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Discussion Paper

Do we have independent visual streams for perception and action?

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The *perception–action* model proposes that vision-for-perception and vision-for-action are based on anatomically distinct and functionally independent streams within the visual cortex. This idea can account for diverse experimental findings, and has been hugely influential over the past two decades. The model itself comprises a set of core contrasts between the functional properties of the two visual streams. We critically review the evidence for these contrasts, arguing that each of them has either been refuted or found limited empirical support. We suggest that the *perception–action* model captures some broad patterns of functional localization, but that the specializations of the two streams are relative, not absolute. The ubiquity and extent of inter-stream interactions suggest that we should reject the idea that the ventral and dorsal streams are functionally independent processing pathways.

Keywords: Visual cortex; Ventral; Dorsal; Perception; Action.

INTRODUCTION

The primate visual cortex is a busy place, estimated to contain more than 40 areas (Tootell, Tsao, & Vanduffel, 2003; Van Essen, 1985, 2005). Neuroscientists have naturally sought a simplifying order to this complexity. Ungerleider and Mishkin (1982) proposed a primary functional division between the ventral and dorsal streams that diverge from extrastriate cortex. They suggested that the ventral stream is specialized for processing visual features, such as shape, pattern, texture and color, while the dorsal stream analyzes the spatial aspects of those features. This framework, though still influential, has been superseded by an alternative formulation, introduced by Goodale and Milner (1992), and receiving its fullest exposition in "The visual brain in action" (Milner and Goodale, 1995, 2006). Milner and Goodale argued that a scheme focused on stimulus attributes cannot capture the division of labor between the visual streams. Since natural selection can act only on real-world outcomes, understanding the design of our visual systems requires that we consider the behavioral goals that vision serves. Vision exists because it improves our actions, but there are more and less direct ways in which it does this. The direct route is via the real-time guidance of action. The less direct route is via the deciphering of visual patterns, enabling us to understand our surroundings and lay down visual memories, and thus to plan actions informed by past experience. Within the *perception–action* model, the latter role, corresponding better to classical ideas of "perception", is fulfilled by the ventral stream. The direct visual guidance of action is the exclusive province of the dorsal stream.

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The *perception–action* model proposes no absolute distinction between the visual attributes of our environment that are analyzed by the two cortical streams. For instance, the spatial layout of visual scenes and the internal geometry of objects are critical concerns for both pathways. This implies no redundancy, however, because the two streams analyze spatial information in different ways, according to their own behavioral goals. Visual representations for action encode egocentric relationships between the observer and the object of an action. These relationships are fleeting, so they are updated continuously and decay rapidly. Our capacity-limited cognitive selves are shielded from the burdensome details of transforming these representations into motor plans, because the dorsal stream is cognitively impenetrable, and neither requires nor evokes visual awareness. Visual representations for perception, on the other hand, must abstract from egocentric viewpoints to encode the more stable, viewer-invariant properties of a scene. Ventral stream representations capture important material for visual memory and higher cognition, and furnish our visual awareness. These contrasting properties of the dorsal and ventral streams are often presented as a series of dichotomies (Table 1).

Milner and Goodale's (1995) updating of Ungerleider and Mishkin's (1982) functional model was accompanied by an anatomical reframing. Ungerleider and Mishkin's model was mapped onto monkey anatomy, with the ventral stream passing to the inferior temporal lobe, and the dorsal stream to the inferior parietal lobe (IPL). However, Milner and Goodale argued that important differences between human and monkey brains imply that functionally homologue cortical areas will not always be found in anatomically similar locations. Therefore they focused on functional properties to identify the human homologues of monkey cortical areas. In particular they proposed that the human dorsal stream does not project to the IPL, but instead to the *superior* parietal lobe (SPL). In contrast, the human IPL was suggested to fall outside of both visual streams, though having closer functional affinity to the ventral stream. The right IPL, given its association with unilateral neglect and constructional apraxia, may be specialized for supramodal spatial cognition, whereas the left IPL, given its association with limb apraxia, may be specialized for complex action sequences and action planning. Rizzolatti and Matelli (2003), however, have rejected the "rather strange proposal" that monkey IPL functions have relocated across the intraparietal sulcus to the SPL in humans. Less controversial is Milner and Goodale's (2006) reassignment of motion-sensitive area MT, classically regarded as part of the dorsal stream. Milner and Goodale argued that MT projects heavily to both dorsal and ventral streams, so that its status should be like that of other prestriate areas that feed information to both visual streams. This is now supported by correlated deficits of perception and action in a patient with akinetopsia following bilateral MT lesions (Schenk, Mai, Ditterich, & Zihl, 2000), and in healthy people undergoing transcranial magnetic stimulation (TMS) to area MT (Schenk, Ellison, Rice, & Milner, 2005).

