Implicit Short-Lived Motor Representations of Space in Brain Damaged and Healthy Subjects

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This article reviews experimental evidence for a specific sensorimotor function which can be dissociated from higher level representations of space. It attempts to delineate this function on the basis of results obtained by psychophysical experiments performed with brain damaged and healthy subjects. Eye and hand movement control exhibit automatic features, such that they are incompatible with conscious control. In addition, they rely on a reference frame different from the one used by conscious perception. Neuropsychological cases provide a strong support for this specific motor representation of space, which can be spared in patients with lesions of primary sensory systems who have lost conscious perception of visual, tactile or proprioceptive stimuli. Observation of these patients also showed that their motor behavior can be ''attracted'' by a goal only under specific conditions, that is, when the response is immediate and when no cognitive representation of this goal is elaborated at the same time. Beyond the issue of the dissociation between an implicit motor representation and more cognitive processing of spatial information, the issue of the interaction between these two systems is thus a matter of interest. It is suggested that the conscious, cognitive representation of a stimulus can contaminate or override the short-lived motor representation, but no reciprocal influence seem to occur. The interaction observed in patients can also be investigated in normals. The literature provides examples of interaction between sensorimotor and cognitive framing of space, which confirm that immediate action is not mediated by the same system as delayed action, and that elaborating a categorial representation of the action goal prevents the expression of the short-lived sensorimotor representation. It is concluded that action can be controlled by a sensory system which is specialized for on-line processing of relevant goal characteristics. The temporal constraints of this system are such that it can affect the action before a full sensory analysis of this goal has been completed. The performance obtained on the basis of this spatial sensory processing suggests that short-lived motor representations may rather be considered as real ''presentation'' of the action world, which share its metric properties. © 1998 Academic Press

1. INTRODUCTION

Perception is often conscious, which allows one to report about the object of perception and to elaborate deliberate actions in the environment. But there is a considerable body of evidence that actions do not always result primarily from such elaborated perceptual processes. These two statements are illustrated in Fig. 1. The experimental data reported in this review represent an attempt to summarize several instances of implicit (or nonconscious) use of sensory information during action. These data make it clear that the idea of a pure serial processing of sensory information from mental representation to action (see Fig. 1, upper panel) is out of date. Examples of such implicit sensory representation will be obtained from various experimental fields ranging from psychology to neurophysiology and neuropsychology. These empirical
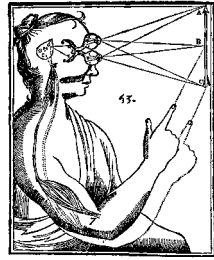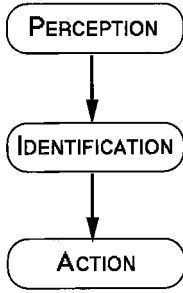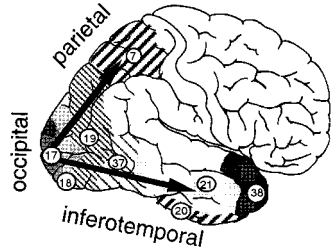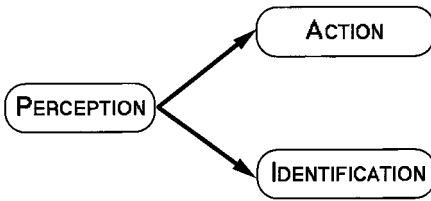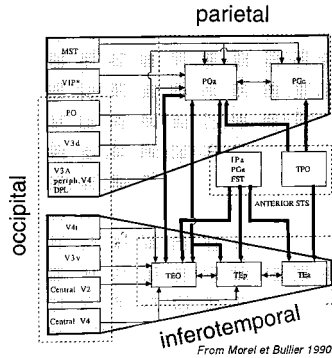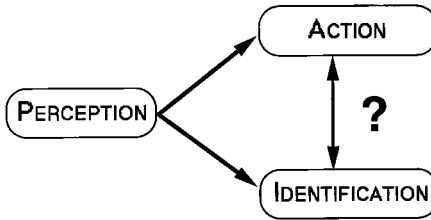
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FIG. 1. Three conceptions of how light comes into muscles. This figure displays three main comprehensions of vision that are discussed in this review (as well as the concurrent evolution of scientific illustration). The Cartesian view of how light comes into muscles is clearly linear (higher panel). The pineal gland, seat of the mind, here considered as interface between sensory input and motor output, could be cognitively described as the potential locus of spatial representation. The modern conception of sensory processing now often focuses on dissociations between spatial and object vision, or vision for action and vision for perception (middle panel). These functionally segregated types of processing would fit two separable anatomical pathways leading visual information to the posterior parietal cortex (dorsal pathway) and to the inferior temporal cortex (ventral pathway). Given this functional dissociation, it is, however, worth noticing that several anatomical cross-connections between the two main streams have been described in monkey (Morel & Bullier, 1990) (lower panel).

data not only make the case for a dissociation between conscious awareness and motor representations of sensory targets, but also provide a basis for understanding how these two representations can interact (see Fig. 1).

Current theoretical and experimental work on consciousness seem to make the assumption that implicit processing may be an intermediate step between brain mechanisms and consciousness (e.g., Rossetti, 1992; Bock & Marsh, 1993). The qualifications of the ''cognitive unconscious'' (Kihlstrom, 1987) may, indeed, very much be shared with conscious processing. It is, therefore, of prime interest to study how sensory inputs can be processed implicitly in the brain and to investigate whether or not this processing can be distinguished from conscious operations. Dissociations between implicit and explicit information processing have been described in psychological fields such as memory, perception, motor behavior, and in neuropsychology (aphasia, prosopagnosia, etc.) (cf. Weiskrantz, 1991). Other kinds of dissociations reported in perception or memory may also be tentatively listed together here. The terminology used to describe these dissociations can be clustered into two main groups.

On the one hand, the attention was drawn to the perceptual side, e.g., conscious vs. unconscious aspects of processing (see Bridgeman, 1992), localization vs. identification of the stimulus (e.g., Schneider, 1969; Paillard, Michel, & Stelmach, 1983); spatial vs. object vision (Ungerleider & Mishkin, 1982); direct parameter specification vs. conscious representation (Neumann & Klotz, 1994); procedural vs. declarative (Cohen & Squire, 1980), and implicit vs. explicit (Shacter 1987) memory systems.

On the other hand, the dichotomy was based on the possible responses provided by the subject: experiential vs. action (Goodale, 1983); cognitive vs. motor (Bridgeman, 1991); cognitive or representational vs. sensorimotor (Paillard 1987, 1991); reaching vs. grasping visuomotor channels (Jeannerod, 1981); sensorimotor vs. conceptual components in memory (Perrig & Hofer, 1989); conscious perception (''what'') vs. action (''how'') visual processing (Goodale & Milner, 1992; Milner & Goodale, 1993); pragmatic vs. semantic representations (Jeannerod & Rossetti, 1993; Jeannerod, 1994a).

This nonexhaustive list of dissociations described in the literature illustrates the great variety of approaches to implicit brain processing and shows the type of confusion that may result from attempts to reconcile their various concepts. In particular, a partial agreement can be found between several theories of automatic vs. controlled processes, or between several conceptions of dissociations within vision, but it appears difficult to unify these different views within one single line of thought. The theoretical objective of this article will thus be rather restricted.

The aim of this review will be twofold: first, I will review some evidence for implicit processing of sensory information during action from the two main lines of research outlined above. As sketched in Fig. 1, I will summarize data indicating that explicit sensory processing and implicit processing for action can be dissociated, but also that they can interfere. Second, I will focus the analysis on a restricted number of parameters that will allow me to propose a common feature for most of the data reviewed. Indeed, this review will highlight the crucial role played by time factors in many of the distinctions quoted above. Further attempts to integrate the concepts

developed in these experimental fields within a unified framework may benefit from this observation.

2. MOVEMENT FUNDAMENTALS

2.1. Eye Movement

Following Bridgeman (1992: p. 76), it can be stated that, with respect to exploratory movements, ''the vast majority of behavioral acts are saccadic jumps of the eye, unaccompanied by any other behaviors.'' It is particularly striking that most eye movements are not consciously elicited. This is particularly true for the low amplitude saccades, like the microsaccades occurring during fixation. But, as is shown below, even larger saccades performed in response to a target jump exhibit a similar automatic component.

The orientation of gaze toward an eccentric target (presented as a step from an initial fixation point) is composed of a main saccade, that usually undershoots the target, and a corrective saccade. Corrective saccades have an amplitude of about 10% of the target eccentricity, and their latency is about half that of primary saccades (Becker & Fuchs, 1969). This reduced latency does not mean that corrective saccades are fully preprogrammed. Indeed, when the target jumps again during the main saccade (the so-called double-step stimulus), an appropriate corrective saccade is elicited with a short latency (Prablanc & Jeannerod, 1975). When the second jump is larger than about 4°, then a new decision has to be made, resulting in an increase in latency of the secondary saccade, in the same range as the latency of the initial saccade. The authors thus suggested that the planning of a corrective saccade at the end of the main saccade can bypass the normal decision time, i.e., that this fast eye movement can be unconsciously elicited.

Another interesting phenomenon related to eye movements is called **saccadic suppression.** As early as 1900, Dodge noted that seeing his own eye motion in a mirror was impossible. Indeed, it is easily demonstrated that one's own eyes can be seen in successive positions but never in motion. Psychophysical studies revealed that human subjects are unaware of displacements occurring within the visual world if these displacements are tightly timed during the saccade (example: Bridgeman, Hendry, & Stark, 1975). Saccadic suppression thus refers to the apparent loss of perception occurring during saccades (Campbell & Wurtz, 1978).

The experimental paradigm using double-step stimuli with the second step synchronized with the first saccade has proved to be a powerful tool for investigating both eye and hand motor control. Later investigation of visual perception during saccadic eye movements demonstrated that eye and hand movements do not become disoriented after saccades as could be expected from the perceptual effect. Indeed, the eyes can saccade accurately to a target that is flashed during a previous saccade (Hallett & Lightstone, 1976; but see Honda, 1990). This maintenance of such visually guided behavior may appear contradictory to the loss of perceptual information described as the saccadic suppression. One possible solution to this paradox results from the comparison of the responses used. Saccadic suppression experiments required a symbolic response (verbal report or key-press), whereas maintenance of fairly accu-

rate eye orientation requires a quantitative information (cf. Bridgeman, 1992, p. 79). This crucial distinction will be followed throughout the present review.

2.2. Arm Movement

2.2.1. *Reaching*

As is the case for eye saccades, two phases are classically described in arm movements. Reaching movements are initiated in a ballistic way, but are then subjected to feedback from several sensory systems. Given this parallelism, the effect of abrupt stimulus change on arm movements has been investigated in conditions allowing or not the conscious detection of this change by the subject.

Pointing. The saccadic suppression paradigm described above has also been applied to arm responses. In one early experiment, subjects were asked to point to the position of a target that had been displaced during the saccade (by a stroboscopic induced motion) and then extinguished (Bridgeman, Lewis, Heit, & Nagle, 1979). These authors made similar conflicting observations to those reported for eye movements: the saccadic suppression effect was not followed by a motor disorientation. Moreover, it was found that a pointing movement following a target jump remained accurate, irrespective of whether this displacement could be verbally reported or not. These experiments, therefore, suggested that two psychophysically separable visual systems can be distinguished, one system for a ''cognitive'' response, and a second one for motor behavior.

