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4 Several 'vision for action' systems: a guide to dissociating and integrating dorsal and ventral functions (Tutorial)

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Abstract. There is a well-established argument for a double-dissociation between vision for action and vision for conscious identification. The distinction between these two visual systems applies to both the attributes being processed and the outputs of the processing. However, numerous direct and indirect interconnections and convergence have been described between cortical and subcortical visual pathways as well as between the dorsal and the ventral streams. This chapter presents an attempt to solve this apparent contradiction between neuroanatomy and behaviour, by organizing our knowledge about several aspects of how vision can be involved in the various aspects of action. First, several cognitive → motor interactions can be observed, which suggest that action can rely on cognitive representations. Reciprocally, examples of sensorimotor → cognitive interactions have been provided by the reorganization of cognitive representation of space induced by sensorimotor plasticity. Second, it is shown that introducing a memory delay between the target presentation and the action emulates a cognitive representation of the target that is used for action. Conversely, adding a speed constraint to a simple pointing task seems to allow a specific activation of the sensorimotor system: for fast movements no influence of cognitive representations or of intention is observed. Neuropsychological data suggest that the most typical function of the dorsal stream is the on-line control of an ongoing goal-directed action. It is concluded that, depending on the time-scale considered, no interaction or two-way interactions between the dissociated vision for action and vision for identification can be observed. These functional data are fully compatible with the temporal constraints of the complex anatomical network involved in the processing of visual information, in relation to fast (magnocellular) and slow (parvocellular) streams. Recipes are proposed to isolate or integrate a sensorimotor or a cognitive sensory system, according to the type of stimulus, the type of response, and the temporal link between the stimulus and the response.

4.1 Perception and action: a perfect couple?

The question of the relationship between action and perception is central to many areas of philosophy, psychology, and neuroscience. The perception–action couple has been said by ecological psychologists to be inalterably inseparable, whereas specific experimental conditions and neurological patients have suggested that a divorce can be achieved. One of the two partners, Action, is the more forthright and does not trouble itself with non-concrete aspects of life. Therefore everybody agrees about what it is up to. But so many people have flirted with Perception that everyone has their own view of it. Some think that it is only able to deal with proper mental objects which can be manipulated by the mind, while others believe it is a simple-minded character who is under the direct influence of the senses. Still others have rather argued that it is a thoughtful creature that is very aware of objects or events, and tends to interpret them in the most appropriate fashion. It has also been claimed that perception has an impressionable character, being easily influenced by its environment. With such a many-faceted personality, it is no wonder that Perception and Action have a rather chaotic relationship. In order to go beyond these vaudevillesque considerations and try to consider their relationship in a less conflictual way, let us specify which view of perception will be adopted in the present chapter. Following the usage of Milner and Goodale (1995), we will consider perception as an integrated process that gives rise to identification. The usual way to investigate the content of perception implies that this content is mediated by conscious awareness before an output (e.g. a verbalization) can be produced. In more general terms, this way of dealing with sensory inputs has been termed 'cognitive' processing by Bridgeman (1991) and Paillard (1987, 1991), as opposed to 'sensorimotor' processing.

Most of the current debates on sensorimotor versus cognitive processing refer respectively to dorsal and ventral streams of the visual brain. As will be detailed in a further section (4.3.2.), the dorsal stream is defined here as the projections from the primary visual area to the posterior parietal cortex, in particular to the superior parietal lobule. The ventral stream can be defined as the projections from the occipital visual areas to the inferior temporal cortex. Based on neuropsychological observations reviewed below, these two streams have sometimes been associated with implicit (non-conscious) versus explicit (conscious) processing. This issue will be discussed at the end of the present chapter (Section 4.8.4.)

Following this introductory section (4.1), we will first summarize the evidence for the dissociability between perception and action in both normals and brain-damaged patients (4.2). Then we will demonstrate that the complex neuroanatomical networks involved in vision, perception, and action do not show a strict segregation between two cortical visual pathways (4.3). Our main aim will be to review the different ways by which this apparent gap between anatomy and behaviour can be filled (4.4).

On the one hand, several lines of evidence for double interactions between the two visual systems will be presented. It will turn out that both visual systems can contribute to action, suggesting that neuroanatomical data are right (4.5). On the other hand, we review several aspects of the effect of time variables on space processing by the visual system, which suggest that pure anatomical data are not sufficient to account for behavioural observations. We will argue that dissociations between cognitive and sensorimotor processing can result from temporal limits of visual processing (4.6).

Then some simple and more complex experimental recipes will be proposed for either isolating or integrating dorsal and ventral types of function (4.7). Among others, the method of choice for isolating the sensorimotor mode of vision in normals appears to be to apply time constraints to the task. The purest expression of the dorsal processes may consist of an 'automatic pilot' able to on-line drive the hand to a selected visual target, irrespective of the subject's own intention.

To end with, a few concluding remarks will be made on neglected aspects of visuomotor processing (4.8). Instead of seeing dichotomies between sensorimotor and cognitive, dorsal and ventral, implicit and explicit processes, we propose that transitions between these aspects can be viewed as continuous gradients.

4.2 Dissociations

The discovery of reflex reactions at the end of the nineteenth century has given rise to an enormous amount of experimental and theoretical work. The discovery of unconscious nervous processes, as already postulated by von Helmholtz in the case of visual perception, opened new areas of investigation of the mind (e.g. psychoanalysis) and of perception and behaviour. It is interesting to note that the pioneering work of Helmoltz or Freud not only emphasized the distinction between the conscious and the unconscious but also clearly addressed the issue of the interaction between these two aspects of mental life. Unfortunately, for about one century there has been more and more attraction towards the power of unconscious processes as opposed to the conscious mental life, and the report of dissociation between the conscious and the unconscious has become more fashionable than it really deserves to be. This bias has applied to the study of sensory and motor processes separately, and especially to the distinction between implicit processing for action and explicit processing for perception (review: Milner and Goodale 1995; Place 2000; Rossetti and Revonsuo 2000b). As a consequence, more is known about the dissociation than about the interaction between sensorimotor and cognitive processes.

4.2.1 The double-step paradigm

The double-step paradigm refers to experimental conditions where a visual target is first presented to the subject (step one: between fixation point and the target), and then displaced during the action (step two: between the initial target position and the secondary target position). Psychophysical studies have revealed that human subjects are unaware of displacements occurring in the visual world if these displacements are synchronized with the saccade (see e.g. Bridgeman, Hendry, and Stark 1975). Several experiments have explored the consequence of this saccadic suppression phenomenon, which refers to the apparent loss of perception occurring during saccades (Campbell and Wurtz 1978), on arm movement production. In one early experiment, subjects were asked to point at a target that had been displaced during the saccade (by a stroboscopic induced motion) and then extinguished (Bridgeman *et al.* 1979). These authors observed that the saccadic suppression effect was not followed by related visuomotor errors. 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 sensorimotor behaviour. This distinction has been more recently referred to as 'hand sight' (Rossetti, Pisella, and Pélisson 2000).

Following this work, a long series of experiments was initiated by Prablanc and colleagues to explore on-line arm movement control. In a first experiment, they required normal subjects to orient their gaze and point to visual targets presented in full darkness (at fixation point offset). These targets could be unexpectedly displaced forward or backward during the saccade, so that a shorter or a longer hand movement had to be performed for the finger to land on the target. Since eye movements are usually initiated before arm movements, these target jumps occurred well before the hand had reached the target. The use of virtual images of the targets (seen in a mirror) allowed a continuous presentation of the target, without the reaching hand hiding it to the eyes (and thus this differed from the Bridgeman *et al.* 1979 study). The interesting question raised here was whether the motor system would be able to update the hand movement in conditions where the target jump had been performed unbeknown to the subject (Fig. 4.1). Their results were straightforward: (1) as in the Bridgeman *et al.* study (1979), subjects altered the amplitude of their movements such as to compensate for most of the target displacement ('hand-sight'); (2) this hand path correction did not imply a significant increase in movement time; (3) not only did subjects not detect the target jump, but they also remained unable to detect their own movement corrections; (4) forced-choice guesses about the direction of the jump could not discriminate between forward and backward target perturbations (Goodale, Pélisson, and Prablanc 1986; Pélisson Prablanc, Goodale, and Jeannerod 1986). This seminal work has been followed by many studies on motor control versus conscious perception. First, Prablanc and Martin (1992) replicated the same experiment for perturbations in direction and performed a detailed kinematic analysis of perturbed as well as unperturbed reaches. Using an analysis of the direction of the tangential velocity vector, they showed that the two types of trials could be discriminated as early as about 110 ms following movement onset. Knowing that this duration includes both sensory processing time and motor pattern activation time, this result suggested that the specific access of the motor system to visual information was operating at an extremely fast rate. In addition, they observed that the transition from the unperturbed pattern of trajectory to the updated one was produced very smoothly, suggesting that movement correction was integrated in the initial motor programme. Recent work using transcranial magnetic stimulation applied to the posterior parietal cortex has shown that inhibition of this structure was disrupting the on-line correction system (Desmurget *et al.* 1999). A further experiment triggered the target jump at different times with respect to the saccade peak velocity (Komilis, Pélisson, and Prablanc 1993). It revealed that identical corrections were observed in conditions where the subjects could or could not detect the target jump, provided it was applied early enough in the movement (i.e. no later than the hand peak velocity).

These findings were then extended to more complex actions. For example, smooth corrections were also observed for grasping movements perturbed either in target orientation (Desmurget *et al.* 1995; Desmurget and Prablanc 1997) or in target location (Gréa, Desmurget, and Prablanc 2000) at the onset of the movement. We shall mention other experiments performed with simulated perturbations of target objects and on the respective timing of the processes involved in following sections (4.6.2 and 4.7).

4.2.2 Illusions

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) extended a finding made on eye movements (Wong and Mack 1981) and compared the amount of the 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 the cognitive system. It was concluded that apparent target displacement affected only perception whereas real target displacement affected only motor behaviour, which provides a case for a double dissociation between cognitive and motor function (see Bridgeman 2000; this volume, Chapter 5).

In about the last five years, a substantial number of experiments have been performed to explore the effect of visual illusion on a grasping action. We shall only review a few of them here and come back in a further section (4.7.6) to this issue, which is becoming controversial. Aglioti, DeSouza, and Goodale (1995) made use of size-contrast illusions (or Titchener's circle illusion). In this illusion, two circles in the centre of two circular arrays, 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 version of the illusion adapted in pseudo-3-D, Aglioti *et al.* required subjects to grasp the central circle between thumb and index finger, and measured their

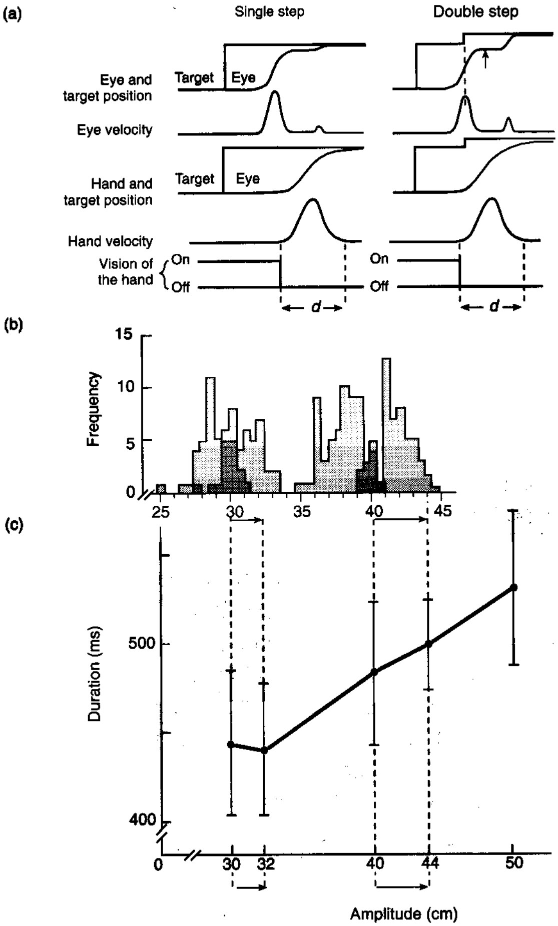


Fig. 4.1 Saccadic suppression and hand pointing performance.

(a) *Experimental procedure*: Schematic representation of single- and double-step trials randomly presented during an experimental session. In all trials, the target was displaced from a central position to a randomly selected position in the right hemifield, and vision of the hand was turned off at the onset of the hand response. In double-step trials, the peripheral target jumped again to the right at the time the saccadic eye response reached its peak velocity, i.e. nearly at hand movement onset. The second target step represented 10% of the first step amplitude and was not detected consciously by subjects.

(b) *Spatial distribution of hand pointings*. Distributions of the endpoints of hand pointing responses, pooled over 4 subjects, towards single-step targets at 30and 40cm and towards double-step targets (30–32 and 40–44 cm). Note that pointings to double-step targets undershoot the final target location (a characteristic of hand movements performed without visual feedback) to the same extent as pointings to single-step targets, demonstrating the existence of corrective processes compensating for the target position perturbation. (From Pélisson *et al.* 1986.)

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 by 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 this '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. In contrast, the motor representation for grasp remained much less affected by the illusion.

Another such experiment was performed by Gentilucci *et al.* (1996) to explore the effect of the Müller–Lyer illusion on pointing behaviour (see Fig. 4.21). 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 (see Rossetti 1999). When the two arrows are directed to the centre of the line, it appears shorter. When they are oriented away from the line, it appears longer. Gentilucci *et al.* (1996) compared pointing responses made from one to the other end of lines linked to 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 the 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. As in the Haffenden and Goodale (1998) study, the influence of the illusion on the goal-directed action was much less than on perception, because the perceptual effect usually covered about 20% of the physical line length used by Gentilucci *et al.* (Rossetti, unpublished). Interestingly, early movement kinematics were also altered, which suggests that the illusion affected the programming of the movement, and not only its final execution. We shall come back later to précis the effects of illusion on action and examine possible points of controversies between authors. For the moment let us consider that visual illusions seem to affect the perceptual system in a more pronounced way than the action system, which may further support the idea of a dissociation between perception and action.

4.2.3 *Masking*

Visual masking has been used extensively as a probe to study conscious experience and cognition (reviews in: Price 2001; Bar 2000), and may explain some of the effects observed during saccadic suppression (Matin, Clymer, and Matin 1972). We will consider here some 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 lit 50 ms prior to the onset of the surrounding LEDs.

(c) *Duration of hand pointings.* Relationship between hand pointing duration (mean and standard deviation) and target step amplitude for three single-step targets (30, 40, and 50 cm) and for two double-step targets (30–32 and 40–44 cm). Same responses as in (b) It can be seen that the same relationship accounts for both types of trial, indicating that motor correction in response to a target perturbation (see panel (b)) is not related to an increased pointing duration. (Modified from Goodale *et al.* 1986, and Pélisson *et al.* 1986.)

This last stimulus could evoke both metacontrast (masking by a surrounding shape) and backward masking (masking with a subsequent light of greater intensity than the small test light). Three motor responses of various complexities (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 and 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 prcessing 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 along 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 (1994) have specifically explored several aspects of this phenomenon. They showed that similar effects could be observed on RT (measured by keypressing) even in a two-choice situation that required integrating form information with position information. In addition, this priming effect influenced the error rate as well as speed of the motor response, and could appear despite of the use of variable stimulus–response couplings, showing that it is not restricted to preprogrammed responses. Taylor and McCloskey (1996) also replicated this finding in their experimental design.

Interestingly it has been shown that the brain-activation pattern triggered by a masked stimulus is very similar to that triggered by unmasked ones. In a very elegant experiment, Dehaene *et al.* (1998) have shown that a masked stimulus used in a semantic priming task could activate up to the primary motor area (see also Eimer and Schlaghecken 1998). Similarly, recordings of the Lateralised Readiness Potential (LRP) in motor areas provide a physiological basis for the Simon effect (review in Hommel 2000).

The double-step paradigm, applied to both reportable and non-reportable target perturbations, as well as experiments exploring the effect of visual illusions or masking on action, suggest that the neural pathways leading to visual awareness are distinct from those involved in visuomotor processing. The implicit processing of sensory information during action may affect the release of a preprogrammed motor output as well as motor planning or on-line control of the execution. The experimental study of neurological cases allows researchers to speculate on the possible anatomical substrate for this dissociation.

4.2.4 Optic ataxia

Descriptions of the effects of lesions of a restricted area of the posterior parietal lobe were reported in groups of patients by Jeannerod (1986) and Perenin and Vighetto (1988). These patients had difficulties in directing actions to objects presented in their peripheral visual field although they were not impaired in the recognition of these objects, a neurological deficit that was termed 'optic ataxia'. Visually directed reaching movements made by these patients are inaccurate, often systematically in one direction (usually to the side of the lesion). In addition, these movements are kinematically altered: their duration is increased, their peak velocity is lower, and their deceleration phase is longer. This alteration of movement kinematics becomes particularly apparent when vision of the hand prior to and during the movement is prevented. Restoration of visual feedback reduces the reaching errors, but the movements remain slower than normal (Jeannerod 1986). Object grasping and manipulation are also altered by posterior parietal lesions. Patients misplace their fingers when they have to visually guide their hand to a slit (Perenin and Vighetto 1988). During prehension of objects, they open their finger grip too wide with no or poor preshaping, and they close their finger grip when they are in contact with the object (Jakobson, Archibald, Carey, and Goodale 1991; Jeannerod 1986). They exhibit deficits not only in their ability to reach to the object, but also in adjusting the hand orienting and shaping during reaching. In contrast, they seem to remain able to indicate the orientation of a stimulus by a wrist movement that is not aimed to the stimulus (matching task: see Jeannerod, Decety, and Michel 1994). These results strongly suggest that the posterior parietal cortex plays a crucial role in the organization of object-oriented actions, whether the visual processig required for a given action is concerned with spatial vision (location) or with object vision (size or shape) (see Jeannerod 1988; Jeannerod and Rossetti 1993; Milner and Goodale 1995; Rossetti 1998, 2000). One interpretation of optic ataxia is that patients present a deficit in programming hand movements (Jakobson *et al.* 1991). Recent evidence rather suggests that deficits result primarily from a disruption of on-line motor control (Gréa *et al.* 2002; Pisella *et al.* 2000).

4.2.5 Visual agnosia

Pathological conditions may also result in disconnecting parietal mechanisms for processing object attributes from those for programming the hand configuration. Jeeves and Silver (1988) reported the case of a patient with callosal agenesis who was unable to grasp objects correctly if they were briefly presented within either half of his visual field. The hands remained wide open throughout the movement and did not adapt to the object size. Jeeves and Silver speculated that, due to the absence of callosal control, the crossed corticospinal pathway (normally responsible for the control of finger movements) could not be activated by visuomotor mechanisms. Instead, the patient had to use the ipsilateral motor pathway, which was inappropriate for carrying the correct commands. These results have prompted a reappraisal of the respective functions of the two cortical pathways. The posterior parietal cortex exerts a role in organising object-oriented action, whether movements are executed by the proximal or the distal channel. This role must be dissociated from the role of other cortical structures specialised for object identification and recognition.

