird equivalent of the multisensory superior colliculus in mammals).

Wallace and Stein (2007) presented an elegant study that demonstrated that coordination of the normal sensory binding between a sound source and the visual location of that source was plastic. In their experiment cats were reared from birth into adulthood in an altered sensory environment in which visual and auditory stimuli were coincident in time but originated from different spatial locations. In this sense, the reality of the environment was altered from what is generally found in the natural setting.

Through mapping the receptive fields of neurons in the cats' superior colliculus, the authors showed these neurons developed an anomalous form of multisensory integration in which spatially disparate visual-auditory stimuli were integrated in the same way that neurons in normally reared animals integrated visual-auditory stimuli from the same location.

Their results show that there is no innate specification that visual and auditory input from the same spatial location should be integrated. Instead, it was the *co-occurrence* of the stimuli, even if they happened at different spatial locations, that brought them into spatial register in the superior colliculus. That the temporal element was the determiner for intersensory binding can be understood with reference to Hebb's rule, which requires that neurons that fire together to wire together. This finding by Wallace and Stein (2007) suggests that the 'normal' spatial register found between audition, vision and touch in the superior colliculus is a reflection of the common characteristics of events that occur in the environment. For instance the buzz and sensation of the landing of a bee on the skin are all apprehended as arising from the same location.

These findings highlight the fact that space and spatial coupling of the senses is not a fundamental aspect of mammalian reality. Rather, the temporal coincidence of events is the determiner for their being bound together in nervous tissue. This raises the interesting prospect of the spatial decoupling of the different colours in visual processing.

There have been earlier indications that co-temporal visual-somatosensory stimulation altered the receptive fields of bimodal visual-somatosensory neurons in the superior colliculus of newborn mice. In the experiments mentioned earler, Benedetti (1995) connected two cutaneous regions by implanting a pig-hair bridge between (a) the mouse's ear and nose and (2) its ear and shoulder.

Physical contact with the connected body parts or the bridge led to their co-stimulation, which was also witnessed visually by the mice. It was found that the visual receptive fields of bimodal visual-somatosensory neurons in the superior colliculus in the adult mice were extended into the portion of visual space where the artificial bridge was directed. This result supports the view that multimodal integration is learned and demonstrates the role played by coincident stimulation in altering visual receptive fields within the multimodal setting.

Similar plasticity in the bimodal visual-auditory receptive fields in the barn owl was mentioned earlier (Knudsen et al., 1982; Knudsen, 1999) adding further support to the view that multimodal integration is learned.

Finally, it is worth mentioning that the extensive plasticity demonstrated by studies of sensory deprivation uphold the view that sensory integration is acquired through a process of learning.

5.1.5 Binding and Unbinding of Sensory Input

The phenomenon of multisensory integration highlights the fact that the senses function in concert even though the outputs of the sensory receptors are processed in diverse parts of the brain. The question of where and how these features become integrated into percepts and unified processes is reminiscent of the integration of unimodal processing into coherent percepts.

Visual percepts are derived from input to the rods and three types of cones in the retina, whose outputs, in the form of action potentials, are processed in parallel for colour, size, motion, shape etc. in many disparate brain regions. The early processing takes place initially in the retina, the LGN and the striate cortex (see chapter 3), and subsequently in more than 20 extra-striatal areas and two major processing pathways: the dorsal and ventral streams, specializing, respectively, in object localizing and recognition (see, for instance, Desimone et al., 1990). Despite these distal spatial regions in which processing takes place, we nevertheless apprehend a unified *visual* percept, and know that we see it rather than be unsure if we felt or heard it.

Furthermore, reflecting on the visual input we are nevertheless able to distinguish between the different properties and functions of the visual percept (i.e., separate the colour from the motion of the object, and its shape from its size and so on). So also in the case of the multisensory input, reflection allows us to distinguish between, for instance, the auditory and somatosensory etc. aspects of the multimodal percept. The key, then, is knowledge of the different sensory functions and their names that allow the discrimination process.

The process by which both multisensory input and unisensory input present the subject with coherent percepts (the binding problem) remains the subject of debate and is yet to be solved (Feldman, 2012).

For the present purposes of identifying the sensory modalities that inform about the fundamental dimensions mass, time and length, the above discussion highlights the fact that knowledge of the different senses and their functions is required to enable their identification. There is no difficulty in this matter with regard to the sense of touch, vision and audition. However, it cannot be generally assumed that those not acquainted with robotics or sports-physiology can distinguish between proprioception, kinesthetics, active touch, haptics and the vestibular sense, given that these distinctions are generally not well known. As such, the topic of proprioception is briefly elaborated upon below, particularly because this sense plays a central role in informing the apprehension of mass.

5.2 Proprioception and the Vestibular Sense

The human body may be considered to be a mechanical system composed of the trunk, the head and limbs, and an array of connecting joints, providing diverse degrees of freedom of motion within and between the parts. The body parts all have mass, and can be moved precisely relative to one another by the muscles, as well as be held rigid by them. The muscles also provide means for locomotion of the body as a whole in a variety of modes, from walking upright to crawling or rolling to swimming and so on. The limbs can wield tools, carry, push, kick and throw masses. Equally, the head can butt against an object or be used to carry one, and in performing these activities, upon which survival may depend, the body as a whole must be able to sustain an appropriate posture, be it static or in a state of motion, without sustaining damage to itself or its surroundings. These requirements are supported in the human body by the senses as a whole, but particularly by proprioception.

Our daily doings are coordinated by what has been referred to as a ‘trinity’ of independent sensory systems: proprioception, vision and the functions provided by the vestibular organs of the inner ear, all mediated by action potentials in the nervous system. Proprioception is not widely known to be one of the bodily senses, but plays a central role in the human apprehension of both inertial and gravitational mass. It may be regarded as the sense by which the blind guide their movements, through sensors that precisely measure, dynamically, body joint angles, muscle extensions, tendon tensions and deep pressure within body tissue as well as in the skin, that provide a sense of the presence of the body, its posture and motion. Sensors in the skin also innervate the hair follicles so that fluid movements too may be detected.

The sensory category proprioception incorporates what are referred to sometimes as dynamic touch, kinaesthetics or the haptic system. The coupling of proprioception with the afferents from the vestibular senses enables the whole body itself to be regarded as a sense organ, and promotes a sense of self, manifested with particular acuity in the blind (Ma and Han, 2011). Details of the many proprioceptive receptor types may be found in, for instance, *Neuroscience* (1997, pp.152-4).

The afferents from these receptors, coupled with a continuous feed of signals from the vestibular system, vision and the sense of touch, update complex sensory-motor maps of the body (see §5.3). These maps store information about the momentary distribution and dynamics of forces on the limbs and their highly nonlinear interactions. The stored information not only guides bodily movements but also helps in determining the size and shape of objects and the geometry of external space. Clearly, proprioception informs about the apprehension of both length (L) and mass (M).

The vestibular system acts as a miniaturized accelerometer and inertial guidance device, continuously providing information about the motion and position of the head and body to integrative centres located in the brainstem and cerebellum, and is a key component in the control of posture and eye movements.

Angular motion of the head is detected by hair cell displacements in the semicircular canals. Linear motion of the head is detected in separate parts of the vestibular organ known as the utricle and saccule. These contain the otolith organs that transduce linear accelerations and provide information about the orientation of the head with respect to the direction of gravity.

The otolith organs, comprising small particles of calcium carbonate and a gelatinous matrix, are contained in the labyrinth, an elaborate set of interconnected canals buried in the temporal bone. The movements of the particles stimulate hair cells, similar to those found in the cochlea, to transduce motion into neural impulses. These motions are those that arise from the inertial effects of head movements and the effects due to gravity, ground-borne vibrations, and support various cognitive functions including spatial navigation and memory. For details see, for instance, *Neuroscience* (1997, Chapter 13) and Benson (1982, Chapter 16).

The body's posture and movement-receptors are processed in the brain in much the same way as the conventional senses of vision, audition and so on, and the signals from the proprioception receptors, mentioned above, are sent by afferent nerves through the spinal cord via the thalamus to areas 2 and 3a of the somatosensory cortex and the motor and parietal cortices, where they continuously feed and update sensory-motor maps of the body mentioned earlier (*Neuroscience*, 1997; Colby and Goldberg, 1999; Maravita et al., 2003; Smetacek and Mechsner, 2004; Price et al., 2006).

Vestibular functions are achieved by signals originating in the vestibular nuclei in the brainstem, projecting via several thalamic nuclei to the cerebellum and to many regions of the cerebral cortex. They are known to be coupled with the mechanoreceptors within and on the surface of the body and also with the afferents that inform the orientation of the limbs and body segments. However, details of the locus of function of vestibular afferents in the human cortex and their integration with the other sensory modalities are still the subject of on going research (Lopez et al., 2012). However, it would appear that the multimodal integration of the vestibular system with the other senses is learned.

The proprioceptors along with the vestibular system provide a subjective, internal body consciousness. They also provide information about physical properties of external reality such as space, weight and inertial mass. Given that these systems provide feed-back to the brain about the body's state of motion and the positions of its limbs, a child born without proprioception and vision would not sense internally that it had a body (Smetacek and Mechsner, 2004).

This view was emphasized by study of the rare individual Ian Waterman who lost all sense of proprioception from the neck downwards at the age of 19 (Carello and Turvey, 2000; Robles-De-La-Torre, 2006). Though still able to feel temperature and pain, he lost, permanently, all touch and sense of movement and position sense below the neck. Waterman could move his limbs, but could not control them in a precise way. When he was not looking at his limbs, he could not tell their position or whether they were moving. When not looking at them, his fingers and particularly his arms would move uncontrollably. He could not sustain the upright position in the dark.

It is worth noting that anyone who has learned to walk has attained mastery in the dynamic control of his own mass (for an elaboration, see Taylor, 1962, p. 70). Proprioception has been documented in a variety of living systems including fruit flies (Walker et al., 2000), nematode worms (Li et al., 2006), African clawed frogs (Shin et al., 2005) and zebra fish (Sidi et al., 2003).

5.3 Space Maps

A brief account is presented below on how dynamic maps of both personal and extra-personal space participate in the apprehension of distance between objects even though the

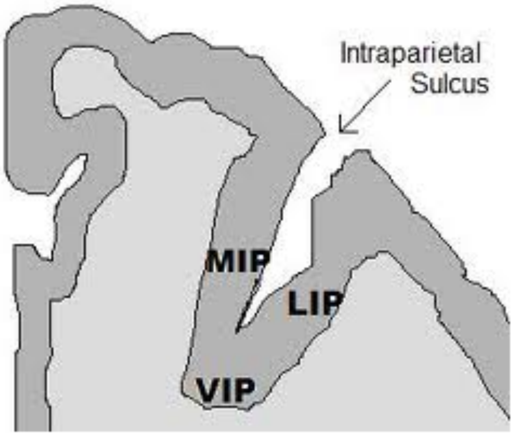

Fig. 5.1 Coronal section showing the intraparietal sulcus, the site of space maps.

sensory receptors that provide this information are often in constant motion. Much of the information has been obtained from Colby and Goldberg (1999). Maps involved in length perception through haptics are reviewed by Lederman and Klatzsky, 2009 (see below for a summary).

We can estimate an object's spatial location from many different sensory cues: vision,

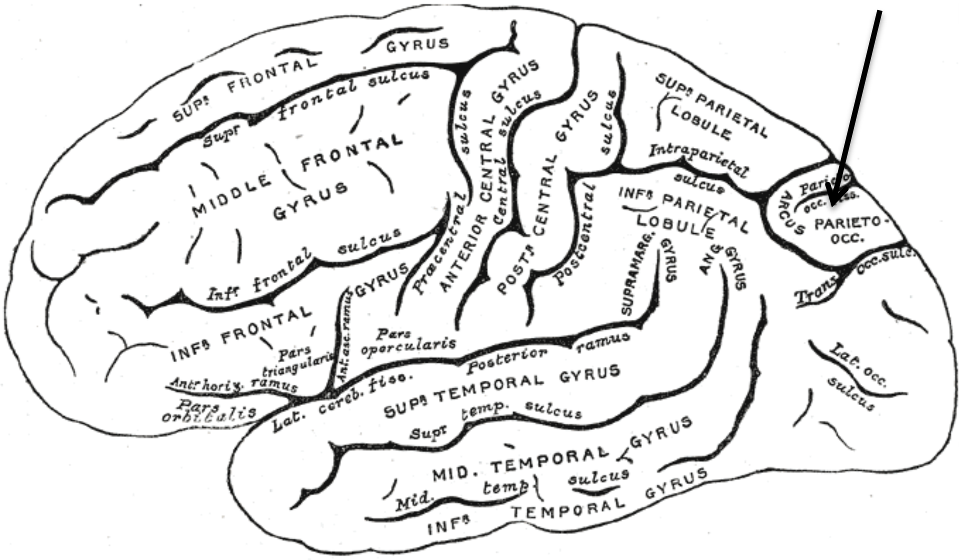

Fig. 5.2 Lateral view of the human brain with arrow marking the intraparietal sulcus.

audition and proprioception. Using these sensory sources multiple spatial reference frames are constructed dynamically in the parietal cortex. For example, retinocentric, body-centric and environment-centered. Subjects with lesions in the parietal cortex suffer a variety of forms of neglect.

Every time we move the location of our head and eyes, each object in our surroundings activates a new set of retinal receptors. Despite these changes in retinal activation, we experience the world as being stable. The same applies to our apprehension of objects in space using touch (or proprioception) and audition. Although the sensory receptors are attached to movable body parts, we generally have the impression of static or moving objects located within a stable spatial backcloth.

The reason for the stability is that what we see is not a dynamic pattern of the external world as it impinges upon the sensory epithelia, but a pre-processed internal representation of it. The visual representations of extra-personal space, for instance, are compensated for by eye movements, and reside in the lateral intraparietal (LIP) cortex. LIP represents the space that we explore best with our eyes; the space is not constrained to the immediate grasp of our arms or mouth.

Maps in the ventral intraparietal (VIP) cortex associate vision and touch. The tactile receptive fields are generally restricted to the head and face, and they match in size and location. Neurons in VIP with visual receptive fields near the fovea have tactile receptive fields close to the mouth, indicating that the maps are mutually aligned with respect to the most sensitive regions of the receptor surfaces. Some neurons in VIP are sensitive to vestibular stimulation, encoding motion of the head. The representations facilitate directed movement of the head, lips and tongue, and reaching with the mouth.

Neurons in the medial intraparietal (MIP) cortex are specialized for responding to stimuli within reaching distance. They have differing response properties. Some are purely somatosensory; others are bimodal for somatosensory and visual inputs, and yet others are purely visual. They bind, for instance, hand-eye coordination and are responsible for facilitating the control of arm movements. MIP neurons also show dynamic changes in their receptive fields when the arm's functionality is extended by tool use (Iriki et al., 1996; Maravita et al., 2003). Similar multisensory maps exist also in the superior colliculus (Stein and Meredith, 1994). A popular account of body maps may be found in Blakeslee and Blakeslee (2007).

Space maps and vestibular functions that support multimodal integration are dynamically updated. However, it has been shown in the experiments described that the capacity to make the intersensory links is acquired through learning, and the specific co-ordinations that are formed appear to be arbitrary.

5.4 Capacity for Visual Apprehension of Length

Articles by Braddick and Atkinson (1982) and Cutting (1997) described the means by which length may be perceived visually. Cutting (1997) provides a graph showing the range of depths over which the different depth discrimination systems are thought to operate. The processes for visual length perception have been classified according to whether they require the use of one eye, both eyes and those that involve motion. It is evident, as shown below, that all the methods require the capacity for the perception of structure (or contours) in the visual field.

5.4.1 Monocular Depth Determination

Direct Comparison of a length entails the lining up of two pairs of edges (or points), and can be accomplished using one eye; the degree of accuracy would depend on the vernier acuity of the eye (see, for example, Fig. 5.3).

Fig. 5.3 Use of a calibrated tape to measure length.

Occlusion occurs when one object hides or partly obscures another from view. Occlusion provides information only about which object is closer to the observer, but nevertheless enables depth perception.

Fig. 5.4 Depth is depicted in this painting by height in the visual field, occlusion, relative size, texture density, linear and aerial perspectives (Gustave Caillebotte: *A Rainy Day in Paris*).

Height in the Visual Field measures relations among the bases of objects in a three-dimensional scene as projected to the eye. It relies upon the assumption of a ground plane and knowledge about the sizes of the objects in the scene to allow the observer to infer their distances away from him.

Relative Size is a measure of the angular extent of the retinal projection of two or more similar objects or textures to indicate relative depth of the two objects. Once again, prior knowledge about the nature of the objects is required for the inference of depth using the measure of relative size (for example, the relative distance to humans in a landscape).

Texture or Relative Density is concerned with the indication of depth through the projected number of similar objects or texture elements per solid visual angle. The repeated objects or texture elements need to be familiar to the observer if absolute values of depth are to be extracted using this measure.

Aerial Perspective refers to the increasing indistinctness of objects with distance caused by light scattering in the atmosphere.

Accommodation refers to the eye's capacity to focus the lens to obtain a sharp image of the object at a particular distance from the observer. Objects at other distances are blurred, particularly under poor lighting conditions. This visual function clearly provides information about depth. Since the use of accommodation as a cue to depth perception requires the ability to distinguish between a sharp and blurred image (Currie and Manny, 1997), it too must depend on the capacity for perceiving structure in the visual field.

Linear Perspective refers to the extraction of depth information from the property of parallel lines converging with distance from the observer. An example is the appearance of the decreasing width of a road as it recedes into the distance. This property allows the estimation of the distance of objects within a landscape with parallel lines.

Fig. 5.4 shows cues to depth perception by all the above-mentioned categories apart from accommodation. They all require the capacity for structured vision.

5.4.2. *Visual Motion*

It is worth reflecting at the start that the notion of visual length perception involving motion inevitably entails the capacity for the perception of structure. This is because without the presence of a discernable structure it begs the question: motion relative to what?

Directionally selective cells for visual motion have been reported to exist in the visual cortex and in the superior colliculus of, among others, cats, monkeys and ferrets (see also §10.7). A compelling sensation of motion results from seeing a stimulus at just two positions at just two moments. The continuum of positions at a continuum of times is not necessary for motion detection. This highlights the fact that motion detection requires *resolution* both in space and time. If either of the positions or times cannot be distinguished, motion cannot be detected. If one could not tell that the stimulation at one place occurred before the other, one could not even decide that motion had occurred, and one certainly would not know its direction (Woodhouse and Barlow, 1982, p.159).

Motion Perspective refers to the optic flow field of objects stationary in the ground plane relative to a moving observer. Optic flow from objects nearer the observer is more rapid than those further away and thereby indicate the relative distances away of the objects in the ground plane from the observer. A special case of this phenomenon is looming, where the optic flow field directly ahead of the observer is under consideration. In this case the speed of the observer relative to the ground plane determines the rate of dilation of the optic flow, with objects nearer the observer expanding faster than those further away.

5.4.3. Binocular Depth Determination

Binocular Disparity or Stereopsis. The two eyes being set apart give rise to separate viewpoints, which in turn give rise to a difference in the relative position of an object as projected on the two retinae. The integration or synthesis of the images on the two retinae provides a three-dimensional image of a scene from which depth may be apprehended (see, for instance, Braddick, 1982, p. 192). Clearly, for this ability to develop the capacity for structured vision is required. Evidence obtained from preterm infants that stereopsis is learned during early development is given in § 6.3.

Convergence is a measure of the angle between the foveal axes of the two eyes. The angle is large when a viewed object is close to the face, and it decreases for objects further away. Convergence can be classified, strictly, as a proprioceptive function and operates in conjunction with stereopsis, with information from the extensor detectors in the muscles controlling eye movements encoding depth (see, for instance, Braddick, 1982, p. 193). Convergence associated with depth perception manifests only when there is the capacity for structured vision.

It was shown in the summary of work by Hubel and Wiesel, presented in §3.5.8, that the capacity for structured vision is learned. Given that these examples presented above show that visual length perception requires structured vision, it may be claimed that the capacity for visual length perception is learned.

5.5 Proprioceptive Apprehension of Length

Haptics is a sub-set of the broader sensory category proprioception. It focuses on perception through exploration, and omits issues associated with the sensing of body presence through receptors in deep tissue that the term proprioception includes. The haptic receptors reside in glabrous skin and in the limbs that are involved both in the exploration as well as in the performance of motor activities.

Haptics is mediated by two afferent subsystems: the cutaneous and the kinaesthetic, and typically involves active manual exploration, through which the dimension length may be obtained. While vision and audition provide precise spatial and temporal information respectively, the haptic system is highly effective at processing the material characteristics of surfaces and objects. It has been claimed that spatial extent and the concreteness of physical reality is obtained through haptics rather than vision (George Berkeley, cited in Heller, 2000, p. 6). However, in general, all haptic processes are guided by vision, and it would seem that Berkeley seems to have neglected both multisensory integration and the vivid depiction of spatial extent obtainable particularly through stereopsis, especially when accompanied by motion.

The hand, in particular, is acutely sensitive for the perception of the dimension length because of its mechanical structure, which consists of an intricate arrangement of 19 bones with some 40 muscles that activate 22 degrees of freedom (Srinivasan[13]). The compliance and frictional properties of the skin together with sensory and motor capabilities of the hand and arm enable its gliding over surfaces to be explored, without losing contact, as well as for stably grasping objects to be manipulated. The mechanical loading on the skin, the transmission of the mechanical signals through the skin, and their transduction by the

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[13] Source: Srinivasan, M.A. (date unknown) *What is Haptics*, http://touchlab.mit.edu

cutaneous mechanoreceptors are all strongly dependent on the mechanical properties of the skin and subcutaneous tissue (for further details on cutaneous receptors see, for instance, Iggo, 1982).

The information obtainable by the hand can be divided into two classes: (a) tactile information, referring to that obtained from the low threshold mechanoreceptor and (b) kinaesthetic information, concerning the position and motion of the limbs, along with the associated forces, conveyed by the sensory receptors in the skin around the joints, joint capsules, tendons and muscles, together with neural signals derived from motor commands. All sensory tasks entailing manipulation, performed actively, involve both classes of information. In addition, free nerve endings and specialized receptors which signal skin temperature, mechanical and thermal pain, as well as chemogenic pain and itch are also present in the hand.

These two classes of information are processed into the haptic equivalent of the visual ventral and dorsal ‘what’ and ‘where’ analytical streams in respect of haptic determination of object properties and their localizations. Haptically accessible object properties can be divided into broad classes: material and geometric. Surfaces can be explored manually to find ridges or gaps embedded in them that may define markers between which lengths may be estimated. Equally, external geometrical boundaries may be detected haptically, and lengths may be estimated between the boundaries (Lederman and Klatzsky, 2009).

Changes in temperature and thermal properties can also be used to define lengths. As long as the temperature of the object and the skin temperature are not identical, the temperature of the skin changes on contact with an object to an interface temperature. The interface temperature is determined by the material touched, its thermal conductivity, density and specific heat. Such temperature changes, together with surface roughness and so on, can act as markers to define lengths.

Lengths can be, clearly, also measured using human body parts as units of distance, for example the hand span, or the length of the foot or the cubit, referred to earlier. Such measures can be augmented by the use of tools such as yardsticks and so on (Lederman and Klatzky, 2009). Equally, length may be estimated, for example, *within* the closed hand or the mouth. In fact, any combination of kinesthetics and touch can be used to obtain a measure of length. Furthermore, locomotion in conjunction with either counting paces or timekeeping can be used to provide measures of length. Indeed the domain of athletics, and sports in general, dwell, in effect, on measures of distance, *viz.* high and long jump, javelin, shot put etc.

There is in addition an extensive literature on the mechanisms for length perception by use of dynamic touch. These indicate that humans can estimate the length of a rod simply by holding it still at an inclination to the vertical, or by wielding it, without need of any accompanying visual information. The inertial properties of the objects provide the sensors in the muscles and other parts of the body information about the objects wielded. This initial resistance to change in its state of rest or motion is specified by the distribution of mass in the object (Carello and Turvey, 2000, p. 34; Asao et al., 2012).

It has been shown, further, that the striking of an unseen object by an unseen wielded rod can improve its length judgement (Stephen and Arzamarski, 2009), as can increments in the speed with which the unseen object is struck (Lobo and Travieso, 2012). Rod wielding, primarily by movements of the trunk, while the unseen rod was attached to the shoulder girdle, also permitted rod length determination (Platinus et al., 2011).

All the above-mentioned measures of length rely on dynamically updated maps and, as such, haptic memory stores, of which there are many within the nervous system (Colby and Goldberg, 1999). In general, a frame of reference defines a coordinate system for localizing points with respect to an origin. Multiple frames of reference are generally available simultaneously, and the performance of any task may use a single frame or several at once. Points may be localized with respect to body parts as the origin, such as a fingertip, or the location where the 'actor' stands, in *egocentric* terms, or with reference to landmarks external to the observer, in an *allocentric* frame. Haptic measures of length on the body depend on motor and tactile memory, which are organized somatotopically, and act in conjunction with body maps residing in the parietal cortex.

Memories of the properties of stimuli such as size (and therefore length), as detected by touch receptors in the skin, are stored in the anterior part of the parietal lobule. Memory of spatial information, such as the spatial location of stimuli, involves the right superior parietal lobule and the temporoparietal junction (Gallace, 2009). For further details, see Colby and Goldberg (1999) and Lederman and Klatzsky (2009).

5.5.1 Behavioural Plasticity in Haptic Length Apprehension

In the realms of geometry, length is defined as the distance between two points. In order to assess if the capacity to apprehend length using active touch is derived or primitive, there is need to examine (among other factors) the behavioural mechanisms underlying the processes involved in determining the distance between a pair of points. Two experiments are described below that provide insights into this issue.

Fig.5.5 Crossed fingers reversed the perceived positions
of the points of contact (Benedetti, 1991).

Benedetti (1991) noted that crossing two adjacent fingers produces a distorted perception of spatial extent when the fingertips are stimulated by the two ends of an object (see Fig. 5.5; object not shown). This is because in the normal course of handling objects, the fingers are not crossed, and the haptic information of the length of a handled object is determined by the mechanoreceptors in the fingertips providing information about the location of the fixed points at the ends of the object, whilst the muscle extensor receptors and those in the joints provide information about the distance between the points to yield information about the length of the object. Vision acts to confirm and fix what is usually a multimodal property of the length of an object.

With the fingers crossed, there is a reversal of the points of contact with the object compared to what is usually encountered, and there is an alteration in the haptic assessment of direction. This is because the fingers have a functional range of action within which spatial perception is correct (with fingers uncrossed), beyond which (with fingers crossed) the perceived location of the endpoints is felt to be wrong.

However, Benedetti (1991) reports that with practice (of up to six months) the range of action was enlarged such that spatial perception was correct with crossed fingers as well. This finding suggests that the perceptual organization of the hand in the estimation of length depends on experience, and is not determined on a genetic basis. This view is supported by the observation that the capacity for object length assessment is preserved whilst hands and digits grow during development. A dynamic learning process underlying such length assessment rather than a hard-wired one seems more likely.

It would seem that a mapping is learned between the haptic receptors and what is termed the length of an object, and when the range of mappings previously learned are exceeded, the system initially fails to provide the desired result: length perception. However, learning over the extended range restores capacity for length perception.

Robbles-De-La-Torres and Hayward (2001) demonstrated that the output from sensory receptors participating in dynamic touch need not involve joint and muscle receptors. We can use our hands not only to manipulate objects in the physical world but also to perceive them. Using our hands to perceive the shape of an object often involves running the fingertips over the object's surface. During such active touch, we obtain both geometric and force cues about the object's shape: geometric cues are related to the path taken by the fingertips, and force cues are related to the contact forces arising from the object on the fingertips. Geometric and force cues are generally highly correlated, and it is difficult to determine the contribution of each to perception.

However, Robbles-De-La-Torres and Hayward (2001) were able to separate haptic geometric perception from force cues about an object's shape by using a robotic device to manipulate the horizontal forces on the object and the fingertip to demonstrate that a mapping could exist between solely force cues and the spatial dimensions of an object. As such, only the forces associated with haptic processing were sufficient to yield information about the shape of an object.

In the experiments, subjects were asked to use a fingertip to slide an object over a surface. Their hand and the apparatus was hidden from their sight (Fig. 5.6). They had to decide whether they perceived a bump or a dip. In all cases (a), (b) and (c) shown in the figure, subjects reported perceiving a bump. In Fig. 5.6 (a) the object went over a real bump, which gave rise to physical forces represented by blue arrows. The horizontal forces initially resist and then assist lateral motion to the right as the object went over the bump. Vertical forces cause the object and the fingertip to rise and fall (but these movements were not visible to the subject). (b) The object slides across a flat physical surface but horizontal virtual forces (red arrows) simulating the effect of a physical bump were applied to the object by the robotic device. Although the fingertip does not rise and fall, the subject perceived a bump. (c) The object slides over a trough, but a virtual force corresponding to twice that in (b) was applied to the object. This resulted in the subject perceiving a bump even though the fingertip follows the trajectory of the dip.

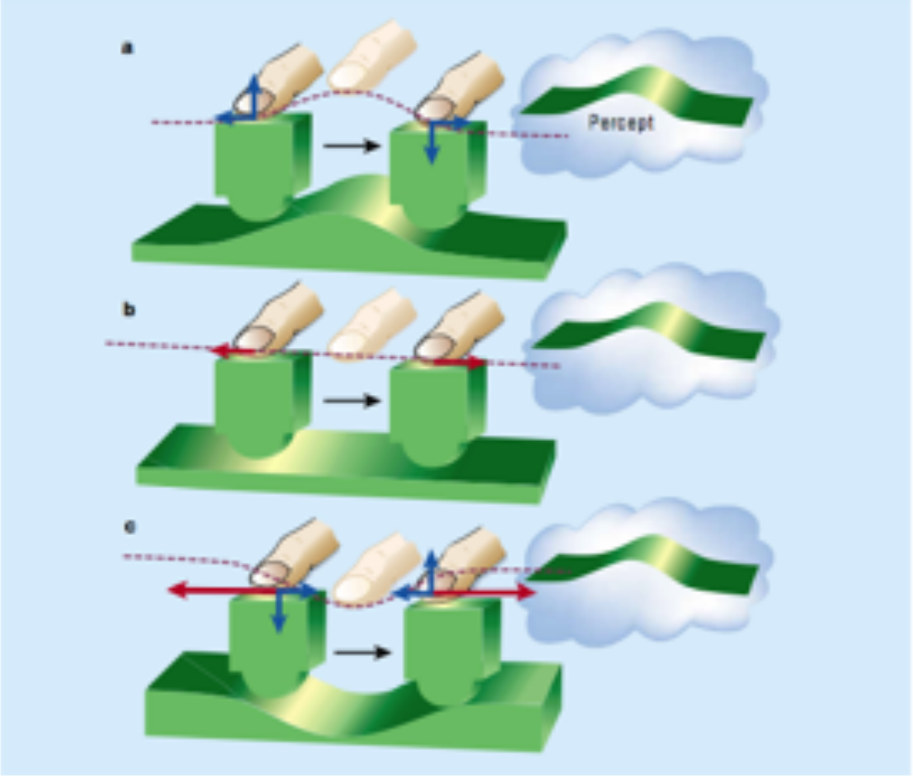

Fig. 5.6 A schematic representation of the experiment by Robbles-De-La-Torres and Hayward (2001). The blue arrows represent forces; the red arrows, virtual forces and the profile depicted in the clouds the subjective percepts. See text for details. (Source: The review by Randall Flanagan and Lederman, 2001).

Given that the geometric cues are learned (see Benedetti’s results above), and that the geometric and force cues are generally correlated, it seems reasonable to take the force cues for shape to also be derived and not primitive, particularly because the underlying neurophysiological substrate supporting force perception is common with those supporting receptors of geometric cues (see chapter 3).

6

APPREHENSION OF MASS

6.0 Introduction

In the realm of classical physics, mass and force are mutually defined in terms of acceleration by Newton's second law of motion,

$$f = ma,$$

which states that the application of a force f to a body of mass m that is free to move, will result in an acceleration a.

The mass of an object manifests as weight (w) on the surface of the earth because of the acceleration due to the earth's gravity, ($f = ma = mg = w$, where g is the acceleration due to gravity, so weight is force due to gravity). Mass also manifests as inertia, or inertial mass. This is a body's resistance to being moved. Inertial mass is a measure of the force that would need to be applied to a body to produce a unit of acceleration. The greater the force required to produce unit acceleration, the greater is the body's inertial mass.

Similar considerations apply when a body is rotated. Its resistance to rotation under the action of a torque is also a measure of its inertial mass and the distribution of that mass about the axis of the applied torque (Amazeen and Turvey, 1996). Inertial mass and gravitational mass are both a measure of the same entity.

In its simplest form, mass manifests as force, sensed through touch. It could be the pressure of a strap felt around the palm of the hand from which a weight is hung (gravitational mass or weight), or it could be the force felt against the hands when pushing off a free-floating boat from a jetty (inertial mass). As the boat moves, its acceleration is both seen as well as experienced in the body through the proprioceptive senses.

Piaget made a distinction between (a) being competent at performing an activity on the level of sensorimotor behaviour and (b) naming and understanding the principles underlying those activities at a conceptual level. At issue in the present enquiry is not the *comprehension* of the term 'mass' *per se,* at the intellectual level or the understanding at a higher-level the principles that govern its behaviour, such as its conservation despite changes in the shapes of objects.

Rather, of interest is competence in the *functions* of the diverse senses that participate in our capacity to deal with objects of differing masses. Clearly, such competence can lead to intellectual reflections about the notion of mass. But that is not specifically at issue in the present enquiry.

In particular, the enquiry addresses the issue whether our capacity to sense and manipulate mass is given innately, and so comes to be in place as a part of the process of maturation, irrespective of the subject's engagement with the environmental setting, or whether this competence is acquired through the subject's exploration of, for example, objects in its environmental setting.

Clearly, someone, particularly an infant or child able to sense mass, would generally be physically competent in dealing with it, but would not necessarily have the higher-level concept of mass.

In the case of mass conservation, the child does not realize that weight, volume and substance are invariant under transformation of shape, even though the infant shows this via competence in its sensorimotor behaviour by the age of 18 months (Mounoud and Bower, 1974). A child comes to understand the principle of mass conservation through his thought processes only at the age of 8 or 9 years (Mounoud and Bower, 1974).

It is the origin of capacity to sense mass through sensorimotor behaviour that is addressed herein, although following Locke (see §2.5), it is also of interest to evaluate the suggestion that there is nothing in the intellect that is not first in the senses. Clearly, the latter precedes the former.

An interesting complication in the case of mass is that the limbs or appendages through whose agency mass is apprehended themselves have mass. However, it is worth observing that anyone competent to walk will have sensorimotor mastery over dealing with his own mass.

6.1 The Senses Involved in the Apprehension of Mass

In the human system, the apprehension of mass (or weight) is often initiated by motor activity leading to an experience of force, usually within a multisensory context. The force can be applied either to resist gravity, to generate (or resist) motion or both. In this regard the somatosensory sense within the context of proprioception constitutes the principal means for the manifestation of mass.

The example of the person pushing off a boat, mentioned earlier, is useful in identifying the separate senses participating in mass perception, particularly when applied to boats of differing masses. The forces felt in the hands and feet are sensed by the diverse mechanoreceptors embedded in glabrous skin, whilst the motor system provides and controls the applied forces. The major classes of somatic sensory receptors are given in *Neuroscience* (1997, Table 8.1, p.149).

As each successive boat, with a different mass, starts to move away from the jetty under the influence of the complex inter-related forces exerted by the muscles, the vestibular system senses the linear movement of the subject's head in the direction of the motion. Meanwhile, the proprioceptive senses provide dynamic information about the body's posture in respect of muscle extensions, joint angles and so on. Notable is the fact that the muscles both hold up the subject's weight as well as provide the net thrust against the boat. Concurrently, the visual system monitors the size and overall motion of the boats as well as that of the body parts providing the motive force.

There is, thus, a degeneracy of multimodal information provided by an array of senses that participate in the example of mass apprehension given above. All human senses bar, audition and the chemical senses, participate in the apprehension of the boats' masses.

Audition, too, can provide information about an object's mass. For example, the sounds heard when a cricket bat strikes different objects can indicate unequivocally their relative masses when there exists prior knowledge of such sounds; consider the situation when the sounds heard are successively those of a cricket ball, a tennis ball and a table-tennis ball being hit by the bat. See chapter 8.

It is generally assumed in the literature that the capacity to apprehend mass develops through learning rather than being given innately. However, for the sake of completeness, an account is provided below of the issues and stages involved in the development of an infant's capacity to apprehend mass or weight.

6.2 Fetal and Neonatal Development

Given that mass apprehension involves the greater proportion of sensory modalities, a brief account is presented of the time course of the initial behavioural manifestations of sensory development pertinent to mass apprehension. These have been studied by following the changes in the associated brain activity or by stimulating the different sensory modalities as the fetus develops (Eswaran et al., 2004).

The fetus is contained in an environment of neutral buoyancy, so the weight of its body is not sensed directly in the womb, although there is a fluid pressure gradient in the womb due to the force of gravity.

The following time-line is provided to emphasize the fact that sensory and some motor competences develop early during gestation. It is intended to provide a perspective for appreciating the significance of the subsequent activities engaged in by the neonate that will enable it to come to apprehend mass at the age of about eighteen months.

Brain development is reflected by the changes in fetal behavior patterns observable over gestation. The time-line for the development of these prenatal activities in terms of weeks of gestational age (g.a.), as determined by behavioral responses, begins with the response elicited by touch (7 g.a.), followed by limb movements (10 g.a.), coordinated movements (16 g.a.), slow (16 g.a.) and rapid (23 g.a.) eye movements, cyclic motor activity (21 g.a.), startle response to vibroacoustic stimulation (24 g.a.), response to light (28 g.a.), sleep cycles (34 g.a.), regular breathing movements (35 g.a.), and habituation to repeated vibrotactile stimulation (38 g.a.) (Eswaran et al., 2004).

There is frequent thumb-mouth contact in the womb by mid-gestation, which the fetus anticipates by opening its mouth prior to contact and a diversity of other bodily movements, that refine somatotopic ordering of the targets of cutaneous mechanoreceptors in brain tissue through mutual contact between fetal body parts and, indeed, between the body and the wall of the womb and other anatomical structures contained therein (Parpia, 2011). These activities have been recorded using ultrasound imaging (see, for instance, Myowa-Yamakoshi and Takeshita, 2006).

6.3 Vision in the Womb

The reason for the inclusion of this topic here is because vision is one of the modalities that participate in the infant development of mass apprehension (see below). It also provides an opportunity to address the issue of the manifestation of visual competence in the neonate which is taken to indicate the presence of innate ‘core knowledge’ by traditional nativist developmental psychologists, who claim that neonatal visual competence is independent of learning or the influence of the environment (see, for example, Streri and Gentaz, 2012).

This belief stems from the widespread assumption that human gestation takes place in the dark. However, a flash of light corresponding to one-eleventh of the intensity of sunlight incident directly on the mother's abdomen is sufficient to provoke a visually evoked brain response from a fetus of 28 g.a. (Eswaran et al., 2004).

This indicates that the womb is far from being a dark place. Furthermore, there is evidence to suggest that the amniotic fluid can be clear (Lebed et al., 1980), thus allowing the structured visual input thought necessary for orientation tuning to occur in striate cortex to enable the development of visual competence. This can only occur once the striate cortex is appropriately configured by the visual experience of edges of a variety of different orientations (Hubel and Wiesel, 1962; Hirsch and Spinelli, 1970; Blakemore and Cooper, 1970; Walk et al., 1988). See also § 5.0.

The development of the fetal visual system has been studied using a number of methods. The maturation of eye-movement patterns accompanying functional development (or pathology) has been analysed using ultrasonic imaging systems in fetuses from 16-42 g.a. (Birnholz, 19981), and several studies have demonstrated the feasibility of recording visually evoked electrical potentials on preterm infants to follow the development of visual function (Herschkowitz, 1988).