Experiments aimed at exploring the type of sensory information involved in motor control further explored this interesting phenomenon (Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986). In this experiment, they asked subjects to point as fast and as accurately as possible to visual targets presented in the dark. In half of the trials, the target simply jumped from a central position to randomly selected positions in the peripheral visual field. In the other trials, the target made a further jump time-locked to the saccade, so that the second target was either closer or farther than the first, but always in the same direction. Subjects were never aware of the second target jump and could not even guess its direction. Nevertheless, it was clearly showed that not only the eye (after a corrective saccade) but also the hand reached the target in all cases, although they were both initially directed toward the first target. It was concluded that vision of the moving hand was not necessary to control the movement, and that movement trajectory could be updated without the subject's knowing it. This study thus demonstrated that perception of target position could be dissociated from visuomotor response directed to that target, i.e., that different types of visual computation are made for visual perception and visuomotor control. Similar results were obtained when the second target jump altered movement direction instead of its amplitude (Prablanc & Martin, 1992). Again, neither the target change in location nor a kinesthetic sensation of correction were consciously detected. Since there was no visual information available apart from the target, the encoding of target in an external frame of reference by the conscious perceptual system could have been misled in both experimental situations to assume that the position of the target, because it was stable before the saccade, had remained un-

changed. The motor coding of target location was, nevertheless, correctly performed with respect to an egocentric reference allowing accurate movements.

One interesting feature of this automatic sensory processing in action is the particularly short latency that is measured between the target jump elicited in the environment and the motor reaction to it. In the previously described experiments, usual visuomotor delays were about 110 ms. Strikingly, this value is very similar to that obtained when the target jump was not synchronized with the saccade and therefore could be detected by the subjects (Soechting & Lacquaniti, 1983; Komilis, Pelisson, & Prablanc, 1994), indicating that conscious awareness may be dissociated from the automatic sensorimotor reaction.

Grasping versus vocalizing. In addition to these pointing experiments, automatic corrections were explored for more complex grasping movements. Paulignan, MacKenzie, Marteniuk, and Jeannerod (1991) reported a similar delay of motor response (about 100 ms) to a perturbation of the location of the object to be grasped. When the perturbation instead affected the object orientation (Desmurget, Prablanc, Arzi, Rossetti, Paulignan, & Urquizar, 1996) or size (Paulignan & Jeannerod, 1991), the motor reaction time increased to about 110 ms and 300 ms, respectively. Related studies stressed the high speed of motor correction and investigated the delay of subjective awareness of the perturbations (Castiello, Paulignan, & Jeannerod, 1991; Castiello & Jeannerod, 1991). In these experiments, a simple vocal utterance (Tah!) was used by the subject to signal his or her awareness of the object perturbation. Comparison of the hand motor reaction time and the vocal reaction time showed that the vocal response consistently occurred after the motor corrections. As in the Paulignan et al.'s experiments, the onset of motor correction was about 110 ms after the object displacement and about 280 ms after the change in object size. However, the vocal responses occurred in both cases about 420 ms after the object's perturbation. It was concluded that conscious awareness of the object perturbation lagged behind the motor reaction to this perturbation.

Altering or prohibition vision. There is additional evidence for the implicit use of sensory information in motor control. In contrast to the above manipulations of the target, another possible approach is to manipulate sensory information about either the target or the acting arm. Jakobson and Goodale (1989) showed that exposure to about a 3° shift of vision through wedge prisms could not be detected by uninformed subjects. Nevertheless, when subjects pointed at visual targets during such exposure, they demonstrated an on-line correction of the prism-induced bias in movement direction, resulting in a modified hand-path curvature of the first few movements of prism exposure. Once again, these results suggest that the sensorimotor system can be responsive to consciously undetected sensory events. Moreover, different arm trajectory types were observed between preexposure and postexposure phases, which suggests that visuomotor adaptation took place in uninformed subjects.

Another experiment investigated the structure of pointing movements made under prism exposure (Rossetti, Koga, & Mano, 1993; Rossetti, Desmurget, & Koga, 1998). In this experiment, subjects were asked to point as fast as possible toward visual targets. Finger trajectory and eye movement analysis showed that subjects took into account terminal errors (knowledge of results) in the processing of the next movement

in the sequence. Subjects could initiate their pointing in the appropriate direction within a few trials exposure. However, the terminal part of their movements exhibited an ''attraction'' toward the virtual location of the target (displaced through the prisms), which resulted in an increased path curvature. A dissociation was thus observed between the initial movement direction, which subjects could easily update between trials, and the terminal movement direction which escaped this updating. Terminal movement direction was indeed subjected to an automatic sensorimotor processing driving the hand off the physical target (i.e., toward the seen virtual target). Trajectory analysis revealed that this automatic processing may be based on an on-line comparison of the proprioceptively defined hand position with the visually defined target location.

Still another example of nonconscious integration of sensory information used for action is provided by studies on the encoding of hand position prior to movement onset (Prablanc, Echallier, Jeannerod, & Komilis, 1979; Elliott, Carson, Goodman, & Chua, 1991; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994; Desmurget, Rossetti, Prablanc, Stelmach, & Jeannerod, 1995). Although subjects are not aware of using visual information about their hand prior to movement, they perform with better accuracy when this information is available. This implicit use of visual information was best demonstrated when view of the hand was displaced by wedge prisms, whereas the target, located outside the prism field, was seen normally (Rossetti, Desmurget, & Prablanc, 1995). Subjects performing pointing movements without sight of their moving hand exhibited a pointing bias reflecting their implicit use of visual information about hand position prior to movement. Interestingly, another study demonstrated that pointing accuracy was degraded when the view of the hand was removed 2s prior to movement onset (Elliott et al., 1991), suggesting that such information has to be used immediately. Similar experiments can be performed by altering proprioceptive input about hand location, by vibrating an arm muscle tendon shortly prior to movement onset (Velay, Roll, & Rossetti, unpublished). It is known that tendon vibration induces illusory motion of the adjacent joint. An interesting effect of time was again reported, since this illusory effect of the vibration needs more time to develop than the effect observed on pointing.

Gentilucci, Daprati, Toni, Chieffi, and Saetti (1995) designed an implicit learning experiment in which subjects had to grasp a cylinder without seeing their hand. Visual information about the object was provided in a mirror, so that the apparent visual size of the object could be dissociated from its actual size encoded through repeated grasping movements. Although the experimental manipulation of the cylinder to be grasped did not reach subject's awareness, measurement of the movement grasp parameters were affected by object size, in such a way that subjects adapted their grip size to the actual size of the grasped object. This experiment suggested that a motor representation of the object could be implicitly constructed from somaesthetic inputs.

Conclusions. All experiments summarized in this section suggest that an implicit use of various sources of sensory information can be made before and during goal directed movements. Extension of the double-step paradigm to arm movements led to the hypothesis that the saccadic suppression effect assessed only a cognitive component of the visual system. The paradigm of fast motor corrections, applied to both reportable and nonreportable target or sensory perturbations, further suggests that

the neural pathways leading to visual awareness are distinct from those involved in visuomotor processing.

2.2.2. Visual Illusions

Another means to distinguish between perceptual and motor responses to visual stimuli is to take advantage of visual illusions. The main idea is that visual perception would be more sensitive to illusion than the visuomotor behavior. Substantial experimental support for this hypothesis can be found.

When a large structured background is displaced during visual fixation of a small target, the latter appears to move in the opposite direction. This phenomenon can be observed for both smooth (induced motion) and step (induced displacement) background shifts. Bridgeman, Kirch, and Sperling (1981) replicated a finding made on eye movements (Wong & Mack, 1981) and compared the amount of perceptual illusory effect with the pointing response to the extinguished target. They showed that the motor system was much less affected by the apparent motion than was the ''cognitive'' system. It was concluded that apparent target displacement affected only perception whereas real target displacement affected only motor behavior, which provides a case for a double dissociation between ''cognitive'' and motor function. Interestingly, a detailed subject-by-subject analysis of a similar experiment showed that only half of the subjects exhibited a motor effect of the visual illusion (Bridgeman, 1991). This observation became all the more interesting when it was observed that interposing an 8 s delay before the response forced all of the subjects to use spatial information that is biased by the perceptual illusion, again replicating the finding made on eye movements (Wong & Mack, 1981). This result suggested that subjects may switch from motor to cognitive modes of sensory processing at differing delays after stimulus offset.

Aglioti, DeSouza, and Goodale (1995) made use of size-contrast illusions (Titchener's circle illusion) to explore the effect of visual illusion on a grasping action. In the Titchener's circle illusion, two circles in the center of two circular arrays each composed of circles of either smaller or larger size, appear to be different in size even though they are physically identical. The circle surrounded by larger circles appears smaller than the one surrounded by smaller circles. Using this principle, one can build configurations with central circles of physically different sizes that will appear perceptually equivalent in size. Using this smart version of the illusion adapted in pseudo-3D, Aglioti et al. required subjects to grasp the central circle between thumb and index finger and measured their maximal grip aperture during the reaching phase of the movement. Strikingly, they observed that grip size was largely determined by the true size of the circle to be grasped and not its illusory size. In a later study, Haffenden and Goodale (1998) compared the scaling of the grasp to a matching condition, in which subjects had to indicate the central circle size with thumb and index finger without reaching it. The effect of the illusion on the matching task was very similar to the mean difference in actual size required to produce perceptually identical circles, whereas it was significantly smaller in the grasp condition. This result suggests that matching object size with the fingers relies on an object representation similar to the perceptual representation. By contrast, the motor representation for grasp remained much less affected by the illusion.
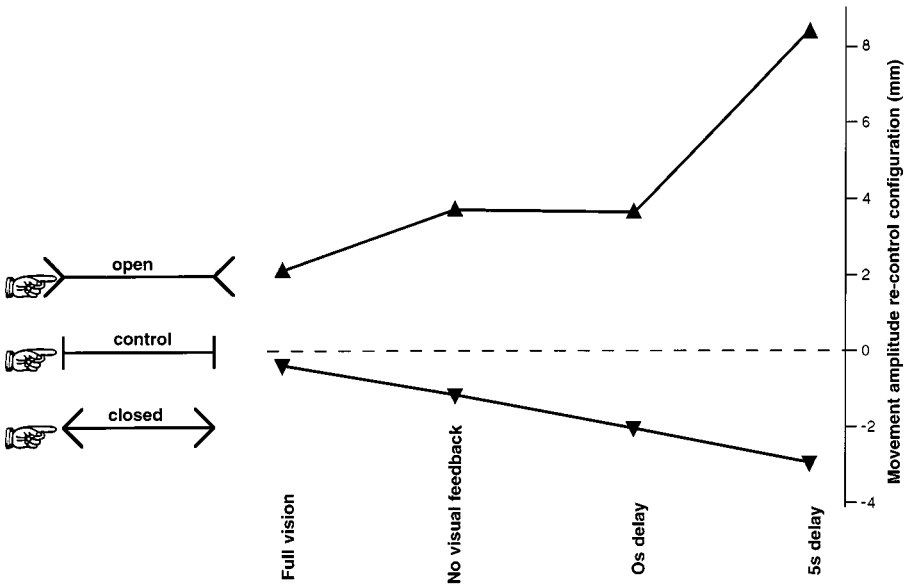
FIG. 2. Visual illusion and action. Pointing biases induced by the two configurations of the Müller-Lyer illusion. Movement amplitude tended to increase in the open configuration and to decrease in the closed configuration, i.e., in the same direction as the perceptual illusion. Values plotted on this figure were normalized by subtracting the value obtained for the control configuration. The effect of the illusion on pointing was very weak in the full vision condition. It is noticeable that the effect of the illusion on movement amplitude increased when less information was available to the subject and when a delay was introduced between the stimulus presentation and the response. (*adapted from Gentilucci, Chieffi, & Daprati, 1995*)

An elegant experiment was performed by Gentilucci, Chieffi, and Daprati (1995) to explore the effect of static visual illusion on pointing behavior (see Fig. 2). The Müller-Lyer illusion induces the perception of longer or shorter length of a line ended by arrows and has been widely used by psychologists and philosophers to argue about the cognitive penetrability of visual perception. When the two arrows are directed to the center of the line, it appears shorter. When they are oriented away from the line, it appears longer. Gentilucci et al. compared pointings made from one to the other end of lines ended by the two types of arrows used in the Müller-Lyer illusion, the subject having to look at the figure for two seconds prior to initiating his movement. Mean endpoints were significantly, though slightly, influenced by the visual illusion, so that movement distance was increased or shortened by a few millimeters, according to the type of illusion produced (see Fig. 2). As in the Haffenden and Goodale (1998) study, the influence of this illusion on the goal-directed action was much less than its perceptual effect, because this latter usually ranges about 20% of the physical line length (Rossetti, unpublished). Interestingly, early movement kinematics were altered, which suggests that the illusion affected even the programming of the movement and not only its final execution. In addition, Gentilucci et al. showed that introducing delays between line observation and onset of movement proportionally increased the illusion effect on the pointing. These findings are very

reminiscent of the idea that perceptual representation can influence the sensory processing devoted to action (Bridgeman et al., 1981). It is also very interesting to notice that this influence becomes particularly noticeable as the delay between stimulus presentation and movement onset increases.

