

On the Perceptual/Motor Dissociation: A Review of Concepts, Theory, Experimental Paradigms and Data Interpretations

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Abstract

With its roots in Ungerleider and Mishkin's (1982) uncovering of two distinct — ventral and dorsal — anatomical pathways for the processing of visual information, and boosted by Goodale and Milner's (1992; Milner and Goodale, 1995) behavioral study of patients with lesions of either of these pathways, the perception–action dissociation became a standard reference in the sensorimotor literature. Here we present briefly the anatomical, neuropsychological and, more extensively, the psychophysical evidence favoring such dissociation and pit it against counteracting evidence as well as against potential methodological and conceptual pitfalls. We also discuss classes of models accounting for a number of 'dissociation' results and conclude that the most general and parsimonious one posits the existence of one single processing stream that accumulates information up to a decision criterion modulated by stimulation conditions, response mode (motor *vs.* verbal/perceptual), task constraints (speeded *vs.* free time responses) and the nature of the task (detection, discrimination, temporal order judgment, etc.). The reviewed evidence is not meant to refute or validate the hypothesis of a perceptual–motor dissociation. Rather, its main objective is to show that, beyond its self-evidence, such dissociation is difficult if not impossible to test.

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Keywords

Perception–action dissociation, visual agnosia, optic ataxia, visual illusions, metacontrast, detection latencies, response time, eye movements, pointing

1. Prologue

One of the major goals of the cognitive sciences is to make clear how a physical stimulus can lead to a motor response, with or without an accompanying conscious experience. According to the most widespread account (Goodale, 2008; Goodale

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and Milner, 1992; Goodale *et al.*, 2005; Milner and Goodale, 1995, 2008), visual information undergoes different and largely independent processes depending on whether it leads to perceptual processing or to a motor action. These two types of treatment are said to occur in two pathways, the ventral and the dorsal, respectively. A very large body of experimental results from the neurosciences and from experimental psychology has lent support to this dissociative view (see Goodale, 2008; Goodale *et al.*, 2005; Milner and Goodale, 2008; Milner *et al.*, 2003). Rather than presenting an exhaustive review of these results, our aim is to provide an overview of the different scientific approaches to the issue of perceptuo-motor relations and discuss the most significant empirical, experimental design, theoretical and conceptual challenges to the two-pathway theory. As a consequence we shall dwell only very briefly on the anatomical and neurophysiological foundations of this dichotomy and will mostly concentrate on behavioral studies with particular focus on those with healthy subjects.

One of the fundamental lines of evidence for the dual-stream theory is the neuropsychological observation of what is currently referred to as a ‘double dissociation’. Lesions of posterior parietal areas (dorsal stream) lead to a condition known as *optic ataxia*, which involves disturbances of what is typically called *visually guided action*. Patients set before a mailbox slot are able to report its orientation, but are incapable of correctly inserting a card into it. Lesions of ventral visual areas, in contrast, lead to *visual agnosia*: these patients are unable to verbally indicate the orientation of the slot, but can correctly insert a card into it (for reviews see Goodale, 2008; Goodale *et al.*, 2005; Milner and Goodale, 1995, 2008). This double dissociation has been challenged based on observations suggesting that (1) optic ataxia is not a general disturbance of visually guided action and that (2) visual agnosia is not a disturbance specific to ‘perception’. Such claims have been contested in their turn.

The first attempts to demonstrate this dissociation in healthy subjects made use of visual illusions. The hypothesis underlying such experiments was that visual illusions, which make use of prior knowledge and contextual information, would affect only perceptual responses, leaving the motor system unaffected. Initial studies validated this hypothesis and concluded in favor of the dissociation (e.g., Aglioti *et al.*, 1995; Brenner and Smeets, 1996; Daprati and Gentilucci, 1997; Gentilucci *et al.*, 1996; Haffenden and Goodale, 1998). They have been mostly criticized for a failure to convincingly match perceptual and motor tasks (Franz *et al.*, 2000) or for allowing alternative interpretations of the results (e.g., Smeets and Brenner, 1999, 2001, 2008; Smeets *et al.*, 2002). Experiments with tighter methodological controls revealed that the motor system is affected by visual illusions no less than the perceptual system (e.g., Bruno, 2001; Franz, 2001; Smeets and Brenner, 2001; Vishton *et al.*, 1999). Be it as it may, the difficulty of matching perceptual and motor tasks reflects the fuzziness of the two concepts so that, ultimately, any such comparison remains debatable (see Neumann, 1990).

Numerous behavioral studies have used masking to scrutinize the relation between perceptual and motor responses. The rationale of most of these studies is

based on a direct conceptual consequence of the dissociation stand which is that vision-for-perception is by definition conscious, while vision-for-action may not be (see Goodale, 2008; Milner and Goodale, 2008). The first studies concluded that simple reaction times (sRTs) to a prime–mask combination are independent of the visibility of the prime (e.g., Fehrer and Raab, 1962; Neumann and Klotz, 1994; Taylor and McCloskey, 1990). While confirming this factual dissociation, recent studies showed however that sRTs do vary with subject's perceptual state: sRTs associated (on a trial-by-trial basis) with correct detections (hits) are shorter than those associated with omissions (misses), supporting the notion of a sensorimotor dependence (Waszak and Gorea, 2004; Waszak *et al.*, 2007). Other masking studies have examined the relation between the identifiability of a masked 'prime' stimulus and its effects on choice response times (cRTs) to its masker (e.g., Klotz and Neumann, 1999; Neumann and Klotz, 1994; Vorberg *et al.*, 2003). These experiments showed, on the one hand, that the cRT to the mask is differently affected by the prime depending on whether the two are congruent or incongruent. On the other hand, they showed that these priming cRT effects are independent of the identifiability of the prime. These results, once again, have been interpreted in favor of a functional dissociation between perception and action. Under this view, the priming effect on cRTs is understood as a motor effect. An alternative interpretation, however, is that the prime affects perception of the mask and that it is this modified perception that modulates cRT (Neumann and Scharlau, 2007). This interpretation is supported by the fact that the moment of the *perceptual* detection of the mask (measured by the method of temporal order judgments) varies as a function of the prime intensity, and, as for the cRTs and sRTs, may be independent of the prime's visibility (a perceptuo–perceptual dissociation).

On the hypothesis that a single processing stream is responsible for perceptual and motor detection, detection latencies inferred from perceptual and motor responses should be identical. This hypothesis is invalidated by a large majority of studies which find that stimulus manipulations (e.g., of intensity) modulate sRTs more strongly than perceptual latencies (for reviews see Jaśkowski, 1996, 1999; Miller and Schwarz, 2006; Sternberg and Knoll, 1973). This difference between perceptual and motor moments has been taken to support the perception–action dissociation view (e.g., Neumann *et al.*, 1993; Steglich and Neumann, 2000; Tappe *et al.*, 1994). Alternatively and more parsimoniously, this difference has been accounted for by models wherein a single internal response evoked by a sensory stimulus grows with time and leads successively to perceptual and motor responses in this or reversed order depending on which of the perceptual or motor criterion is exceeded first by the evoked internal response (e.g., Cardoso-Leite *et al.*, 2007, 2009; Ejima and Ohtani, 1987; Miller and Schwarz, 2006; Sanford, 1974; Sternberg and Knoll, 1973). Such one-stream-two-decisions models may also account for a number of results evidencing or not a perception–action dissociation depending on whether the motor responses are speeded or delayed.

After sketchily presenting the anatomical foundations of the perceptual–motor dissociation, the present review focuses on those behavioral (including neuropsychological) studies having investigated this dissociation. Rather than being exhaustive, its main emphasis is on the multiple experimental approaches that have been taken to this end as well as on the experimental, theoretical and conceptual problems they raise. The review is not meant to reject or substantiate the dual pathway view. Instead, it focuses on its debatable aspects that might never be entirely settled *via* neuropsychological observations or experimentation with healthy subjects.

2. Neuroscientific Theory of the Perception–Action Dissociation

Goodale and Milner’s pioneering proposal (1992; Milner and Goodale, 1995), more than 15 years ago, of a theory wherein the sensory signal is treated by two distinct pathways, one for perception, the other for action echoes similar suggestions made more than a century ago in Wundt’s laboratory by Lange (1888) and by Münsterberg (1889). It stands against the unitary (and intuitive) position which holds that a stable and complete ‘perceptual’ representation must be internalized before any action or thought can occur (the ‘official doctrine’ according to Ryle, 1949). Goodale and Milner’s first argument against this serial view, wherein conscious perception always precedes action, is an evolutionary one (see Note 1). Conscious perception, they suggest, may be a recent product of evolution, the primary and principal function of sensory receptors being to capture information about the environment in order to act (see also Goodale *et al.*, 2005; Milner and Goodale, 2008). Goodale and Milner hold that in highly evolved animals, visually guided behaviors are not rigidly tied to the visuomotor modules, since in the course of phylogenesis a representational system evolved and allowed the brain to model the world and identify objects and events, giving them meaning and establishing causal relations. This representational system is supposed not to be directly linked to the motor system, but instead to the cognitive system including memory, planning, semantics and communication. The function of this representational system is to permit motor actions better adapted to the world, so as to improve the chances of survival of the organism. This stand is countered by the traditional, more intuitive view according to which perception and action share a common representation of the external world (e.g., Clark, 2001). It is also claimed that in fact perceiving *is* a way of acting (Gibson, 1966, 1979; O’Regan and Noë, 2001).

Goodale and Milner, thus, define two systems, one dedicated to visuomotor modules linking specific types of visual stimuli to specific typically skilled/automatic actions performed in an “absolute frame of reference centered on specific effectors, that is, in egocentric coding”, the other permitting knowledge, learning and the voluntary control of actions within a reference frame “beyond the absolute metrics of a particular visual scene” (i.e., allocentric; Goodale *et al.*, 2005, pp. 273–274). The essential arguments in favor of this theory are anatomical, neuropsychological and behavioral. Many of them have been challenged on numerous grounds.

3. Sketchy Overview of the Neural Bases of the Perception/Action Dissociation

Visual perception is subserved by a vast network of specialized areas (DeYoe and Van Essen, 1988; Felleman and Van Essen, 1991; Zeki, 1993). Each area is composed of multiple layers, each with connections to other cortical regions. Despite the apparent complexity of this organization, Ungerleider and Mishkin (1982) revealed two major sets of nerve projections in the monkey brain, both beginning in primary visual cortex, one projecting into the temporal lobe (the ventral pathway), the other projecting into the posterior parietal cortex (PPC; the dorsal pathway: see Figs 1 and 2). According to Ungerleider and Mishkin (1982), these two pathways have complementary functions: the ventral pathway subserves the object identification (the ‘what’ pathway), whereas the dorsal pathway is thought to allow spatial localization of these objects (the ‘where’ pathway). Specific lesions of either the ventral or dorsal stream affect monkeys’ ability either to recognize objects or to situate an object in space with respect to a landmark, respectively, and exclusively.

Slightly more elaborated, the above split was still endorsed in the late eighties (DeYoe and Van Essen, 1988) but its neatness was soon obscured by Felleman and Van Essen’s (1991) thorough tracing of the many afferent, efferent and lateral paths followed by the visual signal from the retina onward. In the same time, the ventral-‘what’/dorsal-‘where’ dichotomy proved to be, well, too, dichotomous

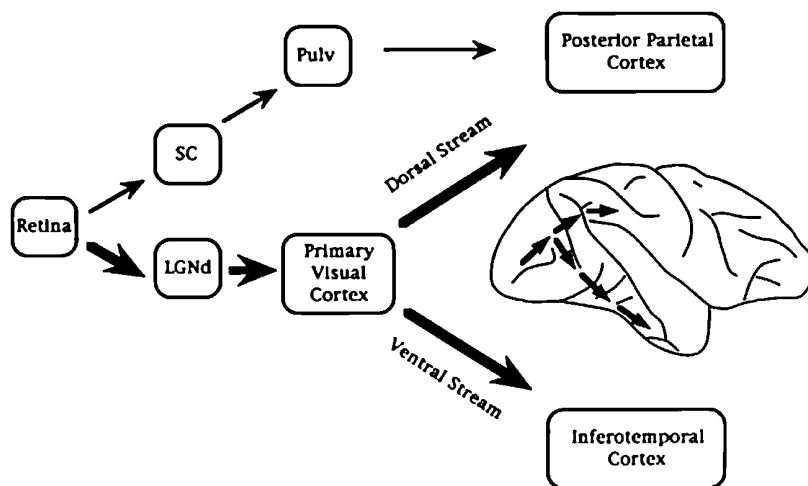


Figure 1. Simplified representation of the two functional pathways for the treatment of visual information according to the model of Ungerleider and Mishkin (1982; following Goodale and Humphrey, 1998). Retinal stimulation is transmitted to subcortical structures (SC, Pulv, LGNd) and then cortical structures (PPC, V1). After having reached the visual cortex information flows along one of two streams: the dorsal pathway, which leads to posterior parietal cortex and is thought to subserve the visual control of action, and the ventral pathway, which is thought to subserve perception, and whose integrity is considered necessary for conscious perception. (LGNd, lateral geniculate nucleus pars dorsalis; Pulv, pulvinar; SC, superior colliculus.)

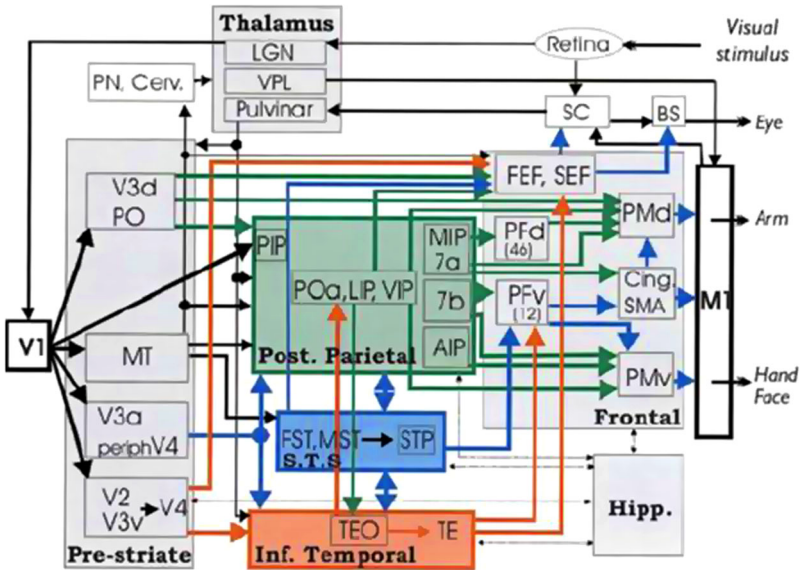


Figure 2. Cortical networks permitting the association of motor responses (M1) to visual inputs in primary visual cortex (V1). The dorsal pathway is shown in green and the ventral pathway in red. Blue arrows represent projections that combine information from the two pathways. There are direct connections between the two pathways, and numerous areas in the frontal lobe receive projections from both pathways. (AIP, Anterior intraparietal are; 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; MIP, mesial intraparietal area; PIP, posterior intraparietal area; MST, medial superior temporal area; MT, mediotemporal area; PF, prefrontal cortex; PM, pre-motor cortex; SC, superior colliculus; SEF, supplementary eye field; SMA, supplementary motor area; STS, superior temporal sulcus; STP, superior temporal polysensory area; TE, temporal are; TEO, temporo-occipital area; v, ventral; VIP, ventral intraparietal area.). From Rossetti, Pisella and Vighetto (2003). This figure is published in colour on <http://brill.publisher.ingentaconnect.com/content/vsp/spv>

as incoming evidence showed that both streams manipulate information about the nature of objects and their locations in space (e.g., Konen and Kastner, 2008; Singh-Curry and Husain, 2009). Milner and Goodale's (1995) work pressed for turning the what/where split into a vision-for-action/vision-for-perception dichotomy subtended by the very same dorsal/ventral anatomical distinction. According to a sketchy account of this new dichotomy, the vision-for-action system operates in real time, is typically involved in skilled actions and computes the absolute metrics and position of a visual object. In contrast, the vision-for-perception path is involved in movement planning based on memory of an object relative to other items and has no requirement for absolute/egocentric coding (Goodale *et al.*, 2004, 2005; Milner and Goodale, 1995). This classification captures indeed many features of the functional architecture of the cortical visual system as revealed by a multitude of techniques such as unitary recordings (see reviews by Boussaoud *et al.*, 1995; Goodale *et al.*, 2005; Guillery, 2003), neuroimaging (with positron emission tomography, PET, functional resonance imaging, fMRI, electro-encephalogram, EEG and transcranial

magnetic stimulation, TMS; see reviews by Culham and Kanwisher, 2001; Culham and Valyear, 2006). It also reveals, however, a number of discrepancies with the mainstream perception/action dichotomy a sample of which is enumerated below.