TABLE 1
Core characteristics of the *perception–action* model

	Ventral stream	*Dorsal stream*
Behavioral function	Vision for perception	Vision for action
Spatial properties	Allocentric coding/ relative metrics	Egocentric coding/ absolute metrics
Temporal properties	Sustained representations	Transient representations
Visual awareness	Critically linked to awareness	Independent of awareness

In the epilogue to the second edition of *The Visual Brain in Action*, Milner and Goodale (2006) survey the ample evidence that has accumulated to support and refine their model since its inception. In the present critical review, we lay more emphasis on empirical and theoretical challenges to the model. We will base our discussion around the core dichotomies listed in Table 1, with an additional section on the topic of illusions-in-action. Here, and elsewhere, the relevant data on vision-for-action will come predominantly from studies of reaching and grasping, reflecting the strong bias toward these actions in the literature. Overall, our discussion will support the broad spirit of the *perception–action* model, but will also identify instances in which its predictions have been refuted, and grounds on which its assumptions may be questioned. A common theme will be that the functional independence of the two visual streams may have been overestimated, and that the specializations proposed may be relative rather than absolute. In the final section we consider the legacy of the *perception–action* model, and future directions for the field.

PERCEPTION VS. ACTION: VENTRAL VS. DORSAL STREAM

The core neuropsychological evidence for the proposed dissociation between vision-for-perception and vision-for action is a set of contrasting behavioral impairments resulting from focal lesions to the ventral or dorsal streams. The most intensively studied patient with damage to the ventral stream is DF, a woman who developed visual form agnosia as a consequence of anoxic lesions, destroying the lateral occipital area (LO) bilaterally (James, Culham, Humphrey, Milner, & Goodale, 2003). DF was shown to use visual size and orientation proficiently to guide her hand for reaching and grasping, despite being unable to discriminate these properties explicitly. It was suggested that her preserved visuomotor abilities result from the sparing of her dorsal visual pathway (see Karnath, Rüter, Mandler, & Himmelbach, 2009 for an even clearer case anatomically). In support of this view, Milner and Goodale contrasted DF's condition with that of patients with optic ataxia, who show inaccurate visually guided movement following damage to the SPL (Karnath & Perenin, 2005; Perenin & Vighetto, 1988). Naturally occurring lesions do not respect anatomists' boundaries, and neither DF nor most optic ataxic patients have a perfectly selective, let alone complete, lesion of either visual stream (see James et al., 2003 for a detailed analysis of DF's lesion). Nonetheless, at least to gross analysis, vision-for-action and vision-for-perception are separately susceptible to disruption from brain damage, suggesting that they are segregated in the normal brain.

Of course, vision-for-perception and vision-for-action must interact at some level, since we are manifestly capable of deciding a course of action on the basis of what we consciously see. Milner and Goodale (2008) have underscored a distinction between action planning and programming as the critical barrier between dorsal and ventral stream influences on behavior. Vision-for-perception informs awareness, and influences action planning, but these actions are programmed via the transformation of afferent visual information into motor commands, which is the domain of vision-for-action. As neat as this scheme seems, it will not work without exceptions and qualifications. First, not all metrical parameters of our actions can be programmed on the basis of bottom-up information. When we lift an object, visual size and memory cues influence our fingertip forces (Flanagan & Beltzner, 2000; Gordon, Forssberg, Johansson, & Westling, 1991; Mon-Williams & Murray, 2000), as must visually based judgments of the object's material. Force programming thus involves visual recognition, of either a specific object or the stuff of which it is made. A critical role for the perceptual pathway is supported by the finding that DF does not use visual cues to program her fingertip forces (McIntosh, 2000). The ventral stream's influence on action thus reaches down to the programming level, at least for these force parameters.

