Implications of the "initial brain" concept for brain evolution in Cetacea

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Abstract: We review the evidence for the concept of the "initial" or prototype brain. We outline four possible modes of brain evolution suggested by our new findings on the evolutionary status of the dolphin brain. The four modes involve various forms of deviation from and conformity to the hypothesized initial brain type. These include examples of conservative evolution, progressive evolution, and combinations of the two in which features of one or the other become dominant. The four types of neocortical organization in extant mammals may be the result of selective pressures on sensory/motor systems resulting in divergent patterns of brain phylogenesis. A modular "modification/multiplication" hypothesis is proposed as a mechanism of neocortical evolution in eutherians. Representative models of the initial ancestral group of mammals include not only extant basal Insectivora but also Chiroptera; we have found that dolphins and large whales have also retained many features of the archetypal or initial brain. This group evolved from the initial mammalian stock and returned to the aquatic environment some 50 million years ago. This unique experiment of nature shows the effects of radical changes in environment on brain-body adaptations and specializations. Although the dolphin brain has certain quantitative characteristics of the evolutionary changes seen in the higher terrestrial mammals, it has also retained many of the conservative structural features of the initial brain. Its neocortical organization is accordingly different, largely in a quantitative sense, from that of terrestrial models of the initial brain such as the hedgehog.

Keywords: ancestral brains; brain evolution, Cetacea; Chiroptera; columnar organization; cortical columns; cortical modules; Insectivora; isodendritic neurons; prototype brain

I. Introduction

We have been studying the morphology of the dolphin brain for many years (see Morgane et al. 1986a; 1986b) and, like earlier investigators (Beauregard 1883; Breathnach 1953; 1960; Kükenthal & Ziehen 1889; Langworthy 1931; 1932), we were struck by the extreme size and convolutional complexity of cetacean neocortical formations. Our histological studies, however, revealed a relatively simple underlying neocortical organization in the dolphin·that is in many ways similar to that of hedgehogs and bats (Morgane et al., 1985; 1988 in press). The studies of Sanides (Sanides & Sanides 1972; 1974) and Valverde (Valverde 1983; Valverde & Facal-Valverde 1986; Valverde & López-Mascaraque 1981) on the cortical neuronal structure of the hedgehog and bat provide further evidence of neuroarchitectonic similarities with the neocortex of the dolphin. Our recent studies (Morgane et al. 1985; 1986a; 1986b) have accordingly led us to interpret the dolphin brain in terms of an initial or prototype brain concept that we now propose to elaborate in this target article.

The initial brain concept concerns the evolution of the mammalian nervous system and suggests that the full spectrum of extant patterns of brain organization in mammals arose from a common ancestral mammalian brain (Elliot Smith 1910; Filimonoff 1949; Herrick 1921; Wirz 1950). A number of well-established evolutionary concepts documented by comparative neuromorphology and physiology have been drawn upon in this account. (Ariens Kappers et al. 1936; Brodmann 1909; Ebbesson 1984; Ebner 1969; Elliot Smith 1910; Filimonoff 1949; 1965; Herrick 1921; Kaas 1980; Kesarev 1970; Le Gros Clark 1932; Morgane et al. 1985; 1986a; 1986b; Northcutt 1984; Poliakov 1958; Sanides 1969; 1970; 1971; 1972). The following major features of brain evolution recognized by camparative neuroanatomists will be used in discussing the initial brain concept:

1. There is a general trend toward an allometric increase in the absolute and especially the relative mass of the brain with respect to body size. This implies an increase in the number of functional units (neurons), an increase of interneuronal communication due to the corresponding growth of neuronal processes (dendrites and

axons), and an associated increase in related structures (glia and blood vessels).

2. Components of the telencephalon, especially the cerebral cortex as a whole, exhibit greater quantitative development compared to other brain regions.

3. There is relatively greater development of neocortical areas than of the other cortices (paleocortex, archicortex, and intermediate cortical formations).

4. In specific sensory/motor systems the sensory component is quantitatively predominant.

5. There is intensive development of the associative zones of the neocortex located between the specific primary zones along with a relative decrease in size of specific projectional zones with respect to the entire cortex as well as to the secondary zones, despite their high degree of morphological and functional differentiation.

6. There is progressive differentiation of specific cortical laminae in all regions of the neocortex, although the directions of laminar differentiation taken are different in the projection and associative zones. Thus, in the sensory projection zones the layers have undergone an overall increase in the number and type of granular, short-axon elements and the granular cells themselves have become smaller (a granularization trend). The inner granular layer (layer IV) has progressed quantitatively and here the granularization trend is the most prominent feature in the primary sensory cortices. On the other hand, in the motor projection zones magnocellularity appears to have become the main evolutionary trend, with its strongest expression seen in the differentiation of layer Vb (the giant pyramidal cells of Betz). In the associative zones the main trend of laminar differentiation has apparently been an overall gracilization of the cells and an extreme development of the supragranular layers, particularly the associative layer IIIc.

7. There is an immense absolute increase (in the number of cellular elements, connections, and processing units [nuclei in subcortex, laminae in cortex]) – and especially a relative one – in the sensory systems mediating the biophysical senses (vision, audition, proprioception, and general somatic sensation) as compared to the chemical senses (olfaction and taste).

8. There are characteristic trends in neuronal development, including the appearance of a diversity of cell types arising from the distinctive geometrical patterns of dendritic and axonal trees. In the cortex of whales, these evolutionary changes may account for the extensive pyramidization of the major cell population and the appearance of a great variety of stellate cells, including the most phylogenetically advanced granular elements.

Overall, the above characteristics could each have evolved independently in the separate mammalian groups by convergent evolution. If we accept these eight major morphophysiological features of brain evolution then we can begin to reconstruct the stages of evolution from the prototype brain. The concept of the initial brain was introduced by the Russian neurologist I. N. Filimonoff (1949) and then developed by his collaborators (Kesarev 1975; Kesarev et al. 1977; Poliakov 1958; Preobrazhenskaja et al. 1974; Zvorykin 1971). The idea was based on the widely accepted paleontological assumption that the different groups of eutherian mammals extending to the most advanced have a common ancestral form from

which all varieties of eutherian mammals have evolved through various evolutionary mechanisms, such as natural selection, geographic isolation, radiation, and so on (Dillon 1973; Eisenberg 1981; Mayr 1966; McKenna 1975; Moody 1962; Simpson 1945; 1949; 1953; West-Eberhard 1986). According to Simpson (1945), this initial species should resemble some types of primitive insectivores in its functional and structural features. Newer revisions of mammalian phylogenetic systematics on the basis of recent paleontological data and cladistic methods (McKenna 1975) indicate, however, that all contemporary eutherian groups (i.e., Insectivora, Ferae, Archonta, and Ungulata) evolved from a common ancestral group, the Tokotheria (Figures 1A, 1B).

Morphologically, at least on the basis of their skeletal features, these tokotherians were actually similar to some of the ancient Insectivora, especially the erinaceids (McKenna 1975). According to McKenna (1975), all Cetacea evolved from ancient Ungulata at the end of the Cretaceous period or at the beginning of the Paleocene. With these revisions of Simpson's original view of mammalian evolution, his postulate that extant insectivores have retained many more conservative (plesiomorphic)[1] features than other mammalian eutherian groups seems to be accepted by most mammalogists (Eisenberg 1981). It can thus be deduced that in these extant insectivores one would find brains that retained various features of the hypothetical ancestral form. The search for the features of this initial brain was facilitated by the findings of Stephan (1967; 1969; 1972), Stephan and Andy (1969), Stephan et al. (1970b), Stephan et al. (1981) on the quantitative characteristics of the brains of a variety of insectivores. Stephan identified a group of the most conservative insectivores, which are characterized by the lowest degree of encephalization, and especially of neocorticalization, among all extant eutherian mammals and among the order Insectivora itself (Figure 2). This group he, as well as others (Hall & Diamond 1968; Jolicoeur et al. 1984; Pirlot 1986; Sanides & Sanides 1972; 1974; Valverde 1983), designated as basal Insectivora, which include three families: Soricidae, Erinaceidae, and Therenacidae. These basal insectivores are thus considered possible models for the initial steps of brain evolution in eutherian mammals. It is accordingly assumed that in species of these families one can expect to find more clearly recognizable features of the ancestral initial brain. This grouping into basal and specialized insectivores is not to be construed as a taxonomic one; rather, it is based on the relative degrees of conservative brain features.

II. Major morphological features of the hypothetical "initial" brain

Based on features of cortical brain evolution we can tentatively reconstruct morphological characteristics of the initial mammalian brain (Figure 3) and then attempt to verify this reconstruction by examining the brains of present-day species that retain a dominance of conservative features and thus serve as models of the initial brain. Some extant mammals such as basal insectivores can be thought of as comparatively close models of ancestral prototypes of the mammalian brain, having retained many of its fundamental features. Of course, some
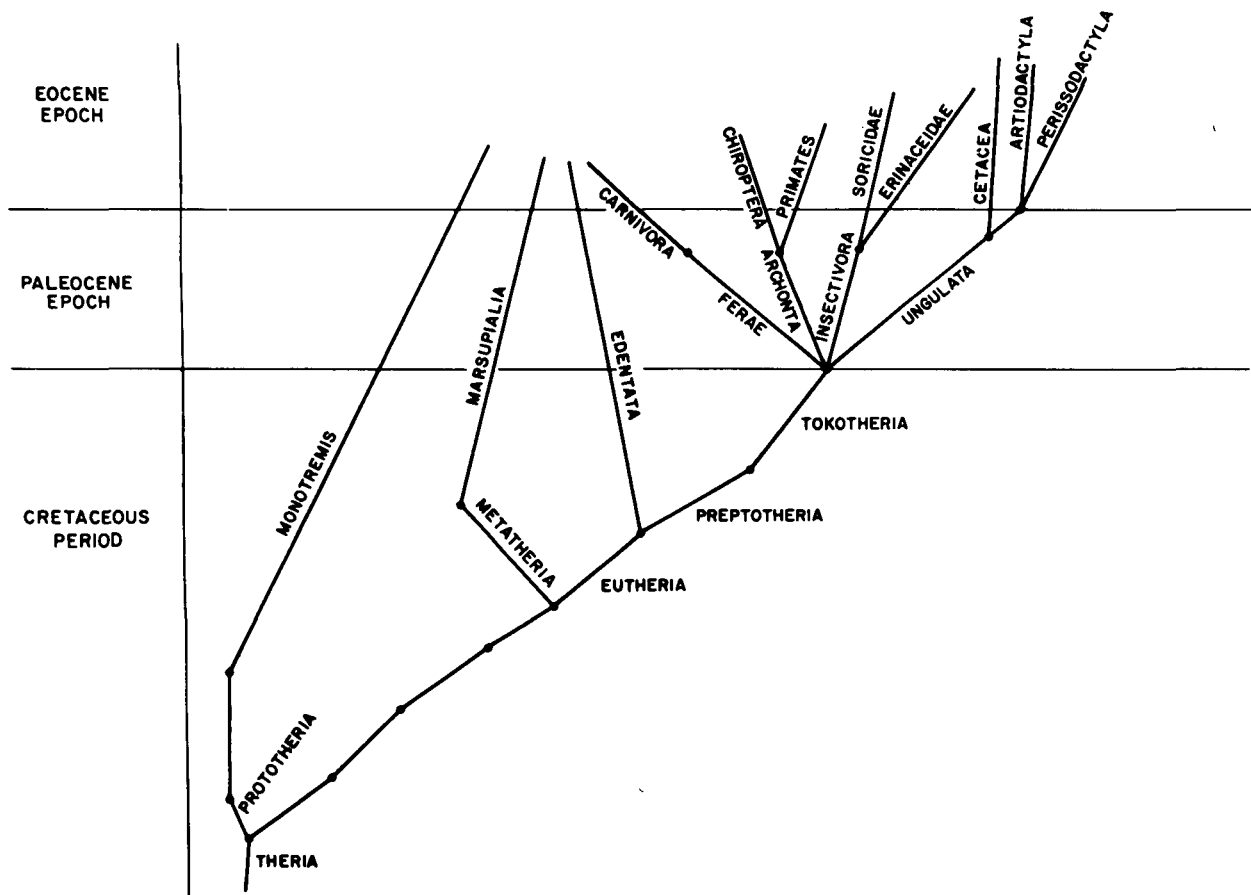
EOCENE EPOCH

PALEOCENE EPOCH

CRETACEOUS PERIOD

MONOTREMIS
MARSUPIALIA
EDENTATA
CARNIVORA
FERAE
CHIROPTERA
PRIMATES
ARCHONTA
SORICIDAE
ERINACEIDAE
INSECTIVORA
CETACEA
ARTIODACTYLA
PERISSODACTYLA
UNGULATA
TOKOTHERIA
METATHERIA
PREPTOTHERIA
EUTHERIA
PROTOTHERIA
THERIA

EOCENE EPOCH

PALEOCENE EPOCH

CRETACEOUS PERIOD

CARNIVORES
PRIMATES
CHIROPTERA
SORICIDAE
ERINACEIDAE
ARCHEOCETI
ODONTOCETI
MYSTICETI
ARTIODACTYLA
PERISSODACTYLA
FERAE
ARCHONTA
INSECTIVORA
CETACEA
UNGULATA
TOKOTHERIA

Figure 1A. Cladogram showing the main directions of mammalian origin and evolution. Note that major placental mammalian groups radiated from tokotherians between the Cretaceous and Paleocene periods. The bushlike branching of the tokotherian mammals suggests that four major placental groups originated from one common stock. This implies the existence of an initial mammalian group with generalized features from which different specialized groups evolved through ecological adaptation. The cetaceans appear to have arisen from ancient ungulates by bushlike radiation in the beginning of the Paleocene. This cladogram is a combined and simplified scheme based on the original schemas of McKenna (1975) and Eisenberg (1981).
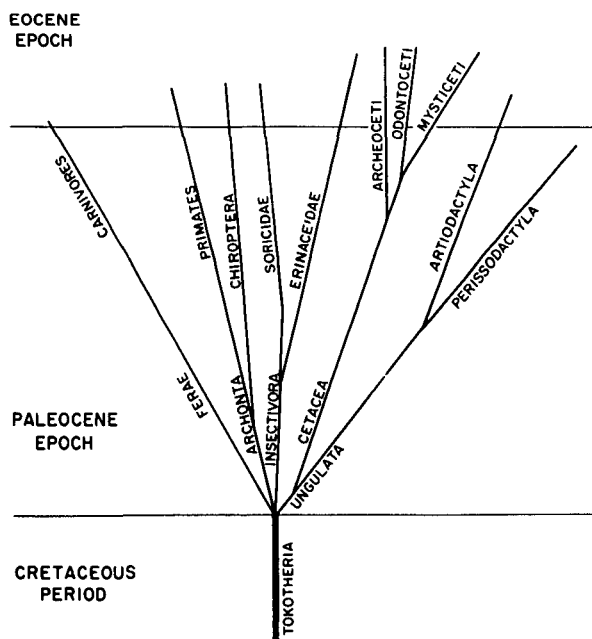
Figure 1B. Detail of one component of the previous cladogram showing the bushlike radiation of the contemporary mammalian groups. This cladogram is our modification of the McKenna views on the evolution of placental mammals, based on comparative neuroanatomy and molecular biology (genetic distances between species; Goodman 1975; Shoshani 1986). According to the initial brain concept, extant Insectivora, Chiroptera, and Cetacea branched much earlier from the initial mammalian stock and thus preserved many initial morphological features, including the structure of their neocortex. The wider initial branch indicates the period when this branching most probably took place.

additional changes have also occurred over the millions of years of their subsequent phylogenetic history.

Various Russian investigators (Filimonoff 1949; Poliakov 1956; Zvorykin 1977; 1980) have presumed that the initial group of mammalian ancestors is likely to have been characterized by small brains with relatively little cerebral cortex, with the paleocortex, archicortex, and

intermediate cortex predominant over the neocortex. The organization of the pallium in the ancestral eutherian group, however, is thought to be more advanced than in more ancient Prototheria (Monotremata) and Metatheria (Marsupialia). It was shown by Abbie (1940; 1942) that in the latter most of the cortical surface is occupied by the so-called parahippocampal and parapyriform formations
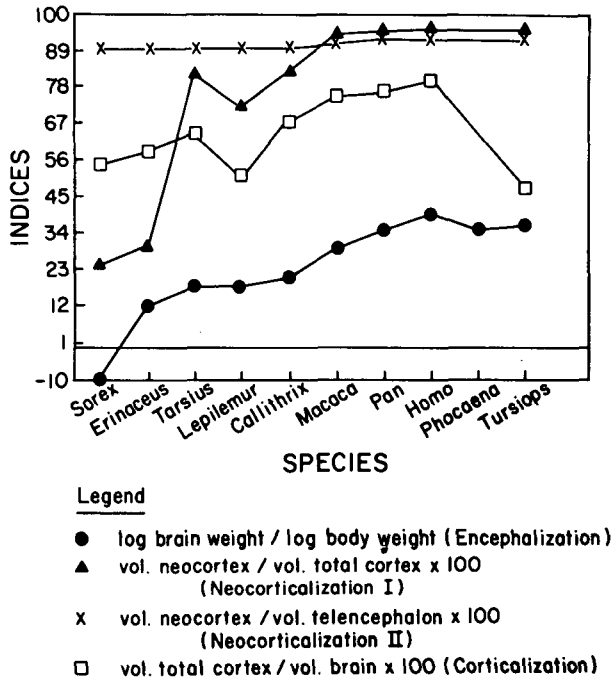
Figure 2. The indices of encephalization, corticalization, and neocorticalization in a comparative series of placental mammals. The indices were calculated from the empirical tables of Fil-iminoff (1949), Stephan and coauthors (1967; 1970a; 1970b; 1972; 1981) and Haug (1987). Note that the index of *encephalization* (log of brain weight/log of body weight), and *neocorticalization* (volume of neocortex/ volume of cortex × 100) reveal a strong increase from basal insectivores to primates and ceta-ceans. The index of *corticalization* of the telencephalon (volume of cortex/volume of telencephalon × 100) shows high stability across all species of insectivores, primates, and cetaceans. The index of brain corticalization (volume of cortex/volume of brain × 100) shows a moderate increase in this comparative series.

Figure 3. Schematic presentation of the main cytoarchitec-tonic features and neuronal (Golgi) types in the initial neocortex. Our reconstruction is based on the data of Sanides and Sanides (1972) on hedgehog and bat brains, Valverde (1983) and Val-verde and López-Mascaraque (1981) on hedgehog brains, and our own data on the dolphin brain (Glezer and Morgane, in press; Morgane et al., in press; Morgane et al. 1985; Morgane et al. 1986a). The scheme of cytoarchitectonic structure (left part of Figure 3) shows the following features: an extremely wide layer I, an accentuated layer II, and an absence of layer IV (so that layers III and V have no distinct boundaries). Subdivision into sublayers in layers III and V is not well expressed. As a result of the absence of sublayering and the absence of layer IV the overall subdivision of the neocortical plate into definitive layers is weak. The main neuronal types of the initial neocortex are presented at the right part of the scheme: 1 - extraverted neuron of the second layer; 2 - isodendritic stellate cell; 3 - atypical (transitional) pyramidal cell; 4, 5 - bipolar cells.

that represent intermediate or transitional cortex but not true neocortex. In ancestral eutherian mammals, on the other hand, the neocortical formations were very distinct from all other cortices, though still in relatively non-differentiated form. Moreover, the morphological organi-zation of the functionally distinct neocortical components of the sensory/motor systems was similar, and of these the chemical sensory systems (taste and smell) are likely to have occupied more surface area than the other sensory systems (vision, audition, general somesthesis, and pro-prioception), since this is the pattern seen in extant models of the initial brain such as that of the hedgehog. It is also probable that the primary projection zones in the protomammalian neocortex were considerably larger than the secondary and tertiary zones, which were in the very beginning of their phylogenetic development. It is even possible that the latter were not developed at all, in which case the boundaries of the sensory cortical projec-tion zones were in direct contact with each other (this is called the "principle of cortical adjacency," Supin et al. 1978).

Based on characteristics of the cerebral cortex in the models of the initial brain we can hypothesize that cytoarchitectonic and neuronal features of neocortical organization were poorly differentiated (Figure 3). The neocortex was absolutely and relatively thin, and its laminae were not distinct, largely because of the relative
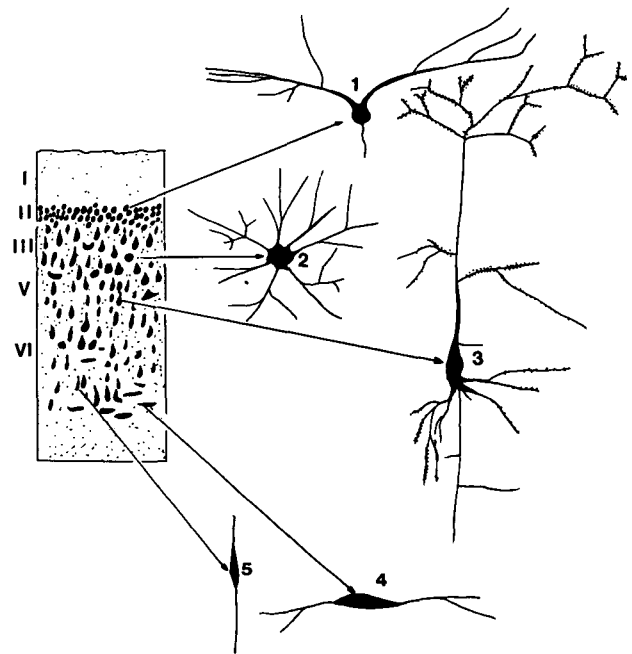
homogeneity of the cell populations. The numbers and diversity of cell types in the initial neocortex were proba-bly very limited. The ancestral neocortex may have been populated predominantly by undifferentiated or transi-tional forms of pyramidal and stellate cells, as seen in extant models of the initial brain. Extreme size variants of particular cortical cell types represented, for example, by small pyramidal and Betz cells found in advanced extant mammals were not yet developed. As a consequence, the differentiation of neocortex into different cytoarchitec-tonic areas was extremely poor. Since the separation of the neocortex from phylogenetically older cortical forma-tions was not yet distinct, it still showed the same main afferent inputs as did the older cortical formations. In paleocortex and archicortex, these inputs are channeled to the molecular layer. It is thus likely that in the neocortex of initial mammalian species, layer I showed a powerful development in terms of thickness and extent of dendrites from layer II neurons as well as from pyramidal neurons in the lower cortical layers. Because of the predominance of afferents to the first layer, layer II became extremely cellular and thus played a dominant role as the main cellular layer for afferent inputs to the

neocortex via dendrites spread widely in layer I. In later phylogenesis, layer IV plays the dominant role as the principal cellular layer for input to the neocortex.

Because of weak development of the associative cortical zones representing secondary and tertiary projections in the initial neocortex, the layers that are considered to be "associative" for intercortical connections were underdeveloped and not subdifferentiated. This would apply particularly to layer III. Layer IV was also likely to have been extremely underdeveloped or totally absent since the main afferent projections apparently reached the neocortex through layers I and II. Layer V, the main neocortical output layer, in contrast, was probably well developed in the initial brain type. Similarly, layer VI, representing the source of intrahemispheric connections, also showed strong development.

The geometric structure and morphological polarization of the dendritic trees of the pyramidal cortical neurons probably originated phylogenetically from the geometric features of neurons of the basic isodendritic cell type (Ramón-Moliner 1962; Ramón-Moliner & Nauta 1966). The influence of layer I afferents was evidently predominant and that factor may have influenced the elongation and lateral spread of the apical dendrites of most of the cortical cells, particularly those of layer II. This contributed to the drawn out saucer shape of these modified pyramidal neurons (the "extraverted" neurons of Sanides & Sanides 1972). Other afferent influences acting on cortical neurons of the initial brain, including additional horizontal afferent plexuses as well as local circuit neurons, are thought to have been minimal or weakly developed. As a result, basal dendrites did not develop sufficiently to influence the shape of the basal portion of the perikaryon. It is hence likely that most neocortical cells in the initial mammals were atypical transitional forms of pyramidal neurons. A relatively great number of neurons of the large undifferentiated or isodendritic type would also be expected in the paleomammalian neocortex. As noted above, local circuitry is likely not to have been well developed; thus, small stellate cells with their richly differentiated axon systems were not prominent. In view of the likelihood of an extremely thin cortical plate in the initial brain, many cells probably had their growth and shape influenced not only by afferents passing to the extremely wide layer I, but also by afferents from the subcortical white matter passing to layer VI where, in the initial cortex, one would expect to find many cells of the double bouquet or bipolar types. We have used all of these features of the postulated prototype cortex as representative of an initial protomammalian model system helpful in interpreting the evolution and present organization of the brains of extant groups of mammals, particularly the Cetacea (Figure 3).

III. Extant mammalian brains as models of the "initial" brain

From the above it can be seen that there are special considerations in selecting possible models of the initial brain among contemporary mammalian groups which could themselves serve as models of ancestral brains and thus be helpful in interpreting the evolution of the neo-

cortex. Phylogenetic changes of the ancestral mammalian brain were highly dependent on the necessities of adaptation to the constantly changing environment. In all cases this should have transformed the generalized, multiadaptive initial mammal into specialized species more precisely adapted to specific environments. This precise adaptation and specialization would, in varying degrees, obscure initial features of brain organization, particularly when it involves marked changes in the predominant types of afferent information and locomotor functions.

To illustrate the importance of major changes in afferentation and locomotion in speciation, one might consider the loss of vision in certain basal insectivores. The moles, for example, have become specialized in a fossorial environment in association with an extreme decrease of their visual acuity and this, to varying extents, obscures some of the initial features of the brain. In this case a weakly differentiated visual neocortex may reflect the secondary process of evolutionary degeneration and not the primary ancestral plesiomorphism found in models of the initial brain. Analogous to this situation we can point to attempts to evaluate the ancestral status of the extremities in terrestrial mammals based on rudiments of the pelvic bones in whales.