An observation by Goodale *et al.* (1991) provides another piece of evidence for this dissociation between perception and action, showing a reciprocal pattern to optic ataxia. These authors reported the case of a patient who developed a profound visual-form agnosia following a bilateral lesion of the occipito-temporal cortex. DF was unable to recognize object size, shape, and orientation (Fig. 4.2). This patient was also unable to purposively size her fingers according to the size of visually inspected target objects based on a representation of these objects (matching tasks). In contrast, when instructed to pick up objects by performing prehension movements, the patient was quite accurate and her maximum grip size correlated normally with object size. This observation suggests that, during action, DF could still process visual information about the object properties she could not perceive. If these results are compared with those following posterior parietal

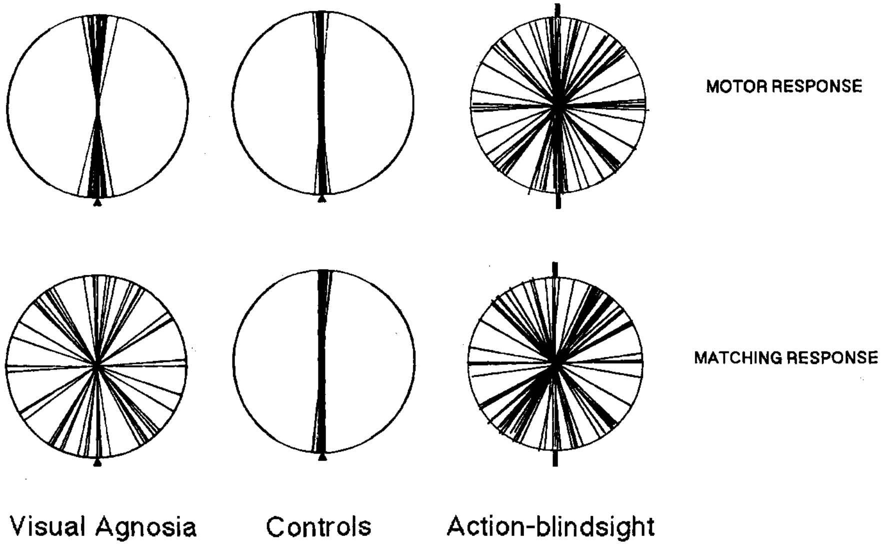


Fig. 4.2 Action and object processing in visual agnosia and blindsight. Polar plots illustrating the orientation of a hand-held card in two tasks of orientation discrimination, from an agnosic patient (DF), a blindsight patient (JCG), and an age-matched control subject. On the perceptual matching task, subjects were required to match the orientation of the card with that of a slot placed in different orientations. On the 'posting' task, they were required to reach out and insert the card into the slot. The correct orientation has been normalized to the vertical. (Adapted from Goodale *et al.* 1991, and Perenin and Rossetti 1996.)

lesions, impairments in perceptual recognition of objects and in object-oriented action appear to be clearly dissociated.

Optic ataxia and visual agnosia patients would support the case for a double dissociation between perceptual recognition of objects and object-oriented action (see Milner and Goodale 1995) (this conclusion will, however, be questioned in a further section). It may be emphasized here that DF 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 visually directed movements. The question therefore arises whether blindsight patients, with V1 lesions, would also exhibit a similar dissociation between perception and action.

4.2.6 Action-blindsight

In addition to optic ataxia and visual agnosia, mentioned above, blindsight is another neurological deficit that is interesting to consider in the framework of the dissociation between implicit and explicit sensorimotor processing. Early studies on patients with lesion of the primary visual area (V1), considered o be amputed from the half of their visual field, showed that they remained able to orient eyes and/or the hand to visual stimuli briefly presented within their blind field (see Weiskrantz 1986). It has been recently shown that some patients could orient their hand and size their finger grip appropriately when reaching out to unseen visual objects (Fig. 4.2) (Jackson 2000; Perenin and

Rossetti 1996). The neuroanatomical substrate proposed to explain this action-blindsight (Rossetti *et al.* 2001) was the projection from the superior colliculus to the posterior parietal cortex via the pulvinar (Bullier *et al.* 1996; Perenin and Rossetti 1996). Therefore this fascinating non-conscious vision, emerging during a goal-directed action, is considered to provide one more instance of dissociation between the dorsal (parietal) and the ventral (temporal) streams of the visual system (e.g. Milner 1998; Milner and Goodale 1995; Rossetti 1998; Rossetti *et al.* 2000).

4.2.7 Action-numbsense

A patient with a left parietal thalamo-subcortical lesion was studied for signs of residual processing of somesthetic modalities. The patient was unaware of any tactile stimuli applied to his arm skin and

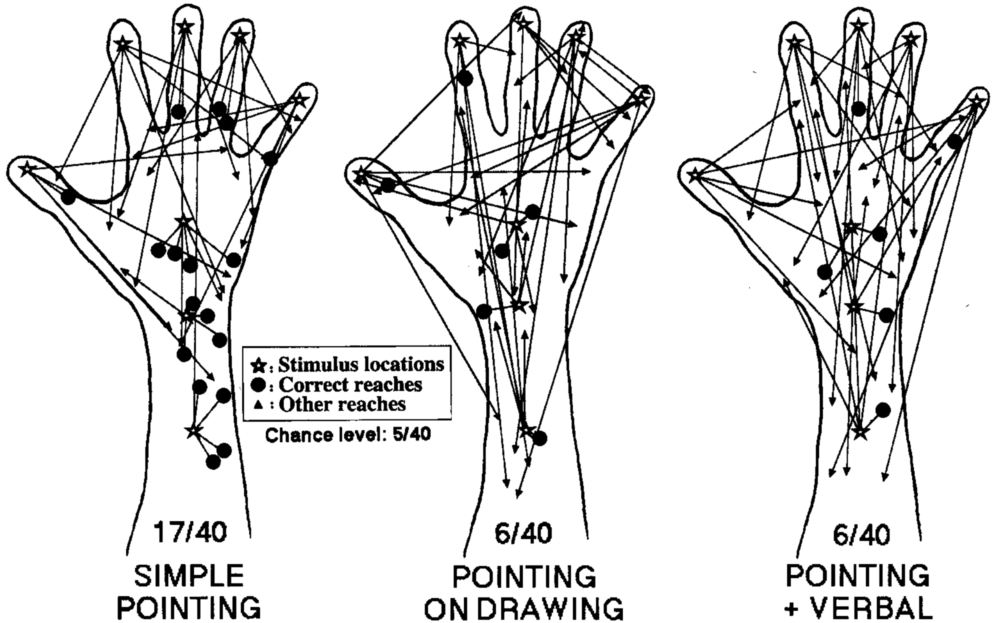


Fig. 4.3 Numbsense: direct pointing versus pointing on a drawing. A set of 8 stimulus locations was used in this experiment: the posterior ungual phalanx of the five fingers + the palm centre + the wrist + the middle forearm of a patient exhibiting action-numbsense following a central lesion of somatosensory afference. Pointing with the left index finger was made toward the locus stimulated (1) directly on the right forearm, (2) on an arm drawing of the right forearm (scale 1). Patient JA was blindfolded when answering directly on the arm. When pointing on the drawing, JA could see the A4 sheet with the arm drawing placed next to his unseen target arm. An opaque curtain was used to prevent him from seeing his target right arm. In addition, the whole arm and face of the investigator delivering the stimuli remained out of sight throughout the experiment, so that no indice (e.g. gaze direction) was available to the patient. (From Rossetti *et al.* 2001.)

failed to demonstrate any significant performance in a verbal forced-choice paradigm. However, he generated above-chance levels of performance when pointing at the stimulus location on the numb arm (Rossetti, Rode, and Boisson 1995, 2001). This observation is similar to that of Paillard, Michel, and Stelmach (1983), who presented a tactile equivalent of blindsight. The question under investigation was whether the residual ability of the patient was linked to the mode of response (motor vs. verbal) or to the representation subservient to these responses (motor vs. symbolic). Interestingly, when the patient had to point to stimulus locations on a drawing of an arm, no significant performance was observed (chance level Fig. 4.3). This dissociation indicates that only a representation of the stimulus linked to the body scheme was preserved, whereas more elaborate representations of the stimulus had vanished. In addition, the patient was unable to localize verbally his right index finger when it was passively positioned in a horizontal plane, but demonstrated significant performance when pointing to this finger with the left hand. Therefore numbsense can apply to proprioception as well. These results reinforce the interpretation proposed above for action-blindsight: there seems to be a sensory system specific for action.

4.2.8 Conclusion

These observations suggest the existence of a specific representation for those (extrinsic as well as intrinsic) object attributes which are used for controlling movement. In the action of grasping an object, the role of the sensorimotor representation will be to transform the visual qualities of the object into corresponding action-specific motor patterns for the hand to achieve the proper action. This mode of representation thus relates to the object as a goal for an action. The object attributes are represented therein as affordances, that is to the extent that they afford specific motor patterns (see Riddoch *et al.* 2001). This pragmatic, or sensorimotor representation seems to specify the metric properties of the action goal in a veridical way, because the hand has to interact with real objects rather than with distorted representations (it would therefore match the theoretical properties of an 'immaculate perception',[1] Rossetti 1999). It is different to the mode used during the process of overt recognition, and by which an object can be named, categorized, and memorized. This process implies a representation of the semantic type, where the object appears as an identifiable entity and remains invariant across different vantage points. Its elementary attributes (size, orientation, colour, texture, etc.) are bound together to form a specific unit. At variance with this cognitive representation, the pragmatic representation implies no binding of attributes into a single percept (see Revonsuo and Rossetti 2000). Instead, each attribute of the graspable object is represented in itself and contributes to the motor configuration of the arm and hand.

The above hypothesis implies that the cortical mechanisms for object recognition or for object-oriented action are selectively activated by the task in which the subject is involved. If the task involves recognizing, memorizing, or forming a visual image of an object, only the ventral visual pathway should be activated. If, on the other hand, the task involves finger movements for grasping or manipulating an object, the dorsal pathway should be activated.

Taken altogether, the findings made on the ability of neurological patients as well as normals to process sensory information specifically for action purposes suggest that vision (or somaesthesia) for action and vision for perception can be dissociated. The dissociations found in optic ataxia, visual agnosia, and blindsight further suggest that the neurological substrates for these two functions could be located selectively in the dorsal and in the ventral streams of visual processing.

4.3 Neuroanatomy of visual-to-motor connections

4.3.1 Cortical versus subcortical vision

About 100 years ago, anatomical studies first suggested the existence of three visual pathways by which the retina was connected to the cortex. Apart from the main route through the lateral geniculate body, von Monakow identified one pathway through the pulvinar and another through the superior colliculus. These pathways terminated in cortical areas outside the striate area (see Polyak 1957). Cajal (1909) described a 'descending' or 'motor' pathway arising from the fourth layer of the superior colliculus and terminating in the ocular motor nuclei and the adjacent reticular formation. This pathway was thought to carry orienting as well as pupillary reflexes. Subcortical vision was thus considered by Cajal to be pure motor vision. Accordingly, extensive lesions of this structure were shown to produce severe impairment in eye movements and visuomotor behaviour (Sprague and Meikle 1965). The distribution of retinofugal fibres between the retinogeniculate and the retinotectal pathways was interpreted within the framework of a dichotomy between two visual systems endowed with complementary functions. Schneider (1969) proposed that the geniculostriate pathway is a system essential in the learning of pattern discrimination, and that the retinotectal pathway is a system for mediating spatial orientation. Using hamsters, he dissociated 'cortical blindness' from 'tectal blindness'. Following ablation of visual areas 17 and 18, animals became unable to learn simple pattern discrimination (e.g. vertical vs. horizontal stripes), although they remained able to orient toward stimuli (e.g. sunflower seeds) presented across their visual field. By contrast, following large undercuttings through the midbrain tectum, spatial orientation ability was lost, whereas pattern discrimination was still possible. This anatomical and functional duality became known as the now classical oppoition between a system specialized for answering the question 'What is it?' and another one specialized for answering the question 'Where is it?' (Schneider 1969). A model of visuomotor coordination built on the notion of two visual channels for movement control was also presented by Trevarthen (1968). This author studied visuomotor behaviour in split-brain monkeys and concluded that the subcortical visual system subserved 'ambient' vision, while the cortical system subserved 'focal' vision.

Pathological destruction of the visual cortex in humans was classically thought to produce total blindness, except for pupillary responses to light and very crude visual perception limited to sudden changes in illumination. This opinion, however, was called into question on the basis of experimental findings in monkeys. Although destriated monkeys also appeared to be profoundly impaired in their ordinary visual behaviour, they were still able to avoid obstacles and to generate motor responses for reaching objects appearing in, or moving across, their visual field (Humphreys and Weiskrantz 1967). These anatomical findings represented a strong argument for the role of subcortical structures in mediating residual visual function in destriated monkeys. Mohler and Wurtz (1977) showed that partially destriated monkeys, which were able to orient visually toward stimuli presented within their scotoma, lost this ability after subsequent destruction of the retinotopically corresponding zones of the superior colliculi. Thus in monkey, the superior colliculi, and possibly other brainstem areas receiving input from the retina, may play a critical role either in mediating pure 'subcortical vision' or in relaying visual input to other structures onto which they project, including extrastriate cortex.

In humans, clinical observations suggestive of incomplete or 'relative' blindness within scotoma of cortical origin had been mentioned previously by several authors (see Weiskrantz 1986, for review). Systematic experimental evidence of residual visual abilities following lesions of the striate cortex was first reported by Pöppel, Held, and Frost (1973). This experiment used a new methodological approach derived from the monkey studies and based on forced-choice responses. Cortically lesioned subjects were requested not to try to see stimuli that were presented within their scotoma, but rather to turn their eyes or point their hand each time a stimulus was presented (see also Weiskrantz, Warrington, Sanders, and Marshall 1974). The amplitude and direction of the responses definitely correlated with target positions. Similar results were obtained by Perenin and Jeannerod (1978) and Ptito, Lepore, Ptito, and Lassonde (1991) in hemidecorticated subjects. In this situation the complete loss of cortex on one side stressed the role of subcortical vision. The fact that subjects tested for 'blindsight' remain unaware of the stimuli, and usually experience 'guessing' rather than 'seeing', would be in accordance with the classical idea that subcortical vision is 'unconscious'. As can be seen in Fig. 4.5, the subcortical network also projects to cortical visual systems (see Bullier, Schall, and Morel 1994; Girard 1995).

4.3.2 Two cortical visual systems

In rodents, lesions of the striate cortex appeared to affect orientating behaviour toward targets located within the rostral visual field, whereas this ability was spared after collicular lesions. By contrast, the superior colliculus was necessary for orienting toward targets placed in the far peripheral visual field (see Goodale 1983). Thus, orientating seems a more complex function than suggested by Schneider's results, and cannot be completely dissociated from pattern discrimination, especially in the most central parts of the visual field.

Later experiments performed on monkeys suggested that both modes of vision were mediated by two diverging corticocortical pathways for processing 'what' versus 'where'. One pathway was the ventral occipitotemporal route, linking striate cortex to prestriate areas and from there reaching inferotemporal cortex on both sides via callosal connections. Interruption of this pathway abolished object discrimination without affecting perception of spatial relations between objects. The other, dorsal, pathway diverged from the ventral one by linking the prestriate areas to the posterior part of the parietal lobe. Interruption of this pathway produced visual spatial disorientation characterized not only by misperception of the relative positions of spatial landmarks (Ungerleider and Mishkin 1982), but also by localization deficits during object-oriented action (Ungerleider 1995) (see Fig. 4.4).

As mentioned above, cases of optic ataxia and visual agnosia have raised the possibility that the anatomical dorsal–ventral division may instead relate to a distinction between the processing of 'what' vs. of 'how' to direct an action (Goodale and Milner 1992; Jeannerod and Rossetti 1993; Milner and Goodale 1995). This renewed conception of parallel visual systems was no longer based on the modalities of visual coding (what vs. where), but rather on the modes of representation of the target object, that is directly linked to the type of response produced by the subject (what vs. how) (Jeannerod 1994). In monkeys, posterior parietal lesions produce a reaching deficit, characterized by the fact that the animals usually misreach with the arm contralateral to the lesion in either part of the visual field (e.g. Faugier-Grimaud *et al.* 1978, 1985; Hartje and Ettlinger 1973). In addition, as discovered by Faugier-Grimaud *et al.* (1978), after lesions limited to the inferior parietal lobule (monkey area 7), the contralesional finger movements are impaired during grasping. These findings are consistent with the properties of neuronal populations recorded in this cortical region; neurones coding for the direction of reaching arm movements were described in this area by Hyvärinen and

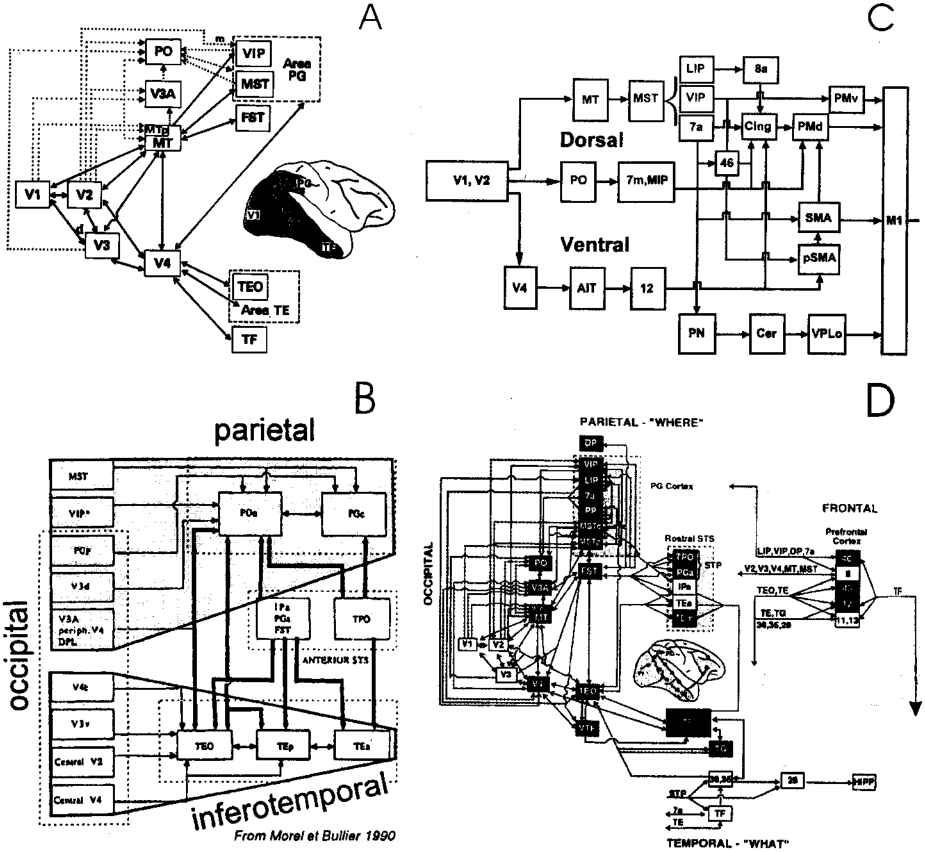


Fig. 4.4 Several sketches of the visual system. Several representative conceptions of the main neural pathways in the visual system. A–C: From the main visual input to area 17, two segregated streams of processing have been described projecting respectively to the posterior parietal cortex (dorsal pathway) and to the inferotemporal cortex (ventral pathway). While the ventral pathway is specialised in processing colour and form and is assumed to play a key role in object identification ('what'), the dorsal pathway is known to be primarily involved in the computation of places and movement ('where') (Morel and Bullier 1990; Ungerleider and Desimone 1986; Ungerleider and Mishkin 1982) and in the sensorimotor processing of the object metrics ('how') (Schwartz 1994). D: Both pathways project onto frontal structures involved in action.
A. Ungerleider and Desimone (1986)
B. from Morel and Bullier (1990)
C. from Schwartz (1994) D. Ungerleider (1995)

Poranen (1974) and by Mountcastle *et al.* (1975). More recently, another population of cells, selectively activated during manipulation by the animal of objects of given configurations, were described by Taira *et al.* (1990). The production of typical visuomotor deficits by lesions and the recording of typical sensorimotor activities in the posterior parietal cortex strengthened the conception of a dorsal visual system specialized for action (review in Sakata and Taira 1994; Jeannerod, Arbib, Rizzolatti, and Sakata 1995; Milner and Dijkerman 2001; Milner and Goodale 1995; Pisella and Rossetti 2000; Rossetti 1998; Sakata *et al.* 1997).