Perhaps the key to ventral stream involvement in action is not high-level planning, but semantic involvement, exemplified by picking up tools, which must be recognized before an appropriate grasp can be selected. DF's behavior suggests that this scheme will not work either. She does indeed make semantic errors when interacting with tools, grasping them in non-functional ways (Carey, Harvey, & Milner, 1996), but she also makes errors when grasping neutral blocks, in that she does not select the most comfortable grasp (Dijkerman, McIntosh, Schindler, Nijboer, & Milner, 2009). Selection of actions that minimize postural awkwardness might be classed as action planning, but it has no obvious semantic component. DF is unable to make accurate memory-guided actions, which should obviously lie beyond the competence of a dorsal stream evolved for immediate visuomotor guidance (Goodale, Jakobson, & Keillor, 1994a), but she also fails at immediate guidance tasks of any significant complexity. She can post a simple plaque through a slot adeptly, but makes systematic errors with a T-shaped object (Goodale et al., 1994b), and is poor at determining contact points for grasping an X-shaped object, supporting the idea that the dorsal stream can process simple spatial attributes, such as the orientation of an object's principal axis of elongation, and its height and width with respect to this, but is unable to process more complex shapes (Carey et al., 1996). When presented with objects to be grasped by holes cut into them, DF's grasping resembles blind groping (Dijkerman, Milner, & Carey, 1998; McIntosh, Dijkerman, Mon-Williams, & Milner, 2004). No simple criterion based on planning level or semantic involvement predicts the visuomotor tasks with which DF struggles and which, by implication, benefit from ventral stream participation in the normal brain.

The empirical evidence suggests that DF's visuomotor competence extends only to the spatially based programming of rudimentary actions to simple, arbitrary targets. However, even her success in such rudimentary tasks may not be supported by the same combination of visual cues that healthy subjects employ for such tasks. Perturbation studies have revealed that DF is almost exclusively reliant on vergence angle and vertical gaze angle for the programming of reach amplitude (Mon-Williams, McIntosh, & Milner, 2001; Mon-Williams, Tresilian, McIntosh, & Milner, 2001), and on binocular disparities and motion parallax to recover object depth for grasping (Dijkerman & Milner, 1998; Dijkerman, Milner, & Carey, 1996, 1999). When these cues are perturbed, DF's performance drops off precipitously. Normal performance is much less vulnerable to these manipulations, suggesting that healthy participants make use of additional depth and distance cues unavailable to DF, presumably mediated by the ventral stream. This implies that the ventral stream participates even in the low-level, spatially based programming of rudimentary actions (cf. McIntosh & Lashley, 2008). DF, with her quasi-isolated dorsal stream, succeeds in simple visuomotor tasks, but this testifies to the robustness of the system in adapting to a degraded perceptual analysis in the ventral stream, rather than being a model of visuomotor control in the healthy brain. The evidence points toward ventral stream involvement at all levels of action planning and programming, leaving only fast online updating of movements, and possibly some implicit forms of obstacle avoidance, as a potentially "pure" dorsal task (cf. Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Rizzolatti & Matelli, 2003; Rossetti, Pisella, & Vighetto, 2003).