Basing their argument on the anatomical intricacy of the ventral and dorsal streams, Churchland *et al.* (1994) were perhaps the first to point out the impossibility of a ‘pure vision’ vs. action theory (see also O’Regan and Noë, 2001). While this anatomophysiological blur was clearly acknowledged by Goodale *et al.* (2005), the mainstream, though more elaborated, perception/action dissociation was maintained based on incoming support from both neurophysiological and behavioral studies (e.g., Goodale, 2008; Milner and Goodale, 2008). However, accumulating neurophysiological evidence was also pointing to many instances where neurons and cortical sites in the ventral and dorsal streams behave contrary to predictions of the dissociation theory. For example, both neurophysiological and neuroimaging studies show evident dorsal stream responsiveness to stimulus features supposed to be processed in the ventral stream such as shape (e.g., Konen and Kastner, 2008; Lehky and Sereno, 2007) and color (e.g., Claeys *et al.*, 2004; Toth and Assad, 2002). Equivalently some prototypical dorsal processing features such as motion are equally well processed in the ventral stream (e.g., Gur and Snodderly, 2007). Also, while the temporal processing characteristics of the two streams have also been cited in favor of their functional dissociation (with magnocellular neurons in dorsal areas responding earlier to visual stimulation than the parvocellular neurons in the ventral stream; e.g., Nowak and Bullier, 1997; Rossetti *et al.*, 2003), the significance of such latency differences has been obscured by numerous reports that visual information processing is not strictly feedforward (as supposed in the classic view) so that frontal areas may respond to visual stimuli at about the same time as V1 (Lamme and Roelfsema, 2000; Schmolesky *et al.*, 1998; Zanon *et al.*, 2009). Hence, efferent signals from the frontal cortex may modulate processing in both the dorsal and ventral extrastriate areas (Moore and Armstrong, 2003; Moore and Falah, 2001, 2004). Demonstrations of neuropsychological conditions such as optic ataxia and visual agnosia being selectively caused by specific damages of the dorsal and ventral streams, respectively (e.g., James *et al.*, 2003; Steeves *et al.*, 2004), have been questioned based on the observation that lesions in the visual agnostic patients showed a diffuse, widespread pattern of neuronal and white matter damages throughout the whole brain. This is particularly the case with the prototypical visual agnostic patient D.F. extensively studied by Milner, Goodale and many others (Goodale *et al.*, 1991, 1994b; James *et al.*, 2003; McIntosh *et al.*, 2004; Milner *et al.*, 1991; Mon-Williams *et al.*, 2001a, b; Schenk and Milner, 2006; Servos *et al.*, 1995; Wann *et al.*, 2001; Westwood *et al.*, 2002). Hence, conclusions based on such neuropsychological evidence on behalf of the ventral/dorsal dissociation remain problematic (Karnath *et al.*, 2009).

Taken together, such evidence progressively blurred the neat neurofunctional two-streams account and led to the revised view according to which the two streams entertain a hierarchically organized interplay and possibly represent basic object

features in similar ways (see Guillery, 2003; Konen and Kastner, 2008; McIntosh and Schenk, 2009; Singh-Curry and Husain, 2009; Zanon *et al.*, 2009). Notwithstanding, a wealth of recent neuroimaging and TMS studies (e.g., Cavina-Pratesi *et al.*, 2007; Cohen *et al.*, 2009; Ellison and Cowey, 2006, 2007, 2009; Rice *et al.*, 2007) continued to support the mainstream ventral/dorsal functional distinction. What one should then conclude other than that “there is a sense of unease about how well the [ventral/dorsal] model accommodates all [these] findings” (Singh and Husain, 2009, p. 1434).

The present introduction to the neurofunctional bases of the perception/action dissociation is purposefully sketchy as the reader may find detailed accounts of the literature in all the reviews cited above. What should be pointed out here is that, be the ventral/dorsal neurofunctional classification correct or wrong, it is by necessity based on the outcome of specific behavioral tasks. That different neural paths and cortices light up depending on whether one is asked to grasp an object or to (verbally) specify its orientation or shape comes as no surprise. However, how such tasks should or whether they actually can be matched for comparison is a whole different story that is discussed at length in the following sections.

4. Neuropsychology

The main argument of Goodale and Milner’s two-pathways proposal is based on their original neuropsychological observation of a double dissociation between perception and action. Patients with lesions of the inferior temporal cortex (Gross, 2007; Schwarzlose *et al.*, 2008) and, more typically, of the lateral occipital complex (like patient D.F. — James *et al.*, 2003; for reviews see Grill-Spector, 2003; Grill-Spector *et al.*, 2001; Karnath, *et al.*, 2009; Valyear *et al.*, 2006), both in the ventral pathway (see Note 2), have trouble with the recognition of objects (including their simple shape features such as their orientation; *visual agnosia*, VA), but remain capable of pointing to and correctly grasping or manipulating the same objects. Conversely, patients with lesions of the posterior parietal cortex (dorsal stream; for reviews see Culham and Kanwisher, 2001; Culham and Valyear, 2006; Sakata, 2003; Valyear *et al.*, 2006) correctly identify such objects, but are significantly impaired in visuomotor tasks such as “using vision to form their grasp or to direct an aiming movement towards objects presented outside foveal vision” (*optic ataxia*, OA — Bálint, 1909; see Goodale *et al.*, 2005, p. 270). That perceptual and motor tasks are eventually subtended by different neurophysiological structures comes as no surprise. There is no surprise either that visuomotor behavior can be impaired in the absence of perceptual deficits; it naturally follows from the intuitive view of perception and action unwinding sequentially. The surprise comes from the standing dissociation credo that perceptual deficits (VA) may not entail visuomotor ones (OA). Its ultimate, debatable consequence is that one may appropriately act on objects that are not ‘perceived’. While such claims will be more thoroughly reviewed in Section 6, the next sections raise issues on the unambiguous distinc-

tion made between VA and OA as well as to another related neuropsychological condition known as *blindsight*.

4.1. Optic Ataxia (OA) and Visual Agnosia (VA)

Lesions of posterior parietal areas can lead to a set of impairments known collectively as OA. Classically, OA is described as an impairment of motor control of visually guided actions. According to Goodale and Milner, it involves a disruption of the perception-for-action system. In their reviews of OA, Rossetti *et al.* (2003) and Pisella *et al.* (2006) conclude that the claim of a perceptuo-motor dissociation is unfounded. They note that, contrary to what is implied by the standard description of OA patients' performance in behavioral experiments, their condition does not prevent many of them from carrying out common daily life tasks, whereas patients with visual agnosia are unable to do so. This observation seems to contradict the idea that the ventral pathway, with its more recent evolutionary origin, is less important than the dorsal pathway in normal sensorimotor interactions. Rossetti *et al.* (2003) also note that the majority of OA patients are able to guide precise actions toward objects, so long as the objects are presented in central vision (Perenin and Vighetto, 1988; Vighetto, 1980). This is the case even for patients with bilateral OA who perform normally or close to normally on many visuomotor tasks requiring foveal pointing and grasping (Grea *et al.*, 2002; Milner *et al.*, 1999; Pisella *et al.*, 2000, 2006; Rossetti *et al.*, 2005). Grea *et al.* (2002) find no difference in the kinematics of grasping movements between the patient I.G. and control subjects when the stimuli to be grasped are static and subjects are free to shift their gaze. Furthermore, if OA patients are instructed to delay their action toward an object (rather than reacting immediately following its appearance), their performance improves (Goodale *et al.*, 1994a; Milner *et al.*, 1999, 2001, 2003; Pisella *et al.*, 2006). Thus, it might be more revealing to dissociate OA — understood as a specific deficit in *immediate* reactions — from impairments observed in patients with frontal lesions — who are unable to inhibit immediate reactions ('environment-dependency syndrome'; Lhermitte, 1986) — rather than from VA (Rossetti *et al.*, 2003).

Pisella *et al.* (2006) present a more subtle classification of behaviors entailed by dorsal, ventral and ventro-dorsal lesions. According to them 'dorsal–dorsal' lesions (in the most dorsal part of the parietal and pre-motor cortices) entail deficits "restricted to the most direct and fast visuo-motor transformations"; 'ventral–prefrontal' lesions (of the stream bypassing the parietal areas) yield anomalies in 'spatial or temporal transpositions' involving intention while preserving visuo-manual guidance restricted to immediate but not to delayed or pantomimed goal-directed guidance; finally, 'ventro-dorsal' lesions (the more ventral part of the parietal lobe and the pre-motor and pre-frontal areas) entail perturbations of "complex planning and programming relying on high representational levels". They emphasize the critical role of the different temporal and integrative constraints of the various tasks used to assess these patients' perceptual and motor capabilities thereby diluting, not to say invalidating, the significance of the double OA–VA dissociation,

the cornerstone of the perception–action distinction view. The major proponents of the latter do not overlook such task-related constraints but use them to reinforce their position.

For example, against Pisella *et al.*'s argument that OA patients significantly improve their pointing accuracy when a delay is inserted between stimulus presentation and response, Milner and Goodale (2008) argue that such behavior conforms to the double-dissociation view as for delayed responses OA patients must rely on information processed by their intact ventral stream. In support to this they refer to Milner *et al.* (1999a) who showed that, as predicted by the dissociation theory, VA patient D.F. (who cannot make good use of the ventrally processed information) displays the opposite delay effect. The argument is weakened by experiments showing that these reverse patterns of performance changes are observed in central vision for VA patients and in peripheral vision for OA patients (see Prado *et al.*, 2005). Milner and Goodale (2008) argue that double-dissociations (in VA and OA patients) are equally observed in central and peripheral vision but the studies they refer to (among others Binkofski *et al.*, 1998; Goodale *et al.*, 1994b; Jakobson *et al.*, 1991; Jeannerod, 1986; Jeannerod *et al.*, 1994) have not tested the effect of delayed motor responses. An additional confusing observation is that, despite potentially based on information processed by their intact ventral stream, delayed movement performance of OA patients remains impaired with respect to normal performance in the same conditions (Himmelbach and Karnath, 2005; Milner *et al.*, 1999, 2001, 2003; Rossetti *et al.*, 2005). Finally, a recent fMRI study by Himmelbach *et al.* (2009) showed that brain activity associated with immediately executed and delayed movements in a OA patient with extensive bilateral lesions was robust and indistinguishable in the intact dorsal occipital and parietal areas adjacent to the patient's lesions. They also found that the BOLD signal in the visuomotor network of healthy subjects was similar for immediate and delayed movements, and that it was significantly stronger in the bilateral occipito-parietal and occipito-temporal areas for movements to visible targets than for delayed movements. Hence, Himmelbach *et al.* (2009) conclude that "in healthy subjects as well as in the OA patient (...) dorsal areas are not only involved in immediate but also in delayed reaching" and question the stance "that residual visuospatial abilities in patients with OA could only be mediated by a system outside of the dorsal stream". A recent concurring observation by Schenk and Milner (2006) with the VA patient D.F. is that her shape-discrimination (square *vs.* rectangle) performance improved from chance to up to 80% when she was asked to name the shape of the object ('perceptual' task) while she was reaching forward to pick it up ('visuomotor' task). This suggests that D.F. can access the object's visuomotor representation in the dorsal stream or, alternatively (see Himmelbach *et al.*, 2009), that the dorsal/motor–ventral/perceptual dissociation is less obvious than frequently claimed. Finally, using a prism adaptation paradigm with healthy subjects, Rogers *et al.* (2009) have shown typical post-exposure negative effects in both an immediate and delayed pointing task as well as an almost complete transfer of the aftereffect between immediate and delayed pointing. They

comment that this latter result contrasts with the standard dissociation view according to which immediate and delayed responses are subtended by different neural representations. Hesse and Franz (2009) argue that differences between immediate and delayed actions are more parsimoniously explained by a single decaying memory trace than by a qualitative switch from dorsal to ventral stream guidance.

In short, OA does not seem to reflect a general impairment of action and VA does not appear to be a general impairment of perception. Both conditions comprise a set of deficits that match specific temporal and integrative task requirements involving, for example, direct and fast *vs.* intentional and more reflective visuo-motor transformations *vs.* complex planning. Even though such distinctions may partially fit the specifications put forward by the dissociation proponents of what they mean by perception and action (see Goodale, 2008; Goodale *et al.*, 2005; Milner and Goodale, 2008), they clearly do not support a neat dichotomy between ‘perceptual’ and ‘motor’ tasks. To repeat Milner and Goodale’s (2008) citation of Weiskrantz (1997, p. 42) “there is no such creature in psychology as a pure task, nor will there ever be”. (See Note 3.)

4.2. *Egocentric vs. Allocentric Issues*

One of the best-known tasks used to demonstrate the supposed double-dissociation between perception and action involves placing subjects in front of a randomly oriented slot and, on the perceptual task, asking them to match its orientation with a card they hold in one hand. In the visuomotor task, subjects are asked to insert the same card into the slot. D.F., a patient with ventral stream lesions was able to insert the card into the slot like a normal subject, whereas ataxic patients failed at this task. Inversely, D.F. was unable to match the orientation of the card in her hand to that of the slot, whereas ataxic patients did so successfully. While the perceptual and motor tasks seem similar, Schenk (2006) has recently noted that there was a potentially confounding factor in the original experiment. The type of processing required by the orientation matching (‘perceptual’) task involves an allocentric judgment (centered on external objects). Instead, inserting the card into the slot involves an egocentric judgment (as it requires the evaluation of the slot’s orientation with respect to the orientation of the subject’s own body). In order to determine whether D.F.’s visual agnosia represents a perception–action dissociation, or an allocentric–egocentric processing dissociation, Schenk retested D.F. in an experiment where these two factors were ingeniously crossed. According to Schenk’s interpretation, D.F.’s results support the latter: D.F.’s performance was disrupted in the allocentric perceptual task but remained intact in the egocentric visuomotor task, with this latter replicating the classic results reported in earlier studies. Contrary to the predictions of the model of perception–action dissociation, D.F.’s performance on the perceptual task was not disrupted in the egocentric task but it was in the allocentric task. In other words, D.F.’s impairment was not specific to the task, *i.e.*, perceptual *vs.* motor, but instead appeared to be specific to the mode of visuo-spatial information processing, *i.e.*, allocentric *vs.* egocentric. Schenk’s interpretation is in agreement

with previous demonstrations of similar deficits in visuomotor control if allocentric stimulus coding was required from D.F. (Dijkerman *et al.*, 1998; McIntosh *et al.*, 2004).

Milner and Goodale (2008) propose an alternative interpretation of Schenk's results. They contend that Schenk's perceptual task is in fact comparable to a motor task and, reciprocally, that his motor task is more akin to a perceptual one. The argument is that Schenk's egocentric/perceptual task allowed D.F. to make the perceptual judgment based on a latent, internalized motor response, while the allocentric/motor task made possible a motor judgment based on a sketchy perceptual representation. Clearly, arguments of the kind can be entertained indefinitely against the dissociation view. It can be argued, for example, that grasping, a prototypical 'action' behaviour, is also a form of motor translation of a perceptual judgment so that it should also be (which, according to the dissociation view, is *not*) subject to visual illusions (see Section 5). The point here is that the notions of egocentric and allocentric processing are as vague and difficult to apprise experimentally (e.g., Bar, 2001) as the concepts of perception and action.

4.3. *Blindsight*

One of the arguments in favor of a perception–action dissociation rests on the behavior observed in patients with cortical lesions of V1. Despite the absence of V1, numerous cortical areas in the dorsal stream, but not in the ventral stream, respond to visual stimulation (Bullier *et al.*, 1994). According to Goodale and Milner's dual-systems theory, patients suffering from such lesions should still be able to execute motor responses toward visual stimuli, since their dorsal stream continues to receive visual information. On the other hand, they should fail to consciously perceive the same objects, since their ventral stream is no longer receiving visual input.

The partial or total destruction of V1 leads to cortical blindness in the parts of the visual field corresponding to the lesioned areas. Despite their apparent blindness (assessed *via* visual perimetry (see Note 4)), visual information corresponding to the blind visual field continues to be treated in the brain by other cortical and sub-cortical areas, and can, under certain circumstances, manifest itself in the behavior of the patient. The fact that this visual information can be used by the brain despite the apparent blindness of patients led to the paradoxical term of 'blindsight', first used by Sanders *et al.* (1974).