It seems likely that species of basal insectivores that are more adapted to many types of environments would provide excellent models of the initial brain structure. Certain species of hedgehogs (Therenacidae and Erinaceidae) and some of the shrews (Soricidae) belong to this group of generalized eutherians that apparently retained a multi-adapted status from the Cretaceous period to the present day (Anderson & Jones 1967; Eisenberg 1981; Vaughan 1972; Walker 1968). Thus, from the ecological and paleontological points of view there are compelling reasons for accepting representatives of the non-specialized families of Insectivora as models of the initial protomammalian brain. Among other orders of mammals one also finds features of the initial brain in Chiroptera that are thought to have radiated very early from the initial stock of eutherians somewhere at the end of the Paleocene (Dillon 1973; Eisenberg 1981; Romer 1966; Simpson 1949; 1953). Although bats as a group departed much more in their ecology and specialization from the initial stock of ancestral tokotherians, they have nevertheless retained many conservative brain features in common with the basal Insectivora (Sanides 1970; Sanides & Sanides 1972). For these reasons, we feel that it is useful to consider the major features of the brain, especially the cortex, in certain of the basal Insectivora and Chiroptera and to similarly regard them as models of initial protomammalian brain organization.

When considering relationships between the original ancestral version or extant models of the initial brain and higher derived mammalian brains, a comparison needs to be made among major parameters of brain structure, including brain size, the size of the cortical and neocortical components of the brain and their cytoarchitectonic and neuronal organization. We will now consider these parameters.

A. Encephalization. Although extremely variable in body size (from 5.3 grams in *Sorex minutus* to 860 grams in *Erinaceus europaeus*), all basal insectivores have the lowest encephalization indices among terrestrial mam-

mals. Based on data of different authors (Blinkov & Glezer 1968) we have estimated the ratio of the logarithm of brain weight to the logarithm of body weight (Figure 2) and its variations to be between −10 and +12 in *Sorex* and *Erinaceus*. If one uses the allometric formula of Dubois-Snell and constants given by Stephan (1969) and Stephan et al. (1970b), this index varies from 83 to 112 in basal insectivores. This equation expresses the relation between brain and body weights and shows that this relation is not linear [$A = B^{.56}$].[2]

B. Corticalization. The degree of corticalization – expressed as the ratio of the volume of the cerebral cortex to the volume of the entire brain – is lowest in the basal insectivores and varies from 49.7% to 60.1% (calculated by us from the tables of Stephan et al. 1970b). However, when the volume of the cortex is compared to that of the telencephalon, the degree of corticalization in basal insectivores is more than 90% (Figure 2) and varies only slightly in the comparative series. It thus appears that one of the major phylogenetic innovations of the initial stock of mammals was a corticalized telencephalon. The presence of such a relatively large quantity of cortex even in animals with small brains represents a distinct phylogenetic advance over the earlier mammalian groups (Prototheria and Metatheria) and appears to have been stable throughout mammalian evolution (Figure 2).

C. Neocorticalization. Although many investigators have identified neocortical areas in the basal insectivores (Diamond & Hall 1969; Ebner 1969; Hall & Diamond 1968; Stephan 1969; Valverde 1983; Valverde & Facal-Valverde 1986; Valverde & López-Mascaraque 1981), it was shown that these areas have a cytoarchitectonic and neuronal organization that is poorly differentiated and, in many features, resembles the structure of the allocortex (Sanides & Sanides 1974; Valverde & López-Mascaraque 1981; Valverde & Facal-Valverde 1986). Moreover, the neocortex of basal insectivores is on the lowest scale of development when compared quantitatively to representatives of other mammalian orders (Figure 2). Only 20–30% of the total cortex in basal insectivores is neocortex, the greater part of the cortical formations being paleocortex. The small amount of the neocortex occupies only one-fifth of the entire brain surface (Figures 2, 4A).

Based on these quantitative data we can deduce that the initial stock of mammals was characterized by a low degree of encephalization, corticalization, and neocorticalization as illustrated in Figure 2. The potential for encephalization and, especially, for neocorticalization under select environmental stimuli expressed itself in the radiation of a number of mammalian orders from this primitive ancestral stock (Figures 1A, 1B).

D. Cytoarchitectonics. According to Valverde and López-Mascaraque (1981), the neocortex of *Erinaceus* can be subdivided into several cytoarchitectonic areas which differ only slightly in their cellularity, cell types, and cell size. Generally, more anterior areas (frontal and precentral) are less cellular and contain larger cells than the more posterior areas (occipital, parietal, and temporal regions). The thickness of the neocortex varies from 600–800 μm caudally to 800–1000 μm rostrally. Of the cortical laminae, the most prominent is layer I with a radial diameter of 200–300 μm, containing mainly tangential
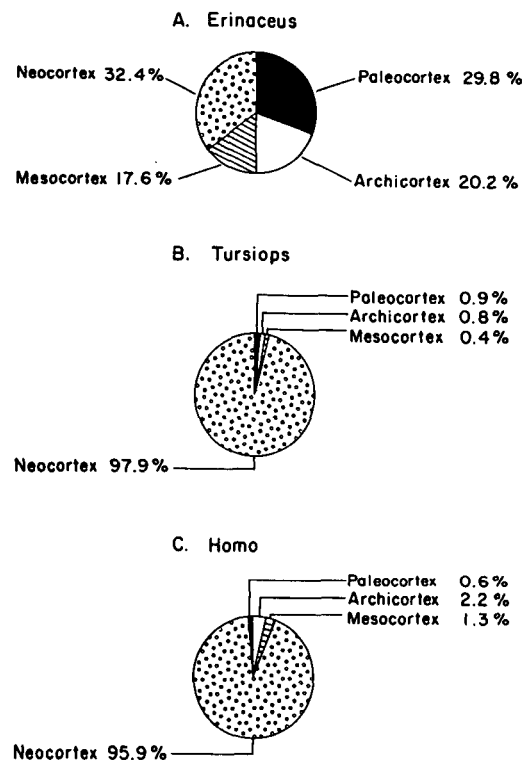

Figure 4. Relative size of the cortical territories in representatives of conservative (A), conservative/progressive (B), and progressive (C) modes of neocortical evolution in mammals. Each of the pie-shaped graphs shows proportionate relationships (percentages) in area size of neocortex, paleocortex, archicortex, and mesocortex (a sum of peripaleo- and periarchicortices). Note the area of neocortex in both conservative/progressive and progressive modes (*Homo* and *Tursiops*) occupies more than 90% of the total cortical surface. Note also that in the conservative mode (*Erinaceus*) the neocortex occupies only one-third of the entire cortical surface, whereas archicortex is almost equal in relative size to neocortex (29.8%).

myelinated and nonmyelinated axons. Layer II (Sanides & Sanides 1974; Valverde & López-Mascaraque 1981; Valverde & Facal-Valverde 1986) is accentuated, that is, it contains an extremely dense packing of polymorphic, so-called "extraverted" neurons. The layer immediately below layer II is interpreted by Valverde as a combined layer III–IV and reveals some signs of columnar organization in the hedgehog. Only in the most posterior parts of the neocortex can layer IV be differentiated as a separate band of granular cells. Layer V contains large pyramidal cells and layer VI is characterized by horizontal rows of polymorphic and pyramidal cells. Thus, the cytoarchitectonic features of the neocortex of *Erinaceus* probably coincide well with the features of the hypothetical initial neocortex. According to Sanides and Sanides (1974), the same type of cytoarchitectonics as that described above is present not only in Insectivora but also in Chiroptera (referred to by Sanides as "flying Insectivora"). Some Marsupialia (*Didelphis delphis, Perameles nasuta*) and Monotremata (*Ornithorhynchus* and *Tachyglossus*) are also characterized by these types of primitive features of the cortical cytoarchitectonics. However, even in these extremely conservative species there is a cytoarchitectonic differentiation along the fronto-occipital axis of the telencephalon. Thus, frontal cortex is less cellular and

more magnocellular than occipital and parietal regions (Abbie 1940; 1942).

To summarize, conservative features of brain evolution include a small radial diameter of the cortex, weak topographic differentiation of cortical areas, with more cellular and granular regions posteriorly and fewer cellular regions anteriorly, an extremely wide layer I occupying from one-quarter to one-third of the total cortical thickness, an accentuated layer II consisting of densely packed neurons with dendrites extending widely ("extraverted") into layer I, overall agranularity or dysgranularity of the neocortex with absent or incipient layer IV, and predominance of layer Vb over layer IIIc in thickness as well as in the size of its neurons.

E. Neuronal structure. One of the major features of neuronal structure in the neocortex of models of initial brains is the presence of large numbers of neurons with extremely divergent apical dendrites ("extraverted" neurons, Sanides & Sanides 1974). According to the latter investigators, such cells belong to the pyramidal type, whereas Valverde and López-Mascaraque (1981) regard them as large spiny stellate cells. Another major initial feature found in some lower extant mammals is that most of the pyramidal neurons are transitional or immature in type and have basal dendrites that are much less developed than the apical dendritic tree. Further initial features include the predominance among the stellate type of large stellate cells with long, widely spread rectilinear dendrites. This "long radiator" type of stellate cell, originally described by Ramón-Moliner and Nauta (1966) as an isodendritic neuron and also studied by Sanides and Sanides (1974), constitutes more than 60% of the entire population of stellate neurons in the bat and hedgehog cortex. Neurons with short radiating dendrites, on the other hand, were found to be much fewer in number in these mammalian species. Thus, the spectrum of neuronal types present in the neocortex of mammals showing features of the initial brain type coincides with the prediction that in the initial brain the overall neuronal typology may have emphasized the general nondifferentiated, isodendritic types of neurons with only a slight development of highly specialized cells such as small stellate neurons (short radiators) and typical neocortical pyramidal cells.

A consideration of the cytoarchitectonic and neuronal characteristics of the neocortex in extant initial model animals suggests that the ancestral mammals already possessed, in primordial fashion, many of the features of later phylogenetic stages of neocortical development. These features included laminar orientation of neurons, a modest spectrum of neuronal types, and rostrocaudal cytoarchitectonic differences of neocortical areas with different functional characteristics. All these features evidently appeared in mammalian evolution at very early stages and have tended to remain stable in phylogenesis.

IV. Organization of neocortex in extant mammals in relation to the "initial" brain

The neocortex in all extant mammals is characterized, to a greater or lesser extent, by columnar and laminar distributions of neurons. These two geometrical features of neocortical organization have been intensively investigated and interpreted both by neuroanatomists and neurophysiologists. The search for an elementary morphofunctional cortical unit has resulted in the recognition of the fact that this unit must include both laminar and columnar features as integral components. In the classical studies of both Ramón y Cajal (1909–1911) and Lorente de Nó (1934; 1949) the different cortical laminae were regarded as playing special roles in afferentation and efferentation in relation to neocortical activity. More recently, however, greater emphasis has been placed on the role of columnar (radial) organization in neocortical activity (Gilbert & Wiesel 1983; Goldman & Nauta 1977; Goldman-Rakic & Schwartz 1982; Hubel & Wiesel 1962; 1965; 1974; Mountcastle 1957; 1975; Szentágothai 1973; 1974; 1975). Although the elementary vertical modules (Szentágothai 1975) as specialized repeating units for stereotyped analysis of afferent stimuli are regarded as essential for cortical function, laminar (horizontal) organization of the neocortex into functional domains is also considered to be critical in cortical activity (Gilbert & Wiesel 1983; Hubel & Wiesel 1974; Wong-Riley 1979).

Based on these views of functional geometry of the mammalian neocortex and on known cytoarchitectonic and neuronal features in a comparative series of mammals, we will attempt to summarize the main directions of neocortical evolution and to indicate the probable evolutionary status of variations in neocortical organization in mammals. The starting point for these reconstructions involves the initial brain concept. The deviations from the archetypal neocortical structure in the evolution of mammalian lines will be discussed below.

We will develop our discussions around two well-defined terms: cortical area (with its subdivisions) and cortical modules. Each of these concepts corresponds to morphophysiological entities that have been widely investigated and discussed in past and recent literature. We will attempt to correlate these terms and to apply them to mammalian neocortical evolution.

The subdivisions of cortex which have peculiar cytoarchitectonic and neuroarchitectonic features and, according to physiological data, receive a particular combination of afferents (specific, nonspecific, associative, commissural, etc.) will be referred to as cortical areas. Each cytoarchitectonically distinct area of sensory cortex is a separate sensory termination zone. Most of these structurally distinct neocortical areas have not yet been assigned a specific function, but we can postulate that since structural individuality is present there must be particular specialized functions different from those in adjacent areas.

The other concept we will use in discussions of neocortical evolution is "module." A module is an elementary columnar unit of the neocortex that is characterized by its vertical and tangential parameters, cell typology, and microcircuitry. This term corresponds to the vertical subdivisions of the cortex similar to those proposed by Mountcastle (columns; 1957), Hubel and Wiesel (ocular dominance and orientation columns; 1962), Woolsey and Van der Loos (barrels; 1970) Szentágothai (modules; 1974), Popper and Eccles (modules; 1981). Each cortical area is in reality an assembly of modules. These modules are connected into a discrete continuum with the help of intermodular connections (Szentágothai 1974) and each group of modules may vary considerably in number and size.

It is well established that the number of cytoarchitectonic areas and subareas depends on the phylogenetic level of the species. In regard to primates, it has been shown that the human neocortex has many more constant areas and subareas in functionally homologous regions than do anthropoid apes, whereas the latter have many more areas of the neocortex differentiated into subareas than the lower primates and particularly the subprimates (Carnivora, Rodentia, etc.; Blinkov & Glezer 1968; Filimonoff 1949; Kononova 1962; Poliakov 1958; Preobrasjenskaja et al. 1973). These earlier findings of Russian morphologists were recently confirmed by physiological mapping studies. It was found that in the owl monkey (*Aotus trivirgatus*) not only is the visual receptive field represented by multiple areas, but, in addition, each of these areas is subdivided into smaller subunits. On the other hand, in prosimians (*Galago*) only one area is present which corresponds to all five areas of the owl monkey (Allman 1982; Baker et al. 1981). The same pattern holds not only for the visual cortex but also for all other functional cortical areas (sensory, motor, etc.) in primates (Wise 1985). In the prefrontal cortex in man at least fourteen functional subareas have been found whereas in the macaque monkey only five have been identified (Allman 1982; Roland 1984; Rosenkilde 1979). Thus, at least in terrestrial mammals, evolution has produced numerous morphofunctional cortical divisions. It is reasonable to suggest that all these morphofunctional cortical areas have developed in the course of eutherian evolution from an initial brain type in which there was minimal subdivision of the cortex into cortical sensory areas. Certain species of Insectivora and Chiroptera appear to have retained this minimal variability of cortical areas throughout millions of years of evolution.

The next question is how the initial minimal cortical variability condition was then transformed into more variable and abundant cortical areas at later stages of brain evolution in terrestrial mammals. At this point we should consider the modular components of the cortical areas to be some of the main targets of evolutionary forces. The major emphasis in work on columnar organization of the neocortex has been on uniformity of the vertical modules in different functional types of cortex, extending beyond taxonomic boundaries (Bugbee & Goldman-Rakic 1983; Hubel & Wiesel 1962; Mountcastle 1957). However, even these studies have shown considerable variation in the size of modules (250 μm to 800 μm) and in their subdivisions into smaller subcolumns (25–100 μm). Based on cytoarchitectonic descriptions of vertical striations in different neocortical areas (Brodmann 1909; Preobrasjenskaja et al. 1973; Vogt & Vogt 1919; von Economo & Koskinas 1925) we can postulate that each of the cortical areas is characterized by a complex of special types of columnar modules. Columns of the cortex as revealed by cytoarchitectonic methods are only cellular "skeletons" of the columns found by immunocytochemical and tracing methods (Goldman-Rakic & Schwartz 1982).

It would appear that in the initial stages of eutherian and, especially, prototherian and metatherian evolution the number of modular types was very limited. This suggestion is supported by the fact that in most nonderived species of mammals the structural homogeneity

of the cortex is extreme (Sanides & Sanides 1972; 1974; Valverde & Facal-Valverde 1986). However, even in these representatives of the initial brain model a fronto-occipital cytoarchitectonic gradient has been found (Abbie 1940; 1942; Valverde & López-Mascaraque 1981). We can accordingly suggest that in most conservative orders of Insectivora and Chiroptera only two modular types of cortex, frontal and parieto-occipital, can be distinguished. It is also likely that at this stage the differences between the two types of modules were very slight and a continuous spectrum of the modules existed along the fronto-occipital axis of the hemispheres.

From this "bimodal" type of neocortex, it is likely that more differentiated cortices of eutherian mammals have been developed through the intervention of two mechanisms, namely, internal modification of the basic prototype columnar modules and multiplication of the modules. We can assume that the initial two types of modules, frontal (magnocellular and less cellular) and parieto-occipital (parvocellular and more cellular), have produced, on the one hand, extremely magnocellular modules of agranular cortices in higher mammals and, on the other, extremely granular modules seen in the koniocortical regions. All other types of modules in neocortical evolution appear to represent intermediate modifications between these two extreme variants of the modules. Not only has the cell density (cellularity) of the modules and their vertical parameters changed but also their inner distribution of cell types, which is expressed in the development of layer IV as a special afferent zone of the module in sensory cortical areas. The combination of all these structural changes, both quantitative (vertical and tangential size of the modules, cell density in each module) and qualitative (microcircuitry and appearance of new cell types) we define as a modification of the columnar module.

The next step (or, in most terrestrial mammalian species, a parallel step) of neocortical evolution was a multiplication of the modified columnar modules. The degree to which this phenomenon of modular multiplication was expressed in each order and species depended on the specific characteristics of the adaptive pressures acting in a particular environment. Thus, the great variety of neocortical regional types in eutherians appears to have been the result of the combined modification/multiplication mechanisms operating on the basic modules (columns) of the initial neocortex. Our columnar modification/multiplication hypothesis proposes a dual mechanism for columnar evolution, whereas the recent hypothesis of Sawaguchi and Kubota (1986) proposed only multiplication of columns in primates. However, the multiplication of the columns alone cannot explain the presence of such a broad spectrum of regional subdivisions of the neocortex in eutherian mammals. On the other hand, the combination of both modification and multiplication of the columns probably accounts for most of the progressive increases in regional subdivisions in neocortical evolution (Figures 5 and 6).

Applying the modular modification/multiplication hypothesis to neocortical phylogenesis we can postulate the existence of the following four modes of neocortical evolution in terrestrial eutherian mammals that have resulted in four distinct types of neocortex:
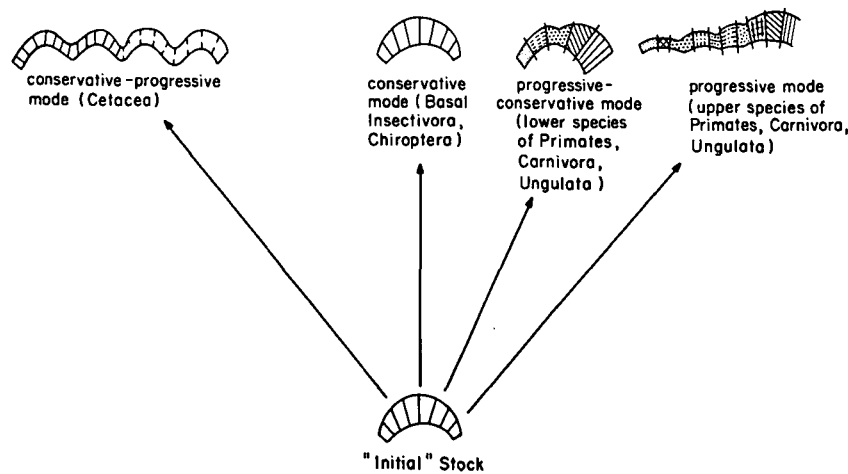
Figure 5. The columnar modification/multiplication hypothesis in four modes of mammalian neocortical evolution. Each sketch of the figure represents schematically a strip of the neocortex with its cytoarchitectonic columns. The latter are shown by vertical lines or other labels (dots, dots and line, etc.). The initial type of neocortical organization is shown at the bottom of the figure. It is characterized by a small number of nonmodified columns (solid continuous vertical lines). From this initial neocortex four main types of neocortical organization have arisen in extant mammals: (1) *Conservative* organization: The initial nonmodified and nonmultiplied columnar organization is retained (basal Insectivora and some Chiroptera). (2) *Progressive/conservative* organization: Several types of columns have developed from the initial type of primitive cytoarchitectonic column. This modification is schematically shown by different combinations of dots and lines in the schematized cortical strip. The number of these modified columns, however, is still comparable to that in the conservative type since the process of multiplication of the columns is not yet advanced. In each order of eutherian mammals there are species that might be regarded as progressive/conservative; for example, among primates, prosimians, and some of the lower species of monkeys (*Cebus, Callithrix*). (3) *Progressive* organization: Both modification and multiplication of the neocortical columns have achieved their highest level. This type is demonstrated by multiple combinations of the vertically oriented dots, lines, and other labels. In each order of extant mammals there are species that represent this type of neocortical evolution. In primates, for example, anthropoids and hominoids can be regarded as having this neocortical type. (4) *Conservative/progressive* organization: only slight modification of the columns or even none at all has occurred. Thus, columnar organization of the cortex is very close to that in the initial type of neocortex. On the other hand, the multiplication of these primitive columns in this type of neocortical evolution has achieved its highest level. This type of neocortical organization is a unique feature of the extant cetaceans. In the figure this type of neocortex is depicted by the long, extremely convoluted cortical strip with the same or slightly changed initial columns. The scheme also illustrates that cortical areas are complexes of differently modified columns and that the more intensive the modification of the columns the more new cortical areas appear during neocortical evolution.
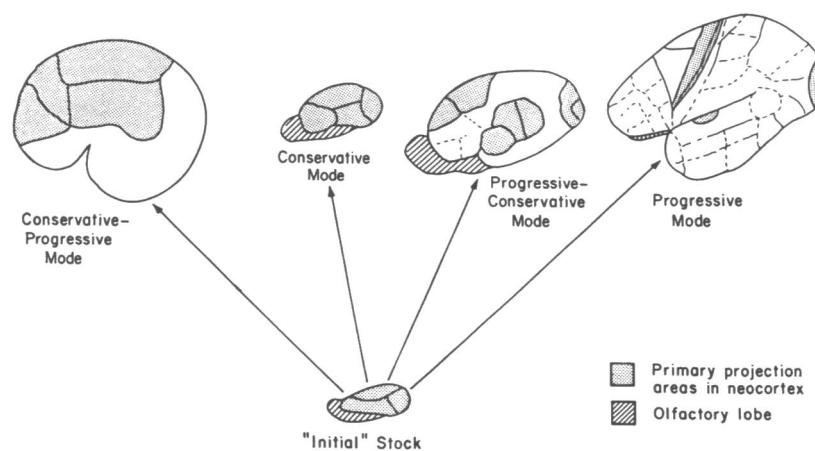

Figure 6. Schematic illustration of cortical areal topography on the lateral cortical convexity maps reflecting primary, secondary, and tertiary projectional zones in four types of neocortex in extant mammalian orders and their relationships to a putative map in the hypothetical initial protomammalian stock. In the latter, the number of cytoarchitectonic areas is presumed to have been very limited and their size small. The functionally different cytoarchitectonic areas in this cortex are adjacent or partly overlapped. This type of cortical topography is retained by representatives of the conservative mode of neocortical evolution (models of the initial stock, such as basal Insectivora and some Chiroptera). In the progressive/conservative and, especially, the progressive modes of evolution the number of cortical areas has increased. The most intensive expansion and differentiation has occurred in the zones located between the primary projection zones. We have described columnar modification/multiplication (see Figure 5) as a possible mechanism for this differentiation and expansion. A special case of neocortical evolution is represented by a conservative/progressive mode and is found only in cetaceans. In this mode the primary and possibly secondary projection zones have expanded immensely without differentiation into local areas. Thus, the main functional projection zones remain adjacent as in models of the initial brain and the whole neocortical pallium has retained a high degree of structural homogeneity.

1. A *conservative* or initial type of neocortex in which the cortical areas are weakly differentiated and almost identical in their cytoarchitectonic structure. Their number and size are also very limited. Each of the cortical areas contains a small number of archetypal modules which are characterized by very limited structural variability. As a result of this combination of archetypal modules and their associated cortical areas, the conservative type of neocortex found in basal Insectivora and most conservative Chiroptera is a generally dysgranular cortex, in which both maximally agranular (gigantopyramidal) and koniocortical formations are absent.

2. A *conservative/progressive* type of neocortex in which the structurally conservative features are dominant. Thus, overall the cortex is cytoarchitectonically homogeneous and the number of cortical areas of different types is very limited. The columnar modules are also weakly differentiated and similar in cytoarchitectonic structure to modules of the conservative type (archetypal modules). However, the number of these modules is extremely high in each cytoarchitectonic area, resulting in an extremely large neocortical surface area, comparable in size with that of most advanced mammals (Figures 4B, 4C, 5, and 6). This type of neocortex is present only in extant Cetacea (see section V of this article).

3. A *progressive/conservative* type of neocortex in which the progressive features are dominant. As a result of modification of the modules, the number of cortical areas has increased greatly over that present in the initial type. The size of the cortical areas, however, remains small, because the process of multiplication of columnar modules has not occurred or is not sufficiently advanced. Thus, although cortical areas contain basic modules comparable in number to the initial type of neocortex, a considerable advance in modular differentiation has occurred. This type of neocortex is found in most extant orders of eutherian mammals, but it is present only in the smallest representatives of each order. For example, in primates the progressive/conservative type of neocortex is present in prosimians and in the smallest simians, such as in *Cercocebus* and *Cebus* genera.