We now turn to the complementary claim, that the dorsal stream is not involved in visual perception. This discussion has been informed by findings from patients with optic ataxia following dorsal stream damage. The clinical diagnosis of optic ataxia requires that perceptual deficits be excluded as an explanation for misreaching under visual guidance, but this has often been done only coarsely. More stringent assessments, focusing on discriminations in the peripheral visual field, for which misreaching is most severe, have often observed impaired discrimination of object location or orientation (Michel & Henaff, 2004; Perenin & Vighetto, 1988; Pisella et al., in press), which may be secondary to attentional disorders (Michel & Henaff, 2004; Pisella et al., in press; Striemer et al., 2007, 2009). Milner and Goodale (1995) recognize that dorsal stream areas play key roles in attention, and that the functional relationship between action programming and spatial attention may be a deep one (Rizzolatti, Riggio, & Sheliga, 1994). It is thus consistent with the *perception–action* model that dorsal stream lesions should influence perception. However, this raises a thorny issue of definition. Some would argue that, where attention plays a necessary role in visual awareness, it should be considered fully part of the perceptual process (Pisella et al., in press). Milner and Goodale, however, class this role as indirect, since attention may filter the contents of awareness, but it is the ventral stream that provides those contents. A true perceptual role for the dorsal stream, on Milner and Goodale's terms, would require the products of dorsal stream processing to enter visual awareness. Possible evidence of this sort will be considered in "Awareness and the two visual streams" below, which addresses the issue of awareness in detail.

We would conclude that, while the mapping of vision-for-perception and vision-for-action onto the ventral and dorsal stream respectively reflects an important, first-order organizing principle, the characterization is hard to maintain in any strict sense. Part of the problem is that vision-for-perception and vision-for-action are not self-explanatory categories, but theoretical constructs requiring further definition; and part of the success of the *perception–action* model may owe to a degree of elasticity in these key terms. If vision-for-action is whatever the dorsal stream does, then this definition can evolve to exclude aspects or forms of action that transpire not to have "pure" dorsal status. We have argued that the shrinking island of "pure" dorsal action may now include only certain forms of online control, all other visuomotor skills being contaminated by contributions from other areas. At some point, this custom definition of *vision-for-action* may diverge so far from what we would normally mean by this term that it becomes counterproductive. This notion figures prominently in three substantive criticisms of Milner and Goodale's account (Jeannerod & Jacob, 2005; Rizzolatti & Matelli, 2003; Rossetti et al., 2003), and similar concerns were noted earlier with respect to vision-for-perception (Pisella et al., in press). However, much of the tension can be relieved simply by relaxing the assumption that the functional domains of the dorsal and ventral stream are independent and mutually exclusive. The broad functional distinction captured by the *perception–action* model is relative, not absolute. It may be possible to identify some simple visual behaviors at the extreme ends of a ventral–dorsal continuum (e.g. color discrimination vs. online movement correction), but most visual behaviors, especially those of any significant complexity, are likely to involve collaboration between the two visual streams, and other brain systems.

SPATIAL CODES FOR PERCEPTION AND ACTION

Within the *perception–action* model, a major rationale for the segregation of vision-for-perception from vision-for-action is that spatial coding requirements differ fundamentally between these domains. For action, an object's position must be coded egocentrically and its spatial dimensions measured in absolute metrics, i.e. in terms of its real physical dimensions. Vision-for-perception, by contrast, is concerned with viewer-invariant relationships in the environment, so spatial features should be coded in allocentric frames of reference. This perceptual strategy applies also to sizes and distances, which will be encoded relative to one another, rather than in absolute metrics. These theoretical considerations underpin the expectation of distinct spatial coding systems in the dorsal and ventral streams. How well do the data conform to this expectation?

There is abundant neurophysiological evidence for egocentric coordinate transformations of visual information in the posterior parietal cortex of the monkey, made possible by the convergence of proprioceptive and visual information. For instance, in areas LIP and 7a, visual targets have been found to be represented in retinocentric (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuña, 1975), head-centered (Andersen, Essick, & Siegel, 1985) and body-centered frames of reference (Snyder, Grieve, Brotchie, & Andersen, 1998). Buneo and Anderson (2006) have recently described a chain of transformations in the parietal reach region, whereby the coding of visual target and hand positions within a common retinocentric frame allows the extraction of the movement vector required to reach the target (functionally equivalent to hand-centered coding). It is clear that the posterior parietal cortex does not construct a purely sensory representation of space, but computes action-relevant, viewer-dependent, encodings. There is also abundant complementary evidence for *viewpoint-invariant* spatial coding in monkey inferior temporal cortex (see Logothetis & Sheinberg, 1996, for a review).