4.3.1. *Perceptuo-motor Dissociation*

Contrary to 'real' blind patients (such as those having undergone the section of the optic nerve), blindsight patients exhibit pupillary responses to stimuli in their blind field that they are unable to identify verbally (Weiskrantz, 1990). These pupillary responses are modulated by the intensity, the spatial frequency and the colour of stimuli in blindsight patients with lesions restricted to striate cortex, but only by luminance in hemidecorticated patients, which indicates that the dorsal stream is implicated even in this basic behavior (Weiskrantz, 1990).

Non-perceived information could also modify voluntary behaviors. Pöppel *et al.* (1973) asked their patients to make a saccade toward a stimulus presented in their blind field which they claimed not to see. Their eye movements were imprecise, but, within a certain range of amplitudes, were correlated with the position of the stimuli. The precision of the localization of stimuli in the blind field is substantially improved when patients are required to point with their finger toward the stimulus (Perenin and Jeannerod, 1975; Weiskrantz *et al.*, 1974). This difference in localization accuracy as a function of the type of motor response has been interpreted as evidence against a unique central representation that precedes action, and in favor of multiple visuomotor representations (Milner and Goodale, 1995).

Voluntary motor responses directed toward an object presented in the blind field can also be influenced by the form of the object. Marcel (1983) reported that two of his patients performed above chance in their arm, wrist and finger movements in grasping objects of different forms and positions.

4.3.2. *Detection*

Zihl and von Cramon (1980) asked blindsight patients to indicate the presence of a visual stimulus presented in their blind field by blinking their eyes, pressing a button, or saying ‘yes.’ After several sessions of practice, detection assessed *via* manual and blinking responses improved greatly. Detection performance as measured by verbal responses, on the other hand, remained very weak. This dissociation in performance according to response modality runs contrary to the intuition of a general effect on visual sensitivity, and raises the problem of defining what constitutes a ‘perceptual’ response. In a similar vein, Marcel (1983) asked his patient G.Y. to report the presence of a visual stimulus, this time presented only on half of all trials, *via* different response modalities. The sensitivity inferred from manual responses was lower than the one derived from eye blinks but higher than the sensitivity measured *via* verbal responses. This pattern of results was maintained even when G.Y. gave the three types of response on each trial: G.Y. could manually detect a stimulus while verbally signaling having perceived nothing at the end of the very same trial. It should be noted, however, that performance was negatively correlated with response latencies. It, therefore, cannot be directly concluded that a distinct representation underlies each response modality, as it could also be that the internal signal simply degrades over time.

Despite the absence of ‘visual consciousness’ when a visual stimulus is presented to the blind field, blindsight patients can see nonexistent stimuli there. In these patients, bilateral transcranial magnetic stimulation of the extrastriate areas V5/MT creates phosphenes that extend into the blind field (Silvanto *et al.*, 2007). Furthermore, blindsight patients can consciously perceive afterimages from a stimulus that is ‘invisible’ due to being presented in the blind field (see Note 5), a phenomenon dubbed ‘prime-sight’ (Weiskrantz, 2002). Visual awareness of a stimulus is associated with increased amplitude in frontal activations (Sahraie *et al.*, 1997; Weiskrantz *et al.*, 2003).

4.3.3. Discrimination

Blindsight patients' detection ability may indeed be explained if one accepts that detection is not accompanied by the experience of visual qualia (Milner and Goodale, 1995) (see Note 6). On the other hand, the possibility that the same patients are able to discriminate textures or objects without being able to perceive them consciously is incompatible with the hypothesis that ventral activation suffices for conscious perception, since these visual attributes are processed in the ventral pathway.

D.B., a blindsight patient, displayed above chance performance on form discrimination tasks (circle vs. square, horizontal vs. vertical line) when the stimuli were presented sequentially in the blind field (Weiskrantz *et al.*, 1974) but performed much worse when they were presented simultaneously (Weiskrantz, 1987). Twenty years later, D.B. managed to identify objects represented by very low-contrast line drawings, and was able to discriminate between pairs of shapes simultaneously presented in his blind field (Trevethan *et al.*, 2007a, b). Curiously, D.B.'s contrast detection sensitivity assessed with a forced-choice technique was better in his blind field than both in his intact field and in healthy subjects (Trevethan *et al.*, 2007a). Nonetheless, D.B. persisted in saying that he had no conscious experience of the stimuli presented in his blind field.

A number of recent studies demonstrate that a form of blindsight can be induced in healthy subjects by means of transcranial magnetic stimulation (TMS). When visual stimuli are presented during such short TMS episodes, subjects report not perceiving them but show a number of motor behaviours indicating that such 'invisible' stimuli do affect a number of motor behaviour features. For example, Ro *et al.* (2004) report that when the TMS 'suppressed' stimuli are used as distractors in a discrimination task, they delay saccade (though not manual) pointing to the target. Boyer *et al.* (2005) report above chance orientation and color discrimination performance despite the TMS induced 'invisibility' of the stimuli and Christensen *et al.* (2008) and Ro (2008) demonstrate preserved online correction of reaching movements toward a TMS obliterated target. All these results suggest the involvement of an 'unconscious' retinocortical pathway subtending blindsight in general. Critically, however, all the above studies based their assessment of blindsight on subjects' *subjective* report of not having seen the target or distracting stimuli and this even in the only case where sensitivity (i.e., d') was assessed and actually found to be well beyond chance ($d' = 2.27$ in Ro's study). Thus, from a psychophysical (Signal Detection Theory, SDT; Green and Swets, 1966) viewpoint, none of these studies does actually prove the existence of blindsight.

It may seem surprising that the blindsight phenomenon is frequently cited in favour of the perception–action dissociation theory (e.g., Milner and Goodale, 1995, 2008). In order to attribute the preservation of visually guided motor responses to the dorsal stream, it must be assumed that these patients show no activity in the ventral stream. At the same time, patients claim to 'feel' that a stimulus was presented, which *prima facie* should be the consequence of ventral processing. To escape from this dilemma, Milner and Goodale (1995) argue that blindsight subjects' experience

is not *visual* experience. They suggest that it results instead from the consequences (possibly proprioceptive) of the weak activations evoked in the dorsal stream. In support of this hypothesis they cite Marcel (1983), who affirms that G.Y. feels different sensations for a same visual stimulus depending on the motor response that is associated to it. This line of reasoning is very similar to the one used by Milner and Goodale (2008) against Schenck's (2006) interpretation of his results (see Section 4.2, *Egocentric vs. allocentric issues*) and raises unsolvable experimental problems. It implies that there is no way to guarantee that a response is perceptual or motor because the former can reflect a non-executed motor activation and the latter could be the translation of an internalized perceptual response.

Does blindsight (assuming it exists) reveal a perceptuo-perceptual dissociation? There is an ongoing debate on whether the vision demonstrated by blindsight patients is qualitatively different from that of healthy subjects (Weiskrantz, 2008), or whether it is simply a form of degraded normal vision (equivalent to vision at the detection threshold; e.g., Fendrich *et al.*, 1992, 1993; Overgaard *et al.*, 2008) possibly entailing a change in subjects' decisional behavior (Campion *et al.*, 1983; Gorea and Sagi, 2002; Klein, 1998). What is known for a fact is that perceptual performance in blindsight subjects is not uniformly degraded across tasks: it is highly impaired, for example, in colour contrast but less or not at all in luminance detection tasks (Kentridge *et al.*, 2007). Also, less or no impairment is noticed when performances are assessed *via* two-alternative forced choice than *via* yes/no paradigms (Azzopardi and Cowey, 1997), an observation supporting the contribution of decisional factors (Campion *et al.*, 1983; Gorea and Sagi, 2002; Klein, 1998). The fact that simple shape discrimination performances correlate with subjects' level of confidence disclaims the proposition of blindsight being a qualitatively different form of vision and argues in favor of it being the consequence of a strongly deteriorated sensitivity (Overgaard *et al.*, 2008). Finally, and despite criticisms by Stoerig (1993) and by Weiskrantz (1993), dense visual field mapping together with nuclear magnetic resonance and positron emission tomography techniques suggest that at least some blindsight patients are not entirely hemianopic, as scattered islands of vision persist in their primary (geniculostriate) visual pathways (Fendrich *et al.*, 1992, 1993). It cannot be excluded that a similar preservation of V1 activity also occurs in artificially TMS induced scotomae.

4.3.4. Conclusion

In the context of the perception-action dissociation, the case of blindsight has been used to illustrate the fact that information which is inaccessible to 'consciousness' remains available for motor responses. The results presented above suggest that this information is nonetheless accessible for a number of perceptual tasks (and subjects), such as simple detection or shape discrimination and that this access may be due to residual, scattered islands of vision in the ventral pathway. The impairments of blindsight subjects, thus, do not license the conclusion of a perception-action dissociation. It should be pointed here, however, that the debate on the blindsight condition and its underpinnings remains open. The most decisive unsettled issues

relate to whether or not such patients are indeed hemianopic (Type I referred to as ‘attentional blindsight’ vs. Type II referring to subjects presenting residual visual abilities ‘with awareness’, Weiskrantz, 1989; Weiskrantz *et al.*, 1995), to the very definition of what is meant by awareness and its different types (see Danckert and Rossetti, 2005) and to the residual subcortical neural structures mediating (Type I) blindsight (e.g., Bittar *et al.*, 1999; Boire *et al.*, 2001; Leh *et al.*, 2006).

In any event, it should be stressed once and again that the very concepts of perception (“the visual experience [thus, consciousness] we have about the current stimulus array”; Milner and Goodale, 2008, p. 775) and action (“the [unconscious] use [of visual information] in the detailed programming and real-time control at the level of elementary movements”; Milner and Goodale, 2008, p. 776), no less than their mandatory associated consciousness/unconsciousness states (circularly used in their definition), remain fuzzy and misleading despite claims made that their definitions are shared by “most experimental psychologists working in the mainstream tradition”; Milner and Goodale, 2008, p. 775). This point is rather obvious from a psychophysical perspective whose main reference frame is Signal Detection Theory (SDT). Mostly ignored in the interpretation of neuropsychological data, SDT is entirely uncommitted to a distinction between conscious–unconscious sensory events other than relating these two states to the evoked internal responses being, respectively, above or below subjects’ decision criteria (see Rouder and Morey, 2009). If such relationship is not accepted, then the consciousness issue remains entirely philosophical, hence quantitatively intractable.

5. Psychophysics of Dissociation in Healthy Subjects: Perception and Action in the Context of Visual Illusions

5.1. Size, Tilt and Depth Illusions

The two distinct visual pathways view led naturally to the hypothesis that the ventral stream should be subject to perceptual illusions, whereas the dorsal stream should be immune to them, notably because the latter does not have access to the perceptual knowledge stored in the ventral stream. A wealth of experiments with size-contrast illusions (Ebbinghaus/Titchener and related: e.g., Aglioti *et al.*, 1995; Amazeen and DaSilva, 2005; Fischer, 2001; Ganel and Goodale, 2003; Ganel *et al.*, 2008a, b, c; Gonzalez *et al.*, 2006; Haffenden and Goodale, 1998; Hanisch *et al.*, 2001; Kwok and Braddick, 2003; Ponzo: e.g., Brenner and Smeets, 1996; Ganel *et al.*, 2008c; Jackson and Shaw, 2000; Müller-Lyer: e.g., Daprati and Gentilucci, 1997; Dewar and Carey, 2006; Gentilucci *et al.*, 1996; Haffenden and Goodale, 1998; horizontal–vertical illusion: e.g., Servos *et al.*, 2000; diagonal illusion: e.g., Stöttinger and Perner, 2006; the rod-and-frame illusion: Dyde and Milner, 2002) suggest that this is indeed the case (see Note 7). As a consequence, it has been concluded that such behavioral studies validate the perception–action dissociation view (e.g., Carey, 2001; Goodale, 2008).

The first serious challenge to this conclusion began with a methodological and conceptual critique by Franz *et al.* (2000). These authors hold that the perceptual and motor tasks in the experiments of Aglioti *et al.* (1995) are not comparable. In the perceptual task, subjects directly compared two Ebbinghaus figures, whereas in the motor (grasping) task, only one figure was presented at a time. According to Franz *et al.* (2000), the comparability of the motor and perceptual responses rests on the premise that simultaneous processing (as in the perceptual task) and sequential processing (as in the motor task) are identical. Franz *et al.* (2000) invalidated this premise. On the one hand, their results show that the perceptual effect of the illusion is greater when subjects compare two simultaneously presented discs. On the other, Franz *et al.* (2000) find no difference between perceptual and motor performance when both are evaluated under comparable conditions (Franz *et al.*, 1998, 2000; Pavani *et al.*, 1999). The motor system's immunity to visual illusions is also contested for other pictorial illusions (for reviews see Bruno and Franz, 2009; Bruno *et al.*, 2008; Franz, 2001; Goodale, 2008). Franz (2001) highlights general concerns with the different ways of assessing the effects of illusions in the perceptual and motor domains as they raise the problem of characterizing the difference between motor and perceptual tasks. Depending on the study, subjects may be asked to match the illusory size of the target stimulus by adjusting either the size of a probe, or the distance between their thumb and index finger. But thumb-index finger separation has been cited both as a perceptual (e.g., Haffenden and Goodale, 1998) and as a motor measure (e.g., Vishton *et al.*, 1999). Another issue is that different perceptual measures yield different results (Daprati and Gentilucci, 1997), and that the differences between these measures can sometimes be greater than the difference between measures said to be 'perceptual' and those said to be 'motor' (Haffenden and Goodale, 1998). Franz, together with several other authors, and in contrast with the dissociationist view, holds that action and perception are based on a common visual representation (Franz, 2001; Franz and Gegenfurtner, 2008; Franz *et al.*, 2000, 2001; Gegenfurtner and Franz, 2007). When perceptual and motor tasks are correctly matched, Franz argues, they yield equivalent performances (e.g., Bruno, 2001; Franz, 2001; Smeets and Brenner, 2001; Vishton *et al.*, 1999).

It has been countered that such non-dissociation results are marginal in number, that they do not fit in with the neuropsychological and neurophysiological evidence and/or that they could be themselves subject to experimental confounds (e.g., Goodale *et al.*, 2005, p. 278). One such possible confound when testing the Ebbinghaus illusion is that, under particular stimulus arrangements, the visuomotor system may treat the surrounding disks as obstacles to be avoided, thus, yielding an 'illusory' visuomotor illusion (e.g., Haffenden and Goodale, 2000; Haffenden *et al.*, 2001; Schindler *et al.*, 2004; but see Franz *et al.*, 2003). At the same time, advocates of the dissociation view also argue that cases where some actions (such as grasping) do mimic the perceptual illusions are not surprising given that "after all (...) perception has to affect our actions or the brain mechanisms mediating perception would never have evolved". (Goodale, 2008, p. 904.)

Yet another instance of countering the perceptual–motor task matching problem is to argue that it becomes immaterial for cases (e.g., Aglioti *et al.*, 1995; Ganel *et al.*, 2008c; Haffenden and Goodale, 1998) where the grip amplitude continues to reflect the physical difference in targets' sizes despite the fact that the illusion displays are adjusted so that these targets appear perceptually identical (Goodale, 2008; see also Goodale *et al.*, 2005). Clearly, the argument does not address the possibility that observers use different cues depending on the (visual or motor) task they are requested to perform. A case in point is Smeets and colleagues' (Smeets and Brenner, 1999, 2001, 2008; Smeets *et al.*, 2002) argument that grasping control is based on the location of the grasping points rather than the distance between them (i.e., the size/extent of the object to be grasped) and is hence immune to size illusions (see also Mack *et al.*, 1985). Such dissociation between location and size should account for most (if not all) size context effects as well as for the absence of Weber's law when applied to the grasping behaviour (Ganel *et al.*, 2008a).