4. A *progressive* type of neocortex in which the cortical afferent units are extremely abundant, much larger in size than in the initial brain, and exhibit greater degrees of differentiation. In this neocortical type both modification and multiplication of modules reaches the highest degree in any given order of mammals. Each cortical area contains not only many more modules than in the initial type and in progressive/conservative types, but the number of modular types is increased immensely. This type of neocortex is present in the largest representatives of each particular order of eutherians. For example, in primates it is present in *Homo sapiens* and to some extent in the highest anthropoid apes (chimpanzee, gorilla, and orangutan).

We may tentatively hypothesize that the four neocortical types of extant eutherian mammals described above represent four sequential or parallel stages of neocortical evolution which took place near the beginning of the Eocene period. The main driving forces of this evolution were processes of modification and multiplication of initial modules. As a result, there occurred an increase in the differentiation and number of cortical areas. The

present scheme of neocortical evolution is only a tentative reflection of the more complex and variable phylogenetic reality of neocortical history in extant terrestrial mammalian species. The conservative/progressive type, found in extant cetaceans, evidently represents a special kind of evolutionary deviation from the general path of neocortical phylogenesis for terrestrial mammals. It combines the most conservative (initial) type of modules with an extreme multiplication of these archetypal modules. This type of neocortex is discussed in section V.

Attempts to identify the types of morphological organization of the mammalian neocortex and their modes of evolution have been made previously by several authors who used different criteria for defining the level of neocortical organization relating to the ancestral initial brain. Zvorykin (1971; 1977; 1980) defined three modes of neocortical evolution on the basis of two main criteria, including an expansion of the neocortex and differentiation of layer III into sublayers. According to Zvorykin, the first mode is characterized by expansion of the neocortex without reorganization of its fundamental six-layered stratification plan and includes the most primitive of lissencephalic (nonconvoluted) brains. The second mode is characterized by further expansions of the neocortex, especially in the frontal direction, accompanied by an increase in its thickness, particularly layer III, and includes contemporary carnivores. The third mode of evolution is characterized by the vigorous expansion of the neocortex in both directions, frontal as well as parieto-occipital, and includes only primates. In this mode the thickness of the neocortex is also increased because of the further differentiation of layer III. Since our studies involve a consideration of the evolutionary status of the cetacean brain, it is of interest to note here that Zvorykin concludes that cetaceans cannot be classified in any of the above three modes, but have a special combination of features including expansion of the neocortex in the mediolateral direction and retention of the original thickness of the neocortex to the same extent as in the first mode. Thus, although Zvorykin did not identify a special fourth mode of cortical evolution he did recognize a unique direction of the cetacean neocortical phylogenesis.

Using their own set of criteria, Ladygina and Supin (1974) and Supin et al. (1978) also discussed the cortical types and modes of evolution of the neocortex. They defined four evolutionary modes and cortical types on the basis of the topographical organization and distribution of projection and associative zones throughout the cortex. In the first type of neopallial structure these authors included extant rodents and insectivores, considering them the least divergent from the ancestral form. In this type, projection zones are all adjacent to each other and are not separated by associative zones. In the second type, they included carnivores and ungulates with their expanded neocortex in the frontal and occipital directions due to the development of the associative zones that separated primarily adjacent projection zones. The third type, according to Supin et al. (1978), includes only primates and is characterized by further expansion of the associative zones in both frontal and parieto-occipital directions. The fourth type of neopallial structure belongs to cetaceans, which have all their projection zones shifted

in the frontal direction because of what these authors considered the great expansion of associative zones in the occipito-temporo-parietal directions. Supin and his co-workers (1978) also postulated a unique condition in cetaceans, one combining the progressive expansion of the neocortex with conservative retention of the adjacency of their projectional zones (Figure 6).

Hence from several points of view, whether purely morphological (cytoarchitectonic) or functional (physiological mapping), cetaceans represent a peculiar deviation from the general eutherian mammalian plan of evolution. It would accordingly be of interest to apply the modification/multiplication hypothesis of neocortical evolution as well as the initial brain concept to the analysis of this extremely specialized group of mammals.

V. The cetacean neocortex and its relation to the modes of mammalian neocortical evolution

Investigating different aspects of cetacean brain morphology we, along with many others, became aware of numerous peculiarities in the cortical organization of these aquatic mammals. We have recently found that these peculiarities encompass not only macroscopic and histological features of the dolphin's brain, but they also can be seen at the ultrastructural levels in synaptic structures, glial cells and blood–brain barrier morphology (Glezer et al. 1987; 1988). In analyzing the convexity cortex of the lateral gyrus· (visual cortex) in the dolphin according to its boundaries as established in the physiological studies of Sokolov et al. (1972) and Ladygina et al. (1978), we have distinguished two cytoarchitectonic types that we have designated as homolaminar and heterolaminar cortex (Glezer et al. 1988; Morgane et al., in press; Morgane et al. 1985). The differences between these are considerably less obvious than those between areas 17, 18 and 19 of higher terrestrial mammals. We do not find either koniocortical or gigantopyramidal formations in the cetacean neocortex. All zones of the various sensory projections in the dolphin exhibit a rather similar overall cytoarchitectonic appearance. As in the hedgehog brain, considered as a model of the initial group of mammals, cellularity in the rostral cortical regions of the hemisphere is less than in the caudal regions (Garey & Leuba 1986; Garey et al. 1985; Morgane et al. 1982).

The topography of the main sensory and projection zones is somewhat unusual in the dolphin in that the position of the auditory and visual areas has shifted rostrally onto the lateral convexity cortex. They have also become localized adjacent to each other in a manner generally similar to that of the initial group of mammals (Figure 6). The neocortex of cetaceans is narrow and not significantly wider than in the hedgehog. The general features of lamination of the neocortex of the dolphin are also similar to those of the hypothetical initial brain, that is, an extremely wide layer I, a narrow but accentuated layer II over the entire convexity, a layer III that is narrower and contains smaller cells than layer V, and a layer IV which, as in the initial group of mammals, is incipient or in some areas totally absent (Morgane et al., in press). As a whole,· the dolphin neocortex can be

defined as dysgranular (Morgane et al. 1985). Layer VI contains polymorphic cells and is, as a rule, wider than layer V. The spectrum of neuronal types in the dolphin neocortex is rather similar to those of the hedgehog model of the initial brain. Thus, in layer II there are large numbers of neurons with wide external ramifications of their apical dendrites evidently analogous to the "extraverted" neurons of Sanides (Morgane et al., in press). The cells in the dolphin neocortex are predominantly pyramidal and are of atypical or transitional types having pear-shaped, club-shaped or ovoid perikarya. However, in our Golgi material we have verified these transitional cells on the basis of their apical dendrites as being pyramidal cells.

An important conservative feature of the dolphin neocortex is the presence of large stellate cells with long dendrites similar to the isodendritic, nondifferentiated neurons (long radiators of Ramón-Moliner 1962 and Sanides & Sanides 1974). We have found these cells in all layers of the cortical plate, especially in layer III of the dolphin. Together with smaller numbers of small stellate cells (short radiators of Sanides & Sanides 1974), the presence of large stellate neurons provides us with the first tentative overall classification of nonpyramidal neurons in the dolphin cortex. The spectrum of neuronal types is largely reminiscent of what has been described in models of initial brain animals such as the basal insectivores (Valverde 1983).

Our recent computerized image analyses of the dolphin's visual cortex have shown the presence of columnar cytoarchitectonic organization extremely different from that of man (Morgane et al., in press). The columns in the dolphin visual neocortex are distributed much more sparsely and their mean diameter is significantly larger than that in area 17 of man. Computerized analysis has also shown that columnar organization of the dolphin visual cortex is even more conservative than in the visual cortex of a bat. Thus, the number of columns per unit of cortical volume in the dolphin is smaller than in the bat and significantly smaller than in area 17 of man.

The structure of the neocortex of the cetacean brain hence appears in many ways to be similar to and in some way even more primitive than accepted models (Insectivora and Chiroptera) of initial brain animals. This similarity, however, exists largely at the microscopic and submicroscopic levels. It is well known that at the gross anatomical level, in terms of such parameters as neocorticalization and encephalization, the cetacean brain, with its greatly expanded neocortex, is in the range of the most progressive mammalian orders (Filimonoff 1949; Jansen & Jansen 1969; Jerison 1973; 1978; Morgane & Jacobs 1972; Ridgway & Brownson 1984) (Figure 4B). Our estimation of the corticalization index in *Tursiops truncatus* based on the data of Haug (1986) and of Ridgway and Brownson (1984), however, has shown that in this parameter dolphins are even below basal insectivores (Figure 2). This somewhat paradoxical finding can be explained by the presence of a very thin cortex in cetacean brains (about 1.5–1.6 mm). Thus, although the cortical surface area in these brains is even larger than in *Homo sapiens,* the overall volume of the cortex is much smaller. As a result, the corticalization index (volume of total cortex/volume of brain × 100) in cetaceans is much smaller

than in other mammals.* We can consequently expect the relative volume of subcortical components, especially the basal ganglia and thalamus, to be increased. Thus, even some of the most important quantitative gross anatomical features of the dolphin brain show resemblances to conservative brains (models of the initial brains). Nonetheless, cetaceans are characterized by a very large brain, especially in terms of its absolute weight and surface area. This extreme enlargement of the neocortex was achieved by the ancestors of the contemporary whales and dolphins somewhere between the Eocene and Miocene epochs (15–20 million years ago; Jerison 1973; 1978).

All the above findings provide a strong basis for considering that cetaceans have a special type of neocortex and, evidently, exhibit a fourth mode of neocortical evolution. We designate this as a *conservative/progressive type* of neocortex. As we mentioned, in this type we observe the most unusual combination of weakly differentiated cortical areas with an immense number of plesiomorphic (archetypal) columnar modules in each. This combination is likely to be developed by multiplication of the initial modules with little or no modification of the module.

This peculiar type of cetacean brain evolution, especially of the neocortex, can be partially interpreted in terms of cetacean phylogenetic history. Retention of the conservative, initial type of cortical area and conservative type of columnar module might be related to the very early origin of the cetacean mammalian group from ancestral initial stock whether they were tokotherians (McKenna 1975) or insectivore-like creatures (Simpson 1945; 1949; 1953). According to paleontologic dating, the most ancient representatives of cetaceans are found in the Paleocene or early Eocene epochs. However, these early cetaceans were quite advanced in their adaptations to the aquatic environment and exhibited many of the features found in extant cetaceans. Because of this, it can be suggested that branching of cetaceans from ungulate stock occurred much earlier, somewhere near the end of

*[This footnote was added in proof and was not seen by the commentators. Ed.] In our estimation of the corticalization index in *Tursiops truncatus* and other mammals presented in Figure 2, we used the data of Stephan et al. (1981) and Haug (1987).

For both of these sets of data, we calculated the index of corticalization using not only the gray matter of the neocortex but also the subcortical white matter. We made this calculation since the main sources of data were papers of Stephan's group which used this unusual method of estimating neocortical volume, i.e., calculations based on both white and gray matter. If we were to use only the volume of neocortical gray matter, the indices of corticalization would be much smaller. We should stress the wide variability in the surface area and volume of the neocortex among individual mammals of the same species (Blinkov & Glezer 1968). Thus, in the older data of Haug (1970), because of the relatively small volume of the whole brain of the specimen *Tursiops truncatus* in relation to its large neocortex, the indices are only slightly smaller than in humans. However, using more recent data of Haug (1987), as well as the data of the Moscow Brain Institute cited by Blinkov and Glezer (1968), the indices of corticalization calculated by using both gray and white matter vary in humans from 80 to 88, and in *Tursiops truncatus* from 33 to 73. The index of corticalization calculated by using only gray matter varies in humans from 47 to 51, and in *Tursiops truncatus* from 19 to 41.

the Cretaceous period (Figure 1B). According to the evolutionary systematics of McKenna (1975), cetaceans evolved from ungulates somewhere around 50 million years ago. In the cladistic tree of McKenna as well as Eisenberg (1981), five groups consisting of Eparctocyona, Cete, Meridiungulata, Phenacodonta, and Tethytheria originated by branching from ancient ungulates. However, the analysis of the genetic distances according to immunodiffusion comparisons with chicken antisera have shown a striking resemblance between the contemporary cetaceans and insectivores, especially erinaceids. When we tabulated the original data of Shoshani (1986), we found that genetic distances between erinaceids and cetaceans were almost 4 times smaller than those between ungulates and cetaceans. We found confirmation of this closeness of cetaceans to the basal insectivores also in other similar works by molecular biologists, for example, Goodman (1975). It is of special interest also that, next to erinaceids and ungulates, representatives of Chiroptera are genetically the closest to cetaceans. Thus, from these data on genetic distances as well as from the paleontologic data, we can tentatively presume that cetaceans originated from the basal stock of insectivore-like ancestors at the very beginning of the Eocene period. Perhaps this is one of the reasons why initial features of neocortical structure in cetaceans are similar to those of the insectivores. It is probable that the conservative/progressive type of neocortex has evolved in parallel with terrestrial lines of progressive/conservative and progressive types of neocortex from a common initial type of cortex present in primitive terrestrial forms. The existence of the conservative/progressive mode of neocortical phylogenesis in a biologically successful aquatic mammalian group demonstrates that under certain environmental conditions phylogenetically conservative but efficient features are retained. These also expand markedly, producing some overall behavioral effects paralleling behaviors in some terrestrial forms that exhibit progressive evolution of the brain, such as complex social behavior, communication, problem-solving abilities, and so on.

VI. Phylogenesis of cortical areas and columnar modules

The hypothesis presented above concerning eutherian neocortical evolution from an initial nondifferentiated stage has to be further elaborated to suggest possible mechanisms for progressive phylogenetic change in neocortical structure as well as mechanisms for the retention of conservative morphofunctional features in species that represent models of initial mammalian stock (basal Insectivora, Chiroptera and, according to our data, Cetacea). It seems that the appearance of the archetypal neocortical columnar module in ancestral mammalian groups was a major phylogenetic event in the sense of Severtzov's "aromorphosis" (Severtzov 1939). In contrast to "idioadaptations" (small, gradual changes) aromorphosis gives particular groups of animals immediate and significant phylogenetic success (Reid 1985). In this case, the modular organization of the neocortex might have immensely improved the functional features of the sensory systems, such as discrimination, integration of different sensory modalities, and so forth. It would accordingly, increase

the chances for survival of this ancestral mammalian group. The preservation of this archetypal modular structure in weakly differentiated neocortices of biologically successful mammalian groups supports the idea of punctuated evolution (Gould & Eldredge 1977) where short periods of evolutionary change (Simpson's quantum evolution) are followed by long periods of evolutionary stasis (arrested evolution of Simpson; cited in Schoch 1986).

The most probable mechanism of neocortical evolutionary differentiation is related to changes in neocortical afferentation. This follows from the fact that the neocortex represents the highest level of sensory integration. The changes in amount of information and type of informational signals coming to this level of integration may affect its internal structure. Thus, based on the Herrick-Elliot Smith conception of a "primitive" archetype of mammalian neocortex, Diamond and Hall (1969) proposed a model for understanding the development of the visual cortex in a line extending from a hedgehog-type ancestor to primates. According to Diamond and Hall, the appearance of multiple cortical cytoarchitectonic areas is causally connected with differentiation of the subcortical projections. Thus, in the hedgehog model of the initial brain the nondifferentiated thalamus as a whole represents a relay nucleus between the optic tectum and neocortex. At the next evolutionary stage partial differentiation of the thalamus into lateral geniculate nucleus and lateral posterior nucleus (the future pulvinar) produced, in turn, two different zones in the visual cortical area: the visual core and visual belt areas. However, at this stage these two zones still overlapped morphologically and functionally, which corresponds basically to the condition in the hedgehog brain. The next stage of differentiation of the lateroposterior nucleus into the pulvinar and growth of the lateral geniculate nucleus has resulted in an expansion and further morphological and functional differentiation between the striate area (the core that receives afferents from the lateral geniculate nucleus) and the visual belt (the cortex surrounding the visual core). This stage is found in the Tupaiidae (tree shrews). In the last evolutionary stage, represented by the primates, the pulvinar elaborated its connections and subdivided into several nuclei which in turn produced a third cortical projection around the visual belt (i.e., visual association cortex). According to Diamond and Hall's hypothesis, these phylogenetic changes and the progression of cortico-subcortical relations, particularly thalamocortical connections, correlated with the redistribution of functional assignments in the sensory cortices. Thus, at the initial or archetypal stage the discriminative (cognitive) and learning abilities of the visual sensory system were assigned to one visual zone that was not differentiated into areas. In later evolution, these two functions are represented separately in the cortex. A tertiary associative zone for visual analysis also appeared at the next stage of evolution, adding a third important component to cortical function.

Further developing Diamond and Hall's idea that subcortical afferentation and its phylogenetic changes caused a differentiation of the cortical areas we can conjecture that cortical columnar modules were the units that were subjected to these evolutionary changes of subcortical afferentation. Using our terminology, the evolution of the neocortex in terrestrial mammals has resulted in a modifi-

cation and multiplication of the cortical modules, thus producing multiple cortical areas. We may theorize as to what kind of structural changes were at the basis of the proposed modifications of the initial cortical modules. We can tentatively answer this most important question by comparing the intracortical distribution of the specific, nonspecific and associative afferents in advanced mammals of progressive and progressive/conservative neocortical types with those of conservative and conservative/progressive types. As mentioned above, in extant basal insectivores almost all subcortical and intracortical afferents feed into the enormously thick layer I and through the extraverted neurons of accentuated layer II. The afferent information then spreads to deeper layers of the cortex. Our preliminary data on Golgi structures of the dolphin visual cortex have shown the same patterns of afferentation of the neocortex in these aquatic mammals as those found in terrestrial models of the initial brain (Morgane et al., in press). We can assume that in aquatic and terrestrial animal models of the initial mammalian neocortex the primitive modules receive all their afferentation through a mixture of different types of afferents that are located in layer I (Figure 7A).

In the later stages of cortical module evolution, the flow of afferent signals is divided into more superficially located associative and commissural afferents and more deeply located specific thalamocortical afferents. This segregation of afferentation of different types was probably a main driving force for the appearance of the short radiators (granular stellate cells) of Sanides and as a consequence, the modification of the initial module into granularized form, where layer IV appeared between layers III and V serving as a relay from specific afferents to pyramidal layers (Figure 7B).

According to the modular hypothesis of Szentágothai (1975), four main groups of afferents are present in layer I of terrestrial mammals: monoaminergic afferents from locus coeruleus, associative T-shaped fibers, commissural fibers, and axons of Martinotti cells. Only a small number of specific fibers from the thalamus reach this layer. The concept of progressive evolution from an initial type of brain can also be extended to include cetaceans. However, as we mentioned above in this particular case, multiplication of modules occurred with or without their modification. It is quite reasonable to expect that the absence of segregation in neocortical afferentation needs an enormous number of initial type primitive modules to process a comparable amount of information in advanced terrestrial mammals. All extant whales and dolphins appear to have adapted to the aquatic environment with limited cortical cellular organizational changes from an initial form. The data of Glezer et al. (1985), Kesarev (1975), and Morgane et al. (1985) show that the brain of the dolphin is a blend of progressive features (neocorticalization, encephalization) and extremely conservative features (neocortical homogeneity, absence of beltlike zoning of the sensory cortical regions, poor overall differentiation of the intrinsic structure of the cortical laminae with a very wide layer I and a strongly accentuated layer II, and an obvious limitation of the spectrum of neuronal types).

Thus, the special case of cetacean brain evolution is not accompanied by multiplication of the basic cytoarchitectonic areas but rather appears to be expressed through an
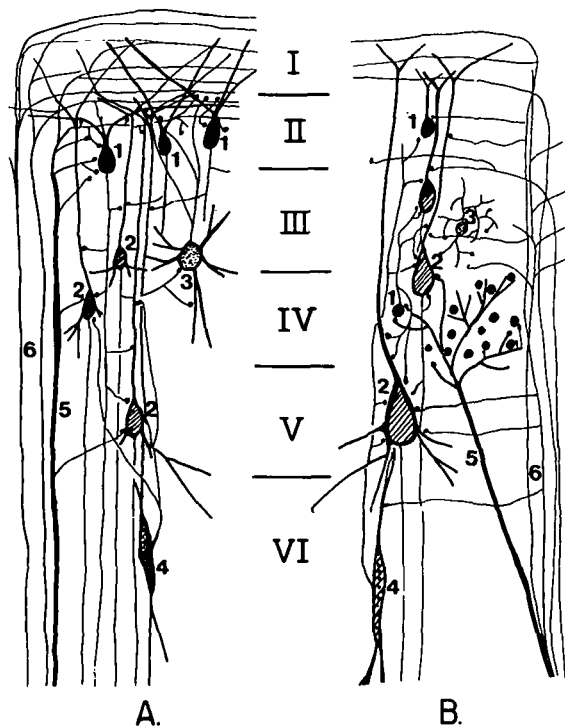
Figure 7. Schematic illustration of the hypothetical mechanism of columnar modification. On the left (A) is a generalized picture of the neuronal types and extracortical and intracortical connections in a nonmodified initial column. In this case both specific (5) and nonspecific thalamocortical afferents as well as other projections (associative, commissural) (6) feed into layer I and thus convey stimuli onto the apical dendrites of all cortical efferent cells (pyramidal and fusiform; 2,4). Large isodendritic stellate cells (3) send their axons to layer II and might be important reverberating circuits in the cortex of this type. The main afferent layer in this type of cortex is layer II, consisting of extraverted neurons (1), which transfer information along cell columns by their descending axons that give off horizontal collaterals at different laminar levels. In the right part of the scheme (B), a modified columnar structure is presented. The main apomorphic evolutionary change has occurred in the segregation of the afferent inputs into the cortex. The specific afferents (5) in this column have developed a specialized afferent layer of cells between two main efferent layers (III and V). All other kinds of afferents (6) are concentrated in the upper (supragranular) region of the cortical plate and in layer I. Special intermediate stellate types of cells have developed, including granular stellate cells or short radiators of Sanides (3). Thus, in the modified cortical column there are two main zones of afferentation, the supragranular (including nonaccentuated layer II) and granular (layer IV). For this reason we have labeled both cells in layer II and layer IV as major afferent cells (both labeled #1), although in this case the sources of afferentation are different. The main efferent elements are represented in this type of column also by pyramidal (2) and fusiform (4) cells.

expansion in size of architectonic areas with a multiplication of the archetypal modules. This special kind of mammalian cortical evolution correlates well with corticosubcortical relations. According to the data of Kruger (1959) and Morgane and Jacobs (1972), the cetacean dorsal thalamus is well differentiated into many nuclei, and the pulvinar comprises the largest single complex in the thalamus of the dolphin (Morgane & Jacobs 1972). There is weak elaboration of the pulvinar into separate nuclear groups, however. The medial and lateral genicu-

late bodies are large and the lateral ones do not display laminar structure. It has been suggested that with massive elaboration of the medial geniculate body, part of the pulvinar became absorbed by this expanding nucleus (Morgane & Jacobs 1972). Thus, pulvinar differentiation in dolphins may be suppressed by the expansion of the primary visual and acoustic thalamic nuclei. This possibility might explain some of the conservative features of the dolphin neocortex. Evidently, enlargement of the geniculate bodies and somatosensory relay nuclei and the presence of the nondifferentiated pulvinar in the dolphin produces only the stage of an extremely expanded core (heterolaminar cortex) and belt (homolaminar cortex), but not the stage of further neocortical differentiation into cytoarchitectonically definable associative areas. In terrestrial mammals, on the other hand, enlargement and further differentiation of the primary and especially the associative thalamic nuclei resulted in the development of functionally and morphologically distinct cortical core and belt zones as well as cytoarchitectonically definable associative areas of the neocortex.

VII. Summary and conclusions

The initial brain concept is important in studying mammalian brain evolution since it provides a valuable morphological frame of reference for comparative neuroanatomy and paleoneurology. It can therefore be of use in helping to establish directions of brain evolution taken by diverse mammalian groups. We have postulated four different modes of mammalian brain evolution. There is both morphological and physiological evidence that in phylogenesis all four modes originated from a single initial (ancestral) mammalian group, with all four types of neocortical organization in extant mammals representing distinct patterns of divergent evolution.

A mechanism for evolutionary change and the preservation of conservative features was proposed in the form of the modification/multiplication hypothesis for neocortical columnar modules and the differentiation and enlargement of cortical areas that result from it.

With respect to the brain of the dolphin and other whales, the initial brain concept stimulates thinking about the causes of development of a large brain with a voluminous neocortex. This morphological substrate underlies the functional mechanisms of these totally aquatic mammals which evolved from a basic stock of ancestral terrestrial forms with small brains. Thus, in the case of whales, which returned to the aquatic environment some 50 million years ago (Barnes et al. 1985; Gingerich et al. 1983) when the insectivore-like stock is thought to have been dominant, a consideration of dolphin brain structure in relation to that of a hypothetical archetypal brain may also provide clues to the influence of the aquatic environment on further brain evolution. Whales are unique in being the main mammalian line which was initially terrestrial and then became totally aquatic. Thus, study of the cetacean brain in relation to a baseline initial terrestrial type may shed new light on the effects of particular life habits and ecological niches on brain organization in a unique group of mammals whose line of evolution was entirely different from the main mammalian line occurring in the terrestrial environment.

A comparison of whales with the most progressive types of terrestrial mammals shows that from an initial brain line, there have evolved two quantitatively large brain lines with many qualitatively different characteristics of brain structure. This indicates that in brain phylogenesis the appearance and accumulation of derived brain features is not the only direction of brain evolution but that, in addition, the retention of conservative features thought to have existed in the initial brain also represents a distinct line of phyletic brain development. Thus, large brains such as those of cetaceans may owe their size to the multiplication of weakly differentiated (nonmodified) columnar modules and, as a consequence, to the retention of the homogeneous character of morphofunctional subdivisions of the neocortex (cortical areas).