Recently, functional magnetic resonance (fMR) adaptation (Grill-Spector et al., 1999), which relies on the reduction of neuronal responses to repeated presentations of equivalent stimuli, has begun to provide insights into representational codes in the human brain. Consistent with expectation, ventral stream area LO adapts to repeated presentations of the same shape, across variations in viewpoint (James, Humphrey, Gati, Menon, & Goodale, 2002; Kourtzi & Kanwisher, 2001; Vuilleumier, Henson, Driver, & Dolan, 2002), including changes in object size (Grill-Spector et al., 1999; Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005). Valyear and colleagues (Valyear, Culham, Sharif, Westwood, & Goodale, 2006) contrasted responses in temporo-occipital cortex with responses in parieto-occipito cortex across repeated presentations of objects varying in identity, orientation, or both. They reported doubly dissociated patterns of activation, such that the ventral stream adapted to identity, regardless of orientation, while the dorsal stream adapted to orientation, regardless of identity. However, Konen and Kastner (2008) found a remarkably close mirroring between ventral and dorsal streams, with early and intermediate visual areas showing fMR adaptation only to low-level visual features, but some higher-level areas adapting to object identity, regardless of changes in viewpoint or size. This viewpoint invariance was observed for area LO in the ventral stream, and for dorsal stream regions in the posterior intraparietal sulcus. This latter result is inconsistent with an absence of allocentric codes in the dorsal stream.

A number of neurophysiological findings also show allocentric encoding of space in dorsal stream areas. Snyder et al. (1998) found that, whereas visual targets were represented in monkey LIP predominantly in head-centered coordinates, the majority of neurons they sampled in area 7a reflected world-centered coordinates, coding target position in an environmental frame. Subsequently, in an object-based spatial task, Crowe, Averbeck and Chafee (2008) found that a transformation from retinal to object-centered coordinates arises, or is at least reflected, in area 7a, suggesting that this area may be capable of a variety of allocentric encodings. If the monkey IPL is homologous with the human SPL, as Milner and Goodale suggest, then the allocentric encoding of space in monkey area 7a should map to the human dorsal stream. If the monkey IPL is homologous to the human IPL, as Rizzolatti and Matelli (2003) maintain, then these allocentric encodings would be compatible with a role for the IPL in higher-level spatial representation, but the homology would imply that spatial representations in the human IPL, as in the monkey, are involved in spatial coding for action. In either case, these neurophysiological data are problematic for the *perception–action* model.

Neurophysiological and neuroimaging evidence for allocentric spatial coding in the dorsal stream needs to be reconciled with evidence from lesion studies. Experiments with patient DF suggest that she is fundamentally limited in her ability to make use of allocentric spatial relationships, whether making a perceptual judgment or an action response (Schenk, 2006). One implication could be that the allocentric representation of space in the dorsal stream relies on input from the ventral stream. This would be compatible with the *perception–action* model, in the sense that allocentric coding would be held to depend on ventral stream processing. However, it would deny the categorical claim that the dorsal stream does not use allocentric codes, and would admit a very close interaction between visual streams in the processing of objects and space, undermining the idea that the two streams are meaningfully independent.

Accepting that the dorsal stream uses allocentric representations does not necessarily challenge its visuomotor role. On the contrary, the need for absolute metrics requires that the object representations guiding action must respect size constancy, a cardinal form of viewpoint-invariance. Milner and Goodale (1995) propose that the visuomotor system employs exclusively absolute metrics, while perceptual representations are concerned with relative metrics. It is argued that relational coding must be used for perception because "if perceptual representations were to attempt to deliver the real metrics of all objects in the visual array, the computational load would be astronomical" (Goodale & Humphrey, 1998, p. 195; see also Milner & Goodale, 2006, 2008). However, it is not self-evident that it should be any less onerous to compute size and distance for every object *relative* to some other object. Nor is it obvious why, if the action system can deliver absolute metrics on demand, the perceptual system could not. We may also question the intuition that egocentric, absolute representations are not useful within visual awareness. If a key role of visual awareness is to inform action planning, then such representations may well be relevant (for further discussion, see "Awareness and the two visual streams" below).