All experiments reported here provide evidence that visual illusions affect perception more intensely than motor behavior. They also raise an interesting point about the effect of the delay in responding to the stimulus. There is a clear convergence of several experimental paradigms to demonstrate that the effect of the illusion on motor behavior is strongly increased when the response delay increases.

2.2.3. Visual Masking

Visual masking has been used as a probe to study conscious experience and cognition (e.g., Price 1998), and may explain some of the effects observed during saccadic suppression (Matin, Clymer, & Matin, 1972). Let us consider here some more specific implications of masking for action control. Taylor and McCloskey (1990) investigated the triggering of preprogrammed motor responses to masked stimuli. Three stimuli were tested: one *small* central LED with a 5 ms pulse, a *large* stimulus composed of the central LED plus four surrounding LEDs, and a *sequential* stimulus, where the central LED was shortly lit 50 ms prior to the onset of the surrounding LEDs. This last stimulus could evoke both metacontrast (masking by a surrounding shape) and background masking (masking with a subsequent light of greater intensity than the small test light). Three motor responses of various complexity (from a single muscle group contraction to a predetermined movement sequence) were used. Reaction times (RT), as measured by EMG, were not affected by the masking of the small stimulus in the sequential condition. Comparison of RTs obtained for the large and for the sequential stimulus showed that motor response registered in the sequential condition was triggered by the short small stimulus preceding the masking surrounding. Although the simple response evoked a shorter RT, a similar effect of the masked stimulus was observed for the three types of movements tested. This experiment thus confirmed that motor reaction to a visual stimulus can be dissociated from the verbal report about detection of this stimulus (see also Fehrer & Biederman, 1962). As stated by Taylor and McCloskey (1990, p. 445), ''the ability to react to such stimulus with a voluntary movement implies that sensory processing during reaction time does not have to be completed before motor processing can commence.'' Indeed, motor RTs are usually shorter than the 500 ms delay that may be required before a conscious sensation can be elicited. Although these results confirmed that unconscious operations proceed faster than conscious ones, they cannot tell whether conscious perception and motor reaction are processed on parallel pathways with different thresholds, or whether these two responses can be elicited at different stages of serial sensory processing.

It appears that masking and metacontrast affect conscious perception of the stimulus, although the ability to trigger a motor response remains largely intact. Neumann and Klotz (see 1994) have specifically explored several aspects of this phenomenon. They showed that similar effects can be observed on RT (measured by key pressing) even in a two-choice situation that required integrating form information with posi-

tion information. In addition, this priming effect influenced error rate as well as speed of the motor response, and could appear despite the use of variable stimulus–response couplings, showing that it is not restricted to preprogrammed responses.

The above results clearly questioned the classical sequential conception of sensory information processing for action. The psychophysical approach to the problem of sensorimotor coordination also suggests that early communication takes place between sensory and motor systems (Nandrino & El Massioui, 1995). This hypothesis was tested on auditory evoked potentials by requiring subjects to press a key with the left or the right hand in response to high and low tones presented dichotically. The main stages of information processing, target feature extraction, response choice, and motor adjustments can be respectively affected by stimulus degradation, stimulus–response compatibility, and presence or absence of a preparatory period. Manipulating these three variables may, therefore, specifically affect early or late components of event related potentials. However, an early interaction between stimulus degradation and preparatory period was observed, which suggests an overlapping of feature extraction and motor adjustments phases. This study provides additional support for the possibility that motor responses can be prepared prior to the completion of stimulus-processing.

2.2.4. Conclusion

Three main conclusions can be drawn from the above experimental data. First, experiments on oculomotor and arm movement control demonstrate that an unconscious integration of visual information can take place during a simple action, and that an unconscious use of proprioceptive information can be made despite contemporaneous conflicting visual information. Second, masking experiments and visual illusions show that object perception can be dissociated from visuomotor processing of the same object. Third, several results suggest that the time required to elicit a motor response may be shorter than the delay observed between a stimulus occurrence and conscious awareness of this stimulus.

3. DISSOCIATION BETWEEN CONSCIOUS PERCEPTION AND ACTION IN BRAIN-DAMAGED PATIENTS

One of the most striking dissociations between conscious and nonconscious processing observed in neuropsychology is blindsight (see reviews in Weiskrantz, 1989; Adams, Bodis-Wallner, Enoch, Jeannerod, Mitchell, 1990; Farah, 1994; Milner & Goodale, 1995). After a lesion of primary visual areas, patients report no visual experience in the whole or part of their visual field. However, some of them can still indicate the location of a contrasted visual stimulus through an eye or an arm movement (e.g., Pöppel, Held, & Frost, 1973; Perenin & Jeannerod, 1975). This phenomenon has raised new conceptions of extra-geniculostriate vision in humans, and provided a model for questioning the neural and phenomenal bases of consciousness (see Weiskrantz, 1991; Dennett & Kinsbourne, 1992; Lahav, 1993; Stoerig & Cowey, 1993; Block, 1995). The discovery of a tactile equivalent of blindsight is more recent, but it has also stimulated both theoretical and empirical work (e.g., Lahav, 1993).

3.1. Blindsight

The discovery of the so-called blindsight phenomenon has been made in a specific context of the knowledge about visual processes and, in particular, about residual visual functions in monkey (Humphreys & Weiskrantz, 1967). The search for functional dissociations within the animal visual system resulted shortly prior to the discovery of blindsight. The idea of a cortical ''focal vision'' and a subcortical ''ambient vision'' proposed by Trevarthen (1968) to account for dissociations observed in split-brain monkeys, and that of cortical blindness (impairing the ''What is it?'' system) and tectal blindness (impairing the ''Where is it?'' system) proposed by Schneider (1969) to account for observations made on rodents with occipital or tectal lesions, emerged a few years prior to the first report of blindsight (Pöppel et al., 1973).

3.1.1. Historical Context

The early publications about blindsight described patients with lesions of the primary visual cortex, who exhibited remarkable residual capacities to orient their gaze or to direct their hand toward targets presented within their blind hemifield (Weiskrantz, Warrington, Sanders, & Marshall, 1974; Perenin & Jeannerod, 1975). Following the distinction made earlier in animal experiments (Schneider, 1969), this residual function was attributed to subcortical vision. The lack of awareness implied that patients usually felt like they were guessing, and was compatible with the idea that subcortical vision is unconscious. Indeed, similar results were then replicated in hemi-decorticated subjects (e.g., Perenin & Jeannerod, 1978).

However, the two visual systems model, as championed by Schneider (1969), was rapidly challenged by new experiments and proved to be unsatisfactory (for a review, see Jeannerod & Rossetti, 1993, p. 442; Milner & Goodale 1993, p. 317). Another conception of vision as a dissociable function appeared that considered both modes of vision as mediated by corticocortical pathways: the **where** function would depend on a dorsal stream projecting from primary visual cortex to posterior parietal lobule, and the **what** function on a ventral stream from primary visual cortex to inferotemporal cortex (see Mishkin, Ungerleider, & Macko, 1983). This well-known distinction has, however, not received unconditional support from electrophysiological and, especially, neuropsychological data (see Jeannerod & Rossetti, 1993, p. 443; Milner & Goodale, 1993, p. 317). The most recent experimental evidence is now converging toward a new interpretation of the cortical systems which emphasizes the final products of vision (see Fig. 1, middle panel). It is now argued that the inferior parietal lobule of primates, rather, provides a set of modules specialized for visually directed action, whereas the inferotemporal cortex is primarily concerned with object recognition. The dorsal pathway would thus be concerned with **pragmatic** motor representations about **''how''** to act toward an object, and the ventral pathway would be involved in building more semantic representations about **''what''** the object is, in which the object appears as an identifiable identity (see Goodale & Milner, 1992; Jeannerod & Rossetti, 1993; Milner & Goodale, 1993; Jeannerod, 1994a).

Let us review some of the recent neuropsychological evidence that has prompted a reappraisal of the respective functions of the two cortical pathways and that will be crucial for interpreting the blindsight phenomenon. Patients with optic ataxia,

following a lesion of a restricted area of the posterior parietal lobule, have difficulties in directing actions to objects seen in peripheral vision, although they are not impaired in the recognition of these objects (Jeannerod, 1986; Perenin & Vighetto, 1988; Jakobson, Archibald, Carey, & Goodale, 1991). They exhibit deficits not only in their ability to reach toward the object, but also in adjusting the hand orienting and shaping during reaching. These results strongly suggested that the posterior parietal cortex plays a crucial role in the organization of object-oriented actions, whether the visual processing required for a given action is concerned with spatial vision (location) or with object vision (size or shape) (see Jeannerod, 1988; Jeannerod & Rossetti, 1993). Interestingly, a reciprocal dissociation was reported by Goodale, Milner, Jacobson, and Casey, (1991) in a patient (D.F.), who developed a profound visual-form agnosia following a bilateral lesion of the occipitotemporal cortex. Strikingly, despite her inability to perceive the size, shape, and orientation of visual objects, D.F. performed quite accurately when instructed to perform movements toward these objects. This observation suggests that, during action, D.F. could still process visual information about the objects' intrinsic properties she could not perceive. Optic ataxia and visual agnosia patients clearly make the case for a double dissociation between perceptual recognition of objects and object-oriented action. It may be emphasized here that D.F. had her primary visual area spared. As a consequence, processing of visual information may have been disrupted only in the ventral pathway and spared in the dorsal pathway, which would explain why she could perform visual directed movements. The question, therefore, arises whether blindsight patients with V1 lesions would also exhibit a similar dissociation between perception and action.