NOTES
1. Plesiomorphic as opposed to apomorphic. The term "plesiomorphic" in phylogenetic literature refers to "evolutionarily primitive characteristics of the organism" (Schoch 1986).
2. Where A = brain weight, B = body weight and .56 is a constant for all mammalian groups. Other mathematical methods have given the same results with different types of equations (Jolicoeur et al. 1984).

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Conservative aspects of the dolphin cortex match its behavioral level

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Glezer, Jacobs & Morgane have done a great service in clarifying the structural comparison between the cetacean brain (as exemplified by the dolphin, *Tursiops*) and the brains of higher terrestrial mammals. They note particularly the profound differences in the macroscopic, microscopic, and submicroscopic structure and organization of the neocortex, which are explained in great detail, but unfortunately not always in the clearest language.

Their contribution is particularly significant given the popular view of the cetacean brain that emphasizes its remarkable similarity to the human brain. The large size of the brain in these mammals, and especially the vast number of sulci and gyri in the cerebral cortex, have led some people to see this brain as possibly more advanced than the human brain. Prominent among these was John Lilly (1967), who vigorously promoted the thesis that the dolphin mind is on a par with that of humans, and that dolphins' vocalizations represent a genuine language in which they regularly converse with each other. Lilly also maintained that captive dolphins often mimic human sounds within the limits of dolphin vocal capacities. From this he concluded that dolphins are capable of learning human language. Moreover, because of the huge dolphin brain, he decided that human–dolphin conversations could develop a substantial intellectual content.

Although Lilly's dolphin research is controversial (Herman & Tavolga 1980), it has influenced many present-day investigators to believe that structurally and functionally the cetacean brain is on a level with that of humans, and that their cognitive and social behavior are distinctly similar.

Glezer et al.'s sophisticated and well-documented anatomical arguments are not matched, however, by the brief simplistic statement about the evolution of behavior, in which they propose that "under certain environmental conditions . . . phylogenetically conservative . . . features are retained" and "expand" so that the cognitive processes and social behavior of the cetacean parallel those of the higher terrestrial mammals.

Both in behavior and in anatomy, Glezer et al. emphasize parallelism in the evolutionary process. However, both the text and the diagrams presented in Figures 5 and 6 suggest to us a process of radiation, with its concomitant significantly different end points. We suggest that a hypothesis which gives equal emphasis to differences and similarities is more appropriate than that of parallelism offered by the authors. Complex social behavior, trainability, and complex communicative systems, although sufficiently impressive to lead to a misguided extrapolation endowing the animal with far greater psychological capacities than are warranted, may each have very different processes underlying them. For example, the complex social behavior may be related to endocrine as well as to neural factors. Trainability is not necessarily correlated with problem solving ability (Krushinsky 1988) and the communication system may be related to the environmental context in which foraging and feeding take place (Würsig & Würsig 1979; Gaskin 1982).

Higher level processes (behavior) cannot be equated with lower level (morphological) techniques. The anatomical concept of homology, which forms the background for the arguments put forth by Glezer et al. simply does not work for comparative behavior as it has for comparative anatomy (Atz 1970; Aronson 1981; 1984), although many have tried (Hodos & Campbell 1969).

The alternative is the concept of levels of integration and organization as formulated by Needham (1937), popularized by Novikoff (1945), and elaborated by Schneirla (Aronson et al. 1972) and his colleagues (Greenberg & Tobach 1984). The integrative-levels concept makes it possible to deal with the similarities and differences among different levels of behavior (Tobach 1987). Although the process of communication is continuous on many phyletic levels, each level presents a disjunctive break expressed as a difference in the communicative process (e.g., language, the human communicative process).

Gaskin (1982) points out that although dolphins can readily be trained, they are not comparable to higher primates in either their social behavior or their problem solving, and they are certainly not comparable to humans. Gaskin (1982), who has reviewed much of the evidence, especially the field data, concludes that for the extensively studied sperm whale (suborder Odontoceti) there is no evidence of complex social behavior beyond that of an ungulate herd. In the suborder Mysticeti,

where the behavior and social structure are less complex, he finds no evidence that would rank them higher than elephants or hippopotami. Through the efforts of Glezer et al. we are now able to correlate the behavioral level with the anatomical level of the neocortex and probably with the physiological level as well. We see at once that the anatomical level is considerably below that of the higher primates, and far below the human level. Those who favor the hypothesis of a high level of cetacean intelligence almost always emphasize the large, highly convoluted cortical surface area which is larger in *Homo* and which forms a vast array of sulci and gyri. But Glezer et al. show paradoxically that the corticalization index in *Tursiops* (volume of cortex over volume of brain × 100) is even below that of the basal insectivore which is their extant model of the hypothetical "initial" mammalian ancestor.

The target article also suggests a significant direction for future research. In their ascription of a progressive character to the increased quantity of primitive modules in the cetacean cortex Glezer et al. assume that qualitative behavioral changes have accompanied the increased number. Although they use a neuroanatomical version of levels of integration (see particularly sect. VI, para. 2), they do not integrate the structural and functional properties. Doing this might contribute much to an understanding of the level of integration in cetacea. The levels approach has been applied to the understanding of the evolution of the telencephalon, which was helpful in explicating not only the structural changes in evolution, but the evolutionary processes in behavior (Aronson 1981).

We think that Gaskin (1982) put it well: "If I may borrow and embellish a phrase from a paper by the Caldwells, there is abundant evidence that dolphins communicate information about 'what', 'where' and 'who'. There is no substantive evidence that they transmit information about 'when', 'how', or 'why'. So, no matter what some might wish to believe, with respect to Kipling's 'six honest serving men' of learning and intellect (Kipling 1910) the dolphin appears to be three servants short" (p. 152).

Primitive survivors and neocortical evolution

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Although Glezer et al. repeatedly assert that their discussion concerns brain evolution, the only part of the brain actually addressed is the neocortex. The intellectual "superiority" of man is usually attributed to his convoluted neocortex, with highly differentiated layers and many different cortical areas. Only animals with a similar organization are considered to be "superior" or "advanced." These naive notions lead to surprise when seemingly intelligent animals are found with large brains and convoluted hemispheres but cytoarchitectonically simple neocortical organizations, as Glezer et al. have found in *Tursiops*. The large brains and highly convoluted hemispheres may merely reflect the large body size of this group of animals.

Glezer et al. present a list of major features of brain evolution. These trends are most often demonstrated in a series of primates and nonprimates ordered in a *scala naturae* leading to man. Other lineages have not been well enough studied to determine how general they are.

Using the hedgehog brain, "one of the simplest and most generalized of mammalian brains" (Elliot Smith 1910) as a model of the brain of early eutherian mammals is an old idea. LeGros Clark (e.g., 1934) used it in this way when he argued that the tree shrews had diverged sufficiently from the ancient pattern in the direction of primates to merit classification with them. The notion that early eutherians were characterized by small brains with relatively little cerebral cortex and with paleocortex, archi-

cortex, and intermediate cortex occupying more of the hemisphere than neocortex was promulgated by English-speaking workers long before 1949.

It is poor scholarship on the part of Western scientists to ignore the Russian literature, but this may understandably arise from a lack of fluency in the Russian language. However, this factor can hardly be used to explain Glezer et al.'s implication that the idea of a "primitive brain" originated with I.N. Filiminoff. The general approach of choosing a structure with apparently simple morphology in an animal considered to be "primitive" and "generalized," and then using it as a model for the structure in ancient animals itself has a long history. It has been criticized extensively by organismic biologists and has been referred to as the concept of the "primitive survivor."

Martin (1973) points out that this concept can be useful as a first step in the organization of data, but that it involves a circular argument. Take the case of hedgehogs, for example. If their brains were large and covered with an extensive, highly differentiated neocortex, most neuroanatomists would assume that they could not be primitive or generalized no matter what the structure of the rest of their body might be. So, partly on the basis of their brain morphology, they are chosen as the "primitive survivor" and the characteristics of their brain morphology are described as "primitive." Glezer and his colleagues substitute "initial" for "primitive" in this target article but it is the same concept. Martin (1973) also criticizes Stephan's "basal insectivore" concept, relied upon by Glezer et al. Zoologists have more rigorous methods for inferring ancestral states, such as cladistics, and these should be applied here too.

Glezer et al.'s hypothesis is that animal groups with the four major types of neocortical organization diverged from an ancestral stock in the Eocene period that had a neocortex resembling that of some modern hedgehogs, tenrecs, shrews, and bats. This scheme, illustrated in Figures 5 and 6 of the target article, cannot be correct on the face of it. Glezer et al. indicate (Figure 5) that "lower species" of primates, carnivores, and ungulates possess the progressive/conservative type of cortex, while "upper species" of primates, carnivores, and ungulates have the progressive type of neocortex. Precisely what is meant by "upper" and "lower" species is not specified. Aside from the implication that the authors have a *scala naturae* conception of evolution, the use of these terms without explanation leaves the reader in the dark as to which animal groups should be included in the two categories. The authors give a clue in regard to the primates, as they seem to include the prosimians, *Cebus*, and *Hapale* among the "lower" primates. Yet perfectly valid technical names exist for species and for higher categories and ought to be used. For example, often "higher vertebrates" is used for birds and mammals. If only birds and mammals are meant why not use those names?

If both the progressive/conservative and progressive types are found in the orders Primates, Carnivora, and Ungulata, and each of these groups evolved from a single ancestral primate, carnivore, and ungulate, then in each order one of the types must be inherited from that ancestor and the other must be independently derived at some time in the history of the order. This is quite a different pattern from the one illustrated in figures 5 and 6.

Glezer et al. present the interesting hypothesis that phylogenetic changes in subcortical afferentation led to differentiation of the cortical areas principally by increasing the number of cortical modules or modifying their organization. They are expanding on an idea discussed by Diamond and Hall (1969), who infer the evolution of the primate neocortex through a sequence of stages, including a hypothetical reptile-like mammal, tree shrew, prosimian primate, and anthropoid primate. Glezer et al. substitute a hedgehog "initial" brain for the first stage, but otherwise follow the pattern of Diamond and Hall's first stage, in which a brain with an undifferentiated thalamus represents a relay nucleus between the optic tectum and neo-

cortex. Diamond and Hall's principle point about this stage was that the retina did not project directly to the thalamus but was relayed in the tectum to the undifferentiated visual thalamus, which in turn projected to a general sensory cortex. You cannot use the hedgehog brain model for this stage. Hedgehogs have direct retinal projections to a visual thalamus differentiated into lateral geniculate and lateral posterior nuclei, as well as retinal projections to the tectum (Campbell et al. 1967). In addition, Kaas, Hall, and Diamond (1970) have shown the hedgehog visual cortex to be differentiated into core and belt areas (VI and VII).

I have criticized the details of the evolutionary stages and the process of evolutionary inference presented by Diamond and Hall elsewhere (Campbell 1976). In spite of this, the notion that adaptation to challenges from the sensory environment could lead to changes in subcortical afferentation, which could in turn produce changes in the organization of neocortex is a compelling one. Also, the suggestion that the neocortical modules are principal targets of change is appealing. What one would like to see now is the rigorous demonstration that the hypothesis is correct. In doing so, the same methods of phylogenetic inference used by zoologists should be applied to that data. We must abandon such familiar concepts as the *scala naturae*, unidirectional evolution from simple to complex states, and utilization of "primitive survivors" as baselines.

NOTE. The views of the author do not purport to reflect the position of the Department of the Army or the Department of Defense (Para 4-3, AR 360-5).

Evolution of the brain in Cetacea – is bigger better?

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It is generally accepted by evolutionary biologists that contemporary mammalian species evolved from small generalized insectivore-like species similar to some existing insectivores. The target article presents a good general discussion of major features of mammalian brain evolution, with particular emphasis on the description of the brain of basal insectivores, as a background for the authors' proposal that a unique form of brain evolution may have occurred in cetaceans. However, the reader is not presented with a review of data on brain structure, function, or behavior in cetaceans to substantiate "progress" in the members of this order. Rather, the description of neuronal types and laminar differentiation is presented to suggest that the cerebral cortex of the dolphin (*Tursiops*) is not significantly different from that of basal insectivores. The implications of the data presented on cetaceans are limited by considering only a single species and by the authors' failure to address the serious limitations that wide differences in body size present for the interpretation of quantitative brain measures.

Brain size–body size. There has been a general increase in body size in all mammalian orders over the last 70 million years – an increase most dramatically seen in the land-dwelling elephant, of the Order Proboscidia, and the sea-dwelling whales, of the Order Cetacea. The significance of differences in the encephalization ratios or neocorticalization indices between insectivores (ranging in weight from 5 to 860 grams) and cetaceans (ranging in weight from 45 to 130,000 kg) is obscured by these vast size differences. Elephants, as well as some whales, have encephalization indices which exceed that of humans; other whales have encephalization indices comparable to basal insectivores (Bauchot 1978; Hofman 1982). Other factors which limit the significance of these indices of "progressive" changes

in brain evolution are secondary changes in body size such as dwarfing. The talapoin monkey (*Miopithecus*) has a neocortex expansion index second only to humans (Stephan & Andy 1969). The degree of cortical fissurization, the relative amount of neocortex and topographical and cytoarchitectural differentiation in somatic sensory cortex are not reversed following secondary dwarfing in this species (Warren & Carlson 1986). These examples illustrate the limitations of individual or related quantitative indices as indicators of "progressive" evolution without evidence of progressive behavioral changes. The data on neocortex in dolphins in Figure 4 make one wonder whether secondary dwarfing may have occurred in some cetaceans as a basis for the discrepancies in encephalization indices for different species in that order.

Those features of the dolphin brain that are commonly referred to as showing progressive development – fissurization and cortical/neocortical expansion – may increase as a function of body size alone without implying adaptive or behavioral progress, as seen in various large and small carnivores and rodents (Welker & Campos 1963). Head size does not increase at the same rate as body size, and brains of larger species are more fissured than those of smaller species. As the body surface increases, so does the neocortical projection area for somatic sensation, motor control, and other sensory organs so that an increase in body size could lead to an increase in neocortical area without a progressive change in behavioral capacity. Selective expansion of the hand area in many primate species, and in various skin surface projections to somatic sensory cortex in carnivore species, relates to increases in receptor density in the glabrous skin and specialized use of that skin surface in exploratory and discriminative behavior (Welker & Campos 1963). Relative enlargement related to behavioral differences can be interpreted as "progressive" as opposed to a general increase in neocortical size, which may be simply allometric (Northcutt 1984; Radinsky 1982).

Enlargement versus differentiation. Among the finite number of ways that evolution can improve upon a design for a brain, enlargement and differentiation are the two most commonly considered. As mentioned above, a general enlargement of neocortical surface alone (as may occur in the case of the dolphin) may merely reflect increased body size, or secondary dwarfing, whereas differential enlargement may be correlated with increased behavioral capacity. Differential enlargement may occur along with increased functional and cytoarchitectural differentiation, or any of these changes may occur in isolation. Though many of us have speculated about the possible correspondence between physiologically defined cortical columns and cytoarchitectural columns or areas, major functional transitions can occur in cortex without corresponding structural changes (Zeki 1978) and vice versa (Carlson 1985; Warren & Carlson 1986).

In our studies of primary somatic sensory cortex (SI) in Old World prosimian and anthropoid primates, expansion and increased differentiation of the SI hand area was correlated with increased tactile discrimination capacity (Carlson 1985) but the enlargement and greater differentiation of the SI hand area in New World anthropoids was not (Carlson & Nystrom 1986). Enlargement or differentiation may occur together or separately in different species in a variety of mammalian lineages. This strongly suggests that, in any given mammalian order, a single strategy or combination of strategies may not characterize brain evolution.

Comparative and developmental neurobiologists have entertained a variety of hypotheses about possible patterns and processes in brain evolution (Northcutt 1984) and some have been bold enough to speculate about possible ontogenetic processes leading to phylogenetic sequences (Ebbesson 1984). Theories about the processes involved in brain evolution must consider: (1) the relationship between expansion and functional and structural differentiation of cortical areas and behavioral

capacity (Carlson 1985); (2) data on a variety of fossil endocasts (Radinsky 1982), along with data on existing species which approximate the various postulated stages in the evolution of a mammalian order (Carlson & Welt 1981; Clark 1959); and (3) those ontogenetic mechanisms by which genetic mutations lead to phenotypical change in adult organisms (Gould 1977).

When I received Glezer et al.'s target article I was ready to be jarred from my primate-centric complacency by a review of neural and behavioral data on cetaceans but the article raised questions more than it provided information. I was left with the image of a highly convoluted brain (with the cytoarchitecture of a hedgehog) in the large-bodied aquatic dolphin, but still wondering about brains in whales, and other aquatic mammals (Sirenia and Pinnipedes).

Cetacean brains have a structure similar to the brains of primitive mammals; does this imply limits in function?

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The research efforts by Morgane and his associates (Morgane et al. 1986b) have attracted much interest on the part of biologists. This derives from the fact that the organization of the cetacean brain appears to be radically different from that of other extant eutherian mammals. Most of the work on cetacean brains has been conducted with the smaller forms of the family Delphinidae. But sufficient data from other families allows a certain amount of generalization. It is well known that brain weight covaries positively with body weight. What has not been appreciated in the past is that although the brain of the smaller cetaceans is relatively large and the volume of the neocortex is large relative to the volume of the total cortex, the volume of the total cortex expressed as a ratio of total brain volume is relatively low. Glezer et al. attempt to explain this deviation in proportion. They postulate that although all extant eutherian mammals have brains that could be derived from a common ancestor, the brains of cetaceans have deviated in that as cetaceans evolved early in phylogenetic time to occupy their aquatic niche, natural selection produced a brain that is different in structure and may function somewhat differently from those of their terrestrial relatives. In some functional aspects the brain structure of a cetacean is closer to that of an insectivore or some bats. Perhaps this similarity with microchiropterans shouldn't be so surprising since bats and cetaceans use echolocation as their primary means of orientation in a three-dimensional medium.

The target article attempts first of all to establish a basic framework for explaining the morphological divergence as brain structure evolved within the different lineages of extant eutherian mammals. The *BBS* reader may, however, seek a relationship between form and function in the following sense: How does brain structure reflect the behavioral capacities that living species display (see Morgane et al. 1986)? Glezer et al. restrict themselves to the extant eutherian mammals, using the term Tokotheria derived from McKenna (1975). The phylogenetic tree in Figure 1A does not exactly express what McKenna (1975) or I (Eisenberg 1981) meant to imply. In the target article the Insectivora are treated as a unified group, whereas McKenna and I expressed a conviction that the assemblage was artificial. This does not detract from the major thrust of Glezer et al.'s paper; but those who wish to know more about "basal insectivores" would do well to refer to the original works.

An attempt to understand form and function in terms of brain evolution within the vertebrates has preoccupied many workers for the last 200 years. In 1978 P. D. MacLean wrote a provocative article entitled "Why brain research on lizards?" To quote him, "When beginning to plan for the present facility

[Laboratory of Brain Evolution and Behavior, National Institute of Mental Health] 20 years ago, a primary purpose was to use new behavioral approaches in investigating the functions of a basic part of the forebrain that reflects our reptilian ancestry" (p. 1). Recently, Ulinski (1986) concludes from studying the fossil endocasts of therapsid reptiles that the growth of the basal ganglia may have resulted in some of the initial expansion of the forebrain seen in endocasts of early mammals. Thus the real beginning of the mammalian brain lies somewhere in the transition from a reptilian brain to a therapsid brain and thence to an early mammalian brain.

I must accordingly ask the question: Why are the extant monotremes and marsupials omitted from a consideration of the fundamental mammalian brain? The literature on form and function exists (Griffiths 1978; Johnson 1977). This may seem an irritable quibble, but there are remarkable similarities, as well as differences, between eutherian and marsupial brains. It appears from my perspective that the fundamental brain of extant eutherians already existed in marsupials, not to mention monotremes.

This brings us to a further consideration: The brain of a bird is organized quite differently from that of a mammal and yet the bird is able to accomplish extremely complex behavioral acts. A large corvid such as a crow or raven appears to demonstrate a concept of number comparable to that of a mammal, and yet the brain structure is profoundly different (Koehler 1952). Should we be surprised at this? Over and over again in biology we find different paths in the course of evolution leading to the solution of similar problems. This suggests how imperfectly we understand the way vertebrate brains function.

I recall some of my earlier work with Golani, in which we attempted to compare the behavioral repertoire of the marsupial Tasmanian devil *Sarcophilus harrisii* with that of the golden jackal *Canis aureus;* both are functional carnivores but each has evolved independently since at least the Paleocene, if not earlier. There were remarkable convergences in behavioral repertoire and interesting differences that were extremely hard to quantify (see Eisenberg & Golani 1977; Golani 1976). This may serve to highlight some of the paradoxes which become evident when one attempts to relate form and function.

Certainly the structure of the cetacean brain, and in particular that of *Tursiops,* is different from that of most of the other eutherian mammals. Form and function still appear to elude us, especially when one attempts to relate behavioral competence with brain structure. On the other hand, Glezer et al. have performed a valuable service in focusing on the very real differences in brain structure between a dolphin brain and that of a primate. The challenge to explain differences in form and function still eludes us.

Allometry cannot be ignored in brain evolution studies

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Glezer et al.'s target article is very interesting, especially from a histological point of view, and the "initial brain" concept and cladograms upon which it is based seem reasonable. However, a model of mammalian neocortical evolution based on the four modes presented by Glezer et al. is untenable because it fails to incorporate the allometric scaling between neocortex, brain size, and body size that is known to occur in mammals. For various indices to be meaningful, "criteria of subtraction" need to be applied to remove the allometric effects of body size (or brain size) from the neurological data (Pilbeam & Gould 1974). The accepted method for doing this is to calculate a regression

equation that has a neurological feature (e.g., brain size) as the dependent variable and body weight as the independent variable for a baseline group of mammals (e.g., basal insectivores). A neurological index is then defined as a function of the distance between the mean value of the dependent variable for the group in question and that predicted by the regression line for a basal insectivore *of the same mean body size.* That is, neurological indices are usually defined as functions of the "residual" that are equal to the actual value of the neurological feature divided by the predicted value (Falk 1980; Jerison 1975; Stephan 1972; and see Hofman et al. 1986 for details of regression models).

The importance of allometric scaling in studies of brain evolution is made clear by the following example. Relative brain size (brain size divided by body size) is .03 in the squirrel monkey, which is larger than the .02 figure for *Homo sapiens* (Schultz 1969). However, as a general allometric rule, smaller mammals have relatively larger brain sizes than do bigger mammals and .02 happens to be an astoundingly large relative brain size for a mammal with a body size as large as that of *Homo sapiens.* Therefore, comparing relative brain size of smaller primates such as the squirrel monkey with those of larger primates such as *Homo sapiens* is meaningless unless allometric scaling of brain size with body size is taken into account. Unfortunately, the indices presented in Figure 2 of the target article have not been calculated to control for allometric scaling of brain size with body weight or neocortex size with brain size (see Passingham 1975).

Numerous studies of mammalian (including primate) brain evolution have resulted in certain basic allometric principles which are relevant to the target article: (1) Bigger mammalian brains are more convoluted than smaller mammalian brains; that is surface areas (that would ordinarily increase as a radius squared) must buckle in order to keep up with increasing internal volume (which increases as a radius cubed) (Jerison 1982; Falk 1980). (2) Brain size in *Homo sapiens* is approximately three times that predicted for a nonhuman primate of equivalent body size (Passingham 1975; Falk 1980). The human neocortex is also approximately three times as large as expected for a nonhuman primate of the same body size, but the volume of neocortex obtained by humans does *not* differ significantly from that predicted for nonhuman primates of the same brain volume (Passingham 1975). It appears that brain size and neocortex size increased nearly isometrically during recent primate evolution as well as human evolution (Falk 1980; Radinsky 1975; Passingham 1975). (3) Larger-bodied mammals generally have absolutely (but not relatively) larger, more convoluted brains (Jerison 1968; 1982) than do smaller mammals. The implication of 1–3 is that both neocortical area and brain size scale allometrically with body size in mammals.

With these principles in mind, it is apparent that the "columnar multiplication" portion of the columnar modification/ multiplication hypothesis of neocortical evolution needs to be reviewed from an allometric perspective. Glezer et al. note that their progressive/conservative mode is characterized by modular differentiation but *size of the cortex remains small* and that this mode is present in prosimians and the *smallest* simians such as *Cebus;* their progressive types of neocortex, on the other hand, are characterized by *greater areas of cortex* (due to "multiplication of modules") as well as modular differentiation and "this type of neocortex is present in the *largest* representatives of each particular order of eutherians" (emphasis mine). Thus, the differences between progressive/conservative and progressive modes of neocortical organization appear to be related to body (brain) size – bigger animals within a lineage have greater areas of cortex.

In order to substantiate the claim that the four suggested modes are distinct rather than merely the result of allometry, they must be shown to exist *after* body (brain) size has been accounted for. Similarly, cetaceans are larger animals than basal insectivores and bats and therefore would be *expected* to have

absolutely bigger brains, with longer, more convoluted cortices than their smaller-bodied "cousins." Therefore, the cortical morphology of cetaceans also should be reanalyzed in light of allometric considerations. Until the data presented in the target article are reanalyzed from a traditional allometric perspective that takes body size and brain size into account, mammalian brain evolution can at best be viewed in terms of two of the four suggested modes of columnar development. Specifically, the two modes are conservative and progressive columnar *modification* and, as predicted by the literature, neocortex appears to scale allometrically with body size within each of these modes.

Fish, sea snakes, dolphins, teeth and brains – some evolutionary paradoxes

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According to current theory, the earliest vertebrates were fishlike, aquatic, and small-brained. Now, many millions of years later, small-brained fish continue to flourish in our oceans, and many other vertebrates of seemingly minuscule cerebral size have returned to the sea and prospered (e.g., sea snakes and ichthyosaurs). Yet, when mammals become aquatic their brains enlarge not only by comparison to cold-blooded vertebrates, but also by comparison to other mammals. Why? Also, why has the enlargement of the dolphin brain followed such a different anatomical pathway from that of large-brained terrestrial mammals such as higher primates?