In response to Smeets and Brenner's (2008) criticism, Ganel *et al.* (2008b) provide data showing that delayed grasping, that "must rely on a memory of the object that was originally laid down by perception" (p. R1091) *does* obey Weber's law, a result claimed to comply with the dissociation view but, unfortunately, also with the non-dissociation view. To make their point, Ganel *et al.* (2008b) also report data showing the absence of Weber's law for 'real-time' grasping with vision occluded after movement initiation (see an equivalent report for the Ponzo illusion by Ganel *et al.*, 2008c). Their argument seems to be that in this latter case as in the delayed grasping case, subjects must rely on visual cues and yet only the former displays Weber's law. Their concluding comment is that Smeets and Brenner's account "cannot explain these results without making additional assumptions (for example, positing that real-time grasping uses position cues whereas memory guided grasping uses size)" (p. R1091). Because they are 'additional' such assumptions are not necessarily unwarranted. It may well be that memory traces of absolute location and of extent degrade differentially over time so that location memory is more reliable than extent memory for short delays and that this pattern reverses for longer delays.

It is worth noting that although rejecting Smeets and Brenner's (2008) location *vs.* extent account of the many perception–action dissociation results, Goodale and Milner's group acknowledges the fact that the location/extent dichotomy is "difficult to separate" from Goodale and Milner's (1992) and Milner and Goodale's (1995) original distinction between the visuomotor system computing absolute object metrics and the perceptual system using scene based metrics (see Goodale *et al.*, 2005, p. 278). Such acknowledgment together with the numerous studies discussed in Section 4.1, *Optic ataxia and visual agnosia* (see also Pettypiece *et al.* (2009) for similar delayed response results obtained with healthy subjects), changing their response strategies depending on whether their haptic responses are delayed or not (or, equivalently, unpracticed *vs.* well trained; Gonzalez *et al.*, 2006, 2007, 2008) provide ample evidence that motor (but also perceptual) responses can and do appeal to either of the two metrics. Strangely, it is precisely this type of argument

that Milner and Goodale (2008) seem to reject when it comes to interpret Schenk's (2006) data presented above (Section 4.2, *Egocentric vs. allocentric issues*).

Another relevant and critical account given by the dissociationist group of the many discrepancies observed in the visual illusions perception–action studies is the timing of motor appraisal of a pictorial illusion. This point is nicely illustrated by the *hollow mask* illusion. When looking at the concave side of a hollow mask human observers perceive it as convex (Gregory, 1963). Króliczak *et al.* (2006) showed that, when asked to ‘flick’ off a small target stuck to the hollow surface, observers aimed at the real depth, i.e., they were not ‘fooled’ by the visual illusion. The standard interpretation of this dissociation is that the eye-vergence system (consciously impenetrable) is immune to pictorial cues as it has been shown with ambiguous slant stimuli (Wismeijer *et al.*, 2008). In response to failures to replicate the original result with a procedure that did not require subjects to perform a ‘flicking’ movement (Hartung, Schrater, Bulthoff, Kersten and Franz, 2005) Goodale (2008) points out that “such slow pointing movements, (...) can often reflect cognitive/perceptual judgements (...) and need not engage the more ‘automatic’ visuomotor system” (pp. 908–909). Slowed down movements are precisely those for which Króliczak *et al.* (2006) have *not* obtained visuomotor immunity to the hollow mask illusion and are also those for which optic ataxic patients show improved pointing and/or grasping movements (see the preceding section).

The perennial distinction made between fast/automatic and slower/more reflective movements is a key feature of the dissociation view. That (re)acting ‘here and now’ (Goodale, 2008, p. 902) and providing a time unconstrained response are behaviours characterized by distinct properties (and performances) is beyond doubt. Within short time-frames action must rely on poorly processed perceptual information (open-loop); for longer time-frames, action (if not ballistic) may and does profit from online corrections (see Bruno and Franz (2009), Jeannerod (1997), and Section 8.3, *Pursuit and detection of changes in speed or direction*). Equivalently, ‘perceptual’ judgments (including size-contrast illusions; e.g., Fraise, 1971) clearly differ with the timing of the stimuli to be judged. This common sense distinction (supported by myriads of experiments) between slower ‘cognitive/perceptive’ and faster ‘automatic’ visuomotor judgments can by itself account for a large number of dissociation results presented in this and in the following sections without appealing to a perception–action dissociation.

A more conceptualized variant of this same idea has been developed by Glover and Dixon (Glover, 2002, 2004; Glover and Dixon, 2001a, b, 2002) who point to the fact that action tasks involve multiple stages of processing from purely perceptual to more ‘automatic’ visuomotor control (the ‘planning/control’ model) and that illusions would be expected to affect the early but not the late stages of a grasping movement. In their model, each movement draws on both a planning and an online control component (see Bruno and Franz, 2009; Jeannerod, 1997). The planning of an action needs to take context into account, if only to avoid obstacles, and should, thus, be subject to perceptual illusions that are induced by the context. Percep-

tual illusions may not much affect the final precision of the motor act, thanks to corrections from an online context-independent control system. As the large majority of studies have assessed motor performance that bears on the final part of the movement, they may have passed over the illusions' effect on the motor system. Instead, studies of the time course of grasping movements toward a bar subject to a tilt illusion (Glover, 2004; Glover and Dixon, 2001a, b, 2002; Li *et al.*, 2008), to the Müller-Lyer illusion (Westwood *et al.*, 2000, 2001), or toward the Ebbinghaus circle (Glover, 2002), do show significant illusion due perturbations only at the beginning of the grasping response (but see Handlovsky *et al.*, 2004). Careful analyses of similar data suggest, however, that the motor effect of the illusion is constant throughout the movement (Franz, 2004).

5.2. *Illusions of Perceived Position*

The Roelofs effect (Roelofs, 1935) is a change in the perceived position of a small central target due to its position inside a large frame. The centre of the frame is out of alignment with the observer's median plane. When subjects are asked to indicate the position of the central target using a previously learned set of possible positions, they report its location as displaced in the direction opposite to the center of the frame, relative to the subject's median plane. Despite their erroneous perception of the target's position, subjects are able to precisely guide their manual pointing (Bridgeman *et al.*, 1997) or saccades (Dassonville and Bala, 2004) toward it. Dassonville and Bala (2004) argued against taking such results as evidence in favor of a perceptual–motor dissociation. They noted that, while both the perceptual and motor responses bear on the position of the target, the two tasks are very different. In the visuomotor task, subjects can point at the target based on an egocentric encoding only. In the perceptual task, in contrast, subjects must compare the target's position to those of the memorized positions. The errors in perceptual judgments could result, therefore, either from an error in the *perceptual* encoding of the target's position in the direction opposite the centre of the frame (as also concluded by Bridgeman *et al.*, 1997), or from an error in the localization of the memorized positions in the same direction as the frame. In one of Dassonville and Bala's (2004) experiments, subjects had to learn five spatial positions in the dark. In a second phase, they were asked to make a saccade toward one of the memorized positions, in the presence of a frame which was either centered on their fixation point, or slightly shifted to the right or left. The presence of the frame induced a distortion of the memorized spatial positions in the same direction as its displacement, as the authors had hypothesized. They dubbed this the *inverse* Roelofs effect on memorized space. These measured biases in saccadic localization predicted the size of the Roelofs effect. Dassonville and Bala (2004) argued that these distortions occur because the frame induces a bias in the subject's perceived median plane, and the median plane serves as a reference for the egocentric localization of stimuli. To test this hypothesis directly, they varied the initial fixation position of subjects and then asked them to look 'straight ahead', while a frame that was either centered or

shifted with respect to the true median plane was displayed on a screen. The results clearly show that the frame induces a shift in subjects' perceived median plane toward the center of the frame. These results should explain the lack of a Roelofs effect in visuomotor tasks: if the same reference frame is used both to encode target positions and to direct actions toward them, then changes in this reference frame caused by the positioning of the frame will not affect the final movements. Thus, according to Dassonville and Bala (2004), the apparent dissociation between perception and action in the Roelofs effect results from the transient distortion in the subjects' perception of their own median plane induced by the frame. Movements toward targets remain accurate because position encoding and movement planning are based on the same egocentric reference frame. The effect observed on the perceptual task, then, occurs because the positions that the subject is comparing are encoded at one moment in the presence of a shifted frame — and, thus, relative to a biased median plane — and then in the absence of any frame and, thus, relative to the true median plane.

De Valois and De Valois (1991) showed that when a translational movement is applied to the carrier of a Gabor patch, its envelope is perceived as being displaced in the direction of the movement. Yamagishi *et al.* (2001) studied the effect of this illusion on both perceptual localization judgments and pointing movements. As the visuomotor localization error was three times larger than the perceptual error (though only for short — 200 ms — post-stimulus delays), they concluded in favor of a perceptual–motor dissociation. Using the same stimuli, Kerzel and Gegenfurtner (2005) showed that perceptual mislocalizations depend significantly on whether subjects are asked to evaluate the position of the Gabor relative to other Gabors, to static lines, or to flashed lines. As contextual effects do not have equivalent bearings on perceptual judgments and motor pointing, they advise comparing these behaviors with simpler and better controlled stimuli and tasks.

5.2.1. Conclusion

The relevance of the effects of illusions to a hypothetical dissociation between perception and action is highly debatable. On the one hand, the differential effects of visual illusions on motor and perceptual responses disappear when tasks are appropriately matched (e.g., Franz, 2001; Franz and Gegenfurtner, 2008; Franz *et al.*, 2000; Pavani *et al.*, 1999). On the other hand, it is generally possible to give an alternative account of the two response types clearer and more parsimonious than in terms of a dissociation between two functional entities vaguely described as 'perception' and 'action'. Various authors have suggested that behavioral dissociations result from a range of differences between the types of processing required for 'perceptual' and 'motor' tasks, such as semantic *vs.* pragmatic (Jeannerod, 1997), relative *vs.* absolute (Vishton *et al.*, 1999), allocentric *vs.* egocentric (Bruno, 2001; Schenk, 2006), immediate *vs.* delayed (Rossetti *et al.*, 2003), planning *vs.* online control (Glover, 2002; Goodale and Milner, 1992), and simultaneous *vs.* sequential (Franz *et al.*, 2000).

While the discussion above raises serious doubts about the validity or even testability of the perception–action dissociation theory, it clearly points to the undeniable observation that the temporal conditions under which judgments (be they motor or perceptual) are compared is critical. Once this is accepted, it can be argued that ‘automatic’ (thus, rapid) reactions necessarily require a lesser accumulation of sensory evidence than slower, ‘cognitive/perceptive’ judgments (respectively, more liberal and more conservative decision criteria). It is then legitimate to raise the possibility that ‘automatic’ motor and slower perceptual behaviors operate on the same incoming information but at different levels of confidence. This stand is developed at length in the next two sections.

6. Backward Masking and Perceptuo-motor Dissociation

The effects of an unperceived prime on motor responses is known as *subliminal response priming*. This topic sits at the meeting point between the study of subliminal perception and of the perception–action dissociation. The classic response priming paradigm is based on the following logic: in a first condition, subjects’ perceptual sensitivity to a stimulus is tested (direct measure), often in hopes that it will be statistically indistinguishable from zero. Then, in a second condition, the effects of this ‘invisible’ prime on the motor response to the mask are tested (indirect measure).

Here we present and discuss experiments comparing simple reaction times (sRTs) and perceptual detection, on one hand, and studies looking at choice response times (cRTs) and perceptual discrimination, on the other.

Two things should be made clear from the start. On the one hand, using RT as an index of vision-for-action processing is legitimately debatable (see Goodale, 2008) as by itself RTs is not fully indicative of the “detailed programming and real-time control at the level of elementary movements” (Milner and Goodale, 2008, p. 776). On the other hand, the latency of an action is an inevitable segment of the acting (no less than of the perception) process and as such provides significant information on this process as a whole (e.g., Striemer *et al.*, 2009). Rightly or wrongly, it has been used as such by most of the studies referred to below. Their main purpose was to show that RTs can indeed be manipulated by visual stimuli of which subjects remain allegedly ‘unconscious’. This distinction between ‘conscious’ perception and ‘unconscious’ action is one of the key ingredients if not *the* key conception entertained by the dissociation view (Goodale, 2008; Milner and Goodale, 2008). Whether or not their main proponents agree with the use of RTs for assessing this theory’s value is inconsequential. The fact is that a significant number of psychophysical studies have addressed it by such means (see Neumann, 1990).

6.1. Simple Reaction Time and Perceptual Detection

One of the most widely cited demonstrations of the dissociation between perceptual and motor responses is known as the ‘Fehrer–Raab effect’. In the original experiment, Fehrer and Raab (1962) briefly presented a luminous square (prime stimulus)

followed by two flanking squares (masking stimulus) hence yielding for a range of delays strong metacontrast (see Note 8). Under such conditions the central ‘prime’ square was phenomenologically invisible. The task of subjects was to press a key as soon as they perceived any of the stimuli. Even for conditions where the prime preceded the masks by as much as 75 ms (and was phenomenologically invisible), sRT to the prime plus masks complex were similar to those measured in a condition where the prime was presented alone and, therefore, visible. This pattern of results has been replicated many times (i.e., Bernstein *et al.*, 1973; Fehrer and Biederman, 1962; Schiller and Smith, 1966; Taylor and McCloskey, 1990). In their meta-analysis of a part of the data from these experiments, Neumann and Klotz (1994) noted that the distribution of mean sRT to the prime–mask complex could be explained by a race model wherein internal responses to the prime and to the mask grow independently toward a threshold. The internal response which reaches the threshold first sets off the motor response. According to Neumann and Klotz (1994), these data suggest a dissociation between conscious perception of the prime (direct measure) and the ability of the same stimulus to evoke a motor response (indirect measure).

In order to study the relationship between motor and perceptual responses, Waszak and Gorea (2004) measured sRT to a metacontrast stimulus (motor task), followed on the same trial by a Yes/No response as of the presence of the masked stimulus (perceptual task). On each trial, a masking annulus was displayed at a random time on the screen. It could either be presented on its own or preceded by a Gaussian blob that acted both as prime and target. Target intensity was manipulated so as to keep it close to threshold within a range from about 0.5 to 4 d' units. Contrary to suggestions derived from the experiments discussed above, sRT decreased with target’s intensity only when subjects managed to correctly report its presence (perceptual hits). In other words, the motor response was conditional on the perceptual response. This result is surprising given that similar studies measuring both simple and choice RT (cRT: see below) had arrived at opposite conclusions, namely that motor responses are independent of perceptual responses. One of the methodological differences noted by Waszak and Gorea (2004) was their use of a low-contrast (14–16%) prime. Other studies had classically used maximum contrasts. Waszak and Gorea (2004) repeated their first experiment with a higher target contrast while keeping its sensitivity constant by increasing the masking effect *via* a shortening of the prime–mask delay. This time, in accord with previous studies, they found a reduction of sRT when the prime was physically present, whether it was detected by the subject (hit) or not (miss).

To interpret these results, Waszak and Gorea (2004) hypothesized that the motor system operates within two separate functional regimes in response to a visual stimulus. In one of these regimes, active when stimulation has low physical energy (in this case, low contrast), the motor response cannot be directly evoked and depends on the perceptual criterion. In the other, active under stimulations of high physical energy, the prime can directly evoke a motor response, independently of the percep-

tual system. These two functional modes could be implemented in a model wherein the perceptual response is determined by a variable decision criterion which depends on context (e.g., stimulus probability), in accordance with Signal Detection Theory (Green and Swets, 1966). The motor response, in contrast, might depend on a fixed, high threshold. According to Waszak and Gorea (2004), this hypothesis is compatible both with models which postulate two distinct pathways, perceptual and motor, and with those holding that the two responses are determined by a single system, but at different moments.

Waszak *et al.* (2007) repeated the original Waszak and Gorea (2004) experiment and compared its outcome with a condition where prime and ‘mask’ were presented at sufficiently different locations to avoid metacontrast. For this latter condition, sRT to the prime–‘mask’ complex decreased with prime’s contrast only on trials entailing perceptual hits. When the prime was masked, on the other hand, sRT were affected by the prime whether detected (hits) or not (misses), though the effect was weaker in the latter case. Mean sRT computed independently of subjects’ perceptual responses did show a prime contrast dependency and for any given contrast were strictly identical, whether or not the prime was masked. In other words, sRT were determined by the prime’s contrast and were independent of its visibility. Taken together these data are compatible with the notion of a unique incoming signal upon which motor and perceptual decisions are taken independently with the motor decision taken earlier than the perceptual decision. Because the mask appears after the prime, Waszak *et al.* (2007) suggested that masking may only affect the later stages of visual processing of the prime and, thus, modulate perceptual responses only.