4.3.3 An occipito-frontal visuomotor network

The study of the dorsal–ventral dissociation in the motor context led researchers to distinguish specific motor abilities, which are dissociable from conscious experience and preserved by patients with lesions of the ventral stream, from other types of motor responses. The dorsal–ventral distinction finally evolved toward the conception of two parallel visual streams in the occipito-frontal network for visual-to-behavioural motor responses (Rushworth *et al.* 1997; Schwartz 1994; Ungerleider 1995; see Fig. 4.4). Occipito-parieto-frontal networks have been precisely identified for reach and grasp movements (Jeannerod *et al.* 1995; Rossetti *et al.* 2000; Sakata *et al.* 1997; Tanné *et al.* 1995). However, the visual processing of both the dorsal and the ventral streams has to join the motor structures in order to allow the subject to produce behaviour adapted to his or her environment. Indirect projections of the ventral stream toward the motor regions exist: the temporal area TE can connect the primary motor area after a relay in the prefrontal and then in the premotor regions (Tanné *et al.* 1995; see Fig. 4.5). The temporal lobe can also be implicated in action via its connections to the basal ganglia. Two types of behavioural arguments support this idea of a 'dual route' to visuomotor action (Milner and Dijkerman 2001).

The first line of studies distinguished between 'sensorimotor' and 'cognitive' representations underlying actions, either in normal subjects or in neurological patients. The involvement of the dorsal or ventral stream in action was based on the modes of representation of the goal of the movement: egocentric versus allocentric coding, goal-directed action versus matching, implicit versus explicit processing, grasping of meaningless shape versus meaningful objects. We shall describe this distinction in more detail in the following sections.

The second line of studies concerned conditional motor tasks. Not all sensorimotor transformations consist of goal-directed actions and involve the computation of sensorimotor coordinates and the shaping of the hand with respect to object properties. Other aspects of motor behaviour depend on object identity. The functional role of a stream connecting areas involved in object perception and recognition with the motor structures accounts for the usual associations between a specific stimulus and a motor behaviour (like braking associated with red lights). Rushworth, Nixon, and Passingham (1997) conclude from lesion studies in monkeys that neither part of the parietal lobe may play a major role in the selection of movements made to arbitrarily and conditionally associated visual stimuli. Relatedly, a patient with bilateral posterior parietal lesion exhibited no difficulty performing instructed motor responses (stop or redirect ongoing action) to visual stimuli, but lost the automatic visuomotor guidance of action (Pisella *et al.* 2000; see Fig. 4.14).

In search of the detailed neuroanatomical basis for the ventral and dorsal systems, Fig. 4.5 presents an attempt to synthesize the cortical neuronal networks described in monkeys between V1 and M1 allowing visual inputs to be transformed into motor output. Although the dorsal and the ventral streams can be individuated from this network, this illustration displays a possible substrate for common participation of these two systems in action. Strikingly, M1 receives only mixed projections and no pure projections, either from the dorsal system or from the ventral one. Although distinctions can be

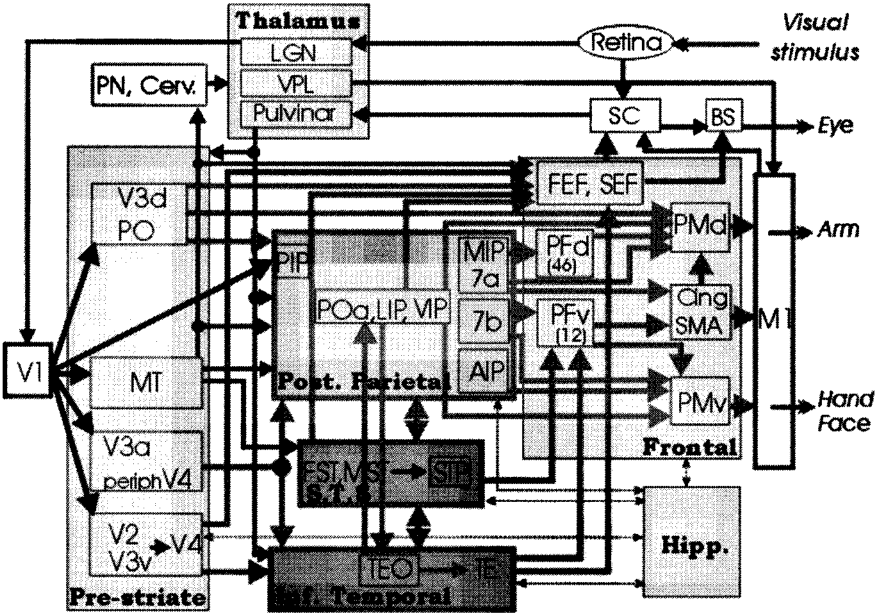
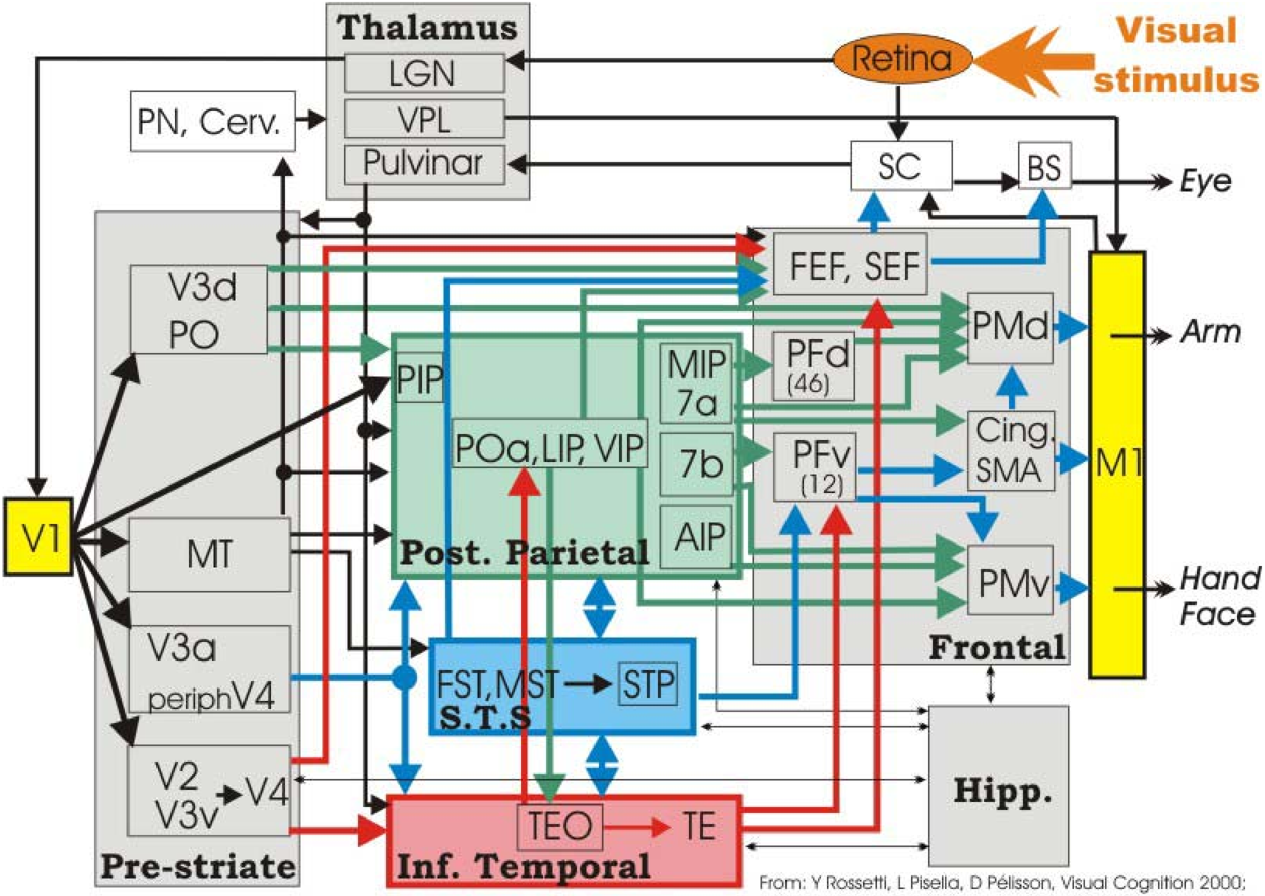


Fig. 4.5 (See also the color plate of this figure.) Overview of the visual-to-motor network. Cortical neuronal networks allowing visual inputs to be transformed into motor output. This illustration displays the possible substrates for dissociation and interactions between ventral and dorsal pathways driving information from V1 to M1. The dorsal and the ventral streams are depicted in green and red, respectively, as well as their efferences. Blue arrows arise from areas receiving convergent dorsal and ventral inputs, either directly or indirectly. Further projections from areas receiving these mixed convergent inputs have also been represented in blue. Even though the posterior parietal cortex and the inferior temporal cortex receive a single direct projection from each other, they were not considered as mixed recipient areas. By contrast, areas in the frontal lobe receive parallel dorsal, ventral, and mixed projections. Interestingly, at the motor end of this network there is no pure projection from either the dorsal or the ventral stream of visual processing.

Abbreviations: *AIP: anterior intraparietal area; BS: brainstem; Cing.: Cingulate motor areas; d: dorsal; FEF: frontal eye field; FST: floor of the superior temporal sulcus; Hipp.: Hippocampus; LIP: lateral intraparietal area; M1: primary motor cortex; MIP: mesial intraparietal area; MST: medial superior temporal area; MT: medio-temporal area; PF: prefrontal cortex; PM: premotor cortex; SC: superior colliculus; SEF: supplementary eye field; SMA: supplementary motor area; STS: superior temporal sulcus; STP: superior temporal polysensory area; TE: temporal area; TEO: temporo-occipital area; v: ventral; V1: primary visual cortex; VIP: ventral intraparietal area.* (updated from Rossetti, Pisella, and Pélisson 2000—derived from Colby *et al.* 1988; Morel and Bullier 1990; Schall *et al.* 1995; Schwartz 1994; Tanné *et al.* 1995; Van Hoesen 1982.)

described between cortical and subcortical vision, between dorsal and ventral stream, and between two occipito-frontal routes, the important point raised here is that all subsystems considered in these distinctions are interconnected.



From: Y Rossetti, L Pisella, D Pélisson, Visual Cognition 2000;
& Y Rossetti and L Pisella, Attention and Performance 2002

4.4 The gap between anatomy and behaviour

The above two lines of evidence make a strong case for the dissociability perception and action, on the one hand, and for the interconnection of visual-to-motor networks, on the other. The examples of dissociation presented here suggest that there must be two independent visual systems which can give rise either to action or to conscious perception. However, taken as a whole, the anatomical data do not support as clear a segregation between two major pathways as they are often considered to establish. Instead, Fig. 4.5 suggests that interaction between the two streams can take place at many levels before visual information reaches the motor output, and that a pure input from the dorsal stream onto the motor areas cannot be isolated within the visuomotor network. A crucial point to note here is that most of the evidence used to support a dissociation between two visual subsystems comes from animal lesion or neuropsychological patients, whereas most of the arguments for an interaction between these two systems comes from experimental work performed in normal subjects.

Is it possible to bring together these two lines of evidence? There must be ways to go beyond the surface of this lack of a direct anatomical correlate of a behavioural dissociation. If there is no doubt, as argued above, that perception and action can be dissociated (at least in some circumstances) then the anatomical data presented in Fig. 4.5 should be revised or improved. In particular, additional features of this anatomical network have to be identified, which would explain this behavioural dissociation. Conversely, if, as argued above, there are numerous interconnections between the dorsal and the ventral anatomical pathways, then interactions should be observed between the two behavioural responses.

4.5 Anatomy is right

Numerous examples of interaction between action and perception systems will be listed below, suggesting that the anatomical evidence for an interconnection between the two systems is followed by functional correlates. Altogether four types of cognitive→sensorimotor interaction can be observed, whereas one type of reciprocal sensorimotor→cognitive interaction has been described (see Fig. 4.6).

4.5.1 Perception can trigger action

Since they don't perceive objects, blindsight patients would never initiate spontaneous actions toward these objects. Their motor ability in pointing and orienting objects has always been observed in forced-choice experiments, where the action was initiated upon a go-signal (see Rosetti 1998; Weiskrantz *et al.* 1974, 1989). The same observation has been made for numbsense patients (Paillard *et al.* 1983; Rossetti *et al.* 1995, 2001). This experimental detail has a strong theoretical impact. It means that in order to allow the sensorimotor system to release an action, the cognitive system has to provide instructions to initiate this action.

4.5.2 Perception can inhibit action

We have seen that perception and sensorimotor processing can be dissociated in action-blindsight and numbsense patients. It is interesting to note, however, that the preserved motor abilities of these patients were disrupted when the elaboration of a cognitive representation of the action goal was activated during the action (see Rossetti 1998). When asked to produce a verbal response simultaneously

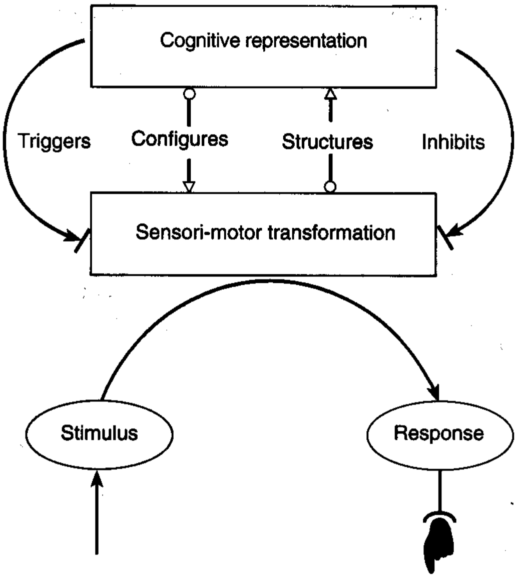


Fig. 4.6 Summary of the various types of interactions observed between the sensorimotor and the cognitive representations of a stimulus leading to behavioural responses.

to the action, the motor performances of blindsight patients dropped to chance level (Fig. 4.7). And the same observation has been made with a numbsense patient, for both tactile and proprioceptive targets (Fig. 4.7): the simultaneous motor + verbal condition was responsible for random responses (see Rossetti *et al.* 1995).

Experiments in normals have also shown that the co-activation of a verbal representation during a motor response changes the configuration of the movement endpoint errors. Immediate pointing toward proprioceptive targets was tested with blindfolded subjects by Rossetti and Régnier (1995). For each target, constant and variable errors were computed. Variable errors were assessed by a confidence ellipse of the endpoint distribution (Fig. 4.8). On each trial a target was presented on one out of six possible locations lying on a circle centred in the starting point. Because subjects were trained to point to these positions in a preliminary session and to associate a number (from 1 to 6) to each target, they could mentally extract the pattern of the target array and use it to encode the target location in an allocentric frame. In this case (as for delayed action, see Fig. 4.10), the distribution of endpoints would tend to align with this target array, that is, perpendicular to movement direction. If they encoded the target position in an egocentric reference frame, then their pointing distribution should remain unaffected by the target array and should be elongated in the movement direction (as in Vindras *et al.* 1998). In a 'motor' condition, subjects simply had to point toward the proprioceptive target after the encoding finger had just been removed from it. In a 'motor + verbal' condition, subjects similarly pointed toward the same proprioceptive targets but were instructed to give simultaneously a forced-choice verbal response of the target number. In the 'motor' condition, as in the condition of arbitrary 'number' verbalization, the orientations of the ellipse main axes were randomly distributed (Fig. 4.9(a)). This lack of influence from the context of the target array was interpreted as the pure

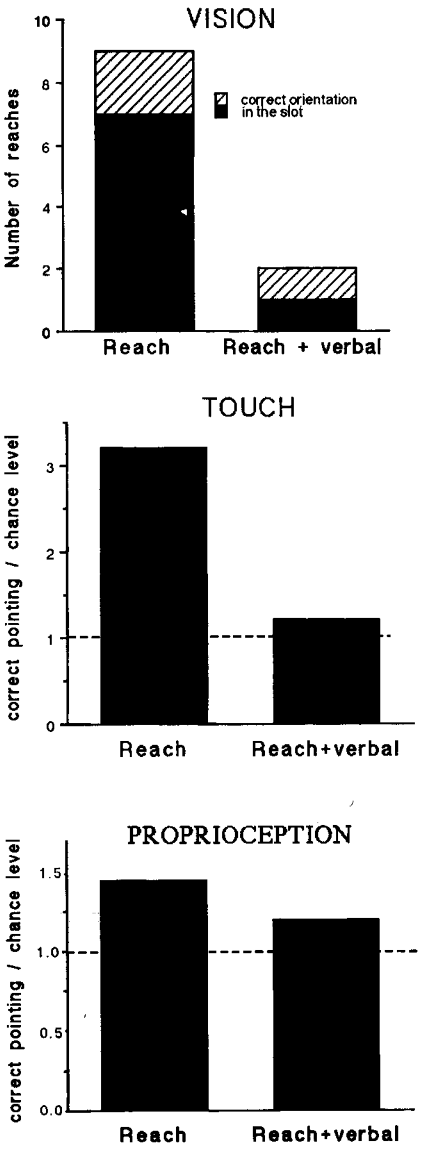


Fig. 4.7 Effect of verbalization on the reach performance of a patient with a lesion in the primary visual area and a patient with a lesion of the primary somaesthesic afferents (tested for touch and proprioception). The vision modality was assessed by testing the reach performance of the blindsight patient PJG toward visual targets presented in his blind visual field. The reaching performance of the numbsense patient JA was evaluated toward tactile and proprioceptive stimuli on the affected side. In these three modalities, the correct reaching responses decreased when a forced-choice verbalization of the target was produced simultaneously to the immediate motor response. (Adapted from Rossetti 1998.)