A consideration of feeding behavior can help resolve these issues. Dolphins, like their terrestrial mammalian kin, are homeothermic. For this reason, the marine environment must present a greater challenge to them than to cold-blooded vertebrates. Dolphins must consume greater quantities of food to sustain their body metabolism. Yet, dolphins have no dental or other anatomical specializations to increase their feeding efficiency. Rather, dolphin feeding skills must result from perceptual and intellectual abilities provided by their enlarged brains.

To digress temporarily from dolphins, the brains of insectivores provide them with feeding skills which are superior to those of most lower vertebrates in several respects. Typical lizards, for instance, are limited to prey which can be detected by visual movement or olfactory cues, captured with little locomotor pursuit and swallowed whole. By contrast, insectivores possess auditory, tactile, and cross-modal sensory integration skills which permit the location and capture of stationary, cryptic or hidden prey. In addition, visual, and perhaps other following skills allow them limited pursuit of moving prey, and neurologically mediated dental and other manipulative skills permit breaking food into small pieces prior to ingestion (Gibson 1986).

The evolution of various mammalian taxa has witnessed selective expansion of these basic insectivore feeding capacities. Carnivores, for instance, have greatly advanced their ability to pursue and capture moving prey while retaining rather limited object manipulation skills. In contrast, many higher primates are supremely skilled in finding hidden foods and in direct-contact manipulation of foodstuffs. They tear fruits, leaves, insects, and small mammals apart with their hands and teeth, unroll leaves and overturn stones to find hidden insects, bang hard-shelled nuts against tree trunks to open them, pluck tiny seeds from grasses or fruits with their fingers and, in some cases, use tools to obtain extractive foods (Gibson 1986; Parker & Gibson 1977). These behaviors demand well developed eye-hand coordination, very precise, fine-grained differentiation of visual, tactile, and motor space and advanced cognition in the

form of an understanding of object structures and object relationships.

Primates also have pronounced social skills that involve the manipulation of the behavior of living animals from a distance. Unlike object manipulation, long distance behavioral manipulation does not demand fine eye-hand coordination. It does, however, demand another advanced skill – the prediction of the future behavior of a living animal. Although nearly all higher primates are social, and many eat insects or small vertebrates, only a few have developed their long distance behavioral manipulation and predictive skills to the extent that they can chase, either cooperatively or alone, vertebrate prey for more than a few feet. No primates, other than humans, habitually "herd" whole groups of animals over long distances.

By contrast to primates, dolphins have no anatomical organs for direct-contact, fine-grained manipulation of object properties. They have even lost the heterodont dentition which provides most mammals with precise oral manipulative skills. They have capitalized, however, on the development of techniques for recognizing and manipulating living prey and living conspecifics. Well developed powers of echolocation, for instance, permit the long distance recognition of individual fish or other objects. Moreover, groups of dolphins are legendary for their habits of communicating with each other and for following schools of fish. Possibly, they do more than this and actually cooperate to "herd" schools of fish in specific directions (Cousteau & Diole 1975). Thus, while falling below primates in direct-contact object manipulation skills, dolphins may well exceed them in long distance detection, manipulation, and prediction of behavioral events.

How, then, do we explain the differential enlargements of primate and dolphin brains? Single unit recording techniques indicate that the sensorimotor areas of the primate neocortex are admirably designed for within-modality, fine-grained analysis of sensorimotor data, such as the detection of very minute differences in visual orientation, tactile pressure, or finger position (Hubel & Wiesel 1974; Mountcastle 1978). Whole cortical columns specialize in the detection and analysis of specific sensorimotor details. Within each cortical sensory area, the cells of layer IV are the most responsive to isolated and minute sensory details, while precision of movement of individual fingers correlates with the development of the long corticospinal tracts which emerge primarily from large pyramidal cells. These considerations suggest that the differences between dolphin and insectivore versus primate brains in terms of columnarization, parcellation into fine cytoarchitectonic areas, and differential enlargement of konio and agranular cortex may well reflect the primate superiority in direct-contact, fine-grained object manipulation skills. By contrast, the fact that dolphin brains have enlarged while still retaining a more insectivore-like neural structure reflects, in part, the lack of these skills in dolphins and suggests that whereas dolphin predictive abilities may require more neural substance than that possessed by insectivores, they require little fundamental change in neural structure.

Both cortical and subcortical neural structures mature and differentiate, in part, in response to sensory input from peripheral structures. Cortical receptive fields can even be changed in adult monkeys by surgical techniques which alter peripheral anatomy (Kass 1987a). Consequently, many of the differences between the dolphin and primate neocortex may, as Glezer et al. suggest, reflect differential input from subcortical structures. This differential input, however, is determined, in part, by peripheral anatomy and behavior during maturation. Hence, the authors' conclusion that subcortical structures help determine cortical anatomy accords with the view presented here: Differences in dolphin and primate cortical anatomy partially reflect differential manipulative behaviors.

Developmental axes and evolutionary trees

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The evolutionary perspective provides the main basis for integrating the wealth of data generated by system-oriented neurosciences into unitary theories or concepts. The task is not easy: As with most theoretical work in the neurosciences, the relevant factual information is both not enough and too much and discouraging amounts of imagination, bravery, and ingenuity seem to be needed.

Previously discussed difficulties (Innocenti 1984) include the construction of the general phylogenetic trees, and the usefulness of the trees for assessing the evolutionary level of neural structures. A prerequisite for identifying the evolutionary relations of neural structures seems to be the availability of comparable sets of data in different species. Important species differences may arise not from evolution but from evolution of the neurosciences. In this respect, the strongest evidence on the phylogenetic position of the dolphin's cortex seems to come from cytoarchitectonic studies and from cytology using the Golgi method. Comparing the number, location, and organization of sensory areas and cortical "columns" in the dolphin with those of the cat and monkey can be misleading – if this commentator is right in assuming that no detailed, single unit recording or tracer study has been performed on the dolphin's cortex.

Another difficulty comes from the trickiness of nature in producing structural homologies, homoplasies (see Northcutt 1984), or their opposites, by convergent or divergent evolution. Because of the uncertain homology of cortical areas in different species, I find the "principle of cortical adjacency" of questionable usefulness. Indeed, the notion that the neocortex may have evolved by a relative increase of the "association" areas between the "sensory" areas has been strongly criticized (Diamond & Hall 1969); the very notion of association areas may have to be revised since the discovery of multiple representations of sensory modalities in the regions traditionally allocated to "association" cortex.

A related difficulty concerns the identification of the direction of evolutionary changes. One gets the impression that the direction usually chosen in making trees is that of "progressive" morphogenetic events (for example, increase in the index of neocorticalization) since this may appear more compatible with the direction traditionally ascribed to ontogenetic changes. The wide occurrence of impressive diverse "regressive" morphogenetic events in ontogenesis make one wonder about the solidity of the trees and even the usefulness of the "initial" brain concept.

Glezer et al.'s target article provides a clear and stimulating overview of the types of morphological changes that probably underlie neocortical evolution. Since there may be developmental constraints on evolution (see Innocenti, in press, for discussion) it is tempting to speculate about which of the proposed changes may be compatible with, or use, mechanisms known to provide flexibility to normal cortical development, and which changes would violate these mechanisms or require them to be modified by genetic mutations.

It is unknown whether in normal development there exists any flexibility in the production or number of cortical neurons as would seem to be required for the neocorticalization index to evolve. In this respect, the dolphin's cortex is particularly interesting since it seems to have achieved tangential growth, unaccompanied by radial growth (i.e., surface growth without corresponding growth in thickness). Thus, two independent developmental modifications may be involved in cortical evolution: (1) an increase in the extent of the germinative layer from which neocortex originates (or perhaps a more widespread distribution of migratory neurons achieved by a multiplication

of the glial channels), leading to tangential cortical growth; (2) a prolonged period of neuronal generation (or a reduction in the number of glial channels), leading to radial increase of the cortex. Both modifications may be caused by the acceleration or retardation of normal developmental processes secondary to DNA changes, in agreement with modern evolutionary views (Gould 1977).

In contrast, changes in the size and shape of cortical neurons may, to some extent, exploit the normal developmental modifiability of neuronal shape, although for more drastic structural and chemical changes in cortical neurons some genetic innovations may be necessary. Normal developmental mechanisms can also allow changes in the number of at least one type of cortical "module" (Van der Loos & Welker 1985).

Finally, cortical connectivity develops through a phase of initial exuberancy (Innocenti, in press; Innocenti et al. 1977) characterized by the fact that an area or part of an area projects to and receives from a broader and more diverse territory than in the adult, followed by focussing or rededication of these projections. As discussed elsewhere (Innocenti, in press), this developmental strategy might have appeared by fortuitous mutation and then been maintained through phylogenesis because of its adaptive ontogenetic value. Since this strategy may also have allowed the incorporation of genetic caprices such as addition or loss of neurons, the invasion of new territories by a projection, and the segregation of projections into separate territories (Ebbesson 1984; Katz et al. 1983), structures that have adopted this strategy, such as cortex, have enjoyed and still may enjoy explosive evolution.

Morphogenetic versus morphofunctional theory

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The target article by Glezer et al. about the "initial brain" concept offers a phylogeny of the cetacean neocortex in terms of its laminar and modular cytoarchitectonics. On that account the Cetacea appear as a unique feature of evolution in the direction of "conservative/progressive" corticalisation. The authors start from an hypothesized archetypal brain model, represented by extant basal Insectivora and Chiroptera. They reconstruct four evolutionary modes by postulating a modification/multiplication model wherein the modular components of the cortical areas are considered to be the elementary functional units and "some of the main targets of evolutionary forces."

In contrast to this, morphogenetic theory starts from extant allocortical (phylogenetically early) formations – that is, reptilian and paleomammalian – preserved throughout vertebrate evolution and considered to be the foundation of species-typical behaviour in man and animal, from the mammal-like reptiles upwards.

Morphogenesis (a well-ordered sequence of transformations) rests on:

1. Allo-isocortical contiguity, that is, "interpenetration" (Edinger 1909) or "interfaces";

2. Hemispheric rotation around the sylvian pivot (Jacob 1911); it involves the sagittal and coronal planes and starts from the peri-insular segment resulting in a maturation gradient (Kahle 1969) which means heterochrony in cortical differentiation;

3. Folding in of the allocortex at the base; there, the allocortex loses contact with the bone (Spatz 1937). These processes are autonomous (Monod 1970) and emerge early in phylogeny and ontogeny (Gegenbaur 1898; Hyman 1962; Kahle 1969; Rose 1935).

4. Different and independent rates and modes of these processes result in lateralisation (dominance) of the two brain halves; that is, in a heterochronic shift of encephalisation.

5. Morphogenesis is closely related to metamorphosis: (a) In both, an orderly sequence of events is involved that cannot be imposed on the evolving system by outside forces; (b) in both, information is transmitted by chemical means, analogous to the mRNA in the Monod-Jacob lactose system. The concept of *morphogenetic induction* (Spemann 1936) is fundamental in metamorphosis and morphogenesis, uniting both under one heading (Monastra 1986).

6. Chemoaffinity (Sperry 1963) is the essential feature of the reptilian type of brain, which forms the core of the "paracrine" neuraxis and constitutes the "chemoarchitecture" of the brain (Nieuwenhuys 1985); it includes the "R-complex" of MacLean (1978) and the allocortices at the base of the frontal and temporal lobes ("basale Rinde" in the human: Spatz 1937; Jakob 1979).

7. Flechsig's original concept (1920; 1927) of "primary" receptive areas having connections only with adjacent "parasensory" areas known as "associative areas" was later developed into a "connectivist" (Pribram 1971) hypothesis of neocortical "crossmodal associations" (Geschwind 1965) supposedly underlying the "higher cortical functions in man" (Luria 1980). Contrary to this, it is found that the association cortices belonging to the late-myelinized areas on the Flechsig scale represent the more generalized architectonic pattern (compared to the sensorimotor cortices) and come closest to the general cyto- and myeloarchitectonic scheme of Brodmann (1909) and the Vogts (1919) (Sanides 1970; 1975).

Thus, in the ontogenesis of higher placentals there is a space-time dislocation between cortices having different rates and modes of differentiation; this results in contiguity of the "primary" areas with paleomammalian and mesocortical (insular) boundary zones (Sanides 1975 and coworkers). According to morphogenetic theory, the crucial feature of this kind of interrelationship is that it is species-typical (innate) and, in the words of Sperry (1983) "largely preorganized independently of sensory input" (p. 95).

Critique of Glezer et al. First, the cortical subdivisions offered in the target article (Figure 5) are artifacts construed to fit a preconceived neocorticalisation scheme. They do not coincide with definite extant mammalian species. Consequently, there is considerable overlap, even with "deviant" Cetacea. Thus, cortical subdivisions based on purely cytoarchitectonic descriptions seem inadequate for speciation and taxonomy. Generally speaking, in the whole cortex there is a definite trend toward progressive differentiation from the paleo- to the eulaminate neocortex (Braak 1980; Brockhaus 1940). Nevertheless, during early development there is a great deal of variability in stratification and myelinization (Humphrey 1966; Kahle 1969; Sanides 170; Stephan 1975), contradicting Glezer's et al.'s emphasis on the uniformity of the vertical modules in different functional types of cortex "extending beyond taxonomic boundaries."

Second, Glezer et al.'s hypothetical mechanism of columnar modification (Figure 7) rests on specific afferent inputs and main efferent layers with intercalated association zones between the primary projection areas (Figure 6). This strongly reminds one of Pavlov's "reflex principle," recently called by Luria (1980) "the modern materialistic psychology" (p. 30). Likewise, Kotchetkova (1960), in studying the specifically human regions in the hominid neocortex, concludes that certain neocortical regions concerned with tool making and praxis ("labour" in the sense of Friedrich Engels), have been the driving forces in anthropogenesis – a view as morphofunctional as that of Glezer at al. (See abstract on Sinanthropus in Edinger 1975, p. 233.)

Glezer et al.'s cytoarchitectonics make the module – a single, variable functional element – the causal determinant, outclassing and superceding all lower levels of neuronal activity; this is not likely to be one of the "main targets of evolutionary forces."

NOTE. Former senior neurosurgeon at the University in Berlin, and (1939–1945) member of the (then Kaiser-Wilhelm) Institut für Hirnforschung in Berlin-Buch (now Max-Planck-Institut für Hirnforschung in Frankfurt am Main).

Whose brain is initial-like?

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The pain of the target article is in the convoluted, strained, logically circling and inevitably futile effort to make an ancestral mammal out of the hapless hedgehog yet again; the joy is in its presentation of more facts to demolish this perverse and ever-tempting inclination to find our ancestors among us. Of course hedgehog brains are models of the initial brain; *but so, and equally so, are those of dolphins – and bats!* Who is going to say with a straight face that the Cetacea and Chiroptera are simple, underived, primitive, and unspecialized beasts, much like our Mesozoic ancestors? The truth is that the brain of every living creature is the product of eons of strenuous research and development; each will thereby have its own advanced and its own conservative features. The possession of any one or any set of conservative characters is of absolutely no value in predicting the advanced or conservative nature of any other independent characters.

Glezer et al. present good evidence of extremes of derivation and of conservation in cetacean brains, and a similar case can be made for even the maligned hedgehog: One of the intriguing results of our own exercise in building phylogenies from a different set of variable brain traits was that, according to our set of characters, *Erinaceus* had to be placed among the most derived of mammals (Kirsch & Johnson 1983; Kirsch et al. 1983).

Glezer et al. list four modes of brain differentiation from the hypothesized initial brain. Their nomenclature for this otherwise felicitous idea is clumsy and does not easily allow for additional modes; I suggest that they rename these modes for the taxa in which they have been found. Calling a mode conservative/progressive sounds like an attempt to be too general (political parties call themselves by these names for similar reasons); why not be honest and call it the cetacean mode? Two or more unrelated taxa may turn out to follow one of these modes of brain organization, but I will bet that every mammalian order, when sufficiently studied, will show its own unique rearrangement of old and new brain characters. For example, edentates by most accounts (see Figure 1A in the target article) left the eutherian stem long before the modern insectivores, bats, and dolphins, and among them sloths have the conservative (initial-like) paucity of differentiation of laminae and distinctive cytoarchitectonic areas (Gerebtzoff & Goffart 1966). However, they have something like the advanced feature of "association" cortex intervening between primary sensory areas (Meulders et al. 1966; Saraiva & Magalhães-Castro 1975). Why make them fit some conservative/progressive, liberal/radical, or other such prematurely-striving-for-generality mode: Let them have their own edentate (or more probably megalonychoid) mode.

Given the independent development of the brains of the various orders of mammals, such unique lines of differentiation are not surprising. Indeed mystifying are the several examples of striking parallels in these independent diversifications. Glezer et al. attempt to elide the question of marsupials – who branched off long before even the edentates – through depriving them of all neocortex by misstating Abbie's conclusion. Abbie was showing the gradual derivation of neocortex from its various paleocortical neighbors; he picked what looked like the most "initial-like" species he could obtain – the bandicoot

Perameles nasuta. But even the lowly bandicoot has perfectly respectable neocortex (specialized layer IV and all), in its most derived sensory and visual areas (Abbie 1942). In addition, in this scheme the North American Virginia opossum, that other abused "initial-like" marsupial, possesses thoroughly advanced features such as pyramidal cells shaped like pyramids and massive thalamic terminals in layer IV, which layer is even subdivided into IVa and IVb (Walsh & Ebner 1970). Brodmann himself had no difficulty in recognizing primate-like cortical areas in marsupials (Brodmann 1906, pp. 360, 388–90, 392); there is general agreement that kangaroos are more distant relatives of chimpanzees than are hedgehogs. The similar placement of sulci in the somatic sensory areas of gyrencephalic marsupials and a variety of eutherian forms (Johnson 1980) is another case of convergence which may be trying to tell us something about "latent" properties of the real initial brain.

The course of brain evolution will not be easy to discern. In the elegant simile expressed in these pages not long ago (Innocenti 1984), existing animal species – and their brains – "are rather like the fruits of a tree, a strange tree which produces different fruits on different branches. The problem with evolution seems to be that all the fruits are on the ground and the tree is gone. If we could put the fruits back on a tree, in their original positions, we would be closer to understanding evolution" (p. 340). In our efforts at this daunting task, I favor an egalitarian/democratic/republican approach to our cornucopia of varied brain-fruits. Each brain-fruit has its own virtues and messages for us. The target article has read some very important ones from the brains of cetaceans: Their advanced features are very advanced, their conservative features are very conservative, and their coexistence gives us rich food for thought about how brains diversify.

Determining species differences in numbers of cortical areas and modules: The architectonic method needs supplementation

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Most neuroscientists agree that neocortex is subdivided into numbers of functionally distinct areas and that at least some of these areas are further subdivided into smaller processing units called cortical columns or modules. Critical questions raised by neuroscientists interested in the evolution of the neocortex include those related to (1) how extant species differ in numbers and kinds of areas and modules, and (2) how evolutionary changes have occurred. Providing accurate information about species differences and similarities will usefully constrain theories about the course of evolution and the mechanisms of change; it is accordingly important to obtain such information.

Early in this century, Brodmann (1909), Elliot Smith (1910), Campbell (1905) and others studied the histological structure of the neocortex of various mammals. Regional differences in structure were noted, but the interpretation of such differences proved to be difficult. There was general agreement only on the location and identity of a few areas, and there were as many theories as investigators. Furthermore, for all cortical areas, with the possible exception of the primary somatosensory cortex of mice, the standard cell and fiber stains failed even to suggest the existence of modules. Subsequently the validity and usefulness of the architectonic method was questioned by Lashley and Clark (1946), among others.

More recently, especially within the last 20 years, other methods (including microelectrode mapping, the use of various tracers of anatomical connections, and a range of histological and histochemical techniques) have led to an increased understand-

ing of cortical organization in a number of mammalian species (see Kaas 1987a; 1987b). In addition, these procedures have allowed a reevaluation of traditional architectonic studies, and, when used in conjunction with traditional fiber and cell stains, open the door for the productive use of these classical methods.

Comparisons of current and classical conclusions on cortical organization suggest that three types of error were common and led to the differences in opinion among early investigators. (1) Since architectonic differences between areas in cortex can be difficult to demonstrate, area boundaries were often missed. (2) Frequently, areas are not uniform in structure and boundaries were commonly placed within areas. (3) Across species, the same area typically varies in structure, while different areas may have similar structure; thus misidentifications were common.

Of course even with modern methods the potential for such errors remains, and mistakes are more likely when single or few criteria are used to identify a field. However, the power of some methods and the reassurance given by agreement across methods are leading to the widespread acceptance of some of the parcellations of cortex as valid. Such parcellations, whether at the level of areas or modules, will provide the basic data for theories about the course of cortical evolution.

The theory of cortical evolution outlined by Glezer, Jacobs and Morgane represents a positive and scholarly step that will certainly generate interest and productive debate. The disappointment is that the proposal relies largely on architectonic evidence, which by itself is often unreliable. The arguments are those that were or could have been made by investigators at the turn of the century. Little is known from more recent methods about the organization of cetacean brains, except for limited electrophysiological evidence for dorsomedially located visual, auditory, somatic, and motor fields reviewed by the authors elsewhere (Morgane et al. 1986b). It is possible, as Glezer et al. conclude, that cetacean brain evolution is characterized by a substantial increase in numbers of cortical modules, with the numbers of cortical areas remaining the same. However, Glezer et al. present no evidence whatsoever for or against the existence of modules of any number, size, or shape in the cortex of cetaceans. Thus, we do not know whether the number increased or not. In addition, Glezer et al. present no credible evidence that the number of cortical areas has remained stable in the evolution of cetaceans. Admittedly, the neocortex is poorly differentiated, and few architectonic borders are evident, but this appearance does not demonstrate that only a few cortical areas exist. In several mammals with expanded brains, large "association" regions of cortex have been described as nearly uniform in appearance in Nissl preparations, but other procedures have demonstrated numbers of functionally distinct areas within such cortex; for example over 15 separate visual areas in extrastriate visual cortex of monkeys (see Maunsell & Newsome 1987 for review).

The concept of association cortex should be abandoned

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Glezer et al.'s target article is provocative and provides a good review of the comparative anatomy and comparative evolution of the marsupial and mammalian brain, in particular the cetacean brain. However, the authors' analysis of brain evolution rests on the assumption that the neocortex can be subdivided into primary (core), secondary (belt), and tertiary (association) areas, following the scheme described by Diamond and Hall (1969). Diamond subsequently revised his views on this subject

in an article published in 1979 in which he proposed that there were no separate regions of "association" cortex that chiefly processed inputs from other primary or secondary cortical areas. Rather, all cortical areas should be viewed as sharing equally in primary, secondary, associative, and motor functions. Within each cortical area, lamina IV could be considered as "primary sensory," laminae II and III as "associative," and lamina V as "motor." Consistent with this concept are the results of anatomical studies which demonstrate a strong visual sensory input to portions of the thalamic pulvinar nucleus, the primary thalamic input to so-called visual association cortex (Benevento & Rezak 1976). Thus, visual association cortex can just as well be considered as another primary sensory cortical area, functioning somewhat independently and *in parallel* with the traditional primary visual cortex of area 17. The concept that the cerebral cortex functions primarily as a *parallel processor* agrees better with the electrophysiological data concerning the sensory receptive field properties of cells in "association" cortex and also avoids the extremely time-consuming sequential cortical processing assumed by the primary⇒secondary⇒association hypothesis (cf. review on parallel processing by Rumelhart & McClelland 1986).

My laboratory (Neafsey et al. 1986; Terreberry & Neafsey 1983) and others (van der Kooy et al. 1982) have recently reported that the infralimbic cortex (area 25), a cortical region formerly assigned (Swanson 1981) to the category of "limbic association cortex," is actually a visceral control cortex with direct projections to the vagal solitary nucleus and other brainstem "autonomic" regions. I believe this finding is just one example of mislabeling cortex as "associative" when it actually is functioning in a "primary" sensorimotor role. The concept of association cortex should be abandoned.

Putting all cetacean brains in one category is a big order

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In their "initial brain" concept and their typology of four kinds of mammalian brains, Glezer, Jacobs & Morgane present a valuable framework for investigating the evolution of dolphin brains. The authors' distinction between the two modes of brain evolution – that is, modular modification and modular multiplication – is especially intriguing because modular multiplication may be a mechanism for saltatory addition of brain tissue, and thereby of terminal addition of developmental stages (Gibson 1981; Gould 1977; Parker & Gibson 1979). Their classification of cortical cytoarchitecture is particularly interesting. It would be interesting to know how the anomalous cytoarchitecture of dolphin brains relates to their behavioral capacities.

It is surprising that Glezer et al. do not discuss the relationship between the total morphological pattern (Le Gros Clark 1965) of the dolphin brain and its behavioral capacities. The authors do not relate the specialized brain structures of dolphins (such as the hypertrophy of the cochlear branch of the acoustic nerve, the large acoustic geniculate and the enlarged auditory projection area on the lateral surfaces of the temporal lobe of the cortex, which make the dolphin brain wider than it is long (Kellogg 1961 citing Langsworthy 1931) to their special behavioral abilities – for example, the ability to identify details of size, shape, and spatial location of objects by sonar (Kellogg 1961), the ability to communicate such information to conspecifics (Lang & Smith 1965), and the ability to learn arbitrary symbols and use them referentially (Shyan & Herman 1987; Herman et al. 1984). Nor do they discuss the location of the

breathing center in the motor area of the cerebral cortex (Kellogg 1961).