6.2. *Choice Reaction Times and Recognition*

This methodological approach capitalizes on the combination of two standard effects: metacontrast, a process whereby a mask interferes with the coding of a prime (as in Fehrer and Raab’s paradigm) and a congruence–incongruence effect whereby the prime interferes with the processing of the mask in a facilitatory–inhibitory way depending on their similarity/dissimilarity. This latter effect is but a variant of a large set of paradigms such as Stroop interference (MacLeod, 1991; Stroop, 1935), picture–word interference (LaHeij and Vandenhof, 1995; Lupker, 1979), or the flanker paradigm (Eriksen and Eriksen, 1974). In the present context it has been used for the first time by Neumann and Klotz (1994), and was subsequently adopted by many others (e.g., Klotz and Neumann, 1999; Neumann and Scharlau, 2007; Scharlau and Ansorge, 2003; Schmidt, 2002; Vorberg *et al.*, 2003). It differs from Fehrer and Raab’s paradigm in that it involves a perceptual *discrimination* (rather than detection) task and a motor *choice* response time (cRT; rather than simple) *bearing on the mask* (rather than on the prime). In contrast with standard interference paradigms where the prime is typically visible, the use of metacontrast is meant to render it invisible. Neuman and Klotz’s introduction of this new paradigm was meant to answer methodological criticisms by a number of authors (e.g.,

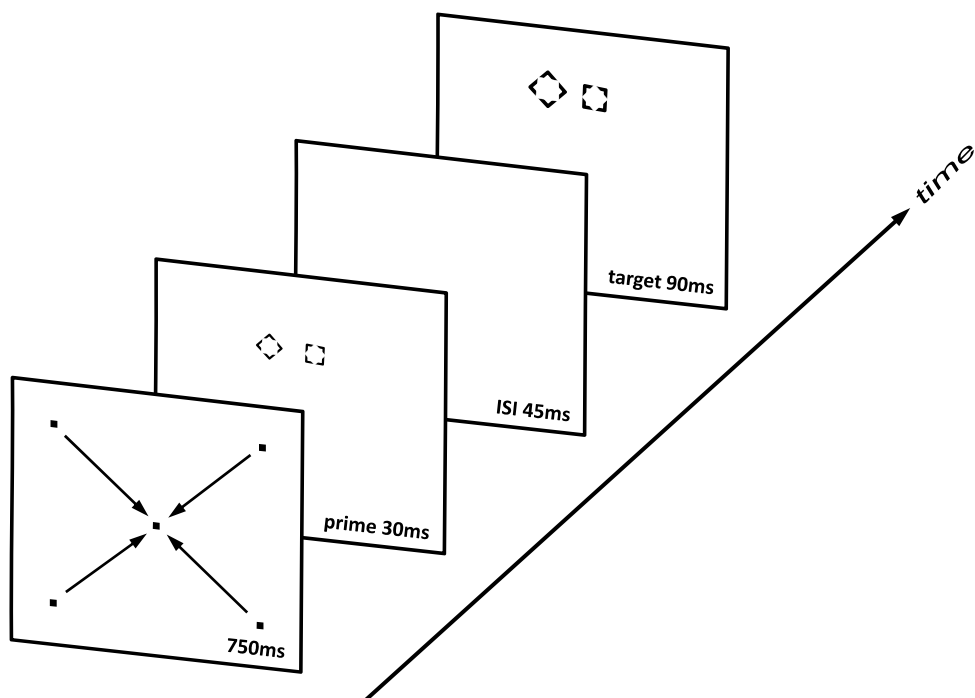


Figure 3. Timecourse and spatial layout of stimuli in a ‘congruent’ trial from Neumann and Klotz (1994). A trial begins with the presentation of four points beginning at the corners of the screen and moving toward the centre. Their purpose is to facilitate fixation. The following frames present the primes, followed after some delay by the masks. Figure from Klotz and Neumann (1999).

Holender, 1986; Reingold and Merikle, 1988, 1990) of the previous techniques. Among those, transgressions of the *exclusiveness* and *exhaustiveness* principles are the most critical. The exclusiveness principle boils down to making sure that any effect of the prime on cRT is observed while the sensitivity to this prime is null (i.e., ‘true’ zero awareness, sic!). The exhaustiveness principle requires that both perceptual and motor tasks use the very same available information, hence a carefully designed stimulation sequence and data analysis.

In one of their typical experiments (see Fig. 3), Neumann and Klotz (1994) present a pair of different stimuli (i.e., square and diamond) on each side of fixation referred to as primes. They are followed by larger size versions of themselves referred to as masks. If they share the same shape at the same location, primes and masks are congruent and incongruent otherwise. The motor task is to press a key corresponding to the position of a mask of a pre-specified shape (square or diamond). The discriminability of the primes (square vs. diamond) is tested in a separate block of trials under the very same stimulation conditions as for the motor trials. The experimental conditions are chosen so that this discriminability is close to zero, thus, complying with the *exclusiveness* principle. The detectability of the primes is non-zero, but this is not an issue as the question asked is *whether*

a non-identifiable (but detectable) prime can influence choice motor responses. The answer is yes: when prime and mask are congruent, mean cRT (to the target mask) are shorter and there are fewer choice errors than when prime and mask are incongruent. This result is extremely robust and has been repeatedly replicated (Klotz and Neumann, 1999; Neumann and Scharlau, 2007; Scharlau and Ansorge, 2003; Schmidt, 2002; Vorberg *et al.*, 2003). In addition to replicating Neumann and Klotz's (1994) congruency effect with (presumably) invisible primes, Vorberg *et al.* (2003) manipulated the stimulation conditions so as to produce an incomplete masking effect that either increased with or followed a U-shaped function of the time-interval between prime and mask. Independently of the type of masking, however, the effects of the prime on cRT remained unchanged: congruent primes yielded faster responses to the masks than incongruent primes, and the effect increased linearly with the increasing delay between prime and mask, that is independently of the visibility of the mask. Moreover, for the condition where prime discrimination performance dropped with the prime–mask interval, cRT increased, an effect termed *double dissociation* by the authors (see Note 9).

To explain these priming effects, Vorberg *et al.* (2003) propose a model wherein a decision mechanism, possibly located in the prefrontal cortex, evaluates the information integrated by two leaky accumulators, each voting for one of the two motor responses (“press left button” vs. “press right button”), mutually inhibiting each other (see Note 10 and Fig. 4). A response is set off when one of the two accumulators reaches a critical value. The model predicts the priming effect on the motor

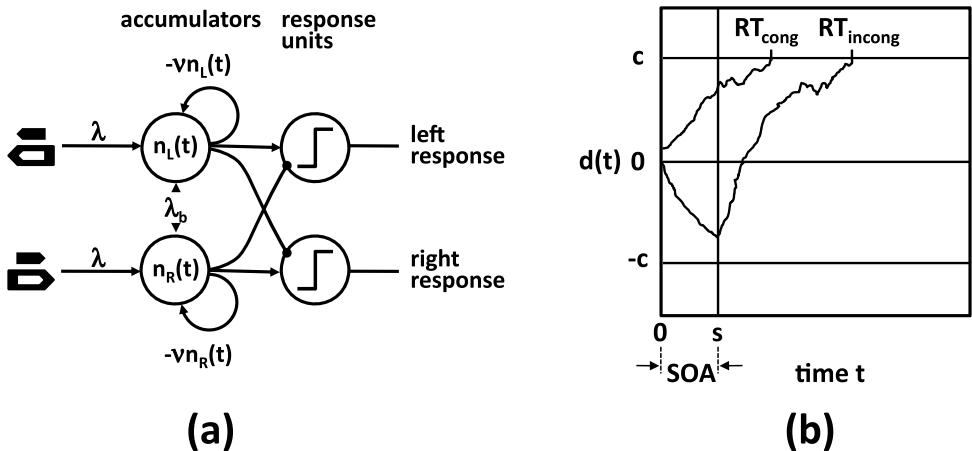


Figure 4. (a) Integration model proposed by Vorberg *et al.* (2003) to explain the priming effect on choice reaction times. Two integration units, each specific to one of the two stimuli (and hence response options), have mutual inhibitory connections. A response is set off when the difference between the two integrators $d(t)$ exceeds a criterion (c or $-c$). (b) Representation of the inter-accumulator difference in the $d(t)$ signal on congruent and incongruent trials. The appearance of the prime corresponds to time 0, that of the mask to time s . See text for more details. Figure adapted from Vorberg *et al.* (2003).

responses by postulating that the primes evoke the same activation in the accumulators as the masks. Accordingly, the primes begin to bias the decision signal toward one or the other of the response thresholds before the appearance of the mask. In keeping with their data, the model predicts priming functions that are independent notably of motor decision criteria and, thus, of subjects' error rate. The function of this decision mechanism would be to permit arbitrary associations between sensations and actions.

Vorberg *et al.* (2003) conclude that not only can a motor response be affected independently of a perceptual response, but that perception and action are under the control of independent systems. On this view, the dissociation between the priming effect on responses to the mask and the masking effect on the visibility of the prime is compatible with the theory of a dissociation between perception and action (Milner and Goodale, 1995) if it is assumed that processing of the prime is interrupted by the mask, rendering it invisible. This understanding is shared by numerous authors (e.g., Bridgeman *et al.*, 1979; Steglich and Neumann, 2000). According to these authors, the motor system has access to information about the shape of non-perceived stimuli, and integrates (rather than substitutes) the image of the mask with that of the prime. The integration of information about the prime and the mask is the central assumption underlying this accumulator model. It should be noted, however, that Vorberg *et al.*'s (2003) model does not specify how the perceptual response is obtained, but simply postulates that it is produced elsewhere, in an independent module (see also Schmidt and Vorberg, 2006).

The hypothesis that priming effects consist in the activation of motor responses associated with the primes seems to be unanimously accepted (e.g., Kiesel *et al.*, 2007; Kouider and Dehaene, 2007). The strongest arguments in favour of this hypothesis come from studies measuring 'lateralized readiness potentials' (LRP) — or the metabolic activity in motor areas using fMRI. Several studies have indeed found that subliminal primes activate motor areas (Dehaene *et al.*, 1998; Leuthold and Kopp, 1998; Westheimer, 1954). In accordance with Vorberg *et al.*'s (2003) model, this pre-activation of motor areas apparently facilitates responses to the mask when prime and mask are congruent, and slows responses when they are incongruent.

6.3. Critique of the Perceptuo-motor Dissociation in Masking Paradigms

As mentioned at the beginning of this section, the logic underlying the majority of these experiments is based on the comparison between a direct measure (detection or discrimination of the prime) and an indirect measure of the prime's effects (e.g., sRT or cRT to the prime-mask complex). The direct measure, thus, serves to demonstrate the absence of 'conscious' detection/identification of the prime, while the indirect measure is supposed to reveal the subliminal effects of the very same prime. For the effects of priming on the indirect measure to be imputed to non-conscious processing, it must be shown (1) that the direct measure reflects only conscious information (*exclusivity principle*: this is thought to be guaranteed when $d' = 0$) and that (2) none of the information affecting the indirect measure is con-

sciously detected (*exhaustivity principle*: this criterion makes it necessary for the tasks yielding these different types of measures to be comparable; see Reingold and Merikle, 1988, 1990). This logic is open to various objections (for reviews see notably Holender and Duscherer, 2004; Schmidt, 2007; Schmidt and Vorberg, 2006). Demonstrating that $d' = 0$ in the direct task yields methodological and conceptual problems. Experiments using congruency–incongruency paradigms (between prime and mask) often use complex geometric figures (e.g., Klotz and Neumann, 1999; Neumann and Klotz, 1994; Schmidt, 2007; Vorberg *et al.*, 2003). When primes and masks have different shapes, their interactions can produce different effects depending on whether or not they are congruent. Klotz and Neumann (1999), for example, used squares and diamonds as stimuli. In congruent trials, the prime–mask sequence produces a movement of expansion, whereas in incongruent trials a rotational movement is added. These supraliminal movement signals may be ignored by subjects in the direct (discriminating the form of the prime) but not in the indirect (RT) tasks, thereby transgressing the exhaustivity principle (Ansorge *et al.*, 2007, 2008; see also Szczepanowski and Pessoa, 2007). An alternative to the ‘null sensitivity’ approach consists in testing whether the manipulation of one stimulation parameter may entail different, or even opposite direct and indirect effects (e.g., Schmidt and Vorberg, 2006; Waszak and Gorea, 2004; Waszak *et al.*, 2007). An affirmative answer is taken as evidence of a perception–action dissociation (Schmidt and Vorberg, 2006). While avoiding the 0 sensitivity problem, this ‘process dissociation’ approach remains vulnerable to criticism. Even when this approach allows the dissociation of processes, it remains that the conscious/unconscious nature of these processes has to be postulated *a priori*.

Let us suppose that any of the two methods above is valid and that the measured effect is real: cRT is influenced by a prime, whether or not the subject is able to discriminate it from another. Can it, therefore, be concluded that perception and action are dissociated? What subliminal priming experiments show is that perceptual detection or discrimination of a prime can be modified independently of the ‘motor’ response to the prime–mask pair. They do not show (1) that the motor system would respond to the *invisible* prime if it were not followed by a mask, nor (2) that the perceptual response to the mask is independent of the prime. Concerning the latter possibility, Neumann (1982) notes that, at least for sRT experiments, the prime could draw attention toward the mask that follows it and lead to more rapid detection (perceptual latency priming effect, see above). Steglich and Neumann (2000) point to the fact that this attentional interpretation cannot be put forward in the case of prime–mask congruency cRT effects (e.g., Klotz and Neumann, 1999; Neumann and Klotz, 1994; Vorberg *et al.*, 2003). Nonetheless, attentional effects are not to be disregarded, as cRT are more rapid in the presence of a prime (congruent or not) than when none is present (Ansorge, 1996).

In order to test the hypothesis that the prime has effects on the perception of the mask, certain studies have used temporal order judgment tasks (TOJs: e.g., Neumann *et al.*, 1993; Scharlau, 2002; Scharlau and Neumann, 2003; Steglich and

Neumann, 2000;). Scharlau and Neumann (2003), for example, studied the effect of primes on perceptual latencies as measured in a TOJ task, depending on whether or not the primes were masked. Their results show that perceptual latencies to the prime–mask complex are independent of the visibility of the primes, just as the experiments cited above found for sRT and cRT. Whereas these results suggest an association between a motor response (i.e., sRT) and a perceptual response (i.e., TOJ), they have been nonetheless taken to support their dissociation. Two arguments speak in favor of the dissociation view. The first is based on the observation that the type of primes (congruent or not) affects cRT, but not perceptual latencies (TOJ). At the same time, it is known that the priming effect (even subliminal) on cRT depends on the task (e.g., Neumann and Klotz, 1994). Since motor and perceptual tasks are by necessity different, the differential effects caused by the type of prime used are unsurprising. The second argument rests on the fact that the effect of the prime on perceptual latencies is weaker than its effect on motor latencies. And yet, this difference in effects on perceptual and motor latencies is not restricted to priming situations, but is also found when, for example, the intensity of stimulation is varied (e.g., Cardoso-Leite *et al.*, 2007; Jaśkowski, 1992; Jaśkowski and Verleger, 2000; Menendez and Lit, 1983; Roufs, 1963, 1974; Sanford, 1974). The crucial point is, thus, to demonstrate that these differences between perceptual and motor latencies do indeed result from a dissociation between perceptual and motor systems. This issue is the focus of the next section.

7. Perceptual vs. Motor Latencies

One other approach to the question of sensorimotor relations is to compare perceptual and motor response latencies (e.g., Jaśkowski, 1996, 1999; Jeannerod, 1997). The logic of this approach is straightforward: if perception and action are controlled by a single system, perceptual and motor latencies should be identical. Castiello *et al.* (1991), for example, asked their subjects to verbally indicate when they detected a change in the position of a target that they must also grasp. When position changes are detected, verbal responses are emitted 420 ms after the start of the pointing movement, whereas kinematic modifications in the grasping movement are registered 300 ms earlier. This result has been interpreted to mean that perceptual detection occurs after motor detection (see Note 11).

Comparing perceptual and motor latencies presupposes the ability to precisely define what characterizes each of these. If we consider that they both reflect decision processes (in addition to those necessary to execute the motor response, for example), the distinction between perceptual and motor processes becomes blurred. Following the literature, we distinguish motor and perceptual responses on the basis of the tasks that are used to evoke them. Tasks requiring a simple and immediate motor response to a stimulus (i.e., sRT) are typically said to be ‘motor’, whereas those allowing for a delayed response or requiring the comparison of one stimulus to another are described as ‘perceptual’.