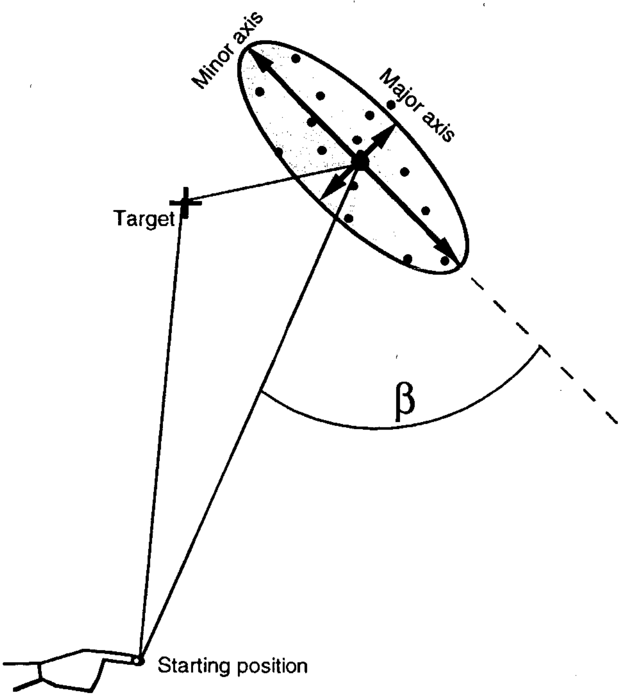


Fig. 4.8 Constant and variable pointing errors. Endpoint recording was made of each individual movement, and each target was used to compute constant and variable pointing errors. Constant errors were measured in direction (angle) and amplitude relative to the ideal reach that would hit the target. Variable errors were assessed by confidence ellipses (95%) of the scatter of finger end positions. The ellipse surface provided an estimate of the global pointing variability. The orientation of the ellipse major axis was computed relative to mean movement direction (angle beta). This most pertinent parameter revealed the sensorimotor or cognitive representation underlying the pointing movement. This parameter was shown to be affected by the various conditions of target coding (review: Pisella *et al.* 1996; Rossetti 1998, see Fig. 4.9) and by the delay of response (Rossetti and Régnier 1995, see Fig. 4.10.)

activation of a sensorimotor representation in this condition (Rossetti and Régnier 1995). In the 'motor + verbal' condition (with a specific spatial verbalization of the 'target number'), the orientation of the ellipse, perpendicular to movement direction (see Fig. 4.9(a)), was interpreted as the result of the influence of an allocentric representation of the target position. Therefore the cognitive integration of the whole target pattern played a role in the immediate action only when a spatial verbal representation was activated (Rossetti 1998). In order to demonstrate that this result could not simply be attributed to an attentional bottleneck or dual task effect, several control experiments were performed (Fig. 4.9(b), and see Fig. 4.20 in the recipes provided in section 4.7). This type of cognitive →sensorimotor interaction effect was later confirmed by the application of this motor–verbal paradigm to the Roelofs effect (Bridgeman 1997, 2000, this volume, Chapter 5).

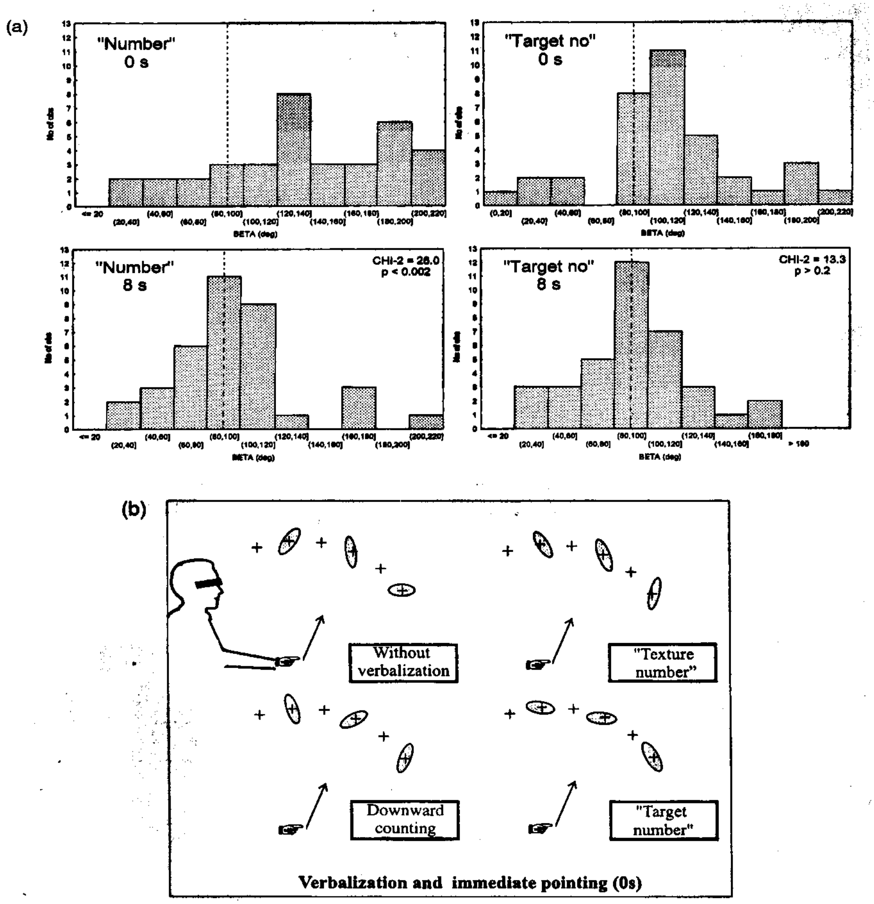


Fig. 4.9 Effect of verbalization on the orientation of confidence ellipses.

(a) Histogram of the beta distribution for immediate (delay = 0 s) and delayed pointing movements (delay = 8 s) when subjects verbally report a number during their pointing responses. This number can result from downward counting ('number' condition) or from a guess about the target location ('target number' condition). With the 'target number' verbalization specific to the spatial location of the target, ellipses orientation tended to be more aligned with the arc array (beta reaches 90 deg). In contrast, with the arbitrary 'number' verbalization, the influence of the context of target presentation appears only for delayed pointing movements. Immediate movements are coded in an egocentric reference frame, independent of the target array as in the condition without simultaneous verbalization [schematized in (b)].

(b) Schematization of the influence of various verbalizations on the ellipse orientation of immediate pointings. Without verbalization, ellipses are randomly oriented. Ellipses tended to align with the arc array (beta reaches 90 deg in mean) only for the specific verbalization of the target spatial location ('target code') but not for the two arbitrary verbalizations: arbitrary number ('downward counting') or learned 'texture code' of the target. (Derived from Pisella *et al.* 1996; Rossetti 1998 and Rossetti and Régnier 1995.)

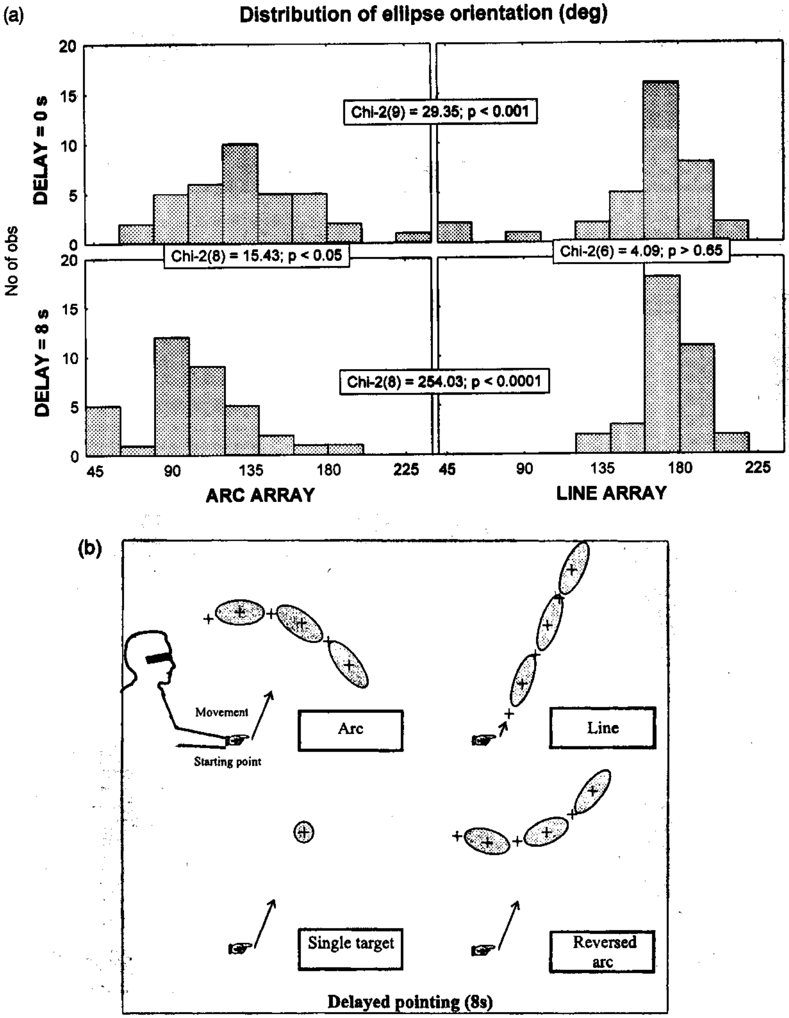


Fig. 4.10 Effect of delay on the orientation of confidence ellipses of pointing errors.

(a) Histogram of the beta distribution for immediate (delay = 0 s) and delayed pointing movements (delay = 8 s) when targets were presented on an arc array or a line array. For immediate pointing, the confidence ellipses are influenced by the direction of the pointing movement (as shown in Fig. 4.9). After a delay, ellipse orientation tends to align with the target array, revealing an allocentric coding of the target location. In the case of the arc array, beta tends to reach 90deg for delayed pointing movements. On the contrary, in the case of a line array aligned with the direction of the movement, ellipses orientation doesn't change between immediate and delayed pointing movements (remains about 180deg). These results for 8 s delay are schematized in (b).

(b) Schematization of the influence of the target array on the ellipse orientation of delayed pointings. The result shown in (a) was replicated with various target arrays. (Derived from Pisella *et al.* 1996; Rossetti 1998 and Rossetti and Régnier 1995.)

As in the case of blindsight and numbsense, the observations made in normals confirm that when a motor and a cognitive representation of a target are simultaneously elaborated, the cognitive representation seems to impose, at any level before the output, its spatial parameters on the final output.

4.5.3 Recognition of the objects to grasp configures the motor program

The preserved motor performances in blindsight patients are classicaly observed after a training session performed in the intact visual field (e.g. Rossetti 1998). This suggests that a configuration of the motor act by the ventral stream is a preliminary step necessary for blind sensorimotor processes.

Non-motor parameters have been shown to influence action in normal subjects after learned associations between objects' features and motor parameters. Clever experimentation demonstrated that after such semantic associative learning, the processing of the colour of an object (Haffenden and Goodale 2000b), or of words written on an object, can interfere with the sensorimotor processing of the physical properties pertinent for grasp, and consequently affect the grip size. The size–weight illusion provides another such example (Flanagan and Beltzner 2000). In the same vein, Jeannerod *et al.* (1994) reported that a patient with a bilateral lesion of the dorsal stream (AT) exhibited normal actions toward familiar objects, whereas her actions toward similar unfamiliar 3D forms were severely impaired. These results suggest that goal-directed actions could be configurated by the visual recognition pathway. Even for normal subjects, the motor parameters of everyday actions made toward familiar objects can therefore be programmed on the basis of the knowledge about the usual physical characteristics of these objects.

4.5.4 Sensorimotor representation structures spatial cognition

Both visuomotor adaptation in neglect patients and the natural ageing process have been shown to affect the elaboration of explicit cognitive representations of spatial information (Pisella and Rossetti 2000; Bhalla and Proffitt 2000). The therapeutic improvement of neglect symptoms mediated by a pointing procedure of adaptation to a prismatic deviation (Rossetti *et al.* 1998b, 1999a) has demonstrated that the spatial cognition of brain-damaged patients can be restructured by adapting sensorimotor transformations. This profound action was shown to affect sensorimotor coordination and classical neuropsychological testing through visuomotor tasks (e.g. cancellation task, copying task, bisection task), as well as pure cognitive representation such as mental imagery (Rode, Rossetti, Li, and Boisson 1999; Rode *et al.* 2001). In addition, we have shown recently that this type of structuring effect of visuomotor adaptation can also alter spatial cognition (midline judgements) in normal individuals (Colent *et al.* 2000). Bhalla and Proffitt (2000) too have shown that evaluation of the slope of a hill was influenced by subjects' age; that is, by a subject's adaptation to his/her reduced sensorimotor and power abilities. This effect is not observed over a shorter time range such as after jogging. This is coherent with Piagetian theory about child development, that is, the brain is structured by sensorimotor associations and learning ('sensorimotor scheme'), which are progressively transferred to cognition (considered as covert action schemes). As shown by these examples of intermediate or long-term interactions between action and cognition, a much larger time-scale seems to be necessary to observe an influence from the sensorimotor level to the cognitive level. It is likely that the cerebellum is involved in this type of profound revision of these several levels of space representation, because this brain structure is the best candidate for the neurological substrate of adaptation (review: Jeannerod and Rossetti 1993). But other structures may be involved as well, as suggested by the lack of contextual influence on delayed pointing performed by blindfolded subjects in the experimental situation depicted in Fig. 4.10 (Rossetti *et al.* 1996).

Based on this short synthesis of the empirical data available on the interplay between cognition and action systems, it appears that explicit and implicit processing of space involved in action cannot be considered as fully dissociated from cognition and that there are multiple possible interferences between them. These interactions are not symmetrical. Cognitive→sensorimotor interactions are observed at the level of the duration of a single slow action, whereas sensorimotor→cognitive interactions can be observed over a much longer time-scale (as a result of many successive actions).

4.6 Anatomy is not sufficient

Whereas our knowledge of brain anatomy is mainly based on monkey data and does still need development and refinement, human behaviour can be observed directly. If there is a mismatch between neuroanatomy and behaviour, then we have to look at anatomy in a more functional way. Let us now consider the neuroanatomical networks connecting sensors and effectors in this light. The dissociation between a dorsal and a ventral stream of visual processing has been initially based on the connectivity of visual areas. More recently, the functional properties of the cells participating in each of these streams have been described. Recent single-unit studies in the monkey also provide evidence for a temporal dissociation between two visual pathways. Comparison of visual response latencies at various locations in the monkey visual system have led Nowak and Bullier (1997) to distinguish two groups of visual areas. Parietal areas from the dorsal stream, projecting onto the premotor cortex, exhibit particularly short visual latencies (about 40–80ms) as compared with other pre-striate areas. In their extensive review of the literature, the dorsal pathway projections towards frontal areas is therefore referred to as the 'Fast Brain', whereas temporal areas are described as the 'Slow Brain' (about 100–150ms). As stressed by Nowak and Bullier (1997), the visual latencies do not match a hierarchical model of purely anatomical organization, but rather follow the distribution of magnocellular and parvocellular inputs. The speed of the occipito-parietal processing seems to be explained by the faster conductivity of the magnocellular channel almost exclusively activating this dorsal stream and by the numerous bypass connections existing in it, whereas the ventral stream seems to be connected in a more serial fashion (Nowak and Bullier 1997; Schall, Morel, King, and Bullier 1995). In addition, neuroanatomical tracing has shown that parietal areas of the dorsal stream project directly to the dorsal premotor cortex, whereas the ventral stream projects only indirectly to ventral premotor cortex via the ventral prefrontal cortex (Schmolesky *et al.* 1998; Schwartz 1994; Tanné *et al.* 1995; see Fig. 4.5).

Can we now identify some behavioural correlates of the functional properties of neuroanatomical projections?

4.6.1 Immediate versus delayed actions

Differences between immediate and delayed actions have been reported in normal and brain-damaged subjects. With respect to the temporal issues raised here, it is interesting to note that visuomotor performance (how) in brain-damage patients and healthy subjects can depend upon the delay and the speed of the motor response.

The effect of a delay can be easily tested in normals with various simple tasks. In general, there is a global decrease in performance when the delay introduced between the stimulus presentation and the response is increased. This effect is mainly observable in terms of an increase in response variability. Interestingly, it has also been observed that the effect of delay duration is not linear (see Fig. 4.11(a)). Using a simple experimental design, Rossetti *et al.* (1994) had subjects point with various delays to visual targets flashed on a monitor. Nine target locations were used, and organized along an arc centred on the starting position (see Rossetti 1998). Several accuracy parameters were investigated (Fig. 4.8). First, the global variability, as assessed by the surface of the confidence ellipse fitting the movement endpoints, continuously increased with the delay. Second, the evolution of the orientation of the main axis of the confidence ellipses fitted for each target followed instead a two slope function: it tended to be aligned with movement direction in the absence of a delay and then rapidly increased for the 500ms delay (see Fig. 4.11(b)). Between the 500ms and the 8s delay, a nearly horizontal plateau was reached, with ellipse orientation tending to be aligned with the target array, that is orthogonal to movement direction (see Rossetti *et al.* 2000: Fig. 4.10). Third, the orientation of the constant error vector in space also followed a similar two-slope trend. As shown in Fig. 4.11(a), it is rather striking that experiments investigating the effect of a delay on eye movement accuracy in the monkey made similar observations (Krappmann 1998; White, Sparks, and Stanford 1994). Although the parameters used in the monkey saccade experiment were not identical to the one used in the human pointing experiment, it is interesting to observe that a similar time course could be observed in both studies. These results indicate that a different type of sensorimotor process is at work in the immediate and in the delayed condition. A short-lived egocentric representation of the target location seems to be used to guide immediate actions. However, an allocentric coding of the visual target seems to participate in the delayed action, which is affected by the global spatial context of the experiment that has been extracted by a trial-to-trial integration over time. In addition, similar results have been observed for delayed pointing to proprioceptively defined targets (Fig. 4.10) (Pisella *et al.* 1996; Rossetti and Procyk 1997; Rossetti and Régnier 1995; Rossetti *et al.* 1996).

Neuropsychological data have also reported the effect of delay on the motor performances of patients with a lesion of the dorsal or ventral stream. The agnosic patient DF can correctly reach and grasp objects that she cannot describe, but loses this preserved motor ability when her action is delayed by only 2 s (Goodale *et al.* 1994). Goodale *et al.* reported that many kinematic landmarks 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 with normal movements. Strikingly, movements delayed by 30 s and pantomimed movements performed beside the object were similar to those observed after 2 s.

Conversely, an ataxic patient (AT) described by Milner *et al.* (1999a) performed imprecise reach and grasp movements when instructed to act immediately to objects, but she was (paradoxically) improved when a delay was introduced between the stimulus presentation and the pointing response (see also Milner and Dijkerman 2001). Action-blindsight and numbsense have also been shown to be disrupted when a delay is introduced between the stimulus and the response (see Rossetti 1998, Fig. 4.12).

These results converge towards the idea that when action is delayed and the object has disappeared, the parameters of object position and characteristics that are used by the action system can only be accessed from a sustained cognitive representation. This type of representation obviously relies on different reference frames with respect to the immediate action system. Furthermore, the neuropsychological data suggest that the dorsal stream is able to build a short-lived sensorimotor representation of the target that is only available for immediate actions.