Eswaran et al. (2004) demonstrated, using magnetoencephalography, that areas like the primary auditory, visual and somatosensory cortex show a basic function, beginning at 28 g.a., similar to that of a fully developed brain. The overall finding is that the visual system develops during fetal life, and becomes functional before birth.

These findings suggest that there is sufficient visual competence in place to enable the fetus to associate visual and proprioceptive inputs (including, of course, the motion resulting from pushing against the walls of the womb), without, however the capacity for binocular fusion, which develops postnatally (see below). It is worth mentioning that with the fetal cornea immersed in amniotic fluid the overall refracting power of the eye is diminished, resulting in a shortening of the near point so that objects closer to than in air may be focussed upon in the womb.

Jandó et al. (2012) report that the age of onset of stereopsis in preterm infants precedes that of full term infants. This is because the visual cortex is ready to accept (enhanced) environmental stimulation right from birth, and that the preterm infant uses the extra stimulation to acquire binocular fusion at an earlier age (counting from conception) than the full term infant. The authors observe from their data that the developmental processes preceding the onset of stereopsis are not pre-programmed, as they might be had this function arisen solely as a function of maturation, and so the mechanisms that initiate stereopsis are experience dependent.

6.4 Development of the Apprehension of Mass

Neonates (aged 18 days) were reported to purposefully monitor visually their control of arm movements against gravity while opposing additional external forces applied to their wrists as a part of the investigation (Fig. 6.1). This suggests the occurrence of a process of proprioceptive learning under visual monitoring, where the weight, length, and motion of the limbs are being assimilated (van der Meer et al., 1995). It is worth noting that not all movements in the neonate are purposeful, because spontaneous reflex activity is manifested during the first few months after birth (for details see §6.7.3).

The importance of vision under such self-monitoring activities is emphasised by reports that short-term visual deprivation induces significant changes in the neural processing of tactile form (Weisser et al., 2005). The findings given above indicate that the multimodal development of precursors of mass apprehension are underway in the neonate.

The capacity to apprehend mass, as a property of objects, can be thought to emerge through perception-action routines similar to those displayed by infants indicated above. This can be interpreted to occur when the sensory prerequisites are sufficiently established to accomplish the further coordinated learning.

Fig. 6.1 An 18 day-old baby whose arm movements were being monitored (Van der Meer et al., 1995).

The exploration of the material properties of objects, such as textures, rigidity, compliance, and so on, in order to respond appropriately to underlying features, or ‘regularities’ common to objects, such as mass, occurs in infants only at the age of 13 months (Paulus and Hauf, 2010), but is not in place at the age of 11 months (Hauf and Paulus, 2011).

These explorations are shown to be visual, auditory and proprioceptive. As such, virtually all sensory capabilities are involved in the development of mass apprehension, with perhaps proprioception and vision playing key roles.

A resumé of some aspects of the experiment by Mounoud and Bower (1974), given below, illustrates the development of the sensory capacities involved in the apprehension and discrimination of weight.

Babies aged 6-18 months were handed test objects they were previously familiarised with visually and haptically. These samples consisted of rods of constant diameter but of varying lengths. Accordingly, their weights varied linearly with their lengths. The infants had to hold out their arms to receive the samples.

The authors recorded if the subjects had visually anticipated (a) the grip-force that they needed to apply to successfully hold the sample presented and (b) whether there was a drop or elevation of their arm in receiving the samples of different weights.

Although the authors were interested in determining the age of onset of the infants' ability to detect that a sample's weight was invariant through transformations of its size (weight conservation), for our purposes, the results of these tests showed that by the age of 18 months babies were competent in anticipating visually the weights of such objects by their lengths. These observations may be taken as evidence that the infants had built an internal model of expectation for object holding, in order to apply an appropriate muscle tension, and were able to anticipate visually the masses of the different objects presented. Indeed, Claxton et al. (2003) have shown evidence of planning in reaching behaviour of 10-month-old infants, and Mounoud and Bower's results (Mounoud and Bower, 1974) show that planning extends to weight apprehension by the age of 18 months. Thus, visual and proprioceptive abilities required for the apprehension of weight were in place by that age.

Younger infants (between 6 - 15 months) were unable to accomplish the tasks, which Mounoud and Bower (1974) took to indicate the babies' lack of experience; the process of development being regarded by the authors as a ‘construction’, reminiscent of the Piagetian notion of epigenesis, and its modern manifestation in theories of constructivism and neoconstructivism (see §3.6).

It is worth elaborating that the forces babies apply in grasping objects has been evaluated also by Molina and Jouen (2003) in their more recent study of weight perception in 12-month-old infants. Their work was directed at evaluating the infants’ capacity to apply an appropriate force when they grasped objects of different weights that were presented to them. During the trials the infants were free to execute uni-manual exploratory procedures on two objects of different weights that were identical in other respects. The exploratory procedures consisted of shaking, banging, waving and squeezing the samples, whilst the palmar grip pressure was being monitored dynamically through the use of transducers within the surfaces of the objects.

From an analysis of the data collected of the infants’ haptic activities, the authors claimed that the temporal variation of the grip force was seen to be adjusted dynamically to suit the motion of two objects of different weight. Thus, the infants displayed the capacity to haptically process mass during their manipulation task. Other work shows that this capacity is not in place until about 9 months (Molina and Jouen (2003).

The above work suggests that the ability to apprehend mass develops through experience and shows that in addition to the use of vision to anticipate mass through size (in the work by Mounoud and Bower, 1974), there are haptic procedures that infants can use to learn to gain information about object mass.

6.5 The Motor System

Taylor (1962) observes that a striking feature of neonatal behaviour is the inability to control head movements, and thereby sense and control the mass of the head. In re-positioning the neonate, the head rolls into a new position as if it were a dead weight. However, within a few days the infant is able to hold its head in fixed positions.

There is no direct evidence that this capacity is due to learning rather than maturation, except for the observation that preterm infants acquire motor control of head position against gravity over much the same period of time post birth as do full term infants. Were the ability to control head movements a feature of genetically ordered maturation, preterm infants might be expected to achieve this ability after a longer time interval after birth, and that post-mature infants (born later than full term) should be able to hold their heads in a fixed position almost at once, which are not observed to be the case. These results suggest that motor control of such head movements is learned and not primitive.

Schmidt (1988) has remarked upon the ease with which motor behaviour can be learned, and indeed, human competence in interactions with mass is demonstrated in virtually all sports, and particularly in gymnastics. There is little doubt that performance improves with practise, which confirms the widely held belief that the motor component of our competence to apprehend mass is acquired rather than being given innately.

Ghahramani (2000) observes that a feature of motor movements is that they entail forces that provide the subject with information about the mass of an object. The central nervous system creates complex behaviours by combining simpler motor primitives, and once learned, these primitives can be assembled to create new behaviours.

Thus, the sequences of motor actions are composed of learned primitives, as is the information contained in gnostic neurons (see §3.6.8), and are structured, in this respect, in a manner similar to those of phonemes that comprise the learned vocal structure of speech sounds (Sejnowski and Rosenberg, 1986). See also chapter 9.

6.6 Discussion

To sum up, the proprioceptive, vestibular, visual and auditory receptors all participate in the apprehension of mass. However, audition, for example, cannot provide much independent information about mass. This is with the exception of cases where prior auditory knowledge is in place within the context of a multimodal setting.

Thus far, work described on the acquisition of competence in mass apprehension has been largely confined to behavioural results involving sensorimotor processes. Of the senses that participate in the apprehension of mass, those considered to be key are vision and touch.

Furthermore, multisensory integration is central in unifying this capacity. The neurophysiological processes underlying plasticity in the visual and somatosensory systems, along with multimodal integration have been described respectively in chapters 3 and 5, and shown to be plastic.

As suggested by Westermann et al. (2007), the maintenance of sensory competence in dealing with mass with changes in anatomical size during development would require the dynamic updating of information in the central nervous system, and it would appear that the apprehension of mass as a multimodal phenomenon is learned through an interaction between the subject and its environment. However, the motor activities used for the sensing of mass may be themselves derived from motor reflexes that might be genetically pre-specified, thereby making the motor aspects of mass apprehension inevitable and not dependent upon learning. With this concern in mind, the next section provides a review of the pertinent studies on human movement with a view to establishing the relationship between the repertoire of human motor actions and their possible dependence on innately given primitive reflexes.

6.7 Motor Behaviour Revisited

This section seeks to establish whether in the absence of any learning, the motor abilities involved in the apprehension of mass might arise as a part of infant maturation irrespective of environmental factors.

A similar issue arose during the era when Behaviourism was the dominant paradigm in psychology. In this case Charles Sherrington and Ivan Pavlov had proposed that coordinated motor behaviour might be regarded as a collection of simple reflexes, so that the response to each stimulus served as the triggering stimulus for the next response in a stimulus-response chain (See, for instance Konczak, 2005; Robinson and Kleven, 2005). The key issue with regard to this proposal was whether human behaviour might be accounted for without evoking the notion of a centralised, top-down, structural organization, or mind.

The resolution of the issue was initiated by Lashley's observation that the developing nervous system could spontaneously generate coordinated motor activity without the need of an initiating sensory stimulus (Lashley, 1917). Boden (2006, p. 266) points out that Lashley (1951) settled the issue in favour of the existence of a volitional controller by considering the example of the generation of a sequence of phonemes in speaking a word. The Behaviourists' view of this activity, as mentioned above, was that it consisted of a chain of stimulus-response reflexes. This implied that what happens next can only depend on what has happened previously, and not on any future links in the uncompleted chain as speech production proceeds.

Lashley (1951) showed that in the case of the generation of linguistic errors, such as spoonerisms and anticipatory slips of the tongue, that speech is actively organized by syntax, not merely describable by it. As such, speech production must be pre-organized in such a way that syntactic agreement must be put in place (along with its errors), anticipating what is yet to be uttered.

However, the issue of interest in the present section in regard to mass apprehension is not whether there exists a centralized controller, but that of learning: whether or not the motor actions through which the infant comes to apprehend mass are determined by native motor reflexes that appear spontaneously during gestation, or if coordinated motor behaviour is generated through learning.

6.7.1 Overview of Motor Control

The large-scale organisation of the motor cortex located on the precentral gyrus is somatotopic, and has a form that is homologous with that of the Penfield homunculus. In it, the feet are represented near the apex of the cerebral hemisphere, and the mouth laterally (Parpia, 2011). The approximate body-map has some overlap between the representation of different body parts, with discontinuities in somatotopy and some multiple representations of body parts (Graziano, 2006).

The stimulation of cells in different parts of the motor homunculus gives rise to overall activity in the muscles corresponding to the respective homuncular locations.

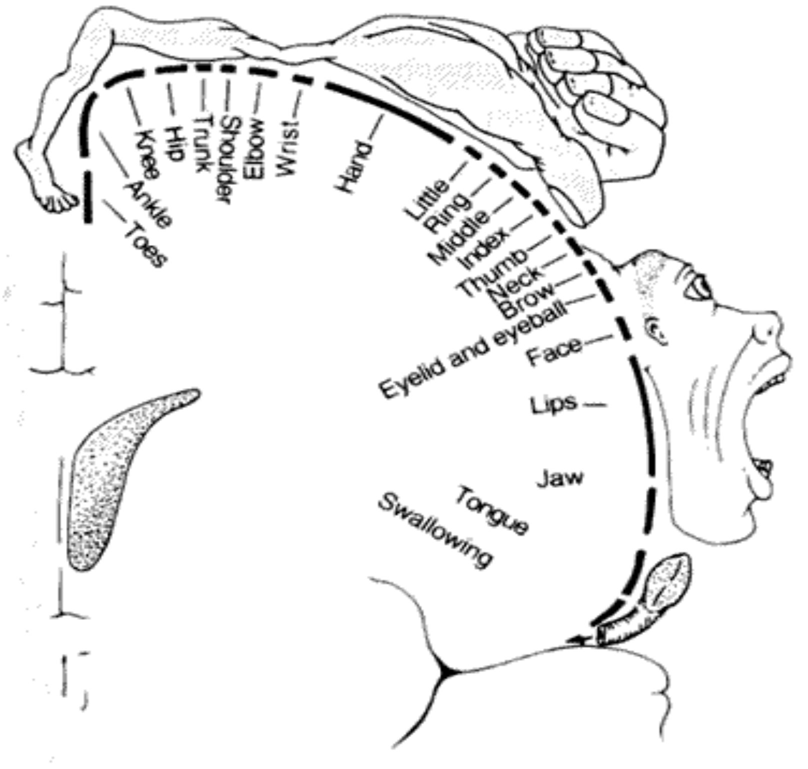

Fig. 6.2 A schematic representation of the motor homunculus (Adapted from Penfield and Jasper, 1954 by Liberman, 2000).

Electrical microstimulation studies of the macaque motor cortex showed that the activation of specific sites resulted in complex coordinated actions that have been interpreted along ethological categories, such as the movement of the hand to the mouth in feeding, reaching and grasping actions and defensive manoeuvres to protect the body from injury.

The present view is that motor cortex is broadly hierarchical in its organisation, in which higher-order categories of behaviour (such as feeding or climbing) are decomposed into its simpler lower order component actions, which are then communicated to the muscles via the spinal cord, for execution.

With advances in research it is becoming clearer that the local cortical layout, particularly at the output stage, consists of a mosaic of regions that influence each other through short-range lateral connections. These regions represent the animal’s movement repertoire, and can be interpreted as being directed to higher-level objectives like escape or grooming.

The resulting seemingly haphazard spatial organisation has been interpreted by Graziano (2006) following Kohonen’s suggestion that the spatial layout of cortical maps result from a self-organization of their adjacency relations, so that neurons that process similar information are located adjacent to one another to facilitate economy in intra-cortical communication (Kohonen, 1987). Such self-organization can lead to a fractured, or apparently disordered appearance of the maps in certain cases because the cortex is quasi-planar while the relevant adjacencies being mapped may be of higher dimensionality. This view is consistent with the suggestion that such a spatial arrangement optimises geometric, biophysical and energy constraints (Laughlin and Sejnowski, 2003).

Individual neurons in the motor cortex do not generally control just a single muscle. Rather, they often influence several muscles, and such ‘synergies’ (or co-activations, or sequences of activations) of muscles generally cooperate in an overall activity, such as, feeding.

The rough map in motor cortex represents spatial locations in the body to which the movements are *directed*. For instance, the stimulation of a particular site in macaque right precentral gyrus results in a movement of the left hand to the monkey’s mouth, irrespective of the hand’s starting position (Graziano et al., 2002). It seems that these complex behaviours are accomplished by combining a relatively small number of simpler building blocks: ‘motor primitives’.

Their significant feature is that many different movements can be derived from a limited number of stored primitive muscle activations, and the resulting movements can be combined through a well-defined syntax of action to form more complex behaviours. Motor primitives have been detected in many different species from humans to frogs to locusts and even in the feeding system of the sea slug *aplysia* (Flash and Hochner, 2005) (see also §6.7.4).

A significant issue that arises with regard to the concern mentioned earlier about the origins of the apprehension of mass, is the origin of motor primitives: whether they are learned independently, or are derived from, innately given reflexes.

6.7.2 Motor Reflexes

Traditionally a reflex is thought to be an involuntary bodily movement that the organism cannot suppress. It might be spontaneously generated, as in the case of kicking *in utero,* or evoked by a sensory stimulus as, for example, when a drop of water falls onto to the eye. In this event, the eyelid reflex closes the eye to protect it from further exposure (Konczak, 2005).

The term reflex is used also to refer to a rapid sequence of motor activity to achieve a behavioural goal, for instance, while playing a sport. In this case, the reflexive action refers not to an innate stimulus-response effect, but to activity that is the result of prior learning, and is, at least partially under volitional control.

The presence of volitional influences in what are referred to conventionally as reflexive actions make it difficult to determine what is and is not a reflex. However, an acceptable definition, for present purposes, is provided by the existence of what are regarded as primitive reflexes that appear to be native in origin.

These behaviours come closest to mimicking simple input-output functions, and are typified by the patella or knee-tap muscle stretch reflex, which is initiated by tapping the patellar tendon just below the knee, and results in the lower leg kicking forwards (see Fig. 6.3). The phenomenon of the stretch reflex is generally considered to facilitate keeping an upright body posture. The reflex is stimulated by muscle spindle receptors that detect an unexpected stretching of muscles either through inattention to body posture or due to an external force. The effect of the reflex is to correct any disequilibrium and to restore an upright posture.

It is worth emphasising that even the patellar reflex, which is misleadingly referred to in many neuroscience texts as ‘ … a monosynaptic reflex arc, consisting of only two neurons (a sensory neuron and a motor neuron) …’, is more complex than the closed sensorimotor loop that its name might imply. As can be seen from Fig. 6.3, that the muscle spindle sensors send afferents also to the central nervous system, which can moderate muscle responses by the action of descending efferent fibres (not shown).

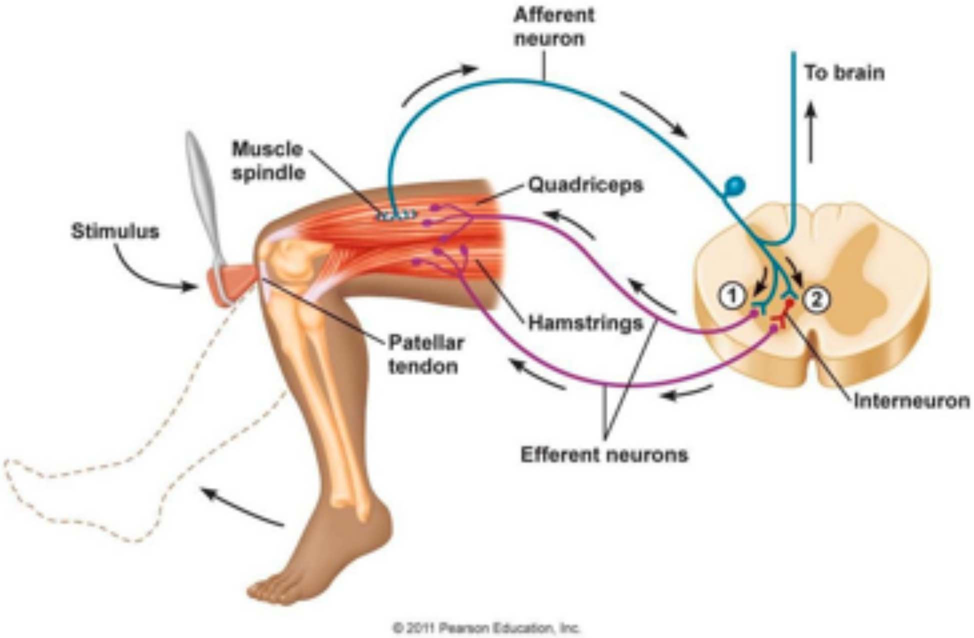

Fig. 6.3 Nerve fibres involved in the sensing and promoting the patellar reflex. The muscle spindle sensors detect muscle stretch, and the reflex arc consists in the activation of (1) the quadriceps and the (2) deactivation of the hamstrings via an interneuron. The afferent action potential is also conveyed to the brain. Source: Pearson Education Inc., www.studyblue.com

Another reflex that persists into adulthood is the eyelid reflex mentioned above. The patellar reflex cannot be voluntarily supressed while the eyelid reflex can, with training, but it is clearly possible to touch one's own eyelid without eliciting the reflex. It will become clearer, as this section proceeds, that what is deemed to be a reflex is more complex than it may at first seem.

6.7.3 Infantile Primitive Reflexes

The motor system does not come as a ‘blank slate’. In a wide variety of species there exist stereotyped inborn movement sequences. The newborn infant possesses a repertoire of coordinated movements. This class of motor behaviours is known as primitive reflexes, and are brainstem-mediated, complex but invariant movement patterns that develop during gestation. They are readily elicited by a specific sensory trigger, and with further maturation of the central nervous system, are gradually supressed and superseded by voluntary or volitional[14] motor behaviour (Konczak, 2005).

Among the reflexive movements that can be elicited *in utero* (by, for instance, vabroacoustic stimulation (van Heteren, 2001)) is the rooting reflex (emerging at 7.5 weeks g.a. (gestational age)), where the embryo will turn its head towards anything that stimulates its cheek or mouth in search of its source. The reflex is thought to assist the act of breastfeeding, and disappears at the age of four months, when breastfeeding gradually comes under voluntary control.

Other primitive reflexes are the Moro reflex, where a sudden lowering of the head and body of an infant supported on its back elicits extension of all four limbs (emerging at 8-9 weeks

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[14] The term ‘volition’ is frequently encountered in the literature on motor behaviour. The motor system is activated by descending (efferent) projections, as are sensory nuclei lower down in the hierarchy of the nervous system. Such volitional, cognitive effects are generally neglected by workers reluctant to acknowledge mental influences on the perceptual process. Traditionally, following the physical sciences, workers in the life sciences have sought accounts of biological activity that have drawn from the Behaviourist tradition of not conceding the notion of mind or mental features (e.g., Kandel’s work on the molecular basis of memory (Kandel, 2006)). It is only from around the turn of the present millennium that credence has begun to be given to mental influences on biological activity (not involving motor behavior). Motor behavior that is under cognitive control provides an example *par excellence* of top-down influences.

g.a., and disappears at the age of around 2 months), and the asymmetric tonic neck reflex, where turning the infant's face manually to one side, when it is lying on it back, causes its arm and leg to extend on that side, and the arm and leg on the other side to flex. It is present *in utero* at 18 weeks g.a., and is abolished at about 4 months. See Fig 6.4.

These reflexes are, thus, a repertoire of complex multi-jointed bilateral movement patterns that can be elicited by specific sensory stimuli, and are supressed later in infancy. The fact that primitive reflexes can be elicited sometimes very early during gestation indicates that the sensory capacity for their perception must also be in place at the corresponding stages.

Fig. 6.4 The Moro reflex and the asymmetric tonic neck reflex that results when the infant's head is turned to its right hand side (source: Konczak (2005)).

The presence of primitive reflexes, mediated by the spinal cord and brainstem (composed of the medulla oblongata, pons and the midbrain), are seen to be a part of healthy development. These caudal regions of the brain, lower in the hierarchy of the nervous system, become functional earlier than the more rostral regions as development progresses along the caudal-rostral arc (Joseph, 2000).

One view for the disappearance of primitive reflexes is that as higher centres in the nervous system mature, and volitional movements emerge, the higher centres begin to inhibit brainstem and spinal cord-mediated responses that would otherwise interfere with volitional activity. It is thought that the suppression of primitive reflexes also allows for the emergence of postural responses responsible for allowing the body to cope with gravitational force and those due to motion (Konczak, 2005).

6.7.3.1 Functions Attributed to Primitive Reflexes

A number of developmental functions have been attributed to the presence of primitive reflexes. Goldfield (1995) reviewed the evidence that kicking *in utero* is related to ontogenetic adaptation for orienting the fetal body into the vertex position (head at cervix). Kicking *in utero* is observed between 28 and 36 weeks g.a., when the fetal body has grown sufficiently to fill the uterus, and the inner surface of the uterus can act as a support for rudimentary locomotion. It is also during the same period that fetuses succeed in changing their orientation into the vertex position, as is appropriate for delivery.

Supporting this functional interpretation of the kicking reflex is the observation that babies born with paralyzed limbs are likely to be in an abnormal position for birth. Further, once the fetus is in the vertex position (by around 36 weeks), there is a decrease in kicking, which may help to not disrupt this posture.

Many of the primitive reflexes that involve extension and flexure of the limbs (for instance the asymmetric tonic neck reflex and the Moro reflexes) would act to integrate activity across the midline, and would bring the cutaneous receptors into contact with objects. Such contacts would serve to create somatotopy in the various somatosensory nuclei and cortex by co-activating adjacent sensory receptors (Parpia, 2011). Activity of this kind would also stimulate diverse proprioceptive receptors in the muscles, joints and, indeed, in the vestibular system. In addition, they would also commence the process of learning hand-eye coordination (Metta et al., 1999), given that there is both light and rudimentary vision in the womb (see §6.3). Such activities would clearly promote the development of muscle tone, begin to activate visual motion detectors and also commence the process of integrating proprioceptive, vestibular and visual maps.

6.7.3.2 Primitive Reflexes and Pathology

The persistence or absences of primitive reflexes are used widely in the diagnosis of neuropathology. As mentioned above, with postnatal development, primitive reflexes are not eliminated but repressed, and can be ‘released’ under particular circumstances.

For instance, the development of the grasp response in an adult patient known to have a frontal lobe tumour or infarct can be an early indication of the extension of that lesion (Schott and Rossor, 2003). Interestingly, the infantile snout reflex, which causes the lips to be pursed when they are tapped, is released in adults with alcohol dependency, and can be abolished by the drug Acamprosate, used to reduce the risk of relapse into alcohol dependency. Thus, reflex release can be abolished also with drug therapy, as has been found also in the case of Parkinsonism, where treatment with Levodopa can lead to a resolution of the released primitive acoustic-palpebral reflex (Guzik et al., 2007).

The absence of primitive reflex suppression can lead to the retention of inappropriate reflexive motions later in life. These have been shown to interfere with voluntary motor behaviour, and result in pathologies of development (Taylor et al., 2004). For instance, the persistence of the asymmetric tonic neck reflex, which is triggered by the vestibular system, will continue to influence limb movements every time the head is turned. As such, writing becomes difficult as the hand and arm involuntarily extend as the head turns towards the hand. For further details see Taylor et al. (2004.

Significantly, such findings show that the muscular synergies associated with infantile primary reflexes occur as fixed parcellations, so that the full sequence of reflexive limb movements recur when the reflexes are triggered, and provides the hallmark of a primitive reflex, which distinguishes it from motor primitives that can occur singly (see below)

6.7.3.3 Habituation of Primitive Reflexes

The complex nature of primitive reflexes is illustrated by the observation that all reflexes, including the patellar reflex, suffer habituation, where there is a gradual decline in response to the point of its annulment when the reflexes are repeatedly stimulated (Prechtl, 1958; Hollis, 1971; Zametkin et al., 1979; Mata-Otero, 2006). Studies of fetal behavior using ultrasound monitoring have shown that the rooting reflex is not self-activated when the fetus touches its own face (Christie and Slaughter, 2007), and that muscle stretch reflexes are abolished when the ventral or dorsal roots were cut, showing that reflexes are not devoid of central nervous system control (Sherrington, 1906). As such, there appears to be no such thing as an enduring pure, input-output reflex in the normal human motor system.

Although it is well known that brain stem and spinal neurons are involved in primitive reflexes, the anatomical localization of their source has remained largely elusive despite the availability of structural and functional imaging systems (Schott and Rossor, 2003). It may be, as in the case of attention, that primitive reflexes are not a purely physiological phenomenon, but have a top-down, origin. This view derives from the observation (made above) that all reflexes are subject to habituation, which has its origins in learning to recognize harmless repeated stimuli. Once the stimulus is found to be benign or irrelevant, responses weaken and ultimately cease (van Heteren et al., 2001).

6.7.4 Motor Primitives

The term motor primitive is defined as a set of dynamic force fields that are voluntarily generated usually by the action of the coupled activity of a number of muscles. They are not stimulus bound like, for instance, the rooting reflex mentioned previously. In this respect they are not restricted to early motor activity, but are also part of the volitional adult motor system, and thought to be learned (see below). Reiterated more formally, the brain has been shown to mediate the control of complex movements through a flexible combination of motor primitives, where each primitive is an element of computation in a sensorimotor map that transforms desired limb trajectories into motor commands (Flash and Hochner, 2005; also see §6.7.4.1.

Shadmehr and Holcomb (1997) have shown that the acquisition of a motor skill involves learning an internal model of the dynamics of that task. Once the task is learned, usually through the engagement of frontal cortex, the brain recruits new brain regions to perform the task; there is a shift from the prefrontal region to the premotor, posterior parietal and cerebellar cortical structures. Fourier analysis of data from subjects learning new motor skills showed that they gradually modified their movements by adding higher order harmonics to the fundamental harmonic of the movement established early in practice (Martinuik and Romanow, 1983).

The notion of motor primitives was inspired by the observation that the electrical activation of specific neurons in the spinal cord of 'spinalized frogs' (where the optic tectum is isolated from the spinal cord to eliminate efferent projections from the brainstem and higher regions) elicits goal-directed multi-joint movements, and that the electrical activation of supra-spinal neurons (in higher regions) of intact frogs co-activate, and thus superimpose, what are inferred to be multiple motor primitives in an additive fashion, resulting in a larger repertoire of meaningful movements.

On a physiological basis, the spinal motor primitives have been interpreted as sets of fixed duration motor unit bursts that can be assembled by the motor system to compose voluntary actions (Bizzi et al., 1995; Hart and Giszter, 2004). These motor neuron burst patterns are distinct from each other and are reused in multiple behaviours.

When comparing motor burst patterns in spinalized frogs with those in brainstem frogs, it was found that the influence of the brainstem was to refine the burst patterns and improve the smoothness of the movements while reducing muscle co-contractions. It is also found that when stroke patients regain better control of their affected limb, the number of sub-movements decreases and their temporal overlap increases, giving smoother trajectories (Berthier et al., 2005).

6.7.4.1 Learning New Motor Primitives

A distinction between primitive reflexes and motor primitives is that there is a fixed native repertoire of the former while the latter are learned, with there being no apparent upper limit on their number. Graziano (2006) notes that the mapping from cortex to muscle is not fixed but is constantly reorganized in response to higher and lower-level requirements.

Work on adults by Thoroughman and Shadmehr (2000) have gone some way towards the mathematical description of new motor primitives that were created when subjects exerted novel forces onto a robot arm. These forces were generated in the subject’s arm while he tried to counter the robot arm’s resistance to the subject’s arm-motion in a pre-specified direction.

In the experiment, the robot arm exerted a force at right angles to the direction of the movement of the subject's arm, so as to convert the desired rectilinear motion into a spiral. As the subject learned to counter the forces in order to continue to move his arm in the target-direction, new motor primitives were generated.

From an analysis of the forces and robot arm trajectories, Thoroughman and Shadmehr (2000) were able to provide a mathematical description of both existing motor primitives and the new ones involved in the subjects' control of arm movement. For further details see Ghahramani (2000). Other examples of the generation of new motor primitives are given in Sakai et al., 2003 and Sosnik et al., 2004. An account of systems for the detection and classification of human motor primitives is given by Jenkins and Mataric (2003).

6.7.4.2 Motor Deprivation as Evidence for Motor Learning

There exist only a limited set of experiments on motor deprivation, since they are difficult to implement and interpret. However, work by Walton et al. (1992) on neonatal rats is among the exceptions. The authors used the system of tail suspension to study the effects of simulated weightlessness in adult rats. In the arrangement used, the neonatal rats were suspended by their tails using an elastic band and a swivel, so that their hindlimbs were raised off the ground, and yet they were relatively free to move about using their forelimbs.

The authors report that motor performance following a period of hind limb suspension, assessed through their competence in walking and swimming, could be significantly impaired after only one day of suspension; that the severity and duration of impairment was related to the age at which the animals were first suspended and on the duration of suspension. The authors concluded that there was a critical period when rats are most sensitive to hind limb unloading. In some cases, the lack of early motor activity caused walking impairment that endured into adulthood.

The authors elaborated upon their earlier investigation of weightlessness by having two litters of rats of different ages spend 9 days in space (Walton et al., 1997). They confirmed their earlier finding, that weightless use-deprivation resulted in impaired function, and weightlessness at earlier age had a greater effect on the subsequent walking and swimming abilities than at a later age (Post natal ages P7-P16 as opposed to P15-P24).

Direct evidence that motor deprivation results in atrophy of the supporting nervous tissue comes from a study by Langer et al. (2012) on right-handed subjects with injury of the right upper extremity whose treatment required limb immobilizing for at least 14 days. Using MRI examination, the authors determined the cortical thicknesses of the left and right sensorimotor cortices before and after the immobilization (an average of 16 days apart), and found there was a decrease in thickness in the left primary motor and somatosensory areas. In addition, the motor skills of the left (non-injured) hand improved, and could be related to the increased cortical thickness of the right motor cortex. They concluded that arm immobilization induces a rapid reorganization of the sensorimotor system, and confirmed the presence of motor learning.

It may seem superfluous to state that the capacity to play a musical instrument is learned. However, the evidence to support this claim demonstrates, not least, that what may be expected in the neurological domain in the case of musical practice is indeed the case. The literature on musical training, which inevitably involves motor activity, shows that players of string instruments have a larger cortical representation of the digits of the left hand than of the right hand. This correlation was stronger among those who started their training earlier (Elbert et al., 1995). Further, Bengtsson et al. (2005) reported that there was a greater myelination in the cortico-spinal tract of professional musicians than non-musicians, and that the difference was related to the hours of music practice in childhood (before the age of 11).

Such findings can be interpreted with reference to the work of Purves (1994) on the role of activity in the mechanisms underlying the development of nervous tissue. He found that trophic interactions, where there is neural activity through a mutual exchange of signals between cells, results in cell survival and neuritic growth. However, the deprivation of activity, either through the severance of axonal inputs or immobilisation, results in synaptic retraction from the surface of the cell and dendritic shrinkage. Conversely, an enhancement of neural activity causes additional synapses to be made, and dendritic growth. Purves (1994) noted that at a macroscopic level, activity through trophic interactions must be reflected in the growth and ultimate size of maps, modules and the brain itself. Trophic interactions are, clearly, manifestations of knowledge acquisition and the experiments described provide support for the view that motor primitives are learned (see §3.6).

6.8 Summary

Following the Behaviourists’ proposal that motor action be regarded as a stimulus-response chain, where there is no overall central top-down controller, and its refutation by, among others, Lashley in favour of the existence of an overall controller, the present work has provided evidence to support the view that mass apprehension through motor behaviour is learned, and the human repertoire of motor activities should not be regarded as being given innately through a chaining of deterministic input-output functions. The issue has been addressed at several levels.

6.8.1 The Motor System Does Not Comprise Deterministic Input-Output Chains

Primitive reflexes appear to be pre-specified, but they do not manifest as simple input-output functions: they all habituate; even the patellar reflex. As such, there can be no such thing as a deterministic closed reflex loop in the mammalian motor system (see §6.7.3.3).

6.8.2 Motor Primitives Are Learned

There is detailed *behavioural evidence* for the generation of new primitive reflexes in the work by Thoroughman and Shadmehr (2000), Sakai et al. (2003) and Sosnik et al. (2004). Furthermore, tail suspension experiments in Norwegian rats (Walton et al., 1992; Walton et al., 1997) confirm these findings, There is indirect evidence of learning from *cortical neuroimaging* in the case of subjects who were deprived of motor activity through limb immobilization (Langer et al., 2012). This is supported by evidence also from neuroimaging experiments on musicians by Elbert et al. (1995) and Bengtsson et al. (2005). These experiments also indicate the existence of a critical period associated with motor learning.

6.8.3 Relation Between Motor Primitives and Primitive Reflexes

A primitive reflex, for instance, the palmar grasp reflex, is composed of a fixed muscle synergy: a single stereotypical motor action in which the infant's fingers and palm will close around an object placed in its palm. As development proceeds, the reflex suffers inhibition during normal development and is repressed thereafter.

In cases of (a) primitive reflex retention beyond their normal period, or (b) their release, the retained or re-emergent reflexes are found to remain intact as a fixed muscle synergy (the retention of the asymmetric tonic neck reflex was described earlier).

However, the palmar grasp, for instance, can be learned during development through the acquisition of the constituent motor primitives, and indeed varied by employing only a subset of the muscle synergy required for the palmar grasp. But the primitive reflex cannot be varied; it results from a single, fixed muscle synergy (Mussa-Ivaldi and Bizzi, 1997).

Now, if voluntary motor activity were composed of primitive reflexes, then the smallest element in the motor primitive repertoire would be a primitive reflex. This is manifestly not the case: voluntary motor activity can generate, through learning, the individual components of all primitive reflexes. This could not be the case if motor primitives were composed of primitive reflexes.

In accord with this view is the observation by Konczak (2005):

> … no theory of motor development has attempted to link motor primitives and primitive reflexes. Based on current developmental and neurophysiological research it seems not warranted to claim that the early primitive reflexive motor patterns somehow need to be inhibited at a neuronal level to allow for the emergence of motor primitives. That is, a viewpoint that propagates early motor development as a transitory period from primitive reflexes to motor primitives is unwarranted.

Capute et al. (1982), who studied the behaviour of infants from birth till the age of one year, as they progressively developed volitional motor primitives whilst their primitive reflexes were being inhibited, anticipated the above observation. In particular, the study involved observing the infants as they used motor activity for moving from the prone to the supine position and back again.

The authors found that several muscular actions present in the infants' primitive reflexes were required for the construction of the motor activity necessary for the rolling actions studied, but that isolated reflexes were not seen to determine individual motor primitives.

6.9 Conclusions

Primitive reflexes do appear to be innately structured patterns of motor behaviour that arise spontaneously during gestation. Their presence can be accounted for in functional terms. For instance, they are related to the birth process and the structuring of the early sensory system. They bear little relation to the motor primitives out of which subsequent motor behaviour is constituted. Many lines of evidence have been provided in this section which show that human movement is composed of motor primitives, and that they are acquired, and not derived from primitive reflexes. As such, the haptic activity leading to the acquisition of the capacity for the apprehension of mass may be regarded as being learned and not given innately, and, indeed leads to the overall finding of this chapter that the capacity for the apprehension of the fundamental dimension of mass is acquired through learning.

The underlying structures of the motor system will not be addressed any further in the current work. For additional information, the reader is directed to the following literature. For instance, there are articles on the control of human movement by Winter (1990); Ghahramani (2000); Graziano et al. (2002) and Graziano (2006). Work on the neural correlates of motor memory has been published by Shadmehr and Holcomb (1997), and that on (a) the plasticity and (b) development of motor learning in rats are presented in Xu et al. (2009); Yang et al. (2009) and by Robinson and Kleven (2005) respectively. Information on the neural correlates of motor adaptation in the (a) primary and (b) supplementary motor cortices in monkeys is presented by Li et al. (2001) and Padoa-Schioppa et al. (2004) respectively.

7

AUDITORY PERCEPTION OF LENGTH

7.0 Introduction

Human auditory capabilities in combination with principles of physical acoustics are analysed in this section with a view to addressing the issue of whether the capacity for the apprehension of sound source distance and direction are native or derived.

As will emerge through this work, human auditory capacity is inferior to those of human haptics and vision in respect to object or event localization, and results in a dynamic auditory compliance as manifests in the ventriloquism effect (see §7.1.3). This poorer resolution also causes neural plasticity in the auditory domain to comply with localizations determined by sensory modalities with greater spatial acuity.

Neurophysiological structures supporting sensory input are generally in the form of topographic maps that preserve the spatial organization of receptors in the many sensory epithelia and their corresponding targets in the central nervous system (§3.7).

Objects in the visual field are localized by focusing the light scattered by them onto the retina by use of the eye's lens, and a retinotopic representation of visual space is generally maintained within the central targets of the nervous system involved in visual processing (*Neuroscience*, 1997, p. 203). Such topographic representations are thought to provide an efficient organization for localized analysis of spatial features via the plentiful short-range connections generally found in nervous tissue (Laughlin and Sejnowski, 2003).

The spatial layout in the various nuclei of the auditory system generally reflects the tonotopic organisation of the basilar membrane of the inner ear (see, for instance, Evans, 1982). There are, thus, tonotopic arrays of neurons in most auditory nuclei that respond maximally when presented with their individual best frequency, and spatially adjacent neurons respond best to similar frequencies (see, for instance, *Neuroscience,* 1997, Ch. 12).

Auditory analysis takes place in the temporal domain, and generally consists in the fine-grain segmentation of sound frequency and amplitude into their temporal primitives, as phonemes in speech analysis or other sequences characteristic of particular events such as the breaking of a twig on the ground or the rustle of the wind in the trees (see chapters 8 and 9).