7.1. *Different Measures of Perceptual Latency*

Numerous methods have been used to measure the time that subjects take to perceptually detect a stimulus (for review, see Roufs, 1974). Here we present a limited sample of these.

7.1.1. *Exposure Duration (ED)*

The key idea in this paradigm is that the integral over time of the internal response evoked by a stimulus grows faster with increasing stimulus salience. This is an established psychophysical finding, represented in the laws of Bloch (1885) and Piéron (1914). According to Ejima and Ohtani (1987), perceptual latencies can be inferred from the function associating the contrast detection threshold of a stimulus to its exposure duration. They postulate that the inverse function relating a contrast value to an exposure duration directly represents perceptual latencies. The advantage of this paradigm is that it permits the measurement of perceptual latencies in response to a single stimulus. Given that only one stimulus is generally presented in sRT tasks, this facilitates the comparison of results obtained with these two methods. Nonetheless, the supposition that the liminal exposure duration directly reflects perceptual latency is debatable, if not invalid (e.g., Gorea and Tyler, 1986).

7.1.2. *Temporal Order Judgments (TOJs)*

The temporal order judgment (TOJ) task is probably the most often used to infer the moment at which a stimulus is perceptually detected relative of the moment of perception of another stimulus. In a classic TOJ task, two stimuli, S_1 and S_2 , are presented to the subject with the temporal separation between their respective onsets (Stimulus Onset Asynchrony, SOA) chosen at random on each trial. The task of the subject is to indicate on each trial which stimulus was detected first. The psychometric function in a TOJ task relates the probability that stimulus S_1 is perceived before stimulus S_2 to their SOA. It is generally accepted that the moment of detection of each stimulus can be modeled by a Gaussian distribution (with its parameters, the mean μ and variance σ^2 , depending on the physical attributes of the stimulus; e.g., Schneider and Bavelier, 2003). Then, the difference between two such moments is itself a Gaussian distribution. Following this reasoning, the TOJ psychometric function is a cumulative Gaussian distribution whose mean — also referred to as the point of subjective simultaneity (*PSS*) — is the difference between the mean detection latencies of the two stimuli, i.e., $PSS = \mu_{S_1} - \mu_{S_2}$. This difference taking eliminates all spurious latencies (that do not depend on the signal; e.g., response execution). The standard deviation of the TOJ psychometric function is the square root of the sum of the variances of the moments of detection of stimuli S_1 and S_2 .

7.1.3. *Anticipation Response Time (ART)*

Cardoso-Leite *et al.* (2009) have recently adapted an anticipation paradigm (e.g., Doehring, 1961; Mamassian, 2008) to measure perceptual latencies in an experimental format similar to the one used to measure motor latencies. In this Anticipa-

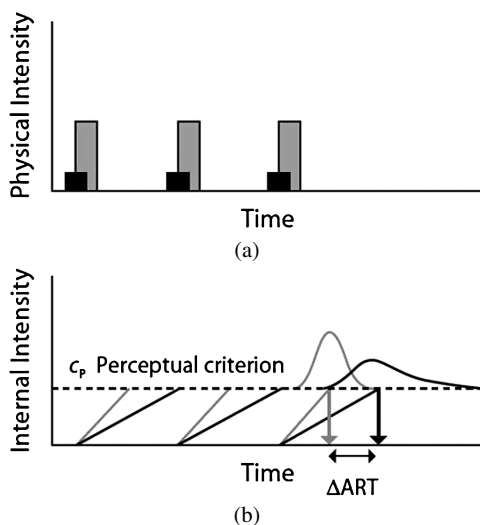


Figure 5. Underlying logic of the ART paradigm (a) Occurrence of signals of two different intensities (black and grey bars) presented at regular intervals. (b) Each of these stimuli evokes an internal response (straight black and grey lines) which causes perceptual detection when it exceeds a critical value, or criterion (dashed horizontal line).

tion Response Time (ART — see Note 12) paradigm, three stimuli are presented on the screen in succession at regular temporal intervals. The task of the subject is to press a button in synchrony with the third stimulus. Figure 5 illustrates the logic of the paradigm. A relatively low-contrast stimulus (black bars, Fig. 5(a)) is perceived later than a higher-contrast stimulus (grey bars). The straight black and grey lines in Fig. 5(b) represent the time course of the corresponding internal responses, which, when they exceed a critical value (dashed horizontal line), lead to perceptual detection. The temporal interval between the detections of the two first stimuli is used to anticipate the appearance of the third stimulus. The internal response reaches the perceptual threshold more quickly for stimuli of high intensity (straight grey lines, Fig. 5(b)) than for those of lower intensity (straight black lines). The perceived interval between two stimuli is the same in each case, but the timing of the synchronization response relative to that of the physical stimuli will vary with the intensity of the stimuli. The difference between the times of synchronization associated with two different intensities, thus, reflects the relative perceptual latency associated with these stimuli.

7.2. Comparison of Perceptual and Motor Latencies

Numerous studies have compared the effects of physical stimulus variations both on perceptual and motor latencies (for reviews see Jaśkowski, 1996, 1999). Physical stimulus properties that have been varied in this context include spatial frequency (Barr, 1983; Tappe *et al.*, 1994), intensity (Jaśkowski, 1992; Jaśkowski and Verleger, 2000; Menendez and Lit, 1983; Roufs, 1963, 1974; Sanford, 1974), lu-

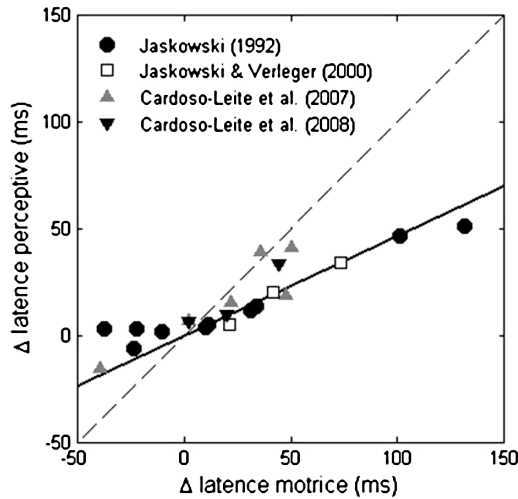


Figure 6. Meta-analysis of 4 studies (various symbols) comparing the variations of perceptual and motor latencies with different stimulus changes. See text for more details.

minance contrast (Cardoso-Leite *et al.*, 2007; Ejima and Ohtani, 1987), changes of color or speed (Adams and Mamassian, 2004), changes of orientation or contrast (Cardoso-Leite *et al.*, 2007), and attentional priming (Neumann *et al.*, 1993; Steglich and Neumann, 2000). These experiments have typically shown that perceptual latencies vary only half as much (or even much less; Liss and Reeves, 1983) with physical variations as motor latencies (see Note 13). This observation in itself justifies the distinction between perceptual and motor latencies.

As an illustration, Fig. 6 presents data from 4 different studies comparing perceptual and motor latencies (Cardoso-Leite *et al.*, 2007, 2009; Jaśkowski, 1992; Jaśkowski and Verleger, 2000) (see Note 14). (1) In the experiments of Jaśkowski (1992), subjects were placed in front of three vertically aligned diodes. The central diode was red and served as a fixation point. The peripheral diodes were yellow and served as stimuli when illuminated, with luminances ranging from 0.4 to 30 cd/m^2 . In the sRT condition, one of the two diodes (fixed position in a given block of trials) was flashed for 200 ms and the subject had to press a key as quickly as possible. In the TOJ condition, the two stimuli were displayed asynchronously, and subjects had to adjust the SOA until the two stimuli appeared to be simultaneous (simultaneity judgment, SJ). (2) In Jaśkowski and Verleger's (2000) setup, the stimuli and sRT task were much like those in Jaśkowski's (1992) study but in the TOJ task the intensity of one of the diodes was fixed (36 cd/m^2) and that of the other varied (0.07 to 2.41 cd/m^2). Subjects had to indicate the position of the stimulus they had perceived first and the SOA was modified correspondingly by one of three parallel psychophysical staircases. (3) Cardoso-Leite *et al.* (2007) used the method of constant stimuli (SOA: ± 100 ms) to measure sRT and TOJ to the same stimuli. A trial began with the presentation of two Gabors, to the left and the right of the

fixation point. These two Gabors successively went through a change that could be either a contrast increment (weak or strong) or an orientation change (weak or strong). Subjects had first to press a key as soon as they detected a change, and then to indicate the position of the first-perceived change. (4) Finally, Cardoso-Leite *et al.* (2009) studied the effect of luminance contrast (from 10 to 80%) on sRT as well as on anticipation response time (see above for a description of this method). The different symbols of Fig. 6 represent a sample of the data obtained in each of these 4 studies. Each point represents the mean of all subjects' data from one experimental condition. The coordinates of each point represent mean relative motor latencies (i.e., ΔsRT ; x axis) and, mean relative perceptual latencies (i.e., PSS ; y axis). Despite large methodological differences, the variations in perceptual and motor latency in these studies are highly correlated (Spearman R : 0.95; $p < 0.001$). Critically, perceptual latencies vary less than motor latencies. A linear fit to these data with a zero intercept (orthogonal regression; continuous straight black line in Fig. 6) yields a slope of 0.47 with a 95% confidence interval between 0.46 and 0.48.

7.3. Explanatory Models of the sRT–TOJ Dissociation

The relation between latencies measured in sRT and TOJ (or ART) tasks is broadly understood as either reflecting the same information integration process followed by distinct decision processes or as evidencing different information integration as well as decision process (for a review, see Miller and Schwarz, 2006).

7.3.1. Two Independent Pathways

Certain authors have suggested that the RT–TOJ dissociation results from the fact that the two tasks involve fundamentally distinct processes, controlled by different cerebral structures (e.g., Neumann *et al.*, 1993; Steglich and Neumann, 2000; Tappe *et al.*, 1994). Appealing to the theory of Milner and Goodale (Goodale, 2008; Milner and Goodale, 1995, 2008), these authors propose that TOJ and sRT are under the control of the ventral and dorsal pathways, respectively. In order to rule out this hypothesis of independence of the two response types, Cardoso-Leite *et al.* (2007) have jointly measured sRT and TOJ on each trial and for the same stimuli. Contrary to predictions of the two distinct pathways hypothesis, their results show that sRT and TOJ are highly correlated.

7.3.2. Single Pathway, Single Decision

Gibbon and Rutschmann (1969) were the first to propose such a model. Aside from a constant execution time proper to the motor task, their model posits the same sRT and TOJ subtending processes (information integration and decision) so that any stimulus variable should equally affect both types of measures. Given the multitude of results contradicting this prediction, Gibbon and Rutschmann's model is to be either rejected or amended. One such amendment is to assume that execution time of the motor response leading to a sRT is also stimulus dependent (Roufs, 1974; Sternberg and Knoll, 1973). Numerous studies show however that execution dura-

tion is relatively constant across a variety of experimental conditions (e.g., Hanes and Schall, 1996; Kammer *et al.*, 1999).

Alternatively, as most experiments have measured sRT and TOJ in separate blocs, their differences could be accounted for by differences in attentional allocation to the stimuli in these tasks. One could for instance posit differential allocation of attention between the two unequal salience stimuli in the TOJ task with more attention allocated to the less visible stimulus (Sanford, 1974), hence facilitating its detection (e.g., Scharlau, 2007; Schneider and Bavelier, 2003). Experiments designed to test this hypothesis invalidated it (Jaśkowski and Verleger, 2000). Finally, dropping the assumption of independence between the two stimuli involved in the TOJ task may also render the predictions of Gibbon and Rutschmann's (1969) model compatible with the psychophysical data. However, this *co-activation* hypothesis has also been invalidated (Miller *et al.*, 2004).

7.3.3. *One Pathway, Two Decisions*

A number of authors explain the differences between sRT and TOJ by supposing that these two responses reflect distinct epochs of a unique internal response. Sternberg and Knoll (1973) posit that a motor reaction is initiated when the internal response evoked by the stimulus exceeds a (relatively low) motor threshold. In the TOJ task, however, these authors posit that subjects base their response on the peak of the internal response, notably in order to minimize the variance of their judgments. The intensity of the stimulus, for example, would have relatively little effect on the timing of this peak, whereas it would have a large effect on the moment at which the motor threshold is exceeded. The idea that the peak of the internal response could be used in this way raises a number of theoretical objections and has been invalidated by numerous experimental results (for review see Miller and Schwarz, 2006).

Various authors suggest that the dissociation between sRT and TOJ can be explained on the assumption that subjects use a higher criterion to detect a stimulus in the sRT task than in the TOJ task (Cardoso-Leite *et al.*, 2007; Ejima and Ohtani, 1987; Miller and Schwarz, 2006; Sanford, 1974) (see Note 15). Ejima and Ohtani (1987), for example, postulate with many others since Carpenter (1981) that the stimulus evoked internal response increases linearly with time, with a slope proportional to the intensity of the stimulus (Fig. 7). On the assumption that subjects place their detection criterion higher in sRT than in TOJ tasks, smaller stimulus intensity effects on perceptual latencies rather than on motor latencies are straightforwardly predicted. Also, random variations in the slope of the internal response (for a given stimulus intensity) will entail smaller variations in decision latency when the criterion is low than when it is high. According to Miller and Schwartz (2006), the main drawback of this model is that it does not explain why the decision criterion should be higher in sRT tasks than in TOJ tasks. Indeed, certain authors have suggested that since the sRT task requires subjects to respond quickly, the sRT criterion should be lower, not higher, than the TOJ criterion (Tappe *et al.*, 1994). Miller and Schwarz (2006) have simulated sRT and TOJ performances with a diffusion model

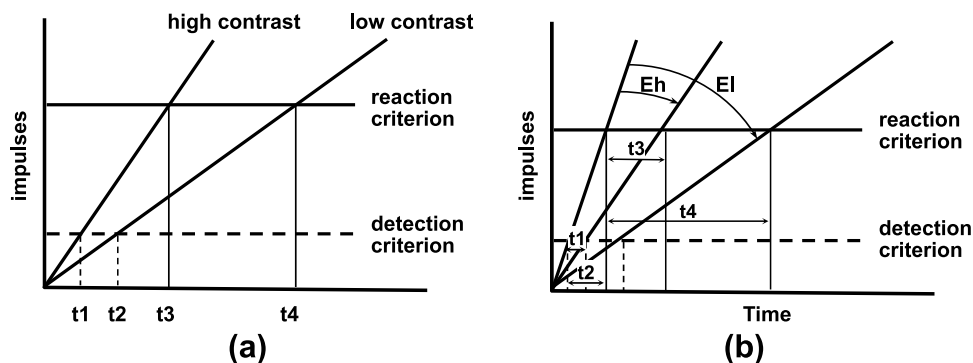


Figure 7. Two-criteria model accounting for differences between perceptual and motor latencies. (a) The rate of growth of the internal response, represented by the slope of the diagonal lines, depends on the intensity of stimulation: the internal response evoked by a high-contrast stimulus grows more quickly than that evoked by a low-contrast stimulus. Each of these internal responses leads to a detection and a motor reaction at the moment when they cross the perceptual criterion (detection) and the motor criterion (reaction), respectively — at times t_1 and t_3 for the high-contrast stimulus, and at t_2 and t_4 for the lower-contrast stimulus. (b) Because of the geometry of this model, identical variations in the slope of the internal response (curved arrows), have different effects on the timing of detection and reaction. The variations E_h and E_l will have systematically greater effects on motor (t_3 and t_4) than on perceptual latencies (t_1 and t_2). This difference in effect size is proportional to the ratio of perceptual to motor criteria. Figure adapted from Ejima and Ohtani (1987).

widely used in the RT literature (see Luce, 1986; Ratcliff and Smith, 2004) (see Note 16). They showed that when the TOJ criterion is lower than the sRT criterion, performance on these tasks is optimal — i.e., faster sRT with a low false alarm rate, and TOJ more often correct. This model offers a parsimonious and theoretically solid explanation of the standard differences in the measured motor and perceptual latencies on sRT and TOJ tasks, respectively. Similar models have been proposed to account for the relationship between perceptual detection and sRT (e.g., Waszak and Gorea, 2004; Waszak *et al.*, 2007). For example, Waszak *et al.* (2007) have proposed that sRT are determined by a fixed motor threshold, whereas perceptual detection is under the control of a variable decision criterion.