3.1.2. Blindsight in Action

Although various residual functions have been reported in cortically blind hemifields, the majority of them are related to extrinsic properties of objects, that is, mainly location and motion (cf. Weiskrantz, 1989; Adams et al., 1990; but see Stoerig & Cowey, 1992). Research on this phenomenon may, however, become even more interesting if we examine their performance on tasks that have been used in optic ataxic patients. It can be predicted that, since patients with V1 lesions showed an ability to direct an eye or an arm movement toward a target presented within their ''blind'' field (and thus not consciously seen), they may also be able to process unconsciously

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FIG. 3. Dissociation between identification and action in blindsight. Patient P.J.G. presented with a complete right hemianopia (see his brain imagery and visual field amputation). He was tested for his ability to distinguish between four stimulus orientations by several responses. The stimulus was a 18 × 3 cm slot presented 20° left from fixation point in the vertical black panel facing the subject. The slot was bordered by two bright white stripes, producing a high contrast with the vertical panel. It was rotated between each trial and presented in each of the four possible orientations (0, 45, 90, 135°) in a random order. Eye fixation was controlled during each trial. Verbal response was a forced choice between the four possible orientations displayed on a sheet of paper. Matching response consisted in showing the orientation of the target with wrist movements. Reaching response was a natural aiming movement to the target, similar to posting a card in a mail box. Performance was assessed by computing the correlation between the slot orientation and the hand orientation, and a significant relationship was observed only in the motor task. (*adapted from Perenin & Rossetti, 1996).*
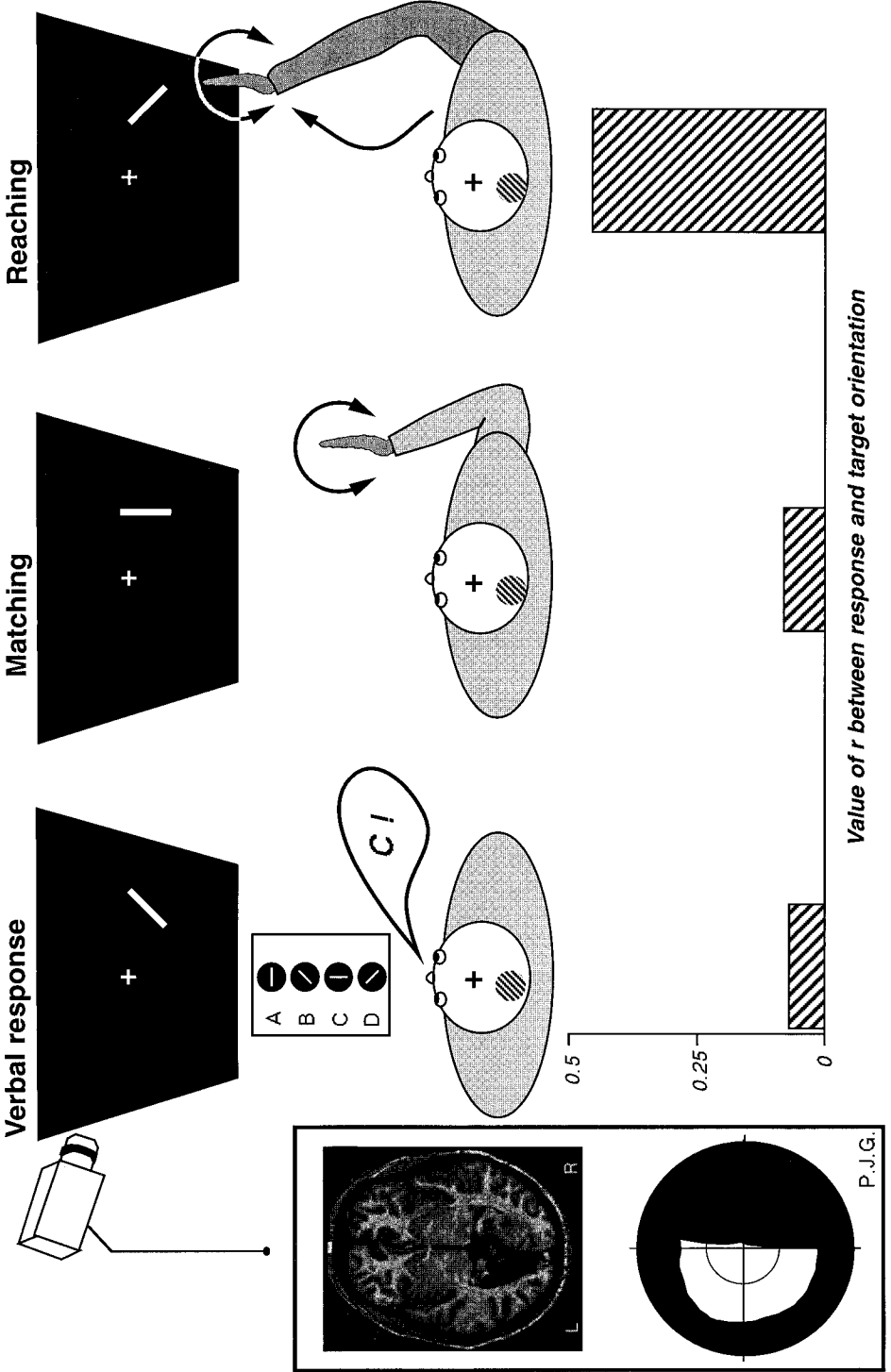
orientation, size, or shape or visual stimuli during action. Indeed, the useful parameters of objects, whose processing is required for guiding an action, include metric properties of an object other than its direction and distance. The following series of experiments was designed to test whether this prediction about action in blindsight patients can be verified.

In these experiments, several patients were tested for their ability to process orientation or size of visual objects. They were presented with slots of variable orientation or with rectangular objects (of equal surface) but variable horizontal length. Their performance was assessed in three kinds of tasks (see Fig. 3). In a **verbal** task, they were asked to produce forced-choice verbal guesses about stimulus orientation or size. In the **motor** task, they had to insert a card in the orientable slot or grasp the rectangle between thumb and index finger. In addition, they had to perform a **matching** task, in which they were asked to match the slot orientation by wrist prosupination movements, or to match object horizontal size with their thumb–index grip. Performances were recorded on videotapes and analyzed frame by frame (spatial accuracy was 0.5 cm).

One of these patients (P.J.G.) was a 32-year-old man who presented with a complete right hemianopia due to a left medial occipital lesion (see Fig. 3; see Perenin & Rossetti, 1996). He could discriminate motion direction in his hemianopic field (Perenin, 1991), but remained unable to discriminate between simple geometric forms (e.g., circles vs. triangles). When instructed to perform each of the three tasks with his left hand in the normal visual field, he performed as well as healthy subjects for either of the two types of stimuli. When required to perform on the right side, he first explained that he could not perform the task since he did not perceive the stimuli. After several encouragements, he agreed to perform the task, performing verbal guesses and making movements ''by chance.'' Performance of P.J.G. in the orientation task is displayed in Fig. 3. The verbal guesses and the matching responses were at chance. However, a significant relationship between the slot orientation and hand orientation was obtained for the reaching responses ($r = .463$, $p < .005$). It should, however, be mentioned that, since he made consistent error in reaching toward the panel, P.J.G. never succeeded in introducing the card into the slot, even when it was well oriented (Perenin & Rossetti, 1996).

Similar results were obtained when P.J.G. had to grasp the horizontal objects. While he performed randomly in the verbal and matching tasks, his maximal finger grip aperture (measured during the transport phase) and his final grip aperture (measured at the time of contact with the horizontal panel) were both significantly correlated with the actual object size (rs $> .414$, ps $< .01$) (Perenin & Rossetti, 1996).

Another patient (N.S.) did not exhibit the constant offset in the final position shown by P.J.G. and was able to introduce the card into the slot, to her own surprise (9 trials ''in the slot'' out of 40 trials, without being informed that only four orientations were used) (Rossetti, Régnier, Perenin, Rode, Lacquaniti, & Boisson, 1995). As P.J.G., she performed at chance level when asked to perform a verbal or a matching task.

These data provide a further instance of dissociation between two modes of visual processing (knowing what the object is vs. how to grasp it). They indicate that the neural pathway responsible for space representation in action (or pragmatic represen-

tation) is much less dependent on V1 input than is the pathway involved in visual discrimination, identification, and perceptual awareness (see also Stoerig, Hübner, & Pöeppel, 1985). This hypothesis is strongly supported by recent neurophysiological findings in the monkey. Indeed, selective brain cooling applied to V1 only partially affected the activity of visual areas (MT and V3A) that constitute the main input to the dorsal pathway, whereas it suppressed the visual activity of the ventral stream (see reviews in Bullier et al., 1994; Girard, 1995). These results provided further argument that neuronal activity of the dorsal pathway may arise from subcortical inputs such as colliculus and pulvinar (see Cowey & Stoerig, 1991; Bullier et al., 1994), and are likely to explain the ability of blindsight patients to process orientation and size to build a pragmatic representation of the goal to achieve.

3.2. Numb-Sense[1]: The Sense of Touch

About ten years after the discovery of blindsight, a case of implicit processing of somatic sensation following a lesion of central somatosensory areas was reported (Paillard et al., 1983). The patient was fully anesthetized at the forearm level and could not report any tactile experience. However, she could point with her healthy hand to a location stimulated on the ''deafferented'' forearm. At that time, this result was interpreted as a tactile analog of blindsight, i.e., as a dissociation between localization and identification. Other related observations have been described (Volpe, Ledoux, & Gazzaniga, 1979; Weiskrantz & Zhang, 1987; Lahav, 1993; Brochier, Habib, & Brouchon, 1994). These ''numb-sense'' observations have raised several questions relative to the type of representation involved in motor performance (cf. Rossetti, Rode, & Boisson, 1995). Indeed, several interpretations can account for it: dissociations between conscious–unconscious, motor vs. verbal, 'What' vs. 'Where,' or 'What' vs. 'How' can be evoked (cf. Ettlinger, 1990).

A patient (J.A.) with a lesion of the thalamic relays of somaesthetic afference allowed us to test these hypotheses. His lesion (left ventrolateral and ventroposterolateral nuclei) is shown in Fig. 4. The tactile and proprioceptive deficit was complete on the right side of the body and so stable that the patient could be tested over several years. To test J.A.'s tactile ability, stimuli were delivered to his right forearm and hand with the tip of a pencil, and left in place until the patient initiated his response. The investigator randomly stimulated locations that had been demonstrated on the left normal arm prior to the session. Since the patient did not feel the stimuli applied, he had to be instructed when to produce his response. No information was provided to the patient about his performance during the experiment. However, given the lack of explicit localization information, considerable encouragement was required.

The first experiment investigated J.A.'s ability to locate tactile stimuli applied to his right hand. The patient was blindfolded and motor and verbal performances were compared. Motor responses involved pointing movements using the left index finger. Verbal responses were obtained by a forced-choice paradigm where the patient chose between stimulus locations that were shown to him before the test. When guesses were made by a pointing movement of the left hand to the stimulated right arm
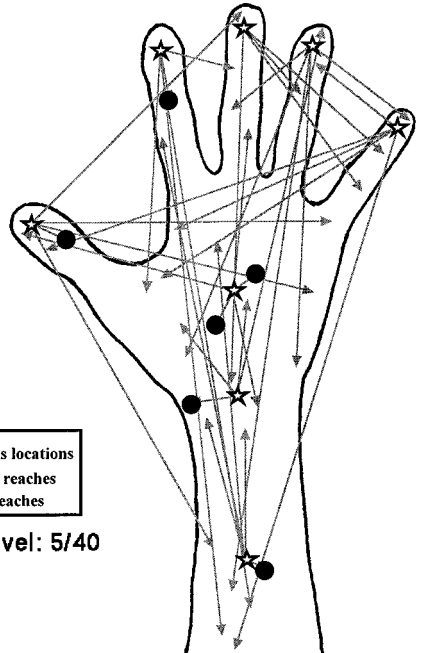
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[1] The term ''numb-sense'' was preferred to ''blind-touch'' following stimulating discussions with Marc Jeannerod and Semir Zeki.

J.A.

**: Stimulus locations
●: Correct reaches
▲: Other reaches
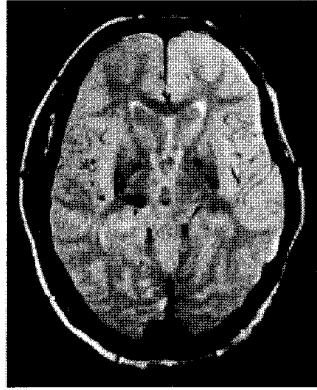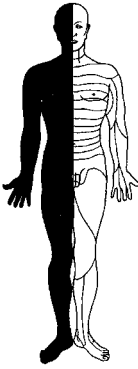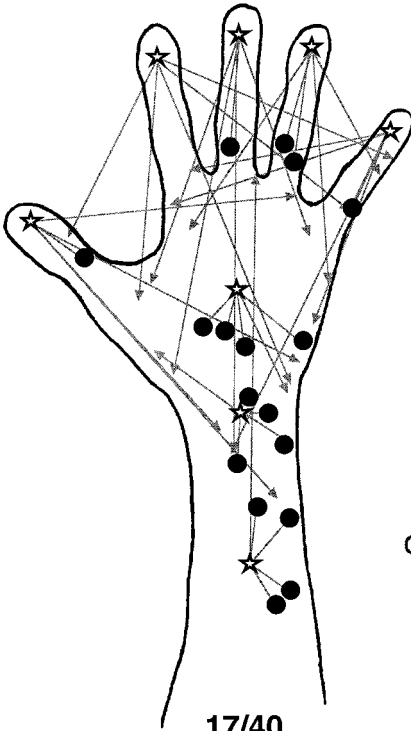
Chance level: 5/40

17/40
SIMPLE
POINTING

6/40
POINTING
ON DRAWING

(pointing-on-arm condition), he consistently performed well above chance level. Several sessions demonstrated that his performance improved when more distal areas were tested on the arm (from shoulder to hand) and when the number of possible stimuli was higher (from 3 to 8). Figure 4 provides an example of results obtained with 8 stimuli. The verbal forced-choice paradigm demonstrated that the deficit exhibited by J.A. could not be explained by simply a conscious–unconscious dissociation since verbal guesses were made randomly.