The theoretical rationale for restricting vision-for-perception to relative metrics can be questioned, but what about the complementary claim that relative metrics are not used by the visuomotor system? This claim has engendered the idea that the visuomotor system should ignore relative sources of size and distance information, such as the majority of pictorial depth cues, processing the action target in isolation from its visual context. Against this view, computational analyses of the information available in multi-cue environments do not support strict distinctions between absolute and relative cues: Relative depth cues can be "promoted" by other cues in the scene to provide absolute distance information (Landy, Maloney, Johnston, & Young, 1995). Moreover, there is a wealth of empirical evidence to show that action systems are sensitive to visual context. Numerous studies have found that visuomotor performance is improved when visual context is available (for example: Bautista & Korienek, 1999; Coello & Iwanow, 2006; Coello & Magne, 2000; Krigolson, Clark, Heath, & Binsted, 2007; Redon & Hay, 2005). Interestingly, these benefits apply not only to action programming (Obhi & Goodale, 2005) but also to online control (Krigolson & Heath, 2004). Action-based responses tend to give proportionately higher weight to binocular and absolute depth and distance cues than do perceptually based responses (e.g. Knill, 2005), but there seem to be no hard barriers to action systems using pictorial depth cues, even those that depend on object-knowledge (McIntosh & Lashley, 2008). The most relevant constraints may be imposed by the latencies with which different cues can be made available (Greenwald, Knill, & Saunders, 2005).

VISUAL ILLUSIONS IN ACTION

Proponents of the *perception–action* model have advocated context-based visual illusions as a simple tool to test the idea that the two visual streams use different spatial representations. Since the relation between a visual target and its surrounding context is presumed to be represented in the ventral, but not the dorsal stream, the action outputs of the dorsal stream should be unaffected by contextual illusions. Initial reports of such dissociations were highly influential (e.g. Aglioti, DeSouza & Goodale, 1995; Bridgeman, Lewis, Heit, & Nagle, 1979). More recently, this methodological paradigm has attracted skepticism on empirical and theoretical grounds, arguably becoming the most controversial pillar in the *perception–action* framework (for critical reviews, see Bruno, 2001; Carey, 2001; Franz, 2001; Franz & Gegenfurtner, 2008; Smeets & Brenner, 2006). Rather than providing yet another review of this topic, we will give only a short summary before considering the implications of the debate for the *perception–action* model.

Many studies have now reported that visual illusions do affect actions, though these effects may typically be smaller than those on perceptual judgements (for reviews and meta-analyses, see: Bruno, Bernardis, & Gentilucci, 2008; Bruno & Franz, 2009; Franz & Gegenfurtner, 2008). Differences in illusion strength between response modalities have been ascribed to a host of methodological factors, such as differences in visual feedback (Bruno & Franz, 2009; Franz, Hesse, & Kollath, 2009, Mon-Williams & Bull, 2000), or the requirement for relative vs. absolute judgments (Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999; Vishton, Pea, Cutting, & Nunez, 1999) in perception- and action-based responses. In the case of the Ebbinghaus-Titchener illusion, appropriate matching between response conditions yields comparable and correlated effects of the illusion on perception and action (Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Pavani et al., 1999). The clear influence of methodological factors on illusion strength, within as well as between perception- and action-based varieties of response, suggests that the *perception–action* distinction does not provide a satisfactory account of the data. Multiple task-specific explanations may be needed (Dassonville & Bala, 2004;

Smeets & Brenner, 2006; Smeets, Brenner, de Grave, & Cujpers, 2002).