Glezer et al. also neglect to discuss the general relationship between cortical size and information processing capacities (Jerison 1982), the positive correlation between cortical volume, surface area, and dendritic arborization (Jerison 1979), or the relationship between neuronal interconnectivity and complexity of behavior (Gibson, in press). They therefore bypass the important questions concerning the universality of the relationship between cortical size and information processing capacity and dendritic branching that their formulation raises. They do not ask, for example, whether the larger cortical modules in dolphins imply more dendritic branching and hence more information processing, or how the cytoarchitecture of the dolphin brain relates to information processing capacity.

A second and related point concerns Glezer et al.'s omission of behavioral and morphological data on closely related forms within Cetacea, on more distantly related mammals that inhabit the same medium (e.g., species of the order Pinnipedia, seals, sea lions, and sea cows) and on more distantly related mammals that use a similar mechanism for object location (species of the order Chiroptera, bats[1]).

Another issue concerns the breadth of Glezer et al.'s claim: Their model covers the whole order, Cetacea, but their anatomical research apparently encompasses only two species of dolphins – *Tursiops truncatus* and *Stenella coeraleoalba* (Glezer et al. 1987a; 1987b; Jacobs et al. 1971; Jacobs et al. 1979; McFarland et al. 1969) from one family (Delphinidae), though in one of their publications, they compare the bottlenose dolphin to four other cetacean species (Morgane et al. 1980). A more explicit enumeration of the taxonomy of Cetacea and the distribution of the brain structures under discussion would have been helpful.

Like most orders of eutherian mammals, Cetacea includes several clades that reflect a sequence of adaptive radiations that occurred at various epochs (Eisenberg 1981; Jerison 1979; Norris 1966). The descendents of the earlier radiations are generally more primitive, that is, more like the earliest common ancestor, while the descendents of the later radiations are generally more "advanced," displaying more complex behaviors, larger brains, and longer life histories. Consequently, it is possible to "distinguish several grades of encephalisation in living cetaceans: the river dolphin (*Delphinus*) and the harbor porpoise (*Phocaena*); the bottlenosed dolphin (*Tursiops*) . . . and other groups" (Jerison 1979, p. 174).

Finally, Glezer et al. erroneously identify cebus monkeys and cercocebus monkeys (mangebeys) as the "smallest simians" and as "lower species of monkeys" (caption of Figure 5). Actually, cebus are not the smallest New World monkeys. Pygmy marmosets, Cebeulla, have that distinction, while the talapoin monkeys (*Miopithecus talapoin*) and not cercocebus are the smallest Old World Monkeys (Harvey & Clutton-Brock 1985; Napier & Napier 1967).[2]

Glezer et al. also conclude on the basis of their erroneous classification (and the implicit notion that small equals primitive), that cebus monkeys have primitive brains. Cebus monkeys are, in fact, anomalously intelligent and large-brained among monkeys. They display intelligent problem solving and tool using abilities that otherwise occur only in great apes (Klüver 1933; Parker & Gibson 1977; Visalberghi & Antinucci 1986; Westergaard & Fragaszy 1987). They also mature at a slower rate and live longer than most other monkeys (Robinson 1987). Moreover, their encephalization index is very high (Gibson 1986) and their cortices are more complex than those of other monkeys (von Bonin 1938).

NOTES

1. Glezer et al. fail to note differences between the two groups of bats, the larger-brained fruit-eating bats and the smaller-brained insect-eating bats (Eisenberg & Wilson 1978). Recent work on the visual system of these two forms suggests that the former may be more closely related to the primates (Pettigrew 1986).

2. The choice of the word "progressive" to describe characteristics that appeared in recent adaptive radiations is unfortunate because it carries implications of progress and hence purposiveness in evolution.

The "initial brain": Initial considerations

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Glezer et al. have performed a worthy task by putting into focus several issues pertaining to cortical evolution. In the absence of data on electrophysiology and connections, their emphasis on cytoarchitecture and neuroarchitecture is understandable. By limiting the scope of their analysis to eutherian mammals, Glezer et al. are able to relate their findings to the initial brain concept, which regards certain insectivores as expressive of a primitive or ancestral condition and thus coincides with the effort to distinguish primitive from derived traits. However, this excludes consideration of monotremes and marsupials, earlier-branching groups for which there are data that could be applied to this analysis.

Certain aspects of Glezer et al.'s presentation appear to be reasonable approaches which would benefit from more explicit codification. In some cases there is simply a need for more data. For instance, cetacean cortical structure is represented largely, if not exclusively, by data from bottlenosed dolphins. To what degree are these data representative of other cetaceans? Likewise, by limiting their discussion to neocortex, Glezer et al. give an inadvertent nod to the long-standing bias against olfaction as a presumably primitive sense. Not surprisingly, species adapted for olfactory functions (such as many insectivores) may exhibit poorly developed neocortices yet have extremely well developed olfactory structures (e.g., the convoluted olfactory tubercle of armadillos). Thus, if one focuses on the rudimentary neocortex of such species and views it as a baseline (ancestral) condition, it should be recognized that only part of the story is being told. While it may be appropriate to view such species as "basal" from the point of view of one set of characters, it does not necessarily follow that the entire organism is basal. If, as Glezer et al. assert, "progressive evolution" has transformed an initially generalized, multiadapted mammal into several specialized species, this has happened for insectivores as well as other groups. Choosing any modern group as basal must be done on the basis of particular characters only, recognizing that other characters will exhibit specializations.

One way to clarify some of these issues is to list discrete characters, score the condition of each character on a presumed primitive to derived scale, species by species, then construct phylogenetic trees based on Wagner algorithms. This has been done for 15 brain characters in 147 species by Kirsch and Johnson (1983), and it would be interesting to similarly quantify the trends described by Glezer et al. Possible starting points might be the volume of isocortex relative to that of mesocortex and allocortex, laminar widths and cell diameters, the branching structure of Golgi-stained neurons, etc. The obvious limitation of this approach is the lack of data for many species. On the other hand, there is a wealth of data for a few species, including those for the bottlenosed dolphin summarized by Glezer et al.

It is intriguing that the great expanse of cetacean cortex is characterized by a thin, poorly laminated structural organization, and Glezer et al.'s hypothesis that this reflects the multiplication of primitive cortical modules seems to be a plausible starting point. One further way to test such hypotheses is through experimental analysis of cortical development in selected species. This approach could include an analysis of the spatial patterns of the duration of proliferation, cell death, and migration, thus assessing the influence of such events on resultant cortical structure. Such an approach would address directly

the question of whether observed adult lamination patterns are primitive or derived.

What about *Sirenia*?

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It is readily understandable that whales have relatively conservative structures of the neocortex with weakly differentiated cortical areas exhibiting a great number of archetypical columnar modules. The change from life on earth to life in water in early antecedents had a conservative effect on all those structures that were sufficient for life in water; this represented relatively uniform conditions for selection. The increase in brain size was correlated with greater body size due to the alleviation of body weight in water (and perhaps Cope's rule).

The next obvious question to ask is whether another phylogenetic line of mammals, the *Sirenia* (Trichechus, Halicore), which also developed at the beginning of the Tertiary, but are herbivorous, would show parallel conservative brain structures with parallel allometrical consequences.

Cetacean brain evolution

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In their thought provoking article, Glezer et al. have substantiated and elaborated the "initial brain" ideas of Filimonoff, Keserev, and others. Whales have evolved two living suborders – baleen whales and toothed whales – comprising about 78 species. Adult body sizes ranging from as small as 30 or 40 kg to over 200,000 kg have been reported. Adult brains as small as 200 g and as large as 9,200 g have been documented. Baleen whales and some river dolphins have brains that are less convoluted than those of the majority of toothed whales. Some whales are much more encephalized than others (Ridgway & Brownson 1984) and brain anatomists have studied only a few species in detail. We point out these facts because cetaceans violate the first major feature Glezer et al. use in discussing the initial brain concept – that there is "a general trend toward an allometric increase in the absolute and especially the relative mass of the brain with respect to body size" (p. 1). Only in the cetacean family Delphinidae do we find a few genera ·in a size range similar to that of humans that have near human-sized brains – *Steno, Lagenorhynchus, Lissodelphis.* The smaller Platanistidae and Phocoenidae have relatively smaller brains than the Delphinidae mentioned and relative brain size drops precipitously for the large-toothed whales and especially for the baleen whales.

In modern cetaceans, adult cerebellar size as a percentage of brain size is generally around 15% for odontocetes and 20% for mysticetes. The massive cerebellum accounts in large measure for the low value of corticalization (volume of total cortex/volume of brain × 100; Figure 2 of the target article). In the earliest cetaceans of 50 million years ago, the cerebellum was the most voluminous portion of the brain. It was wider and partially overlapped the cerebrum (Edinger 1955). This suggests that at first there was an expansion of the cerebellum followed later by the great expansion of the cetacean neocortex.

Although cetaceans are the most diverse of the wholly aquatic mammals, they are not the only mammalian group to have completely abandoned land for the sea. Ancestors of modern Sirenia, the dugongs and manatees, also returned to the sea in the Eocene (Savage 1976). With a similar duration of aquatic

evolution, sirenian brain structure appears quite different. The relative brain size is small and the cortex is much less convoluted and thicker (Supin et al. 1978). We suggest that Sirenia evolved a different brain from cetaceans because they have filled an ecological niche that is quite different. Like their terrestrial ancestors, the Sirenia are herbivores. They graze on aquatic plants and have a low rate of metabolism. In contrast, those cetaceans with the largest relative brain size, the delphinids, have adapted an energetic lifestyle that requires capturing large amounts of active, often elusive, high-calorie prey. Relative brain size among cetaceans has been correlated with ecologic relationships (Wood & Evans 1980).

Although cetaceans vary in their ecology and have a wide range of body size, none of them are small mammals. Since water transports heat from a submerged body about 25 times as fast as does air, we suggest that any early cetacean ancestor would have had to be at least an order of magnitude larger than contemporary insectivores; this suggests a long period of evolution on land. Even the earliest cetaceans were of good size. The cranium of *Pakicetus,* described as the earliest cetacean (Gingerich et al. 1983), is estimated to have been 30 to 35 cm in length and 14 to 15 cm in breadth; Yablokov (1965) has commented on the proportionately small heads of Eocene archeocetes compared with those of modern cetaceans.

In the caption of Figure 1A, Glezer· et al. note that "the cetaceans arose from ancient ungulates by bushlike radiation in the beginning of the Paleocene." In fact, this describes Figure 1B, their modification of the McKenna scheme which placed the branching in the late Paleocene. In any case, both here and in Section V of the text, Glezer et al. indicate their acceptance of the now widely held view that the cetaceans evolved from primitive ungulates. But then, without explicitly rejecting this view, they abruptly drop it in mid-paragraph: "However, the analysis of the genetic distances according to the immunodiffusion comparisons with chicken antisera have shown a striking resemblance between the contemporaneous cetaceans and insectivores, especially erinaceids." Also, "We found confirmation of this closeness of cetaceans to the basal insectivores . . . in other similar works by molecular biologists, for example, Goodman (1975)."

In a recent paper, Miyamoto and Goodman (1986) state that "The Adams (1972) consensus tree and phylogenetic classification of living Eutheria are our best estimate of ordinal relationships based on the present body of protein sequences" (p. 237). This classification places the Cetacea, along with the Artiodactyla and Perissodactyla, in the Superorder Ungulata. This accords with various lines of evidence. Barnes and Mitchell (1978), who accept van Valen's (1966) evidence that cetaceans were derived from mesonichid condylarths, a basal ungulate group, also note that "Neontological studies based upon tooth enamel microstructure (Carter 1948), chromosomes (Makino 1948), serology (Boyden and Gemeroy 1952), and fetal blood fructose (Goodwin 1952) consistently show closest relationships between Cetacea and ungulates, particularly Artiodactylia" (p. 592).

It appears that Glezer et al., having found an acceptable initial brain in the hedgehog (following Filimonoff, Keserev, and other Soviet workers), have attempted to make a stronger case for a close insectivore-cetacean connection, based only on their tabulation of Shoshani's (1986) chicken antisera data. In their "Summary and Conclusions," Glezer et al. cite Gingerich, Wells, Russell, and Shah (1983) in alluding to "whales, which returned to the aquatic environment some 50 million years ago . . . when the insectivore-like stock is thought to have been dominant." Gingerich et al. described *Pakicetus* from the early Eocene as "the oldest and most primitive cetacean known," with dentition resembling that of mesonychid land mammals as well as middle Eocene cetaceans." As for the suggested dominance of the "insectivore-like stock" at that time, insectivores were more prominent in the preceding Paleocene epoch,

though even then in company with abundant primitive ungulates, along with other early mammals (Romer 1966).

To the extent that ontogeny recapitulates phylogeny (Gould 1977), developmental studies on the cetacean brain would seem to be a rewarding approach. Garey and Leuba (1986) have published a study of *Tursiops* visual cortex finding a thin layer IV in two younger dolphins, one 3 years of age and the other 18 days old. Layer IV was absent in brains of animals age 12, 22, 26, and 33 years. If these findings hold up, it suggests that granular layer IV is a regressing characteristic of cetacean brain evolution and would not seem compatible with the initial brain hypothesis. We suggest that brains of cetaceans have evolved in response to their various ecological niches and that they entered the sea to take advantage of its rich food resources after they had developed large bodies and a predatory lifestyle on land.

Elephants have a large neocortex too

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I found Glezer et al.'s target article stimulating and tantalizing. The phylogenies in particular would be useful to evolutionary biologists. Figure 4 intrigued me and triggered my interest – intrigued me for its simplicity and the valuable information it contains, and triggered my interest because it would be an even more meaningful comparison to incorporate the brain of the largest living terrestrial mammal (*Loxodonta africana* or *Elephas maximus*). The elephant does have a large and elaborate neocortex as well as mosaic interwoven plesio- and apomorphic neural characters. We (Shoshani et al. 1982) have reviewed some of the literature on the elephant brain; see also Laursen and Bekoff (1978) and Shoshani and Eisenberg (1982) for additional information.

Concepts of brain evolution

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Evaluations of possible evolutionary changes in the fundamental organization of the neocortex are fraught with a host of dangers often avoided by fuzzy distinctions between assumption and documentation. Yet Glezer, Jacobs & Morgane present descriptions of the basic assumptions they make in proposing various modes of brain evolution and in placing the cetacean brain where they do in this scheme. The conclusion that the cetacean brain more closely approximates the "initial" eutherian plan than that of terrestrial mammals is in direct conflict with the popular notion of the advanced developmental and intellectual status of these animals. Yet this is a good example of the strength of combining and contrasting analyses of micro- and macrostructure. The thin, comparatively undifferentiated cortical laminae, impoverished cellular morphologies, and adjacent sensory projection zones are used to place these animals at a more primitive level than would be expected solely on the basis of an appreciation of their large, convoluted cortices.

Glezer et al.'s basic argument has a simplicity that does no violence to current modes of thought regarding evolution, and yet, involves a great deal of microstructural anatomy, providing a base of data from which to argue the case. In its simplest form, their analysis proposes that the initial mammalian cortex was generalized, multiadaptive, and comparatively poorly differentiated. Subsequent speciation produced a host of organizational changes that accompanied adaptation to specific ecological pressures. These changes took the form of increases in cortical thickness, greater morphological and functional diversity of cortical cell types, alteration of afferent termination and lamination patterns, elaboration of cortical modules, and the interposition of association areas between sensory projection zones. For some reason many of the changes in these organizational features, so prominent in extant species, are not apparent in cetaceans; it is impressive to consider that in the 50 to 70 million years since cetaceans returned to an aquatic environment few changes have been imposed on the prototypical brain proposed by Glezer et al. Yet the changes that have taken place appear to be quite different from those described for terrestrial mammals. The initial brain that is proposed was small and completely occupied by primary projection areas. In cetaceans the juxtaposition of all sensory areas is retained and surrounded (rather than separated as in more advanced species) by "association" areas. Just why the aquatic environment favored the seemingly unique form of neocortical differentiation exhibited by cetaceans is not discussed, but this is an intriguing issue and does warrant consideration.

Although the popularized concept of "ontogeny recapitulates phylogeny" has justly suffered in current biological theory, it is worth noting that while the primitive mammalian brain is proposed as having a thickened lamina I to receive most thalamocortical afferents, the cortex of prenatal and neonatal mammals does receive such afferents (Kato et al. 1984; 1986; Laemle et al. 1972; Luskin & Shatz 1984). In ontogenetic and, supposedly, phyletic development, the corticopetal target shifts from lamina I to lamina IV. Similarly, the morphological diversity of cortical neurons is only realized comparatively late in ontogeny and evolution. Unfortunately, there appears to be little support for the generality of a more highly developed lamina I in primitive species. It is essential to examine this possibility in monotremes and marsupials. With regard to this concept, it should be noted that *Tupaia glis* appears to have a comparatively modest lamina I compared to lamina IV – the same situation that is present in more "advanced" mammals. Similarly, the idea that the olfactory system exhibits greater development in more primitive species is not unequivocal and is contested by others (see Jerison 1976). Yet the idea that more advanced species are generally more encephalized than primitive ones is, of course, an attractive one, and one that continues to be discussed. Unfortunately, Figure 2 gives the impression that there is a direct relationship between advancement and brain/body or neocortex/cortex ratios. However, the ordering of species here seems strange, and the manner of gathering the ratios needs to be discussed in much greater detail. For example, it is not immediately obvious how neocortex/total cortex ratios yield a higher index than neocortex/telencephalon.

Although the argument and the evidence for a progressive evolutionary change from the initial form (could it have been forms?) appear to be compelling, the assumption of a monotonicity in this progression among terrestrial forms does produce some nagging doubts. For example, given the general (and reasonable) assumption that extant species are well adapted to specific environments, can one simultaneously assume that the initial mammal was a generalized form which had to be so in order to adapt to a continually changing environment? Is it possible that this initial form, rather than being the simplest of organizational varieties, was instead one which gave rise to substantial regressive as well as progressive changes in neocortical organization? It is also not clear to me whether we have enough information at present to identify which environmental features are favorable to one or another of the four evolutionary modes proposed by Glezer et al.; this must be addressed at some point.

Although the vast majority of the data presented in the target article are anatomic, Glezer et al. do point out functional distinctions that may covary with different levels of phylogenetic advancement. Presumably, an increase in the number

of vertical modules (i.e., columns) in the cortex and an increase in the number of cortical areas is directly related to advancement, and thus to being more removed from the initial mammalian form. This has the immediate appeal of helping to "explain" the apparent increase in the cognitive capabilities and behavioral repertoires of more advanced species. Although it may be true that modular development and neocortical evolution are directly related, one must be cognizant of the flux of this field. A great deal of interest has been devoted to understanding the functional subdivisions of the cortex in such species as cat and various primates; these would not have been predicted on the basis of cytoarchitectonics or morphometrics. There appears to be a direct relationship between the intensity of the scrutiny and the number of functional areas and subareas (e.g., "modules") identified. Thus, the early descriptions of somatosensory, visual, and auditory cortices identified comparatively few distinct regions in these mammals. However, there has lately been a dramatic rise in the number of these areas exhibiting distinct topographic features (see Clemo & Stein 1982; Mucke et al. 1982; Olson & Graybiel 1981; Palmer et al. 1978; Woolsey 1981). This points out the necessity of a similar effort in more primitive species. Equal effort with basal insectivores and cetaceans is necessary before the number of modules, or the amount of "association" cortex interposed between sensory areas, can be related to evolutionary status.

Glezer et al. also point out that cortical laminae help define functional units. One promising method for comparing different animals with very different cortical organizations may be to consider the influence that the cortex can exert over brainstem centers such as the superior colliculus. In nonmammalian vertebrates the optic tectum (homologue of the superior colliculus) might be expected to perform its sensorimotor roles with less direction from cortical centers than in mammals (see Stein & Gaither 1981; 1983). In mammals the cortex sends massive projections to the superior colliculus and has considerable control over its excitability and the response properties of its constituent cells (see Clemo & Stein 1986; Ogasawara et al. 1984). Knowing about the cortical acquisition of control over brainstem centers and correlating this with four proposed evolutionary strategies (conservative/progressive in cetacean, conservative in basal Insectivora, progressive/conservative in prosimians, and progressive in man) would be of considerable interest. Given the attractiveness of general schemes such as that proposed by Glezer et al., it is likely that such functional evaluations will be provided to supplement existing anatomic data.

What is provided here by Glezer et al. is a "tentative reflection." It serves the major purpose of a theory of codifying existing knowledge and of generating testable hypotheses. It is to be hoped that this will spur an extensive data collection using physiologic as well as anatomic methods in order to answer the queries raised by the current discussions.

Climbing the evolutionary ladder of success: The scala naturae in models of brain evolution

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Some years back, Hodos and Campbell (1969), in an influential article, drew attention to the many sins of comparative psychology. [See also Campbell's commentary, this issue.] Cardinal among these was the then frequent arbitrary arrangement (guided by rules of convenience rather than genetic proximity) of animal groups into a hierarchy along some dimension (e.g., small to large brains) to study the evolution of neurobehavioral

traits. Fortunately, the blossoming of evolutionary biology in the intervening two decades has left its mark on the comparative sciences, and the once popular "rat – cat – human" quasi-evolutionary series has become a historical curiosity.

Another aspect of the problem, however, has not been so quick to retreat into history, namely, the arrangement of traits along a graded phylogenetic scale, in principle unchanged from the Aristotelian scala naturae. As Hodos and Campbell (1969) originally pointed out, such a scale is minimally implied (if not made explicit) in the characterization of morphological or behavioral traits as "higher," "lower," "advanced," or "progressive," especially in comparisons among diverse phylogenetic lineages.

The present attempt by Glezer, Jacobs, and Morgane to reconstruct the stages of mammalian brain evolution, despite its avowed reliance on "well-established evolutionary concepts," does not manage to free itself from the philosophical grip of the scala naturae notion. This is most apparent in the description of the four modes of eutherian neocortical evolution (conservative, conservative/progressive, progressive/conservative, progressive). Though it is nowhere stated, the features (numbered 1–8) of "progressive" brain evolution are assumed to be "recognized by comparative anatomists" on the basis of comparisons among extant mammalian orders. As the brains of insectivores are poorly encephalized relative to certain other eutherians (especially members of Carnivora, Ungulata, and Primates), the latter, so the argument goes, have "progressed" furthest from a hypothetical (insectivore-like) "initial" brain. In keeping with a scale of neural progress, the neural traits of various taxa are then ranked, for example, as being "on the lowest scale of development," "most phylogenetically advanced," "not sufficiently advanced," etc. Species or larger taxonomic groups are similarly conceived as occupying a "higher" or "lower" position (or "phylogenetic level") on this ladder of progress.

BBS is hardly the place for (nor is its readership in need of) a lecture on "why evolution is *not* progress" or on "the abuses of teleology." In fact, I suspect (or hope) that Glezer et al. would not defend an essentially anthropocentric scala naturae of brain evolution. In a few instances they do use more appropriate, value-free terminology in describing brain traits (e.g., "derived" or "specialized"); this suggests that Glezer et al.'s predominant use of teleological terms may be influenced by similar usage prevailing (unfortunately) among neurobiologists.

So, is all this just nitpicking over terminology? I think not, for the terminology betrays a subtle (if unwitting) adherence to an evolutionary scale. The result is a ready acceptance of intuitively appealing assumptions about "stages" of brain evolution. The evolution of cortical areas is a useful example. Glezer et al. claim "It is well established that the number of cytoarchitectonic areas and subareas depends on the phylogenetic level of the species" and that the appearance of association cortex is a progressive (or late) feature in cortical evolution. This is the traditional argument that follows from the idea that the neocortex, and particularly association cortex, is the seat of human-like intelligence, and that evolution therefore progresses toward large, intelligent brains.

An abundance of comparative physiological data, however, show that this view of association cortical function and evolution is untenable (Kaas 1987, for review). Much of the traditional association cortex is not multimodal or "associational," but has specific sensory functions, and by that criterion hedgehogs have "association" cortex (e.g., secondary visual areas, prefrontal cortex) functionally comparable to that defined in supposedly "higher" mammals. Furthermore, compared to small brains, large brains have relatively more sensory areas but not more multimodal association cortex. Thus, multiple sensory areas probably evolved by differentiation of association cortex (Pandya et al. 1988).

One of the aims of Glezer et al.'s effort is to enhance our understanding of the dolphin brain. I cannot see how a characterization of the dolphin brain as less progressive than the brain

of a primate or carnivore provides any novel insight into the peculiarities of dolphin morphological or behavioral adaptation. Despite its apparent retention of generalized insectivore brain traits, the dolphin appears no less evolved than, but only different from, carnivores or primates. The question of the functional-behavioral significance of dolphin brain features remains largely unanswered in the present treatment.

Elegant hypotheses are intellectually rewarding; even more so if more hard data were available

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Apart from its merits as an elegant hypothesis, a considerable portion of Glezer et al.'s target article's appeal comes from bringing into focus much of the classical work of the early German and Russian literature and many of their still surviving traditions that otherwise exercise almost no influence on contemporary neuroscience. We are in some danger of losing perspective under the pressure of the explosive developments in the various fields and disciplines of the brain sciences: From molecular neurobiology, neural genetics, through biophysics and biochemistry of ionic channels, cross identification of neurons and neuron connections by electrophysiology, micro-anatomy, and immunocytochemistry, to brain theories and neurocomputers. It is therefore gratifying when authors (who still are able to do so) step back for a moment, as painters were supposed to do in the good old times, for an overall view.

Conscious of the limits of my knowledge of modern evolutionary theory in general and brain evolution in particular, I do not feel qualified to discuss the specific evolutionary aspects of Glezer et al.'s target article. The basic idea of four different lines of cortical evolution from an "initial (stock) brain": (1) *conservative,* (2) *progressive-conservative,* (3) *progressive,* finally (4) *conservative-progressive* – as in the Cetacea – Glezer et al.'s Fig. 5 seems to be a convincing explanation for the excessive size (or rather, surface extension) of the cetacean cortex.