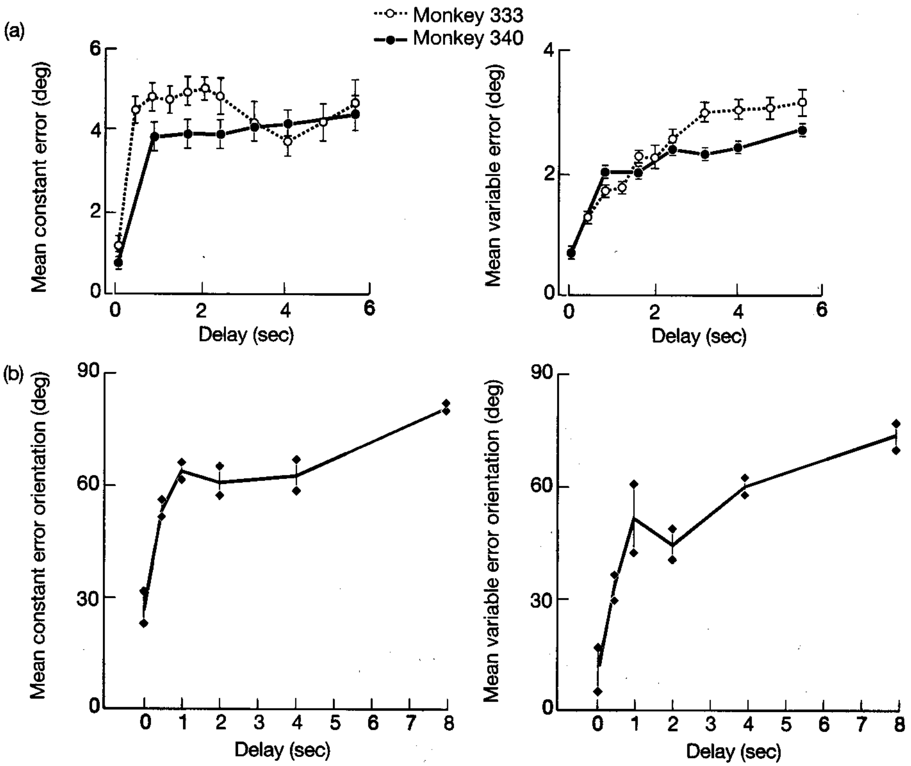


Fig. 4.11 Time course of error distributions. Effect of increasing delay intervals (between the target extinction and the go-signal) on the precision of two types of motor responses. Constant errors (left) and variable errors (right) defined in Fig. 4.8 were plotted as a function of the delays. Plotted points are the errors averaged across all target locations. Similar tendency was observed in two studies on (a) ocular and (b) manual motor errors. (a): Constant saccadic errors showed a drastic increase between 0 and 1 s and stabilized for longer delays in the two monkeys (White *et al.* 1994). Variable errors follow the same evolution with delays at least for one monkey. (b): Both constant and variable pointing errors toward visual targets increased sharply in humans between 0 and 1 s and then reached a plateau. (Drawn from Rossetti *et al.* 1994.)

4.6.2 Fast versus slow actions

Following the initial finding that movements could be updated on-line unbeknown to the subject (Pélisson *et al.* 1986), related studies stressed the high speed of motor correction and investigated the delay of subjective awareness of the perturbations (Castiello and Jeannerod 1991; Castiello, Paulignan, and Jeannerod 1991). In these experiments, a simple vocal utterance ('Tah!') was used

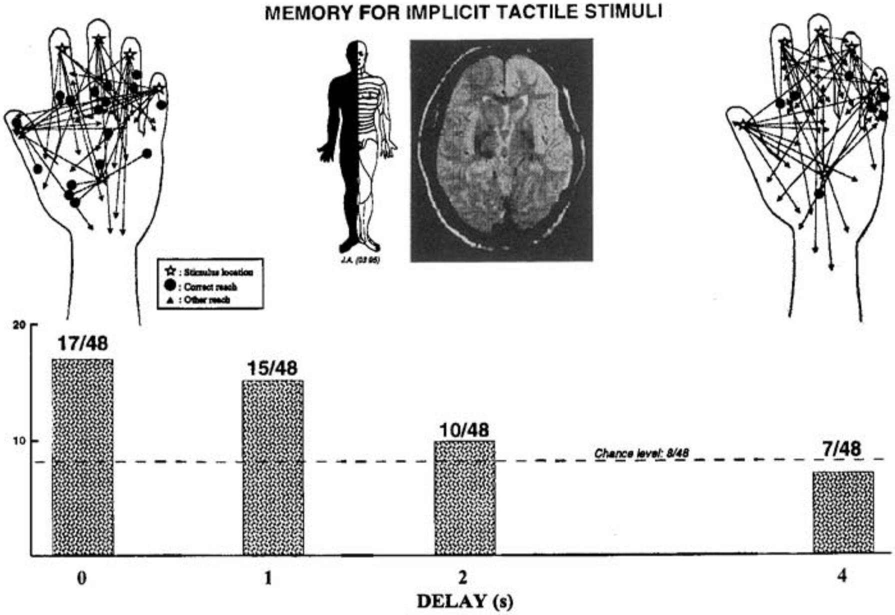


Fig. 4.12 Effect of delayed tasks on action-numbsense. Action-numbsense was tested in JA for tactile stimuli delivered to the hand. Four different sessions tested the effect of 4 delays introduced between the stimulus delivery and the go-signal: 0, 1, 2, and 4 s. In each session 48 stimuli were randomly delivered to 6 possible locations (stars). The number of correct responses (black dots) decreased abruptly from an above chance (immediate and 1 s) to a close-to-chance level (2 and 4 s). This result suggests that the residual somatosensory information used to direct JA's response was available only for a very short period (about 1 s). (From Rossetti 1998.)

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 preliminary experiments (Paulignan *et al.* 1991), 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. These results also stressed the important role played by time factors with respect to the action–perception debate.

The spontaneous variation of response speed in a patient with action-blindsight allowed us to note that faster sessions gave rise to a more significant performance than the slower sessions (see Rossetti 1998). A similar effect was described in an experiment investigating the effect of movement time on the type of action control (Pisella *et al.* 2000: Exp. 1). In a 'location–stop' pointing experiment, one green target was initially presented and subjects were requested to point at it at instructed rates. This target remained stationary on 80% of the trials or could unexpectedly jump to the right or to the left at the time of movement onset. Subjects were instructed to point at the target, but to systematically interrupt their ongoing movement when the target jumped. The direction of the target

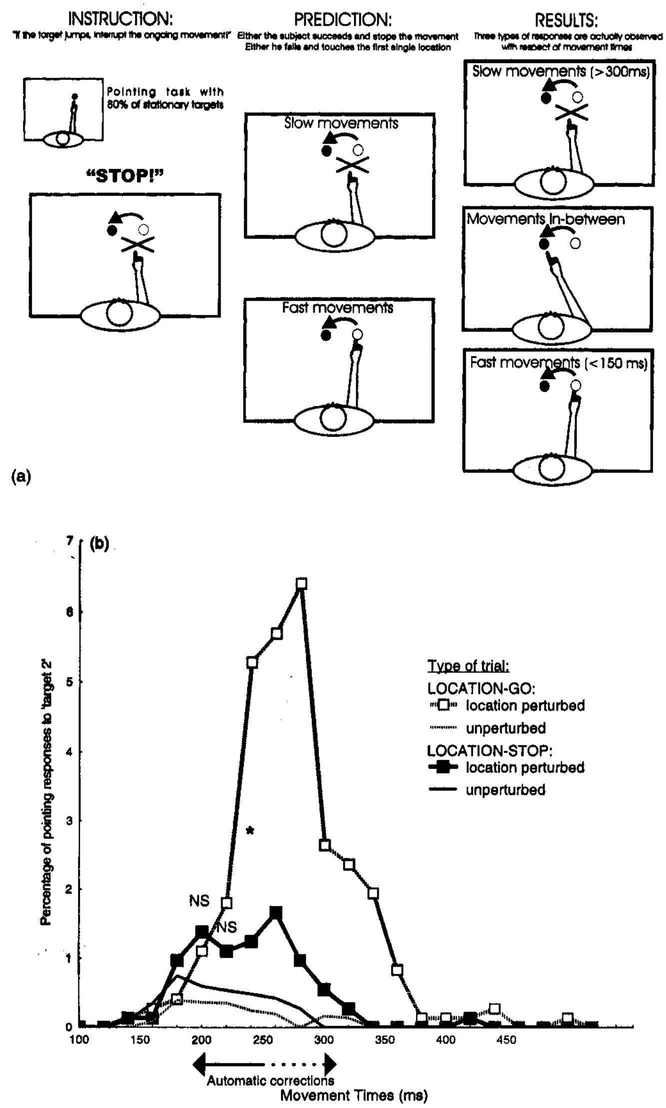


Fig. 4.13 An automatic pilot for the hand.

(a) Schematization of the 'location–stop' protocol, predictions, and results. *Left column*: Protocol. During a pointing task with a 300-ms movement duration constraint, the target could be displaced unexpectedly to the right or to the left at movement onset (in 20% of the trials). The instruction was to stop the ongoing movement whenever the target jumped. *Central column*: Predictions. Slow movements should allow subjects to stop their movement and not to touch the screen, whereas too-fast movements should not be affected by the target jump and thus should touch the programmed target location. *Right column*: Results. Three types of motor responses were successively observed when movement time increased. As expected, subjects touched the first target location for the fastest movements, whereas jump was thus irrelevant for this task. A strict compliance with the 'stop' instruction would imply that subjects would either succeed in stopping their movement or fail to interrupt their action and therefore reach the primary position of the target (Fig. 4.13(a)). In striking contrast to this prediction, a significant percentage of corrective movements were performed in the direction of the target jump in spite of the 'stop' instruction (Figs 4.13(a), 4.16). After touching the displaced target, subjects were fully aware of their mistakes and spontaneously expressed a strong frustration.

We explored whether the ongoing hand movement was corrected or interrupted with respect to movement times. Sampled movement times ranged from about 100 to 450ms with a Gaussian distribution; they corresponded to movement speeds because the distance between targets and starting point was constant in the experiment. Fig. 4.13(b) shows the number of corrected movements with respect to movement durations. Since they occurred in a restricted temporal window, escaping the slower processes of voluntary interruption, the involuntary corrections resulted from a failure to inhibit an automatic process of on-line visuomotor guidance. This 'automatic pilot' (see also Place 2000), systematically activated during movement execution, led subjects to produce disallowed corrective movements over a narrow range of movement times between about 150 to 300 ms. Over a given temporal window (about 200–240 ms), the same rate of correction was found in this location–stop condition and in a control 'location–go' condition where subjects had to correct the action in response to the target jump. Only movements slower than 300ms could be fully controlled by voluntary processes. In contrast to this normal pattern, a patient with a bilateral lesion of the posterior parietal cortex (Fig. 4.14) showed a lack of on-line automatic corrective processes, whereas intentional motor processes were preserved (Pisella *et al.* 2000: Exp. 3). This allows us to conclude that fast movements are controlled by a posterior parietal 'automatic pilot' (PAP) located in the dorsal stream. By contrast, slow movements are controlled by intentional motor processes that remain largely independent of the posterior parietal cortex. Accordingly, frontal patients tested on the same tasks exhibited a complete loss of intentional inhibition of their automatic corrections (see Pisella *et al.* 2000). Thus the notion of automatic pilot extended that of 'hand-sight' in the sense that it refers not only

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they had enough time to intentionally stop their movement during slow trials. However, an intermediate class was also observed, in which subjects performed a significant number of unwilled corrections. (b) Distribution of the unwilled automatic corrections performed in response to unexpected target jumps. Comparison with a control 'location–go' condition in which another group of subjects faced the same stimuli set but were instructed to perform corrections in response to the target jumps. The percentage of corrected pointing responses was calculated with respect to the total number of perturbed and unperturbed trials performed by 6 subjects. Corrected movements in response to target jumps appeared for the movement duration of 150ms and became significant with respect to the motor variability observed in fast, unperturbed trials (speed–accuracy trade-off law) for the movement duration of 200 cms in both location-stop and location–go conditions. Automatic corrections were produced by the location–stop group until movement times of about 300ms, which allow voluntary control to fully prevail over automatic visual guidance. A total of 9% of all the perturbed trials were redirected toward the second location of the pointing target in this stop condition. For movement durations between 200 and 240ms, the correction responses were produced at the same rate by the location–go group (in accordance with instruction) and by the location–stop group (irrepressible reaction despite the instructed stop response). This indicates that these fast motor corrections result from the same automatic pilot in both groups of subjects. (Adapted from Pisella *et al.* 2000.)

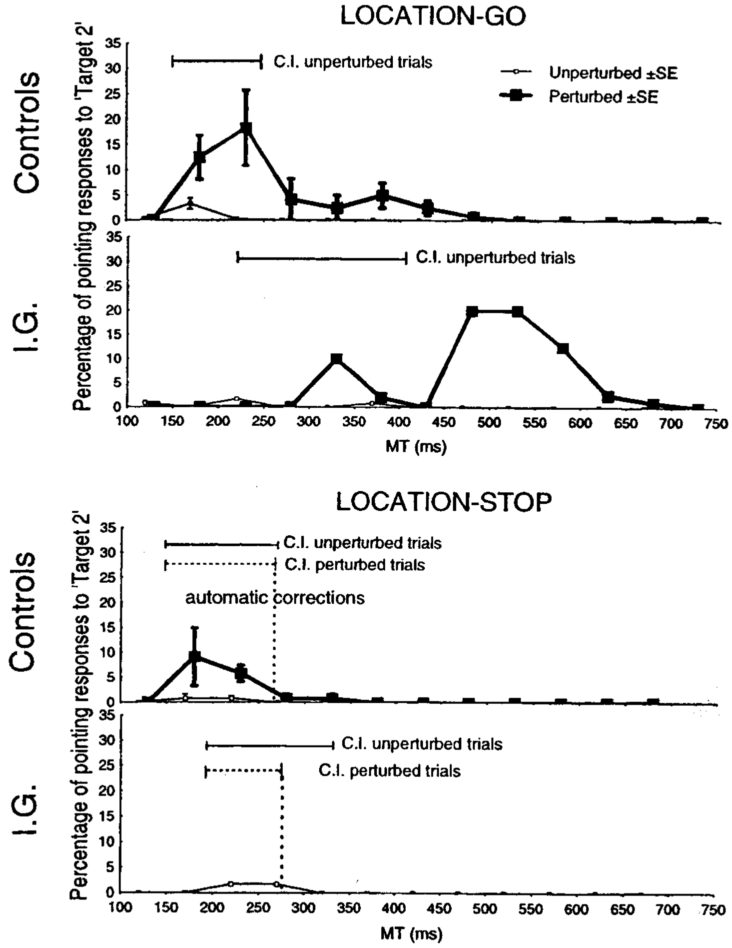

Fig. 4.14 Specific disruption of automatic corrections following a bilateral parietal lesion. This set of figures illustrates the pointing performance of three control subjects compared with a patient, IG with bilateral optic ataxia, in the 'location–stop' and in a 'location–go' condition where correcting movement toward the second target location was instructed. For each condition, the horizontal bars indicate the 95% confidence intervals of movement time computed for all stationary targets. In the lower part of the figure, the vertical dotted line indicates the upper edge of the 95% confidence interval of movement time computed for all non-interrupted perturbed trials (displayed as a dotted horizontal bar). When correction was instructed (upper panel), control subjects mainly produced corrections without increasing their movement time with respect to unperturbed trials (horizontal bar), whereas most of the corrections produced by the patient IG caused a large increase of movement duration. When the stop response was instructed (lower panel), the patient produced no corrective responses, whereas about 10% of the perturbed trials elicited disallowed corrective responses in the controls. For the interruption response, the patient exhibited a performance similar to normal subjects (vertical dotted lines). (Adapted from Pisella *et al.* 2000.)

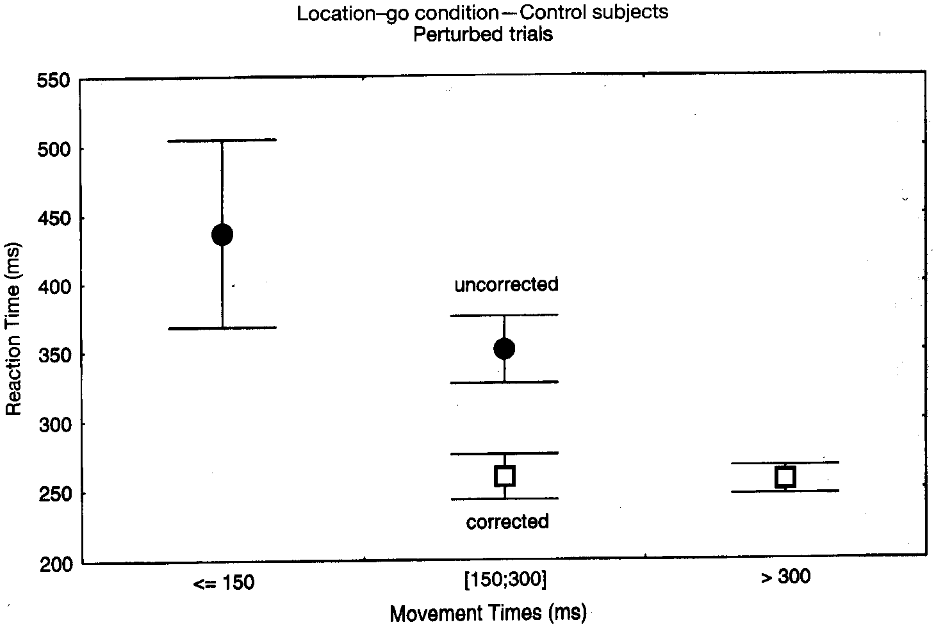

Fig. 4.15 Interaction between reaction time and movement on-line control. Mean latencies of the responses given to target jumps with respect to three classes of movement times during a pointing task. Motor correction was instructed in response to target perturbation in location. A post-hoc classification of corrected versus un corrected movements showed that they corresponded to significantly different reaction time values.

to unconscious visual processing by the action system, but also to an autonomous use of visual information which bypasses and even counteracts intention.

4.6.3 Interaction between movement preparation and execution

In the 'location–go' condition described above, subjects faced the same unpredictable target jumps occurring at movement onset but were instructed to redirect their ongoing movement toward the second location of the target. Figure. 4.15 shows that whether perturbed trials were corrected following the target jump depended on their movement times and their reaction times. Three motor phases were identified with respect to movement times. Movements faster than 150ms were ballistic and always reached the initial location of the target. No reaction was observed in response to the target jump. For durations between 150 to 300 ms, both corrected and uncorrected movements were observed. On-line reaction to the perturbation became possible but errors were still observed. All movements lasting more than 300 ms correctly responded to the target jump.

Figure 4.15 shows that for the same movement time interval, corrected pointings tended to exhibit shorter latencies, that is, shorter durations available for movement programming. These short-latency movements may have been less precisely or less rigidly programmed and they were consequently more sensitive to the on-line visuomotor guidance. In contrast, movements that benefited from a longer and finer programming phase were less reoriented on-line by the automatic pilot in response to the target jump. Long-latency movements appeared therefore to be more rigidly executed as they were better programmed. Accordingly, they showed no flexibility to respond to the target perturbation and reached the initial target location.

4.6.4 Conclusion

As a conclusion, in addition to the anatomical connectivity between areas, we have to take the timing of the activation of cortical networks into account. As the action system seems to benefit from overall faster processing than the identification system, dissociation between action and cognition can result from time factors. Timing and speed-constraints seem to be the keys for a ventral/dorsal dissociation in the cerebral network. The participation of a given area in an anatomical network does not imply that it is absolutely necessary to the task being considered. Temporal constraints may be a reason for a connected area not to participate in a process (but other reasons can be evoked, such as a particular configuration of the network, as shown at the beginning of Section 4.6).

4.7 Recipes

The current chapter is based on a controversy between behavioural evidence and neuroanatomical data and we have proposed that temporal variables can provide a way to reconcile these two lines of evidence. However, numerous other parameters have been evoked throughout the previous sections. We found it useful to take an inventory of these parameters and attempt to classify them in order to compile a user's manual for researchers interested in the relationship between sensorimotor and cognitive processes. For example, these directions for use should be particularly helpful in the field of visual illusions, where a controversy is growing between the arguments for dissociation versus integration of the two visual systems. To enable valid comparisons between experiments, attention should be paid to the use of comparable conditions among the many axes that will be listed below. These recipes could also prove beneficial in a rehabilitation context. In patients with one of the two systems damaged, they can be used to set optimal conditions allowing them to achieve better performance by recruiting residual visual-to-motor networks. Activating these residual functions could provide a means to activate the organization of compensatory mechanisms, and thus become a first step of re-adaptation processes.