A nucleus deviating from the general tonotopic organization found in the auditory system is the superior colliculus in the mid brain. It contains a stack of 3 adjacent layers of neurons responsive to audition, vision and touch that form topographic maps that are in register with the surrounding world in retinotopic coordinates. Thus, neurons in the auditory layer of the superior colliculus, that encode directions in auditory space, are in register with tactile and visual spatial maps. This nucleus is widely connected to other brain regions (see Konishi, 1993; Stein and Meredith, 1994)[15]. Auditory maps also exist in intraparietal cortex (Colby and Goldberg, 1999). Graziano et al. (1999) have discovered neuronal maps representing the distance of nearby sounds in the ventral premotor cortex, a region of frontal cortex (see below).

Audition does provide some autonomous and significant secondary information within a multimodal context about space and distance. In association with haptic and visual cues, audition can aid range finding because it has some degree of directional acuity. This, in conjunction with auditory prior knowledge, can aid the detection of auditory events in space not accessible to vision and touch, to which these latter senses may be then directed for more precise distance determination. An example of the use of prior knowledge

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[15] N.B. Many publications use terms like “spatial localization” and “sound source location” loosely, not distinguishing between the source direction and its distance from the listener. While much work has been done on auditory direction determination, range finding is generally poor in non-echolocating species, and is less frequently addressed in the literature.

combined with auditory directional acuity in object localization is provided by the case of the sound of a dropped coin landing behind the subject (see also §7.3).

Sound waves that the human auditory system can respond to have wavelengths between an inch and several feet (about a foot at 1kHz), and are composed of traveling waves of temporal variations in air pressure that are some six orders of magnitude larger than optical wavelengths, and are therefore unsuitable for precise distance determination.

However, sound waves are vectorially additive, like electromagnetic radiation, so when a region of air compression encounters another undergoing equal rarefaction, they can annul one another. As such, sound waves scattered by objects can suffer constructive and destructive interference. In general, sound waves generated by external sources are diffracted by their interactions with the head and body, and significantly by the pinna (ear-flap), which plays an important role in sound direction perception.

Sound is also reflected and absorbed by body tissue and objects in the environment, with the absorption coefficient depending on frequency. These features of sound waves allow them to be utilized for the estimation of both the directions and distances of sound sources.

The human auditory system has a dynamic range for the detection of sound pressure variations that spans twelve decades, a sub-millisecond temporal resolution (~ 10 μs in owls (Konishi, 1993)) and a capacity to continuously resolve complex sounds into their amplitude and frequency components. Furthermore, for frequencies below ~ 1500 Hz, the auditory system can detect the phase difference between sounds incident upon the two ears. However, the medium through which it propagates (air) is quite substantial, having a density of ~ 1.2 kg per cubic meter, and is subject to motion and variations in its physical characteristics arising from local changes in pressure and temperature, making sound wave propagation deviate from being rectilinear.

Human auditory capacities may be understood through an examination of the human auditory apparatus. It is here that a subtle temporal analysis is made of the sound pressure variations in air. These pressure variations or vibrations are detected by the tympanic membrane and conveyed to the cochlea in the inner ear through a chain of *ossicles* (see, for instance, Evans, 1982, pp. 251-306). In the cochlea, a Fourier analysis is carried out of the vibrations by the basilar membrane, which is then converted into a sequence of action potentials by the inner hair cells, located progressively at different sites along the length of the basilar membrane. Their outputs are conveyed via the auditory nerve to the generally tonotopically organized intervening processing nuclei to auditory cortex (for functional and anatomical details, see, for instance, Konishi, 1993; Konishi, 2000).

The large dynamic range of pressure variations (sound loudness) supported by the auditory system is augmented by muscles in the inner ear[16] as well as by top-down attentional influences that alter the response properties of the outer hair cells for specific frequencies (Xiao and Suga, 2002).

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[16] The tensor tympani and the stapedius muscles act to increase the stiffness of middle ear system and thereby decrease the transmission of potentially damaging lower frequency sounds while increasing the dynamical range of the ear (Evans, 1982, pp. 259-60).

7.1 Localization of Sound Direction

The current section addresses the apprehension of distance as a vector quantity, so both distance and direction with regard to auditory localization are addressed herein. These are generally separated in the literature because, as will become clear, there exist sound principles in physical acoustics that the auditory system makes use of for direction discrimination, whereas the nature of physical acoustics in relation to the human auditory system largely confounds distance determination. The extraction of information about distance to the sound source is largely multisensory, and dependent on prior knowledge. It will be demonstrated that both auditory direction and distance apprehension are learned.

7.1.1 Horizontal Plane

Lord Rayleigh's work at the turn of the 19th century on sound direction localization (Rayleigh, 1907) is referred to as his Duplex Theory. This theory attempts to account for the human capacity to determine the direction of a sound source according to interaural difference cues.

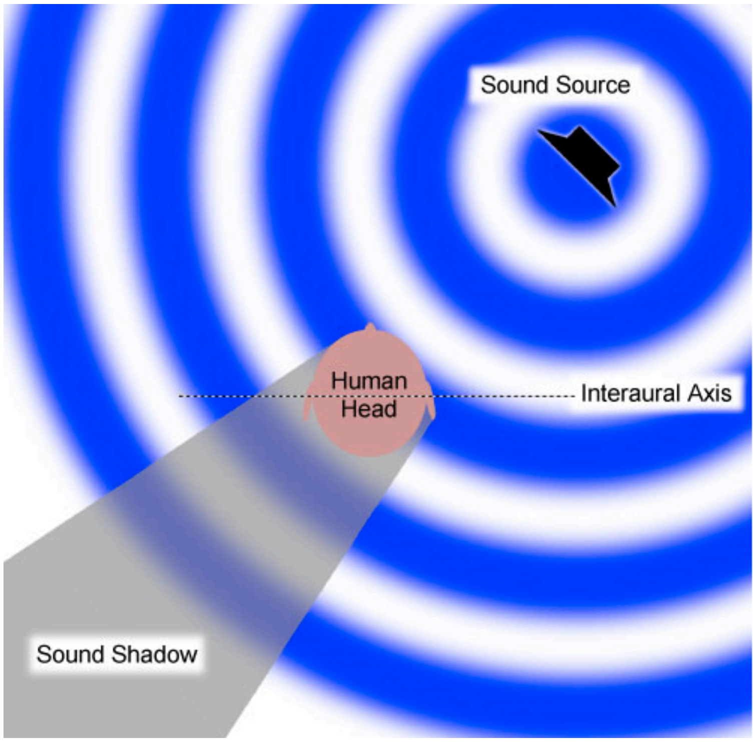

Fig. 7.1 A sketch showing the shadowing of a sound source by the head and a depiction of interaural phase difference. The circles mark contours of constant phase. (Source: Perrett, 2009)

Rayleigh appreciated that when a sound (of a sufficiently short wavelength) was presented from the side, the listener's head would interrupt the path of the sound source to the far ear, and result in an interaural sound pressure level difference (ILD) by an amount dependent on sound absorption by the head (Fig. 7.1). The shadowing would depend on the wavelength of the sound; high frequencies are absorbed more in body tissue than low frequencies (and sound waves of a wavelength of a size equivalent to the human head or larger are mostly scattered by it). For adults, there is a 35 dB[17] difference in sound pressure level (SPL) at 10

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[17] The Decibel (dB) is a logarithmic unit used to measure the ratio of sound levels. The difference in decibels between two sound pressures P1 and P2 is defined to be 20 log (P2/P1). In its application to hearing, setting P1 to being at the threshold of hearing, the sound pressure level for a sound that is twice as loud will have a difference of 6 dB.

kHz between the two ears, and a 20 dB difference at 4 kHz, when the sound source is on the interaural axis (see Fig 7.2).

However, for frequencies below ~ 1 kHz, the wavelength is larger than the size of the head, and sound can travel around it to result in little difference in the SPL between the ears. Nevertheless, directional differences in sound sources may be detected at low frequencies. This ability is attributed to the human capacity for the detection of interaural phase difference (IPD) of the sound waves arriving at the two ears.

Rayleigh noted that when two tuning forks, constructed so that they vibrate at slightly different frequencies, were presented, one close to each ear, the mistuned forks produced a progressive phase difference. This had the effect of producing the sensation of an auditory image of the source that moved back and forth in the plane of the azimuth.

Thus, it was not the difference in time of arrival of the two sounds, but their phase difference that was being detected by the auditory system to evaluate sound source direction. He also noted that this sensitivity to auditory phase difference diminished with increases in frequency, and had an upper frequency limit that is now thought to be 1000-1500 Hz.

The Duplex theory, mentioned earlier, maintains that the interaural sound pressure difference combined with the difference in the phase of the sound waves enable sound direction localization in the horizontal plane.

This view is now generally accepted, and accounts satisfactorily for results obtained from sound localization experiments in the horizontal plane at both low and high frequencies (Middlebrooks and Green, 1991). At high frequencies, as mentioned earlier, sound shadowing plays a significant role in direction determination. It is suggested that at low frequencies, neuronal action potentials in the auditory nerve phase lock, with the auditory input frequency, and a comparison of phase at different frequencies is made in the brain stem (Wightman and Kistler, 1997).

The mechanism has also been explored in barn owls showing similar results, although barn owls, who display the greatest sound localization acuity among vertebrates, have been shown to exhibit sensitivity to interaural phase differences at frequencies even greater than 7 kHz (Konishi, 1993).

The work on humans predicts that localization in the horizontal plane would be poor for the frequency range 1500-3000 Hz because both ILD and IPD would not allow angular discrimination. This is because there is a small ILD at low frequencies, and IPD is restricted to frequencies below about 1 kHz.

Furthermore, a phase difference of up to only 180 degrees can be detected between the sounds arriving at the two ears. As indicated earlier, for greater differences in phase angles there is an ambiguity between phase advances and lags, and it is thought that the human auditory system rejects such ambiguous information. Worthy of note is the fact that in addition to the tonotopic organization of auditory cortex in one direction, there exists at right angles to this direction strips of aural dominance, reminiscent of ocular dominance columns found in striate cortex (see §3.5.4), that might contribute to auditory sensitivity to binaural cues (Pickles, 1982, p. 202).

There exist neurons in cat primary auditory cortex whose activity patterns are found to correlate with the azimuth of sound targets. The units recorded showed sharpened spatial tuning when the subjects are engaged in behavioural tasks compared to when the cats are not being attentive (Lee and Middlebrooks, 2011). Indeed, neurophysiological studies in a range of species have shown that neurons throughout the central auditory pathway are tuned to the direction of a sound source (Knudsen, 1983).

Work by Woods et al. (2006) showed that most neurons in macaque auditory cortex showed direction preferences, with the caudal belt fields having the greatest directional acuity, primary auditory cortex showing intermediate and the rostral and middle medial the least directional tuning. Work in humans (reviewed by Salminen et al., 2012) is even less suggestive of the existence of well-defined auditory space maps in auditory cortex, and attempts at finding systematic topographic mapping of auditory space in monkey or cat cortex has consistently failed (Woods et al., 2006).

Salminen et al. (2012) note:

> It seems clear that the representation of auditory space in cortex is not formed by a set of static feature detectors but rather is an adaptive system sensitive to context.

This view, compounded from a neurophysiological study of auditory cortex, is consistent with the findings of the current analysis of physical acoustics, experimental psychology and psychophysics (see below).

7.1.2 Localization of Elevation

Were the outer ears symmetrical about the interaural axis, sound sources at different elevations on the median plane or on the ‘cone of confusion’ would be indistinguishable (see Fig.7.2). This is because at such locations the source would be equidistant from both ears. Work by Batteau and Plant (1962) and Batteau (1967) show that this is clearly not the case, and that the convoluted surfaces of the pinna provides spatial cues of elevation through interacting differently with sound sources at different heights, even if the sources are equidistant from the two ears. Furthermore, such cues would not need binaural hearing.

Work by Fisher and Freedman (1968) confirmed this prediction in their ear modification and occlusion experiments. On the insertion of a 10 cm tube in the ear canal, bypassing the pinna, led to a loss of localization ability in the vertical plane. Similar findings, emphasising the importance of the pinna, are reported when sounds are presented using headphones.

In general headphones create the sensation of hearing the broadcast sound inside the head. However, when the broadcast microphones are inserted in a dummy head having pinnae, the sounds heard on the headphone are dramatically projected into space (Evans, 1982, p. 330).

Middlebrooks and Green (1991) observe that current theories interpret the pinna as producing changes in the spectrum of the sound source that reaches the tympanic membrane. The influence of the pinna is to create multiple paths to the ear canal, among them a direct path and one reflection from the *cavum concha* of the pinna.

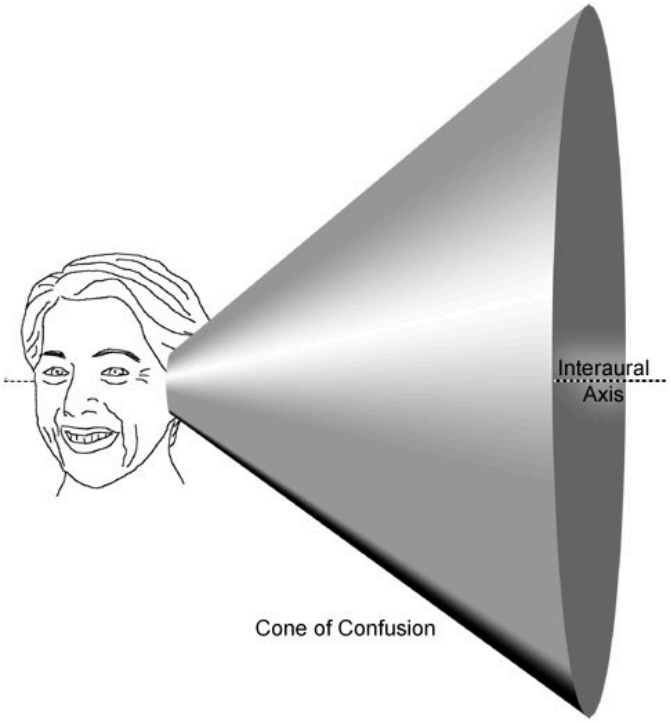

Fig. 7.2 There is no phase difference between sound sources at elevations that maintain the same distance along the interaural axis on the curved surface of the ‘cone of confusion’ and the two ears. (Source: Perrett, 2009)

They state that the addition of the direct signal, with a delayed (reflected) version of the same signal, produces a spectrum containing a characteristic pattern of peaks and notches, and the length of the reflected path varies with elevation of the sound source.

Such spectral shape-cues do not require an interaural comparison, and would account for the observation that localization of elevation can be retained without binaural input. It is concluded that spectral shape-cues are the major factor in sound localization in elevation.

However, it is found that spatial acuity is frequency dependent, and frequencies above about 4 kHz seem to be particularly significant. The pinna shape-cue, and its efficiency for elevation-sensing is found to be dependent on pinna size, with a downward shift in viable frequency being associated with increasing physical size of the subject (Middlebrooks et al. 1989).

2-D Spherical Localization

Middlebrooks and Green (1991) summarized work on the accuracy of sound direction localization in two-dimensional space surrounding the listener. The two dimensions are elevation and azimuth. A broadband spectrum was used to resolve ambiguities that are present in narrowband spectra, and the sound source was moved freely in both the horizontal and vertical directions over a spherical surface of 1.2 m in radius centered on the subject's head.

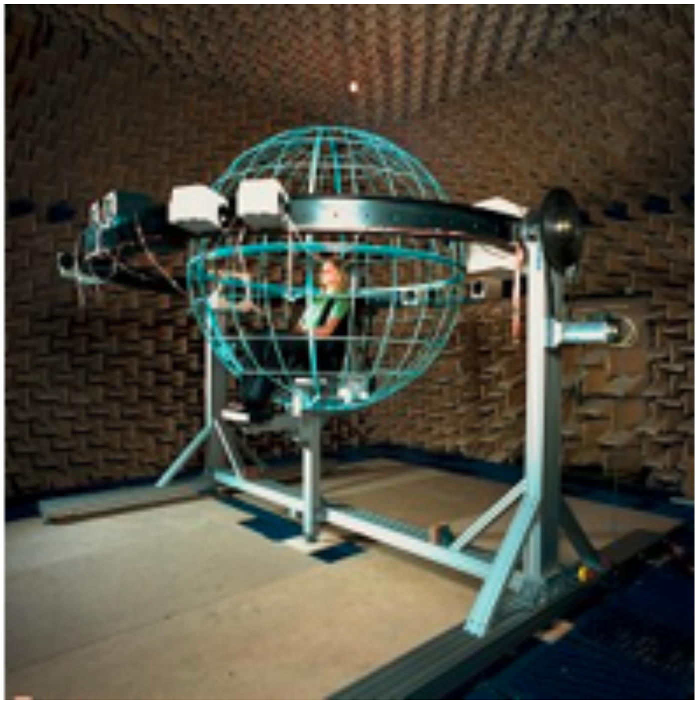

Fig. 7.3 Apparatus used at the University of Southampton Institute of Sound and Vibration Research to investigate sound direction localization. (Source: Virtual Acoustics and Audio Engineering, University of Southampton)

The localization errors were smallest for stimuli directly in front, and increased at more peripheral locations. The smallest errors were about 2° in azimuth and about 3.5° in elevation, increasing to as much as 20° at some rear locations. By comparison, human visual acuity is ~ 0.35 arc-minute, highlighting a significant factor for visual dominance over audition.

The well-known spatial ventriloquism effect, where the perception of auditory space is modulated by concurrently presented visual input, provides an example of such visual dominance. When auditory and visual stimuli occur simultaneously at discrepant spatial locations, the sound is typically mislocalized towards the site of the visual event (Bertelson and Radeau, 1981). This feature is an illusion created by poor auditory spatial resolution rather than being an example of neuronal plasticity, although it has been shown that early experience is responsible for the formation of the visual-auditory coupling between stimulus source directions, and that this generally found accord can be decoupled by altering the developmental conditions (see §7.4.2).

7.2 Auditory Length Perception

7.2.1 Far-Field Distance Determination

The resolution for sound intensity discrimination in humans for noise burst stimuli is about 1 dB. The review by Zahorik et al. (2005) points out that for a stationary source in environments free from physical objects capable of sound reflection, the sound pressure level varies inversely with distance. As mentioned earlier, there is a 6 dB loss in sound pressure for each doubling of distance. The corresponding resolution in distance determination, neglecting the frequency dependence of the sound absorption coefficient, would predict a theoretical error of 10%, i. e., an error of 1 m when the sound source is 10 m away. However, this presupposes that initial conditions are known. As such, only distance ratios may be assessed rather than there being any capability for absolute distance determination. And indeed, distance ratio assessments would depend on other factors like the human capacity to retain a memory of sound amplitude for purposes of making the comparison.

Experiment shows that listeners to speech sounds (whose variations with distance all listeners studied will have had prior knowledge of) in anechoic chambers underestimated the distances, with some experimenters reporting that up to a 21 dB difference is needed in the apparent sound pressure level to perceive a doubling of distance (instead of the theoretical 6 dB). However all listeners showed a monotonic increase in distance estimation with decreases in sound pressure level (Zahorik, 1996; Zahorik et al., 2005).

It is worth noting that the theoretical account applies in the free-field for point sources of sound that are at large distances from the listener. In the near-field, where sound distances are less than one wavelength (and wave fronts cannot be approximated to be planes), sound pressure levels decline exponentially with distance. Accurate distance estimations would have to incorporate all such knowledge.

Use of the received sound intensity to gauge the distance of its source is confounded by the fact that the sound might be soft with the source close by, or soft because it has travelled some distance and lost amplitude in its dispersal through the atmosphere.

All natural sounds generally contain information about their sources, from which they cannot be readily separated. As such, some inference can be made about the distance they will have traversed. This is illustrated by the difference between low amplitude sounds received at the ears of a listener of someone shouting from a great distance, as opposed the soft sound of a whisper close to. Here again a diversity of prior knowledge must participate in auditory distance estimation. The early experiment by Coleman (1962) supports this view.

7.2.2 Coleman's Experiment

Clearly, sounds in an enclosure like a room will activate responses from all physical surfaces within the containment, and have the effect of modulating the sounds received at the ears. In order to minimise these modulations, work has been done in 'free-space', notably that reported by Coleman (1962; 1963), where the subjects' distance judgements of unfamiliar sounds were studied. The experiments were carried out after a heavy fall of snow on a frozen lake in Canada, to attenuate the effects of ground reflections.

Coleman observed that the loudness of the received sound is dependent on both the intensity of the stimulus at its source and the distance of the source from the subject. Furthermore, the frequency spectrum signifies the timbre of the stimulus as well as the distance of the source, and that accurate distance judgements should not be possible upon initial exposure to unfamiliar sounds.

Indeed, it was found that distance judgements on the first trial in Coleman's experiment were unrelated to actual distances. With further trials valid distance judgements became possible. This indicates that learning was involved in making distance judgements and that the subject cannot, in general, make the distinction between distance change with changes in loudness and timbre.

Coleman (1962) tabulated the error of distance judgement as a function of trial number, and showed that the initial response was heavily weighted towards the near end of the speaker array he used, regardless of the true location of the source. By the eleventh trial, localization was more accurate, and the errors generally approach zero with further trials.

Investigations of auditory localization in the azimuth under the conditions of these studies did not yield any evidence of a comparable dependence on familiarity with the stimulus. Initial judgements here were approximately as accurate as later judgements. This finding is consistent with the analysis provided herein that the human auditory system is capable of determining the azimuth of a broadband source without its prior knowledge.

In his subsequent paper reporting elaborations on the original experiments, Coleman (1963) surmised that the intensity versus frequency spectrum is useful only as a relative cue to distance since both these stimulus-correlates may change without any accompanying distance change.

He concluded that the accuracy of distance judgements of the first stimulus presentation was unrelated to the actual location of the source, and that the subjects could not distinguish between distance change and loudness or timbre change. He observed that it is this very lack of unique ‘local signs’ for distance that makes the distance localization of unfamiliar sounds so poor.

7.2.3 Distance Cues in Enclosed Spaces

In environments with sound-reflecting surfaces, the ratio of energy reaching a listener directly (without being reflected) to that arising from reverberations in the room varies systematically with distance. This direct-to-reverberant energy ratio decreases with distance from the subject, and is considered to provide absolute distance information because the reverberation energy is thought to be independent of distance.

This view has been confirmed using virtual sources (Bronkhorst and Houtgast, 1999; Kopčo et al., 2012, see below). King (1999) also observes that distance perception is dependent both on the listener's adaption to the sound source and the acoustical properties of the room. More recent work by Vesa (2009), who studied distance determination in rooms using speech sounds, while treating the task as a learning problem, also found that experience improved accuracy.

7.2.4 *Near-Field Distance Representation in Cortex*

Although neurons responsive to auditory distance cues in the far-field have not been identified in human auditory cortex (Salminen et al., 2012), there is compelling evidence for their existence in the near-field (see below). Their absence in the far-field may be understood in terms of the complexities, previously mentioned, in auditory distance determination in the far-field.

The early work by Graziano et al. (1999) using microelectrodes to map cortical regions in macaques suggested the existence of such near-field distance neurons in ventral premotor cortex, a region of frontal cortex, where individual multisensory neurons represent sound source distance within a range of up to 30 cm around the head. As in the case of gnostic neurons that respond to features such as paws and faces present in the visual field (mentioned in §3.6.8) similar neurons have been reported that respond to learned sound tokens in auditory cortex (see chapter 8). It is likely that the near-field distance neurons obtain their response properties through a process of learning.

More recently Kopčo et al. (2012) have identified, using fMRI, collections of similar distance-encoding neurons in humans for the near-field, within a range of up to 1 m around the head. Virtual sound sources were used to simulate distance using direct-to-reverberation intensity ratio cues. The virtual sources were simulated to lie at varying distances along the interaural axis, and were all presented at the same sound pressure level, thereby removing intensity cues to ensure that the neurons encoded just distance.

The space around the head and upper body is known to be represented by multimodal neurons, also located in the ventral intraparietal area and a poly-sensory zone in the precentral gyrus (Ladavas and Serino, 2008). These neurons respond to objects touching, near or looming toward the body surface. Electrical stimulation of these cortical areas evokes defensive behaviours, for instance, withdrawing or blocking movements, and it has been suggested that the emphasis of these cortical areas is on the construction of a margin of safety around the body (Graziano and Cooke, 2006). These peri-personal space representations are known to be highly plastic as a function of experience, and tool use to act in far-space can drive an elongation of peri-personal space representation (Ladavas and Serino, 2008).

From the analysis presented thus far, direct-to-reverberation intensity ratio cues coupled with sound intensity shadowing by the head seem to be the significant parameters for auditory distance discrimination. Head shadowing effects may be expected to vary with sound frequency composition, and the direct-to-reverberation intensity ratio to depend on the particular environment. As such, successful distance discrimination is likely to result from prior knowledge of these variations (see below). The finding that there exist near-field distance representing gnostic neurons is consistent with the proposal that the capacity for auditory near-field distance discrimination is not native since such neurons are the brain's mode of representing learned features (see §3.6.8).

7.3 Prior Knowledge and Neural Plasticity

Competence in sound direction determination must depend on implicit knowledge of the age-dependent (i.e., size-dependent) sound absorption properties of the head and sound scattering by the pinna, and their variations with sound frequency (see below). There is a plethora of other prior knowledge that must participate in auditory distance estimation, some of which will be elaborated upon below.

7.3.1 *Distance Perception and Prior Knowledge*.

Human auditory distance perception relies for its function on incomplete information from the environment. Distance information is generally obtained through association rather than directly as in the case of vision, because human audition generally relies on one or more distance indicators that are inherently imprecise.

The medium through which sound is propagated and the sound sources and structures encountered in the environment that scatter sound vary. Furthermore, the human auditory system has significant limitations in respect of its capacity for range finding. As mentioned earlier, these factors account for the subserviant role played by audition to vision and haptics in the process of multimodal distance determination.

Physical acoustics shows that the waveform of a sound received at a point depends on the waveform emitted by the source, which in turn depends on source geometry. The source could be the cone in a loudspeaker or a point source as are used in acoustic laboratories. The emitted sound and its progress through the atmosphere will differ in the two cases.

In the context of common human experience over evolutionary time, the source might be a stone dropped into water or the sounds of a baby beginning to cry. The task of auditory distance determination is aided by the contents of the signature of the source. The sounds emanating from a baby beginning to cry contain some information of its probable location and its source. The medium through which the sound travels also imposes its characteristics upon the sounds received by the listener, with high frequencies being absorbed more than low ones, once again providing the experienced listener with information that might aid source distance determination.

The human auditory system cannot rely on the equivalent of optical stereopsis because there is neither auditory lens, nor the equivalent of the retina in the human auditory system to facilitate source localization. Auditory analysis is carried out significantly in the temporal rather than in the spatial domain.

Furthermore, acoustic wavelengths are large, and the human capacity for the detection of phase difference, as mentioned earlier, is limited to a phase advance or lag of 180°, which are restricted to wavelengths below about 1000 Hz. The phase restriction leads to distance ambiguities from phase sensitive triangulation (between the source and the two ears), the lack of knowledge of the source size and the, at best, one foot acoustic wavelength all conspire to make phase-related auditory distance localization fraught with uncertainties.

The only means for distance to be obtained is through explicit or implicit prior knowledge of the different sources and the functional form of their variation with distance in particular environmental contexts. An example of such prior knowledge is the difference between the faint sound of someone shouting in the distance, with its characteristic change in the frequency composition due to a greater absorption of the higher sound frequencies, and the spectral characteristics of shouting as opposed to those of speaking softly in a normal voice (indeed, recognizing that it is a person involved). Such issues are addressed in chapters 9 and 10.

7.4 Neural Plasticity in the Auditory System

7.4.1 Developmental Considerations

Graven (2008) has reviewed fetal and infant auditory development. He emphasised the view that satisfactory development of audition in the fetus requires appropriate auditory stimulation. In the absence of all auditory input, adjacent cortical regions that process other sensory modalities can invade auditory cortex. This phenomenon of cortical plasticity was well illustrated by Sharma et al. (2000) who diverted visual input into the auditory nucleus of the thalamus (the medial geniculate nucleus) of ferret kits. The authors report that rewiring visual inputs into auditory cortex resulted in the formation of visual orientation modules therein. Thus, auditory cortex assumed the function of visual cortex by virtue of receiving input from the eyes rather than the ears.

This suggests that the primitive units for auditory perception, like those that participate in visual perception are derived from experience. Indeed, neural network models using rules of self-organization have demonstrated, in principle, how such auditory and visual primitives might be acquired (Sejnowski and Rosenberg, 1986; von der Malsburg, 1973. Evidence for the existence of such learned primitives in auditory cortex is presented in chapters 8 and 9.

The reviews by King (2009) and King et al. (2011) bring together a number of compelling findings that point towards the existence of widespread plasticity in human nervous tissue participating in auditory distance and direction perception. They have suggested that competence in sound localization must depend on implicit knowledge of the sound absorption properties of the head and sound scattering by the pinna.

As mentioned earlier, with increases in body size during development, a wide range of acoustic parameters would change, and require accompanying adjustments in the various nuclei processing auditory information; not least in the auditory thalamus, which is known to adapt to manipulations of auditory input in the owl (Miller and Knudsen, 2003).

Changes in anatomical sizes would include those of the peripheral auditory apparatus including the pinna (mentioned earlier), the ear canal, the tympanic membrane and their characteristics, and indeed the size and acoustic properties of the chain of processes involved in conducting and processing sound to the point of its conversion into action potentials by the inner hair cells of the cochlea.

All their changes would require updating with development in respect to the interactions between the anatomical structures with the constant parameters involved with physical acoustics. These would include the acoustic reflecting properties of the diverse reflecting surfaces encountered, acoustic absorption in air and other materials for the different acoustic frequencies, the approximately inverse variation of the sound pressure level with distance in the far field, its exponential variation in the near-field, knowledge of the diversity of different characteristics of different geometrical forms of sound sources and so on.

Learning has been documented in the human auditory system that enables the subjective unification of auditory and visual input as arising from the same distant event; plastic compensation mechanisms have been shown to cater for the difference in transmission speed of sound and light in the atmosphere (Alais and Carlile, 2005). Such compensation mechanisms would need to be updated also as development occurred.

Furthermore, the many multimodal maps involving proprioception, vision, and the vestibular senses would also need to be updated as the body size increased because these are mutually linked (Yamamoto and Shelton, 2009). Without dwelling further on this seemingly endless range of interrelated processes that would need updating (see King, 2009 for further details), it seems clear that mutual accord could be maintained through the provision of a massive plasticity in the central nervous system that was being updated dynamically, particularly during the early stages of development, when these changes are most rapid.

7.4.2 Experiments Showing Auditory Neuronal Plasticity

In their classic work on adult guinea pigs, Robertson and Irvine (1989) permanently damaged a range of cochlea cells, so that their targets in cortex received no inputs. The authors report that the deprived cortical regions were reallocated to support output from cochlear cells adjacent to those destroyed. This resulted in an expanded representation of the auditory frequencies responded to by the undamaged cochlear cells, providing an early demonstration that plasticity exists also in adult auditory cortex.

Hofman et al. (1998) pointed out that that sound localization relies on neural processing of implicit acoustic cues; that the brain must learn to calibrate these cues using spatial feedback from other sensorimotor systems. In their experiment on human subjects, they disrupted the spectral elevation cues of the subjects by modifying their outer ears with moulds. Although localisation of sound elevation was dramatically degraded following mould fitting, accurate performance was steadily reacquired.

Long-term dominance of visual over auditory direction perception has been demonstrated by raising barn owls with prism glasses that displace the visual field laterally (Knudsen and Brainard, 1991) and by periodically exposing dark-reared cats to synchronous but spatially incongruent visual and auditory stimuli (Wallace and Stein, 2007). These manipulations have revealed that auditory receptive fields in the superior colliculus are arbitrarily malleable, so that they need not overlap with visual receptive fields.

Wallace and Stein (2007) note that the congruence in receptive fields generally found in normally raised kittens cannot be specified in the genome, and that sensory experience can craft a brain to deal with specific cross-modal contingencies that are suited to a particular environmental setting.

Similar results were obtained by Zwiers et al. (2003) in humans, where sound localization was evaluated in response to spatially compressed vision using lenses for 2-3 days. This procedure induced a corresponding compression of auditory localization that was most pronounced for azimuth, and was restricted to the visual field of the lenses. Bruns et al. (2011) have demonstrated a similar influence of tactile stimuli on auditory localization.

Indeed, strong attention-gated visual guidance signals have been reported in the barn owl's inferior colliculus (a region containing an auditory space direction map) thought appropriate to guide auditory plasticity (Gutfreund et al., 2002). Further, more recent results obtained in the superior colliculus in macaques by Lee and Groh (2012) suggest that the initial head-centered auditory map of space transfers into the dominant eye-centered visual map. It is interesting to note that an artificial neural network can model the formation of the interaural-time-difference versus sound-source-direction map found in the laminar nucleus of the barn owl (Leibold et al. 2001).

The issue of the need of plasticity for the maintenance of competence in auditory direction and distance perception affirms the statement summarizing the stance taken by proponents of neuroconstructivism:

> Neural development occurs in the context of multiple interacting constraints acting on different levels, from the individual cell to the external environment of the developing child.
>
> Westermann et al. (2007).

These considerations provide significant support to the view that the capacity for auditory spatial localization must rely on neural plasticity, and is acquired rather than being provided innately. However, this capacity is clearly augmented by prior knowledge, whose status is addressed in chapters 8 and 9.

8

NEUROSCIENCE OF AUDITION AND THE CAPACITY TO PERCEIVE SOUNDS MADE BY OBJECTS

Preface

This chapter sets out to show that the knowledge stored in the brain about sound sources that participate in their spatial localization is acquired through learning rather than being provided innately. More specifically, the sounds made by living organisms and by man-made objects are addressed in this chapter. The capacity to recognize such sound sources is regarded as a part of the prior knowledge that enables their localization through audition in regard to the capacity to apprehend the fundamental dimension length. Some basic aspects of the neuroscience of audition are also elaborated upon in this chapter.

The origins of the capacity to recognize the sounds of human voices, in regard to recognizing speaker identity, that would provide prior knowledge for their localization is provided in chapter 9. The issue of the development of the capacity for the recognition of speech sounds, carrying semantic information up to the level of words, is also addressed in the next chapter.

8.0 Introduction

The functional anatomy of the auditory system has been described by Evans (1982), and a more recent review of auditory processing in the primate cerebral cortex was presented by Kaas et al. (1999). Additional information about the physiology of hearing can be found in Pickles (1982). Kaas et al. (1999) note that since microelectrode recordings in the auditory cortex of humans are permissible only under very exceptional circumstances advances in knowledge about single-unit physiology and connectivity-correlates are generally inferred from research in homologous regions in macaques, whose brain structure and function, in regard to current interests, are similar to those in humans. The developments of speech perception and also of speech production are reviewed in chapter 9.

Much research on auditory function has also been carried out in cats (see, for instance, Wallace and Stein, 2007). However, with the advent of non-invasive brain imaging techniques[18], information about auditory processing and plasticity under these constraints is now readily available also from human subjects.

Evans (1982, p. 251) notes that in studies of auditory processing, the afferent pathway is subdivided into two regions. (a) The *peripheral auditory system*, comprising the outer, middle and inner ear, along with the primary auditory receptors synapsing onto the spiral ganglion and the auditory nerve, and (b) the *central auditory system*, comprising the nervous pathways and nuclei from the cochlear nucleus into cortical structures (see Fig. 8.1). Evans (1982) observes that the functional anatomy of the central auditory system is particularly well developed in man, compared to other primates, for auditory communication.

The current work, directed at evaluating the role of learning in generating the capacity for auditory perception benefits from the extensive work carried out on hearing within the context of speech perception, its development, and on auditory deprivation as obtained especially from studies of cochlear implantation (mostly described in chapter 9). These, taken together with the work carried out on the neural plasticity in sound source identification, source direction and distance discrimination, permit an evaluation of the degrees to which the human auditory capabilities for sound source localization are native or learned. Essentially, the features addressed within the currently available neuroscience literature are the human capabilities for:

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[18] These are capable of ~ 1 mm spatial resolution at ~ 1 sec. temporal resolution (fMRI etc.) and electrical neuroimaging (EEG) techniques, with an approximately 1 ms temporal resolution, at a poorer spatial resolution (for details, see, for instance, Spierer et al., 2011)

(1) Sound source direction determination;

(2) Sound source distance determination;

(3) Obtaining prior knowledge about the nature of sound sources that participates in enabling (1) and (2).

As discussed previously on a behavioural level, prior knowledge plays an important role in the human discrimination of the distance and direction of a sound source. The capacity to identify an object from sounds associated with it can assist the listener in directing his attention through other sensory resources towards localizing it in space. The issue addressed herein is whether prior knowledge, in regard to the capacity to recognize sounds originating from man-made objects and living organisms is learned or native.

The neuroscience literature appears not to distinguish between sound source direction and sound source distance, and terms such as 'localization' or 'spatial location' are used without elaboration. They are generally found to refer to sound source direction (as in the case of previous studies described on physical acoustics), and not to its distance from the subject.

The current discussion on the neuroscience of the auditory system will be restricted to aspects that are of relevance to the issues itemised above, where basic auditory function will be described initially followed by issues concerning neuronal plasticity associated with prior knowledge. A review of the physical acoustic and behavioural findings associated with auditory distance and direction discrimination was given in chapter 7.

As in the visual cortex, there are multiple auditory fields that fulfil different functions. The auditory cortex comprises of regions referred to as the core, belt and parabelt (see below) that receive afferents originating in the cochlea. The information comes into the core regions via a diversity of auditory nuclei in the brainstem and midbrain, and after processing in these primary cortical regions, auditory information is projected to other parts of the cortex, including the temporal, parietal and frontal lobes.

Auditory cortex also receives *efferents* from regions of cerebral cortex that are higher in the cortical hierarchy, and project both laterally as well as to regions lower down in the processing hierarchy. Some efferents are projected all the way back to the brain stem and even to the outer hair cells in the cochlea, via the olivocochlear bundle, that are thought to sharpen frequency discrimination in the presence of noise.

It is thought that cortical participation is necessary (but not sufficient) for auditory *awareness*, even though there is much processing that occurs in the brainstem and the midbrain. As might be expected, damage to auditory cortex leads to a loss of auditory awareness. Bilateral lesion of the core area leads to a deficit in source direction and auditory object identification. Most prefrontal and posterior parietal neurons respond more strongly or exclusively to contralateral auditory stimulation (Kaas et al., 1999).

8.1 Maps and Pathways

The earliest stage of central processing of the ascending auditory fibres occurs in the cochlear nucleus in the brainstem, where the peripheral auditory information diverges into a number of parallel central pathways (see Fig. 8.1). The output of the cochlear nucleus, equally, has several targets (not all shown). One of these, the superior olivary complex, is the first location where information from the two ears interacts, and is the site of the initial processing of the cues that enable sound direction discrimination. The cochlear nucleus also projects to the inferior colliculus of the midbrain, where the auditory input first interacts with the motor system. From this relay station, auditory information in the main auditory pathway travels to the medial geniculate nucleus (MGN) of the thalamus, and thence to auditory and other cortical regions, where more complex aspects of sound, including speech and environmental sounds are further processed in an increasingly multimodal context. Auditory direction discrimination also relies on cortical processing even though the initial binaural analyses occur in the brainstem (see below).