What I do not feel quite comfortable with is the emphasis given to so-called primitive features of the "initial brain." The routine Golgi cytoarchitectonics illustrated in Glezer et al.'s Fig. 3 do not warrant any final judgment on the local connectivity of the cortex of the "initial brain." If the several cell types were studied in the same depth as has been done in the last 20 years, or with today's vastly improved combined cell-level physiology, and with the cell- and synapse-level anatomical and immunocytological analysis of the last 10 years on the higher mammals and primates, the initial brain might reveal itself to be at least as sophisticated in local connectivity as that of the higher primates.

Let us remember the fact that all principal neuronal types of the neocortex that we know of today were described correctly by Ramón y Cajal (1900a;b; 1902; 1903; 1906) as early as the turn of the century (apart from a single cell type, the "chandelier" or "axo-axonal" cell). Why was the understanding by Ramón y Cajal and all of his contemporaries of cortical connectivity so limited? Why did the superb attempt by Lorente de Nó (1949) – in spite of fundamental insights about the vertically oriented intracortical neuron chains – not lead to the breakthrough that started with the 1960s? Simply because nobody knew much about cortical synapses prior to the application of electron-microscopy. It is very much to the credit of the Russian neurohistologists, particularly Poliakov (1953), that they assumed the most important synapse target in the cortex were the dendritic spines; but this was not accepted until the axon-spine synapses could be seen under the electron microscope. Only then was it possible to reason about cortical connectivity much

the way this could be done in the case of most other neural centers over fifty years earlier. Even this level of understanding – as exemplified by my own papers from the early 1970s – was at best marginal, when compared with the revolution in "fine grain" cortical structural analysis started by Peter Somogyi in 1977 (Somogyi 1977; 1978; Somogyi et al. 1979). Routine Golgi architectonics, even when supported by degeneration studies or the latter generation tracing techniques and electron microscopy convey, only a very limited picture of the real local connectivity of the cortex. Only a complete reconstruction of (1) intracellularly studied and labeled neurons, (2) their local axon arborizations, (3) both the synapses they project to and receive from other neurons, and (4) the biochemical or immunocytochemixal studies of these very synapses (soon to be completed by the study of their subsynaptic receptors) can give us a reliable picture.

There would be no justification requiring the authors of the target article to present comparable data on the cortex of the cetaceans, but a few firm landmarks might strengthen our confidence in the major assumptions of their hypothesis. It would certainly have been relatively easy to obtain some acceptable GAD or GABA immunocytochemical slides of the hedgehog and the dolphin cortex that would allow some crude guesses as to whether or not the relative proportion of GABA-ergic and non GABA-ergic cells is significantly different in the "initial brain" and the cetacean cortex from what it is in the monkey or cat cortex. (I would venture to wager that the ratio will not be significantly different.) Reconstruction of a few (near complete) Golgi stained cells, both on the light and the electron microscopic scale, might also yield some crucial information. Old expressions, such as "granular cortex" or "konio cortical regions," ought to be used with more reservations than practiced by Glezer et al. because they do not tell us much about the real connectivity. The concept of isodendritic, allodendritic, and ideodendritic arborizations was introduced by Ramon-Moliner and Nauta (1966) for the cells of the lower centers; they do not have any useful application in cortical structures, where it is the axonal arborization that is really characteristic for the several cell types, with the exception, of course, of pyramidal and Purkinje cells (but in their case the question is almost trivial).

One of Glezer et al.'s most important assumptions is that there is an enormous increase in the number of cortical modules in the cetaceans. But how do we know? For all we know it may be the other way round; the modules may have vastly larger diameters. The total cortical volume increases steeply over the phylogenetic scale in the conventional laboratory animals (mouse, rabbit, cat, dog, monkey) and even more so in ape and man. This goes in parallel with the increase in the number of modules. Conversely, the size, structure (cell types and number), and internal connectivity of the modules change very little. An increase in the number of modules should go in parallel with the increase of the neuropil/cell volume ratio. As shown by Haug (mentioned in Glezer et al.'s text, but not in their list of references), this is indeed so from mouse to man. However, if the number of modules increased as spectacularly as assumed in the case of cetaceans, it would be difficult to explain the low neuropil/cell ratio. Alternatively, the large scale (distant) connectivity would have to be fundamentally different.

This commentary is intended only to point out some of the major difficulties. This does not detract from my appreciation of the elegance of Glezer et al.'s most stimulating hypothesis.

Competition for the sake of diversity

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Comparative neuroanatomists reconstruct the process of evolution through the study of some living species (commonly re-

ferred to as *living fossils*) which are thought to be almost exact replicas of those found in the fossil record. Among these, the insectivore hedgehog (*Erinaceus*) has been considered a direct descendant of primitive eutherians, and therefore its brain organization offers a possible model for brain evolution. I would like to present some complementary material pertaining to the brain of the hedgehog as a model for the "initial" brain, the diversity of cells found in neocortex of mammals, and a possible explanation for the development of specific connections.

Glezer, Jacobs & Morgane have found that the neocortical organization of the dolphin brain is similar to that of hedgehogs and bats, concluding that the brain of Cetacea evolved by multiplication of archetypal cortical modules with little modification of its intrinsic neuronal circuitry. A number of arguments suggest that the brains of modern mammals evolved from primitive "smell-brains" (Johnston 1911; Herrick 1924; Ariëns Kappers et al. 1936) and that successive differentiations took place by "invasion" of other somatic systems into this primitive brain (Herrick 1921). This concept has been revised, and recent discoveries led Ebbesson (1980a) to suggest that this "invasion" hypothesis was not operating in evolution. The "parcellation" theory (Ebbesson 1980a; 1984) states that neural systems evolve by differentiation and parcellation involving competition and redistribution of inputs, and selective loss of connections. I would add that these mechanisms are not mutually exclusive.

The most distinctive features in the brain of the hedgehog are the large extension of the olfactory structures and the presence of a small neocortex. In neocortex, layer I is exceedingly thick. It contains thalamic afferent fibers (Valverde et al. 1986), ascending axons of deep cortical cells, association fibers and a host of ascending dendrites of "extraverted" neurons located mainly in layer II. It is the degree of extraversion of layer II pyramidal cells that reminds one most of the structure found in the primary olfactory cortex. It indicates the preservation of an architectural design by means of which horizontally running fibers are capable of contacting the largest possible number of cells, similar to the system of parallel fibers of cerebellar granule cells in the molecular layer. These horizontally running fibers never form complex terminal arborizations, and so they exert a widespread influence on relatively large cortical territories. This special design of layer I in extant mammals seems to be a successful evolutionary achievement which was later found advantageous for other neural systems (invasion). At the same time, however, the invaders competed with the invaded for target neurons, resulting in an imbalance in favor of more specialized types of connections, with eventual loss of connections (parcellation). Dolphins might have been caught in a period of partial invasion and partial parcellation, similar to the insectivore stage, when they returned to the aquatic environment.

The neocortex is organized into basic modules or columns which form elementary units for thalamic, association, and callosal afferent fibers. Glezer et al. postulate that the great variety of neocortical regions might have been the result of modification/multiplication operating on these basic modules of the initial neocortex. This hypothesis is in agreement with the column/multiplication hypothesis of Sawaguchi and Kubota (1986) for the evolution of neocortex in primates. New columns accumulate genetic variations by analogy with the hypothetical creation of new genes from a redundant duplicate of an old gene proposed by Ohno (1970). The result is the paradox that similar arguments are used to explain the evolution of the primate neocortex by Sawaguchi and Kubota (1986) (a progressive type of neocortex according to Glezer et al.) as well as the mode of evolution in Cetacea (a conservative/progressive type).

I agree with Glezer et al. that neocortical evolutionary differentiation may be related to changes in the laminar distribution of cortical afferents. These might have shifted from layer I in initial cortical modules, to predominate in the lower part of layer III and in layer IV, as seen in all extant mammals. There is no doubt that this shift modified the intrinsic organization of neo-

cortex, but I believe that it was secondary to modifications occuring first in neocortical target cells receiving these connections. In the study of the forms of cells with spiny dendrites one gets the impression that all of them may share a common phylogenetic origin and that a continuum can be traced from lower forms to the primate brain. In the neocortex of the hedgehog a complete series of intermediate forms between the most extraverted pyramidal cells and fully developed pyramidal cells can always be found (see Valverde 1986 for details). At a later stage of development, some pyramidal cells lose their apical terminal branches in layer I, retaining a thin apical dendrite tapering at some distance from the cell body. The cell becomes stellate in form, and perisomatic dendrites appear concentrated in more restricted volumes. This seems to be the case of stellate or grain pyramids of the barrel field in the somatosensory and visual cortices of some rodents. In the final elimination of the remnant of their apical dendrites, these turn into typical spiny stellate cells like those found in the visual cortices of the cat and monkey (Valverde 1971). The stages of pyramidal cell differentiation also involve variations in the axonal patterns which change from long projecting neurons (hedgehog, rat, cat) to intrinsic cells with axons remaining inside the cortex (monkey). I have placed emphasis on the differences in intrinsic neocortical organization (Valverde 1986) because the multiplication of columns will not explain the diversity of cell types found in different animals, some of which may be unique for a given species.

The growth of specific neocortical afferents during ontogenetic development represents an example which might be a recapitulation of phylogeny. The axons make first contact with a transitory population of cells in the subplate layer which is largely eliminated by cell death during the early postnatal life (Kostović & Rakic 1980; Luskin & Shatz 1985; Valverde & Facal-Valverde 1987), suggesting that cortical afferents compete for a final target represented by newly developed cells in the middle cortical layers.

Evolutionary events and the "modification/multiplication" relationship

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Describing a pattern of species-typical characters can be a prelude to phylogenetic hypotheses about evolutionary processes. Glezer et al.'s outline of cortical organization across eutherian mammals is such a description. It begins the discussion of the events creating the observed pattern of mammalian cortical organization by proposing "modification/multiplication" processes that occur to various degrees in different mammalian lines. Their presentation also stimulates thought about the processes themselves.

First, however, one must consider the possibility that there really is no pattern at all. Any morphological trait will vary among individuals from large to small or from many to few. Perhaps we are simply making arbitrary categories and ranking them according to a preconceived notion of how evolution should occur. That has often happened in comparative neurobiology, but I think it is not the case here. The composition of Glezer et al.'s categories is not arbitrary. Taxonomic groups identified as generalized or primitive by nonneural criteria tend to have the "conservative" telencephalic structure while specialized or advanced species (Glezer et al.'s "higher" groups)

manifest the more "progressive" patterns. Furthermore, the two processes of modification and multiplication have a curious relationship to each other. They neither vary randomly across species with respect to each other, as might be the case for arbitrarily assigned character states, nor are they inextricably linked. The description of cetacean brains is a key piece of evidence as it shows that a multiplication process can occur relatively independent of modification. By contrast, the overall mammalian pattern suggests that, at the gross taxonomic level presented by the authors, modification does not exist without coincident multiplication.

Why does this pattern occur? The facile answer that brains are simply getting better over time is really no answer at all. In fact, when measured in the biological terms of number of species and geographic range (indicators of adaptability and the capacity to invade new areas and fill a range of niches), the more "conservative" brains appear to have served mammals better; rodents (not discussed by Glezer et al., but presumably in the "conservative" or "progressive/conservative" category) and Chiroptera are the two largest, most successful mammalian orders. I suggest instead that the modification associated with "progressive" modes coincides with the movement of a relatively few late-appearing groups into very restricted, highly specialized niches. Later mammals do not have more complex brains because evolution has made them better in some absolute sense; they have these brains because they are the latest results of a competition among generalized forms that has moved some species to more specialized niches. One implication of this conjecture is that the "progressive mode" category may be a highly artificial assembly. That is, if its members arrived via independent, parallel paths, they may have little in common beyond the superficial fact that they have a large modified cortex. It would be very interesting to explore the details of the cortical subdivisions in various "progressive mode" mammals. My suggestion would predict that, within the confines of the starting condition (the "initial brain" characters outlined by Glezer et al.), the details of the differentiation would vary widely among members of this group.

An expansion, or "multiplication" process, also marks "progressive mode" forebrains. Like "modification," it may have resulted from interspecific competition or selection associated with the specialized niches adopted by the species in this category. However, for the sake of discussion, I would like to present an alternative possibility: that the increase in brain size in the "progressive" categories has no adaptive significance in itself. Rather, I advance for consideration the speculative proposition that "multiplication" is found in those groups only because it is a required prerequisite for the necessary (adaptive) modification. I suggest that selection can experiment with modifying a modular system like the mammalian cortex only when there is an abundance of extra modules with which to work. I hesitate to call this proposition a hypothesis because of the difficulty in finding a way to test it. However, one could begin by determining whether the amount of modification covaries tightly with a degree of multiplication within eutherian groups, and whether modification is necessarily linked to multiplication in marsupials and in the many lines of nonmammals in which a similar pattern of pallial expansion and differentiation occurs (Ebbesson 1980b; Northcutt 1981; 1986).

As noted above, the converse of this proposition is clearly not true. Cetacea show that "multiplication" can occur without substantial "modification." Why cetaceans have developed a telencephalon that is essentially an enlarged version of an insectivore/chiropteran model is an interesting question. I find Glezer et al.'s explanation concerning a close genetic relationship among cetaceans, insectivores, and chiropterans less convincing than one based on an evolutionary and functional similarity between cetaceans and generalized chiropterans. Consider the suggestion that, figuratively speaking, cetaceans have enlarged chiropteran brains because they are enlarged

underwater bats. Both orders emerge from an evolutionary transition that moved them into virtually unique niches with little or no competition from other mammalian groups. A single sensory system, audition, is specialized as the primary information processing channel for navigation, prey catching, and social behavior. Even the foraging behavior (and its attendant decision-making processes) may be similar in cetaceans and insectivorous bats. Perhaps the relative immunity from competition with other mammalian groups that both orders enjoy has eliminated the types of intense selection pressure that lead to the cortical modification characterizing specialized "progressive mode" mammals. The increase in neocortical size in cetaceans relative to bats might then be seen more as a quantitative change in computational capacity than a qualitative change in processing ability.

This suggestion does not explain why cetaceans have a large brain, only why their brain is unmodified. In truth, each proposition put forward in Glezer et al.'s target article and in my commentary leads to another question, and each of *those* questions to still others. I do not see this as a problem. On the contrary, the fascination that evolutionary biologists have with describing characters across organisms comes in part from the ability of a pattern once noticed to engender discussions about governing processes. Each step in such a discussion can lead to another as layers of causality are considered and fundamental processes are uncovered. Glezer et al. have done a good job in describing a pattern that can foster a consideration of the evolutionary and mechanistic processes underlying neural evolution.

Brain evolution: Some problems of interpretation

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The topic of brain evolution as exemplified by cetacean phylogeny certainly deserves attention in *BBS*. Even noncomparative neurologists have long been intrigued by the sheer size of the cetacean brain and its suggestion of a superior intelligence. Glezer et al. are to be congratulated for their thorough discussion, in which, rather than following the traditional approach of simply treating gross morphology, they adopt the fresh one of studying histology. As a nonneuroanatomist I accept the authors' neurohistological findings on various cetaceans and other mammals. It is mainly about their evolutionary speculations that I have some questions, most of which seem to boil down to problems of interpretation.

1. Interpreting intraspecific differences as evolutionary changes. In Section I, Glezer et al. refer to a number of scholars who recognize eight features of mammalian brain evolution. The theoretical, evolutionary, and paleontological bases of that classification, however, are hardly mentioned by the authors; yet there are some problems with such an interpretation. For example, the statements in the last paragraph of Section II made me wonder how the authors could know the histology of extinct mammals! That section's last sentence even seemed circular. I also sensed this in Section III, paragraph 3 where the authors state that "Although bats . . . departed . . . from the initial stock . . . they have nevertheless retained many conservative brain features." Does early branching automatically imply the preservation of initial features? (legends, Figure 1B). Also, in the absence of any paleoneurohistological or, for that matter, any other paleontological observation, the statements in paragraph 2 of Section II that "neocortical formations *were* very distinct" and that "the morphological organization . . . *was* similar" sound rather apodictic (my emphasis).
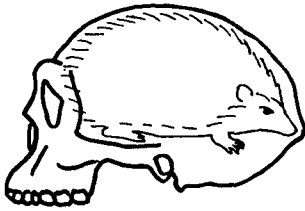
Figure 1 (Wind). Glezer et al. seem to suggest that primitive insectivores can readily be thought of as close models of ancestral brains.

2. Interpreting size. The second sentence of Section III C runs: "Moreover, the neocortex of basal insectivores is on the lowest scale of development when compared quantitatively to representatives of other mammalian orders." Do Glezer et al. mean: "The neocortex in basal insectivores is smaller than in other mammals?"

3. Evolutionary-biological terms. I did not quite understand: "major phylogenetic innovations" and "distinct phylogenetic advance" (Section III B); "conservative features" (Section III D) – possibly indicating "primitive?"; "the phylogenetic level of the species" (Section IV, paragraph 5); "non-derived species" (Section IV, paragraph 6); and "phylogenetic success" (Section VI, paragraph 1).

4. Interpreting cortical histology in terms of ecological pressures. The proposal that such selective pressures occur is fascinating and intuitively attractive, but what I missed, however, is any indication of the links – however hypothetical – between the two. What ecology causes what cortex? For example do the quietly grazing whales have other cortices than the hunting Odontoceti? Would not interesting indications be deduced from similarities or differences of ecological pressures by comparing terrestrial with aquatic mammals?

5. Facts and hypotheses. "The bushlike branching" (in the legends of Figure 1A) does not "suggest," but rather reflects the assumption, "that four major placental groups originated from one common stock." In other words, the reasoning should start with paleontology and comparative zoology, not with a cladogram.

6. Comparative-anatomical language. I had little difficulty with the first two sentences of Section II because the hedgehog can indeed quite readily "be thought of as" one of the "close models of ancestral . . . brains" – at least of those of *Homo erectus* (see my Figure 1). And although I initially had some doubts about features other than the hedgehog's form and size providing a model for ancestral brains (be they somewhat spiny), I was completely reassured by Glezer et al.'s recognition that "some additional changes . . . occurred." Real problems only arose in Section III's first sentence stating that "mammalian groups . . . could themselves serve as models of ancestral brains." This leaves me feeling like a punctualist suffering from too little imagination.

The initial brain concept: A work in progress

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The comparability of the isocortical (neocortical) structures in Cetacea with the "Grundtypus" of Brodmann (1909) has already been discussed by Riese (1925; 1927) and Rose (1926). Since the "Grundtypus" was proposed by Brodmann as the common structural factor for all mammals, a deviation in Cetacea could be of special importance for general concepts of cortical morphology. Riese (1925) emphasized the differences between the

cortex in Cetacea and the "Grundtypus," whereas Rose (1926) contradicted this interpretation, without presenting convincing findings or arguments.

Glezer and coworkers have now considerably expanded the catalogue of criteria for a new approach to this topic of comparative neuromorphology. The inclusion of the modular concept of the neocortex appears to be especially fruitful. The result leads to a corroboration of a standpoint emphasizing the distinct and unique structure of the cortex in Cetacea. In addition, the increase of weakly differentiated columnar modules explains the size of the cetacean neocortex, but simultaneously underlines its conservative mode of organization.

Despite this highly interesting concept, some questions arise regarding the value of the brain of the European hedgehog, *Erinaceus europaeus*, as the model for a conservative mode of neocortical organization. *Erinaceus* is classified by Stephan (1967) as a member of the basal insectivores, but within this group the hedgehog occupies an advanced position. The subfamily tenrecinae (not the family tenrecidae in general, because this group includes the subfamily of oryzorictinae, with progressive members) including, for example, *Echinops*, and the subfamily of geogalinae, including *Geogale*, show a much lower degree of encephalization (Rehkämper et al. 1986). More important, the neocortical lamination pattern of *Erinaceus* and *Echinops* differs from that of *Erinaceus*, showing the more progressive type (Rehkämper 1981). To summarize these findings, *Erinaceus* is *not* a typical representative of a real *basal* insectivore.

It is justified to discuss the microchiropteran species *Myotis* (Vespertilionidae) as a model for a conservative brain (Sanides 1969; 1970), but Stephan and coworkers (Stephan, Frahm & Baron 1987; Stephan, Frahm, Stephan & Baron 1987; Stephan et al. 1981) have shown, based on a huge bat brain collection that, within the same family, *Tylonycteris* is much less encephalized and neocorticalized than *Myotis*. It might thus be a more likely candidate for illustrating simple conditions that could help in reconstructing a basal situation.

Finally, the evaluation of Monotremata and marsupials as ancestral forms is questionable. The interpretation of Monotremata, marsupials, and mammals as three branches of a parallel evolution seems to reflect the situation much better (Starck 1978). The concept of the monotreme neocortex as a solely periallocortical (parahippocampal and parapyriform; Shellshear 1929) unit, and therefore less differentiated as the neocortex proper, is based primarily on anatomical studies of the blood vessel supplies in the brain of *Echidna* (= *Tachyglossus*) rather than on the cytoarchitecture. The laminar pattern, however, which includes a well differentiated inner granular layer, an atypical characteristic for periallocortical areas (Armstrong et al. 1986; Stephan 1975; Zilles et al. 1986), argues against regarding the monotreme neocortex as a primitive structure. The functional studies by Lende (1969) and our own unpublished studies on *Tachyglossus* are indicative of a unique and advanced neocortex. The counting of neurons in cortical columns as defined by Rockel et al. (1980) leads to a 2.5 to 3.5 times higher number in primary neocortical areas of *Tachyglossus* (Zilles, unpublished observations) than in placental mammals. This suggests a considerable degree of differentiation within single cortical modules and speaks against viewing the monotreme neocortex as a model for basal conditions.

Generalized statements about the primitive character of marsupialian brains should also be made very cautiously. Allometric analyses by Nelson and Stephan (1982) indicate a great variation in encephalization within this group and nothing is known about the telencephalization or neocorticalization. More data must be gathered before a balanced position about the degree of cortical organization can be adopted.

It is an old dream of neuromorphologists to differentiate between primary and association cortices and to calculate exact quantitative proportions between both groups of cortical re-

gions, as provided in the paper by Glezer and coworkers. Passingham (Passingham 1975; Passingham & Ettlinger 1974) has published careful and inspiring papers on this topic, but this could lead us to overlook the fact that the data base is very small and that existing data are burdened by severe problems, since the problem of reproducibly defining and delineating associative areas in differentiated neocortices is still unsolved.

The appearance of a layer IV has been interpreted by Glezer and coworkers as a progressive sign of neocortical organization. This, too, must be carefully substantiated and does not seem to be valid in general. *Tarsius*, not being a member of the progressive group among primates, has an extremely broad and differentiated layer IV in its primary visual cortex, with numerous very small cells and the highest degree of laminar differentiation within primates including man. Zilles et al. (1982) have shown that this cortical organization should not be interpreted as a sign of progressiveness, because it is simply a special adaptation to an increased number of visual afferents without a concomitantly high development of structures for intracortical information processing.

A further point we would like to address concerns cytological features. We do not know of any quantitative study supporting the idea of a lower number of neuronal cell types in basal insectivores (including *Erinaceus*) than in higher primates. Golgi observations cannot give a definite answer, because a quantitative statement about cell type proportions is not possible with this method. Werner and coworkers (Werner et al. 1985; Werner et al. 1982) have developed a method based on Nissl stained material for cell typing. This typing is corroborated by Golgi stained, deimpregnated material. With this approach it is possible to identify all types of neurons, including several types of interneurons in the neocortex of *Echinops* (personal communication by Dr. L. Werner). Since a sufficiently broad data base for definite statements about proportions of cell types is presently unavailable, Glezer et al.'s discussion remains at a hypothetical level.

The target article of Glezer and coworkers is truly inspiring and proposes a fruitful hypothesis for the understanding of the cetacean cortex. Nevertheless, much work is necessary in the future for a better definition of the "initial" and conservative mode of cortical organization and the quantification of cell type distribution in a comparative context. At the same time, an interpretation of the functional properties of the special cetacean neocortex must be elaborated, one that explains the selective advantage of this cortical type, which seems to be functionally competent as a primate neocortex despite being structurally less differentiated.

Authors' Response

The "initial" brain concept: Its uses and misuses

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Before replying to the various commentaries in detail, we would like to present an overview of the most general comments on our target article.

Most of the commentators seem to find the "initial" brain concept a plausible hypothesis, worthy of further study and analysis. Most commentators find merit in our view that there are four possible types of neocortical organization in mammals and in our hypothesis of the four likely modes of mammalian neocortical evolution. Our conjectures about mechanisms of evolutionary changes in the eutherian-mammalian neocortex (the columnar multiplication/modification hypothesis) also produced valuable commentaries and further queries. Most commentators accept our finding of ancestral neocortical features in the large-brained cetaceans. Because of the heterogeneity of the research interests of the commentators, the commentaries were especially valuable and multifaceted, covering a wide field of contemporary neuroscience.

It is evident from the commentaries that our article generated more questions than answers, thus fulfilling one of our main objectives. We have pondered these questions about neocortical evolution for several years and they now seem ripe enough for this type of open discussion. There are several points of contention which various commentators brought up; these can be briefly summarized as follows:

1. We recognize the obvious difficulties in assessing true ancestral features of the neocortex in extant mammals who have themselves passed through millions of years of evolution. We certainly understand that all animal species are well adapted and specialized to particular ecological niches. If they had not evolved in both their bodies and brains, it is unlikely that they would be with us today. This is true of cetaceans, which we propose as models for the initial brain concept, and it is also true of basal Insectivora and Chiroptera, among others. We consider these species to show unobscured prototypic or initial neocortical features. They serve only as *models* of ancestral brains, even though they also show many derived (progressive) features in their neocortex.