8. Dissociation in More Complex Tasks

The experiments presented in the preceding section mainly use relatively simple tasks (e.g., detection) and use latencies to manual key presses as a motor measure. Some hold that ‘non-spatial’ responses are not motor responses (e.g., Bridgeman *et al.*, 1979). Below we present a few examples of experiments on the perception–action dissociation which measured motor performance by hand, arm and eye movements.

8.1. Classification Images

Several studies have used classification images to study the perception–action relation (e.g., Beutter *et al.*, 2003; Eckstein, Beutter, Pham, Shimozaki and Stone,

2007). The analysis of classification images makes it possible to study the visual representations underlying perceptual or motor decisions. In a visual search experiment using classification images, a target and some distractors are presented within white noise that varies across trials. Subject's task is to localize the target. The central idea of this method is that subjects' judgment errors are due to the fact that the noise presented at the location of the distractors randomly contains information that the subject confuses with information carried by the target. By taking the mean of the noise images having led to incorrect decisions, it is possible to estimate the spatial representation of the target used by the subject (Abbey and Eckstein, 2002). Eckstein *et al.* (2007) used a visual search task wherein five Gaussian luminance blobs were positioned on a virtual circle. Among these five blobs, four had low intensity and were used as distractors. The fifth blob was the target, and had a higher intensity. The positions of target and distractors were randomized. White noise was additively superposed to each of the 5 blobs, with the luminance of each pixel chosen randomly from a Gaussian distribution. Noise was, thus, specific to each blob, and changed from one trial to the next. Each noise pattern was saved, and presented once in the motor task and a second time in the perceptual task. In the motor task subjects had 4 s to inspect the scene and determine the position of the target. The landing point of their first saccade was considered to be the motor decision, and the duration of visual treatment associated with this decision was estimated from the latency of this saccade. In the perceptual task, stimulation was strictly identical to that used in the motor task, with the exception of display duration: each stimulus was shown for the amount of time corresponding to the duration of its processing in the motor task. Subjects had to indicate target's position at the end of each trial using a manual key press.

Using the incorrect responses from these two tasks, Eckstein *et al.* (2007) obtained the configuration of noise leading to motor and perceptual responses. The classification images associated with the two tasks are illustrated in Fig. 8 for 2 of the 6 subjects tested. For all subjects, these two configurations were strictly identical (once normalized in amplitude): they differed from the luminance profile of the target (a Gaussian luminance distribution) and followed instead a 'Mexican hat' profile, revealing an inhibitory surround. Thus, not only are perceptual and motor decisions based on the same visual representation but, in addition, this representation is different from the physical stimulus. According to Eckstein *et al.* (2007) these results suggest the existence of a single neural center which encodes the spatial luminance profile of the target and is responsible for both perceptual and motor decisions. They hold that a common representation for perception and action is necessary for optimal search performance.

8.2. Saccade Curvature and Perceptual Detection

The trajectory of saccadic eye movements is affected by numerous factors such as the displacement of a saccade-target prior to its execution (e.g., van Gisbergen *et al.*, 1987), the presence of a distractor in the vicinity of the target (e.g., Findlay and

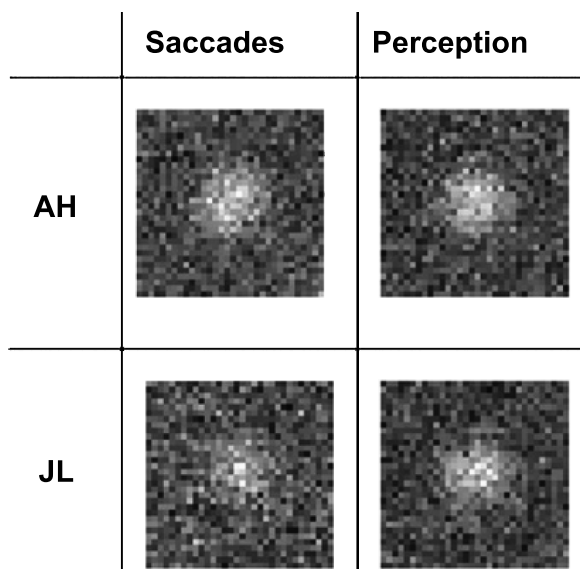


Figure 8. Classification images obtained with 2 subjects on the motor task (saccades) and the perceptual task. See text. Figure from Eckstein *et al.* (2007).

Harris, 1984), prior knowledge of target and distractor locations (e.g., Walker *et al.*, 2006), or spatial attention (e.g., Sheliga *et al.*, 1994). Depending on the experimental conditions, saccades curve either toward (attraction), or away (repulsion) from the distractor (for a review on saccade curvature effects, see Van der Stigchel *et al.*, 2006).

All studies having documented these saccade-trajectory perturbations have used highly suprathreshold distractors so that their effect on the oculomotor behavior could not be assessed in relation to their visibility. Such an enterprise is however of direct relevance to the appraisal of the perceptual–motor relationship. This was precisely Cardoso-Leite and Gorea’s (2009) motivation for comparing on a trial-by-trial basis the perception of a close to threshold distractor with its effects on a saccade directed to a highly visible target. In their experiment, participants performed a saccade to a high contrast Gaussian blob target (10° above fixation) while a low-contrast Gaussian blob distractor was presented 50 ms before the target onset at 5° eccentricity along the horizontal meridian on either side of fixation with independent probabilities of 0.5. After each saccade, participants provided a confidence level (out of 6) of having seen the distractor for each of its putative locations. This procedure allowed the specification of the perception-related receiving operating characteristic (ROC) functions (Green and Swets, 1966) which in turn permitted the inference of the distractor-evoked internal response associated with each confidence level.

Saccades deviated away from the distractor only when it was perceived (perceptual hits), or believed to be perceived (perceptual false alarms). The magnitude of

the deviation was proportional to the magnitude of the evoked perceptual response (as inferred from the ROC functions) *provided the latter exceeded the perceptual (detection) criterion*. This pattern of results fully supports the notion that motor perturbations depend on subject's perceptual state. What's more, motor biases (saccades deviations in the presence of two distractors) correlate with participants' perceptual left/right decision bias (but not with their left/right sensitivity differences). This result suggests that the perceptual criterion plays a crucial role in determining the direction of the saccade deviation. Overall, Cardoso-Leite and Gorea's data provide strong evidence in favor of the association between perceptual and motor responses.

8.3. *Pursuit and Detection of Changes in Speed or Direction*

Osborne *et al.* (2005) successfully modeled eye pursuit behavior in primates as a process involving a variety of noise sources of which target movement inference from sensory data accounts for about 90%. As the estimated variability of this inferential process is in agreement with perceptual discrimination thresholds for speed and movement direction, Osborne *et al.* (2005) suggested that perceptual and motor responses are based on a common representation of the moving stimulus. Comparisons between perceptual and motor responses on a pursuit task yield, however, contradictory results (for review, see Gegenfurtner and Franz, 2007). For example, the speed discrimination thresholds derived by Gegenfurtner *et al.* (2003) from the perceptual and motor responses of their subjects were similar, whereas perceptual and motor errors on the same trials were not correlated. This pattern of results is compatible with a model wherein perceptual and motor responses are under the control of distinct systems. In contrast, Stone and Krauzlis (2003), who studied perceptual and motor responses to changes in target direction found such a correlation, suggesting that perception and action are based on the same internal signal. Most recently, Tavassoli and Ringach (2010) confirmed the absence of correlation between eye pursuit fluctuations and perceptual responses evidenced by Gegenfurtner *et al.* (2003); their data also show that eye pursuit is sensitive to velocity perturbations that are not perceptually detectable.

Perhaps the most eloquent example of a perceptual *vs.* eye–pursuit dissociation is the case of Duncker's (1929) perceptual illusion (and its variants) that does not seem to 'fool' the eye–pursuit system. Duncker has shown that a stationary, fixated object is perceived as moving in the opposite direction to another moving object and, equivalently, that the perceived direction and speed of a moving target is perceptually distorted by another moving object or by a moving background. A number of studies showed that this is not the case for the eye–pursuit behavior (e.g., Carlson *et al.*, 2006; Spering and Gegenfurtner, 2007a, b; Spering *et al.*, 2006; Zivotofsky, 2005) although Duncker's illusion does appear to affect saccades (Zivotofsky *et al.*, 1998), pointing movements (Soechting *et al.*, 2001) and the initiation of slow-phase optokinetic nystagmus (Zivotofsky, 2005).

Spering and Gegenfurtner (2007a), for example, recorded the eye pursuit of a horizontally Gaussian dot moving at constant velocity in the presence of two vertically oriented sinusoidal gratings (flankers; one above and one below the stimulus trajectory) that were either stationary or drifted at different velocities into the same or opposite direction as that of the target. For the case of the drifting flankers, they found that, despite the modulation by these flankers of the perceived velocity of the target, pursuit performance was enhanced irrespective of its motion direction. When flankers' speed was briefly increased or decreased, eye velocity changed accordingly, but only when the context was drifting along with the target. Perturbing flankers' velocity into a direction orthogonal to target's direction evoked a deviation of the eyes' pursuit in the direction opposite to the perturbation. Taken together, the data provide evidence for the use by the smooth-pursuit system of both absolute (unlike perception) and relative motion cues (i.e., motion assimilation and motion contrast, respectively). In a study comparing on a trial by trial basis perceived and smooth pursuit eye velocities with a display requiring the segmentation of the target from the context motion, Spering and Gegenfurtner (2007b) showed that perceived velocity was accounted for by the subtraction of the motion context velocity from the target velocity (motion contrast). Instead *steady-state* pursuit velocity appeared to be determined by the averaging of the two velocities (motion assimilation).

Here as elsewhere (Masson and Stone, 2002; Montagnini *et al.*, 2007; Spering *et al.*, 2006; Wallace *et al.*, 2005; Zivotofsky, 2005), the distinction between steady-state and open-loop recordings is crucial. The most likely account of this and of similar kinds of perceptual *vs.* eye-pursuit dissociations is that action profits from online adjustments *via* feedback loops but does so only after some delay (e.g., Lisberger and Ferrera, 1997; Lisberger *et al.*, 1987; Niemann and Hoffmann, 1997; Osborne *et al.*, 2005; Recanzone and Wurtz, 1999; Spering and Gegenfurtner, 2007a, b; Spering *et al.*, 2006). Osborne *et al.* (2005), for example, point to the fact that only the 125 first milliseconds of the pursuit response provide information about the existence of a noise source common to the two types of response, because, they claim, other processes which do not reflect perceptual treatment begin to interfere beyond this interval. The correlations calculated by Gegenfurtner *et al.* (2003) were based on ocular pursuits beyond this 125-ms period. Gegenfurtner and Franz (2007) also emphasized the fact that eye movements and perceptual responses are necessarily interdependent, given that motor errors affect the signal available to the perceptual system, rendering results difficult to interpret. Other accounts of the observed discrepancies between ocular pursuit and perceptual performances appeal to late independent noise sources (perhaps at the decision stage), late nonlinearities involved in perceptual judgments, and/or different motion integration windows (see Tavassoli and Ringach, 2010).

The close link between ocular pursuit and perception is confirmed, nonetheless, by studies using ambiguous stimuli. Madelain and Krauzlis (2003), for example, used a bistable stimulus composed of a row of squares which jumped horizontally by half of the distance separating two squares every 66 ms. Subjects could perceive

that the squares were moving to the left or to the right with equal probability, and even voluntarily induce a change in the perceived direction. Their task was to follow the apparent movement of one of the squares (physically indistinguishable from the others) with their gaze — starting for example from the left of the screen — and to induce a change in both the perceived movement and tracking direction when the square reached the center of the screen. At random moments, subjects heard a tone and had to evaluate whether it had occurred before or after the perceived change of direction. The results show that the perceptual interpretation that the subject gives to the ambiguous stimulus precedes (by about 50 ms) the pursuit behavior.

To estimate the speed and direction of an object such as a bar in movement, spatially dispersed information is often required (for reviews, see, e.g., Masson and Stone, 2002; Montagnini *et al.*, 2007; Sperling and Gegenfurtner, 2007a, b; Weiss *et al.*, 2002). Motion-sensitive neurons whose receptive fields cover the center of the bar have access only to ambiguous local (1-D) information, since the movement they detect is compatible with an infinity of movements of the bar (the ‘aperture problem’). Neurons whose receptive fields cover an end of the bar, on the other hand, have access to unambiguous 2-D information. The process of integration of local information to infer the global movement of the object unfolds in time. Very brief presentations of moving stimuli lead to directional judgments dominated by 1-D information (Lorenceanu *et al.*, 1993): objects are perceived as moving in the direction orthogonal to their edge. Similarly, when subjects must pursue with their gaze the center of an object carrying both ambiguous and non-ambiguous information, their pursuit speed is initially biased by the ambiguous local information before converging progressively toward the global movement of the object (Masson and Stone, 2002; Montagnini *et al.*, 2007; Wallace *et al.*, 2005). According to Montagnini *et al.* (2007), the correspondence between initial pursuit and perceptual errors suggests that motor and perceptual responses are based on a single representation, initially determined by local movement information. These authors also note that the pursuit error reaches its maximum about 100 ms after the beginning of pursuit and, thus, before the eye movement feedback information becomes available (open-loop phase). By their account, this suggests that the oculomotor bias and its dynamic correction are essentially a perceptual phenomenon.

Montagnini *et al.* (2007) present a dynamic Bayesian model to account for the evolution of such pursuit errors due to contradictory local information. The model posits that pursuit results from an inferential process wherein subjects attempt to determine the most likely movement of the object by combining *a priori* preferences (in this case, for low speeds) with the likelihood of the given sensory data to calculate the *a posteriori* probability density function. The *a posteriori* distribution at time t serves recursively as the prior at time $t + 1$. The model provides a simple link between static (such as SDT) and dynamic decision models, and can in principle be as easily applied to perceptual data (such as verbal judgments given at the end of trials; e.g., Lorenceanu *et al.*, 1993), as to continuous motor behavior (e.g., Montagnini *et al.*, 2007). Nonetheless, its authors note that this model of Bayesian

inference does not specify the transit from the decision process (e.g., the peak of the *a posteriori* distribution) to the motor command and cannot, therefore, be validated against the recorded oculomotor trace or perceptual responses.

8.4. 3-D Perception

The main function of 3-D vision is to enable visually guided action. However, the large majority of studies on 3-D perception require subjects to give perceptual rather than motor responses. Generalizing from such data to the related motor behavior would be unwarranted on a perceptual–motor dissociation hypothesis. To test this contention, Knill and Kersten (2004) compared the effects of the delay between stimulus presentation and subject's perceptual and motor responses in a visual tilt discrimination task. The underlying idea was that, according to the dissociation view, the visuomotor system, in contrast to the perceptual system, has little or no memory; for stimulus–response delays exceeding 2 s the motor response should be based on a perceptual representation (Goodale *et al.*, 1994a). Response delay should, therefore, affect motor and perceptual responses differently. Knill and Kersten's (2004) visual stimulus was a plane surface with a texture printed on it (white noise). The surface was attached to a computer-controlled robotic arm, which could position it in front of the subject at variable orientations and depths (see Fig. 9).

In the motor task subjects had to place a cylinder — initially set upon a horizontal surface above and to the right of the test surface — on the inclined surface, tipping the cylinder so that the contact surfaces be parallel. The test surface was presented for 2 s, and after a variable delay of 1 to 3 s, an auditory signal indicated to subjects to place the cylinder ('open-loop' motor response). The measure of motor performance was based on the 3-D position of the cylinder during the trial. The perceptual task was a two temporal intervals forced-choice task. Following the same inclined surface presentation and response delays as in the motor task subjects were presented a new inclined surface, also for 2 s. Subjects indicated which

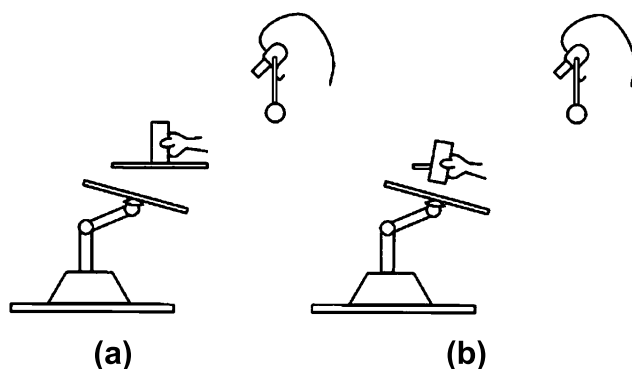


Figure 9. Experimental setup of Knill and Kersten (2004). The equipment surrounding the subject's head serves to limit the field of vision and to control the duration of observation of the inclined surface. Figure from Knill and Kersten (2004).

of the two surfaces was tilted further forward with a manual key press. Contrary to the perception–action dissociation stand, results showed that perceptual and motor sensitivities drop similarly with increasing stimulus–response delay, and that perceptual sensitivity is always superior to motor sensitivity. According to Knill and Kersten (2004), these data are compatible with a model wherein a unique representation of the 3-D orientation of the stimulus is used for both perceptual and motor responses (see also Mamassian, 1997) with the additional motor noise involved in the visuomotor task accounting for the lesser sensitivity assessed therein.