8.1.1 Initial Sound Direction Segmentation

While listening, the subject has to accomplish two functions: he has to segment the sounds into acoustic features to enable an analysis of their contents. He also has to attempt to categorize them into auditory objects, or invariants, (such as phonemes – see §9.1) despite the variability present in these primitive acoustic tokens that make up spoken words. Indeed, it is widely acknowledged that the representation of auditory objects within nervous

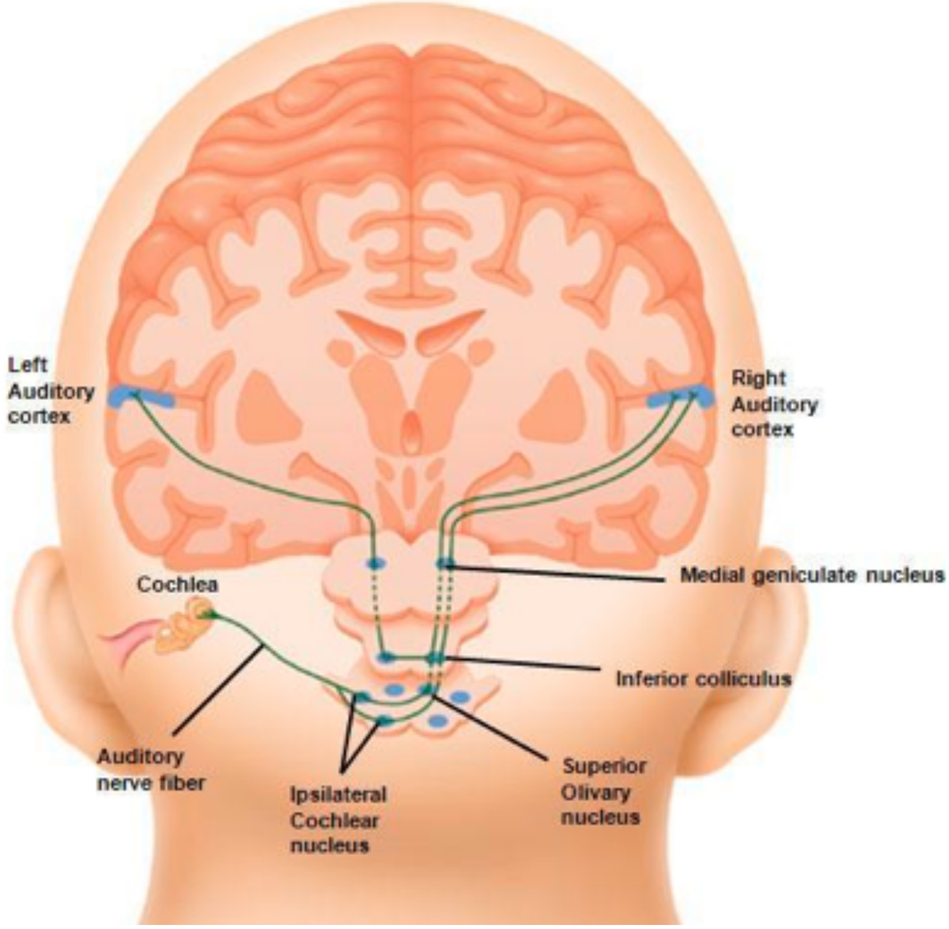

Fig.8.1 The main auditory pathways between the cochlea and primary auditory cortex. Source: www.PositScience.com. For more detailed pathways, see Evans (1982), Figs 14.1 and 14.2.

tissue is individual (subjective) and critically dependent on learning (Kral and Sharma, 2012; see also chapter 9). During learning, there is a dynamic reorganization of the features associated with the sensory stimulus, and the receptive fields in the auditory cortex change with training, usually reflecting improvements in performance (Recanzone et al., 1993). Both cortical and subcortical analyses contribute to this process.

The identification of auditory sources requires the capacity to track the sounds that may be associated with the same source. In the realm of speech perception, this entails identifying and tracking the different speakers; the semantic contents of what is being said helps in the process. In the realm of vision, *spatial* features help to discriminate between different objects in the visual field. However, in following environmental sounds, such discrimination needs to be carried out by tracking the frequency composition (and its variations) in order to identify the separate sound sources. Some of the relevant initial analysis is carried out in the superior olivary complex in the brainstem. Subsequent analysis of the object according to its semantic class is carried out later in brain regions higher in the processing hierarchy than the loci for initial object recognition (see §8.6).

It is worth mentioning that within the context of a noisy bustling environment, the overall segmentation process cannot be wholly reliant on the auditory sense; multimodal integration is an important aspect of source identification and the determination of its direction and distance relative to the listener. For instance, the superior colliculus in the midbrain creates a spatial register of the senses of vision, audition and touch (see, for example, Stein and Meredith, 1994 and Wallace and Stein, 2007) that helps to track the sound source.

It has been known for some time that individual cochlear fibres synapsing onto the inner hair cells at specific locations on the basilar membrane have a preference to discharge in a given half-cycle of the acoustic stimulus period for frequencies below 5 kHz. This phenomenon is known as ‘phase locking’ of discharges (or neuronal firings). Furthermore, individual cochlear fibres carry information that is band passed for the frequency range associated with its particular location on the basilar membrane. This frequency-segmented temporal information contained in the auditory nerve fibres is of significance for the localization of the direction of a sound source as well as for tracking the identity of the source when binaural cues are united in the superior olivary complex.

Evans (1982) notes that there appear to be three modes of analysis carried out by cells located in the superior olivary complex. Mode 1 cells are more sensitive to variations in binaural intensity (i.e., to intensity variations that are *correlated at* the two ears) than to differences in intensity *between* the two ears, and appear to fulfil the function of simultaneously tracking sounds from a common source incident at both ears.

The cells involved in mode 2 are particularly sensitive to changes in the intensity *difference* between sounds incident at the two ears (ILD). This second mode is relevant for the localisation of high-frequency sounds, where head-shadowing and pinna effects, mentioned earlier, can cause significant differences in interaural intensity, depending on the direction of the sound source relative to the mid-line of the subject (see Fig.7.1). The third mode of cell interaction deals with input frequencies below about 1 kHz, and is sensitive to interaural time delays between sounds reaching the two ears (ITD). In much the same way that visual orientation tuning is manifested in both primary visual cortex as well as in higher visual cortical regions, auditory direction signatures are detectable in most auditory nuclei, and, as mentioned earlier, there are reports of the existence of binaural interaction bands in cats and ferrets, homologous with ocular dominance bands in striate cortex, that may participate in auditory direction discrimination (Schreiner, 1995).

8.2 Auditory Processing in Cortex

The primary stage of cortical processing occurs in the central ‘core’ area (Brodmann’s area 41, see Fig. 8.2). This is followed by processing in the various surrounding regions forming an auditory ‘belt’ (Brodmann’s area 42), and subsequently in parts of area 22 (the parabelt).

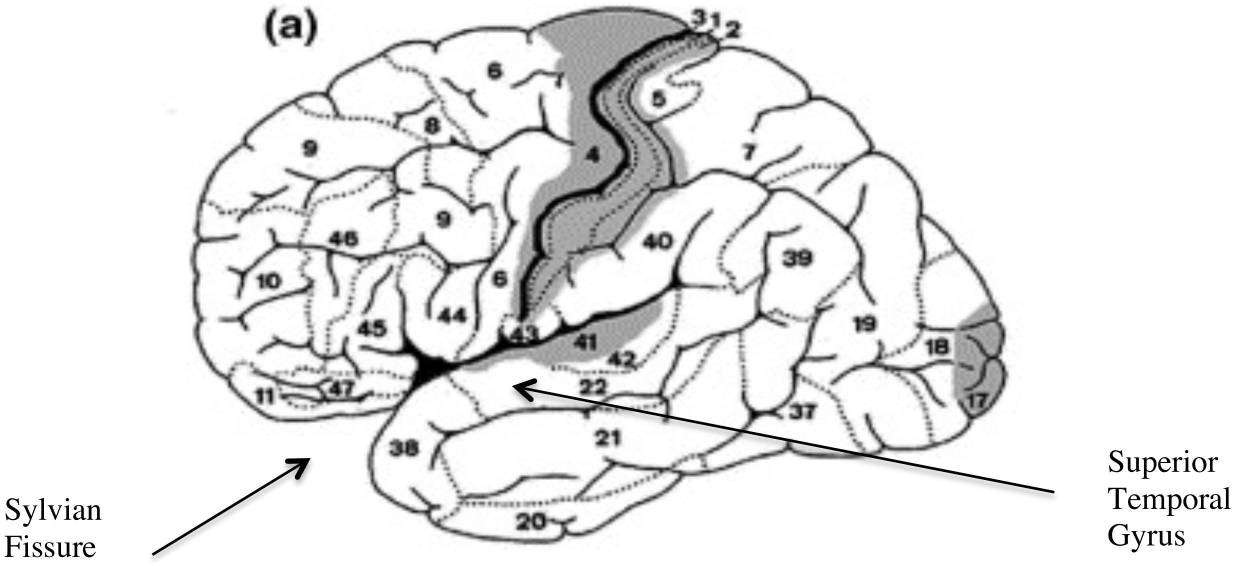

Fig. 8.2 Lateral view of the human brain, with various Brodmann’s areas indicated. Regions 41, 42 and 22 lie inferior to the Sylvian fissure on the superior temporal gyrus and within the superior temporal plain. Source: Pulvermüller (2001).

These regions are partially buried in the Sylvian (lateral) fissure in superior temporal cortex (see Figs. 8.2, 8.3 and 8.4).

The core area contains three cochleaotopically-organised fields (AI, R, RT in Fig. 8.4) that receive input in parallel from the MGN. AI, the largest, receives most of the direct input, and the surrounding belt areas receive inputs in parallel also from other thalamic nuclei that process afferents from other sensory modalities. Consequently, some belt areas are multisensory. For further details see Kaas et al. (1999), Fig. 2. These belt regions (so called because they surround the core) appear to be a second stage in the cortical processing hierarchy, and consist of seven fields, identified on the basis of separate cochlear representations (see Fig. 8.4, which shows the surface of the superior temporal plane that is mostly buried in the Sylvian fissure).

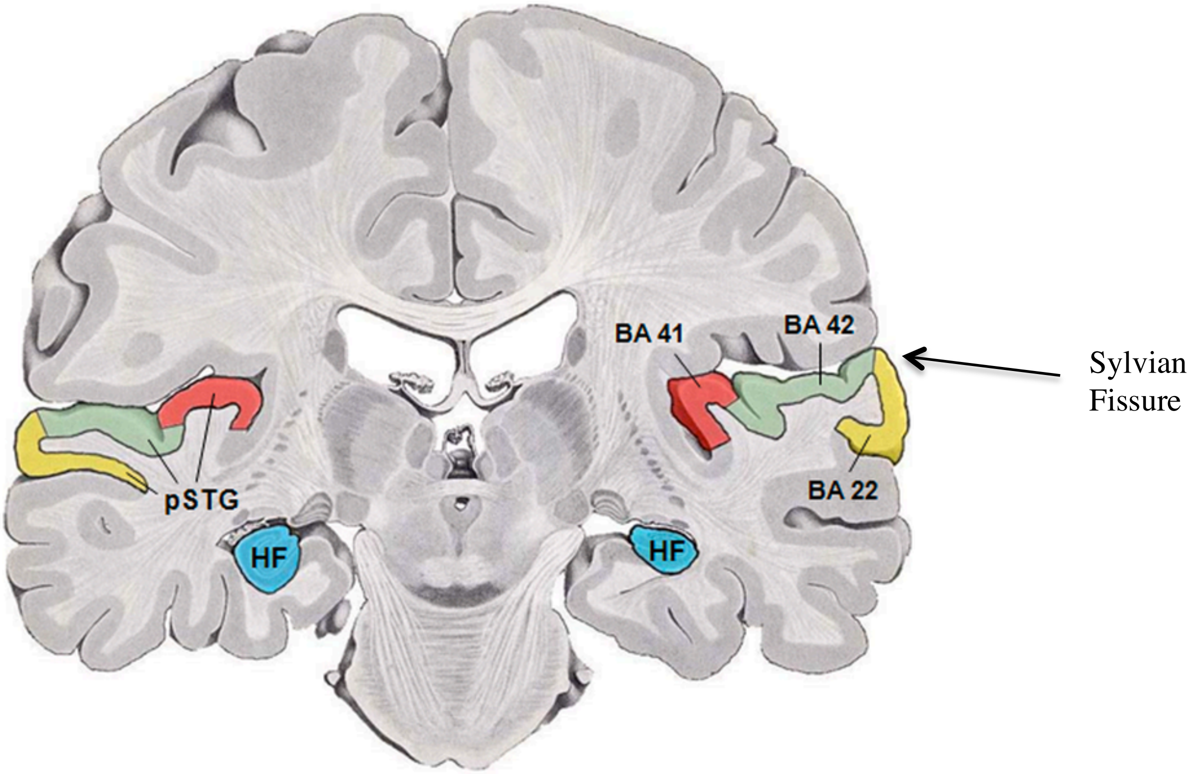

Fig. 8.3 Coronal section showing Brodmann's areas 41, 42 and 22. Source: Talbot et al. (2011). (Labels 'HF' and 'pSTG' are not relevant to the present work)

These belt fields abut parabelt regions laterally, caudally and rostrally (depicted in green in Fig. 8.4), and are thought to represent a third stage of cortical processing within the MGN -> core -> belt -> parabelt hierarchy.

Kayser et al. (2009) report that multisensory integration of auditory input occurs not only in higher associational cortices but also in early primary and secondary processing regions. Their work was carried out using fMRI and electrophysiology in primate auditory cortex. Visual-auditory and somesthetic-auditory inputs have been reported also in the caudal parabelt region (Kaas et al., 1999; Kayser et al., 2009).

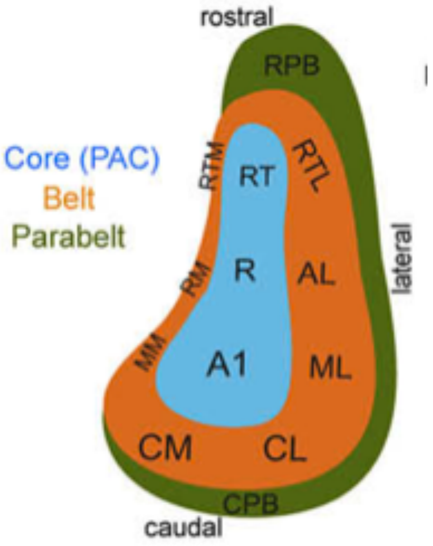

Fig. 8.4 A schematic representation of the monkey auditory cortex. The core (primary auditory cortex (PAC)) is shown, surrounded by the belt regions. Also shown are the rostral parabelt (RPB) and caudal parabelt (CPB) auditory fields. Source: Kayser et al. (2009).

8.3 Functional Organization of Auditory Cortex

It was suggested a decade ago that auditory cortical processing is organized according to separate functional 'what' and 'where' pathways, in a manner similar to that now established for visual cortical processing by Mishkin et al. (1983). In both sensory modalities, the ‘where’ pathways project from each of the primary sensory areas (visual and auditory) into posterior parietal cortex; the ‘what’ pathway projects into anterior temporal cortex. As in the visual system, the posterior parietal pathway is identified with spatial (direction) processing in audition, while the temporal pathway is involved in the identification of complex auditory patterns like speech sounds or those associated with objects. These pathways are referred to as the postero-dorsal and antero-ventral streams (Rauschecker, 1998; Rauschecker and Tian, 2000; Rauschecker and Scott, 2009).

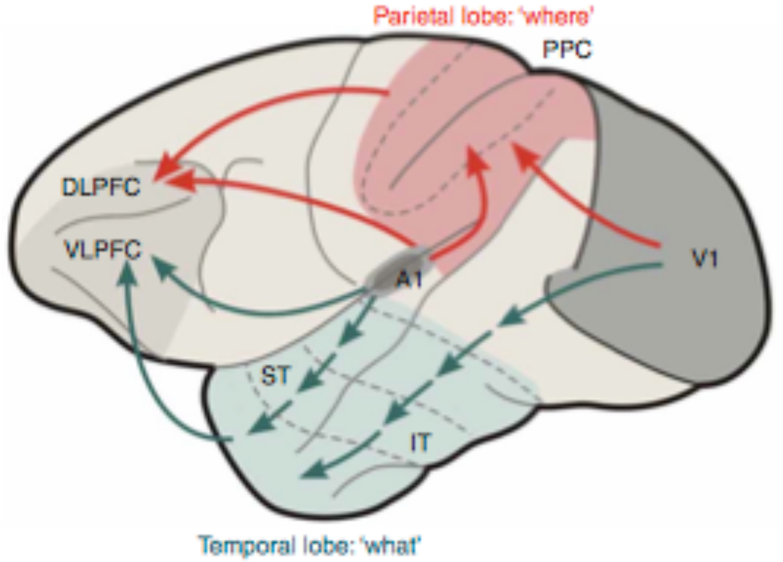

Fig. 8.5 The ‘what’ and ‘where’ pathways for auditory and visual processing in primates. V1, primary visual cortex; A1, primary auditory cortex; IT, inferior temporal region; ST, superior temporal region; PPC, posterior parietal cortex; VLPFC, ventrolateral prefrontal cortex; DLPFC, dorsolateral prefrontal cortex. Source: Rauschecker and Scott (2009).

In the auditory system, the long-range connections from the belt areas project from the anterior belt directly to the ventrolateral prefronatal cortex (VLPFC in Fig. 8.5) and from the caudal (posterior) belt to dorsolateral PFC. These pathways are hierarchically organised so that more complex analysis in both processing streams is carried out in the higher regions of the prefrontal cortex than in the lower or primary regions.

In accord with the pathways delineated above, Kaas et al. (1999) note that bilateral ablation of the core area or its inputs leads to a profound deficit in both sound source identification and localization, suggesting that both processing streams rely on the core region. In support of the two processing streams schema, Rauschecker and Scott (2009) point out that single-unit studies in the lateral belt areas of macaques show that when species-specific communication sounds are presented from different directions, neuron responses in the antero-lateral belt area (AL, in the ‘what’ stream, see Fig. 8.4) are more attuned to identifying the type-of-monkey-call than other regions. By contrast, neurons in the caudo-lateral belt (CL area, part of the ‘where’ stream) are more likely to process direction cues than neurons in the core or the anterior belt regions (see Fig. 8.4 and 8.5). Other evidence supporting the functional separation of the dorsal and ventral auditory streams may be found in the reviews by Kaas et al. (1999), Rauschecker and Scott (2009) and Spierer et al. (2011).

8.4 Hierarchical Organization for Auditory Object and Speech Processing

The role of the ventral stream in the hierarchical processing of object sounds is now well established in primates. The same hierarchical organisation in the antero-ventral auditory pathway in humans is important in auditory pattern recognition and object identification. Like their visual counterparts, auditory objects have their distinctive temporal signatures compounded from features such as timbre, pitch, and loudness that give each object its distinctive perceptual identity. As in animal models, preferred features of lower-order auditory neurons combine to create selectivity for increasingly complex sounds, so that regions can be identified in humans that are specialized in distinguishing different object classes (see Spierer et al. 2011 and §8.7). Indeed, sound source localization is aided by the capacity to recognize the source. In this respect, the cortical processing that enables the recognition of speech sounds and those made by certain classes of objects will be evaluated to determine whether these capabilities are derived from learning or given innately.

Rauschecker and Scott (2009) note that a meta-analysis of imaging studies of speech processing shows that there is an antero-lateral gradient along which the complexity of preferred stimuli increases, from tones and noise bursts to words and sentences. There is, thus, a hierarchical organization in which preferred features of lower-order neurons combine to create selectivity for increasingly complex sounds. This finding is reinforced in work by Belin et al. (2000) who were able to identify, using fMRI, the upper bank of the superior temporal sulcus (STS), bilaterally (with a greater activation in the right hemisphere), as areas that responded only to speech and other vocal sounds, and not to the non-vocal sounds of bells, clapping, finger snaps and synthetically generated amplitude-modulated sounds.

Belin et al. (2000) note that the area concerned forms a part of a hierarchically organized system extending anteriorly and ventrally, beyond the lateral belt that is specialized for extracting auditory object features (the ‘what’ pathway). They conclude that in humans the

STS may be homologous in its function to the fusiform gyrus where visual face-selective regions have been identified (Kanwisher et al., 1997; McCarthy et al., 1997).

8.5 Speech and Voice Perception

In their review, Rauschecker and Scott (2009) cite evidence for the localization of a hierarchical organization in the 'what' stream, of speech related functions like vowel and consonant recognition, raising the possibility of the existence of a phonetic map (as suggested by Kohonen, 1987 and Sejnowski and Rosenberg, 1986). They also suggest the existence of a human voice area related to speaker recognition, processing detailed spectral properties of individual speakers.

This latter function of the anterior-lateral temporal lobe area may be regarded as an example of a derived rather than native processing capability. This is because each voice carries with it the signature of the speaker's identity in the same way as handwritten signatures contain invariant features that allow the writer to be identified. It is proposed (without providing a formal proof) that there are too many unknowns, as in the case of innate phoneme recognition (Nittrouer, 2001; Nittrouer, 2002, see also §9.1.1) to allow the genetic pre-encoding of all voice signatures, present and future. Indeed, the American Bar Association allows a voice to be used as a legally binding signature[19]. It seems reasonable to conclude that the ability to recognise individual voices cannot be given innately. The listener must have to learn each voice signature separately through exposure to it (For a

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[19] See, for instance, http://www.tradeharbor.com/what-a-voice-signature-is.html

review of biometric recognition methods see, for instance, Delac and Grgic, 2004). This issue is treated in some detail: see §9.3.2.

Of interest in respect of the existence of functionally specialized auditory regions is the finding that there exists the well-known Wernike's area, located in the left posterior superior temporal gyrus, associated with the comprehension of language. Lesions in this region, and more particularly damage to the underlying white matter, leads to the syndrome of Wernike's aphasia, where affected subjects are unable to understand language in both its spoken and written forms. There exists another syndrome known as 'pure word deafness', reported to occur in subjects with lesions involving the primary auditory cortex bilaterally, and is characterised by the inability to hear speech sounds, while preserving the capability of recognising other sounds such as music or sounds from the environment (Belin, 2006)

8.6 Brain Loci for the Auditory Representation of Environmental Sounds

Previous studies have identified specialized networks for specific categories of environmental sounds within the auditory 'what' pathway. For instance, Lewis et al. (2005) demonstrated using fMRI that sounds of animal vocalizations activated bilaterally the middle temporal regions of the superior temporal gyri, whereas tool sounds preferentially elicited a response within a wide left-lateralized network overlapping largely with the mirror system (Rizzolatti et al., 2002).

Furthermore, studies visual identification and auditory comprehension have shown selective impairment in the identification of living things and foods while retaining the capacity to identify inanimate objects. In some patients this pathology was found to exist for both visual and verbal presentation of these categories of objects (Warrington and Shallice, 1984). Evidence for the segregation of auditory processing for living versus non-living items has been noted in neuropsychological patients with lexical retrieval deficits due to brain lesions (Silveri et al., 1997), and more recently a similar segregation has also been observed in healthy participants by the use of multiple neuroimaging methods, reviewed by Spierer et al. (2011).

The capacity to decipher environmental sounds is a part of the prior knowledge that humans bring to localizing the distance and direction of the sounds emitted by objects. This section addresses two such sound categories: those made by living organisms and the ones emanating from man-made objects.

The human auditory processing that takes place on the presentation of sounds made by living creatures and man-made objects, both in behavioural priming-based recall and in brain responses, as elicited by electrical neuroimaging techniques (Spierer et al., 2011), will be used in the present analysis to argue that they are both learned. It is gratifying to find these results in common for both categories of sounds because it can be claimed independently that the ability to identify sounds from man-made objects could not have been embedded genetically in the time-scales involved.

8.7 Auditory Discrimination of Living versus Man-Made Objects

Of interest in this respect are the results from experiments carried out by Murray et al. (2006; 2008) to study the spatiotemporal brain mechanisms involved in discriminating sounds of living and man-made objects. The work was carried out on healthy subjects using a 64 channel electroencephalographic (EEG) system to measure and localize acoustically evoked potentials (AEPs); a methodology referred to as 'electrical neuroimaging'. Murray et al. (2008) also employed functional magnetic resonance imaging (fMRI) to chart more precisely the overall localizations of the generators of the electrical potentials during the processing of these different sound categories.

Murray et al. (2006) found that processing of sounds from both man-made and living sources began within 70 ms of stimulus onset in the posterior middle temporal regions of the right hemisphere (Brodman's areas 21/22). As processing proceeded, the initial activity associated with object identification shifted over the time scale of 155-257 ms to networks involving bilateral electrical sources within the posterior portion of the superior and middle temporal cortices as well as to the pre-motor cortices.

Responses to sounds of man-made objects exhibited an earlier shift between generator configurations than those to sounds of living objects. These latter activations (in the time scale of 155-257 ms) have been associated with semantic categorization of the acoustic stimuli (see below). For details of responses from other object categories that have been studied see (Spierer et al. 2011).

Examples of sounds from man-made objects were those from bicycle bells, cuckoo clocks, police sirens, telephones, car horns etc., while sounds of living objects included human coughing, laughing, screams, gargling, baby crying, rooster calling and so on.

8.8 Indications that Auditory Knowledge of Sound Sources Are Learned

Objects of auditory and visual perception share some common behavioural responses. The repeated exposure to newly learned visual or auditory objects leads to an improvement in performance in implicit memory tests involving an object discrimination task (Tulving and Schacter, 1990). This phenomenon is referred to as *repetition priming*. There are two classes of repetition priming: perceptual priming and semantic priming. Perceptual priming is linked to the physical features of the object, such that changes to these features lead to a reduction in the behavioural facilitation in object differentiation tasks. Conceptual or semantic priming continues to occur despite such changes. Indeed performance enhancement continues to occur even when the physical features are altered. This is because such changes do no alter the class of object, but only its particulars. Semantic priming has also been demonstrated in both visual and auditory domains (Spierer et al., 2011).

Repetition priming is often accompanied by a reduction in the brain's electrical response to the stimulus, referred to as *repetition suppression*. This phenomenon was first observed using visual stimuli, and it is thought that the neural mechanisms for learning and memory both dynamically modulate and permanently alter the representations of visual stimuli in the brain (first observed in the adult monkey cortex (Desimone, 1996)). The suggestion that a prior learning experience leaves a structural trace in cortical circuits is supported by numerous findings cited by Hofer et al. (2009), who followed-up prior work by studying the dynamics of apical dendrites of pyramidal neurons in functionally defined regions of adult mouse visual cortex during visual deprivation experiments involving eye closure. Their results showed a link between functional plasticity and specific synaptic rearrangements revealing a mechanism of how prior experience could be stored in cortical circuits.

Repetition suppression is typically considered as an index of plasticity, in that it reflects experience-dependent modulation in neural activity that supports perceptual learning (e.g., Desimone, 1996). Although the phenomenon of repetition priming manifests a similarity to that of habituation, the precise mechanisms leading to this reduced activity remain unresolved.

More recently, repetition suppression has also been demonstrated in humans using auditory linguistic and auditory environmental stimuli (Spierer et al., 2011). Neuroimaging investigations have elucidated priming-related effects within extrastriate *visual* and frontal cortices (Spierer et al., 2011). The existence of common loci for the occurrence of both visual and auditory repetition suppression can be interpreted on grounds that these higher regions are multimodal. This is not to say that other regions are not involved in the perceptual priming of auditory stimuli; indeed, it has been shown that auditory cortices in the temporal lobe are involved in responses to the priming of sounds from environmental objects (Bergerbest et al., 2004).

Murray et al. (2006) monitored AEPs in subjects as they performed an ‘oddball’ target sound detection task based on the semantic category of stimuli. The target sound for each semantic category was embedded in odd-ball sounds not belonging to either of the semantic categories. For both categories of sounds, repetition priming effects were observed as a speeding up of the reaction times for discriminating the target versus oddball sounds, and there was a greater accuracy in discrimination. In addition, there was a suppression of the strength of the electrical response to repeated sound presentations for both categories of target sounds over the 156-215 ms post stimulus period. The reduction in brain activity in the processing regions was found to be similar for both sound source categories.

As mentioned earlier, fMRI was used for localizing more precisely the electrical sources, and at poorer temporal resolution. Use of this technique also demonstrated a suppression of the hemodynamic responses associated with repetition suppression within the previously identified but overlapping brain regions[20].

Spierer et al. (2011) concede that they are far from having a full understanding of the processes that change in the brain, and result in alterations in the AEPs when discriminating acuity improves in auditory object recognition capacity. However, these authors remark

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[20] The superior temporal resolution of electrical neuroimaging permitted the localization of the time course of the electrical activity at a poorer spatial resolution than obtained by fMRI. However, the poorer temporal resolution of latter technique resulted in overlapping images being integrated over the region showing the electrical response.

that there is a direct correlation between these changes in the AEP signatures and the shortening in the reaction times with trial number, and indeed in the improvement in the discrimination scores between the target sounds and distractors.

In summary, results from the repetition priming experiments, showed shorter reaction times and greater accuracy for target sounds in both object categories. Repetition of sounds from both categories resulted in reduced brain activity in the processing regions (repetition suppression). These results support the view that the auditory prior knowledge associated with the identification of sounds made by both living and man-made sources is learned rather than given innately.

It is interesting to observe that in all the above experiments sounds from both categories elicited equivalent brain and behavioural responses. Given that it can be claimed that prior knowledge of sounds of man-made objects could not be innate, their common responses reinforces the view that the capacity to recognise sounds from living organisms is learned.

Given that the sounds made by these classes of objects can be an indication of their masses, these findings affirm the earlier finding that the human capacity for mass apprehension (within these auditory limits) is acquired through learning (see chapter 6).

8.9 Sound Direction Discrimination

It was indicated earlier that the initial histogram of cochlear segmentations according to frequency in the cochlear nerve fibres and the band-pass rectification of the signal they carry from the two ears to the superior olivary complex appear to be a mechanical process not requiring any component that may be interpretable as learning.

In this respect, it would appear that the capacity for such processing to occur might be given innately in much the same way as the pinna transform occurs simply by virtue of the shapes of individual pinnae. Reinforcing this view is the finding that electrophysiological studies, mostly using mismatch negativity (MMN; see below) has demonstrated that auditory spatial information is processed preattentively (Spierer et al., 2007). This might be expected to be the case if the processing in the superior olivary complex occurred, as proposed above, in the same manner as occurs with the pinnae transforms.

However, even though the auditory system of infants is well developed at birth, the infant still needs to make sense of what it hears. In this respect, it seems comprehensible that despite the innate provision of interaural time difference (ITD) information from the midbrain, the association of the signal from the midbrain containing direction information still needs cortical activity for directional capacity to be established. This is in analogy with the predisposition of babies to respond to the sounds of language, but their understanding of these sounds has to develop for them to use the speech sounds of their own language[21].

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[21] In: *The Early Development of Audition and Vision in Hearing Infants* By Susan Gregory. Reader in Deaf Education University of Birmingham.

Indeed, Benson et al. (1981) observe that cortex is profoundly involved in the ability of animals to localize sound in space, because the ablation of either auditory or prefrontal cortex leads to deficits in sound localization.

Wright and Fitzgerald (2001) have demonstrated that humans can improve their performance in discriminating between different sound source directions, which reinforces the view that the capacity of sound direction discrimination is learned. In their experiments, the authors altered the interaural level differences (ILD) and ITD of sounds presented to subjects on headphones in order to simulate the different sound directions. As might be expected, the study demonstrated that subjects could rapidly improve their ability to discriminate between sounds differing by small ILD or ITD.

8.9.1 Auditory Mismatch Negativity

Brain processes give rise to measurable electrical potentials in the microvolt range that may be measured by scalp-mounted electrodes. On being provided with an oddball in a sequence of identical sounds that the subject has learned to recognize, the AEP recorded from the deviant stimulus gives rise to electrical activity in the brain that differs from the brain responses from the identical components in the sequence (Näätänen et al., 2005; 2007). The difference in electrical activity arising from the oddball is referred to as mismatch negativity (MMN). This is observed only when the subject has learned to recognize the repeated sounds, and the MMN is observed even when the subject is not directing his focal

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attention to the sequence of sounds. If the sequence of identical sounds is not one the subject has been trained to recognize then MMN is not observed. The magnitude of the MMN is considered to be an index of the difference between the electrical activity elicited by the oddball stimulus and the memory trace (or signal) arising from the identical stimuli in the series.

The term 'negativity' in MMN is confusing, in that it refers only to the fact that AEPs are plotted with the negative electrical potential represented as increasing on the ordinate of the AEP graph; the oddball stimulus gives rise to an increase in the negative electrical potential, and the increase in the negative electric field arising from the mismatch with the previous identical stimuli is referred to as the MMN.

8.9.2 Loci of Brain Processing of Sound Direction Discrimination and Learning

Spierer et al. (2007) sought to identify brain loci associated with learning to discriminate sound source directions using AEPs and electrical neuroimaging analysis. In their experiments, the investigators recorded AEPs from subjects before and after training sessions during which the subject learned to distinguish between sounds from two different sound source directions. Psychophysical evaluations of performance were made at intervals during the training process. As expected, the authors found that before training, when the subjects were unable to reliably distinguish between two spatial positions, there was no evidence of MMN in the subjects' AEPs on being presented with an identical sound but emanating from an oddball direction. However, after 40 minutes of discrimination training, performance improved from near chance levels to ~ 75%, and AEP modulations, measured as a MMN, were observed in subjects with improved performances.

Using electrical neuroimaging analysis (essentially the electrical generator configurations) of the AEPs associated with the MMNs, the investigators identified the changes to the positions in the electric field topography that accompanied changes in the behavioural performances of the subjects, and were able to identify the regions where plastic changes had occurred. By manipulating the sound source directions the authors were able to reveal that training selectively changed the topography within the left inferior parietal cortices, contralateral to the hemisphere of the stimulus. These regions that lie within the auditory 'where' pathway have been previously associated with sound localization (Spierer et al. (2007).

The authors concluded from an analysis of their results that auditory spatial discrimination relies on spatial comparisons rather than on absolute direction determination. This view is reinforced by experiments on cats (Wallace and Stein, 2007) and in owls (Knudsen et al., 1982; Knudsen, 1999) that it is possible to dissociate the normal spatial alignment between the visual and auditory senses.

In their review of the work described herein on auditory object and sound direction discrimination, Spierer et al. (2011) conclude that the auditory system is specialized in its structure and function for detecting the identity and location of objects from the temporal sequence of sounds they make. The capacity to identify the object and its location is learned, and reinforced by multimodal input. Objects are identified according to learned categorical boundaries, aided by multimodal inputs that are processed hierarchically in the temporal lobe and the prefrontal region through recursive activity. The authors conceded, however, that they are far from having a clear understanding of the details of the processes.

In sum, a detailed account has been presented here, based in auditory neuroanatomy and physiology, to support the view that the capacity for the apprehension of auditory prior knowledge of sounds made by both living and man-made objects that support sound source distance and direction discrimination is acquired through a process of learning.

9

DEVELOPMENT OF SPEECH PERCEPTION AND PRODUCTION

Preface

This chapter explores the origins of our capacity to recognize and produce speech sounds in regard to the issue of the status of prior knowledge that aids auditory sound source localization. For instance, the capacity to distinguish a human voice from another sound source might facilitate the estimation of the distance away of, for example, a person humming in the dark.

Furthermore, vocal exchange of semantic knowledge forms a significant additional source of prior knowledge that informs the human capacity to apprehend physical reality. In this regard, it would be interesting to explore if the capacity for human vocal exchange at the semantic level is native or derived from environmental input.

An examination of the human capacity for vocal information exchange at the level of the use of language is too large a topic to address in the present work. However, this may not be necessary because vocal exchanges are based upon the capacity to recognize and produce the primitive constituents of speech sounds: the phonemes. Furthermore, given that speech recognition and production can be shown to be hierarchically organized, with phoneme recognition and production lying at the bases of the two hierarchies, some consensus may be arrived at about whether or not the capacity for vocal exchanges are dependent on a process of learning from environmental input. This argument is similar to the one used previously to support the view that the capacity for visual length perception is learned on grounds that the visual primitives are derived from environmental input (see chapter 5, §5.7). Thus, the issue of whether prior knowledge about physical reality obtained through vocal exchanges is primitive or derived may be, nevertheless, evaluated by confining the debate to the status of phoneme recognition and production.

The exploration of the development of speech recognition and production is, inevitably, associated with the issue of the generation of the meanings of words. This issue is central to the domain of semantics. The findings concerning this topic are discussed at the end of the chapter.

9.0 Introduction

Given its central role in human communication, much work has been carried out on speech perception. The results generally support the view that the capacity to decipher speech sounds entails a period of learning. Indeed, speech recognition does not occur spontaneously when a deaf person is fitted with a cochlear implant any more than is clear vision given to a blind one on the provision of a corneal transplant.

Some of this work will be recounted below in support of the broader stance that our capacity to apprehend physical reality is derived rather than primitive. An overview of the cortical organization for the processing of speech and environmental sounds in the adult was provided in chapter 8. This chapter addresses mainly the development of the perception of speech sounds, although, as mentioned above, some observations are also made on the associated topic of the development of speech *production* and how they may be related.

Auditory speech perception shares with the capacity for the recognition of other environmental sounds its ability to provide contextual information about the distance and direction of a sound source. As mentioned earlier (Ch 8, §8.4), they are both processed at the higher-level in the auditory antero-ventral ‘what’ pathway in the cortex. Given the inherent plasticity of the cortex and that sounds both of man-made and living sources appear to be learned, it would seem likely that the capacity for speech sound recognition, rather than its semantic contents, for the present, is also derived rather than given innately.

§9.3 elaborates upon some aspects of the neurophysiological correlates of speech perception.

It has been demonstrated that familiarity with a sound source can improve the human capacity to localize it (Coleman, 1962, 1963; Vesa, 2009). In this respect, the characteristics of speech sounds and the way they vary with context are familiar to humans. For instance, speech sounds differ when made by a child or by an adult, and on whether the person is shouting in the distance or talking quietly close by. Vesa (2009) showed that sound source locations could be accurately charted when recordings of speech sounds were used as sources in an enclosed space. Thus, our capacity to distinguish a speech sound from other sounds would facilitate its localization.

Although the present work will address our capacity for the apprehension of physical reality at a level close to its perceptual primitives, I will also examine the suggestion that our capacity to apprehend the semantic content of spoken instructions for the identification of a sound source is also derived[22] rather than being native.

It is proposed that such a claim about our capacity to perceive spoken words can be extended to incorporate the comprehension of *all* spoken instructions that may be communicated concerning the apprehension of physical reality (and beyond). With the incorporation of speech production as well as speech comprehension in the present work, I

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[22] It must be born in mind that the term ‘derived’ extends to the capacity of the individual to make and incorporate new associations through reasoning and so on, to enlarge his corpus of knowledge. Such additions to his corpus of knowledge through inference, for instance, are, of course, seen as distinct from innately provided knowledge.

will evaluate the claim that the capacity for all human vocal *exchanges* is derived through a process of learning.

It is worth bearing in mind that the recognition of speech sounds in their common manifestations as meaningful words is based upon our capacity to segment them into their primitives: the phonemes (see below), although it will be shown that the distinction between speech and non-speech sounds is made during development prior to the apprehension of the semantic content of the speech sounds (O'Connor, 1973; Binder et al., 2000; Ambridge and Lieven, 2011; also see §9.3.

Houston (2005) and Werker and Tees (2005) have reviewed the literature on the hierarchy of the neonatal and early speech perception skills that are relevant for learning words: speech discrimination (from other sounds), segmentation of words from fluent speech and construction of lexical representations of the sound patterns of words. The ubiquitous behavioural evidence that there exists a hierarchical construction of such competences is supported by the existence of processing hierarchies in the temporal cortex (see chapter 8, §8.4 and chapter 9, §9.3).

9.1 Phonemes

Spoken words are composed of repeated 'primitive sounds' in much the same way as written words are composed of letters of the alphabet. In addition, even though no speaker pronounces the same word in exactly the same way every time, the listener is, nevertheless, able to decipher words from their sounds. Handwriting and typescript also vary in their detailed forms, and the reader also successfully adjusts to these variations in form.

Words spoken by different speakers are understood, despite differences in their gender, accent, age or the speed at which the words are uttered. The primitive speech-segments that are considered to be functionally equivalent despite these variations are referred to as phonemes (see, for instance, O'Connor, 1973).

Ambridge and Lieven (2011) observe that different languages use different sets of spoken sounds to make up words, so they may share certain phonemes but not others. For infants learning their native language, a first step is the recognition of the sound properties that distinguish the meaning of words from one another.

However, speakers of different languages may not distinguish between certain speech sounds as constituting different phonemes. For instance, the difference between /r/ and /l/ is phonemic in English (i.e., if /r/ is changed to /l/ a different word is perceived (e.g., *rap* -> *lap*)) but not in Japanese. Japanese speakers perceive /r/ and /l/ as phonetic variations of the same phoneme (/r/). In having not previously experienced the distinction between the sounds in their language they do not perceive the difference when used in English. So a Japanese listener would not distinguish between the words *lap* and *rap*.