4.7.1 Brain lesion

One obvious way to specifically isolate the dorsal stream is to study an individual with a lesioned ventral stream. Reciprocally, one obvious way to specifically isolate the ventral stream is to study an individual with a lesioned dorsal stream. As shown above, the neuropsychological double-dissociation observed between optic ataxia and visual agnosia has provided a key argument for building up the notion of a perception/action dichotomy on the top of the ventral/dorsal segregation. In the absence of one of the two visual systems, the processing performed by the other one can be expressed in the most pure fashion. In the same way, primary sensory lesions, such as encountered in action-blindsight and action-numbsense, seem specifically to restrict visual processing to the action system. It would be tempting to propose that it should be easier to study the properties of the dorsal stream in patients with blindsight rather than in patients with a bilateral ventral stream lesion. Indeed, neurologists much more frequently encounter hemianopsia, which is a prerequisite to blindsight, than the kind of ventral stream lesion exhibited by DF (see Milner and Goodale 1995). However, the dissociation observed in this patient is more pronounced than that observed in action-blindsight patients (see Rossetti 1998). Although both types of patient fail to produce significant verbal guesses about the object property being tested, Fig. 4.2 illustrates the greater variability observed in the motor task for a blindsight patient. This difference can be attributed to the different lesion sites. A V1 lesion is responsible for a full loss of cortical visual inputs, whereas a ventral lesion should leave the dorsal stream intact. In the case of blindsight, the only input to the dorsal stream appears to arise from subcortico-cortical projections (see Fig. 4.5), which obviously do not provide a normal input. Conversely, a difference may be noted between the two types of patient for the matching task, the performance also being poorer in action-blindsight than in visual agnosia (see Fig. 4.2).

4.7.2 Specific inputs

As specific dorsal versus ventral brain lesions can result in a pure activation of one of the two visual systems, the functional properties of the anatomical network suggest that some visual features can selectively activate these systems. For example, it is known that most of the neuronal activity related to colour processing is found in the ventral stream, whereas the processing of location would be more specific to the dorsal stream (Heywood, Shields, and Cowey 1988; Ungerleider and Mishkin 1982).

In a pointing experiment, Pisella *et al.* (2000: Exp. 2) tested whether the parietal automatic visuomotor guidance would extend to other visual attributes than target jump. In particular, would it also be observed when the change in target location is encoded through a chromatic perturbation? To test this, a green and a red target were presented simultaneously in the two positions used for the location–stop task. The subjects were instructed to point at the green one, and the colour of the two targets could be unexpectedly interchanged at movement onset. As the 'location–stop' group, subjects in the 'colour-stop' group were instructed to interrupt their ongoing movement in response to the perturbation. In contrast with the 'location-stop' group, no automatic corrective movements were observed in the 'colour–stop' group (Fig. 4.16). It was concluded that only intentional corrections can be produced on the basis of a colour cue and that the visuomotor transformations of the hand's 'automatic pilot' may be specific to location processing and spatial vision. This specificity for 'dorsal attributes' can be related to the partition of magnocellular and parvocellular inputs between the dorsal and the ventral stream. Another related explanation is that this specificity is due to the processing time required for 'ventral attributes', which is not compatible with the expression of automatic processes. Indeed, irrepressible visuomotor corrections result not only from their automaticity (the processes of visuomotor guidance are inherent to movement execution) but also from their high speed relative to the slow process of voluntary control. It may be hypothesized that normal subjects produce unintentional corrections because the slow intentional inhibition process from the frontal lobe leaves enough time for the fast automatic corrective processes to alter the motor output.

It is interesting to consider the strong contrast between the absence of a colour effect on the PAP (Pisella *et al.* 2000) and the significant colour guesses performed by blindsight patients (Stoerig and Cowey 1992). The main difference between these two experimental situations seems to lie with the type of response investigated. In the case of the Pisella *et al.* study, movements are all programmed and initiated before the relevant event (target change in colour or location) appears. Therefore the target perturbation is only relevant to movement guidance and it is found that colour processing does not affect on-line motor control. In the case of colour-blindsight, simple responses have to be simply initiated (and there is no proper execution control in simple key pressing). This discrepancy suggests that different sensory coding can be involved in different motor responses, and specifically in action preparation versus execution. In the same way, the use of simulated object jumps in conditions where a coloured light indicated which object to grasp from an array of several objects (e.g. Paulignan *et al.* 1991) should be reinterpreted in the light of the Pisella *et al.* (2000) results. The abrupt changes observed in the trajectories obtained by Paulignan *et al.* indicate that the ongoing movement was interrupted and replaced by a secondary movements directed towards the new object to grasp. Indeed, conditions where a real object displacement (and not a colour code) was triggered at movement onset gave rise to much smoother trajectories (Gréa *et al.* 2000), which are compatible with the activation of the automatic pilot. This is confirmed by the observation that these corrections are completely disrupted following a posterior parietal lesion (Gréa *et al.* 2002).

To summarize, using colour stimuli is more likely to activate the cognitive than the sensorimotor system. The on-line control of action has specific access to metric object properties, but remains unaffected by categorical properties such as colour. The issue of depth apprehension will be addressed in a further section (context processing).

4.7.3 Specific outputs

The study of the dorsal–ventral dissociation in the motor context enables us to distiguish specific motor abilities, which are preserved by visual agnosia and blindsight patients, from other types of motor responses. These patients, with impairment of the ventral stream, remain able to direct an action and even to adapt the hand to unidentified or even unseen objects. The preserved, immediate goal-directed action thus seems to be implemented in the dorsal stream. In contrast, matching, delayed, slow, and indirect motor responses are performed very poorly by these patients. Several types of indirect (in space) action have been tested.

In action-numbsense, the patient was unable to indicate where he was stimulated on a drawing, whereas he pointed at an above chance level to these unperceived stimuli in a direct pointing task (Rossetti *et al.* 1995, 2001; Fig. 4.3). A related type of response is derived from the classical antisaccade paradigm. When subjects are requested to make a reverse movement with respect to what would be a direct action, they usually perform with a reduced accuracy. Interestingly, the pattern of errors observed for visually guided antisaccades is similar to that of the memory guided antisaccades (Krappmann 1998). This result is again coherent with the observation that movements shifted in space share their representation with movements shifted in time with respect to direct action. This idea was further confirmed by experiments investigating antisaccades in a visual agnosic patient (DF). Dijkerman *et al.* (1997) observed that DF was performing accurate saccades in natural conditions but was strongly impaired for delayed and antisaccades (Milner, Dijkerman, and Carey 1999b). More recently the same idea was applied to hand pointing. As in the Pisella *et al.* study (2000), it was shown that fast movements are under the control of an automatic process. Interestingly this automatic guidance could participate in the direct pointing performance, but counteracted the anti-pointing task derived from the antisaccade paradigm (Day and Lyon 2000). Schneider and Deubel (this volume, Chapter 30) have also shown that the automatic orientation of attention that is observed around the location of the target of a saccade being prepared, is not observed in the case of antisaccades. Other experiments have also shown that anti-pointing performance in response to masked stimuli would be poorer than direct pointing (Price *et al.* 2001).

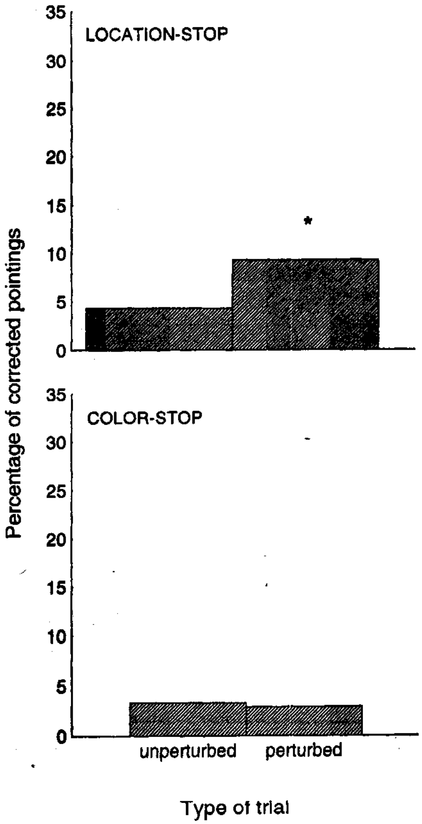

Fig. 4.16 Specific inputs.

(a) In response to target jumps, unwilled correction movements occurred even when countermanded (location–stop condition). Corrections were performed to a significant extent as compared to unperturbed trials despite the opposite instruction.

(b) A colour switch between two targets ('colour-cued' target jump) was not able to elicit automatic corrections. Although the change in target location was physically the same as in the 'location–stop' condition, no significant corrections toward the new green target were observed compared with unperturbed trials. In this condition, responses to the perturbation always complied with the stop instruction. (Adapted from Pisella *et al.* 2000.)

Another type of action to consider is pantomime. In the Goodale *et al.* (1994) study of delayed actions in DF and normals, it was observed that the kinematic structure of pantomimed movements was similar to that of movements delayed by 2 or 30 s. 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.

The effect of subtle changes in the type of motor output requested from subjects can also strongly affect the type of processing involved. A rather clear example has been provided by Bridgeman (this volume, Chapter 5) when he compared communicative pointing to instrumental pointing. Subjects could be asked either to point at an object or to really act on it to push it down. The latter condition provided a stronger difference from the perceptual tasks used in the same experiments, suggesting that the former type of response could result from a less pure activation of the sensorimotor system.

One should note that the issue of the reference frames used by the two systems (an egocentric one for the action system and an allocentric one for the perceptual system) has been more or less implicitly addressed in several sections of the present review, and is strongly dependent on the type of task performed (for recent reviews, see Desmurget *et al.* 1998; Goodale and Haffenden 1998).

From the strong effect of the response on the type of process involved in an action, it seems easier to activate the cognitive mode rather than purely the sensorimotor mode of action control. Any experimental conditions departing from the natural, direct goal-directed action appear to less selectively activate both sensorimotor and cognitive systems in various proportions. As will be addressed below, this is true not only for spatial but also for temporal factors. One interesting parameter to consider when different tasks are compared is the respective amount of programming versus on-line control that is required by the task. Clearly reaching tasks, directly aimed at a real object (Day and Lyon 2000; Goodale *et al.* 1986; Pisella *et al.* 2000; Prablanc and Martin 1992), would generate the maximal activation of on-line control processes.

4.7.4 Delaying the action

'Delaying an action can transform a theory.' Agreeing with this quote from Goodale *et al.* (1992), the review presented in the previous sections demonstrates that there are numerous examples of a dramatic effect of delay on sensorimotor processes. Probably time appears to represent the most crucial dimension in the control of sensorimotor–cognitive interactions. Two conclusions can be reached on this issue: (1) sensorimotor representations are short-lived; (2) cognitive representations take over when a delay is introduced. In terms of recipes, one should note that the titration of the effect of delay on action seems to depend on the sensory modality. As shown in Fig. 4.12, the crucial delay to switch from a dominant sensorimotor activation to a dominant cognitive control would lie between 1 and 2 s in the tactile modality. Other experiments with the same action-numbsense patient showed that this delay was of about 4-s for the proprioceptive modality (Rossetti 1998; Rossetti *et al.* 2001).

In the visual modality, most experiments used delays of several seconds (e.g. Bridgeman, this volume, Chapter 5; Goodale *et al.* 1994; Milner *et al.* 1999a). A 2-s delay appears to be long enough to strongly affect the motor output. Fewer experiments tested delays below this value, but it seems that a delay value of about 500ms would be sufficient to generate sensible changes in the type of motor output (see Fig. 4.11; see Krappmann 1998; Rossetti 1998; White *et al.* 1994).

There is a large amount of converging evidence, arising from three sensory modalities, that the sensorimotor representation can only be expressed within a short delay following stimulus presentation, providing a very simple recipe to study sensorimotor versus cognitive control of action. Another aspect worth mentioning here is that introducing a delay between the stimulus and the response should rapidly disrupt the ability to process on-line control of the action.

4.7.5 Speed constraints

In the same way as normal actions can be delayed, a speed constraint can be added on any given task in order to explore short time-range phenomena. For example, the Pisella *et al.* (2000) and the Day and Lyon (2000) experiments showed that only very fast movements could be considered as fully driven by an automatic pilot. Different values have been reported in the literature about the minimum movement duration compatible with on-line corrections (see Day and Lyon 2000; Pisella *et al.* 2000; Rossetti 1998). This value depends on the type of task, on movement amplitude, and on the experimental set-up. For example the value of about 200ms reported by Pisella *et al.*, obtained for vertical pointing against gravity (and thus with higher torque values) on a computer screen, is higher than the usual value obtained in the horizontal plane, closer to 100ms (e.g. Desmurget *et al.* 1996; Gréa *et al.* 2000; Prablanc and Martin 1992). In terms of recipe, values of movement time between 200 and 250ms in the vertical plane (Pisella *et al.* 2000) and between 125 and 160ms in the horizontal plane (Day and Lyon 2000) seem to correspond to movements dominated by the parietal automatic pilot for the hand.

4.7.6 Visual illusions

The two experiments on the effect of static visual illusions on action presented earlier in this chapter (Aglioti *et al.* 1995; Gentilucci *et al.* 1996) have given rise to a flurry of research on this topic. Other related experiments, using illusion-like phenomena linked to motion perception, are summarized by Bridgeman (2000). Until now we have referred to only a few experiments on visual illusion and action, but we have counted at least 12 articles published on this topic between 1999 and mid 2000. Most of these studies replicated the initial findings made by the first two papers, namely that the effect of visual illusions appears to be stronger on perceptual reports than on action performance. Nevertheless, a number of interesting features emerge from this hot topic, which may help the reader to prepare his own illusion recipe.

First, a variety of visual illusions have been investigated, for which there is a relatively weak effect of the illusion on action. In addition to the Titchener's circle (or Ebbinghaus size-contrast illusion) effect on grasping (Aglioti *et al.* 1995; Haffenden and Goodale 1998, 2000a) and pointing (Fisher, unpublished), the Müller–Lyer illusion has been studied during both pointing (Gentilucci *et al.* 1996) and grasping tasks (Otto-de Haart, Carey, and Milne 1999; Westwood, Chapman, and Roy 2000). Grip aperture during prehension was also shown to remain unaffected by the Ponzo illusion (Jackson and Shaw 2000) or less affected than perception by the horizontal–vertical illusion (Vishton *et al.* 1999: Exp. 1, but see below). Other illusions have been used to show that the positioning of the grasp remained less sensitive than perceptual tasks (Ellis, Flanagan, and Lederman 1999).

Also, the developmental aspect of these effects was addressed by investigating the sensitivity of children to illusion (Kovacs 2000). It was found that children were less sensitive to the perceptual illusion than adults. The authors suggested that this may indicate a slower maturation of the ventral stream with respect to the dorsal stream of visual processing, which would be another way of supporting the dissociation between the two visual systems.

Second, several limits of the relative insensitivity of the action system to visual illusion should be considered. In order for a visual illusion to produce no effects on action, one has to speculate that the neurological substrate that is responsible for generating the illusion lies somewhere around the ventral visual system. However, some illusions have been described as affecting very early visual processes, even at the retinal level (see Gentilucci *et al.* 1996). If an illusion does affect the visual processes taking place between the retina and the primary visual cortex, then the effect of this illusion (or at least of some of its components) would feed both the dorsal and the ventral stream, and one would expect action to be affected by this illusion. In the same vein, one has to address the issue of the visual subsystem that is involved in the action. For example, it has been shown that the Ponzo illusion would affect grip size but not the force programmed to lift a target object (Jackson and Shaw 2000; see also Brenner and Smeets 1996). It is interesting to note that grip size is one of the metric properties of space that has been proposed to be processed within the dorsal stream (see Milner and Goodale 1995; Rossetti 1998), whereas the object weight has to be inferred from previous learning of the relationship between objects' appearance and their weight. This association has to involve other structures than just the dorsal stream, for example the ventral stream and its connections to memory systems (see Jeannerod *et al.* 1994). Therefore it involves more off-line processing (prior to the action) than on-line motor guidance.

Third, the issue of relative versus absolute coding of object metrics has been raised by Pavani *et al.* (1999), Vishton *et al.* (1999), and Franz *et al.* (2000). They observed that previous studies with the size-contrast illusion (the Titchener circles) presented subjects with two stimuli to compare in the perceptual task, whereas only one object was used in the pointing task (Aglioti *et al.* 1995). They performed experiments in which only one illusory object was presented at a time. Pavani *et al.* (1999) and Franz *et al.* (2000) used the size-contrast illusion and found that both perceptual and motor responses were affected by the illusion. Vishton *et al.* (1999), using the horizontal–vertical illusion, extended the initial observation made on the size-contrast illusion when two stimuli were presented at once, but showed that the perceptual effect could be suppressed when only one element of the display was presented. They also observed that grip scaling was strongly influenced by the illusion when subjects had to scale their movements to both vertical and horizontal dimensions of the triangular figure. The more complex visuomotor processing required by this latter task suggests that it may be assimilated to matching tasks in which the hand has to reproduce an object size between two fingers. In contrast to natural grasping action, these tasks have been proposed to involve ventral stream processing (Haffenden and Goodale 1998; Milner and Goodale 1995). Other experiments have shown that such tasks are much more influenced by illusory context than natural direct actions (Westwood *et al.* 2000). However, it remains that a relative judgement made between two stimuli seems to be more sensitive to illusion than the absolute estimate required by a simple action to one stimulus.

Fourth, another possible confound has been raised to account for the discrepancy observed between several studies. Haffenden and Goodale (2000a) have explored the effect of the target-surrounding elements gap in the Titchener illusion. They first showed that a smaller target-flanker gap produced an apparent effect on grip scaling (see also Pavani *et al.* 1999). Then they investigated the effect of two neutral rectangular flankers that could be presented along the horizontal or the sagittal axis of the object. While a perceptual effect was observed in the two conditions, a motor effect appeared only when the flanker lay on the sagittal direction, that is when it could interfere with the two grasping fingers. The effect of these flankers on action also varied with the target-flanker distance, suggesting that elements from the 2-D stimulus could be considered as potential obstacles by the action system. Alternatively the difference between the effects of a visual context aligned with the depth or the frontal axis presented on figure 4.17 may explain such a result. These findings are likely to explain the variety of the effects reported in the literature.

Altogether there seems to exist a reproducible effect of visual illusion on perception while the action system is less sensitive to illusory context. The variety of results found in the literature suggests that careful attention should be paid to the design of the stimuli, however, since the perceptual and the action systems may be sensitive to different stimulus properties. For example, the action system appears to be sensitive to motion-induced illusions (Smeets and Brenner 1995) and to depth cues (see below).

4.7.7 Context processing

A tentative explanation for the effects of illusions on perception and action is that only the former system would be influenced by visual context. Arguments for this interpretation come from experiments performed with illusory set-ups. For example, the Roelofs effect was used by Bridgeman to compare perceptual and motor effects (Bridgeman, this volume, Chapter 5). As for illusions, a pronounced effect was found for perceptual estimates, whereas no significant influence was observed on pointing responses. It has therefore been argued that the sensorimotor system would not be influenced by the visual context, as this seems to be the case for immediate (vs. delayed) pointing (e.g. Bridgeman 1997, 2000, this volume, Chapter 5; Rossetti 1998).

However, several examples can be found of an influence of visual context on action. Several levels of context complexity may be considered here: intrinsic, extrinsic, and inferred contexts. First, the minimum level of visual context that can be tested during a simple action seems to be the size of a target. When subjects have to point to targets of different sizes, they exhibit a spontaneous modulation of their movement time as a function of both target size and distance. The expression of this relationship has been provided by Fitts (1954). If one accepts that the size of a target is the simplest context in the task of pointing to the centre of the target, then the effect of target size on pointing may be considered as an effect of intrinsic context. Not only normals but numerous types of brain damaged patients do comply with Fitts's speed–accuracy trade-off law. This is also true for schizophrenic patients, who are known to be impaired for context processing (Saoud *et al.* 2000).