8.5. *Automatic Piloting of Motor Responses*

Online motor control — or automatic action piloting — is among the most robust and often-cited phenomenon speaking in favor of the perceptuo-motor dissociation (e.g., Pisella *et al.*, 2000). One of the major functions of the posterior parietal cortex is to permit ‘online’ modifications of pointing or grasping movements in response to changes in the position or orientation of the target during the movement (for reviews see Culham and Kanwisher, 2001; Culham and Valyear, 2006; Milner *et al.*, 2003; Pisella *et al.*, 2000) (see Note 17). Responses produced by this automatic pilot are said to be independent of consciousness. Online motor control is at work during all visually guided pointing. In a typical paradigm used to quantify the action of this system, subjects are asked to simultaneously perform a saccade and a manual pointing movement toward a peripherally presented target. On half of trials, the position of the target is fixed until the end of the pointing movement, and in the other half the target is displaced at the moment when the saccade toward it reaches its peak velocity — making it very difficult to perceive this position change. Subjects in fact declare that they have not perceived the change, and when their sensitivity to such displacements is tested with a forced-choice method (see Note 18), they perform at chance levels. Nonetheless, their pointing movements reach the new position of the target (Goodale *et al.*, 1986; Pélisson *et al.*, 1986; Prablanc and Martin, 1992). These results have been unanimously interpreted as a demonstration that the motor system has access to visual information that the perceptual system misses. One criticism of these experiments, due to Gaveau *et al.* (2003), concerns the simultaneous execution of two motor, ocular and manual, responses with the former meant to render the change in target position hard to perceive. Several studies are not subject to this criticism: in the experiment of Gaveau *et al.* (2003) subjects made only a saccade toward the target, whereas in that of Pisella *et al.* (2000) subjects pointed without making a saccade.

Gaveau *et al.* (2003) measured online modifications of saccades toward a target which, on certain trials, changed position at the beginning of the saccade. When asked at the end of the experiment if they had perceived a jump in target position during their saccades, only two of fourteen subjects said ‘yes’. The saccades of all subjects were nonetheless affected by the spatial perturbation of the target: saccade landing point was displaced toward the new position, and the saccade’s peak velocity was reached earlier (a phenomenon known as short-term saccadic adaptation;

McLaughlin, 1967; Straube and Deubel, 1995). Gaveau *et al.* (2003) concluded that the motor system has access to a signal that does not reach consciousness. The similar oculomotor behavior across subjects that said having perceived or not perceived target's position change was interpreted as evidence that online saccade corrections and perceptual detection of displacements are independent. On the other hand, Bruno and Morrone (2007) showed that spatial shifts induced by saccade adaptation are equally evidenced whether observers are asked to verbally report (relative to a memorized reference) the position of stimuli flashed long before (about 150 ms) the saccade onset, or to point to the target's position directly. In the same vein, Burr *et al.* (2001) (see also Morrone *et al.*, 2005) showed that the well documented spatial mislocalizations induced by saccades (Morrone *et al.*, 1997; Ross *et al.*, 1997) are also equally evidenced when observers report verbally or point to (without visual feedback of their hand) the position of the (mislocalized) probe. Interestingly, pointing mislocalizations were not observed in the absence of post-saccadic visual information. These authors hypothesized the existence of a plastic and of a static visual space map; depending on the task setting and on the response mode, the contribution of the two maps would be differently weighted when producing perceptual and motor responses hence yielding different patterns of results (Morrone *et al.*, 2005).

Pisella *et al.* (2000) studied the online correction of manual pointing movements in the absence of saccades. In one of their experiments subjects were presented with a peripheral target, and had to point at this stimulus while maintaining fixation on the center of the screen. On 20% of trials, this target was displaced upon the initiation of the manual movement. Subjects were assigned to a 'go' and a 'stop' group. The 'stop' group was instructed to interrupt their pointing movement upon detection of a target displacement, while the 'go' group was told to point toward the new target position. Results showed that both groups had a strong tendency to point toward the new position of the target after a displacement, although this tendency was weaker in the 'stop' group. As the pointing responses of the 'stop' group were affected by the target displacement, although these subjects had not been instructed to point toward the modified position, Pisella *et al.* (2000) concluded that signal processing for visual perception and for online motor correction are independent processes. According to these authors, the fact that these 'stop' subjects did not interrupt their pointing movement suggests that online motor corrections have priority over intentional responses. This interpretation, however, raises the question of the meaning of the instruction 'point toward this stimulus'. Does this mean that subjects must point toward the spatial coordinates occupied by the stimulus, or toward the stimulus itself? If the subject's task is to point toward the stimulus, its displacement creates a conflict between two intentional actions: one to point toward the target, the other to interrupt the movement. This type of behavior is generally modeled as a 'race' between two internal responses, one each for the two potential actions (e.g., Kapoor and Murthy, 2008). Subjects' ability to inhibit their movements rather than correcting them will depend on the 'salience' of the two internal responses leading to one of these two decisions. The study of Pisella *et al.* (2000) contributes to the

understanding of the functions of the dorsal pathway, but does not tell us about the relations between perception and action.

Do the studies cited above showing that ongoing movements can be modified online despite the failure to detect changes perceptually allow us to conclude that perception and action are independent? The answer is no, even if we accept that subjects' motor responses are perfectly corrected and that the target displacement is perceptually undetectable (in the sense of $d' = 0$). What happens when the subject fails to detect the target displacement? At least three scenarios are conceivable. (1) Possibly, subjects having failed to detect the transient signal due to the position change, also fail to initiate the comparison of target's positions before and after the saccade. (2) The saccade may erase subjects' memory of the initial target position. Finally, (3) the poor perceptual detection performance may be due to subject continuing to perceive the target at its original position, i.e., before the execution of the saccade. Of these three scenarios, only the third is compatible with a functional dissociation as the perceived and pointed to positions are incongruent. This scenario is not plausible, as it implies that eye movements do not affect perception. Furthermore, such dissociation between perception and action would often lead to the (not experienced) impression of pointing toward a location that does not correspond to the perceived position. In the other two scenarios, perceptual localization and pointing movements are both determined by the actual position of the stimulus after the saccade with the observed perceptual–motor discrepancy due to the failure of either comparing or registering in memory the original position. Thus, contrary to the usual interpretation of these data, they suggest a strong *association* between perception and action (see also Mamassian, 1997).

This conclusion is corroborated by the results of a recent study which compared spatial localization performance of a Gaussian luminance blob with perceptual judgments and pointing movements toward it (Gegenfurtner and Franz, 2007). In this study, two collinear vertical lines were presented above and below the blob, and on each trial subjects were to point and indicate whether the blob was to the left or the right of the two lines. The results showed that the precision of perceptual judgments is superior to that of pointing movements, but that the partial correlations between perceptual and motor responses (controlling for variations in responses due to variations in the physical position of the blob) were significant and on the order of 0.28. Gegenfurtner and Franz (2007) concluded that the internal responses which determine perceived position are also used to guide the motor system in the pointing task. This perceptuo-motor conversion, they suppose, introduces noise into the measures and accounts for differences in perceptual and motor sensitivity.

9. Conclusion

In view of the vast neurophysiological, neuropsychological, and psychophysical evidence collected through the past 20 years or so, but also on pure common sense grounds, it would be ludicrous to contest the patently obvious dissociation between

perception and action. What this review has challenged is the evidence supporting one of the major claims of the dissociation view according to which, when tested under strictly matched conditions (inasmuch as they exist), subjects' (be they healthy or stroke-patients) action system may use incoming information that is omitted by their sensory systems (e.g., Goodale, 2008). This claim raises the critical dilemma of where one should set the frontier between perception and action, between perceiving and not perceiving and, equivalently, between acting and not acting. Despite strenuous efforts to define such a frontier, the alleged differential characteristics of 'perception' (e.g., "the visual *experience* we have about the current stimulus array", equated to the "*conscious* experience of seeing"; Milner and Goodale, 2008, p. 775; our *italics*) and 'action' ("not the use of visual information for abstract planning, but rather its use in the *detailed programming and real-time control at the level of elementary movements*", op. cit. p. 776; our *italics*) remain nebulous or, in the best case, reduce to a trivial timing difference. Equally, all efforts of separating 'conscious' from 'unconscious' perception (or action) faced the unsettled issue of what consciousness is (e.g., O'Regan and Noë, 2001). This fundamental conceptual fuzziness translated into pervasive methodological problems relating precisely to the empirical (im)possibility of 'strictly matching' perceptual and motor tasks.

The study of optic ataxia, one of the cornerstones of the dissociationist position, led a number of neuropsychologists (e.g., Pisella *et al.*, 2006; Rossetti *et al.*, 2003) to reject the hypothesis of a general disturbance of action, and to formulate instead a planning-control model similar to that of Glover (2002). The latter rejects the use of punctual motor responses, and emphasizes the importance of movement kinematics as well as of the multiplicity of processes at play in each action. Similarly, the argument of a poor correspondence between motor and perceptual tasks put forward by Franz *et al.* (2000) seems virtually identical to Schenk's (2006) critique of the spatial reference frame (allo- vs. egocentric) within which these two tasks are performed. This distinction between spatial reference frames (see also Bruno, 2001), as well as between the discriminating use of extent/size and of spatial location in perceptual and motor tasks (such as grasping), respectively (Smeets and Brenner, 1999, 2001, 2008) was also raised in connection to studies on what visual illusions tell us about the perceptuo-motor dissociation. The perceptual-motor discrepancies evidenced in the priming-plus-backward masking literature have been discussed in the context of likely transgressions of the exclusivity and exhaustivity principles (Holender, 1986; Holender and Duscherer, 2004; Reingold and Merikle, 1988, 1990) and of unsatisfactory accounts of the concept of consciousness. Independently of such criticisms, data obtained with this paradigm have been shown to comply with predictions of single processing stream models with independent perceptual and motor decision processes modulated by stimulus and task characteristics (Waszak and Gorea, 2004; Waszak *et al.*, 2007). The same models have been invoked to account for the different perceptual and motor decision moments (as inferred from temporal order judgments, temporal integration characteristics or anticipation response times, on the one hand, and from reaction time experiments,

on the other; Cardoso-Leite, *et al.*, 2007, 2009; Ejima and Ohtani, 1987; Miller and Schwarz, 2006; Sanford, 1974; Sternberg and Knoll, 1973). Obviously, such models should also account for other observed perceptual–motor discrepancies such as those observed when comparing the perception of a moving target with the ocular pursuit behavior, or the perception of a transient position change of a saccadic target with the landing position of the saccade. Moreover, in such experiments, what one may call a perceptual–motor dissociation according to one stimulus processing scenario may be taken as evidence of a perfect perceptual–motor association according to another scenario. Considering Perception and Action as two global and independent entities has been a fertile scientific approach. Maybe the time has come to consider them as intimately related (Gibson, 1966, 1979; O’Regan and Noë, 2001) and to try to understand why and how different response modes (e.g., speeded *vs.* delayed) affect the observed performance.

Acknowledgement

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Notes

1. This evolutionary article is common-sensical inasmuch as one accepts that more primitive species lack consciousness. Clearly, this remains a matter of speculation.
2. In fact, D.F., like most of studied VA patients, suffered from a carbon monoxide (CO) inhalational intoxication. CO induces a diffuse and widespread pattern of neuronal and white matter damage throughout the whole brain including (in D.F. as well as in other VA patients) the intraparietal sulcus, the postcentral sulcus, the inferior precentral sulcus, the parieto-occipital sulcus (bilaterally), the left calcarine sulcus and the left posterior parietal cortex. James *et al.* (2003) and Steeves *et al.* (2004) speculated that all this widespread brain damage might not be relevant for the deficits of D.F. and focused instead on the relative concentration of bilateral damage in the ventro-lateral LOC (see Karnath *et al.*, 2009). In the same time, the case of the VA patient J.S. showing circumscribed brain lesions (due to stroke etiology) of the fusiform and the lingual gyri as well as the adjacent posterior cingulate gyrus (medial structures of the ventral occipito-temporal cortex) fit well with the dissociation theory (Karnath *et al.*, 2009).
3. “This of course is an important reason why the kind of dual processing model that we have advocated is difficult to test using healthy subjects and non-invasive experimental paradigms” (Milner and Goodale, 2008, p. 776). Most obviously, neuropsychological studies are equally prone to this same testing difficulty.

4. Visual perimetry consists of presenting a flash of light at various locations on the retina and instructing patients to indicate when they appear. In this way, retinal areas that are insensitive to the flashes can be mapped.
5. Several conditions have been tested to better characterize these afterimages, which are typically negative. They were found to last almost twice as long as in healthy subjects but, as in healthy subjects, they followed Emmert's law, which holds that the size of afterimages is proportional to the distance to the surface on which they are perceived. The slope of this relation is flatter than in healthy subjects.
6. The radical notion that ventral pathway activation and consciousness are identical is wrongly associated with Goodale and Milner's (1992, 1995) theory positing that ventral activation is necessary for the perception of certain attributes (e.g., faces), but that this activation is not sufficient for conscious perception.
7. *Ebbinghaus/Titchener*: where a central circle appears subjectively smaller (or larger) when surrounded by larger (or smaller) circles; *Ponzo*: where two equal length horizontal segments appear unequal when displayed on two lines converging in depth with the more distal horizontal segment perceived longer than the more proximal one; *Müller-Lyer*: where a segment bounded by two chevrons with inward apexes appears longer than when bounded by outward pointing chevrons; *diagonal illusion*: where two equal length lines are perceived as unequal depending on the shape of the quadrilateral polygon in which they are inserted; *rod-and-frame illusion*: where the perceived orientation of a segment depends on the orientation of a rectangular frame circumscribing it.
8. Metacontrast is a type of backward masking where the onset of a test stimulus precedes that of a masking stimulus. The effect of the mask is to reduce the visibility of a test stimulus, to a degree which depends on the delay between the two stimuli. The distinctive property of metacontrast in relation to other forms of backward masking is that the test and masking stimuli do not overlap spatially (for a review of the literature on masking in vision, see Breitmeyer and Ogmen, 2000).
9. Further analysis of these data was meant to rule out transgressions of the exhaustiveness principle such as the possibility of the priming effect resulting from a 'fast guessing' type process set off by the detection of the prime, or consisting in facilitation of the mask processing independently of its congruency with the prime.
10. This model is similar to that of Hanes and Schall (1996) describing neural activity in an area of the frontal lobe and predicting the distribution of ocular saccade latencies.

11. The observation of differences in mean latency in these different response modalities is not a decisive argument in favor of a dissociation. It must be shown that these differences result from the decisional component (i.e., latency of change detection) and not from the motor component (i.e., arm movements vs. pronouncing words).
12. Not to be confused with *Attention Reaction Time* introduced by Reeves and Sperling (1980).
13. Which in turn vary about 1.5 less than attention reaction times (Reeves and Sperling, 1980).
14. Not all published data can be represented in this way (e.g., Ejima and Ohtani, 1987). Whenever possible we used the median rather than the mean (i.e., Cardoso-Leite *et al.*, 2007, 2009).
15. It is interesting to note that certain authors (e.g., Miller and Schwarz, 2006) suppose that sRT and TOJ are controlled by the same perceptual criterion, whose value depends on the current task. In one of our experiments, we measured sRT and TOJ on the same trials, and we found a pattern of results similar to that observed when the two tasks are carried out in separate experimental blocks (Cardoso-Leite *et al.*, 2007).
16. Contrary to deterministic models, diffusion models explicitly represent the noise in the coding and decision processes.
17. Automatic piloting as discussed here excludes those processes subtending the initiation of open-loop responses sometimes included in this category (e.g., Jaśkowski *et al.*, 2003; Waszak *et al.*, 2007).
18. This objective test is rarely performed: in general the invisibility of target displacements is affirmed based on an interview at the end of the experiment (which leads to strong underestimation of sensitivity).

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