A similar effect is present in English. Consider the example (provided by Werker et al., 2012, p. 1) where a parent points to a doll and says, "Look at this doll! That's your doll!"

To a Hindi speaker the “d” sounds in “this doll” versus “your doll” represent a phonemic distinction, between the dental “d” [da̪l] (as in dal, meaning lentil) and the retroflex “d” [ɖal] (meaning branch). In English they both signify the same phoneme (/d/), whose sound changes depending on its context within the sentence. Young English-learning infants easily discriminate the two Hindi “d” sounds, whereas English-speaking adults find this much harder. By 10 months, English learners begin perceiving speech according to their native language and can no longer discriminate these two “d” sounds, whereas Hindi-learning infants maintain the capacity to make the distinction beyond infancy.

In the present work the criterion that will be used to distinguish between speech sounds and other environmental sounds will be guided by previous work on speech sounds both in the behavioural domain as well as in neurophysiology. The former deals with the development of phonemic distinctions in infants, and examines the development of phonological aspects of speech perception associated with the extraction of lexical and semantic information (see below).

The latter focuses on brain imaging studies evaluating cortical responses to diverse classes of speech and non speech sounds varying between unstructured noise, frequency modulated noise, pseudo-words and words. These inform both about speaker identity perception, which appears to be carried out bilaterally in a separate hierarchy from the left-lateralized hierarchy for the analysis of lexical, semantic information. This latter cortical hierarchy appears to process particular speech sound classes such as vowels and vowel-consonant combinations, suggesting the existence of phonetic maps. See §9.3. Work on both these hierarchies will be reviewed to assess whether the capacity to apprehend speech sounds as human sound sources is primitive or derived.

As observed earlier, a demonstration that the capacity to recognise speech primitives is learned, rather than innate, would support the view that the ability for the comprehension of all speech in any individual is derived. This is based on the finding that structures at the higher level in the auditory cortical processing hierarchy are determined by structures that develop at the lower level (see, Rauschecker and Scott, 2009; Tsodyks and Gilbert, 2004; Werker and Tees, 2005). Thus, a demonstration of plasticity at the lower phonemic level, may be taken as sufficient to support the view that the ability to recognise higher-level auditory objects such as words is acquired. As mentioned earlier, a similar argument was employed in respect of visual length perception in chapter 5, §5.7.

The converse may also apply. For instance, a display of the capacity for speech comprehension through conventional auditory means, given the existence of a phonetic hierarchy, would imply the ability for phoneme recognition. This rationale will be used later to argue that cochlear implant-derived-speech-comprehension supports the view that speech segmentation into its phonemic constituents is learned rather than primitive. Both the capacities for speech segmentation into its phonemic constituents and speech comprehension will be addressed as criteria for assessing whether speech sound recognition requires a period of learning.

9.1.1 Speech Comprehension and Speech Production

Given that the deaf cannot speak and that children become competent in the language(s) spoken in their developmental setting, it is claimed without elaboration that speech production is learned through recognition. However, these gloss over the divide between speech comprehension and production, and the association between them needs justification (see below). It may be claimed, alternatively, that both are given innately because the co-occurrence of both deficits in the congenitally deaf arise from a common genetic source, and that there may exist core knowledge that facilitates the recognition of all phonemes.

Results from the domain of auditory deprivation can inform about this issue, particularly from findings within the context of cochlear implantation, where it has been shown in deaf humans that implantation, when carried out within a critical period, can lead to the development of speech comprehension and production (see §9.7). The non-comprehension and absence of speech in feral children also inform this issue (see §9.9).

9.2 Behavioural Development of Speech Perception

Following the development of responses to tactile stimulation at approximately 7.5 weeks g.a., responses to auditory stimuli have been observed at 16 weeks g.a., and there is much evidence to suggest that auditory competence in the neonate stems from auditory learning that has taken place during the fetal stage of development. This feature is sometimes overlooked by workers on child language acquisition. For instance, Ambridge and Lieven (2011) neglect this issue, while devoting much space in their textbook to the nature-nurture debate in infant speech processing.

9.2.1 The Nativist – Constructivist Debate for Phoneme Segmentation

Peter Eimas (1985) proposed that infants are born with the capacity to discriminate all the speech-sound contrasts that exist in all languages. He and colleagues found that 1 - 4 month olds could make the [pa]-[ba] distinction (Eimas et al., 1971). Furthermore, Swoboda et al. (1976) found that 2 month olds could not only make the [i]-[ê] segmentation but could do so across formant frequencies (see O'Connor, 1973), indicating that this categorical distinction was made at a semantic level rather than only a phonetic one. Also, Trehub (1976) found that English-learning 1 - 4 month olds discriminated not only the vowel contrast [pa]–[pã] but also the [r˘a]-[za] contrast, which is not linguistically distinctive in English.

Unlike infants, English-speaking adults cannot generally make this distinction, suggesting that there may be a critical period for learning this difference. This finding was reinforced by work carried out by Werker and Tees (1984) who tested English, Hindi and Nthlakapmx (a Native Canadian language) consonant contrasts in English-learning infants across different ages (over the age span 6 - 12 months), and found the existence of a window period of 6 - 10 months during which the infants could discriminate all the consonants in these languages. The 10 - 12 month olds could not discriminate any of the non-native contrasts.

Although languages differ in the number of phonemic categories they utilize, there are regularities within the languages of the world in respect to where phonemic boundaries are placed. Infants can become sensitized to these boundaries until the age of about 6 months, even if the contrasts are not present in their native language.

These findings led some researchers to suggest that infants' categorical perception of speech was a part of a biological endowment for language: that infants are *born*[23] with the ability to discriminate any phonetic contrasts relevant to segmenting speech sounds of all languages (Eimas et al., 1971; Houston, 2005).

Ambridge and Lieven (2011, p. 13) have elaborated upon this issue and summarise the nativist claim as follows. The nativists suggest that the child builds its phonemic inventory on the basis of a small set of *innate distinctive features* [italics inserted], and that the child analyses the incoming sound to determine which values and combinations of these features are relevant for the language being learned.

Even contemporary nativist psychologists do not elaborate upon how these distinctive features are stored in the many cortical and sub-cortical regions involved in auditory

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[23] As mentioned earlier, many workers neglect the fact that some auditory frequencies contained in speech sounds are accessible to the fetus and learned prenatally.

processing, or indeed, how they might be encoded in DNA and chromatin (e.g., Carey, 2012; Spelke, 2000).

The alternative constructivist position holds that phoneme recognition is constructed bottom-up from the regularity in the statistics of the vocal signal as manifest within the environmental context. The constructivists point to the literal construction of the hierarchical neuroanatomical structures that parallel the behavioural development as evidence for their stance. Indeed, they also provide an account of how memory might be encoded in these structures at both a neuronal and molecular level that relates to the construction of new synaptic connections between the neurons and the variations in their connection strengths. Furthermore, sensory deprivation and lesion studies support their stance. The details were presented in chapter 3. Computational modelling of speech recognition provides extensive 'existence proofs' for the learning of phonemic segmentation (see, for instance, Hinton et al, 2012).

An analysis of how phoneme segmentation might be achieved during development by Pierrehumbert (2003) concludes that it would be impossible to build a phonemic inventory from an innate and fixed set of acoustic features. She points to the extensive acoustic variability present in the articulation of phonemes bearing their invariant labels, and proposes that the phonemic inventory of the articulatory contrasts must be built bottom-up from the actual input and contextual features. Essentially, she proposes the constructivist solution to the problem of phoneme segmentation. See also Ambridge and Lieven (2011) for a summary.

In accord with the position adopted by Pierrehumbert (2003), Werker et al. (2012) propose that the repetitions of the phonemic tokens is crucial for the infant's phonetic learning; that phonetic categories are identified at least in part by information contained in the statistics of the repeated sounds (and aided by contextual information). This view was affirmed by Maye et al. (2002) using the [da̪]-[ɖa] contrast discussed earlier (§9.1) in infants of 6 – 8 months. For a summary of the experiment see Werker et al. (2012).

Clearly, semantic feed-back must also participate in establishing phonemic categories. After all, lexically informative categories are those that are likely to prevail, and language-specific categories are thought to 'solidify' as infants come to treat speech as a means of communication. Work by Yeung and Werker (2009) coupling a pair of phonemic sounds, respectively, with two pictures was shown to promote the establishment of phonemic categories. Such associations are reminiscent of those that promote multimodal learning. That the establishment of phonemic boundary distinctions rely on semantic categories suggest that it is *unlikely* that there exist innately given phonetic structures.

Nittrouer (2001, 2002) too has cautioned against the oversimplified view of infant speech perception in which infants are innately provided with the capacity to discriminate the world's phonetic contrasts.

It is thought that with exposure and experience infants lose this early ability as part of the phenomenon of interlinked critical periods during development proposed by Werker and Tees (2005). They suggest that distinct critical periods are associated with each of the several subsystems (phonetic, phonological, lexical etc.) involved in the overall process of vocal language acquisition, and that these interlinked parts of the system and their separate periods of rapid learning contribute to the establishment of a hierarchy of processing in a cascading fashion. There is, thus, a sequential bottom-up modular growth, where the critical period of the lower element, for example the phonetic phase, ends before the onset of learning of phonological structures and so on. Such an organization during development is thought to promote the maintenance of coherence in the overall analytical structure.

Piaget commented on the existence of a common sequence of events in child development, which is found to exist across cultures, even though the temporal extent of the individual developmental phases of the sequence may vary. Work on cochlear implantation in congenitally deaf children demonstrates the importance of critical periods and early intervention if verbal communication is to be established (see §9.7).

The view that speech sounds do not trigger innately embedded phoneme-recognition-tokens is reinforced by the observation by Grieser and Kuhl (1989) that English-learning 6-month-olds generalize over (i.e., fail to discriminate between) variations of the English vowel [i], and learn the typical version of the vowel [i] rather than the less frequently encountered atypical version of [i]. This observation suggests that it is the frequency with which the sounds occur in the input data stream that determines the distinctions that are learned, and casts doubt on the existence of a set of innate distinctive features that specify phonemic boundaries. This phenomenon is referred to the ‘perceptual magnet effect’. Kuhl et al. (2008) provide further details of this effect in their excellent review on phonetic learning.

Nativists claim that the brevity of the exposure required for infants to distinguish between phonemes indicates the existence of an innate phoneme recognition module. Given that the procedure followed in all tests of phoneme discrimination entails the repeated presentation of the same isolated phonemes to the infant prior to testing, it can be equally claimed that infants can become sensitive to the range of sounds presented to them even for the short duration whilst they are being tested in the laboratory. For instance, Werker et al. (2012) reported that in their study it took about 2 min for the establishment of new phonemic categories by adjusting the statistics of the variation in the sounds [da̪]-[ɖa] in infants aged 6 – 8 month. These infants were previously naïve to the distinction, and were tested immediately after being presented with the tokens in semi-random order. During normal development, however, where the infant is exposed to continuous speech, this learning process may be expected to take longer.

9.2.2 Prenatal Auditory Development

Given that auditory function can be detected at 16 weeks g.a. it would be reasonable to assume that auditory experience is available to the fetus for a period of over five months. As such, the finding that infants are born with some ‘processing biases’ that were previously attributed to native endowments can be accounted for by auditory learning in the womb.

For instance, Ambridge and Lieven (2011) observed that fricative sounds (such as the English [sa] versus [za], made by forcing air through a narrow channel), are more difficult for neonates to discriminate than vowel sounds and consonants. These high frequency airborne sounds in the mother's speech would not be readily transmitted through human tissue to the fetus in its aqueous environment. That the distinctions between fricatives can be made only later during postnatal development is consistent with the view these differences are not readily learned postnatally because of a lack of their experience in the womb.

Belin et al. (2004) observe that babies cannot talk or understand speech, yet they are able to distinguish between individual voices. In support of the view that the process of speech recognition begins in the womb, Susan Gregory[24] states:

a) The mother's voice is recognized at birth, and the neonate can distinguish it from other voices (evidence was obtained using high amplitude sucking by infants to express a preference for the mother's voice (DeCasper and Fifer, 1980).

b) The human voice is preferred by the neonate to other sounds of similar pitch and intensity (Friedlander, 1970).

c) The neonate shows preference to sounds within the human voice range compared to those outside it (Eisenberg, 1975). As mentioned before, infants can distinguish between the phonemes /p/ and /b/ at the age of 1 month (Mehler, 1993), and also distinguish between these consonants and vowel sounds in general (Clarkson and Berg, 1983).

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[24] In: The Early Development of Audition and Vision in Hearing Infants, by Susan Gregory. Reader in Deaf Education University of Birmingham http://www.deafnessatbirth.org.uk/content2/defelop/lang/01/content.pdf Its date of publication could not be obtained.

d) At 2 days of age, neonates can distinguish between their mother tongue and other languages (Werker and Desjardins, 1999).

e) Neonates can distinguish between stories the mother read to the fetus in the last 3 months of pregnancy from other stories (DeCasper and Spence, 1986).

Although findings (a) - (d) display prenatal auditory competences, they do not unequivocally allow the claim that these competences are derived through learning. However, finding (e) clearly suggests prenatal auditory learning. However, findings (a) - (d) are supportive of the position that speech recognition is learned, particularly when considered in association with the other evidence.

This view is reiterated in more recent work by Houston et al. (2012), who point out that most children’s access to auditory information begins before birth, and that such exposure affects their auditory development in respect of speech perception, and indeed speech production. Furthermore, it is found that infants adopted at birth by step-parents who speak a language different to that spoken in the birth parents’ setting, nevertheless acquire the language spoken in their adoptive environment[25] (Pallier et al., 2003). This provides further support for the view that speech recognition is learned, which is consistent with the view that infants become sensitive to the range of sounds presented to them. See Houston (2005) for further discussions.

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[25] The window period for phoneme learning extends to approximately 6-8 months after birth.

9.3 Neurophysiological Correlates of Voice and Speech Perception

9.3.1 Introduction

Belin et al. (2004) observed that the human voice is not only the carrier of speech, but also contains paralinguistic information about the speaker's identity and his emotional state. Even when the semantic, or speech information is not available in a voice, because it is a baby crying or a cough, humans are able to rapidly extract information about the identity and affective state of the person who produces the vocalizations.

As stated before, interest in human speech-sound recognition in the present work arises from the observation that our capacity to identify such sounds enables the provision of contextual information for sound source localization. In particular, it is of interest whether the capacity for the recognition of human vocalizations requires a period of learning or is given innately.

In regard to the capacity for the recognition of speaker identity, results of experiments carried out on adults will be utilized to evaluate whether this human capability of speaker identification is derived through learning or provided innately. In the case of semantic processing of speech sounds, for reasons mentioned in the Preface to this chapter and in §9.1 (also see Werker and Tees, 2005), attention will be restricted to speech sound recognition processes that occur early in the speech recognition hierarchy (see below). The cortical substrates that exhibit the neurological correlates of speech learning will also be described. Work describing the neurophysiological correlates of speech acquisition will be provided (Kuhl et al., 2008).

As observed, interesting associated issues are generated by this investigation that can inform also about the origins of the vocal exchange of all semantic information: whether or not the capacity to perceive speech sounds bearing semantic information contained in all spoken languages is derived rather than being primitive. This question will be addressed in §9.11.

It appears that all thalamo-cortical auditory input is initially analysed bilaterally in the core region of primary auditory cortex (AI). As indicated earlier, there is also extensive subcortical processing of auditory input, and some of it is pertinent to speech processing (see, for instance, Guediche et al., 2014; Johnson et al., 2008 and Song et al. 2008). However, the cognitive content of speech sounds appears to be derived from cortical analysis, which the current work will dwell upon.

A large number of studies using positron emission tomography and fMRI (cited in Binder et al., 2000) show that the initial cortical activity generated by speech sounds extends bilaterally in both directions from AI along the posterior-anterior axis in auditory association areas comprising the superior temporal sulcus (STS) and the superior temporal gyrus (STG).

The anterior regions of the temporal lobes comprise the anterio-ventral ‘what’ stream, in which the early stages of speech signal processing take place. In agreement with this view are clinical reports (also cited in Binder et al., 2000) that show that bilateral lesions restricted to the superior temporal lobes result in the syndrome of ‘pure word deafness’, so that individuals who are afflicted cannot discriminate between the sounds of different words.

The bilateral anterior temporal ‘what’ streams and the corresponding postero-parietal dorsal ‘where’ streams converge on prefrontal and premotor cortical regions to form an interacting network. For details see Rauschecker and Scott (2009).

Earlier work by Binder et al. (2000) using fMRI to chart activation in the temporal lobe of adults suggested the existence of two bilateral hierarchical organizations for the processing of sounds that were dedicated to non-semantic analysis.

In their experiments, the subjects were presented with unstructured noise, frequency-modulated (FM) tones, reversed speech, pseudo-words and words. The authors were able to identify (a) dorsal areas around Herschl’s gyrus that were activated bilaterally more by FM tones than noise, suggesting their role in processing simple temporally encoded auditory information, and (b) regions bilaterally in the superior temporal sulcus that were more activated by speech stimuli: words, pseudo-words and reversed speech than by non-speech sounds.

Previous work had identified separate left-lateralized activations that were in regions that were more ventral-temporal and temporoparitetal than those reported by Binder et al. (2000), and considered to be involved in processing linguistic information associated with words.

These findings pointed to the existence of two hierarchical areas involved in *speech* sound analysis: (i) a left-lateralized region for analysis of speech sounds associated with language and (ii) bilateral regions for the early processing of non-semantic speech sounds.

Belin et al. (2004) summarize these and other findings to suggest that voice information processing is dissociated into three functionally independent hierarchically organized systems: (i) analysis of speech information, involving anterior and posterior STS as well as inferior prefrontal regions predominantly in the left hemisphere; (ii) analysis of vocal affective information, involving temporo-medial regions, anterior insula, and amygdala and inferior prefrontal regions, predominantly in the right hemisphere; (iii) analysis of vocal identity, involving 'voice recognition units' – probably instantiated in regions of the right anterior STS – each activiated by one of the voices known to the person, and a subsequent supra-modal stage of *person* recognition ('person identity units').

The above summary is reinforced in a more recent review by Rauschecker and Scott (2009), suggesting that cortical speech processing is sub-divided hierarchically into a number of separate streams according to levels of complexity, or abstraction. However, complexity is not the sole criterion for the existence of different processing pathways.

There is common, often bilateral, early processing that is utilized later in distinct categorical hierarchies similar to those found in the visual system, in which, for example, orientation tuning for visual object discrimination is applied in common, for instance, to colour and motion processing (Desimone, 1990).

The two aspects of cortical speech processing that the current work will dwell upon are those pertaining to the apprehension of speaker identity and the phonological content from which semantic or lexical information is derived.

9.3.2 Speech Identity Processing Regions

Following the exploratory work by Binder et al. (2000) charting the regions of the human temporal lobes responding to speech and non-speech sounds, Warren et al. (2006) used fMRI to investigate temporal lobe mechanisms involved in the analysis of voices as sound sources. They observed that human voice analysis is a significant auditory recognition task, in that it enables the identification and localization of an individual.

They surmised that speaker identity discrimination must involve the spectro-temporal analysis of individual voice characteristics such as pitch, intensity and timbre, and made an analysis of over a dozen previous brain imaging studies that had been directed at localizing brain areas involved in the pre-semantic analysis of human voice processing. From their analysis Warren et al. (2006) concluded that voice-specific analysis must occur in the temporal lobe; a view reinforced by human lesion evidence for the syndrome phonagnosia, where those afflicted are unable to form memories of new voices nor identify previously known individuals from their voices. The condition does not affect speech comprehension. For details see Van Lancker et al. (1988) and Wikipedia using search item: phonagnosia.

In order to identify the specific human brain substrates for the different stages of voice analysis, Warren et al. (2006) used monosyllabic words made up of consonant-vowel-consonant sequences spoken by a number of different individuals. The sequences were vocoded into different numbers of frequency bins in order to vary the information available to the subject about the identity of the speaker, and the intelligibility of the vocoded speech. fMRI was used to monitor the activity in the subjects' temporal lobes whilst the differently synthesised speech sounds were presented to them.

The authors reported that as the spectral information in the stimuli increased (through the increase in number of frequency bins being used for the vocoded voices), and the identity of the speaker became clearer, there was a corresponding increase, bilaterally, in the activity in the temporal lobes. Such results of increased bilateral activity associated with speaker identity processing has also been reported by Salvata et al. (2012).

Warren et al. (2006) surmised that there was a mechanism for the analysis of voice information in a bilateral network extending from the posterior to the anterior superior temporal lobe surrounding the superior temporal sulcus. They claimed that there was a hierarchy of greater abstraction from the posterior to the anterior regions. The detection of the generic human voice sound, defined by its elementary spectrotemporal properties, was found to occur in the posterior superior temporal plane. The discrimination of features of greater abstraction and the analysis of the speaker identity mechanisms took place in higher order anterior areas.

Warren et al. (2006) charted the temporal lobe processing regions and established that there exists a 3-stage speaker identification hierarchy involving: (a) general source attributes that are analysed in the posterior superior temporal lobe, (b) the abstraction of voice identity features in the posterior STS and (c) further analysis of speaker identity in the anterior STS and higher order cortices in the middle and anterior temporal lobe. The authors did not address explicitly the issue of speaker identity learning.

Rauschecker and Scott (2009) observed that the areas in humans that were related to speaker recognition might be homologous to similar areas found in monkeys that contain detailed spectral information of separate individuals. Petkov et al. (2008) also found a posterior–anterior hierarchy with an anteriorly directed flow of vocal information for discriminating the identity of conspecific calls in the macaque.

9.3.3 Evidence for Learning Speaker Identity

Latinus et al. (2012), elaborating upon similar earlier work by Andics et al. (2010) set out to provide evidence for the previous suggestion by and Belin et al. (2004) that there exist anatomically separable cortical regions for processing voice sounds carrying affect as opposed to speaker identity. With this end in mind, the subjects used by Latinus et al.

(2012) were scanned using fMRI whilst listening to sound samples in which the initially unknown speaker identity was continuously varied (morphed) between those of two individuals. The affect in the voices was also varied.

The subjects were scanned intermittently as they learned to recognize the initially unknown identities of the individual voices and the degrees of affect in them. The intervening training sessions, during which the subjects were allowed to learn both speaker identity and affect, consisted of two stories, words and vowels spoken by the 3 individual speakers lasting about 20 minutes per session.

The results obtained can be summarised as follows.

1) From the loci and the varying amounts of cortical activation observed in the successive fMRI scans for the different voice samples the authors claimed that affect and identity information were seen to be processed in separate cortical regions.
2) Behavioural learning for speaker discrimination was demonstrated.
3) There was a decrease in the BOLD signal in the processing regions as behavioural learning proceeded. This is in accord with the view that learning, and the associated cortical plasticity, lead to repetition suppression of the activity in the regions involved (see §8.8).

Furthermore, comparison of the initial and final fMRI scans showed that learning speaker identity recruited activity to the initial activations in the STC and the superior temporal pole, and also those in the inferior frontal cortices. The experiments showed behaviourally that speaker identity was learned. The work also identified the cortical correlates of the plasticity. For further details of the experiments the reader is referred to the original report (Latinus et al., 2012).

It is worth noting that Warren et al. (2006) had previously demonstrated that the neural substrates involved in the processing of identity information are hierarchically organized. It can be surmised that speaker identity discrimination from voice sounds is not provided innately because the phonemic features upon which the hierarchy rests has been shown behaviourally to be learned. In sum, it seems unequivocal that speaker identification by voice is based on learning.

9.4 Semantic Processing of Speech Sounds

It has been known for some time that there is a left-lateralization in the temporal lobes for language perception. For instance, Werker and Tees (2005) recount that phonetic perception involves networks in the left temporal lobe in both adults and children, and that studies of dichotic listening[26] in adults and children show that there exists a left hemisphere advantage for this faculty. These authors also cite studies showing preferential activity in the left hemisphere language areas during signing in subjects whose first language was American Sign Language. Furthermore, that French speakers of Korean extraction who had been adopted during early childhood by French step-parents, and had not spoken Korean

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[26] Where the subject is required to attend to different spoken inputs to different ears over headphones and tested about their contents.

since adoption, showed activation in the left hemisphere to French and not to Korean (Pallier et al., 2003). These findings affirm that the capacity for linguistic exchange is not assigned by the language spoken by the mother, and that the language faculty is left-lateralized in cortex.

It seems that the critical periods that apply to language learning restrict the acquisition of competence in speech perception in a second language even if the exposure is extensive and early. Pallier et al. (1997) reported that Spanish-Catalan bilinguals who learned their second language (Catalan) during the most sensitive period, i.e. before the age of 6 years, nevertheless could not master the contrast between the Catalan [e] and [ɛ].

The processing of speech sounds early during *development* can be regarded as being non-semantic. Although the infant may be able to distinguish between some phonemes, it has no linguistic knowledge. In keeping with this view, Werker and Tees (2005) observed through event related potential (ERP) studies that at 13 months of age, when infants are presented with words known by them, higher amplitude bilateral activation is observed over temporal and parietal lobes than in other regions, whereas at 20 months of age, higher amplitude responses are restricted to left-hemisphere temporal and parietal recording sites. It may be surmised that left lateralization is a feature of the development of the capacity for the extraction of semantic information. Put another way, left lateralization may be understood as a departure from the bilateral non-semantic processing hierarchies for word sounds, and marks the initiation of linguistic processing.

Werker and Tees (2005) have elaborated upon the development of the semantic hierarchy, and note that that there exist separate critical periods for the different processing categories *viz.*, phonetic, phonological, lexical-semantic etc., with mutual interactions between the cortical regions supporting the different processes.

The distinction between the bilateral speech processing hierarchy and that for semantic processing has been demonstrated by clinical studies that implicate *left* posterior superior temporal sulcus as the region directed at deriving semantic content from the speech signals. Such left lateralisation has also been demonstrated for primate neural responses to conspecific vocalizations whereas the right superior temporal gyrus and superior temporal sulcus have been associated with stimuli containing dynamic, melodic pitch variation and musical patterns (Binder et al., 2000).

As indicated earlier in §8.4, semantic processing of speech sounds take place in a hierarchical order beginning in the auditory core region (AI), and extending into the belt and the parabelt regions, where higher-order specificity is generated by combining input from the lower-level neurons that are sensitive to relatively simple features. Rauschecker and Scott (2009) point out that the left-middle and left-anterior superior temporal sulcus are more responsive to consonant-vowel syllables than auditory baselines. Within these speech-specific regions of the anterior superior temporal cortex, there may be sub-regions selective for particular speech-sound classes, such as vowels, raising the possibility that phonetic maps have some anatomical correspondences in anterior temporal lobe areas.

9.5 Investigation of Early Semantic Processing in Adults

As mentioned in the *Introduction*, non-linguistic speech sounds evoke bilateral responses in temporal cortex, and phonological sounds that form the basis of linguistic analysis in adults evoke left lateralized responses (Scott et al., 2000). In order to further investigate the early parts of the hierarchy for linguistic speech sounds Scott et al. (2006) charted activity in the rostral and caudal auditory cortex (essentially the anterior and posterior temporal cortices respectively) using positron emission tomography (PET) of the superior temporal gyri and sulci in adult human subjects.

By mixing the speech sounds with varying amounts of noise, an 'intelligibility criterion' was established to determine whether or not the modified speech sounds could be decoded by the subjects. It was found that the regions that were active when speech could not be decoded were located bilaterally in the speech-sound areas, whereas when the speech sounds became intelligible activity was recorded also in the left anterior superior temporal sulcus.

Scott et al. (2006) noted that the posterior STS showed sensitivity to aspects of the acoustic sequence from which meaningful structures might emerge. Cortical response to speech-sound amplitude modulation was found to occur early in the hierarchy in the caudal region, close to AI in lateral superior temporal gyrus, which also shows sensitivity for the phonological structure of speech. The anterior region was more closely associated with the extraction of meaning.

Their results are in accord with the existence of a left-lateralized posterior-anterior hierarchy along which the complexity of preferred stimuli increases from tones and noise bursts to words and sentences. This hierarchy for speech intelligibility, as charted by Scott et al. (2006), extends from the core to the belt and on to the parabelt regions.

9.6 Neural Substrates for Language Acquisition

The review by Kuhl and Rivera-Gaxiola (2008) on studies using a variety of brain imaging techniques for the elucidation of the neural correlates of language development demonstrates that there is little doubt that the capacity for language comprehension is acquired through learning.

In their review, these authors describe studies using ERP (EEG), MEG, fMRI and near infrared spectroscopy (NIRS) that uncover neural substrates varying between those associated with the learning of phoneme recognition in neonates and those involved in the encoding of words and the processing of semantic and syntactic information in sentences that occur in the second and third years of life. Two of these studies are briefly described below.

As mentioned earlier, behavioural studies have demonstrated that infants exhibit a universal capacity to learn to detect the phonetic contrasts of all languages at birth. This capacity is significantly altered by their experience of spoken language that leads to a transition in their capacity for phonetic perception as early as 6 months for vowels and by 10 months for consonants.

The two important changes that occur at the transition in phonetic perception are that the infants' capacity for learning phonetic contrasts in their native language increases significantly, while the ability to discriminate phonetic contrasts in other languages declines between 6 and 12 months of age. Rivera-Gaxiola et al. (2005a) have studied the neural correlates of this change by comparing the group data of electrophysiological responses to native and non-native consonant contrasts of infants at the ages of 7 months and 11 months. In their study using event related potentials (ERP) they showed that there was a change in the P150-250 and N250-550 time windows on presentation of non-native consonants at 7 months. This change in the ERP response was absent at the age of 11 months in the group data. However, there were subgroups of infants who showed differences in the ERP signals in the P150-250 and N250-550 time windows.

Rivera-Gaxiola et al. (2005b) hypothesised that the extension of the critical period for the learning of non-native phonemic contrasts in the above mentioned subgroup might be associated with a slower rate of later native language word learning among these infants. In this follow-up work the authors found that they could predict from the characteristic of the ERP data the existence of this effect, in that infants in the subgroup showed a slower rate of word learning at 18, 22, 25, 27 and 30 months than those whose critical period for the learning of non-native consonant contrasts ended by the age of 11 months.

The analyses presented thus far show that there is a close correspondence between the behavioural evidence that supports the view that the human capacity for the recognition of human speech sounds is learned, and the hierarchically organized plastic anatomical structures that support these functions.

9.6.1 Origin of Concepts

The Concise Oxford Dictionary definition of the term concept reads: 'A class of objects, general notion'. Boden (1987) elaborates thus: 'An abstraction or general notion that may serve as a unit (or an 'atom') of a theory'. She notes that a major part of [analytic] philosophy is to clarify them. Thus, the term concept may be regarded as an idea of something formed by mentally combining all its characteristics or particulars.

In this regard, Kornorski's notion of gnostic neurons (Kornorski, 1967; see §3.6.8 Hierarchical Processing and Gnostic Neurons), as being the ones that produce their optimal responses for the presentation of a particular visual image, idea or word, provides a descriptor in the neural substrate for a specific concept. For example, the general face neuron responds optimally to faces regardless of whose face it may be (Rolls, 2011), and neurons in the listener's temporal cortex that are tuned to the presentation of particular phonemes (which are abstract notions), respond optimally to them irrespective of the fundamental frequency of the speaker's vocal cords.

In his analysis of the development of speech recognition, Huyck (2007; 2012) endorses the view that the process of speech recognition is an acquired skill. He regards the generation of Hebbian cell assemblies as the neural substrates that accrue from the learning of concepts, and has proposed a neural network model comprising hierarchically organised set of such cell assemblies that classify auditory input into concepts. This goes some way towards providing a constructivist account for the generation of concepts. It is such an account that is taken to hold while addressing the notion of time as being an acquired concept in chapter 10.

Further evidence in support of the view that our capacity for the recognition of human vocalizations are acquired through a period of learning rather than given innately is provided by studies of auditory deprivation.

9.7 Auditory Deprivation

The early onset of auditory function makes it difficult to evaluate the role of learning in the gaining of auditory competence through experiments using auditory deprivation in humans. As mentioned earlier, it is acknowledged widely that the congenitally deaf lack the capacity for speech production, suggesting that production is contingent upon perception.

The study of deafness and work on cochlear implantation in congenitally deaf children, particularly in the context of speech perception, has provided much information about neural plasticity and the development of the auditory system. Through a brief review of this work, it is hoped to reinforce the view that human auditory function is gained through learning, and that auditory deprivation leads to auditory and speech deficits.

Kral and Sharma (2012) note that to be able to categorize acoustic features into auditory ‘objects’, distinctive features must be accurately represented in the brain. A deficient early representation of acoustic features complicates discrimination of auditory stimuli and subsequently affects the starting point for learning.

9.7.1 Cochlear Implants

A cochlear implant device is a small electronic acoustic prosthesis designed to bypass absent or damaged hair cells of the cochlea, and stimulates the auditory nerve. It is composed of four parts: an external microphone that picks up sound from the environment; a speech processor, which performs a coarse Fourier analysis on the sounds picked up by the microphone; a transmitter which converts the sounds from the speech processor into electric impulses that are conveyed by radio waves to the implanted receiver. The electrodes of the receiver are surgically inserted to make contact with the spiral ganglion in the non-functioning cochlea to enable the auditory nerve to transmit the electrical impulses into the brain (see Fig. 9.1).

The device differs from a hearing aid in that it bypasses the outer ear, which the hearing aid stimulates. Instead, the cochlear implant directly activates the auditory nerve with electrical impulses. For details, see Kral et al. (2004).

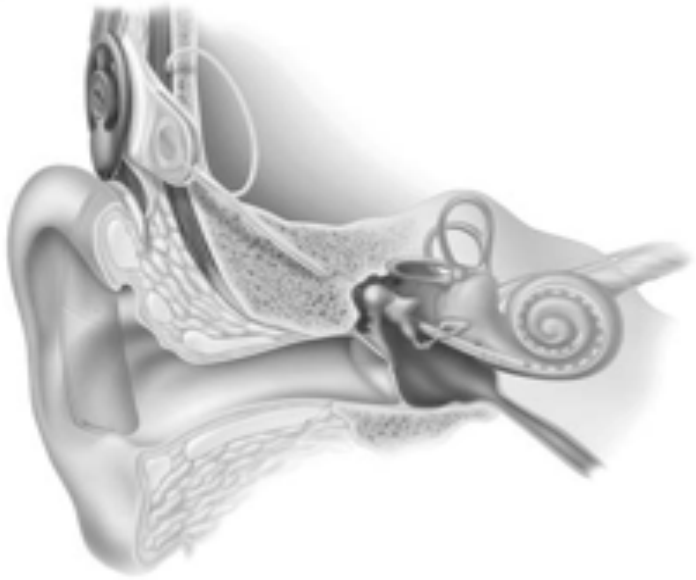

Fig. 9.1 A commercial cochlear implant device consisting of an extracorporeal sound processor with a microphone and an attached transmitter coil that relays signals through a radio link to the receiver unit connected to the intracochlear electrode array inserted into the cochlea (Source: Kral et al. 2004).

Congenital deafness is frequent in humans (0.2 – 0.5 cases per 1,000 live births), and since its advent in the mid 1950s[27] there have been 200,000 cochlear implants performed worldwide, including 80,000 in infants and children (Kral and Sharma, 2012).

The general wiring pattern in the subcortical afferent auditory system develops, in part, before hearing onset at 16 weeks g.a., and is generally preserved in deafness. The auditory nerve often survives the loss of inner hair cells in the cochlea, and is available for artificial electrical stimulation by use of cochlear implants. These are contrived to mimic the pattern of activity that would be otherwise obtained from the coding provided by the basilar membrane, and cochlear implant stimulation results in the activation of the auditory system

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[27] For a history of cochlear implantation, consult Wikipedia using search item: ‘Cochlear Implant’

from the auditory nerve up to auditory cortex in implant recipients (Kral and Sharma, 2012).

The view that auditory perception is acquired through experience is amply supported by the finding that if children congenitally deaf due to hair cell loss are fitted with cochlear implants before the time for the onset of language production (at around 10 months, see below), they can successfully acquire speech perception and production. Since there is a critical period for language acquisition (Houston et al., 2012), it is considered that implantation is best carried out before the age of 2 years, but success is reported also for implantation up to the age of 6.5 – 7 years.

Children for whom implantation is carried out later in childhood can nevertheless detect auditory stimuli, but are not able to discriminate complex sounds even after long periods of implant use, and late implantation leads to compromised language understanding, poor speech perception and production.

Kral and Sharma (2012) note that during auditory learning, a sensory stimulus gains new behavioural significance, resulting in a dynamic reorganization of the representation of the features and objects associated with that sensory stimulus. Receptive fields in auditory cortex change after sufficient training with cochlear transplants, reflecting improvements in the performance of the learned task. Both subcortical and cortical mechanisms contribute to this process. These effects might also be expected to occur as the hearing infant progresses from the early stages of vocalization into the canonical stage of babbling (See below: §9.8.2).

Approaching the issue of auditory learning from the point of view of the underlying neural substrate provides an alternative evaluation of the origins of auditory function. Kral and Sharma (2012) review studies exploring developmental changes in the molecular machinery of synaptic plasticity associated with critical periods for different behavioural functions, and suggest that these differences arise because of differences in underlying neuronal structures and maturation rates. They go on to elaborate upon environmental factors that might affect the prolongation of critical periods. They also confirm that children implanted after 6.5–7 years of deafness (too late for the acquisition of auditory competence) show normal metabolism in high-order auditory cortices, suggesting that these cortical areas were unavailable for auditory processing, presumably due to their recruitment by other sensory modalities[28]. As mentioned in §7.4.1, work by Sur's group at M.I.T. on ferret kits demonstrated that diverted visual input resulted in orientation tuning capability in *auditory* cortex.

In sum, the findings presented above provide support for the view that the capacity for human speech perception is acquired rather than given innately. The next section will provide an analysis of human speech *production* directed at supporting the earlier suggestion that the deaf do not speak because speech production is learned, and is reliant upon speech perception to enable its function.

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[28] Cortical regions deprived of the sensory input they would normally process are generally found to be recruited to perform processing for other sensory modalities. Such recruitment would result in their showing 'normal' metabolic function associated with their new roles.

9.8 Dependence of Speech Production on Speech Recognition

Speech sound production takes place in the vocal tract comprising the lungs, vocal cords, oral and nasal cavities and the articulators in the mouth (the tongue, lips etc.). Studies of vocalizations in the congenitally deaf, who are deprived of auditory input even during gestation, provide useful information about the link between speech recognition and speech production. Such studies reveal the existence of speech production reflexes that occur both in the deaf and in the hearing, which hearing infants develop into speech sounds. These are reminiscent of ‘primitive reflexes’ described in §6.7.3. However, speech reflexes arise spontaneously rather than being triggered by an external sensory stimulus.

9.8.1 Development of Speech in Hearing and Deaf Infants

Infant vocalizations have been categorised into two broad categories: (1) *vegetative sounds* (coughing, sneezing, burping and so on) and fixed vocal signals (crying, laughter, moaning etc.) and (2) *critical sounds* that are specific precursors of speech (the ‘protophones’).

It is recognised among medical practitioners screening infants for deafness that the progression in the capacity to speak through the development of critical sounds can be classified into 4 stages (Oller and Eilers, 1988).

As development proceeds there is a change from the preponderance of fixed vocal signals, as in crying and laughing, where the vocal tract is at rest, to one in which there is posturing of the tongue, jaw and lips that characterize vowels in natural languages.

There is an increased engagement also of the vocal cords and use of the larynx (or voice box), previously high in the throat to let the baby breathe while swallowing, which descends allowing the pharynx to develop, and the sounds of human speech to be formed.

The engagement of the vocal cords is accompanied by the articulation of the vocal tract to form resonant cavities for the production of different formant frequencies and the engagement of the tongue to shift their frequency characteristics rapidly.