Second, we compared pointing responses made in different conditions, which involved distinct levels of representation. In order to test whether the somatic sensation was processed only for motor interaction with the stimulus or if it had also a value for proper location perception, we used another pointing response which was not directed to the stimulus. In this experiment, a drawing of an arm (scale 1) was placed on the table 20 cm left of his hidden, stimulated right arm. J.A. was then asked to point on the drawing to the point matching the location of the stimulus applied to the arm. In this condition, he had to know ''Where'' to point instead of simply knowing ''How'' to point, as was the case in the pointing-on-arm condition. Comparison of the two conditions showed clearly that the patient could not perform accurately in the pointing-on-drawing condition (see Fig. 4).

In the same way that a neuroanatomical basis has been proposed to account for blindsight (cf. Bullier et al., 1994; Girard, 1995), it is interesting to consider the possible pathways that are compatible with numb-sense (see Fig. 5). Besides the main pathway from the ventro-postero-lateral nucleus of the thalamus to the primary somatosensory cortex, another pathway links the posterior nucleus of the thalamus to the posterior parietal cortex of the monkey (see Jones, 1985; Martin, 1985). The parietal opercular region (second somatosensory area) would be responsible for ''object touch,'' whereas the posterior parietal areas would mediate ''spatial touch,'' and can be considered as analogs of the visual posterior parietal and inferotemporal areas respectively (Mishkin, 1979; Ettlinger, 1990). Interestingly, these two regions are also highly interconnected (e.g., Pandya & Seltzer, 1982; Neal, Pearson, & Powell, 1987). When the main pathway is lesioned, as in patient J.A., the other pathway may still provide information to the areas processing spatial information and projecting to the premotor cortex.

3.3. Numb-sense: the Sense of Proprioception

Patient J.A. was also tested for his ability to process proprioceptive information (Rossetti, Rode, & Boisson, 1995). As for touch, J.A. was blindfolded. A tablet was

FIG. 4. Numb-sense: a tactile equivalent to blindsight. Patient J.A. was fully deprived of right-side tactile and proprioceptive sense after a left thalamus VL-VPL lesion (higher panel). Clinically, no tactile stimulus could be detected or located on his right body. He was then blindfolded and instructed to perform a pointing movement with the left normal hand toward the locus stimulated (stars) on the right hand. To assess his performance, we assigned the value 1 or 0 to each trial, respectively, for correct and incorrect responses, i.e., inside vs. outside the stimulated territory (e.g., the whole finger in the case of fingertip stimulation). Although his errors (arrows) were much greater than in normals, he could perform strikingly well above chance level ($p < .001$) (lower panel). By contrast, when he had to make a similar pointing movement toward a picture of his right arm (the right arm being hidden from his view), he performed at chance level. In addition to the dichotomous correct–incorrect evaluation of the performance, the distance between each stimulus and the corresponding responses was measured, and significantly increased in the pointing-on-drawing condition. (*from Rossetti, Rode, & Boisson, 1995*)
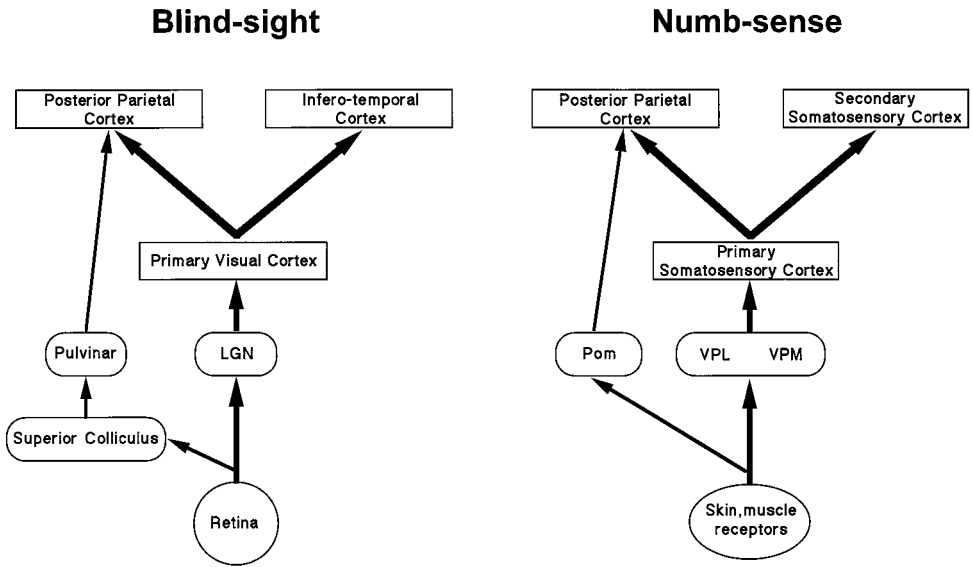
Blind-sight   **Numb-sense**

FIG. 5. Anatomical pathways bypassing primary sensory areas for vision and touch. Blind-sight and numb-sense observations raise the interest for finding sensory pathways bypassing the primary areas. Such pathways can be isolated within the central sensory networks described for both visual and somatic systems. The lateral geniculate nucleus (LGN), the medial region of the posterior nucleus (Pom), the ventrolateral nucleus (VL), the ventroposterior lateral nucleus (VPL), and the ventroposterior medial nucleus (VPM) are thalamic nuclei. Square boxes indicate cortical areas. Thickness of the arrows reflects the probable importance of projection for driving neurons in the target area in the absence of lesion.

The main thalamic projection to the primary sensory areas can be bypassed by a subcortical–cortical projection to the posterior parietal cortex for vision, and a projection from Pom to posterior parietal cortex for touch. Although the temporal cortex may play a role in object touch (Keating & Horel, 1971), there are similarities between the properties of inferotemporal cortex in vision and SII cortex in touch (Mishkin, 1979; Ettlinger, 1990). Patients P.J.G. and N.S., described in this review, had lesions of the primary visual cortex, whereas patient J.A. had a VPL lesion. The ability of these patients to perform an action toward an undetected stimulus may be sustained by these secondary pathways. *(Drawn from data found in Jones (1985: chap. 11); Martin, 1985; Garraghty et al., 1991; Bullier et al., 1994).*

used above which the patient's right fingertip was positioned. Figure 6 shows the results obtained in the pointing condition. (The pointing + verbal condition depicted in Fig. 6 will be described in the following.) The right, numb arm was manipulated by the investigator in such a way as to place the right index fingertip on one of two locations. In order to avoid interference between tactile and proprioceptive information processing, attention was paid to provide the arm with as little tactile stimulation as possible. Since no conscious processing of arm proprioception was available to J.A., two guessing responses were evaluated. In one session, he was asked to point underneath the tablet to the point corresponding to his right target-fingertip location. In another session, J.A. was asked to guess verbally whether his target-fingertip was on the right or on the left location. J.A. was significantly influenced by the target-finger locus in the pointing task only (Fig. 6, pointing condition). In contrast, the distribution of verbal forced-choice responses was not significantly different from a random distribution.
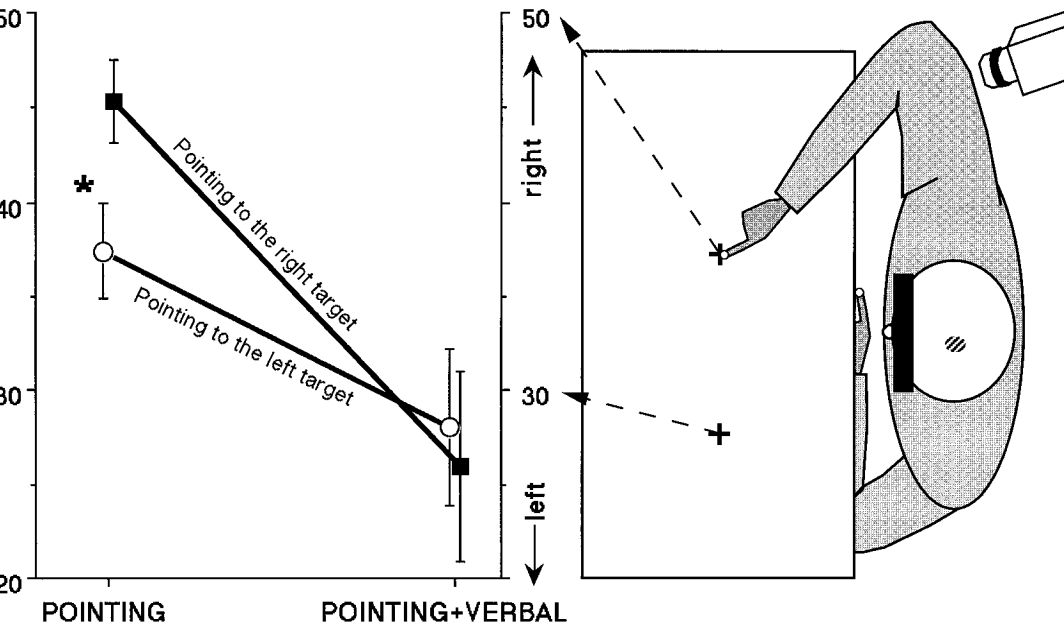
FIG. 6. Interference between pragmatic and semantic representations in numb-sense. Patient J.A. was tested for his ability to process proprioceptive information. He was asked to locate proprioceptively defined target locations encoded with the left arm. Two locations were tested. When asked to produce a forced-choice verbal response (left vs. right) about the target, he performed at chance level.

When J.A. was asked to perform a pointing movement with the right hand underneath the table, he performed above chance and could discriminate between the two positions (POINTING condition). Despite the high variability found in the pointing responses, the difference between the pointings made toward the left target and toward the right target reached statistical significance. When he was required simultaneously to point to the target and to provide a verbal response, his performance was dropped to chance level, and he could no longer discriminate between the two loci (POINTING + VERBAL condition). Simultaneous activation of the pragmatic and the semantic representations thus produced a deleterious effect on the motor performance. *(from Rossetti, Rode, & Boisson, 1995).*

3.4. Conclusion

The failure of these patients to perform above chance in the verbal forced choice condition shows that sensory information (visual, tactile, proprioceptive) may be processed, not only implicitly, but also specifically for motor purposes. Therefore, these results can be interpreted as a dissociation between a motor system responsible for the stimulus-driven pointing and a semantic system responsible for the verbal depiction of the same stimulus location (see Perrig & Hofer, 1989). A similar kind of dissociation has been previously proposed between a What system, responsible for a semantic processing, and a How system, responsible for a pragmatic processing (Goodale & Milner, 1992; Jeannerod & Rossetti, 1993; Milner & Goodale, 1993; Jeannerod, 1994a). It is now accepted that the posterior parietal cortex is primarily involved in visual processing for action purpose (see also Jeannerod, 1994b; Rizzolatti, Riggio, & Sheliga, 1994; Sakata & Taira, 1994). By contrast, the dissociation

observed in the present case holds for stimulus location (i.e., Where vs. How) instead of stimulus intrinsic qualities (i.e., What vs. How), and can be described for both tactile and proprioceptive stimuli. This view is strengthened by the results obtained when J.A. pointed on the arm drawing. In this case, he had to produce the same pointing movement, but combined with a more elaborated representation of where the stimulus was applied, and consequently his performance was reduced to chance level. The dissociation observed here would, therefore, not result from the difference in the response provided (pointing vs. verbal), but from the difference between the representations underlying the responses (How vs. Where). This dissociation fits with the more general description of sensorimotor and representational modes of spatial information processing that would respectively use a body-centered and an environmental frame of reference (see Paillard, 1991). Following Paillard's hypothesis, J.A. appears unable to process the tactile information at levels higher than a direct sensorimotor system, i.e., at more symbolic levels, as was the case in the matching task used with Goodale et al.'s patient D.F. and Perenin and Rossetti's Blindsight patients. The following section will further demonstrate that attempts to make use of a more elaborated representation of the stimulus will disrupt these patients' implicit sensorimotor ability.