2. Some of the commentators reproach us for neglecting allometric issues in discussing the evolution of the mammalian brain and neocortex. We do of course consider the quantitative relations between brain and body (as well as neocortex/total cortex, neocortex/telencephalon) to be of major importance in analyzing brains and their component parts in a comparative series. In our target article we do present certain allometric data (section II), that we consider essential in our assessments. The main focus of our target article, however, was not on quantitative relations between the brain and body or between brain components; rather than concentrating on allometric analysis, our attention was focused more on qualitative characteristics of the mammalian neocortex, particularly the cetacean neocortex, such as the differentiation of neuronal types, areal cytoarchitectonic subdivisions and characteristics of lamination. In our target article we stressed that the neocortical structure of the dolphin has many features similar to those of the neocortex of hypothetical initial neocortical models. The most interesting feature of the cetacean brain is the presence of a large and extremely convoluted neocortical surface with relatively simple inner structure and, in fact, an organization suggesting an allocortical plan of upper cortical layers and more typical neocortical deeper layers.

3. Several commentators pointed out that our hypotheses are mainly based on morphological data without

involving enough physiological and behavioral facts. We certainly agree that a more functional approach would be of great importance. To date, many behavioral and physiological features of Cetacea are not well documented – for obvious reasons related to the special difficulty in studying marine mammals in the laboratory and under conditions in which behavior can be properly assessed. Physiological studies have been carried out relative to mapping of main cortical and motor sensory areas. We hope that morphological findings on the cetacean neocortex will provide incentives for further study of cetacean behavior.

4. Several commentators focused on our interpretation of the direction of evolution in conjunction with the initial brain concept. We were reminded of our somewhat loose usage of evolutionary terms, implying that we had accepted the *scala naturae* concept. We should point out that we agree that such a concept is largely outdated and of limited use. Our main objective was to emphasize the wide diversity of neocortical types in extant mammals. The terms "conservative," "conservative/progressive," "progressive/conservative," and "progressive" were used only as relative descriptors to emphasize the diversity of existing neocortical types and their relations to the hypothetical initial brain. We do not suggest that the term "conservative" implies *less* adaptation or specialization. Likewise, the term "progressive" does not necessarily imply *more* adaptation or specialization. These terms are only used to convey the extent to which mammals retain initial features in their neocortex.

5. Although our suggestion that the evolution of neocortex was influenced by selective pressures on afferent inputs into the neocortex was found to be compelling by several commentators, it created some controversy related to our discussion of "associative" cortex. We agree that the term "associative" lost its meaning once it was discovered that associative cortex usually consisted of multiple, specialized sensory subareas. However, the morphological and physiological facts still remain that the size and number of these specialized areas located at the periphery of the projectional area are larger in *derived* species than in *nonderived* species (Allman 1982; Baker et al. 1981; Blinkov & Glezer 1968; Preobrasjenskaja et al. 1973; Roland 1984; Rosenkilde 1979). Relative to the dolphin brain, we stated facts based on physiological mapping by Russian authors who reported that there were no additional specialized sensory areas between visual and acoustic cortices and no multimodal association areas. The vast region of dolphin neocortex lateral and medial to the visual and acoustic areas is still in need of physiological mapping.

Relative to certain points brought up by **Aronson & Tobach,** it is likely that the behavioral status of the dolphin is exaggerated in literature. Obviously, caution is needed in comparing intelligence among different species living in various ecological niches. Our investigations do not suggest any direct correlations between neocortical morphology and behavior, but they point out the obvious morphological fact that dolphin neocortical organization bears a close resemblance to that of the hedgehog.

Our response to **Campbell** is partly contained in our general remarks above. We disagree with Campbell about our use of the hedgehog neocortex as a model for the initial neocortex. We of course recognize that every

extant mammalian neocortex shows a variety of derived and nonderived features. Although the hedgehog is a very well adapted and specialized mammal, its neocortex is overly dominated by generalized or conservative initial features. We would like to reiterate that we are not promulgating the *scala naturae* concept in our target article. We are stating that the generalized Bauplan might be transformed during phylogenesis into different types of neocortical organization in extant mammals, some of which have neocortices dominated by the features of the original initial mammalian Bauplan. Of course, all brains are the heirs of their past but some are overgrown by derived features which completely obscure the fundamental plan. Brains that do not have their original neocortical Bauplan obscured allow one to study internal organization relatively unimpeded by newer acquisitions. We agree that the terms "upper" and "lower" species are quite inadequate. In using these terms we were only evaluating species from the point of view of how many initial features they retain.

In response to **Carlson:** Our main task was to develop hypotheses about the evolution of the mammalian, especially the cetacean, neocortex, within the framework of the initial brain concept. We do not necessarily consider a "bigger" brain to be a "better" brain in any sense. On the contrary, we have found that the neocortex of cetaceans, which is enormous in its surface area and convolutional complexity, shows multiple features of the generalized neocortex of insectivores. This does not imply that the cetacean neocortex is incapable of processing information as well as the primate neocortex. Each cortex functions well relative to its own ecological situation and must be adequate for species survival. However, each is clearly different and, in the case of the dolphin, the cortical organization resembles that of the basal insectivore neocortex which has long been considered a model of early mammalian neocortex.

Eisenberg notes that we oversimplified his schema of mammalian phylogenesis regarding the subdivision of insectivores into *basal* and *nonbasal* groups. We did this only for the sake of clarity in Figure 1 (target article). In the text, we acknowledged the subdivision of Order Insectivora into basal and nonbasal groups according to the data of Eisenberg and Stephan et al. (1981). Regarding the objection that we do not take reptilian, marsupial, and monotreme brains into consideration, we would like to point out that our task was to evaluate eutherian neocortical evolution. To date, there are limited data on the morphology of the marsupial and monotreme neocortices and little of this is definitive. For example, there are almost no data on the Golgi structure of the neocortices of these orders.

Falk notes that the four modes of mammalian neocortical evolution we present are not tenable because we fail to incorporate allometric principles into our classification. We recognize the importance of evaluating the macroscopic correlative growth of the brain and its parts for assessing the evolutionary changes in the brain during the course of phylogenesis and ontogenesis. In classic (Dubois 1914) as well as in recent literature (Falk 1980; Jerison 1973; Passingham 1975; Pirlot 1987; Radinsky 1975; Stephan 1972), allometric relations in the phylogeny and ontogeny of the mammalian brain are well recognized. In our target article we did not emphasize

this important problem (though we mentioned it in section II) because it relates to our concepts somewhat tangentially and our hypotheses are based mainly on inner structural changes of neuronal typology and connectivity. The main point we made in our columnar modification/multiplication hypothesis relates to the proposed mechanism of cortical expansion: multiplication of cortical modules (either nonderived modules in cetaceans or derived ones in advanced terrestrial mammals). It is certainly possible that part of the reason for this expansion relates to demands for more rapid processing of large amounts of information. This postulate is widely accepted in the allometric literature. Nowadays, the situation has become even more complicated. Thus, according to Jerison (1973) and Fox and Wilczynski (1986), the traditional allometric equation ($y = bx^a$) should be changed to the biomodal equation: $E = k_v P^a + k_c P^a$, where two parts of the right side of the equation consequently represent the so-called *somatic* and *nonsomatic*[1] parts.

We agree completely that in the testing of our hypothesis on different mammalian models allometric relations will eventually have to be taken into account, and we would point out that there is great variability of brain and body mass in cetaceans, which is well-documented in the literature (Jansen & Jansen 1969; Morgane & Jacobs 1972; see also the commentary of **Ridgway & Wood**). The problem is further complicated by great seasonal variation in the body weights of cetaceans (Jansen & Jansen 1969). However, if we concentrate attention on the cetacean species most studied morphologically and physiologically, for example, some Odontoceti, and especially *Tursiops truncatus*, we can conclude that, in comparison with even higher primates (*Homo sapiens; Pan troglodytes*), the neocortex of these species appears expanded, even if we take into consideration the allometric coefficient.

According to our data (Morgane et al., in press) and the data of Zvorykin (1977), the surface of the neocortex in *Tursiops truncatus* is about two times larger than that in *Homo sapiens*, although the differences in body size between these two species are only 1.5 fold. As we pointed out in the target article, however, and as Zvorykin (1977) showed previously, the absolute volume of the dolphin neocortex is almost the same as in humans, and relative to the total volume of the brain is even less than that of basal insectivores. This result, paradoxical at first glance, is easily explained by the features of dolphin neocortical cytoarchitectonics; for example, though the extent of the cortex is greatly expanded, the width of the neocortex is small. As we have suggested, this feature appears to reflect the conservative type of modular structure of the cetacean neocortex in addition to poor lamination and granularization. It is of interest that the general number of neurons estimated by Zvorykin (1977) to be present in the neocortex of one hemisphere is about twice as small in the dolphin (*Tursiops*) as in humans, but comparable with this parameter in chimpanzees. These quantitative estimates, with or without allometric corrections, show clearly that the absolute and relative parameters of the neocortex put even the most derived species of cetaceans in a special category of mammals closer to the models of the ancestral brain.

It appears to us that **Gibson** has proposed a quite plausible hypothesis regarding the differences between primate and cetacean manipulative behavior. It might be worthwhile to correlate, indirectly, these differences with features of brain morphology. However, new data on dolphin behavior and neural hardwiring must be obtained before it will be possible to make these correlations.

We agree with **Innocenti** that comparing the morphology of different species should be done only on the basis of comparable sets of data. In the case of columnar cortical organization, we tried to be especially conservative because there are no tract-tracing studies on dolphin cortices, although we are fully aware of the recent progress in assessing new data on so-called association areas of neocortex. In the case of the dolphin, we simply pointed out that according to electrophysiological data there appear to be no association areas (as defined in the old literature) between the primary and secondary projection zones. Relative to Innocenti's comments about regressive morphogenetic events in phylogenesis, we would like to note that, at least in eutherian neocortical evolution, we cannot provide clear examples of regressive changes. In the case of the dolphin, which lacks peripheral olfactory receptors, there is still a highly developed paleocortical formation (Morgane & Jacobs 1972). Thus it is likely that in many systems regressive evolution in phylogenesis did not occur.

We could hardly agree more with **Irsigler's** comments about the use of cytoarchitectonic subdivisions for evolutionary generalizations about the neocortex. However, in our case, we are using not only cytoarchitectonic subdivisions of the dolphin neocortex, but also correlations with electrophysiological mappings by Russian authors along with our own Golgi and electron microscopic studies (Glezer et al., in press; Morgane et al., in press). The second point made by Irsigler is evidently based on a misunderstanding. Although vertical cortical modules are accepted as basic components of morphofunctional organization in the neocortex, there is great variability in the dimensions of the columns as well as in their inner structure. We believe that the quantitative and qualitative variability of columnar organization may reflect functional specializations of different cortical areas. In our view the cortical module is likely to be one of the main targets of evolutionary forces through the influence of subcortical and peripheral neural mechanisms subjected to selective pressures in specific ecological niches (see also the commentary of **Wind**).

In response to **Johnson**: In our attempt to provide a basic plan of eutherian-mammalian neocortical evolution we certainly did not intend to label the hapless hedgehog a "primitive" mammal. We are well aware that all extant animals are conglomerates of conservative (nonderived) and progressive (derived) features in their morphophysiology. The same is true of the features of their cerebral cortices. However, the balance between derived and nonderived features of the neocortex in different extant mammals varies greatly. One of the purposes of our target article has been to compare our data on the dolphin neocortex with the concepts of Sanides and Sanides (1974) and the data of Valverde and Facal-Valverde (1986) showing that, of all extant mammals, the neocortex of basal insectivores is the least masked by evolutionary changes. Our article stresses that dolphin convexity neocortex, when examined with Golgi and Nissl methods, has a basic

internal organization similar to that shown by Sanides, Valverde, and ourselves (Morgane et al., in press) in the hedgehog. The remarkable combination of a large neocortex and the relatively primitive structure of its modular units is something not previously described. Our goal was never to denigrate either the hedgehog or the dolphin but to point out the remarkable similarities between the internal neocortical organization in both. To worry about "political" connotations of the terms (conservative, progressive, etc.) suggests that words are more important than substance. Given that there are only a few acceptable terms for brain phylogenies we – in the interest of economy and comparison with past work – used terms that need have no political connotations to them. We recognize that the fundamental idea of an initial plan or Bauplan of the brain goes back a long way, has many problems, and needs a modern-day analysis.

We agree with **Kaas** that the validity of subdividing the neocortex into areas can be tested by physiological mapping and morphological studies of cytoarchitectonics, neuronal typology, and microcircuitry. Our hypothesis of cetacean neocortical evolution is not only based on cytoarchitectonics but also on Golgi studies, electron microscopy (Glezer et al., in press), and computerized image analysis (Morgane et al., in press). We do not wish to speculate at this time on how many functional cortical areas exist in the dolphin. However, the relative cytoarchitectonic homogeneity of dolphin convexity neocortex suggests that functionally the number of physiological areas will be less than in mammals with more differentiated neocortices. This is certainly but a tentative proposal, which can only be verified by direct experimentation (i.e., tract-tracing, local circuit analysis, and electrophysiological mapping).

In response to **Neafsey** on "associative" and "nonassociative" cortices, we wish to note that concepts such as "primary," "secondary," and "tertiary" associative cortices are in a regular state of revision as newer physiological data appear. Also, based on comparative anatomical data, Sanides and Sanides (1974) have proposed nontraditional views of "projection" and "associative" cortical areas. According to new physiological data, the so-called associative areas are nothing more than special organized projectional areas, processing subcortical information differently as compared with classic projectional areas (see the commentary of **Steklis,** in which this new concept is well described). These new physiological data confirm, in general, the views of Sanides and Sanides (1974), who first suggested that so called association cortex is the least differentiated, that is, most generalized, of the cortical areas. Evidently, the whole concept of multimodal association cortex must be revised (Kaas 1987a) and we agree with these newer interpretations. However, they do not change the fact that in dolphin cortex there is no such multimodal or associative cortex between physiologically defined areas of different functional modalities (Supin et al. 1978). In the advanced or "progressive" mode of classification, additional sensory areas (secondary, tertiary, etc.) clearly separate the primary sensory areas (Baker et al. 1981; Roland 1984).

Parker has noted that we fail to discuss the relationship between "the morphological pattern of the dolphin brain and its behavioral capacities" and that we do not relate the specialized brain structure of the dolphin brain, such as hypertrophy of the acoustic sensory system, to the special behavioral abilities of the dolphin. Although these questions are interesting, our main goal was to present and discuss the neocortical structure of the dolphin brain and to relate these to the concept of the initial mammalian brain. It was not our goal to correlate the specificities of dolphin behavior with structural peculiarities of large neocortical areas, nor can it be done at this time, given the absence of more data on behavior. Also, until more data are obtained on the hardwiring of the dolphin neocortex, especially by use of contemporary EM-Golgi methods, immunocytochemistry, and histochemistry, all discussions of "dendritic arborization and information processing capacities" in the cetacean brain are premature. Our group has only now started such Golgi and EM work (Glezer et al., in press; Morgane et al., in press) in conjunction with computerized image analysis of the modular structure of the dolphin cortex. Whether dolphin cortical neurons are characterized by larger or smaller dendritic arborization fields than seen in other species or whether there are peculiarities in distribution of the GABA-ergic and non-GABA-ergic neurons in their cortical modules can only be decided after immunocytochemical studies.

Parker also mentions that we do not compare the dolphin cortex with the cortex of animals inhabiting the same medium as the dolphin. Once more, our task was a comparison of the dolphin neocortex with that of the presumed terrestrial ancestors. The Pinnipedia and, especially, the Sirenia, though they inhabit the same aquatic niche and have adapted excellently to aquatic life, are not directly comparable with Cetacea in terms of aquatic adaptation. The Pinnipedia only spend part of their lives in the sea, returning to land for procreation, whereas the Sirenia have only adapted to living in shallow water. Cetacea are unique among mammals in their total adaptation to ocean life, including deep diving capacity. The small body of data on cortical structure in Pinnipedia and Sirenia has shown features more similar to those of terrestrial mammals of a noninitial or more derived mode than to those of Cetacea.

Parker evidently did not note our inclusion of the initial models of the bats (Chiroptera), although we are not sure that primitive features of their neocortex as well as those in Cetacea can be directly referred to echolocation capacities. We are aware that the Order Cetacea contains a wide variety of species which differ immensely in their allometric brain indices. However, we concentrated our attention on three species from the Family Delphinidae which have been more commonly used for morphological and physiological studies. It is particularly to one of these species that popular opinion ascribes high intelligence (*Tursiops truncatus*). The detailed morphology we have done concerns only a few cetacean species; we cannot, of course, generalize the details of our data across all Cetacea. However, by using these three species (*Tursiops truncatus, Delphinus delphinus,* and *Stenella coeruleoalba*) we can characterize well the basic cortical structure of this cetacean family. We accept Parker's comment that particular species of Haplorhini and Strepserhini are among the smallest in body size. However, the point we made concerned comparison between species of the same order. Although we do not equate "smaller" with "primitive," as a rule, the more

advanced species of the same order also seem to reveal a progressive increase in body size. With all due respect to the intellectual abilities of Cebidae, these species are far less advanced when compared to anthropoids. The quantitative data of von Bonin (1939) on *Cebus capucinus* clearly showed that its cortical structure is far more "primitive" than that of anthropoid primates.

In response to **Reep:** Our task was to concentrate mainly on the organization of the cetacean neocortex in relation to the organization and evolution of eutherian neocortices. We decided to limit the range of our comparative series by not including Monotremata and Marsupialia because of their earlier branching from the mammalian stock. As Reep notes, our data base includes only representatives of the Family Delphinidae: *Tursiops truncatus, Delphinus delphinus,* and *Stenella coeruleoalba*) and is hence limited with regard to broad generalizations across Cetacea. However, data of other authors (Kesarev 1971; Kesarev & Malofeeva 1969; Zvorykin 1977) which also include other species of Odontoceti (*Phocaena phocoena, Delphinus delphinus, Orcinus orca*) and some of the Mysticeti (*Balaenoptera physalus*) show that the general architectonic features of cetacean neocortex, such as narrow cortex with a low degree of granularization, accentuation of layer II, and extreme width of layer I, are the same for all these cetacean species. We also agree that the initial brain model should only be applied to particular features of extant mammals. In our target article we consider only some characteristics of neocortical organization in some of the Insectivora, Chiroptera, and Cetacea as having retained features of the ancestral neocortex. Other features of the species show that they have clearly evolved and progressed so that each mammalian species is adapted and specialized to its own specific environment.

Regarding the comments of **Rensch,** it is possible that retention of the initial features in cetacean neocortex was somehow mediated by the change from a terrestrial to an aquatic environment where selective pressures were not as strong, or where the aquatic medium acts differently in comparison with the land environment. The sirenian brain may well be useful for comparisons with the cetacean brain, but to date there are too few facts in the literature on the internal organization of the sirenian neocortex. The data of Welker et al. (1986) showed that the brain of the manatee is not comparable in its allometric parameters with the brain of the dolphin. Also, gyrification and cytoarchitectonic organization of the manatee neocortex is quite different and the development of gyri and sulci in its cortex is poor.

As noted by **Ridgway & Wood,** Cetacea are represented by an impressive number of different species varying in their brain and body sizes. There is no contradiction between this fact and our postulate that "there is a general trend toward an allometric increase in the absolute and, especially, the relative mass of the brain with respect to body size" because our postulate relates to the derived species of main eutherian–mammalian orders. Among the Order Cetacea, it is likely that there is some variability of derived and nonderived neocortical characters and the same is true also for primates. Ridgway & Wood also note the likely derivation of cetaceans from an ancestral mammalian group. We also agree with Ridgway & Wood regarding the view of McKenna (1975) that

cetaceans probably evolved from primitive ungulates. It is of interest that these primitive ungulates were also very close to the ancestral insectivores.

A third comment by **Ridgway & Wood** relates to the possibility that regression of layer IV in the ontogenesis of dolphin visual cortex is contrary to the initial brain hypothesis. We have found a narrow (incipient) layer IV in one of the areas of visual cortex in the adult dolphin; we do not feel that the finding of an extremely narrow and weakly developed layer IV, whether in young or adult mammals, undermines our main postulate that dolphin neocortex is agranular or dysgranular and hence comparable in structure to models of the initial brain. Our recent Golgi studies (Morgane et al., in press) show that the incipient layer IV in dolphin visual cortex contains aspinous stellate cells which are very different from spinous stellate cells of typical layer IV in advanced terrestrial mammals.

It is of interest, as pointed out by **Shoshani,** to compare the whale brain with the brains of the largest extant mammals, such as elephants. According to the data of Zvorykin (1977), the cytoarchitectonics of various areas of the elephant brain are not very different in general features from those in other terrestrial mammals. Thus, the width of the cortex is well within the range of that of other mammals and is correlated with the large size of the brain.

Stein comments on the development of lamina I in nonderived mammalian species: Well-documented facts exist only for the hedgehog (Valverde & Facal-Valverde 1986) and bat (Sanides & Sanides 1974). The neocortex of *Tupaia glis* is characterized by a narrow layer I and, accordingly, we do not consider the neocortex of this species to be a representative model of the initial neocortex. It is obvious why the neocortex/total-cortex ratio yields a higher index than neocortex/telencephalon. The first of the indices depends on the size variance of cortex exclusively, whereas the second depends on the size of the cortex and basal ganglia as well as white subcortical matter. We agree with Stein that ancestral initial brain features were not acquired by a singular species but rather by a group of prototypic species which were generalized; because of this generalization of brain features, the latter acquired a higher potential for adaptation to new environments. This statement is equivalent to the view of Sanides and Sanides (1974) concerning generalized features of the cortex.

We concur with the comment of **Szentágothai** that quantitative estimation of GABA-ergic and non-GABA-ergic neurons in dolphin neocortex will help us understand the principles of its structure and function. However, the main difficulty lies in obtaining fresh specimens for immunocytochemical studies. Relative to Szentágothai's comment on columnar organization, our data on cytoarchitectonic columns in the visual cortex of the dolphin show that they are twice as large as in the human brain (Morgane et al., in press). The vast surface of the dolphin neocortex (almost twice that of human) also implies that the total number of columns in the dolphin is comparable to that in humans.

The commentary of **Valverde** is especially interesting and constitutes substantive theoretical extension of our paper. We agree that "dolphins might have been caught in a period of partial invasion and partial parcellation,

similar to the insectivore stage, when they returned to the aquatic environment."

We also concur with **Wilczynski** that so-called derived groups of mammals developed their "progressive neocortices" because of having moved into restricted and specialized ecological niches at relatively later periods of evolution. Other very interesting points are made by Wilczynski, particularly his assumption that "selection can experiment with modifying a modular system like the mammalian cortex only when there is an abundance of extra modules with which to work." We think this is the situation prevailing in the evolution of the dolphin neocortex.

Wind comments on our attempts "to translate the intraspecific differences into evolutionary changes." We certainly realize that only in the hypothetical sense can we consider the neurohistological features of extant and well-adapted mammals to be similar to features of eutherian ancestors. In our target article we stressed that basal Insectivora and Chiroptera are only *models* of the so-called initial type of mammal. We are well aware that these models of ancestral mammals themselves appeared as a result of long-term evolutionary processes and hence only some of their features can be considered to reveal the prototypic signs unencumbered by new evolutionary brain acquisitions.

Wind also notes that we imply early phylogenetic branching as a reason for the preservation of conservative features. We really did not specifically claim this. However, facts of evolutionary anatomy show that the brain is a true reliquary of its past. It is also well demonstrated that "relics" of the paleonotological past can survive through millions of years without any substantial change in their morphology (Coelocanth, Elasmobranchs, etc.). It *is* therefore not unreasonable from our point of view to suggest that one cause for the retention of the ancestral features of the neocortex in extant basal Insectivora, Chiroptera, and Cetacea was their early branching from general protoeutherian stock.

Wind *seems to have misunderstood our second sentence in Section IIIc, namely, "the neocortex of basal insectivores is on the lowest scale of development when compared quantitatively to representatives of other mammalian orders."* Taken out of context, the phrase seems awkward. However, in context, it is clear that we are discussing the relative characteristics (% of area, and volume) of the neocortex, which in basal insectivores (according to Filimonoff 1949; Stephan et al. 1970), is relatively smaller than paleo-, archi-, and mesocortices. In most other types of neocortical organization in mammals (conservative-progressive, progressive-conservative, and progressive) neocortex prevails over other phylogenetically older cortices.

Zilles & Rehkämper correctly point out that the basis of the initial brain concept can be found in the classic works of Brodmann (1909), Elliot-Smith (1910), Riese (1925; 1927), and Rose (1926). We also agree that *Erinaceus europaeus* is not the most typical representative of basal Insectivora. However, in using the hedgehog as a model of the initial mammal, we are taking into account the whole group of nonderived species of Insectivora. It is useful to consider the rare species of Insectivora such as *Echinops* and *Geogale* in comparison with cetaceans. However, in the literature to date, the best-studied

neocortex of basal Insectivora is still that of the hedgehog. We concur with **Zilles & Rehkämper** that the inclusion of Monotremata and Marsupialia would create obstacles for the evaluation of neocortical evolution in eutherians.

- **Zilles & Rehkämper** point out that granularization should not be used as a derived feature of the neocortex because in some primitive species of primates (*Tarsius*), layer IV in area 17 is very well developed. By way of reply, we do believe that granularization should be used, but only for comparison between orders. Thus, the well-differentiated layer IV in area 17 can be found in primates, whereas in Carnivora this layer in the same area is much less developed (Shkol'nik-Yarros 1971). Not only should the neuronal structure of layer IV be taken into account but also a general number of granular cells, especially spinous stellate cells. By these criteria, neocortices of initial animals (Insectivora, Chiroptera, and Cetacea) are much less derived than those of other eutherian mammals (Poliakov 1958a; 1964; Morgane et al., in press).

NOTE
1. The pool of neurons which do and do not depend on body size, respectively (Jerison 1973; Fox & Wilczynski 1986).

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