Second, the effect of target size applies to sequential movements. The first stroke of a two-stroke sequence is altered even if the size of only the distal target of a two-stroke movement is manipulated (e.g. Marteniuk *et al.* 1987). This robust effect even applies to schizophrenic patients (Saoud *et al.* 2000).

Third, another example is derived from the experiments designed by Bridgeman about the Roelofs effect, where an illusory displacement of a target, caused by a change in position of a surrounding rectangular frame, affected phenomenological experience of target position, but not pointing responses (Bridgeman 1991; review in: Bridgeman 2000, this volume, Chapter 5). One of the conclusions from this work was that the sensorimotor system would be insensitive to the visual context. However, this interpretation stands in contrast with the reported finding that visual context influences the perception of the egocentric distance of a visual stimulus (e.g. Coello and Magne 2000). In order to unravel this issue, a recent study addressed the question of whether the dissociation between verbal identification and reaching holds when the illusory target's displacement is radial instead of horizontal, as was the case in the original report (Bridgeman 1991). The task for the participants was to verbally determine whether the second target was presented in the same location as the first one, or to make a non-visually controlled pointing movement towards the second target. The results showed that a similar illusion of target displacement was obtained with verbal reports when the illusion stemmed from a horizontal or radial rectangle displacement (thus confirming Bridgeman's findings). However, the striking outcome was that no effect of the rectangle position was observed in motor performance, but a very significant effect was obtained with the displacement made along the radial axis (Fig. 4.17). This latter effect confirmed the involvement of visual context in distance but not direction perception (Coello and Magne 2000). In addition, the amount of the illusion-induced effect was identical in the perceptual and the motor tasks. This finding has an important implication for theories of visual perception, in the sense that it shows that the distinction between visual perception for identification and visual perception for action is task-and-stimulus

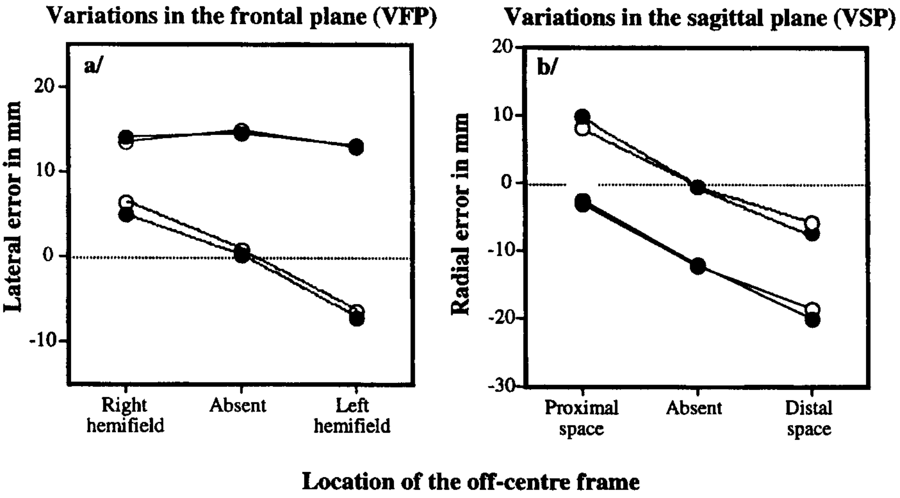

Fig. 4.17 Context processing in the depth dimension. Participants were shown for 0.4s a visual target (diameter 8 mm) presented at 23cm and centred according to a radial or horizontal rectangle. Black and white symbols depict the results obtained for the two test-targets. Then both the target and the rectangle vanished for a period of 0.5ms, before reappearing for 0.4s at a similar or different location. Furthermore, the target was presented alone, or inside an uncentred rectangle (96×38mm), displaced either on one side or the other with respect to the target. The task was to verbally determine whether the 2-D target was in the same location as the first, or to make a non-visually controlled pointing movement towards it. Perceptual and motor responses exhibited the same bias only when the rectangular frame was presented in the radial orientation: the pointing distance was overestimated when the perceptual matching of the target was overestimated, and vice versa. (From Coello *et al.* 2001.)

dependent. It should be emphasized though, that the absence of the visual target at the time of movement completion may also have reduced the influence of on-line motor control on movement guidance.

Other experiments have shown that the depth dimension has a specific status with respect to the relations between perception and action. Dissociations can be observed between cognitive and sensorimotor responses to depth stimuli (see Dijkerman *et al.* 1998). However, interesting comparisons can be made concerning the ability of DF (the case with bilateral visual agnosia) to perform orientation judgements. She seems to perform better on perceptual judgements of orientation in depth under binocular viewing conditions than she would have when judging the orientation of an object (or slot) in the picture plane (Dijkerman *et al.* 1996; Goodale *et al.* 1991). On the basis of DF's performance it seems that there is less difference between perception and action with regard to the orientation of objects in the depth plane than in the frontal plane (see also Carey, Dijkerman, and Milner 1998).

Altogether, the effect of context on action seems to strongly depend on the experimental procedure. As shown by simple or sequential pointing, intrinsic properties of the goal of an action do affect motor parameters. More distal contexts, such as those responsible for the generation of static illusions or illusory movement, appear to be less effective on action, unless the depth dimension is considered. As mentioned in the visual illusion recipe section, the most relevant issue here appears to be the level of processing concerned in each type of context. Intrinsic context such as target size or position in depth refers to a primary metric property of objects, whereas more complex contexts, such as a target array or an illusory set-up, imply integration mechanisms over time or space. In the latter case of the complex integration of a spatio-temporal context (cf. Fig. 4.17), only delayed actions are strongly affected. One should pay attention to these parameters when building an experiment to investigate the role of context on action.

4.7.8 Actual versus represented stimulus

A remaining question about the difference between immediate and delayed tasks such as those presented in Fig. 4.10 is whether the observed effects can be attributed to the duration of the target presentation or to the delay from target onset to the response. In other words, does the availability of the target just prior to the initiation of the action in the immediate condition account for the difference between the two conditions? This question was explored in a simple experiment where subjects had their target finger held in place for a given delay prior to the go-signal versus shortly positioned on the target location, followed by a similar delay. A 2-s memory delay was sufficient for the cognitive representation to affect the pointing distribution (as for the 5-s delay shown in Fig. 4.11). In contrast, no such effect was observed for the 2-s duration of the target presentation; that is, when no memorization was required (see Fig. 4.18). In this case, both types of visual representation are available: (1) the cognitive one, because the 2-s delay enabled the subject to encode the target location with respect to the target array, and (2) the on-line sensorimotor one, because the object has just disappeared upon the movement onset. The result (Fig. 4.18) shows that only the sensorimotor one seems to contribute to the motor output. Therefore priority seems to be given to the sensorimotor mode of processing when it is available (as shown by the Pisella *et al.* 2000, results described earlier). This result indicates that the effect of delay cannot be solely attributed to the slowness of the cognitive system, but is also due to the absence of a real target object that has to be represented because sensorimotor processes are short-lived (see Rossetti 1998).

A similar logic can be used to explore the nature of the representation involved in action in neurological patients. In order to test for the ability of optic ataxia patients to process visuomotor information on-line, we performed another experiment with our patient with a bilateral posterior parietal lesion (IG). When IG was asked to delay her pointing or grasping action, she improved her poor ability to perform accurate actions (review in: Milner and Dijkerman 2001). Knowing that the effect of a memory delay is different from that of a long presentation of a stimulus in normals (see Fig. 4.18), we investigated this possibility with IG. She exhibited a better performance in both tasks, suggesting that both the long presentation and the delay enabled her to form a representation of the object that could be used by the action system. Given her lesion, this representation was postulated to be formed via the ventral stream (see also Milner *et al.* 1999a). An interesting question that leads from this is whether it is possible to generate a conflict between this sustained cognitive representation and short-lived motor representations. Together with Prof. David Milner and Dr Chris Dijkerman, an experiment was designed in which an object was presented for 2s, then hidden behind a panel for 8s, then shown again. This procedure improved her grip scaling compared with an immediate action condition. Then a special session was performed in which, in some trials, the small object could be unexpectedly replaced by a large one, or vice versa. The specific question asked here was whether the grip formed by IG would follow the size of the present object or that of

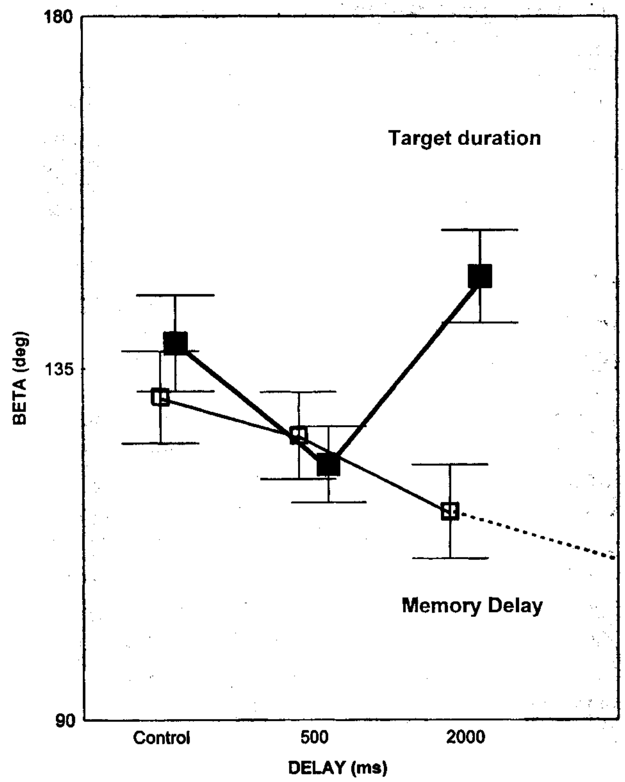

Fig. 4.18 Long presentation versus memory delay. Mean of ellipse orientations (beta in deg, see Fig. 4.8) as a function of various delays between target onset and go-signal, with the target remaining present during the delay (delay = 'target duration') or not ('memory delay'). When the target remained present, for immediate pointings (control), 500 ms or 2 s delays, the orientation of the ellipses remained approximately around beta = 135 deg, i.e. as for immediate pointing movements. In the absence of the target as soon as there was 2 s of memory delay the beta tended to displace toward the orientation of 90 deg (illustrated by the interrupted line). This graph shows that the ellipse orientation fitting the pointing distribution is contingent upon the presence or absence of the target during the delay.

the internal representation formed after the presentation of the initial object in the same trial. The results clearly showed that her grip was initially scaled to her internal representation rather than to the actual object she was aiming at (see Fig. 4.19). Control subjects tested in the same conditions exhibited an on-line grip formation that was adapted to the object present in front of them at the time of the grasp (see also Milner and Dijkerman 2001). In addition to the effect found on grip size, the time to maximal grip aperture was reached earlier in the large→small condition than in the large condition for each of the six control subjects, whereas IG exhibited a similar value in the two conditions. On the particular trials where she 'correctly' opened her hand widely on 'small→large' catch trials, the wide grip aperture actually occurred abnormally late in the movement. This strongly suggests

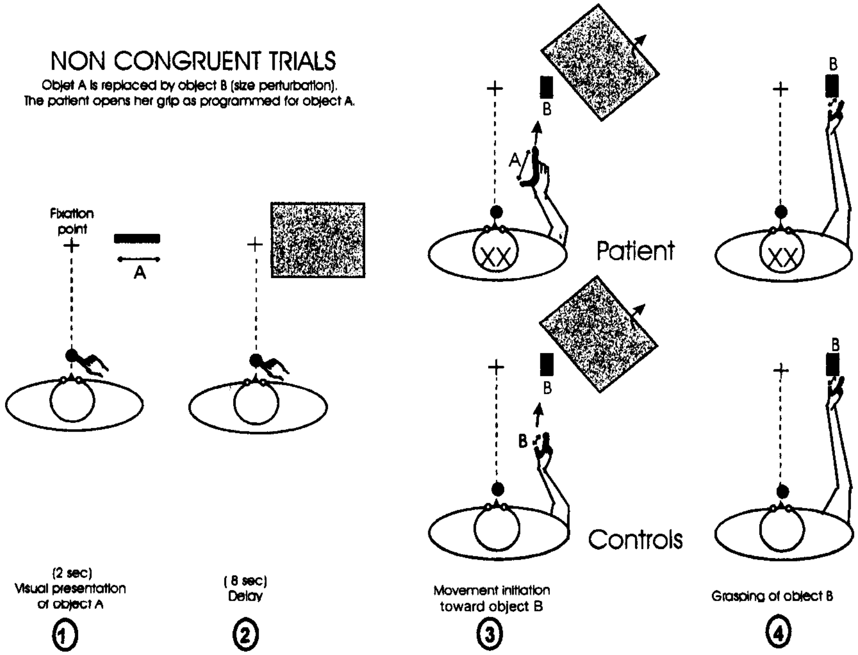

Fig. 4.19 Represented versus actual object. This figure presents the four steps constituting one non-congruent trial of the delayed grasping task, producing a kind of object-size perturbation. In these non-congruent trials, occurring only in 20% of the trials, the object of size A presented before a 8-s delay is replaced by an object of size B for the initiation of the grasping movement. The figure illustrates the results obtained for controls and for patient IG, who has bilateral optic ataxia. IG produced a movement with a grip size based on the first object visualized. She executed her movement quite rigidly as it was programmed during the memory delay, before finally adapting her grasp to the second object. Control subjects were less influenced in their grip size by the first object presented, they rapidly adapted their finger aperture to object B and seemed to behave as in the case of immediate movements toward object B. Control subjects can use the on-line information to perform their movement, whereas the patient with lesion of the dorsal stream seemed to use slower and more rigid sensorimotor processes.

that she was unable to process the change in size that had occurred during the delay fast enough to be able to update her ongoing movement.

These results clearly confirm that sensorimotor and cognitive representation have different time constraints: while sensorimotor representations can be elaborated in real time and are very short-lived, the cognitive representation needs more time to emerge and can be evoked off-line in the organization of action.

4.7.9 Motor and perceptual co-activation

We have referred earlier to experiments where there appears to be a simultaneous activation of the sensorimotor and the cognitive systems in normal individuals and patients (Bridgeman 1997;

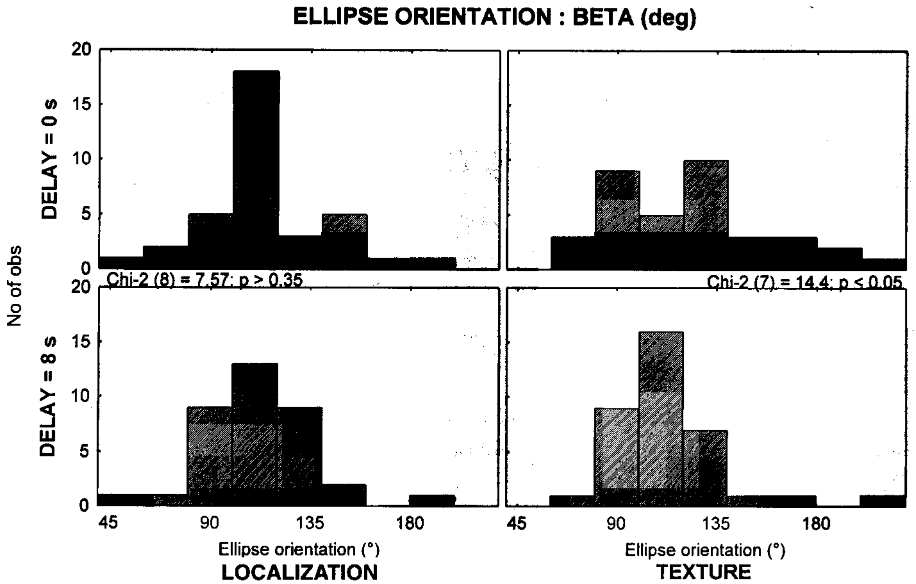

Fig. 4.20 The specific effect of object feature verbalization. As in Fig. 4.9, subjects were requested to produce verbal estimates during a simple pointing to a proprioceptive target. A change in the distribution of the confidence ellipse main axes was only observed when the verbalization concerned the target location (relevant to the action) and not when it concerned the target texture.

Rossetti and Régnier 1995; reviews in Bridgeman 2000; Rossetti 1998). In a further experiment derived from the Rossetti and Régnier study, subjects were trained to identify two target features: location and texture (Pisella *et al.* 1996). During this training, a texture could be presented on any target location, without any systematic association between location and texture. Then on two different days, experimental sessions where performed in which subjects were requested, on each trial, to provide a verbal guess about the current target being presented. The number of verbal errors made during the pointings was similar in the two conditions, suggesting that the two tasks were equally difficult. When the guess applied to target texture, no specific effect was observed on ellipse orientation (see Fig. 4.20). By contrast, a significant modulation of the endpoint spatial distribution was observed when the guesses applied to the target location. This result suggests that for an interaction to be observed between the cognitive and the motor system, experimental conditions have to activate verbal representation of particular features that are relevant to the action being performed. Only in such conditions does the representation elaborated in the cognitive system seem to overwrite the sensorimotor one.

Another observation worth taking into consideration before trying this recipe was made on our action-blindsight (Rossetti 1998) and numbsense (Rossetti 2001) observations. We have seen earlier that the simultaneous motor–verbal task disrupted action performance. We have also had several opportunities to note that, once the subject was asked to provide a verbal guess at the end of a trial, then the following series of trial would show a disruption of performance as well. This is as if the only fact that the patient knew he might have to describe the stimulus activated cognitive processes which interfered with the residual sensorimotor ability.

4.7.10 Complex recipes

Several of the ingredients described in the previous recipes can be combined into more complex recipes. For example, the effect of illusion and that of delays can be coupled. A detailed subject-by-subject analysis of the experiment testing the effect of the Roelofs effect on action 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 (Bridgeman 2000), replicating an earlier finding made on eye movements (Wong and Mack 1981). This result suggested that subjects might switch from motor to cognitive modes of sensory processing at differing delays after stimulus offset. In an elegant experiment, Gentilucci *et al.* (1996) also showed that introducing delays between line observation and onset of movement proportionally increased the effect of the Müller–Lyer illusion on the pointing response (see Fig. 4.21). It is also very interesting to notice that the influence of the illusion becomes particularly noticeable as the delay between stimulus presentation and movement onset increases.