4. INTERACTION BETWEEN CONSCIOUS PERCEPTION AND ACTION IN BRAIN-DAMAGED PATIENTS

All the neuropsychological data provided in the previous section support the hypothesis of a dissociation between two streams of sensory processing, respectively devoted to perception and action. However, the degree of anatomical segregation between the dorsal and the ventral pathways remains questionable. Indeed, neuroanatomical connections have been described between the occipito-parietal and the occipito-temporal pathways (e.g., Morel & Bullier, 1990 (see Fig. 1, lower panel); Knierim & Van Essen, 1992). In addition to these direct or indirect anatomical links, the two visual streams converge onto the superior temporal sulcus (Watson, Valenstein, Day, & Heilman, 1994) and onto several cortical areas of the premotor cortex, which results in two ''interconnected networks'' (Ungerleider, 1995; Bullier, Schall, & Morel, 1996; Boussaoud, di Pellegrino, & Wise, 1996). The above hypothesis of two dissociated representations of space may ''imply that the cortical mechanisms for object recognition and for object oriented action are selectively activated by the task in which the subject is involved'' (Jeannerod & Rossetti, 1993, p. 445). Indeed, the attention has been continuously focused on dissociation rather than interaction between the two modes of visual processing (e.g., Goodale & Milner, 1992). If this hypothesis holds true, then only one of the two types of representation may be activated at a single time. Alternatively, one may attempt to explore the possible functional interaction between pragmatic and semantic representations that could be allowed by the anatomical cross-connections between the dorsal and the ventral streams (Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994). In this context, it becomes interesting to underline the specific conditions in which each of the two types of processing is involved in order to better understand to what extent they

are dissociated. For 20 years, research on blindsight has been continuously exploring the extent to which stimuli can be perceived implicitly (position, movement, color, etc.). Because the discovery of new residual abilities in these patients was stressed over this period, the limiting factors of the implicit processing received less attention. Only a few attempts have been made to explore the limitation of the motor processing performed by patients deprived of the ability to identify objects. One main limiting factor seems to be the time constraints attached to the pragmatic representation. Another crucial factor may be found in experiments trying to simultaneously activate both types of representations.

4.1. Time Constraints

An interesting observation was made on a blindsight patient (N.S.) performing the task at different paces (Rossetti, Régnier et al., 1995). It was observed that N.S.' performance was first at chance level as she was reacting slowly to the stimuli. Performance improved significantly when movement latency decreased from about 500 ms (0 trial ''in the slot'' + 1 correctly oriented out of 40 trials) to about 300 ms (7 trials in the slot + 2 correctly oriented). This result suggests that sensory information responsible for blindsight in action is available only during a short period following stimulus presentation. An inverse relationship between the latency of the response and performance was also reported in another blindsight patient (G.Y.) in an experiment comparing several types of response with several delays (Marcel, 1993). It was found that the several detection reports made to identical trials could be dissociated. An eye blink response (latency about 290 ms) provided more accurate detection than did button press (latency about 365 ms). In addition, a speeded condition produced better performance in both motor responses. A similar observation was also made on the agnosic patient D.F., presented above. Although she was able to preshape her hand in flight, her grip size was no longer related to object size when a delay between object viewing and movement initiation was imposed (Goodale, Jacobson, Milner, Perret, Benson, & Hietanen, 1994).

The same effect of time was also observed for touch and proprioception (Rossetti & Rode, 1996). Patient J.A. demonstrated that latencies up to 1 s for tactile stimuli and up to about 4 s for proprioceptive stimuli were compatible with above-chance performance in motor tasks, but longer delays completely disrupted his performance (see Fig. 7). There is thus converging evidence arising from three sensory modalities that the pragmatic representation can only be expressed within a short delay following stimulus presentation.

These results may lead to a reinterpretation of the data obtained in the verbal and matching tasks. In spite of encouragement to perform faster, it took more time for subjects to respond in the verbal task or in the matching task (in some trials between 1 and 2 s) than it took in the reaching and grasping tasks (see Perenin & Rossetti, 1996). It could, therefore, be argued that time is the decisive variable for explaining the difference between the fast reaching and the matching tasks. However, results obtained with numb-sense are not compatible with this interpretation. Indeed, J.A. performed at chance level when asked to point on the arm drawing, although the latencies observed in these cases were shorter than 2 s. This result suggests that the
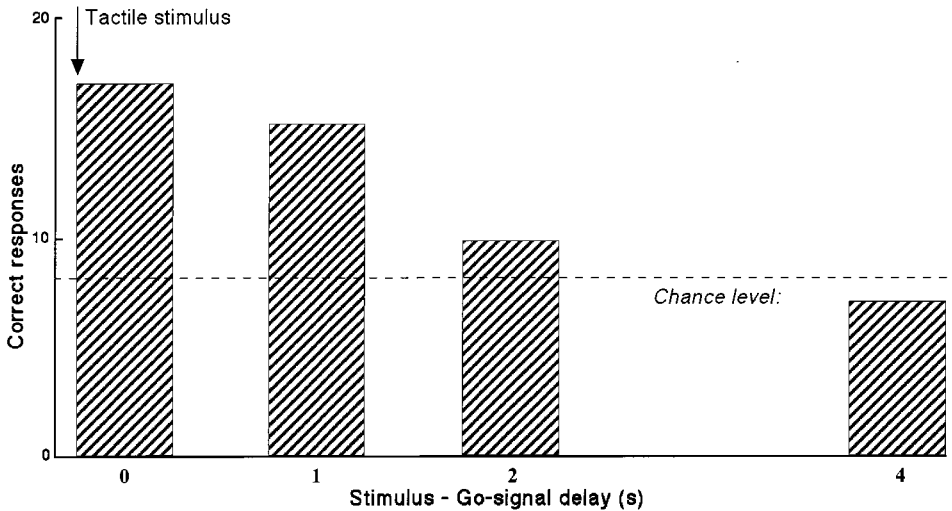
FIG. 7. Time and implicit perception: short-lived representations in numb-sense. This experiment was performed with the same methodology as in Fig. 4. Six locations of stimulus were used on the patient's left hand. Each stimulus was presented 8 times in a random order. Since J.A. was never aware of the stimulus, a delay could be added between stimulus application and the go signal provided to the patient. No information was provided to the patient about his performance during the experiment. The effect of four delays was investigated in separate sessions. The patient was able to perform above chance level for delays up to 1 s, but his pointing was not influenced by stimulus location for longer delays.

failure to perform above chance in the verbalization task cannot be due to a problem with time. In addition, experiments presented in section 5 will show that similar effects of verbalization and time can also be observed in healthy subjects.

4.2. Semantic–Pragmatic Interference

The deleterious effect of time on motor representations suggests that delayed actions may be based on more cognitive representations. Experiments were specifically designed to search for such a possibility. The logic of this paradigm, in contrast with the previous experiments, consisted of coactivating the two types of representation and then looking for effects on the patient's performance. In this experimental condition, patients were instructed to simultaneously produce a movement toward the stimulus and a verbal forced-choice response about the same stimulus. This task could be performed easily after little training, and the verbal response generally occurred during the second half of the arm movement. Three predictions could be put forward: (1) if there is a complete independence of the pragmatic and the semantic systems, then the verbal and motor responses will be performed without any modification of their respective performances; (2) if a transfer of information is possible from the pragmatic to the semantic stream, then the verbal response will become more accurate; (3) if a transfer of information is possible from the semantic to the pragmatic stream, then the previously accurate performance observed for the arm movement will disappear. Surprisingly, responses provided by the patients showed that the si-

multaneous task totally suppressed the ability to process implicitly the sensory information.

Patient N.S. could introduce the postcard into the slot of which she could not perceive orientation. When required to perform the same task again, but to guess aloud the orientation of the slot during the movement, her performance deteriorated considerably (1 vs. 9 trials in the slot) (Rossetti, Régnier, et al., 1995). In addition, no facilitation of the verbal response by the simultaneous pointing movement was observed. An observation possibly related to the competition between the two representations was also reported by Weiskrantz about blindsight (1989, p. 379): ''. . . it was actually better to use less salient stimuli to improve performance by switching the subject into an 'implicit' rather than an 'explicit' mode, in which [the patient] depended upon his real but non-veridical experiences.''

The effect of semantic–pragmatic coactivation was also investigated for touch and proprioception. In the tactile modality, J.A.'s pointing responses were at chance when he was required to produce the two responses at the same time (correct trials: 6/40 for 6 possible locations). There was a congruency between the pointing and the verbal responses in this condition. However, in addition, the mean distance between the stimulus and the response increased up to a similar value as when pointing on the arm drawing (Rossetti, Rode, & Boisson, 1995).

When the verbal and the pointing responses were produced simultaneously in the proprioceptive task (see Fig. 6), they always were congruent, but the pointing performance was reduced to random (17/40, $p > .10$). This was confirmed by the mean locations reached for the two locations explored: the mean pointing toward the left location was located right of the mean pointing to the right location. As for touch, activation of a semantic representation of where the target finger was (required for the verbal response) disrupted J.A.'s ability to point to this finger. Section five (5.2) will provide evidence that the interference effect does not appear when the verbal response is not specific to the representation of the goal.

4.3. Conclusion

When the pointing was delayed or associated with verbal responses about the stimulus for visual, tactile, or proprioceptive targets, the pointing performance was reduced to random. These findings first suggest that the implicit processing observed in these patients is specifically observed during aiming movements rapidly and directly oriented toward the stimulus. They also confirm that attempts to elaborate a semantic representation of the stimulus location can have detrimental effects on the relatively intact sensorimotor processing. Whether this may be due to interconnections or convergence between the dorsal and the ventral stream will be discussed further.

5. RELATIONS BETWEEN CONSCIOUS PERCEPTION AND ACTION IN HEALTHY SUBJECTS

Results obtained with visual illusions have raised the problem of the reference frame used to perform an action. It was suggested that the egocentric reference frame could only be used during a restricted delay following stimulus presentation. Observations made on patients also revealed that the representation of space at work shortly

after target presentation was likely to have a rather limited lifespan. Action requires an encoding of metric properties of objects. In particular, object location must be encoded relative to the body. In the external frame of reference used by the perceptual system, however, the same point has to be encoded, but as a part of the visual context. It is this visual context that can induce illusory perception. Consequently, we may apply the experimental paradigms used by the neuropsychological approach to healthy subjects to seek dissociation and interaction of the two frames of reference that can be used in action.