Smeets and colleagues (2002) argue that specific visual illusions affect specific visual attributes but not others, in ways that may be mutually inconsistent. Whether or not a given response will be affected by the illusion depends simply on whether it uses the affected attribute. For example, several investigators have noted that pointing responses to the endpoints of Muller-Lyer figures may be more susceptible to illusory effects when initiated from a point on the shaft as opposed to from outside the figure (Bruno et al., 2008; see also Post and Welch, 1996; Wraga, Creem, & Proffitt, 2000). Smeets et al. (2002) note that the fins of the Muller-Lyer figure change the apparent extent of the central shaft but not the apparent positions of its endpoints (Gillam & Chambers, 1985; Mack, Heuer, Villardi, & Chambers, 1985). They thus argue that a movement toward an endpoint may be scaled to the extent of the shaft if it begins from a point on the shaft, but be directed at the endpoint position if it begins elsewhere, being prone to the illusion of extent only in the former case. More generally, apparent dissociations between different responses to illusions may always reflect a mismatch between the attributes guiding the different responses. To explain any such pattern requires an understanding of which visual attributes are affected by a specific illusion, and how these attributes are weighted in the guidance of specific responses. These details are not reducible to any general dichotomy.

Finally, even if we have a good functional model of how an illusion works, its behavioral consequences cannot inform any anatomical hypothesis, such as the anatomical component of the *perception–action* model, unless we also know where in the brain the illusion is represented. Until recently, for example, an untested assumption of the illusions-in-action paradigm was that pictorial depth is interpreted in the ventral stream, so that only the ventral stream should represent illusions induced by pictorial depth. However, a recent fMRI study concluded that the perceptual enlargement of objects presented against a receding linear perspective background (Ponzo illusion) is reflected in primary visual cortex (Murray, Boyaci, & Kersten, 2006). Even if we allow that these effects may depend on top-down feedback from ventral stream areas, the implications of this finding for the illusions-in-action paradigm are severe. If the Ponzo illusion can affect early visual representations, the *perception–action* model predicts that the illusory changes should affect perception and action equally, and prior reports of action resistance to the Ponzo illusion (Brenner & Smeets, 1996; Jackson & Shaw, 2000; Stöttinger & Perner, 2006) must have some explanation other than that previously offered by the model. This in turn undermines the idea that dissociated responses to *any* visual illusions would provide differential support for the *perception–action* model.

The illusions-in-action paradigm now looks quite jaded. Its inconsistent results may be better explained by task-specific accounts, and at least some of its key assumptions may be wrong. Consequently, this large literature supports remarkably few firm conclusions regarding the *perception–action* model, except to reinforce the evidence, reviewed in the previous section, that action responses are not generally immune to the influence of visual context or pictorial depth. Whether such influences stem from early vision, from the ventral stream, or from the dorsal stream itself is mostly unclear. Context-based illusions remain an unreliable localizer for ventral stream involvement, a fact that has repercussions in the next section, concerning the temporal properties of the two visual streams.

TEMPORAL PROPERTIES OF PERCEPTION AND ACTION

Vision-for-perception can inform working memory representations that outlast the visual stimulation by several seconds, and enable long-term memories to be formed. Milner and Goodale (1995) propose that visuomotor representations, by contrast, decay rapidly so that only afferent vision can guide action via the dorsal stream. The strongest version of this view proposes that vision-for-action lacks all capacity to store information (Goodale, Westwood, & Milner, 2003; Westwood & Goodale, 2003). Only actions to targets visible at the time of movement initiation are guided by visual information in the dorsal stream; any delay between target viewing and movement initiation forces visual control to switch over to stored representations from the ventral stream. Because ventral stream representations are optimized for visual recognition rather than action guidance, delayed actions should show predictable changes in character, as well as reductions in quality.