9.8.2 Stages in Infant Vocalization

Stage 1	0 - 2 mths	Comfort sounds, precursors to vowel production.
Stage 2	2 - 3 mths	Gooing, precursors to consonants.
Stage 3	4 - 6 mths	Expansion: raspberries (labial trills and vibrants), whispers, and squeals.

Divide between Hearing and Deaf

Stage 4	7 - 10 mths	Controlled production of well-formed syllables:

Canonical stage, reduplicated sequences bababa etc. Phonetic sequences available for assembly into words

(Source: Oller and Eilers, 1988).

Stages 1-3 are common to hearing and deaf infants. Both groups produce spontaneous vocalization (including raspberries and fricatives, squeals and growls). Also, the shift from the articulations of the gooing sounds from the rear of the oral cavity in stage 2, to the more frontal productions of stage 3, appear to occur at similar ages in deaf and hearing infants.

Stages 3 and 4 have been recognized as being distinct from one another in hearing infants, in that the boundary between the stages marks the onset of the 'canonical' stage. Whether there is a continuous change, with the abject sound making evolving into spoken language in a causal chain, or whether the transition is more abrupt is debated in the 'continuity' and 'discontinuity' hypothesis. This debate is not of further interest here, but the transition marks a divergence in the development of speech production between hearing and deaf infants.

Van Beinum and Doppen (2003) have compared the utterance structures of deaf and hearing infants, and report that many deaf infants produce multi-syllabic utterances in the manner that hearing infants do, but deaf infants do not proceed to the 'canonical' utterances characteristic of stage 4.

9.8.2.1 Babbling

Human infants are thought not to be excited or upset when babbling, but babble spontaneously when emotionally calm. Babbling entails learning to use the sound production apparatus without any particular voluntary communications objective in its initial phases. The early vocalizations of ‘protophones’ do not generally contain any meaning or refer to anything specific, and arise in a similar manner to the primitive reflexes mentioned in the context of learning to apprehend mass (§6.7.3).

At the age of 10 months there is a divergence in the vocalizations of the hearing, who will learn to speak and the deaf who will not. At this stage, the structure of the syllabic productions of the deaf differs from those of hearing infants. Hearing infants enter the canonical stage, where they produce well-formed syllables that can be parts of words, which deaf infants cannot. A delay in the onset of the canonical stage has been shown to indicate an extreme risk of hearing impairment (Oller et al., 1999).

The occurrence of the precursors of babbling also in deaf infants suggests that this process may be innate (it is seen to be present also in other species), and that babbling is a facilitator in the development of spoken language, much as primitive reflexes are in ordering the proprioceptive and somatosensory systems, and developing tone and control of the musculature involved in haptic manipulation that volitional factors then utilise in order to learn motor primitives.

In the case of babbling-sounds made by hearing infants during the transition between stages 3 and 4, there would be feedback to inform the infant about whether or not its volitional motor activities were meeting their targets (normally determined by speech sounds heard by the infant in its setting). Indeed, Oller et al. (1999) observe that what the infant hears and parental influences both act to adjust infant vocal patterns, especially at the beginning of the canonical stage. In the case of the congenitally deaf, both targets and feedback would be absent.

The finding that phoneme production (articulation) is limited to those that are recognized by the infant indicates that speech production is strictly determined by what is learned through speech perception. Thus, it seems that it is this lack of auditory feedback in the case of deaf infants, despite parental encouragement, that stops them from acquiring speech. This view is widely held in the current language acquisition literature (Ambridge and Lieven, 2011), and is consistent with the view that speech recognition is a prerequisite for speech production. Further evidence is provided below.

It is interesting to note that during canonical babbling and the early stages of word production, the infants' efforts are directed at the composition of *phonemic sequences* rather than attempting to mirror the speech sounds of its carers. Clearly, these usually arise from adult productions and the infant cannot match the timbre of adult sounds. As such, at this stage the infant has come to apprehend the abstract nature of the phonemes it seeks to reproduce.

9.9 Feral Children

Feral children have long fascinated workers in many disciplines; especially those involved in the fields of linguistics and human psychology. Unable to perform ‘The Forbidden Experiment’ - that is, to raise a child deliberately isolated from human contact, in search of the elusive ‘natural’ human condition– there remains interest in reports of feral children because they may provide insights into the mechanisms of human development. In particular, they may have helped illuminate the nature-nurture debate. However, there is concern about the veracity of many of these reports (Aroles, 2005). The following account about feral children is summarized from Ward (2004).

Throughout ancient and modern times, there have been tales of children rescued from the wilderness who had been reputedly adopted by wolves, bears, monkeys and so on. Stories about wild or feral children elicit both heart-rending pity for their abandonment and wonder for their survival against terrible odds. Ancient mythology has many tales of children nurtured by animals; witness the legend of Romulus and Remus.

One of the earliest written accounts was by the Roman historian Procopius, in *De Bello Gothico,* of a baby boy abandoned by his mother during the chaos of the Gothic wars in about AD 250, and suckled by a she-goat. He was found in her company when the survivors returned to their homes. Procopius states that he saw the boy himself.

Feral children are portrayed in reports as being like wild animals and sharing a common experience of isolation from human society from an early age: lost, stolen, abandoned or strayed. They were then supposedly nurtured by animals or somehow survive on their own during their formative years. Devoid of human cultural influences, they are thought to have grown up often moving on all fours, and with distinctly animal-like behaviours. Regardless of their gender or the nature of any other animal companions, they had one thing in common: their inability to communicate using speech, while showing no signs of any hearing impairment.

Dr Jean Itard published the story of Victor, the wild boy of Aveyron in a book at the end of the 18th century. Itard recounts that the boy was found roaming alone in the woods of Lacaune in Southern France. He had been sighted on several occasions by villagers and was eventually captured by peasants, and displayed in the village square. He soon escaped, only to be recaptured a year later.

Around the age of 12 when he was discovered, Victor had clearly survived in the wild for at least two years, perhaps longer, on his own. It is conjectured that he was abandoned at the age of six by a father who couldn't cope with his learning difficulties, although there is no reliable information about this matter.

Victor eventually found a champion in Dr Jean Itard, who then devoted five years to making a study of the boy during which time he attempted to instruct Victor in human behaviour, and to impart skills such as speech, reading and writing. His study is recounted in Itard (1962).

Although Itard did have some significant successes when it came to humanizing Victor, there was much that he was never able to achieve: in particular, the boy was never able to use any conventional means of communication.

From the analysis provided above, a lack of speech comprehension and production can be understood as arising from the fact that speech production is learned and depends on the capacity for speech comprehension. The latter cannot be learned if a child has been isolated from humans during infancy. In the case of Victor the capacity for speech perception may have been forgotten if the child had been isolated from human contact for a period of about 7 years (a number estimated from the ages presented above).

This view of the effects of auditory deprivation is supported also by the history of the life of Alexander Selkirk, upon whom Defoe possibly based his novel *Robinson Crusoe*. Selkirk, a Scott (b. 1676) lived for 4 years and 4 months without human company on the Pacific island Más a Tierra. When he was rescued on 2.2.1709, it is reported that he was initially unable to speak to his English-speaking rescuers[29]. These findings are consistent with the view that the competence for speech perception and production are not native, and can be lost through a lack of use.

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[29] See for example: http://en.wikipedia.org/wiki/Alexander_Selkirk
http://www.ini.unizh.ch/~tobi/fun/alex/alex2.php.

9.10 Summary

- Auditory competence in the perception of contextual information about the identity of different classes of objects from the sounds they make is acquired.
- The importance of the capacity for speech perception for the development of speech production; evidence from differences in babbling between stages 3 and 4 in hearing and deaf infants. The deaf do not speak because speech production is contingent on speech recognition.
- Deaf children fitted early with cochlear implants learn to recognise speech and can speak, once again endorsing the view that both abilities are acquired.
- Feral children with normal hearing do not speak because they have been deprived of the human speech sounds occurring in their environments.
- Normally developing children speak local language(s) irrespective of their mother tongue. This is because infants can learn all phonemic sounds during a critical period.
- There appears to be an arbitrary mapping between speech sounds and their meanings. The infant is imbued with the capacity for making meaning from these mappings.

In sum: we need to learn to recognize sounds in order to gain the capacity for structured hearing, and this allows us to learn to speak. It may be concluded that the prior knowledge about sounds made by objects, and, indeed, that obtained from vocal exchange are both learned. As such, the capacity for the auditory perception of length is learned.

9.11 Relevance of Above Findings to the Status of Linguistic Philosophy

The current work shows that the capacity for the recognition and production of sound patterns involved in vocal exchanges, e.g., speech, is derived. Given that speech is constituted by physical patterns of variations in sound pressure level at the location of the listener, this finding is consistent with the view that the capacity for the apprehension of physical reality associated with speech is derived.

In the process of the naming of objects by an infant, spoken words, taken to be physical tokens, accessed through hearing, are mapped onto physical objects. Such associations have been described, for instance, by Yeung and Werker (2009) as being a part of the assignment of sounds as tokens for objects.

The establishment of the mapping (or memory) between these physical entities entails the *creation of a meaning* by the subject for each new word. After all, it is indisputable that words at their very basis have meanings. As such, *the human being may be regarded as a meaning-maker*. Such a process of learning is something that every individual who can understand words has had to accomplish during infancy and childhood (and into adulthood).

The sound tokens that refer to objects in the world are learned, and the mapping between the sound token and the object can be arbitrary. This is because any object may be referred to by *any* human-speech-production. As such, the word sounds in themselves carry no innately accorded absolute or fundamental status. After all, the words as tokens are mapped onto the referents, for example to objects, and the process of making meaning seems to be arbitrary in regard to there being no biological pre-requisite for the establishing of any particular token-referent association. However, it is the individual who is the meaning maker when it comes to the attribution of meaning to word sounds.

10

APPREHENSION OF TIME

10.0 Introduction

The Foreword to Jean Piaget's *The Child's Conception of Time* (Piaget, 1969) begins thus:

> This work was prompted by a number of questions kindly suggested by Albert Einstein more than fifteen years ago[30] when he presided over the first international course of lectures on philosophy and psychology at Davos. Is our intuitive grasp of time primitive or derived? Is it identical with our intuitive grasp of velocity? What if any bearing do these questions have on the genesis and development of the child's conception of time?

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[30] The Translator's note in Piaget (1969) states that the French original was published in 1946.

These questions can best be understood to have arisen in Albert Einstein's mind after he had radically altered the previous notion of Newtonian time by proposing his Special Theory of Relativity. His questions set the stage for the current chapter on the origins in the human cognitive system of our capacity for the apprehension of the fundamental dimension of time, as used in science (T), and whether it is primitive or derived.

In the present work I seek to identify and explore the major themes that contribute to the Western notion of time with a view to showing that time is a learned concept. In addition, I will provide an analysis of how clock-time and Newtonian times are related to the notion of time as used in Special Relativity and Quantum Mechanics (scientific time). I hope to also provide answers to Einstein's questions, mentioned at the beginning of this chapter, within the context of current thought on child development and neurophysiology.

The author acknowledges his debt for some of the thoughts expressed in this chapter to the book by Mary Sturt, *The Psychology of Time* (Sturt, 1925), which predated by many years the publication of Jean Piaget's work *The Child's Conception of Time* (Piaget, 1969). It would appear that Piaget was unaware of Sturt's book, in that he does not cite it. However, both authors conclude, along with perhaps all recent reports on the topic that time is a concept acquired through learning. That said, some of Sturt's acute observations will be, nevertheless, quoted, and it is the purpose of this chapter to provide support for the view of time as a learned concept.

As with addressing the notion of physical reality, and the influence of the physical environment on the configuration of the senses to enable its perception, when evaluating the notion of time, I will show that the cultural setting is germinal in establishing the particular conception of time that develops in a given social environment. The work will be directed at showing that time, as used in science, is related directly to what is referred to as ‘objective’ time, i.e., time defined in terms of physical processes (see §10.1). In this way it will be shown that time, as used in science, is acquired rather than imbued innately.

The notion of time, and systems for time keeping, have been in existence for millennia (See, for instance, Sturt, 1925), and the term, as it is used conventionally by the scientific community, does indeed bear a relation to the human capacity to *learn* from experience what is referred to in Western thought as duration. Along with this endowment there also exist innate processes governing ageing that are common to virtually all organisms (See §10.5). However, it is doubtful if the existence of these clock-like structures in the human body can in themselves ensure the establishment of the notion of objective-time in the mind. Had such a transfer been feasible we might not have had to wait for Newton’s genius in contributing to the development of dimensional analysis and classical mechanics in the seventeenth century (See chapter 4).

It will be shown that the notion of time as it is used in modern science has not remained fixed historically, but has been subject to alteration with the changing requirements of scientific development and refinement. However, in the present work the attempt to provide a perspective on these changes will be confined to discussions of clock-time, time in Newtonian mechanics and their relation to time in modern physics. Broader reviews of this popular topic are readily available (see, for instance, Evans (2004) and

The Web Encyclopaedia of Philosophy

http://www.utm.edu/research/iep/t/time.htm#MIND).

In pursuit of the origins of time within the human cognitive system, it is important to keep in mind that not all societies have a word for time that might be recognized to mean what it does in Western cultures. It is claimed that none of the hundreds of Australian Aboriginal languages has a word for time (Lawler, 1991); see §10.4. These findings are in accord with the suggestion that time is a non-universal concept rather than being a thing that has material properties that all human sensory systems might come to apprehend should it be present in the developmental environment irrespective of cultural influences. This is despite the central role time occupies in defining physical reality within Western thought, where everything can be thought to exist in time, or to occur at a specific time. Indeed, time is central for the description of dynamic processes that lie at the core of the Western understanding of the physical universe. It is interesting to reflect that the absence of temporal expressions in Australian Aboriginal languages point to the influence of culture in giving rise to a separate reality (See §10.4). Needless to say, however, that there exist Australian Aboriginals who are bilingual in English.

Many philosophers, physicists, mathematicians and psychologists, among others, have written about time: Aristotle and Zeno the Stoic regarded time as being non-material, and due to our own minds. Heidegger's view that one's existence precedes the development of the notion of time is consistent with the suggestion that the concept of time has been built up through individual and cultural influences. And, although Kant regarded time as *a priori* (given innately to the human cognitive system prior to experience), Sturt (1925, p. 10) points out that time cannot be *a priori* because knowledge of time develops in individuals, and the capacity to apprehend it and deal with temporal ideas can vary from person to person. This ability seems to change with the age of the individual through childhood, and the culture within which the individual is embedded (see §10.3.1 and §10.4).

Such a view of the abstract nature of time is generally held despite the fact that most languages have a proper noun for it. Witness, in English: ‘What is the time?’; ‘the time has come’; ‘how much time?’; ‘the time it took’. Boroditsky (2011) observes that time occupies a central role in Western culture: the word ‘time’ is the most frequently used noun in the English language, with other temporal words, like ‘day’ and ‘year’ also ranking in the top 10. It is ubiquitous and yet it is not tangible. Evans provides a useful review of the notion from a wider linguistic perspective (Evans, 2004).

To deny time a material existence does not mean that time cannot be defined in an objective manner, in that it may attain its objective status through its definition by association with the external world of objects. This view has been widely accepted, and lies at the core of any elementary study of the sciences (see §10.1). However, it is also widely acknowledged that there is something within the human subjectivity that lends itself to the apprehension of clock-time, even though this something may differ from clock-time in significant ways. This capacity has been widely attributed to the human ability to apprehend and conceive of duration (Piaget, 1969). A word of caution is appropriate here because it would appear that the notion of duration is not current within the vocabulary of all cultures. Indeed, children in Western societies below the age of about 4 years of age, who do not yet have the idea of clock-time, will not have the notion of duration (See §10.3.1), and as mentioned earlier, Australian Aboriginal languages do not have temporal concepts.

Helman (2005) observes that in the more traditional agrarian societies, for example, time is often experienced as being cyclical or spiral-like, in being repetitive and advancing slowly. The religions of these regions, especially in parts of Asia, often incorporate a cyclic view of human experience, and can include concepts of reincarnation found both in Hinduism and Buddhism (Nakamura, 1966), while the Western world's conception of time as linear, has been the basis of intellectual and religious thought for many centuries. The term linear is intended to indicate that it does not double back upon itself when viewed as a path or line (as depicted in the conventional Newtonian representation). Joseph Needham (1966) saw this linear aspect as originating in the Judaeo-Christian [and Islamic] worldview, with its sense of time beginning at the point of Creation and ending at the Second Coming. This provides an insight for Newton's formulation of time, and consequently for the Western, scientific, view of time, which is directional, advancing and non-repetitive.

The review by Boroditsky (2011) illustrates the many different spatial forms used by different cultures to represent time, with an emphasis on spatial analogies that exist in diverse languages that are echoed in gesture, and reflect the spatial ordering of the flow of time in their respective cultures (See §10.4.2).

However, it would be inappropriate to go only thus far because virtually all living organisms incorporate within them a multitude of timing mechanisms: 'biological clocks'. Their modes of function are based on either (1) oscillations, or (2) unidirectional processes that trigger development and aging (hourglass clocks) governed by circadian (and circa-lunar) rhythms. Both mechanisms determine time intervals (duration). The function of the first is based on a genetic transcription-inhibition feedback loop, which is common to all living organisms, from primates through rodents, fish, frogs, insects to even cyanobacteria (the prokaryote, blue-green algae). The mode of operation of the second is governed by the limited number of cell division cycles that can be performed before the breakdown of the ability for cell replication (mitosis). It is debatable, however, whether the body clock is able to directly inform the human cognitive system about the concept of time. External factors that provide the human system with the concept of time are principally those of night and day and the seasons; the constant cycle of the phases of the moon is also an important indicator for reckoning time.

As will be elaborated upon in §10.3.1, young children are notoriously bad at dealing with the concept of time, and it is clear that children need to learn about it. And, not until the age of about 10 does the adult capacity to recognize universal time emerge. However, Australian Aboriginal societies, as noted earlier, have no notion of objective-time. These findings indicate that time as used in science is a culturally derived concept.

The notion of clock-time will be addressed initially because it highlights the basic concept of objective-time that has been refined and elaborated upon to acquire the meaning that applies to its usage in modern scientific thought.

10.1 Clock-Time

The following example provides a simple illustration of the generally accepted principles underlying the measurement of time by conventional clocks. It will be assumed in the idealized model of the 'earth and the heavens', that the fixed stars can be thought of as point sources of light embedded in a spherical shell of sufficient astronomical proportions centred on the earth, so that the sun and stars may be regarded only as point sources of light from particular directions.

Consider a long cylindrical candle of uniform composition and cross-section that has equal graduations along its length, so that the length of candle burned between successive sunrises may be measured. Neglecting seasonal variations, it will be found that the lengths burned are much the same between any pair of sunrises, enabling this length to be taken as a standard, and may be given a name 'one day'. Thus, a candle *length* comes to *represent* an abstract notion 'day' through its association with physical events and processes, *viz.* sunrises and candle-lengths burned. This is an example of the establishment of objective time.

It will be found also that the same length of candle is burned between the successive *settings* at the horizon of an appropriately selected fixed star during the course of each *night* (the criterion of suitability being that the star selected is one for which star-set may be observable at night). Once these mappings are established it may be found that the angular distance traversed by the sun and the star are the same for any arbitrary length of candle burned. Such findings allow the suggestion that both the angular distance traversed by the sun (and the star) and candle lengths they map onto may be regarded as being arbitrarily sub-divisible.

It is by such means that in conventional time-keeping, time comes to be regarded as being infinitely sub-divisible, and the graduations on the candle between the successive fixed points of sunrises (and star-sets) can be appropriately attributed the familiar abstract concepts of days, hours, minutes and seconds. The duration of one day is widely considered to be the most convenient universal standard measure of time (Kaye and Laby, 1962).

All instruments employed for the measurement of time use, in principle, cyclic variables that map onto the angular position of the earth with respect to a fixed direction. Thus, the hands of the conventional analogue clock essentially represent, relative to the dial they move over, the angular rotation of the earth relative to a fixed direction; the angular distance traversed by the clock hands indicate, relative to a mutually agreed fixed point (midnight), clock time. The key point is that clock time is defined as an abstract concept based upon a physical mapping between the angular positions in the rotation of the earth relative to a fixed direction.

It is interesting to observe that the Babylonians, who were well known for their astronomical observations and calculations, developed a sexagesimal (base-60) positional numeral system[31] around 3100 BC, which was used to divide time into the cyclic 60-based system of minutes and seconds, with 360° allocated, in geometry, to the circle.

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[31] This is a system of representing numbers, where the end-position of the numeral denotes the units, so that the value of a particular digit depends on the digit itself and its position within the number.

10.2 Time in Newtonian Mechanics and Modern Science

10.2.1 Newtonian Time

The key feature that has led to the development of the notion of Newtonian time has been the adaptation and elaboration of the concept of clock-time, so that it might be brought within the mathematical domain, for the description and analysis of physical phenomena.

Newton's views on space, time and motion dominated physics from the 17th Century until the formulation of Einstein's Special Theory of Relativity in 1905 (Einstein, 1905). Newton proposed in *Philosophiæ Naturalis Principia Mathematica,* of 1687, the concepts of absolute time and space as an independent aspects of objective reality that do not depend upon physical events, but provide a setting within which physical phenomena occur. In this regard, objects can be thought of as being either stationary or moving at an absolute speed in respect to absolute space.

His proposed notion of time, too, was regarded as being absolute and was thought to "evolve" of its own accord in a constant manner irrespective of anything external. Absolute time was in itself imperceptible, and could only be understood mathematically. However, relative time became manifest through the motion of objects, for instance heavenly bodies, and through these movements we could infer the passage of time.

In Newtonian mechanics, time is treated in the same way as a spatial dimension. There is the mathematical notion of a point in time, and between a pair of such points one may draw a straight line, along which the parameter time evolves in a continuous manner from the first point to the second. Thus, it is considered that there is an orderly sequence in the evolution of time.

Further, time may be segmented into isolated arbitrarily short or long intervals, and be treated in the same way as an arbitrary length. Thus, dynamical events that might have occurred in two separate intervals of time may be compared, regardless of the possibility that the events may have taken place at different geographical locations, on different days, at different times of day and so on. This was a significant advance on Locke's seventeenth century view of subjective time that held that no two events that occurred at different times could be brought together.

In this regard, Newtonian time is universal, in that time everywhere is considered to be the same. This is implicit in Newton's universal law of gravitation, since the force of attraction between masses was taken to act instantaneously between objects, even though they may be separated by astronomical distances.

In Classical physics, the establishment of a metric for time is treated in much the same way as the construction of the temperature scale. In the latter case, it is found that most substances show a variation in some easily measurable property, like electrical resistance, volume or length-change when heat is applied to or removed from them.

In the case of the mercury-in-glass thermometer, the device relies on the variation of the volume of a fixed mass of mercury with changes in temperature. The substance is contained in a glass bulb and is free to flow into an evacuated and sealed fine-bored tube of uniform cross-section. The length of the column of mercury is graduated into equal intervals between a pair of fixed points. The fixed points used are, once more, decided upon pragmatically. With the mercury-in-glass thermometer, for instance, they are the freezing point and boiling point of pure water at standard atmospheric pressure. Both these fixed points are relatively easily reproduced in most laboratories, and the physical properties of materials generally chosen for the measurement of temperature are those that show mutual accord in the fractional changes they suffer as heat is applied to them.

A *post hoc* analysis reveals that these are properties that change linearly with temperature (with negligible higher order components) for materials that get used for temperature measurement. These remarks apply to the commonality in the establishment of the scales for temperature and time. However, the significant difference between these two quantities is that we can provide a physical account for temperature in terms of the kinetic theory of matter, and do possess cutaneous temperature receptors, while objective time, as mentioned previously, is an abstract concept defined in terms of physical events and processes.

The same principle for establishing a metric for other physical standards is applied to the measurement of time. These comprise devices based on diverse physical phenomena that are found to manifest changes with time parameters that are in mutual accord, illustrated by the plurality of physical principles upon which clocks are based. These have generally been cyclic phenomena like the period of oscillation of a pendulum of a fixed length under the standard gravitational field, or in more recent times, the frequency of the electromagnetic emission of a spectral line associated with the outer shell electron of the caesium atom (Markowitz et al., 1958). Both of these can be compared to the mean length of the day or to the cyclic variation of the positions of the fixed stars. Once again the units can be arbitrary but become fixed by the choice of the standard. As observed earlier, this forms the basis for clock time.

10.2.2 Time in Modern Physics

It is worth noting that work in physics subsequent to Newton has used, in essence, the same foundations proposed by him with regard to the manner in which time is thought about and manipulated algebraically. For instance, Einstein's Special Theory (1905) treats both space and time in the conventional Newtonian sense in the mathematical analyses presented therein; Einstein, essentially, took on board all of Newtonian mechanics while holding the two postulates to be true.

It is as a result of the insertion of the two Postulates of the Special Theory of Relativity ((1) that all inertial frames are equivalent in regard to the physical laws of physics and (2) that the speed of light is independent of the speed of the source) into what are otherwise thought-experiments using classical mechanics that causes time to emerge as being non-universal for frames of reference in relative motion. And, whereas the concepts of space and time were treated as independent variables prior to the advent of Special Relativity, the theory created a mutual association between the two variables and showed them to be dependent on the relative velocity of moving observers. Einstein carried out his analysis using the general structure of Newtonian time in regard to its infinite divisibility and so on, and indeed relativistic time can be shown to be identical to Newtonian time when the relative velocity in Einstein's equation are set to zero. However, as a result of the two postulates, mentioned above, in Einstein's theory Newton's concepts of absolute time and space were superseded by the notion of space-time. It is the adoption of the two postulates of Special Relativity, that distinguish Newtonian Mechanics from relativity theory and alter our notion of space and time, and indeed reconciled theory with empirical observations in respect of the interpretation of, for instance, the Michelson-Morley experiment and the observation of the anomalously long half-life of muons (See, for instance, White (1965)).

In Quantum Mechanics too, time is treated both conceptually and algebraically in essentially the same way as Newton formulated it, with refinements applied due to the advent of Einstein's work.

For instance, the time-energy relation of Heisenberg's Uncertainty Principle puts an upper limit on the precision with which we may measure the energy, E, of, for instance, a sub-atomic particle and the time, T, at which the particle had that energy. This is expressed as

$$\Delta T . \Delta E \geq h/2\pi,$$

where ΔT is the uncertainty, or error, in the time measurement and ΔE is the uncertainty in the energy, and h is equal to Planck's constant. Time expressed thus is treated in the conventional Newtonian sense.

The evolving conception of time as used in science does not make it any more real or lead to a change in its status. It remains a concept, whose formulation is deemed by a process of refinement, which the dialectics of empirical observation and theory-generation dictate. The notion of time works because this modifiable concept is variously crafted to suit empirical observations. As Mary Sturt remarked:

> … time will have its nature decided in accordance with the necessities of physics and mathematics, and when these necessities change so will time.
>
> Sturt (1925, pp. 7-8)

10.3.1 Development of Temporal Concepts in Children

This section provides in outline aspects of the development in children of the basic concepts of time in order to emphasise the view that the concept of time is learned rather than given innately. The following observations are summarised from Miller and Johnson-Laird (1976), with page numbers in the source cited below. Their work addresses child development in Western society.

10.3.1.1 The Development of Distance-Time Relations and the Role of Language

p. 465

The first temporal expressions of the younger child are locative in function and deictic in form (‘now’, ‘today’). Only later does the child begin to express temporal relations, durations, and frequencies, and, at first, with one term of the relation anchored to the present moment.

It seems plausible that children’s grasp of language of time develops out of their grasp of the language of space. This relation has been suggested by a number of investigators, and it is consistent with the many parallels between the linguistic systems of time and space. Piaget has shown how children until the age of seven or so readily confound differences in distance with differences in time.

p. 27

The complex interaction of space and time that are required to describe the observed properties of motion need elaborate analysis and linguistic representation before competence may be achieved in the application of these concepts; much of the machinery of language is devoted to making such localizations communicable.

p. 462

As such, time in its application to mechanics, which requires the ability to organise it into spatial and temporal dimensions, is acquired only after a child has achieved considerable conceptual sophistication. The conceptualisation of time in terms of movement seems to be a central feature of the Western concept of time. Indeed, when a person is in motion through space there is reciprocity between temporal and spatial designations.

p. 463

Although the time concept may seem easy to an adult who has mastered it, there is evidence that its simplicity is not obvious to young children. A variety of experiences, both situational and linguistic, involve this ubiquitous abstraction in one way or another, but apparently they are not perceived by the child as being related in any simple way. It is not until he reaches what Piaget calls the stage of concrete operations that he seems to have the conceptual basis needed to integrate his diverse temporal experiences in the adult manner.

p. 464

Three-year-old children who can easily distinguish between one and two concrete objects have difficulty distinguishing between one and two flashes of light. In order to succeed, they must use some kind of verbal coding scheme. It has been observed that the concept of two is defined not by the light itself, but by the idea that ‘something went before’. This requires that the previously perceived but now absent stimulus (i.e., the first light) be retained and combined with the second light so as to form a meaningful distinctive entity. In the greater proportion of cases, this achievement seems to demand of the child that he resort to a coding system. In this sphere, accurate perception seems to depend, critically, on language.

p. 414

The simplest way to visualize time [for an educated westerner] is as a line without beginning or end. Conceptually, the time line and the number line are very similar; they may develop together in children. The number line can provide an ordering of magnitudes; the time line can provide an ordering of events. We will say that events are mapped onto the time line by linguistic expressions.

10.3.1.2 Development of Time and Culture

p. 76

The growth of a child's grasp of temporal relations and concepts requires a number of years, as Piaget has shown, and the final articulated system is likely to depend on the technology of the culture in which the child is raised.

p. 415

Young children are as happy with a right-left orientation for ordering events in a story and may even adopt a vertical orientation, as if they were moving upwards or forward into the future. This flexibility is manifested in the diverse ordering for time representation observed in different cultures (see §10.4).

10.3.1.3 Reason for Not Addressing Timing

p. 79

A theory of time perception must also provide some explanation for temporal groupings and rhythms, which are important in auditory and proprioceptive perception, and for the recognition of simultaneity of events in different sensory modalities. The accurate timing of the component parts of a skilled synergic act is critically important for sensorimotor mechanisms – hand-eye coordination, for example – that contribute to our impression of a stable perceptual world, and speech production and perception both require very accurate appreciation of the temporal relations between different speech sounds. Such temporal relations, however, are usually built into mechanisms so automatic that they are inaccessible to introspection and will not support the kinds of attentional-judgement abstractions about time that the conceptual system can call for.

Such temporal relations reflect *the machinery, not the content, of perceptual experience* [my italics], and are considered not to be of significance for the development of clock-time. I observe that an Aboriginal child develops aspects of timing as manifest in sensory-motor coordination and rhythm etc., as do children raised in a Western setting without having any conception of time

10.3.1.4 The Flow of Time

p. 462

The development of the time line, flowing from the past into the present and thence into the future must constitute one of the major cognitive developments of childhood.

p. 466

Children start to ask 'where' questions before they ask 'when' questions; the period of greatest growth in spatial vocabulary is from two to two-and-a half years, whereas the spurt in temporal vocabulary occurs about six months later.

p. 467

One observation that is constant in all accounts of the conceptual development of time is that as a child grows older his temporal horizons widen. He looks further into the future and further back into the past. Similarly, he is progressively better able to orient himself to the clock and calendar; starting from the unit of the day and working up to the year and the day of the month.

10.3.1.5 Episodic Memory

p. 467-468

Accompanying this growth of time perspective is the growth of episodic memory. If we think of episodic memory, not as an isolated memory system, but as one way we have of organizing our general memory, in order to facilitate search for particular information, then the development of the time concept and its use in organizing memory must be a critical component of normal cognitive development. Presumably, the various linguistic devices that are available contribute in some way to this organization. But it seems more likely that episodic organization, and the ability to judge fairly accurately the relative age of an episodic-memory trace, are general-purpose cognitive mechanisms, independent of language[32]. As episodic memory grows, and as it enables the child not only to retrieve the past but also to extrapolate more imaginatively into the future, the need for more flexible and precise ways of referring to time and temporal relations also grows.

Given that the concept of time, and its use in ordering memories, is a higher-level brain function, these abilities might be expected to reflect the general course of hierarchical brain development. Indeed Joseph (2000) notes in his review of fetal brain behaviour and development that brain maturation proceeds along a caudal-rostral arc. This finding is consistent with the later development of prefrontal cortex, and its involvement in higher-order cognitive function. Significantly, Klob et al. (2012) emphasise that the development of prefrontal cortex is associated with experience and involves learning.

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[32] This is a moot point. Miller and Johnson-Laird's proposal is open to dispute because Aboriginal languages do not have temporal terms. As such, episodic memory might not be independent of language.

10.4 Cultural Differences in Time Apprehension

10.4.1 Australian Aboriginal Time Consciousness

Perhaps the greatest difference in time cognizance or consciousness between cultures is represented by the Australian Aboriginals who, as mentioned earlier, appear to have no notion of time. In this regard, Lawler (1991) notes:

> Because Indo-European language dictates that we express all our thoughts in past, present, or future tense, we have the notion that time is an abstract backdrop moving in one direction, like the hands of a clock, from past to the future. None of the hundreds of Aboriginal languages contain a word for time, nor do the Aborigines have a concept of time. As with creation, the Aborigines conceive the passage of time and history not as a movement from past to future but as a passage from a subjective state to an objective expression. The first step in entering into the Aboriginal world is to abandon the conventional abstraction of time and replace it with the movement of consciousness from dream to reality as a model that describes the universal activity of creation.
>
> The ritual dances and songs that the Aborigines perform every day celebrate the movement from subjective to objective that created the world. This perception guides every aspect of daily life.

This mental orientation cannot be due to a unique genetic disposition because Australian Aboriginals, too, can acquire competence in the application of the notion of time. TenHouten (2004) carried out a lexical-level content analysis of transcripts of a corpus of 658 biographical interviews of, among others, Aboriginal individuals from throughout Australia who had had varying amounts of contact with Western thought.

The amount of their previous contact with Western concepts was inferred by their decade of birth, between the years 1900 and 1949, and their transcripts were analysed for the occurrences of words that would indicate the four basic kinds of time-consciousness listed by Roget's 1977 *International Thesaurus*. For details, see TenHouten (2004).

TenHouten (2004) shows that the number of words indicating time-consciousness in the transcripts had a general upward trend when plotted against their decade of birth, which suggests that Aboriginals could learn temporal concepts and the frequency of temporal terms used in the histories correlated with the inferred degree of Western contact. Indeed, as is well known, many Australian Aboriginals are bilingual in English (see footnote 33).

10.4.2 Spatial Metaphor in Time Representation

In her review Boroditsky (2011) has explored how people construct their mental representation of time. In particular, she has examined the role played by spatial metaphor in determining representations of time across languages. Significantly, her work shows that there exists a correspondence between the differences in the spatial representations and those of time for different cultures.

That spatial metaphors might influence temporal representations is consistent with the observation that during child development, spatial vocabulary acquisition precedes that of the acquisition of temporal vocabulary. Miller and Johnson-Laird (1976, p. 466) also point out, as mentioned earlier, that children in the West start to ask 'where' questions before they ask 'when' questions; the period of greatest growth of spatial vocabulary is from two to two-and-a-half years, whereas the spurt in temporal vocabulary occurs about six months later.

Boroditsky (2011) observes that among English speakers, for example, spatial metaphors for the depiction of time are forward-backward; long-short. The future is regarded as being ahead with the past behind. However, among the Aymara people of the Andes, the future is behind and the past is in front, so that when talking about the past, the Aymara gesture in front of them, and while talking about the future they gesture behind them. Among the Mandarin Chinese, who think about time vertically, the future is regarded as being below and the past above.

A further interesting issue with regard to the direction of flow of time is the general propensity among Western scientists to depict time as flowing from the left to right. However, as mentioned earlier, Miller and Johnson-Laird (1976) observe that young children in the West are as happy with a right-left orientation for ordering events in a story, and may even adopt a vertical orientation, as if they were moving upwards or forward into the future, thus not displaying an innate preference.

However, there appears to be striking reversals in the direction of time between different cultural groups. People who read text from left to right tend to lay out time as proceeding from left to right, and people who read text arranged from right to left (e.g., Arabic, Hebrew) arrange time from right to left. This directionality applies also to Mandarin, which is written, traditionally, in columns, with the sequence running from top to bottom.

Interestingly, these spatial metaphors in the representation of time are subject to change through learning, as work by Boroditsky (2001) showed. Her experiments were carried out on Mandarin-speaking participants who had learned English at different stages of life. The participants' response-times to target questions about time, following either vertical or horizontal linguistic primes, were compared. It was inferred from response time considerations, that the greater the experience subjects had with talking about time vertically, the shorter were their response times for vertical primes. Both of the above findings suggest that these spatial aspects of time as a concept are learned.

The same conclusion could be derived from experiments where native English and native Mandarin speakers were asked to spatially arrange temporal sequences shown in pictures. Mandarin speakers arranged the pictures more often in a vertical array, whereas English speakers never did (Chan and Bergen, 2005). A similar vertical bias in spatial organization was found in Mandarin-English bilinguals when the tests were conducted in Mandarin compared to when they were tested in English.

Boroditsky (2011) provides an interesting example of how temporal concepts are represented by the highly specialized culture of the Australian Aboriginal community of Pormpuraaw, who, Boroditsky affirms, have no temporal terms in their languages. Unlike English, the Pormpuraaw languages do not routinely use relative spatial terms like left and right. Instead, they rely on absolute-direction terms that indicate the cardinal directions: North/South/East/West. For example, in specifying a direction in which a cup should be moved they would say, for example, "move your cup over to the NNW a little bit" or "the boy standing to the south of Mary is my brother". Members of such linguistic communities need to orient themselves with respect to the cardinal directions in order to communicate effectively.

To discover how members of such a culture might represent time, Boroditsky and Gaby (2010) presented English speakers and the Aboriginal subjects, who were fluent in English, with shuffled sets of pictures on separate cards depicting temporal progression (an example is shown in Fig. 10.1). Their task was to arrange the set in temporal order. The English speakers arranged the cards so that time proceeded from left to right (as shown). The Aboriginals arranged the cards from East to West[33]. That is, when they were seated facing south the cards were ordered left to right. When they faced north, the cards were ordered right to left; when they faced east, the ordered sequence were arranged towards the body and so on. These results demonstrate that spatial factors play a significant role in determining a cultural influence on the representation and the concept of time, and indeed how communication may be realised in the absence of temporal terms.

Fig. 10.1 Example of the set of picture cards the Aboriginal participants were asked to arrange in chronological order. Source: Boroditsky and Gaby (2010).

It is interesting to observe that modern Western science derives its sense of physical reality from the fundamental algebraic dimensions of mass, length and time, whereas traditional Australian Aboriginal culture appears to lack the concept of time. The

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[33] The results cited should be assessed in the light of the fact that the Aboriginal subjects studied were bilingual in English and their native language, and could therefore understand the instructions of what was required of them. I interpret the results to indicate that they arranged the photographs in the manner that their monolingual peers, who would have no notion of time, might have done, or that their Aboriginal spatial bias was the dominant one.

growing literature on Australian Aboriginals, as witnessed by the journal publications cited by TenHouten (2004), Boroditsky and Gaby (2010) and Boroditsky (2011), would suggest that much more can now be learned about their apparently separate sense of reality.

10.5 Circadian Mechanisms

In the enquiry of whether or not the notion of time is given innately to the human cognitive system, this section considers influences on bodily functions that may be suggestive of time. There are clearly many such influences, and cyclic variations in the environment might constitute cues to the formulation of the notion of time as used in the sciences. Some astronomical effects and their regulatory influences upon living organisms are reviewed herein.

Although it is common knowledge that the human biological system expresses a rhythmic variation in a diversity of bodily functions, manifesting, for instance, in the activity–rest cycle, their origins have only been studied in any depth since the 1960s. It is now clear that there exist body clocks, located separately, for instance, in the liver and kidneys (See, for instance, Couture and Hulbert, 1995). These clocks have various periodicities and are under the regulatory influence of a central clock lodged in the hypothalamus. The coordinating influence of the central clock is thought to establish temporal order or duration of one or many physiological events in the body.