Relevant experiments performed by Graves and colleagues should be mentioned here (Meeres & Graves, 1990; Graves & Jones, 1992). Interestingly, these experiments were aimed at describing a possible analogue of blindsight in normal subjects. Short-duration masked patterns were presented tachistoscopically to subjects who were asked to produce three verbal responses indicating detection, identification, and localization of the stimulus. Their results showed strikingly that undetected stimuli could be localized by the verbal guesses. Although it is not directly related to action, this observation shows that attempts can be made to seek ''neuropsychological phenomena'' in normals, and that threshold for unconscious localization may be lower than for unconscious detection (cf. Price, 1998). It may be hypothesized that threshold for locating a target for an action purpose could even be lower.

5.1. Time Constraints

Effects of the delay between stimulus viewing and movement onset have been repeatedly reported in the present review. In particular, the work performed on visual illusions demonstrated that motor behavior can be affected by perceptual illusions when the response is delayed by a few seconds (Bridgeman, 1991; Gentilucci, Chieffi, et al., 1995). A possible explanation of why a slight but significant effect of the visual illusion could be observed in the Aglioti et al. (1995) and the Gentilucci Chieffi, et al. (1995) experiments may be found in the retinal component of the illusion (see Gentilucci, Chieffi et al., 1995). But it may also be found in the several seconds' delay used between stimulus appearance and movement onset.

The results obtained with visual illusions suggest that healthy subjects may exhibit an effect of time on their natural aiming movements, as patients did. Several experiments were performed to seek such an effect.

Goodale et al. (1994) applied the delay paradigm used with their patient D.F. to a group of healthy subjects. They reported that many parameters of the grasping movement were affected by a 2 s delay introduced between stimulus viewing and movement onset. In particular, the opening and closure of the finger grip was altered and maximal grip size was reduced as compared to normal movements. Strikingly, movements delayed by 30 s and pantomimed movements performed beside the object were similar to those observed after 2 s. Allowing a good comparison with experiments performed on patients, this study further supported the view that brain mechanisms underlying perceptual representations are quite independent of those activated during action, and stressed the necessity for motor representations to have an on-line access to target parameters.

Grasping movements are, by nature, dependent on the metric properties of the object. Because they impose less constraint on the final posture, pointing movements

may provide a better tool to address the problem of frame of reference. Following this idea, we studied pointing movements to memorized targets. The first series of experiment was carried out with visual targets briefly presented on a computer screen (Rossetti, Lacquaniti et al., 1994). Subjects were required to point accurately to the target location when a go signal was provided, i.e., between 0 and 8 s following target presentation (see Fig. 8). The results clearly showed that both constant and variable error parameters were strongly affected when the delay reached about 1 s, but then a plateau followed. Analysis of the pointing distributions observed with two experimental setups suggested that endpoints obtained at the shortest delay were coded using a reference frame centered on the starting position. In contrast, pointing distributions obtained for longer delays suggested that endpoints were encoded in an external frame of reference that was based mainly on the target array used in the current experimental session (see Fig. 8). It resulted that movements aimed to the same physical target could be affected by different biases, according to the delay and the experimental set-up. As in Bridgeman's experiment (1991), it seems that the target was encoded as part of the visual context in the delay condition.

Experiments in monkeys have shown that saccades to memorized target were much less accurate when the delay became longer than 400 ms (White, Sparks, & Stanford, 1994). The time course of saccadic errors measured with several delays is comparable to that obtained in our experiment. This may further support the idea that two distinct systems can be activated during eye movements as well as arm movements. Alternatively, this alteration of eye movements might also explain the results obtained for arm movements. A control experiment was thus realized on a subject performing an eye fixation during the memory delay. Pointing scatters obtained in this condition were larger, but they were elongated as in the previous experiment.

Our findings may result from the strong capacity of vision to process information about several spatial targets in parallel. Although only one of the targets forming the visual context appeared in each trial, each could be located relative to the others using the additional reference provided by the screen border. A similar experiment was designed to determine whether the above results were dependent on the sensory modality (Rossetti & Régnier, 1995). In order to provide the subject with minimal side information during each target location encoding, the proprioceptive modality was chosen. For a wider generalization of the results obtained with vision, targets were proprioceptively defined in the subjects' sagittal plane by a passively guided movement of the left arm, the index finger being shortly held on the target. Subjects were then required to point with their right index to the memorized target location. Again, two different arrays of 6 targets were tested in separate sessions, and two delays were used (0 and 8 s). As for vision, the effect of the context was strongly apparent only after the 8 s delay, so that pointing scatters became elongated in the same direction as the target array (see also Rossetti, Gaunet, & Thinus-Blanc, 1996; Rossetti & Procyk, 1997).

These three experiments strongly supported the existence of two distinct ways of encoding spatial information for action. As has been suggested earlier by Bridgeman (1991), an immediate sensorimotor system would depend on an egocentric frame of reference, whereas a second, slower system would represent the target within an external context. As a function of the delay between target encoding and the motor
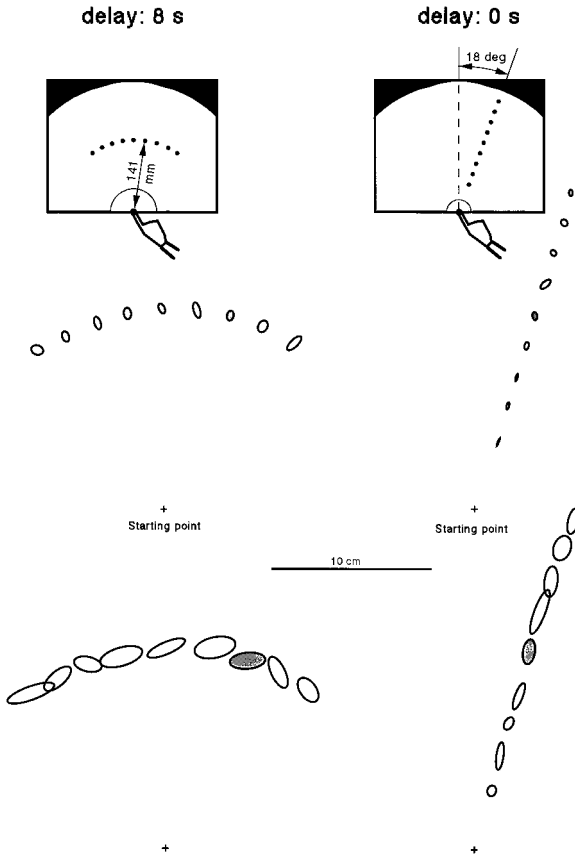
FIG. 8. Time and the representations in action in healthy subjects. Subjects had to point to visual stimuli briefly presented on a computer screen (300 ms). The delay between stimulus offset and the go signal provided to the subject (change in color) was randomly varied from 0 to 8 s within each session (0, 0.5, 1, 2, 4, or 8 s). Two different arrays of 9 targets (arc and line) were used in different sessions. Ellipses presented on the figure are confidence ellipses (60%) of the pointing scatter obtained for each target for a representative subject. The shaded surfaces correspond to ellipses obtained for the same physical point in space. It can be observed that ellipse size is increased by the delay. The most interesting observation can be made about the ellipse orientation. With the 0 s delay, ellipses tend to be aligned with movement direction. With the 8 s delay (and other delays longer than about 1 s), comparison of the results obtained for the two target arrays shows that ellipse orientation tended to be aligned with the target array, and thus became dependent on the visual context provided by the experimental design. These results suggest that different frames of reference were used according to the delay. Movements are likely to be encoded in an egocentric reference frame for immediate responses, whereas they may be encoded in the extrapersonal space after the delay. *(from Rossetti, Lacquaniti, Carozzo, & Borghese, unpublished).*

response, the result of the action would reflect exclusively one type of organization. Alternatively, and according to Gentilucci, Chieffi, & Daprati (1995), the effect of time shown in Fig. 2 suggests that the two systems can gradually interact. The experiment reported in the next section attempted to coactivate the two types of representations.

## 5.2. Semantic–Pragmatic Interference

The effect of the simultaneous activation of semantic and pragmatic representations was tested in healthy subjects pointing to memorized proprioceptive targets (Rossetti, Régnier et al., 1995). Prior to the session, subjects were instructed to associate a number with each of the six target positions from the arc array. As in patients, they were then required to speak aloud the number corresponding to the pointed target during each movement (target number condition). In a control condition, subjects were required to count backward aloud (from 6 to 1 and so forth), so that an utterance (without spatial content) would accompany each movement (number condition). The orientation of the pointing scatters was analyzed as in the experiments reported in the previous section. Distributions of these orientations is shown on Fig. 9. It can be seen that the ''target number condition'' affected only the distribution obtained for the 0 s delay, so that no difference was observed between the two delays. Indeed, results of the ''number condition'' were comparable to those previously obtained without verbal response (see 5.1) and with a less specific verbal response (Rossetti & Régnier, 1995). This finding suggests that activation of a semantic representation of target position had the same effect as the memory delay. Indeed, similar distributions were observed after a delay but without verbalization and without delay but with verbalization of target position. In other words, it is likely that the specific verbalization forced the motor system to immediately use the same frame of reference as was normally used after the delay, namely, an external frame dependent on the target array.

5.3. Conclusion

These experiments performed on healthy subjects were aimed at replicating the situations found to activate sequentially or simultaneously a motor and a more cognitive representation of the goal. A great convergence is found when results of the present section are compared to those presented in section 4. Patients could perform accurately only in the ''natural'' condition, in which they neither delayed the response nor attempted to represent the stimulus at a higher cognitive level (matching, pantomiming, verbalizing). The performance observed in healthy subjects in the same ''natural'' condition may also suggest that a motor representation was used, whereas the representation used after the delay or the verbalization became contingent upon the external context. The effect of the simultaneous verbalization was crucial to demonstrate that segregation of the two representations is based not only on the response delay.