Another combination of ingredients from the previous recipes was made between a specific input and a specific output, namely colour and movement interruption. To co-activate the direct sensorimotor representation of the target responsible for automatic on-line motor control and the higher level cognitive representation of the same stimulus, we designed an experimental device producing double perturbations of a visual target at movement onset. These double perturbations involved a change in location, mainly processed in the dorsal stream and known to trigger a fast updating of the ongoing action, and a simultaneous change in colour, known to be mainly processed in the ventral stream and implying a categorization process. Unperturbed trials (80%), simple perturbations in either location or colour, and double perturbations were intermixed in each session (Pisella *et al.* 1998b; Pisella *et al.* 1999). Subjects had to point to the green targets, and to redirect their movement if the green target had jumped. The change in colour was associated with an instruction to immediately stop the ongoing movement. The double perturbation contrasts a combination of a dorsal visual input (location) and a dorsal motor response (automatic visuomotor guidance of a goal-directed movement) with a combination of a ventral visual input (colour) and a 'ventral' motor response (stop is a conditional motor response to colour change). On the one hand, a faster processing of the location attribute as with compared with the colour attribute is expected (Pisella *et al.* 1998; Rossetti *et al.* 1997). On the other hand, the 'dorsal' visuomotor guidance inherent to goal-directed execution is swift and automatic, contrary to the arbitrary association of a stop response with the red colour (Pisella *et al.* 2000). The double-perturbation condition therefore brings together the association of specific inputs and specific responses that offers the greatest temporal difference, allowing us to dissociate the systematic corrections driven by the dorsal 'automatic pilot' from the intentional motor control of the movement execution. A long temporal window of automatic behaviour should therefore be observed. The results of six subjects confirmed these predictions. For pointing movements with durations shorter than about 200 ms, no effect of the perturbation was observed. For movement times ranging from 200 to about 280 ms, subjects behaved fully automatically in response to double-perturbed trials: they systematically redirected their movement toward the forbidden displaced target and touched it as frequently as when correction was actually instructed (in response to the simple location perturbation). The instructed response to movement interruption appeared progressively only for slower movements (Fig. 4.22). But finally, in this condition, subjects produced automatic disallowed corrections for movement times ranging from 200 to 450ms (a total of 15% of all trials) and expressed a strong frustration linked to the sensation of being unable to control their action intentionally.

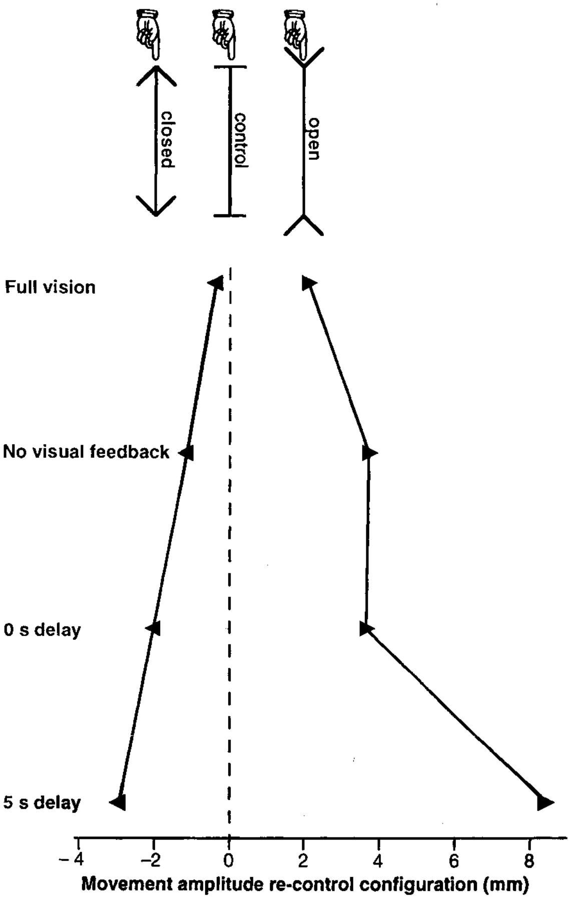

Fig. 4.21 Visual illusions and delayed action. Pointing biases induced by the two configurations of the Müller–Lyer illusion. Movement amplitude tended to increase in the open configuration and to decrease in the closed configuration, i.e. in the same direction as the perceptual illusion. Values plotted 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. (From Rossetti 1998 based on Gentilucci *et al.* 1996.)

These two latter cases of sensorimotor and cognitive coactivations took place at different time-scales. In most of the data reviewed here, it has been shown that interactions between sensorimotor and cognitive processing of spatial information can occur only from the cognitive to the sensorimotor system (Bridgeman 1999; Rossetti 1998). In motor + verbal tasks tested with normals and patients, for example, the response production was affected in an 'all or none' pattern, the semantic representation of the target overwhelming the sensorimotor representation. More recent experiments have shown that the reverse pattern of interaction can be observed on a longer time-scale, through

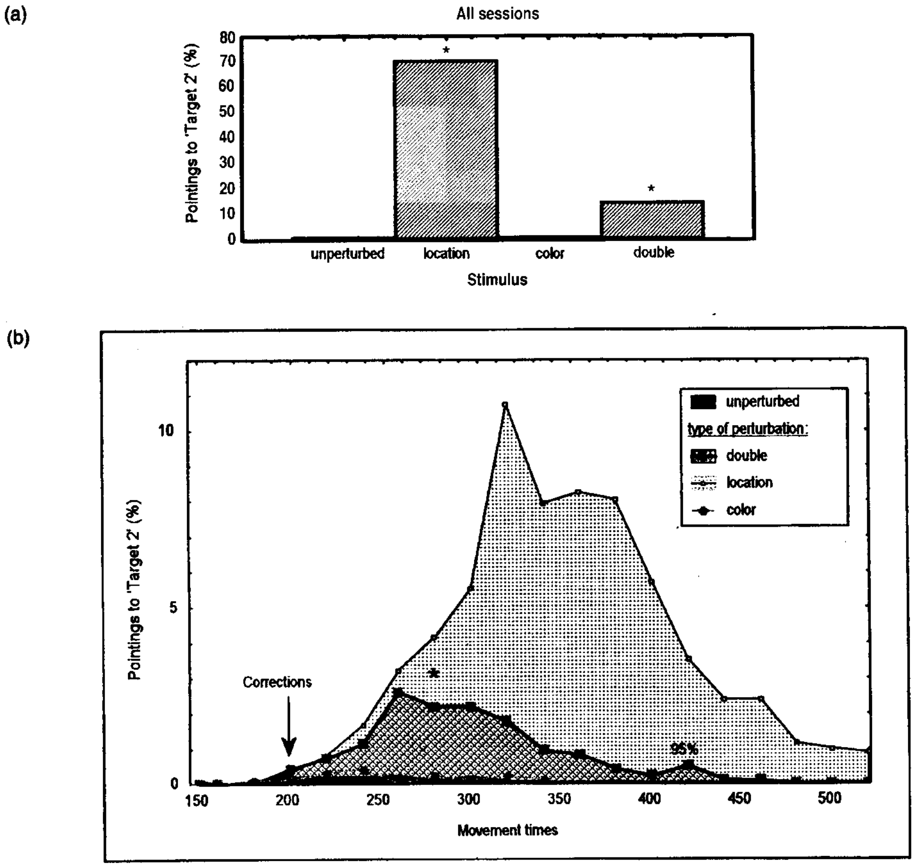

Fig. 4.22 Double perturbation experiment.

(a) Histograms of the percentage of corrected movements for each type of trials. Corrections were produced as instructed in response to the simple target jump (location perturbation) but also, despite the associated stop instruction, in response to the double perturbation.

(b) The automatic corrections escaping subjects' intentional motor control in response to the double perturbation were produced for movement times between 200 and 450ms. Surprisingly, in a temporal window including movement durations from 200 to 280ms, subjects showed the same rate of correction in accordance (in the simple location perturbation) and in contradiction with instruction (in the double perturbation). This result indicated that corrections from this restricted temporal window surely result from the same automatic processes of on-line visuomotor guidance.

adaptative changes (Bhalla and Proffitt 2000; Rossetti *et al.* 1998b). This suggests that several time ranges have to be considered in the discussion of interactions between sensorimotor and cognitive processing of spatial information. As reviewed above, the effect of time can be fully explored by comparing immediate and delayed responses. However, some portion of reaction times inevitably pertains to the production of motor responses, whether produced immediately or delayed. Although reaction times may be short (about 250ms in normals), one cannot exclude the possibility that this period of time is likely to favour an early effect of delay and/or of early semantic representations on sensorimotor processes. The experiments with specific target perturbations during ongoing aiming actions allowed us to explore possible interactions within a shorter time range following the stimulus onset. These series of experiments led us to distinguish programming and control of sensorimotor processes with respect to the direction of interactions between explicit and implicit processes. Programmed sensorimotor processes are more likely to be overwhelmed by cognitive processes. Automatic processes of on-line motor control, however, seem to escape to the influence of cogitive processes during a given temporal window following the target perturbation.

In short, in order to obtain more involvement of the cognitive system in a motor output one may combine several of the ingredients listed above. Such complex recipes typically should associate a time constraint (delayed or speeded action) with any one of the spatial dimension parameters (illusion, context, specific stimuli, or ouputs).

4.8 Concluding remarks

We have examined the link between behavioural evidence for a dissociation of the visual brain in two sensorimotor and cognitive subsystems and the neuroanatomical evidence for a complex and interconnected visual-to-motor network. We have found not only that neuropsychological evidence favours two separate visual systems, but also that it indicates that action, under specific circumstances, can be organized from one or the other of these two systems, confirming that there is 'a dual route to visuomotor action' (Milner and Dijkerman 2001). The numerous results exposed here about the influence of delay or verbalization of specific inputs or outputs, in normals and patients, strongly support the existence of two distinct ways of encoding spatial information for action. Then we have provided recipes to control for the respective contribution of the two visual-to-motor systems to a given motor output. As a conclusion, it appears useful to consider a few neglected aspects of this complex organization of action toward visual goals.

4.8.1 A gradual time effect

Our review of the literature demonstrates that an effect of time can be observed over several time ranges. Figure 4.23 attempts to describe these time ranges. Let us first consider the level of a single action. For the shorter reaction time, and for tasks performed without delay, we have seen that implicit processing provides the only representation that can affect the motor outcome. This exclusive influence of short-lived sensorimotor representations may be carried out by the dorsal stream of visual processing. Then the voluntary control, which is activated more slowly, can influence the motor response, and gradually supplant the pure sensorimotor system. This influence may be supported by the ventral stream, probably through indirect projections made to the motor cortex via the prefrontal and premotor cortex. Different results can be reached if we consider a broader time-scale, which allows for slow adaptative processes to take place through sensorimotor plasticity. Both visuomotor adaptation in neglect patients (Rossetti *et al.* 1998b, 1999b) and ageing (see Bhalla and Proffitt 2000) have been shown to affect the elaboration of explicit cognitive representation of spatial information.

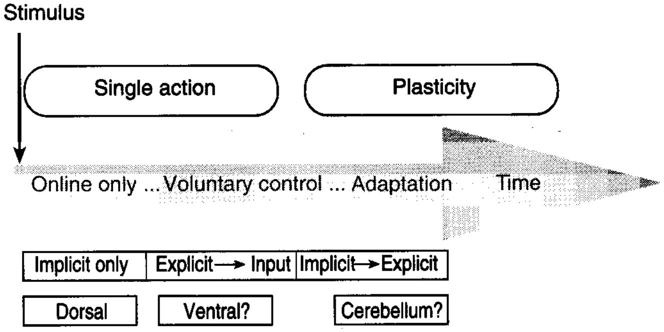

Fig. 4.23 Time constraints and implicit–explicit processing. Tentative synthesis of the temporal constraints on the relationship between sensorimotor and cognitive processing. As reviewed in the present chapter, sensorimotor processing can be performed faster than cognitive processing, which is particularly useful for on-line motor control. The plausible neural substrate for this particular speed seems to be the dorsal pathway. Slower action can be supervised by voluntary control, which implies a transfer from the explicit to the implicit system. For example, the verbalization of the movement goal location during the action induces a loss of the implicit residual abilities observed in blindsight and numbsense patients and a change in the reference frame used to control the action. Interestingly, these effects are similar to the effect of a delay between the stimulus delivery and the action. These interactions might involve the posterior or the anterior portion of the ventral pathway. To evoke a transfer from the implicit to the explicit mode of sensory processing, one has to study a more extended time-scale. This time-scale allows for plasticity to gradually develop and thus implies that several movements are involved. Prism adaptation provides an example of such transfer from an implicit sensorimotor level to an explicit space representation. (From Pisella and Rossetti 2000.)

4.8.2 An action–perception gradient

Although the dissociation between perception and action found in neurological patients is often used to argue for a clear segregation between two visual systems, it should be noticed that the performance exhibited by these patients cannot be taken as identical to normal performance. The motor production obtained in visual agnosia, and especially in blindsight and numbsense patients, is much more variable than that of normals. In our view, this suggests that both visual systems have to cooperate in order to produce normally accurate behaviour.

On the one hand, neuropsychological investigations have shown that matching responses (such as indicating an object size or orientation with the hand) provide similar results to purely perceptual tasks (e.g. Goodale and Milner 1992; Goodale *et al.* 1991; Jeannerod and Rossetti 1993; Milner and Goodale 1995; Milner *et al.* 1998; Perenin and Rossetti 1996). On the other hand, an elegant series of experiments investigating slope perception in normals (see Bhalla and Proffitt 2000) have shown a dissociation between ann (action-like) matching response and a perceptual–verbal report. The distinction between instrumental and communicative pointing described by Bridgeman (this volume, Chapter 5) also emphasizes such a progression from pure sensorimotor responses to verbal reports, via intermediate processes such as pointing to designate. Taken as a whole these results therefore suggest that motor matching responses may lie somewhere in between the action and perception sides of vision, thus offering a third term to the dichotomy that is usually defended (Rossetti, Pisella, and Pélisson 2000).

If one accepts the idea of a continuum between a pure sensorimotor system and a pure perceptual system, then the results summarized in this review suggest that the main parameter of this gradient would be the amount of on-line processing participating in a given task. Thus the sensorimotor end of this continuum would be pure on-line motor control. The only way to observe pure sensorimotor activation appears to be to favour the hand automatic pilot. A pure automatic pilot produces a greater output variability than a natural behaviour, because an unconstrained movement is usually slow enough to also allow some participation of the cognitive system in the action. In addition, this automatic pilot is not capable of planning action. By contrast, a pure 'perceptual control of action' (Milner and Dijkerman 2001) is only seen for very slow actions or in patients with damage to the dorsal system. This indicates that both routes to action have to cooperate under natural circumstances, even if each of them in turn can dominate a given aspect of behaviour. For example, a movement can be initiated toward a target that has been selected by the cognitive system and then be corrected on-line by a sensorimotor system such as the parietal automatic pilot. The example of the Ponzo illusion shows that the force applied to lift an object at the end of the movement is not controlled by the same mechanism as the grip aperture (Brenner and Smeets 1996). Nevertheless, both systems participate in the action, grip force probably simply being specified before the action is initiated while grip aperture is controlled on-line.

As a whole, performing an action cannot be considered as only a sensorimotor process and, once again, the two ends of the perception–action gradient do participate in daily behaviour.

4.8.3 A dorsal–ventral gradient?

Within the purest 'vision for action' system there seem to be an anatomical gradient between the area responsible for space-based action and those responsible for object-based action. Electrophysiological data in monkeys (Sakata and Taira 1994) and lesion studies in human subjects (Binkofski *et al.* 1998) seem to agree that, within the intraparietal cortex, the more rostral part is primarily involved in simple actions such as pointing, whereas the more ventral part is involved in grasping. This anatomical organization seems to constitute the first step of a more global gradient between two extremes whose prototypes would be visual pointing (simple space-based action) and object recognition (object-based cognitive processing) (see Pisella and Rossetti 2000; Rossetti *et al.* 2000). As argued above, the action end of this continuum would be the parietal automatic pilot (Pisella *et al.* 2000).

At the neuropsychological level, the dichotomy of the visual system is best argued from the double dissociation between optic ataxia and visual agnosia (see Goodale and Milner 1992; Jeannerod and Rossetti 1993; Milner and Goodale 1995; Rossetti 1998). However, the very notion of this 'double-dissociation' may be questioned. Unlike visual agnosia, it should be kept in mind that optic ataxia does not impair patients in everyday life. In order to observe a motor deficit one has to require the patients to perform goal-directed actions in *peripheral* vision, that is, in non-natural conditions. This condition is well-known to increase the need for on-line control, because it allows only for a crude target position encoding prior to movement onset. The main problem encountered by these patients in central vision may be the automatic sensorimotor control performed by the PAP.

In this case, one has to consider that the double-dissociation lies between cognitive identification and automatic motor control rather than between cognitive processing and action in general.

Along this line, it is interesting to consider the effect of lesions lying in the brain area just between the focus of lesions producing optic ataxia and that of lesions producing visual agnosia, that is the temporo-parietal junction. The best-documented deficit following such a lesion in a human is hemispatial neglect. On the one hand, neglect has been considered to be dissociated from optic ataxia, in that visuomotor deficits reported for the latter are not observed for the former (Milner 1997). On the other hand, visual neglect has been shown to involve some deficit on the action side (e.g. Mattingley *et al.* 1998), which implies that neglect can also be distinguished from visual agnosia.

To conclude, we propose that the action-perception gradient can be matched onto a dorsal–ventral gradient. The end of this latter gradient would be represented by the PAP.

4.8.4 Implications for visual awareness

One of the key distinctions described between sensorimotor and cognitive processing is the poor level of visual awareness associated with the sensorimotor processing. Whereas movement guidance can be based on a partial analysis of the target attributes, identification and consciousness imply that a binding of all object properties is achieved (see Revonsuo and Rossetti 2000). However, it would be oversimplistic to identify action and implicit processing on one side and identification and consciousness on the other. Not all implicit processing takes place in the posterior parietal cortex, and not all actions rely only on this structure. Unconscious control of more complex sequential actions may involve other structures, such as the basal ganglia (e.g. Rolls 1999). It has also been known for a long time that unconscious processes, either at a low level (Helmholtz) or at a high semantic level (Freud), can affect not only actions but many aspects of cognition as well, and that semantic processes are not necessarily conscious. Still, particular aspects of sensory processing for the purpose of action, and especially for movement guidance, remain fully independent from conscious perception. Therefore action can be directed to unconsciously perceived stimuli, even though conscious awareness allows for a perceptual control of action. Specifically, consious visual perception and intention select the goal for the action, but the realization of the action may escape from their control. In the same way as unconscious processes may participate in goal specification, as is clearly shown by the Simon effect (see Hommel 2000), such processes play an even stronger role in the action control.

Although dissociation has proved to be a useful tool to understand the basic functions of the brain, which have been atomised by most scientific approaches, the understanding of complex functions requires a more global account of how our mind works—an account that implies a synthetic rather than an analytic approach (see Rossetti and Revonsuo 2000b). We propose that the temporal dimension is one of the keys to understanding complex interconnected networks such as the visual brain. Because of the links between the perception–action debate and issues of conscious awareness and intentionality, we suggest here that the strength of temporal factors may be relevant to these issues as well. As proposed by Milner and Dijkerman (2001), it may be that the role of consciousness is primarily to delay action in order to gain behavioural efficiency. Further, if an animal becomes able to slow down, delay, or inhibit immediate actions, it may also become able to reach for a better (hidden or internal) goal. Restricting the use of automatic processes such as the PAP to the regulation of action can improve the execution of intentional actions, without interfering with decision processes.

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Note

1. . . . Contrasting with naïve conceptions of perception as a pure bottom-up process, the idea has been proposed by von Helmholtz that perception results from unconscious inductive inferences. Although physiological studies of the visual system have long been focused on how visual images are constructed through hierarchically organized stages of processing, the same idea of a dialogue between bottom-up and top-down processes is now being applied to the understanding of vision. This two-way description of vision and perception in general is also widely acknowledged by psychologists and philosophers, so much so that the idea that 'there is no such thing as immaculate perception' has been defended (Kosslyn and Sussman, 1995). The most cited experimental evidence for the implication of descending influences on perception is the case of ambiguous figures, for which perception can alternate between two possible interpretations of the visual input, even through the memorized image can be subjected to other interpretation. Visual illusions are also often considered as a clear example of the interpretation (and contamination) of retinal information involved in perception. (Rossetti 1999, p. 141.)

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