The body clocks are responsible for regulating the predominately neuroendocrinal and autonomic rhythms, which, nevertheless, have far reaching influences on human behaviour. These rhythmic variations are available for the human cognitive system to apprehend, by simply noticing that one becomes sleepy at night, or that one becomes hungry at certain times of the day. And, depending on the culture in which the human being is situated, these cycles are interpreted by each in its own way.

Most cultures have emerged with their own unifying concept of time. This is suggested by coordinated cyclic behaviour. It is clear that the circadian variations in bodily functions are closely entwined with the day/night cycle imposed by the rotation of the earth on its axis. It is worth noting that the unity of these two (circadian rhythms in the body and the diurnal cycle of the sun) has been given credence within human thought throughout antiquity. Indeed, in the modern scientific metric adopted for time, the period of rotation of the earth is regarded as a fundamental unit. The scientific aspiration in what may constitute an ideal timekeeper is expressed as follows:

> The ideal time-system would keep in step with the mean length of the day indefinitely, and would also be strictly uniform.
>
> Kaye and Laby (1962)

Given the close correspondence between body rhythms and the circadian cycle in providing cues to the formulation of clock time they will be treated together in this section.

The effect of the day–night cycle, with its regular variations in ambient temperature and light with a 24 hr. period has effects on almost all living organisms. That living organisms demonstrate patterns of internal (as in cell division) and external behaviour that have a diurnal periodicity can be accounted for by evoking arguments concerning survival and ecological factors (Dunlap, 1999; Hastings and Maywood, 2000; Rensing et al., 2001; Ouyang et al., 1998). In addition, there are other rhythms to which many organisms are also sensitive. These are the circa-lunar, circa-tidal and the sidereal rhythms. Sidereal rhythms are in synchrony with the seasons, and result from the revolution of the earth around the sun.

Given that the axis of rotation of the earth is inclined at an angle of 23.5 degrees to its axis of revolution around the sun, both (1) the distance between a point at any given latitude and the sun, and (2) the period of time during which this location receives sunlight each day, vary as the earth revolves around the sun through the seasons.

The period of revolution of the moon around the earth, between successive moon rises, is unaffected by the seasons, and has a period of the lunar day (24.8 hr.). The moon's effect on the tides is well documented (Winfree, 1980; 1986), and it is easy to see how its influence might affect organisms living in tidal regions.

The earth rotates on its axis from west to east, i.e., in an anticlockwise sense, when the North Pole is viewed from above. The moon revolves around the earth also in an anticlockwise direction, when viewed from the same position, and completes its revolution in 29.53 days. This is the time period between, say, successive full moons, and is known as the synodical month. The moon has a slower rate of revolution around the earth than the earth has around its own axis (24 hrs. per rotation). As a consequence, the moon is later to rise on successive days. This amounts to a delay of about 50 min, and the lunar day consequently has a length of 24.8 hrs. Neither the length of the lunar day nor the synod is an integer multiple of the length of the year.

Circadian rhythms have now been found in most eukaryotic species that are subject to the diurnal light-dark cycle due to the sun. These species range from mammals to fruit flies to fungi, and also including the prokaryotic cyanobacteria *Synechoccocus* (Aschoff, 1984; Hastings and Maywood, 2000; Rensing et al., 2001; Mihalcescu et al., 2004). Circa-lunar rhythms are, curiously, found also to exist in various species of blind shrimps that live in complete darkness in aquifers found underground in the northeastern Yucatan, in Mexico.

The apparent coincidence that the free-running circadian period, in virtually all organisms, also has the period of the lunar day has not yet been fully investigated. It is worth noting that the average duration of pregnancy, from ovulation to birth, in the human is nine lunar months (Kak, 1996). Further, that the menstrual cycle in women has an average period of one lunar month. It may turn out, however, that this coincidence has no deeper significance. On the other hand, as has been suggested (Ferraro et al., 1995), the free-running cycle is itself regulated by the moon's cyclic gravitational influence.

An attempt has been made to investigate the possibility that the gravitational effect of the moon regulates the free-running cycle of the fungi *Neurospora crassa* by having the organism carried on a space shuttle flight. It was found that the specimens retained rhythmicity, with a lengthening of their circadian periods and an increase in their growth rates (Ferraro et al. 1995). However, these researchers found it difficult to assess whether or not the observed period-lengthening indicated that the free-running cycle is entrained[34] by the moon's gravitational field. Circa-lunar, circa-tidal and sidereal rhythms have been widely documented, but have not been studied in the same depth as circadian rhythms.

10.5.1 Circadian Rhythms in Humans

It was discovered only in the early 1960s that humans had an endogenous free-running circadian rhythm that was demonstrably stable and apparently not passively following environmental cues (Aschoff and Wever, 1962). In their study, Aschoff and Wever (1962) found that nine individuals lodged in an underground bunker, had a stable rest-activity cycle of about 25 hours when removed from the influence of the diurnal 24 hour solar cycle of light and dark. This pointed towards an internal system for the temporal regulation of bodily functions, which they found could be altered to conform to the daily cycle of light and dark. Similar findings have been reported in studies of humans living in caves, where they are shielded from the influence of the diurnal variation in sunlight (Winfree, 1986, p. 31). In other words, there appears to exist a free-running endogenous rhythm, which has the same period as the lunar day. This period can be entrained to have the 24-hour cycle of the solar day.

In humans, apart from determining the sleep cycle, circadian rhythms manifest as a cyclic variation in bodily effects as diverse as sensitivity to tooth-pain threshold, which is higher during the afternoons than in the mornings or evenings, and curiously, in susceptibility to dental anaesthesia, which is greater in the morning than in the afternoon. There is a circadian variation in the body temperature by about 1° C

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[34] Entrainment is the term used to refer to the regulation of the free-running rhythm through external influences, for instance, by altering the light-dark cycle, to shift or change the period.

(Aschoff, 1965), it being lowest in the middle of the sleep period; blood alcohol clearance rate is lower at 10 pm than in the afternoon (Winfree, 1986, p. 26-27).

There is also a circadian variation in urinary sodium and potassium content. Melatonin production in the pineal gland at night and cortisol release by the thyroid gland just prior to waking up also follow the diurnal rhythm. Further, visual and auditory reaction times as well as the subjective estimation of temporal durations, against the clock, show a circadian rhythm. For instance, when asked to estimate a period of 10 sec, subjects generally generated estimates that were longer than 10 sec, but the overestimates were greater during hours of darkness, and were found to have a cyclic variation with a 24-hour cycle time (Aschoff, 1984, p. 451). More recently, it has been found that moods in individuals suffering from depression also follow the circadian rhythm (for a review see Bovin, 2000).

Many kinds of body cells have a propensity for replication determined by the circadian rhythm, and indeed cancer therapy for the elimination of malignant cells is better carried out at particular times in the cycle, when most of the cells are replicating their DNA, than at others (Haus et al., 1972).

10.5.2 The Circadian Clock

A significant clue about the mode of regulation of the body’s biological clock came from the behaviour of a blind squirrel monkey lodged in a laboratory, whose periods of rest and activity had been carefully recorded over a period of about 3 years. Averaged over this period, it was found that the blind monkey showed a 24hr 46min rhythm

(Richter, 1968), reminiscent of the free-running cycle exhibited by humans isolated from the light/dark of the day/night cycle. This result implied that the visual system was somehow involved in the process of entrainment to the 24 hr. diurnal pattern exhibited by normal monkeys. It is now known that most totally blind humans are free-running (Sack et al. 2000).

In the past twenty years much progress has been made in chronobiology, and particularly in the physiology of the body clock in both the mammalian and other systems (Hastings and Maywood, 2000; van Esseveldt, 2000; Rensing et al., 2001). The brain region thought to be the body's 'master' clock resides in the hypothalamus, a region involved with hormonal and autonomic control. The clock is located above the crossing of the optic nerves from the two eyes, in a region called the suprachiasmatic nucleus (SCN), and is connected to the brainstem systems, which are important in controlling sleep and wakefulness. A further role of the circadian clock is to monitor day length and its rate and direction of change. This forms the basis for seasonal timing, crucial for migration, reproduction and so on.

Perhaps the most convincing evidence of the SCN's role as a biological clock is that its removal in experimental animals abolishes their circadian rhythm of sleep and waking (Purves et al. 1997, p. 505). Further, neural transplantation experiments, in which fetal tissue containing the SCN was grafted into the brains of previously lesioned animals, restored their circadian rhythm. Crucially, reciprocal grafting studies between wild type hamsters and tau-mutant hamsters, with a 20 hr. cycle, showed that the restored period was determined by the genotype of the grafted tissue and not by that of the host (Ralph et al. 1990).

10.5.3 Mode of Function of the Suprachiasmatic Nucleus

The bilateral SCN in humans consists of about 20,000 neurones (approximately the size of a rice-grain). It receives direct retinal afferents along the retino-hypothalamic tract. This is a dedicated pathway from a sub-population of retinal ganglion cells. The SCN receives inputs indirectly from the intergeniculate leaflet of the lateral geniculate nucleus via the geniculo-hypothalamic tract. The SCN in turn projects to the subparaventricular zone and the dorsomedial nucleus of the hypothalamus and to the paraventricular nucleus of the thalamus (van Esseveldt et al. 2000). The efferent pathways are involved in the regulation of the physiology and behaviour of their targets. One of these pathways leads to the pineal gland, which produces the hormone melatonin, involved in the communication of circadian time to the other organs.

In mammals, as in other organisms, the clock mechanisms are endogenous to the cell, and embedded in their genomes. They consist in the expression of a few clock genes. In brief, the products of the clock genes, that is, clock mRNA and clock proteins, undergo concentration changes with the circadian rhythm. The oscillations are caused by positively acting transcription factors binding to clock gene promoters, and initiate clock gene expression. Then, the encoded clock proteins enter the nucleus to suppress further expression of their cognate genes. Gene expression is not restored until the negatively acting proteins are inactivated. This process has a precise cycle time (Hastings and Maywood, 2000; Rensing et al., 2001). Eight such genes have been identified in the mouse, which forms the model for the mammalian system (Foreman, 2002).

Virtually all eukaryotes have clock genes that function according to the same basic principle. In contrast with many other neural systems, where behaviour is an emergent property of networks, the core elements of circadian behaviour in the SCN is cell autonomous (Hastings and Maywood, 2000). The same conclusion was reached by workers studying the endogenous clock in the prokaryotic cyanobacteria (Young and Kay, 2001; Mihalcescu et al., 2004).

The SCN expresses circadian timing at all levels of organization. The mode of time-regulation of the target tissue of SCN efferents appears to be governed by the precise circadian variation in the firing rate of the individual neurones in the SCN. In the free-running state, this period is precise to a few parts in a thousand and is not susceptible to variations due to temperature changes. The origin of the spontaneous rhythm of electrical firing, which drives the cyclicity in the SCN target structures, is not yet established. However, it is found that the same circadian periods are found in the firing rates of individual SCN neurons held in dispersed primary culture, and in the abundance of mRNA in whole tissue *in vivo* due to the cyclic expression of the clock genes (Hastings and Maywood, 2000).

During the 1990s chronobiologists developed a unified model of the molecular mechanisms that underlie the circadian clock in all organisms from bacteria to humans (for a review, see Rensing et al. 2001). All clock genes so far identified in mammals are components of the autoregulatory transcription-translation feedback loop mentioned earlier. Many biochemical details are now documented, which, however, go beyond the scope of the present work. For a review see Rappert and Weaver (2002). Clock genes affect between 2% and 10% of the human genome, and we observe, in consequence, the diversity of bodily effects referred to earlier. In cyanobacteria, clock genes affect almost the entire genome.

10.5.4 Entrainment

As stated earlier, the human free-running cycle has a period of a lunar day, in common with virtually all other living organisms. Aschoff (1984, p. 445) points out that the average free-running cycle time for 147 subjects isolated from external time cues was found to be 25 ± 0.5 hours.

By artificially controlling the light-dark cycle in an isolated underground bunker it was found possible to synchronize subjects to periods other than the diurnal 24 hr. cycle. As indicated earlier, entrainment is the term used to refer to the regulation of the free-running rhythm through external influence to having a periodicity other than the free-running period. Aschoff reports that a unified cycle time of almost 27 hours is about the limit to the extension of the free-running cycle with all the bodily processes still remaining in synchrony with the imposed rhythm of light and dark. It was found that when the imposed cycle time exceeded this value, the different bodily functions were no longer in synchrony with the imposed cycle time. This finding led to the suggestion that there was probably more than the single body clock. And indeed it is known now that there are oscillators in many parts of the body, referred to as ‘slave’ oscillators. These are synchronized by the ‘master’ clock in the SCN (Reppert and Wever, 2001).

A further role of the circadian clock is to monitor day length and the rate and direction of its change. This forms the basis of seasonal timing, which is crucial to migration and reproductive behaviour in animals, and generally for metabolism and appetite. The principal entraining stimulus is the cycle of light and darkness.

The clock is, however, not equally sensitive to light at all times. Brief exposure of a free-running individual to light around the time of the expected dusk and dawn can delay and advance the clock respectively, whereas light presented during expected day is ineffective. This phase-dependent resetting by light is observed across taxa, regardless of the morphological and biochemical details of photo transduction, and whether, in the case of animals, organisms are nocturnal or diurnal in their habits. The clock in humans can be completely re-set in about 7 days.

The anatomical basis to photic entrainment is well established. It is mediated by direct retinal afferents to the SCN. This pathway, the retino-hypothalamic tract (RHT), arises from a specialised population of retinal ganglion cells, and forms a privileged line to the SCN, independent of other visual projections and, *crucially, does not participate in the direct conscious perception of light-level monitoring* (Van Gelder, 2008; Do et al., 2009). The pathway encodes general luminescence, rather than feature detection, from a retinal transduction pathway that has a wide receptive field and very slow adaptation. It is therefore suited to convey information about the light/dark cycle to the SCN. The specialised receptors activate the production of a pigment called melanopsin in the photoreceptor cells. The SCN releases a chemical signal (glutamate), which acts on one or more clock genes in the nucleus of the SCN cells. Gene induction by light appears to be the basis to resetting the SCN clock.

Classical retinal photoreceptors, the rods and cones, with their opsin-based visual pigments, are necessary for the conscious perception of light and images. However, these opsin-based photoreceptors do not participate in evoking the pupillary constrictor reflexes or in clock resetting information to the SCN (Reppert and Wever, 2002).

The resetting effects of brief light pulses are very rapid and can be blocked by glutamatergic antagonists delivered directly to the region of the SCN. A very dramatic observation is that light pulses, which reset the clock, also induce the expression of a number of immediate-early genes.

Given that these genes encode transcription factors, this was the first indication that changes in a transcriptional loop may underlie resetting. It has now become clear that the gene inductive effects of light in the SCN follow a well established cellular pathway, in which RHT synaptic glutamate acts through post synaptic NMDA-type receptors to increase intracellular levels of calcium (Ca^{+2}), which in turn trigger a kinase cascade to activate transcription factors

The correlation between gene induction in the SCN and resetting the behavioural rhythms of mice is very tight, both in its phase dependence and intensity/duration curves. Exposure to light at dusk will turn on the gene at a time when levels of mRNA are falling, probably because of negative feedback by clock proteins. Consequently, induction will delay the progress of the spontaneous cycle. Conversely, light falling around dawn, when gene expression is low but soon to rise in the absence of protein feedback, will cause an early increase, and thereby advance the cycle. In general terms, therefore, the phase-dependent resetting of behaviour observed at the level of individuals can be explained by the known interaction between light and a spontaneous cycle of clock gene expression (Hastings and Maywood, 2000). Further details of the biochemical processes involved in entrainment may be found in the review by Rappert and Weaver (2002).

It is interesting to note that in the human fetus, the fetal clock is already functioning and its cycles can be detected. However, instead of being re-set every 24 hours directly by daylight, the fetus's rhythm is controlled by chemical signals that cross the placenta from the mother. Melatonin and dopamine, generated by the mother, can cross the placenta and affect the fetus's brain clock.

Infants at birth, lacking the entrainment by the mother, have a haphazard sleep/wake cycle until approximately their 17th week. Thereafter periods of waking and sleeping move to a 25-hour cycle, only to acquire a 24-hour cycle at the age of about 26 weeks (Winfree, 1986, p.31).

A study conducted on 62 babies born at least 10 weeks premature, and weighing on average 2 pounds, exposed to different conditions of light and dark, showed that those exposed to cycled light, mimicking the diurnal cycle, grew faster than those held in other conditions. They gained at least 23 gm per week more than those held in constant lighting conditions or light/dark cycles remote from the diurnal one (Brandon et al., 1999).

10.5.5 Communication between the SCN and the Body

The SCN functions as a master clock, using chemical messengers and direct neural connections to other parts of the brain to keep the rest of the body in synchrony with the diurnal cycle. There appears to be a plurality of oscillators dispersed in the body that are all regulated by the light-entrained master clock in the SCN (Repert and Weaver 2002). These are referred to as 'slave' oscillators. They exist in a diversity of locations in the body, including the liver, the kidneys, vascular tissue and so on.

In an *in vivo* study of circadian gene expression in the heart and liver of mice, it was found that although there is a similar number of genes with circadian expression in both, the dynamics of circadian gene regulation in the heart and liver were markedly different. This is despite that fact that the molecular clocks in the two tissues were synchronized (Storch et al. 2002). The divergence of liver and heart in the timing and content of circadian gene regulation suggests a specialized role of circadian clocks in each tissue.

In vitro, tissue from the liver, kidneys and the heart can sustain 24-hour oscillations for a few days without input from the SCN. The molecular composition of the timing mechanism in slave oscillators is very similar to that in the SCN. However, the actual mechanism that distinguishes the self-sustaining oscillatory function of the master clock from the damped oscillations of slave oscillators is unknown (Reppert and Wever, 2002).

To be biologically useful, the phase information encoded in the transcription-inhibition loop has to have an output beyond the closed autoregulatory circuit. Temporal information is thought to be conveyed between the SCN and the rest of the body through a combination of (1) direct neural contacts, and (2) the promotion of hormone release.

For some time it has been known that the synthesis of the neuroactive peptide aginine vasopressin (AVP) by a distinct group of SCN neurons exhibits a circadian rhythm, and that this is matched by a circadian rhythm in the concentration of AVP in the cerebrospinal fluid.

This finding points to a paracrinal link between the SCN and surrounding tissue, where secreted products act upon adjoining regions by diffusion. Further, the release of hormones like melatonin and dopamine into the blood by brain tissue in the pineal and the thyroid glands, to which the SCN has direct efferents, have been proposed as means by which the entire neuroaxis comes under regulatory influence of the master clock (Hastings and Maywood, 2000).

Although it is not entirely clear how the central biological clock in the SCN communicates with individual cells in the body, it is known that electrical synapses have the function of synchronizing activity among a population of neurons, and that particular hormone-secreting neurons in the hypothalamus are connected by electrical synapses (Purves et al. 1997, p. 86). Such an arrangement would ensure that all cells fire action potentials at about the same time to maximize a burst of hormone secretion into the blood. This would synchronize the individual oscillatory circuits, both of nervous tissue as well as the other cells of the body, with the central clock in the SCN.

However, it is worth noting that although melatonin release in the pineal gland can be triggered by the SCN, melatonin production occurs autonomically both here as well as in the retina (Hastings and Maywood, 2000). As such, the role of the SCN as the master clock should, perhaps, not be over emphasised.

The system of clock function outlined above is widely accepted to be the intracellular machinery for circadian rhythm generation, but the model is thought to be incomplete since it cannot fully account for the precision and stability of circadian rhythms in living cells. Interlocked multiple feedback loops have been considered as additional components to stabilize the molecular machinery (Yu et al., 2002). The topic appears to be highly complex and is not yet fully resolved (Honma et al., 2002; Alvarez and Sehgal, 2002).

10.5.6 Hourglass Clocks

While oscillatory clocks can be entrained to keep time with environmental periodicities, hourglass mechanisms mainly determine intervals of time or trigger events such as developmental processes. In both cases, events not belonging to the clock processes are triggered or regulated by signals or actions of the clock.

Hourglass clocks are based on linear or exponential processes that initiate or gate events mainly in the course of development, differentiation or ageing. These events are usually irreversible. They usually depend on external variables such as temperature, nutrients or cytotoxic agents, as well as internal ones such as metabolism. This leads to a strong dependency of development and longevity on these external and internal variables (Rensing et al. 2001).

The ageing process can be considered, for instance, as an accumulation of damage in DNA and other cellular structures, mainly due to mitochondrial generation of reactive oxygen species. This eventually leads to a complete breakdown of cells by means of programmed cell death (apoptosis), culminating in the death of the organism.

Ageing can also be accounted for by the number of cell division cycles between developmental events. Other hourglass timers determine the time of menopause in women, the initiation of labour and so on, and there appears to be a connection between these hourglass periods and the lunar cycle referred to earlier. For instance, the average gestation period in women from ovulation to birth is rather precisely nine lunar months (Kak, 1996).

An important hourglass mechanism within the aging process is governed by the limit on the number of divisions a cell is capable of. This capacity depends on the length of telomeres that mark the ends of chromosomes. In 1965, Hayflick showed that fibroblasts from embryonic lung tissue have the capacity to undergo 50±10 population doublings *in vitro* (Hayflick, 1965). Adult cells cannot replicate as many times. Freezing embryonic cells stops replication. Thawing permits the process to resume. The counting process is thought to take place in the nucleus, because when aged nuclei are transplanted in embryonic cells, they cannot undergo as many replications. These findings suggested that there was an internal clock within the cell that counts the number of cell division cycles that had been completed. It has been confirmed that the clock is located in the nucleus of the cell.

We know now that the ends of chromosomes have 10-12kb of telomeres that terminate the sequences. During each round of replication, 50-200 nucleotides are lost due to incomplete replication of the DNA strand. Eventually, the complete loss of the telomeres allows the chromosomes to fuse and undermines faithful replication of information in the DNA.

The cells in most human tissues are not able to replace their shortened telomeres. The loss of these sequence-end delineating nucleotides allows end-to-end chromosome fusions, as observed earlier. The only cells that are able to survive indefinite replications are those able to stabilize their shortened telomeres by activating telomerase (Rensing et al., 2001). Cancer cells are among these, and the mechanisms controlling the stabilization process is providing interesting avenues of exploration in the fight against cancer (see, for instance, Tarsounas et al., 2004).

There is, however, no suggestion from a study of the physiology of hourglass clocks that they are able to communicate clock time to the human cognitive system in any direct way. The outward manifestation of the process of development and ageing, in themselves, do not necessarily convey a sense of clock time as used in science.

10.5.7 Conclusions

We have thus far dwelt on a physiological investigation of circadian and hour glass mechanisms with regard to internal time regulation, and have not found any mechanism that might endogenously convey clock time directly to the human cognitive system.

The variability in human judgements of duration has provoked the suggestion of the existence of an internal pacemaker (Hoagland, 1933). Triesman (1984) has investigated the possibility that this pacemaker might have its rate of time keeping altered in step with what he terms ‘temporal arousal’. A shortcoming of his account is that in the event that this is the case, a higher degree of temporal arousal will lead to a speeding up of the pacemaker, and lead to a shortening of the estimate of a given duration, as measured by a clock. Furthermore, Triesman does not propose any anatomical location for the pacemaker, and this notion appears to be, at present, purely hypothetical.

It is worth dwelling for a moment on the relevance of this experiment to the present enquiry. What has been of interest is the documentation of the cues to the human cognitive system that contribute to the notion of clock time. The alpha rhythm, or for that matter, a great diversity of temporally regular events that occur in the brain (see, for instance, Miller (2000)) are not directly accessible to human cognition. As such, one might become aware of their existence and variations only if they had some direct effect on other manifest phenomena, or by the application of monitoring instrumentation. This is clearly not the case with regard to our knowledge of common indicators of time.

Triesman found that alpha rhythms had a smaller variability than subjective judgements of duration. Further, that the patterns of variation of the two parameters were not such that they might have a common source. He too concluded that alpha rhythms could not be the source of the variability of subjective duration production.

There is no indication in the present study to suggest that clock time may be conveyed from the diverse timing mechanisms in the body directly into the human cognition. It is worth remarking that despite the fact that Australian Aboriginals have both circadian rhythms and hourglass clocks, nevertheless they have no concept of time. This finding supports the view that the presence of these mechanisms in the human body does not enable the embedding of the concept of scientific time in human cognition.

10.6 Suggested Answers to Einstein’s Questions

To briefly address Einstein’s questions quoted at the beginning of the chapter, the work presented herein has shown that time is an acquired concept and not a primitive. It is a higher-level construct.

Addressing “velocity” as motion in a specific direction within the sensory modality of vision, there is much evidence to support the view that motion can be perceived directly, without the involvement of cultural induction and linguistic analysis.

For instance, it is well known that the cortical region V5 (or middle temporal, MT) has been linked to the higher order processing of visual motion. The columnar organization found for ocular dominance and orientation preference is also present for visual motion detection, so that cells within entire columns in the cortex select for motion in a particular direction. Together these columns form a topographic map of the visual field. Indeed, these directions are defined as vectors, with columns of neurons responding to visual stimulus in one direction but not its opposite direction.

Work on ferrets reported by Li et al, (2006) shows that direction selectivity is not detected in kits at eye opening, but acquired several days later, and strengthened to adult levels in the following 2 weeks. Dark-reared animals do not develop motion selectivity if they have not had experience of visual motion before the end of a critical period. Similar findings have been reported in a diversity of mammals.

It is reported that in the developing *Xenopus* tadpole retino-tectal system, the receptive field of tectal neurons can be 'trained' to become direction-sensitive within minutes after repetitive exposure of the retina to moving bars in a particular direction. The induction of direction-sensitivity depends on the speed of the moving bar (Engert et al., 2002).

The authors observe that their results suggested that experience-evoked activities in the developing brain can influence the refinement of developing nerve connections into mature neural circuits. They found that this occurred in a manner consistent with Hebbian synaptic modification as a mechanism for activity dependent changes in visual circuits.

Interestingly, the capacity for both the apprehension of time and the perception of velocity through visual motion are acquired through experience of the environment, with the development of the capacity to perceive velocity dependent only on experience of the physical environment, while the child's development of the conception and apprehension of time also requires an appropriate cultural setting.

As pointed out in §2.1, Einstein recognised that scientific theories are crafted to derive their worth through their capacity to relate abstract thought to the physical world. In this respect, the concept of time is a part of that theoretic structure. It plays the role of providing culturally derived input to enable diverse assemblies of the tangible (but nonetheless acquired) variables of length and mass to provide a mathematical account of what we perceive the physical world to be.

11

CONCLUSIONS

11.0 Thesis Summary

The current work has addressed the age-old enquiry about the origins of knowledge. This has been carried out at the level of scientific knowledge because at the present time the scientific method is considered to be the most reliable source of knowledge, and scientific enquiry is regarded as being able to provide knowledge on an objective level. Indeed, some scientists go further and consider that the objective stance provides unique, ‘ultimate truths’.

Rather than enter the discourse of whether scientific objectives are conditioned by popular opinions, or engage at the level of the analytical philosopher to consider what it might mean to be objective at the level of the meanings of words, in the present work the status of objective, scientific truths has been addressed through an examination of the mode of function of the human perceptual system upon which empiricism relies for the evaluation of scientific theories.

For scientific results to be regarded as unique and representing ultimate truths, empiricism must be capable of generating veridical ‘sense data’. It has been assumed that for the human senses to apprehend unique percepts the sensory capacity should be somehow defined in human genetics. If, instead, the function of the perceptual system were defined by environmental factors during sensory development, then the claim of uniqueness could not be supported.

I have sought to address this issue in the realms of neuroscience, which has led to an examination of the development of the representation of perceptual knowledge in human nervous tissue.

Among scientists who are persuaded that a strict application of the scientific method can yield ultimate truths, there has been a tacitly held belief that because science employs the language of mathematics for the representation and manipulation of physical relations this adds more than precision to the results. Indeed, it imbues the findings obtained by, for instance, theoretical physicists with a deeper, universal reality.

After a discussion of the notion of physical reality the issue of the formal representations in science was addressed by examining the status of formal systems and in particular Newtonian mechanics and Einstein’s theory of special relativity. In addition, the history of the development of the method of dimensional analysis was reviewed. This is the process that underlies the physicist’s ability to use the precise language of algebra for the description and formulation of scientific theories about the nature of matter. These enquiries showed that none of the above formulations had any intrinsic worth and that their developments were all ultimately reliant on empiricism.

However, dimensional analysis provided a means for more formally defining physical reality. This is because all physical phenomena can be described in terms of the three fundamental dimensions of mass, length and time. Thus, it narrowed the problem of considering the status of empiricism to addressing only the apprehension of mass, length and time in regard to evaluating the status of scientifically derived truths.

Within the realms of neuroscience, the key findings by Hubel and Wiesel and the theoretical insights of Hebb were described in some detail. These supported the suggestions of the early workers on sensory deprivation that the senses needed experience in order to become functional. Hebb's theoretical stance and Hubel and Wiesel's experimental results at a cellular level had found support also from the computational modellers of brain function. In this realm, a significant finding was that models that made provisions for constructive growth of neural networks were capable of creating arbitrary mappings between 'sensory' input and their representations in artificial neural nets. Furthermore, modelling showed that common learning rules for the representation of knowledge could be applied across the different sensory modalities.

The growing consensus was that the structuring of cortical material that supports sensory function is dependent on experience from the environment to enable humans to perceive the physical world. Extensive results were cited to support the constructivist stance: a theoretical position that essentially supports Piaget's theory of how children acquire the cognitive competence to function in the physical world.

These findings have led to a reformulation of the traditional nurture-nature debate so that it is now surmised that the development of the structures required for representation of knowledge in the brain, and indeed to support the capacity for perception, consists of an environmentally dependent process that involves the construction and alteration of nervous tissue using inherited cellular machinery to transcribe information contained in the genome.

In the case of vision, the nature-nurture *divide* between the endogenously given sensory pathways and those that developed thereafter through activity in the sensory receptors was found to be at the location of the inputs from the LGN to layer IV in striate cortex. The 'hypercolumnar' structure in cortex was seen to be provided innately, but it was shown that cortical material might be thought of as general-purpose tissue that was capable of supporting the creation of 'arbitrary' representations of input from, perhaps, any sensory modality. As mentioned, theoretical analysis at the level of neural network modelling was cited to support this view.

An order of magnitude calculation was presented of a comparison between the information contained in the genome and in the brain, which showed that the information contained in the nucleotides in the human genome was insufficient for the genetic pre-specification of all the information in the brain. A multitude of experimental findings were cited to show that the capacity for perception required a long period of learning, which entailed the generation of a variety of sensory primitives whose hierarchical representation was manifested by the activation of specific neurons when the items learned were presented in their receptive fields. This endorsed Locke's view that learning from the environment was the means by which the brain was furnished. The present work addressed specifically the information the brain contained about the physical world.

As mentioned earlier, in co-opting the method of dimensional analysis to provide a rigorous definition of physical reality enabled a basis for differentiating between the roles of genetics and input from the environment in the establishment of the sensory capacity for the apprehension of mass and length. This analysis was carried out for the individual senses of vision, proprioception and audition, both behaviourally and at the level of the underlying nervous tissue, where possible, that supported these senses.

A study of sensory development and reviews of deprivation studies in both humans and animals indicated that the capacity to apprehend the fundamental dimensions of mass and length in all the sensory modalities were derived from environmental input. This result was inferred from the finding that visual competence was hierarchically organized and that the capacity for structured vision relied on the initial establishment of the visual primitives through a process of learning.

It was found that auditory length perception in the near field was learned and represented in auditory cortex in the form of neurons that had learned to respond to sound sources at particular locations in the vicinity of the head and body. The raw information for the capacity for sound source direction discrimination was provided innately at the level of the superior olivary complex through a comparison of the inputs from the two ears, but the capacity for sound source direction discrimination required learning at the level of primary auditory cortex. On the whole, use of prior knowledge about the sound source and the environment were shown to be an important aspect for auditory sound localization.

The capacity for obtaining auditory prior knowledge was examined in some detail, particularly in the realms of the cortical representation of sound. Sounds from a variety of sources were addressed and it was shown that as in the visual system cortical cells that responded best to particular sounds were organized in a hierarchical manner in a posterior-anterior direction. It was also found that there existed cells that responded best to natural sounds and others that responded to the sounds made by man-made objects, and that these capacities were learned rather than given innately. Furthermore, that there were cells that had learned to respond best to non-speech sounds made by humans and others that had learned to respond to speech sounds. The latter are dwelt on later in this chapter. However, as mentioned, evidence was provided to show that the capacity for the apprehension of all these sounds had been acquired through learning. It was therefore surmised that the capacity for length discrimination by audition was acquired rather than a native endowment. A similar conclusion was reached about the capacity for mass apprehension through an examination of the development of this ability in the infant.

The origins of the process of multimodal integration was also examined, and it was found that the capacity for the integration of information in separate sensory modalities was found to be plastic, so that the relations between the different sensory modalities become coordinated, essentially, according to Hebb's rule. That is, the ordering process relied on the co-occurrences of the patterns of activity in the sensory inputs that cause them to be bound together. As suggested earlier, this finding was consistent with the view that the repeated co-occurrences of events gave rise to the construction of cell assemblies, where the nature and form of the new material generated was dependent on information derived from the genome under the influence of the activity generated by the sensory receptors.

An analysis was presented to define the notion of time as it is used in the scientific context. It was shown that even though Einstein had modified Newton's initial conception of absolute time, time was, nevertheless, treated in its original way by Newton with regard to how it is applied in the algebraic formulation of dynamics in modern physics.

It was shown that time is a learned concept, and that its formulation has not remained fixed during the development of physics. Rather its definition has been altered though the ages to conform to the demands of empiricism. The view that time is a concept derived from cultural influences was endorsed by showing that the child's acquisition of the notion of time required an extensive period of learning. The conclusion that time is an acquired concept was affirmed by the finding that Australian Aboriginals do not have any notion of it.

The origins of the phenomenon of circadian rhythms was examined both at the behavioural and physiological level. Although there existed an innate link through the suprachiasmatic nucleus in the hypothalamus that regulated diurnal rhythms in the body's behaviour, it was surmised that such a link was not capable of necessarily generating the concept of clock time. Indeed, despite having diurnal rhythms, the Australian Aboriginals do not have the Western notion of clock time.

Given that time is one of the fundamental dimensions that defines Western physical reality, the finding of an absence of the notion of time among the Australian Aboriginals provided an example of a culture in which an entire population of human beings have an altered sense of physical reality.

In sum, the overwhelming finding was that the capacity for the apprehension of physical reality was critically dependent on learning from environmentally derived input. This view was supported by citing an extensive range of experimental results. Further support for this view is given below.

11.1 Further Support for the Thesis

11.1.1 Dreams of the Blind

Much information was provided in Chapter 3, *Plasticity in the Nervous System,* to show that the sensory organs used to perceive the physical world do not become functional simply through a pre-determined process of maturation. Instead, the capacity for perception is acquired through a process of learning. Thus, restriction of input to specific features during the relevant critical period will result in sensory competence for the apprehension of structures reliant only on those features, as shown in the case of visually deprived kittens by Blakemore and Cooper (1970) and Pettigrew and Freeman

(1973). Indeed, the deprivation of input to a specific sensory modality will result in an absence of function of that sense.

Significant evidence in support of the view that the senses are the portals for cognitive knowledge in humans comes from work by Hurovitz et al. (1999) who analysed reports of the contents of 372 dreams recounted by 15 blind adults who had lost their sight at different ages. The methodology of this work is reminiscent of that by TenHouten (2004), mentioned in §10.5.1, concerning the use of temporal terms in accounts of life histories recounted by Australian Aboriginals who had experienced varying proportions of their lives exposed to Western thought.

In the work by Hurovitz et al. (1999), the adult subjects had been blind for different proportions of their lives, and therefore had a varying proportion of their lives spent gaining visual experience. The results of the analysis of reports on dreams showed that the subjects who had been blind from birth had no visual dreams. Further, there was a correspondence between the amount of visual dream content and the proportion the lives the subjects had been sighted. These findings are confirmed by other such studies (cited by Hurovitz et al., 1999).

In particular, individuals who became blind before the age of five seldom experienced visual imagery in their dreams; those who had lost their sight between the ages of five and seven did retain some visual imagery in their dreams. Most people who had lost their vision after the age of seven continued to experience at least some visual imagery, although its frequency and clarity often faded with time.

The work by Hurovitz et al. (1999) also provides support for the refutation of the suggestion by nativist psychologists of the existence of core knowledge at birth, in that if those who had been born blind had been imbued with core knowledge that was visual, such information might have manifested in a visual form in their dreams.

11.1.2 Stability of Perception and Sensory Primitives

It is perhaps worth summarising the findings arrived at earlier to support the view that although the sensory system is plastic, nevertheless we apprehend a stable world and there is agreement between humans about physical reality to the extent that we can engage in the study, for instance, of physics across cultures. This support is required because it could be argued that if sensory organ-function is reliant upon environmental configuration, then the senses would be reconfigured continuously as the subject moves from one environment into another, which is, clearly, not found to be the case.

This issue can be resolved on grounds that the sensory system is organized hierarchically, with the higher levels dependent upon sensory primitives at the lower level. The primitives at the lower levels are learned before those at a higher level and become fixed after their critical periods.

The ones at higher levels retain, by varying degrees, their capacity to be re-configured to acquire different compositions. However, in the constructive approach they are considered to be built upon in a hierarchical manner. In language acquisition, as pointed out in §9.2.1, there are, indeed, interlinked critical periods corresponding to each of several subsystems associated with the bottom-up modular growth contributing to the acquisition of competent language function.

This scheme can be understood in analogy with the letters of an alphabet forming the primitive set from which words may be composed. As such, words (and non-words) may be formed arbitrarily from different arrangements of the fixed letters of the alphabet. The existence of such sensory and motor primitives was shown to exist in the visual, auditory and motor systems (see respectively chapters 3, 9 and 6). There is also evidence for such primitives in the somatosensory system in regard to, for instance, reading Braille, with its cells of 2x3 elements representing alphanumeric characters (Hamilton and Pascual-Leone, 1998; Hannan, 2006).

Thus, the perceptual and ontological stability manifested is made consistent with a view that sensory function is acquired by the fact that there exist critical periods of rapid learning. On the whole, physical environments across cultures are able to support the generation of common sensory primitives that enable the common configuration of the senses. Where these environments differ, as in the case of the different phonemic sets used in different languages, the fact that sensory configuration lies at the base of sensory competence manifests in the existence of different languages.

11.2.0 Additional Findings from the Enquiry

11.2.1 Thoughts on the Making of Meaning and Human Volition

It is perhaps worth elaborating upon what appears to be an interesting finding about assigning meaning to words, discovered during the course of examining the development of the infant's capacity for speech recognition and production in chapter 9.

The enquiry had been initiated by interest in the capacity for obtaining prior knowledge with respect to auditory length and direction discrimination. This work was extended to, ultimately, the origins of the capacity for the use of human vocal discourse as a means for obtaining prior knowledge about the spatial localization of sounds. It was concluded that this capacity for vocal discourse was derived. The issue of interest that was revealed during the investigation of the origins of the capacity for speech perception is concerned with the attribution of meaning to words (see below).

It was interesting also to find that the ability of speech generation was dependent hierarchically on the capacity for speech recognition, and given that the latter is an acquired function, it may be claimed that the capacity for vocal discourse is also learned.

The capacity for speech production being dependent on the capacity for the generation of motor primitives to enable the process of speech vocalization, which are under volitional control, brings to the fore the issue of human volition. Both meaning making and volition will be considered below.

11.2.1.1 The Problem of Semantics

In their text: *Language and Perception,* Miller and Johnson-Laird (1976) remarked on the absence of a psychological theory of meaning, and that it was unlikely that formal semanticists will solve the problem.

If the problem of the origin of the capacity to assign meaning to words may be thought of as being the same issue addressed in the domain of semantics regarding what is absent in the psychological theory of meaning, then the study of infant phoneme recognition, elaborated upon in chapters 8 and 9 appears to provide some insights into this problem.