6. GENERAL CONCLUSIONS

Considered together, empirical data reviewed here show that the implicit processing of sensory information for action is not an anecdotal curiosity, nor restricted
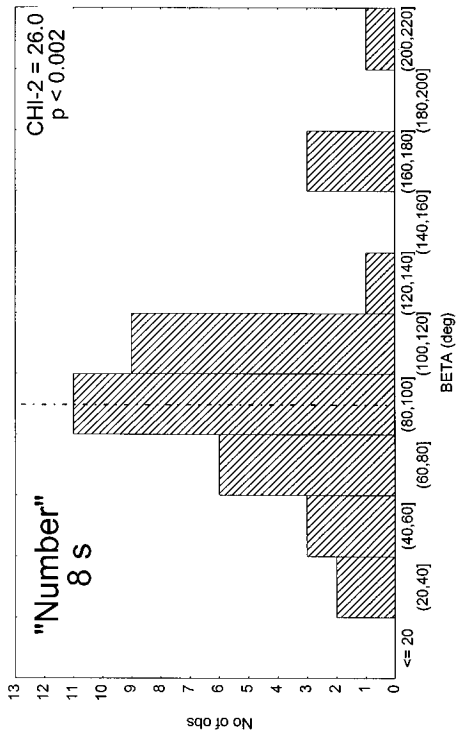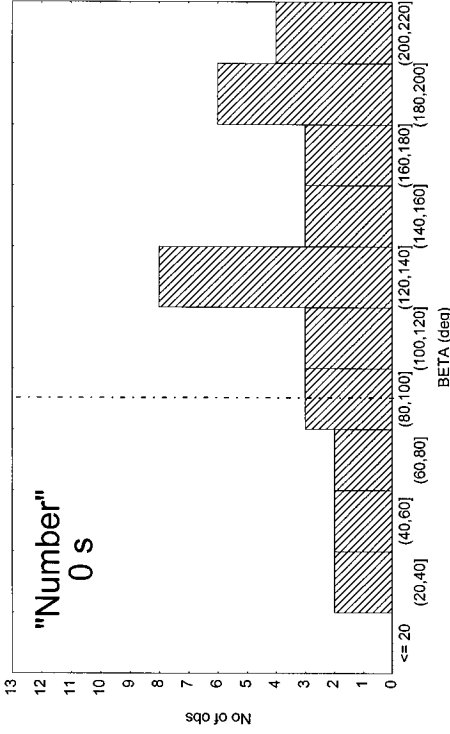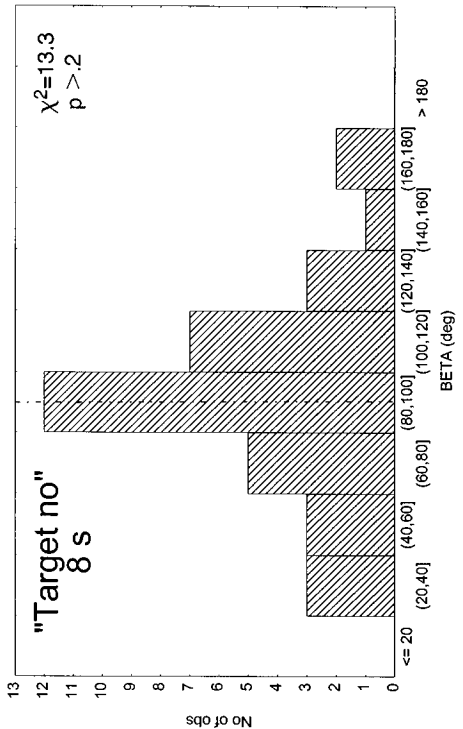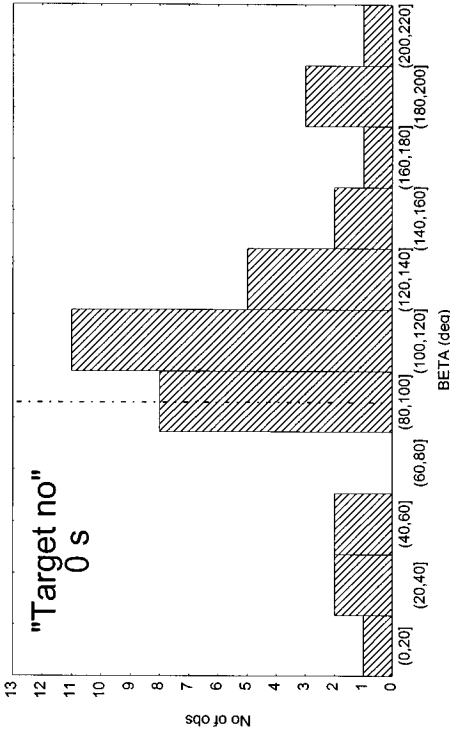
to some very limited control process operating at a low level of motor organization. They rather provide evidence for two distinct representations of space and suggest that these sensory representations can interact before motor output, which allows us to better understand spatial functions involved in action. Automatic processing has long been thought to result from a bottom-up processing and to be unrelated to current intention (see Imanaka & Abernethy, 1992, p. 690). Examples provided here demonstrate that this is not always the case. None of the patients or healthy subjects would respond to the stimulus unless they had been trained to do so or are instructed to perform a guessing action. This major top-down component suggests that the function studied here can be affiliated to the representations of the ''cognitive unconscious'' (Kihlstrom, 1987, 1993).

A considerable amount of evidence for short-lived motor representations can be found in the various experimental fields reviewed in this paper. These examples of dissociation between behavior and awareness share the feature that a stimulus can affect an action in a way that is not congruent with the manner in which it is consciously represented. In this respect, all these examples depart from the naive conception of a linear process leading from sensors to muscles, such as depicted by Descartes (cf. Fig. 1). Other common features can be listed below: (1) Dissociations reviewed here support segregation of sensory processing between two streams respectively devoted to identification and action. (2) Sensory information can be processed at an implicit level to perform an object-oriented action. This implicit pragmatic processing seems to be faster than the explicit one. (3) Although the two types of space representation can be dissociated under particular circumstances, other conditions provide evidence for a possible interaction between the two systems. (4) Pragmatic representations are at work in conditions where the subject performs an immediate goal-directed movement directly aimed at a stimulus. (5) Any attempt to elaborate a higher level representation of the spatial goal to be achieved apparently disrupts the pragmatic processing of the goal. Demonstration of similar dissociation between the two systems in normal subjects, as well as in brain-damaged patients, makes these distinctions all the more believable.

These common features allow us to outline a specific representation of space, whose limitations are coherent with its implication in action. First, and as emphasized

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FIG. 9. Simultaneous activation of pragmatic and semantic representations in healthy subjects. This experiment involved a similar methodology as is described in Fig. 8, unless the target location was defined in the sagittal plane through a movement of the left arm guided by the investigator and left in place for about 300 ms. Histograms show the distribution of ellipse orientations relative to movement direction obtained in 6 subjects for 6 target locations located on an arc array. In addition to the experiment presented in Fig. 8, the subject was required to perform a verbal task during each pointing movement. When the verbal response consisted in counting backward from 6 to 1 repeatedly, providing a single number during each movement, confidence ellipses' orientation varied with the delay: as for visual targets, they tended to be aligned with the target arc (i.e., angle = 90°) only for the longer delay. By contrast, when the number provided by the subject expressed target location (1 for the nearest to 6 to the farthest), ellipse orientations were clustered around 90° for both delays. This result strongly suggests that building a semantic representation about target location is responsible for a change in the frame of reference used by the motor system, which becomes dependent upon the target array. *(drawn from Rossetti & Régnier, 1995).*

by Milner and Goodale (1993), performing an action requires an on-line treatment of pertinent goal characteristics. Thus, there may be no need for long-lived representations in such a process. Second, action is primarily concerned with virtually all metric qualities of objects in space which are useful to guide an action, and does not require a binding of all object properties into a conscious unified percept. Thus, only a partial specification of the goal is requested in pragmatic representations (cf. Jeannerod & Rossetti, 1993). Indeed, a recent experiment demonstrated that normal subjects can react with a motor correction to a stimulus unexpectedly altered in location prior to having processed its color (Pisella, Arzi, & Rossetti, 1998).

The rather restricted function of pragmatic representations makes it a system highly specific to a simple action performed toward a physical goal. This partial representation is built up faster than identification, but it allows less general and less flexible types of response (cf. Lahav, 1993, 1997). In contrast to visual awareness (Milner, 1995), the sensory capacity of the motor system may be restricted to a single or a few features of the goal at a single time. For example, when the location of J.A.'s hand was unexpectedly modified between two trials of a tactile numb-sense experiment, he consistently pointed to the previous location of his hand, even though he could discriminate between the two hand positions during proprioceptive numb-sense sessions. In the same way, when Goodale et al.'s agnosic patient was required to perform a task in which she had to insert a T-shaped object into an appropriate slot, she failed even though she was able to perform the task with a simpler object characterized by a single orientation (Goodale et al., 1994). It may well be that such complex tasks cannot be performed in an egocentric frame of reference (Milner, 1995). The inteference observed between pragmatic and semantic representations also relates to different frames of reference. The verbal requirement may accelerate the elaboration of the context-dependent representation built in an external frame of reference, or may increase its influence on the brain structures responsible for movement control.

Discussion of the interference in terms of coactivation or competition should include anatomical data. Recent neuroanatomical data obtained in monkeys provide support for an extension of the segregation between the two visual systems in their frontal connections. A vision-for-action pathway would project from the dorsal visual system directly to the dorsal and ventral premotor cortex (Watson et al., 1994; Ungerleider, 1995; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Tanné, Boussaoud, Boyer-Zeller, Rouiller, 1996). By contrast, projections from the ventral visual system to the premotor cortex are less direct and involve prefrontal areas. In the same way, projections from the two visual systems to frontal areas involved in eye movements can be distinguished (Bullier et al., 1996). Indeed, convergence of inputs in the premotor cortex may be more relevant than the interconnections found between the two streams. The anatomical organization of the projections to the premotor cortex may provide a basis for understanding the timing difference observed between motor reaction to a stimulus and identification of the same stimulus. Indeed, visual activation of neurons in area MT (a major input to the dorsal stream) appears earlier than in V4 (a major input to the ventral stream) (see Bullier & Nowak, 1995). There seems to be no evidence in the literature, however, that the density of premotor projections from the ventral stream is higher than that from the dorsal stream. As far as eye movements are concerned, projections from the dorsal stream onto FEF (frontal eye

field) are even more numerous than projections from the ventral stream (Schall, Morel, King, & Bullier, 1995). Two alternative hypotheses may then be put forward to explain why pragmatic representations are supplanted by semantic ones as soon as these latter have been elaborated. First, an ephemeral activation of the dorsal stream could account for short-lived motor representations. Second, a hierarchy of the frontal inputs may then be evoked. Indeed, afferents from the ventral stream may project on frontal regions (prefrontal) more anterior than do the direct dorsal afferents. If one assumes that the most anterior area of the frontal cortex is involved in higher level action control (e.g., Norman & Shallice, 1986), ventral projections may well dominate dorsal projections after a short delay. It is also worth noticing that prefrontal cortex is a key structure for short-term (working) memory (Ungerleider, 1995, p. 774). It may be hypothesized then that prefrontal cortex would be involved in forming representations in an external frame of reference, such as can be observed in the many delayed tasks described in this review.

7. SPECULATIONS

Lesions restricted to primary sensory areas seem to be compatible with the sparing of many activities performed in the whole sensorimotor system (involving sensory and motor areas from the parietal to the frontal cortex) (see also Stoerig & Cowey, 1993). It is remarkable that the most patent deficit observed after such lesion is the loss of conscious perception reported by these patients. In line with the current thinking about connections within the visual system, blindsight raises the question of the possible implication of V1 connections in perceptual awareness (see Milner, 1995). Synchronization has been considered as essential for conscious awareness (see Picton & Stuss, 1994). For example, synchronization of neuronal activity can be observed between V1 and V2 and V2 and MT, and may involve other areas (see Bullier & Nowak, 1995). Such mechanism may theoretically explain why many functions of vision are partially spared after V1 lesion (because of subcortical projections), while conscious awareness is lost. Although the current experimental data do not allow further speculation, it should be mentioned that similar thinking has been evoked to explain conscious touch: primary components of S1 response recorded from human somatosensory evoked potentials (Libet, Wright, Feinstein, & Pearl, 1979) and backward projections from S2 to S1 reported in monkeys (Cauller & Kulics, 1991) could provide such physiological correlates of consciousness. As is the case for vision, implication of several sensory areas including the primary area could explain the dissociation between the loss of consciousness and the sparing of other functions.

If it is true that understanding the cognitive unconscious may provide a basis for exploring conscious events (Rossetti, 1992), then time factors should be worth considering in future investigations. However, one should be cautious not to amalgamate the simple processes reviewed in this review with the complexity of consciousness. Several discrepancies may be emphasized to illustrate possible misunderstanding. First, most of the phenomena reported here are subjected to statistical analyses and are endowed with a probabilistic nature. They can be observed and described only as such ''probable tendencies'' that obviously contrast with the usual winner-takes-

all decisions made about environmental stimuli in conscious perception, which provides a basis for global and integrated responses (see also Perrig & Hofer, 1989; Norman & Shallice, 1986; Merickle, 1992; Lahav, 1993, 1997; Cabanac, 1996). In addition, it should again be noted that consciousness may refer to different concepts. Let us consider, for example, Block's recent distinction between access consciousness and phenomenal consciousness (Block, 1995). Access-consciousness may be considered as a continuous stream of serial, unlinked sensory experience of the surroundings. Such phenomena may share mechanisms with the short-lived representations described here and involved in specific responses. It is, indeed, questionable whether it actually belongs to consciousness at all (Revonsuo, 1995). However, phenomenal consciousness may well not be linked to a specific time nor restricted in duration (cf. Dennett & Kinsbourne, 1992). In this respect, it might relate more to the binding processes involved in other nonmotor types of representations. If one considers that consciousness may have evolved from sensation (Cabanac, 1996), the distinction defended in this review between two types of perception may become crucial for understanding conscious states.

ACKNOWLEDGMENTS

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