From the analysis provided in chapters 8 and 9, it seems clear that the capacity to recognize sounds made by a variety of sources is acquired, and that the cells in the temporal cortex acquire their ability to respond to sounds of increasing complexity, from tones to frequency modulated tones and so on. These cells are hierarchically organized in a caudal-rostral order, as is the left-lateralized region of temporal cortex associated with the recognition of speech sounds.

A spoken word is a string of phonemes. It may be also thought of as a temporal variation in sound pressure levels in a travelling wave as it arrives at the tympanic membrane. As such, the arrival of a word at the listener’s ear can be thought of as the receipt of a composite ‘object’, in that the reception of the word can be decomposed into a sequence of physical events: the reception of the successive phonemic elements.

Extensive behavioural results were cited to show that the capacity for the recognition of phonemes was also learned rather than native. During development, following the capacity to recognize phonemes the infant proceeds to acquire the capacity recognize words. Given that phonemes are learned, and words are composed of phonemes, it was inferred that the capacity to recognize words must be learned. This argument has been used previously in regard to visual length perception (see §5.4). Thus, following the acquisition of the capacity to recognize words, the infant proceeds to attribute meaning to word sounds.

The process of assigning a meaning to a word might be viewed as the arbitrary creation of a mapping between a sound and, for instance, an object. As such, where there was previously no meaning assigned to an arbitrary sound, the infant has created one. There is, clearly, no genetic predisposition for the forming of certain associations and not others. As such, what is essentially an arbitrary mapping process results somehow in having a string of phonemes imbued with a meaning.

The study of speech recognition during infancy displays the process of the assignment of the meaning of words at its inception. This is, for instance, the assignment of a sound token for an object. We have here an example of the meaning making process in the lexical domain, where use of the term ‘meaning’ seems unequivocal.

Einstein, Hebb and in their wake, the computational modellers of memory formation are in agreement with the need for the repeated presentation of pairs of stimuli for an association between them to be established. Einstein endorsed the need for the repeated presentation of objects for the notion of a bodily object to embed as did Hebb, at the level of the co-firings of neurons and in the generation of cell assemblies, and so do computational modellers of memory formation using the paradigm of, for instance, Competitive Learning (that lies within the broader category of self-organizing artificial neural networks) where the repeated presentation of the stimulus vector to the input units of the artificial neural network is employed as a means for the gradual updating of the weights representing the information contained in the net.

Clearly, the association initially made between the sound and the object is one that is then elaborated upon through the formation of further associations, and indeed words prime other meaning-bearing words to imbed the newly learned word so that, in time, the meaning initially made becomes multiply defined to the point that we may be persuaded that the *association* generated might have an absolute status.

However, despite the fact that the word-meaning mapping is universally acknowledged and defined with some precision in dictionaries, it is, in fact, no more than the creation of a mapping, which has no fundamental significance, in that the association has been in no way genetically pre-specified.

The result that we acquire the capacity to identify word sounds through learning could have been established by insisting that word-sounds are physical entities, and since we need to learn to recognize all physical entities through appropriate sensory configuration derived from environmental input, the capacity to perceive word sounds, too, would need to be acquired. As might be expected, the analysis of the process speech recognition at the behavioural and neurophysiological levels has endorsed the view that the capacity to recognize words (when considered to be objects) is acquired through learning.

To recapitulate, the enquiry has traced the sequential, hierarchical learning process in the fetus and the infant that enables it to develop the capacity for speech perception. The initial state of the fetal brain can be claimed to resemble a *tabula rasa* in regard to not having any pre-assigned semantic attributes associated with any particular sound. It was shown that the capacity to apprehend phonemes was learned. Further, in developing competence in the use of words, the infant can be thought to be imbued with the capacity to attribute meaning to words. Thus, it is the infant that attributes meaning to words even though the process of creating the associations between the sound and the named object is generally facilitated by the parent or other caregiver.

11.2.1.2 The Issue of Human Volition

The development of motor behaviour was evaluated in some detail in §6.6.0: *Motor Behaviour Revisited*, where a distinction was made between primitive reflexes and motor primitives. In the extensive motor literature the term ‘reflex’ is, nevertheless, widely used even though, as was pointed out, these, too, are subject to habituation and are under the influence of the central nervous system rather than being ‘pure’ stimulus-response reflexes. There is also a widely applied distinction between primitive reflexes and motor primitives that are found to be concatenated to generate sequential motor activity. These are considered to be under volitional control. It would appear, therefore, that workers in the field of motor behaviour concede the existence of human volition. This view is explored below.

The storage and ‘release’ of primitive reflexes in cases of brain injury indicate that these reflexes are provided as an innately given set, and are retained in the nervous system even when motor primitives take over from reflexive activity in the enactment of volitional motor control. It was also demonstrated that motor primitives are learned, and are not derived from primitive reflexes. Furthermore, whereas motor reflexes are initiated by a stimulus, motor primitives are voluntarily generated.

Indeed, the example of speech production, elaborated upon in chapter 9, showed that as both hearing and deaf infants develop they vocalise a set of ‘babbling’ reflexes, which are, however, spontaneous rather than being responses to specific stimuli (as are primitive reflexes). A number of stages of babbling were documented in chapter 9, where it was noted that only hearing infants proceed into the stage of canonical babbling. It is in this stage that the early babbling is superseded by the learned motor primitives that are used for the utterance of speech sounds of the infant’s native language. Deaf infants do not proceed to the canonical stage and do not acquire the capacity for speech production. It was shown that this is because the process of speech production is dependent on the capacity to learn to recognise speech sounds. The process of speech acquisition may be thought of as one where learning to recognize the sounds of its native language enables the infant to assign meaning to the spoken words that it hears, a process that the deaf are deprived of.

Thus, the hearing infant proceeds to learn the motor primitives for the articulation of the speech sounds of its native language that enables it to use these volitional motor manipulations in speech production. The process of the creation of the mapping between perceived speech sounds and the vocalization of these sounds, then, entails the volitional making of meaning in learning to recognize word sounds. This is then followed by the volitional act of using the learned motor primitives associated with uttering speech sounds that the infant uses to meaningfully convey its needs, and intentions to its carers.

Thus, the enquiry into infant speech recognition and production appear to demonstrate that the infant (and, indeed, the adult) is imbued innately with the capacity for meaning making and volition. Time constraints forbid the exploration of the relation between volition and free will.

11.2.2 Time Scale for Altering Physical Reality

If the proposed thesis that the human at conception may be regarded as a *tabula rasa* in regard to its capacity for the perception of physical reality, then it may be claimed that this capacity will have been acquired and participated in the generation of the contents provided by input from the apprehension of the physical entities over the lifetime of any individual.

Indeed, granting this claim would imply that a totally new sense of physical reality might be imbued in any individual during the time interval between conception and maturity, defined as the time of expiry of all relevant critical periods. Clearly the creation of a new reality would require the containment of the individual in a ‘new’ environment. Thus, it may be possible to create a new mind-set within the period of one generation.

11.3 Consequences of the Findings

If it is accepted that the developmental environment and the agency of Hebbian learning significantly mediate our sense of physical reality, there results circularity in the definition of what is physical. This is because we can no longer uphold the view of having an objective stance with regard to having independent access to the physical world. The perceptual system, in having been ‘configured’ by the environment functions in a way determined by it. This results in interdependence between the perceptual system and what is being perceived. The complexity brought by such a situation to the status of the percept goes beyond the problems associated with the distinction between *phenomenon* and the *noumenon*.

As used in philosophy, the term *noumenon* may be distinguished from phenomenon, where the latter refers to the thing as it appears to the sensory system. While, the thing in itself; the underlying basis for the phenomenal experience, from which it may be considered to arise is referred to as the noumenon. See, for instance The Stanford Encyclopedia of Philosophy; Dictionary.com.

To elaborate briefly, it has been proposed that our perception and cognition can only provide us with *phenomena*, knowledge of external objects that are knowable by the human senses, whereas the underlying reality, the thing in itself is the *noumenon,* which is destined to remain forever inaccessible on grounds of the limitations of the human condition. We can nevertheless think in terms of the notion of the origin of the sensory phenomenon, and consider the noumenon to be singular.

In accepting the thesis that physical reality is acquired through the individual's interactions with input from the environment would deem that a pair of individuals, raised in radically different physical and cultural settings, would perceive physical reality differently. Each would insist that his empiricism and scientific enquiry in regard to, for instance, description of the nature of fundamental particles that make up matter was allowing him to approach his notion of the *noumenon*, the true reality. In this way, each person practising the science appropriate for his environment and culture would obtain results that were in accord with his own setting.

However, the analysis presented in this thesis shows that none might be justified in claiming a privileged position, and the notion of the *noumenon* would lose meaning in regard to its being singular, and there would be need to concede the possibility of a plurality of *noumena*.

This change in perspective is more problematic than the one encountered by followers of Copernicus when the Ptolemaic view of the earth-centred planetary system was superseded by the sun-centred one. This is because in having had our sensory systems configured at the level of the primitives of perception in a particular environmental settings we do not have the capacity to conceive of another model of reality as the followers of Copernicus had.

They were able to discard the analysis involving epicycles in an act of exercising Occam's Razor in having found a simpler model to account for their observations of planetary motion in the solar system against the background of the fixed stars. They were able to reformulate their model of celestial mechanics using the same mathematical methodology and sensory primitives.

What we have to come to terms with is that the very ontology of our capacity to apprehend physical reality is plastic and crucially dependent on the developmental environment. An insight can be provided of the significance of this situation through a thought experiment reflecting upon the condition of a human embryo, raised in the manner of Pettigrew and Freeman’s kittens (Pettigrew and Freeman, 1973) in an environment consisting only of uncorrelated point-sources of light (see § 3.4.6). Such an individual would be furnished with visual primitives consisting only of moving dots. In somehow reaching maturity, the individual would, clearly, be unable to formulate or comprehend, for instance, Euclidean geometry, which is composed of stationary points and lines.

Thus, in accepting the findings of this thesis, it has to be conceded that science, may not be capable of yielding unique results, and indeed, the scientific method, being empirically defined cannot be regarded as being a unique method, but one dependent on the environment in which the practitioner’s sensory systems developed.

The findings of the thesis do not change the worth of science as a methodology for obtaining results that are in accord with empiricism; the same methodology may be applied regardless of the way the sensory organs are configured, and the results of science will remain true for each set of individuals that have in common the same sense organ configuration scheme. In the case of individuals living in the conventional terrestrial setting, they will continue to see the world as before: GPS will work and bridges will continue to stand up (or fall down) and jets fly. That is, until it is realised that underlying our acquisition of physical reality was a circular process: what we perceive as matter is also that which has participated in furnishing us with the ability to perceive it. As such, the notion of objectivity loses its sense of its previously claimed independence. Thus, the previous objective stance espoused by scientists changes into one that acknowledges the status of matter is not absolute and the scientific method cannot claim to generate ultimate truths. Instead, the results obtained using the scientific method are contingent upon the developmental setting of the scientists practising their science.

These finding have implications for the use of terms like ‘fundamental particle’, ‘fundamental physical constant’ and so on, and indeed for the basis of empirical science. It can also be seen to have metaphysical consequences in regard to matters religious and in relation to the nature of the self and living organisms. However, these are matters that lie beyond the scope of the current thesis.

Epilogue

Western science claims that it provides us with reliable, unique, objective information about objects and processes in the world around us.

I question this view, and sketch a brief example, without explicit support, to illustrate my stance. I suggest that there is no such thing as a unique reality across human populations. The practice of science is dependent upon our senses to inspire its theories and to evaluate them through experiment (both rely ultimately upon perception). This being the case, there cannot be a unique science, as will be demonstrated in the example below. Rather, there are a plurality of physical realities and so a plurality of sciences.

Native speakers of English can distinguish between the phonemes
/v/ and /w/ (Indians/Germans cannot);
they can also distinguish between
/l/ and /r/ (Japanese cannot).

Sounds are physical patterns of temporal variations in air pressure. So the example is about the apprehension of physical reality.

Native speakers of English have been exposed to these sounds in a cultural context within a critical period, so can distinguish between both pairs, and indeed, can also produce them. Lip-reading too has a critical period, and this process aids auditory discrimination.

Hypothetically, a scientific theory may be devised about phonetics that might rely for its evaluation on distinguishing between different phonemes, that the Japanese and Indian researchers might be persuaded to adopt as a part of their science of phonetics. Let us assume that their science will be determined by how they respond below.

The Japanese and Indians are presented with all four phonemes, and asked to evaluate the following propositions.

Proposition 1: sounds /v/ = /w/.
Proposition 2: sounds /l/ = /r/.

Indians say: Prop 1 Right
Prop 2 Wrong These form the basis of ‘Indian Science’.

Japanese say: Prop 1 Wrong
Prop 2 Right These form the basis of 'Japanese Science'.

Indian Science is at variance with Japanese Science. There is a plurality of realities and a plurality of sciences.

The intended point of the above example is that native English speakers can see two groups, who are equivalent, each with a deficit the other does not have. We as native English speakers can see that they can regard each other as different, and therefore come to accept that there can be differences in realities and sciences.

The above narrative provides a simplistic example of the formation of realities.

Native English speakers are, of course, in a privileged position and can see and accept that this is how realities form – early experience being defining. We remain secure in having all our science to help delineate in sonograms (or spectrograms) that analyse acoustic formants and their differences, so can pinpoint the deficits in both the Japanese and Indians' auditory capabilities.

The underlying point being made in the example is that realities are made in the mind by early experiences. Whatever there is deemed to be out there, by way of our notion of molecules and all of science, has been learned. There is no knowledge of anything that is innately given: this is part of the current thesis. It has all been acquired in the same way as we have learned to distinguish between /l/s and /r/s while the Japanese have not.

The reader is perhaps still attached to his science and its powers for providing explanations that make sense of what is experienced: all of Newtonian mechanics, electronics and the kinetic theory of matter, and so on, to keep him squarely in his reality.

But the reader is urged to consider the view that every one of the ‘atoms’ out of which his phenomenal reality is constructed has been built on what has been acquired through early experience. His reality has been acquired in the same way as the experience of /l/s and /r/s, that allow the reader to experience and distinguish between them, and indeed, to produce them in order that the utterances are different.

There are two sources of environmental inputs: those directly experienced phenomenally and those communicated (usually by others, who are also a part of the environment) in an abstract form, usually through the use of language, that might help ‘tune’ the senses via a cognitive route to coming to apprehend new forms.

To recap, the above example presents two groups who are in an equivalent position, with each having a deficit that the other does not have, and each having a capability the other does not. They can regard one another as being different, and therefore come to accept that there can be differences in their realities and consequently their sciences. This narrative provides an example of the formation of realities. Each group may say to the other:

> There are more things in heaven and earth, Horatio,
> Than are dreamt of in your philosophy.
>
> Hamlet (1.5.166-7).

The same can be said of us!

This work was carried out on the assumption that science has within its scope the capacity to assess its own limitations. Indeed, this has proven to be the case.

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APPENDIX

Parpia, P. (2011) *Reappraisal of the Somatosensory Homunculus and its Discontinuities*, Neural Computation, **23**, 3001-3015.

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Reappraisal of the Somatosensory Homunculus and Its Discontinuities

Pasha Parpia
d.y.parpia@sussex.ac.uk
Centre for Research in Cognitive Science, Schools of Informatics and Life Sciences, University of Sussex, Brighton BN1 9QJ, U.K.

Neuroscience folklore has it that somatotopy in human primary somatosensory cortex (SI) has two significant discontinuities: the hands and face map onto adjacent regions in SI, as do the feet and genitalia. It has been proposed that these conjunctions in SI result from coincident sources of stimulation in the fetal position, where the hands frequently touch the face, and the feet the genitalia. Computer modeling using a Hebbian variant of the self-organizing Kohonen net is consistent with this proposal. However, recent work reveals that the genital representation in SI for cutaneous sensations (as opposed to tumescence) is continuous with that of the lower trunk and thigh. This result, in conjunction with reports of separate face innervation and its earlier onset of sensory function, compared to that of the rest of the body, allows a reappraisal of homuncular organization. It is proposed that the somatosensory homunculus comprises two distinct somatotopic regions: the face representation and that of the rest of the body. Principles of self-organization do not account satisfactorily for the overall homuncular map. These results may serve to alert computational modelers that intrinsic developmental factors can override simple rules of plasticity.

1 Introduction

Somatotopy in the primary somatosensory cortex (SI) provides the paradigm case of spatial adjacency, or topographic, mapping between the arrays of cells in cortical tissue and cutaneous mechanoreceptors. Penfield and coworkers compiled the familiar somatosensory homunculus (see Figure 1 and Table 1) in the mid-1950s by eliciting patients' responses to electrical stimulation of their exposed cortex prior to surgical intervention for epilepsy.

Such topographic mapping is recognized as a common feature of the correspondence between the spatial organizations of receptors in many sensory epithelia and their targets in the central nervous system (Pickles, 1982; Udin & Fawcett, 1988; Kaas, 1991, 1997; Buonomano & Merzenich, 1998; Wong, 1999; Jones, 2000). The presence of topographic mapping in

Neural Computation **23, 3001–3015** (2011)

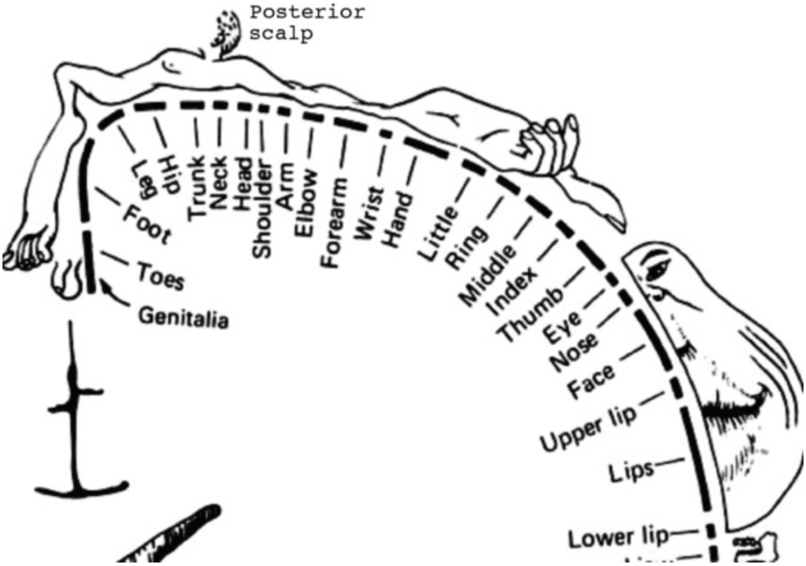

Figure 1: The Penfield homunculus. The penile representation is located inferior to that of the foot. The face representation is inverted and displaced as a whole from that of the neck and posterior scalp. (Modified from Penfield & Rasmussen, 1950.)

the nervous system has been interpreted on grounds that such an arrangement optimizes geometric, biophysical, and energy constraints (Laughlin & Sejnowski, 2003).

However, the genesis of topographic mapping is a subject of continuing debate between those who hold with the protomap or the protocortex position. The protomap view proposes that the spatially specific molecular signaling of neural progenitor cells in the proliferative zone establishes both spatial location and function of neurons within the primary subdivisions of cortex. By contrast, the protocortex view asserts that activity-dependent mechanisms alone give rise to topographic mapping in an otherwise homogeneous cortex (Killackey, Rhoades, & Bennett-Clarke, 1995; Wong, 1999; Sur & Rubenstein, 2005; Stiles, 2008). However, it is likely that both genetic and epigenetic factors contribute. The primary somatosensory region includes the separate architectonic fields 1, 2, 3a, and 3b. For reasons of probable homology with SI in other mammals, area 3b representation is referred to as SI in this view.

1.1 Homuncular Discontinuities. The familiar somatosensory homunculus (Penfield & Rasmussen, 1950) contains two notable discontinuities in SI: between the hands and the face and between the feet and the genitalia (see Figure 1). Farah (1998) assumed the protocortex position by proposing that the discontinuities occur because "mechanisms of self-organization, in combination with the normal position of the fetus in the womb will incline the map towards just this organization." In the womb, the fetus generally has its hands abutting its face, and its feet the genitalia, creating coactivations of the respective body parts.

Farah's suggestion is supported by the generally accepted notions of cortical plasticity and self-organization (Hebb, 1949; Willshaw & von der Malsburg, 1976; Kandel & O'Dell, 1992; Florence et al., 1996; for a review of theoretical approaches to map development, see Goodhill, 2007) and by experiments entailing the simultaneous activation of body parts, which have revealed integrated, overlapping receptive fields in monkeys (Clark, Allard, Jenkins, & Merzenich, 1988; Wang, Merzenich, Sameshima, & Jenkins, 1995). Furthermore, computer simulations of the fetal position, using a Hebbian variant of Kohonen's self-organizing neural net, have provided an "existence proof" for the plausibility of Farah's proposal (Stafford & Wilson, 2006).

A review of recent literature reveals, however, that there is in fact no discontinuity in the genital representation in SI for cutaneous sensations (summarized in section 2). An analysis is presented of body parts that might be costimulated in utero and be expected to lead to somatotopy (see section 3). It is concluded that the rule that generally applies for the refinement of topographic mapping (Kandel & O'Dell, 1992) is inapplicable across the hand-face boundary in SI.

The displacement of the face representation from that of the neck and posterior scalp (see Figure 1) is explored in section 4, and it is suggested that this results from separate innervation (or parcellation) and development of the sensory fibers innervating the face from those innervating the rest of the body. With cutaneous somatotopy present elsewhere in the body, I propose that the boundary containing the facial representation constitutes the only homuncular discontinuity in SI.

Such a finding serves also to alert computational modelers of neuronal dynamics to pay heed to possible underlying developmental constraints, since computational models are inevitably limited by their axiomatic bases. Innervations within the oral cavity are not addressed.

2 The Foot-Genital Discontinuity

Previous work on the localization in SI of sensations from the male genitalia is summarized in Table 1. The Penfield homunculus (Penfield & Rasmussen, 1950) sites the penile representation in SI discontinuously inferior to that of the foot, in the paracentral lobule of the mesial wall (see Figure 1).

However, an analysis of previous investigations that used a diversity of techniques for localizing brain activation in conjunction with (1) tactile stimulation of the penile skin (Pfeifer, 1920; Kell, von Kriegstein,

Table 1: Previous Work on the Foot-Genital Discontinuity in SI.

Author	Detection Method	Stimulation Method
Authors who located the penis discontinuously inferior to the foot in the paracentral lobule		
Foerster (1936)	Subjective report from patient	Electrical stimulation of cortex
Penfield and Boldrey (1937)	Subjective report from patient	Electrical stimulation of cortex
Penfield and Rasmussen (1950)	Subjective report from patient	Electrical stimulation of cortex
Penfield and Rasmussen (1968)	Subjective report from patient	Electrical stimulation of cortex
Narici et al. (1991)	Magnetoencephalography	Electrical stimulation of DNP
Guérit and Opsomer (1991)	Elcctroencephalography	Electrical stimulation of DNP
Allison et al. (1996)	Electrodes in cortex	Electrical stimulation of DNP and Electrical stimulation of cortex
Nakagawa et al. (1998)	Magnetoencephalography	Electrical stimulation of DNP
Mäkelä et al. (2003)	Magnetoencephalography	Electrical stimulation of DNP
Authors who found the penis to be represented continuously with rest of the lower body in the postcentral gyrus		
Pfeifer (1920)	Subjective report from patient and location of brain trauma site	Tactile stimulation
Penfield and Jasper (1954)	Subjective report from patient	Electrical stimulation of cortex
Bradley et al. (1998)	Electrodes in cortex and subjective report from patient	Electrical stimulation of DNP
Redouté et al. (2000)	Positron emission tomography	Erotic visual images
Kell et al. (2005)	fMRI	Tactile stimulation
Moulier et al. (2006)	fMRI	Erotic visual images
Mouras et al. (2008)	fMRI	Erotic visual images

Note: DNP indicates Dorsal Nerve of the Penis.

Rösler, Kleinschmidt, & Laufs, 2005), (2) electrical activation of the dorsal nerve of the penis (DNP) (Guérit & Opsomer, 1991; Narici et al., 1991; Allison, McCarthy, Luby, Puce, & Spencer, 1996; Bradley, Farrell, & Ojemann, 1998; Nakagawa et al., 1998; Mäkelä et al., 2003), (3) the presentation of erotic images (Redouté et al., 2000; Moulier et al., 2006; Mouras et al., 2008), and (4) electrical stimulation of the cortex (Foerster, 1936; Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950,1968; Penfield & Jasper, 1954; Allison et al., 1996) reveals at least two separate loci in SI dedicated to sensations arising from the penis. Those for cutaneous touch, which the somatosensory homunculus is intended to represent, are indeed located somatopically with the thighs and lower trunk.

It would appear that Penfield and coworkers and many of those using electrical activation of the DNP localized sensations of tumescence, which arise from the engorgement with blood of erectile tissue, discontinuously in the paracentral lobules (Penfield & Jasper (1954), revised the earlier findings of Penfield & Rasmussen (1950), and sited the penile representation continuously with that of the lower trunk and thigh in the post-central gyrus). The penile representation proposed by Bradley and coworkers (1998), although stated to be continuous with the trunk and thigh, was exaggerated, and extended into the mesial wall. This issue has been discussed by Kell and coworkers (2005). Electrical stimulation of the population of axons carried in the DNP can simultaneously activate myelinated cutaneous and slow, narrow Aδ fibers that carry sensations of tumescence (Nakamura et al., 1998; Georgiadis & Kortekaas, 2009) and lead to ambiguous results.

In sum, although many standard texts depict a foot-penile discontinuity (Styles, 2005; Purves et al., 2008), cutaneous sensations from the penis are represented continuously with those of the adjacent body parts in SI.

To summarize, there appears to be no disjunction in the penile representation in SI for cutaneous sensation. Previously reported penile representation in the paracentral lobule may be attributed not to cutaneous sensations but to those of tumescence. Georgiadis and Kortekaas (2009) support this view.[1]

3 Analysis and Further Considerations

Despite there being frequent foot-penile contact in utero, penile somatotopy with the lower trunk and thighs is observed in SI. Furthermore, although there is costimulation of the face and the neck where they abut in the body, somatotopy is absent in SI between the face representation and that of the neck. Similarly, costimulation at the face and posterior scalp boundary does

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[1] The original Penfield homunculus, reproduced in Figure 1, wrongly represents face and body parts in the ipsilateral hemisphere. This error is repeated in other work cited here (Bradley et al., 1998, Figure 6; Kell et al., 2005, Figure 3; and Nakamura et al., 1998, Figure 3).

not lead to somatotropy in their representations in SI (see Figure 1). The overall findings are:

- Foot-penile costimulation in utero, no SI adjacency
- Neck-face/face–posterior scalp costimulation in utero, no SI somatotopy
- Hand-face costimulation in utero, SI adjacency present

From these findings, we can surmise that costimulation and somatotopy in SI representation cannot be causally linked. Thus, even at this level of analysis, we may infer that the above data are at variance with Farah's proposal for the origin of homuncular discontinuities. These results are further considered below.

3.1 Simultaneous Firing and Somatotopy. Kandel and O'Dell (1992) have proposed molecular mechanisms to support the finding that simultaneous activity in adjacent presynaptic retinal ganglion axons leads to a refinement of retinotopy in subcortical nuclei. Such trophic mechanisms have been widely invoked to account for the pruning of inappropriately targeted axons (Purves, 1994; Wong, 1999). Applied to the somatosensory system, the coactivation of adjacent mechanoreceptors would refine cortical somatotopy and might be thought to support Farah's suggestion that frequent hand-face contact will place the face representation adjacent to that of the hand.

However, a hand-face contact event in utero would coactivate two distinct groups of mechanoreceptors—one group in the hand and the other in the face. On subsequent hand-face contacts, the same two groups of mechanoreceptor cells might not fire simultaneously because the hand is free to move over the face. Such hand-face contact events might create somatotopy separately in the hand and in the face, but not across the hand-face boundary in SI. The situation is the same in the case of foot-genital contact, where the feet are free to move over the genital region. However, as shown in section 2, there is no somatotopy present in SI between the foot and the penis representations. As such, hand-face adjacency in SI is likely to be generated by other causes.

This view is reinforced by findings in congenital amelics (e.g., thalidomide teratogens) studied by Flor et al. (1998) and Montoya et al. (1998), who examined the homuncular organization in individuals with only one affected upper limb. The frequency of prenatal hand-face contact in these cases may be expected to be asymmetrical. Localization of cortical activation generated by cutaneous touch, using brain-imaging techniques, nevertheless allowed bilateral hand-face adjacency to be inferred in SI despite unilaterally affected upper limbs.

In the case of the experiments entailing costimulation by Clark et al. (1988) and Wang et al. (1995), the body parts whose representations were found to be merged had not been free to move independently. In the former experiment, the digits were constrained and costimulated, and in the latter, the digits had been surgically fused.

In the examples (Clark et al., 1988; Wang et al., 1995), the body schema (Maravita, Spence, & Driver, 2003; Price, 2006) associated with proprioception and cutaneous sensation (whose nervous pathways are co-parcelled) would adapt to reflect body-part fusion in SI. However, in the case of hand-face contact, the body schema would be at variance with a bodily configuration representing hand-face fusion. Furthermore, costimulation of the facial skin and that of the posterior scalp and the neck does not lead to somatotopy across their respective boundaries with the face, even though the body schema would support such a configuration.

This finding casts doubt on the universal applicability of Kandel and O'Dell's (1992) mechanism for the refinement of topographic maps and reinforces the view that hand-face adjacency in SI arises from other causes. These are explored below.

4 Face Parcellation

The overall map of the human somatosensory homunculus for cutaneous sensations that emerges from the results obtained thus far can be interpreted as follows. There exist two distinct regions exhibiting cutaneous somatotopy in SI: the face representation and that of the rest of the body. I observe that the face representation is inverted and displaced as a whole from that of the neck and posterior scalp to lie discontinuously adjacent to that of the thumb (this anomaly is also noted by Penfield & Rasmussen, 1968, and Itomi, Ryusuke Kakigi, Hoshiyama, & Watanabe, 2001; see Figure 1 here). The soundness of this classical finding by Penfield and coworkers has been confirmed more recently by Moulton et al. (2009), who charted the two-dimensional onion skin face representation in SI using fMRI (see section 4.1).

In the owl monkey, the face representation is displaced from that of the neck but is not inverted with respect to that of the body. Here, the representation of the chin vibrissae is adjacent to that of the glabrous thumb in area 3b (Merzenich, Kaas, Sur, & Lin, 1978). Cortical face representation in many rodent species, by contrast, is continuous with that of the neck. It should also be noted that in the human homunculus, the part of the face the thumb abuts is the vertex of the head (I am grateful to P. D. McLeod for this observation), not the mouth, with which it has frequent contact during the fetal stage (Myowa-Yamakoshi & Takeshita, 2006).

Factors underlying separate facial representation are sought through an analysis of facial skin innervation and the time of onset of its sensory function in relation to those of the rest of the body.

4.1 Anatomy. Cutaneous sensations from peripheral mechanoreceptors in the face are carried to the thalamus in the trigeminal somatic sensory system. Those originating in the rest of the body project separately in the dorsal column-medial lemniscus pathway (Purves et al., 1997; Larsen, 2002; Upadhyay, Knudsen, Anderson, Becerra, & Borsook, 2008; see Figure 2).

Afferents from cutaneous receptors in the three well-defined facial zones of the onion skin representation (Kunc, 1970; Borsook, DaSilva, Ploghaus, & Becerra, 2003; Moulton et al., 2009) are carried in the three components of the trigeminal somatic sensory system (ophthalmic: V1, maxillary: V2 and mandibular: V3), providing somatotopic organization related to the afferent projections of the three components (Borsook et al., 2003). These zones cover the bulk of the face and mouth (Moulton et al., 2009). All sensory fibers from these pathways make first-order synapses in the trigeminal nucleus (main V), which has detailed maps of these components. There is also evidence that an inverted facial representation is present in main V (Brodal, 1981). The sensory outputs from main V that originate in the facial zones are carried by the trigeminal lemniscus, and make second-order synapses in the ventral posterior medial (VPM) nucleus of the thalamus.

The afferents from cutaneous receptors from the rest of the body, including the posterior scalp (innervated by cervical spinal nerves, C2 and C3) and part of the external ear (Nihashi et al., 2002, 2003), are carried to the thalamus by the dorsal column-medial lemniscus pathway. First-order synapses form in the two dorsal column nuclei in the medulla (the cuneate and gracile nuclei, innervating, respectively, the upper and lower parts of the body), and the medial lemniscus carries axons from these nuclei to form second-order synapses in the ventral posterior lateral nucleus of the thalamus (VPL). This nucleus has ordered maps of the remainder of the body (Purves et al., 1997).

From VPM and VPL in the thalamus, separate thalamocortical pathways target different regions of somatosensory cortex. These pathways have been explored in monkeys and provide further support for separate face parcellation:

- Jain, Catania, and Kaas (1998) report that a morphologically distinct septum separates the hand-face boundary in cortex.
- Lesion studies (Jones, Manger, & Woods, 1997) showed that silenced cortical hand representations were not encroached on by adjacent face representations.
- Hand-face adjacency is reported to exist in the ventroposterior nucleus (VP) of the thalamus (Jain, Qi, Collins, & Kaas, 2008). However, lemniscal afferents (to VPL) and principal trigeminal afferents (to VPM) do not overlap across these two subnuclei of VP (Raussel, Bickford, Manger, Woods, & Jones, 1998).
- Similarly, in the same study (Raussel et al., 1998), injections of anterogradely transported tracers in VPM and VPL showed that cortical projections from these thalamic nuclei targeted distinct

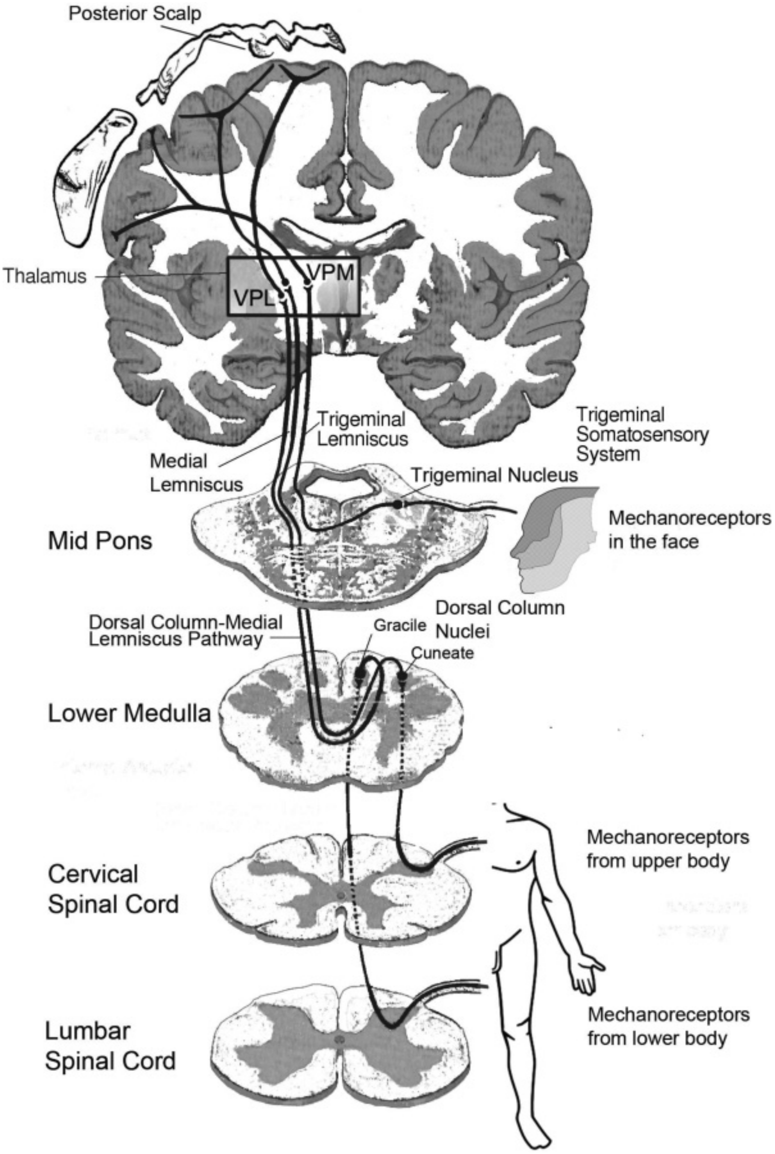

Figure 2: A schematic representation of the trigeminal and dorsal column-medial lemniscus pathways. Afferents from cutaneous mechanoreceptors in the face and the rest of the body form separate cortical representations. The somatosensory homunculus is depicted at the top-left of the diagram. For further details, see section 4.1. (Adapted from Purves et al., 1997, Figure 8.6, and Kell et al., 2005, Figure 3.)

nonoverlapping regions in SI (representing separately the face and the rest of the body).
- Horizontal corticocortical connections, which are extensive within dorsal column-lemniscal and trigeminal representations, do not cross the border between the hand and face representations (Manger, Woods, Muñoz, & Jones, 1997; Fang, Jain, & Kaas, 2002). Similar results are found in the thalamus (Fang et al., 2002).
- VPL and VPM are separated by a prominent cell-sparse border of white matter, the arcuate lamella, dividing face representation from that of the rest of the body (Jones, 2000).

These findings reinforce the proposal of a separate parcellation of the trigeminal pathway from those innervating the rest of the body.

In chronically deafferented animals, however, an invasion of the jaw representation into that of the body's has been previously reported (12 or more years after surgery) (Brown, 1974; Jain et al., 2008) and attributed to expansions of regions innervated by the mandibular nerve, which overlaps input from the upper cervical nerve representation in macaques (Manger et al., 1997). This phenomenon is discussed by Jones (2000) in relation to atrophy of the arcuate lamella.

The septum referred to in Jain et al. (1998) differs from those found at partial discontinuities in receptor sheets that follow the rule: " The terminations of sensory projections with discorrelated activity segregate" (Catania & Kaas, 1995). Rather, it appears to be of another kind that delimits mechanically the spread of new connections in adult brains (Catania & Kaas, 1995). Both Jones (2000) and Jain et al. (2008) remark that normal cortical tissue is capable of setting up boundary conditions that effectively localize representation of body parts, notably the face.

In sum, what appears as the separate face representation in the homunculus is innervated by the separately parcelled trigeminal pathway. The posterior scalp and the neck are innervated by C2 and C3 (Larsen, 2002), not by the trigeminal nerve. These body parts mark the limits beyond which the face is displaced as an island.

4.2 Ontogeny. Topographic mappings emerge sequentially, beginning from the array of cutaneous mechanoreceptors at the periphery and ending in cortex, with somatotopy generally maintained throughout the neuroaxis (Killackey et al., 1995; Scott & Atkinson 1999; Rubel, 2004).

Separate face parcellation is reflected also in its earlier onset of function compared to the rest of the body. During human gestation, at 7.5 weeks gestation age (g.a.), the mouth is the first location that elicits motor responses to cutaneous stimulation; by contrast, the first bodily response occurs at 10.5 weeks g.a. (Brown, 1974). The earlier development and consolidation of the trigeminal pathway is consistent with its separated parcellation in cortex.

5 Conclusion

The analysis leads to the proposal that the somatosensory homunculus results from two distinct, separately developing nervous pathways: one innervating the face and the other the rest of the body.

These separately parceled bundles of nerves, originating in the cutaneous mechanoreceptors, synapse in different sets of intervening nuclei and form separate representations in cortex. The boundary between these two regions constitutes and creates the homuncular discontinuities.

Face-posterior scalp/neck disjunction in SI is consistent with this view. The irrelevance of the frequency of hand-face contact in utero in determining the overall homuncular plan can be supported on two counts. Such contacts can create somatotopy separately only in the hand and in the face (as explained in section 3.1). Furthermore, even if body schema constraints were removed, there remain boundaries between these distinct bundles of nerves across which rules of plasticity do not apply.

Computational modelers may do well to take note that these findings point to the existence of intrinsic developmental factors, other than simple epigenetic rules, that determine the overall form of the homuncular map.

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