Delayed grasping movements show reduced precision (Elliott & Madalena, 1987; Rossetti, 1998; Westwood, Heath, & Roy, 2001), and kinematic changes indicative of greater uncertainty, such as extended movement durations and larger maximum grip apertures (Bradshaw & Watt, 2002; Hu, Eagleson, & Goodale, 1999). However, such changes could be explained by a single visual representation that decays on the removal of visual information. Indeed, the performance decrement observed in grasping with increasing delay is well approximated by an exponential decay function, common across a wide range of memory-based tasks (Hesse & Franz, 2009). To assess ventral stream involvement specifically, Hu and Goodale (2000) compared the influence of a size-contrast illusion on immediate and delayed grasping. They found illusory effects only in delayed actions, taking this as evidence that such actions depend on ventral stream guidance (see also Westwood & Goodale, 2003). However, this pattern has not been replicated for other illusions. For instance, the effect of Müller-Lyer figures on grasping depends on whether or not visual feedback is available during execution, not whether initiation is immediate or delayed (Bruno & Franz, 2009; Franz et al., 2009; Westwood, McEachern, & Roy, 2001; Heath, Rival, Westwood & Neely, 2005). Moreover, as noted in "Visual illusions in action" above, there are sufficient problems with the assumption that illusion strength indexes ventral stream involvement to render moot the significance of any such evidence.

The effect of (non-illusory) visual context provides slightly better quality evidence. Obhi and Goodale (2005; see also Hay & Redon, 2006) found that immediate and delayed reaches both benefited from visual context (environmental structure), but that this benefit was enhanced with delay. An increased weighting of contextual information in delayed reaching is consistent with an increased contribution of allocentric, relative to egocentric, spatial coding. However, as Obhi and Goodale (2005) pointed out, allocentric coding cannot be inferred unambiguously from the influence of visual context. The positions of non-target elements could be computed egocentrically yet influence target localization, perhaps by supporting a more accurate calibration of available distance cues (Magne & Coello, 2002). Nonetheless, if we are prepared to assume that allocentric spatial coding does underlie these contextual influences, and to accept the idea that allocentric coding requires ventral stream involvement ("Spatial codes for perception and action" above), then these findings suggest that delayed actions do have an increased reliance on the ventral stream.

More conclusive evidence might be expected from patients with selective damage to one or other visual stream. If the control of delayed actions switches to the ventral stream, then delayed actions should be impaired relative to immediate actions following ventral stream damage, but *improved* following dorsal stream damage. With respect to ventral stream damage, Goodale et al. (1994a) confirmed that DF's good grip scaling was abolished by a 2 s delay. Subsequently, several studies have found the predicted complementary improvement with delay in patients with optic ataxia following dorsal stream lesions (Himmelbach & Karnath, 2005; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner et al., 2001; Rice et al., 2008; Rossetti et al., 2005). However, analysis of the time-course of improvement does not support an abrupt switch from dorsal to ventral stream control, but rather a gradual improvement with delay duration (Himmelbach & Karnath, 2005). Moreover, optic ataxic performance remains severely abnormal, even with delay (Milner et al., 1999, 2001; Himmelbach & Karnath, 2005), suggesting that delayed actions do not bypass the dorsal stream. Functional imaging supports this inference, as immediate and delayed actions produced similar activation of surviving dorsal stream tissue in a patient with optic ataxia (Himmelbach et al., 2009).

Dorsal stream activation during delayed action is further supported by functional imaging in healthy subjects (Connolly, Andersen, & Goodale, 2003). However, an interesting qualification has been suggested by Singhal and colleagues, who observed reactivation of ventral stream area LO at the time of delayed action (Singhal, Kaufman, Valyear, & Culham, 2006). Consistent with this, Rice-Cohen and colleagues found that TMS over LO affects only delayed action, but TMS over dorsal stream anterior intraparietal area (AIP) disrupts both immediate and delayed action (Rice-Cohen, Cross, Tunik, Grafton, & Culham, 2009). Overall the data suggest that the dorsal stream is involved both in the control of immediate and delayed action (see also Rogers, Smith, & Schenk, 2009), but that the ventral stream may provide crucial support for delayed action, so that such actions are severely impaired by damage to the ventral stream (Goodale et al., 1994a). Our conclusion is thus close to the original proposal of the *perception–action* model, though with important distinctions. First, delayed actions depend on collaboration between the two visual streams, not the substitution of dorsal by ventral stream control. Second, this collaboration is not unique to delayed actions, but also underlies immediate control (see "Spatial codes for perception and action" above), though the ventral stream contribution may be *relatively* more important when the flow of afferent visual information is turned off.

AWARENESS AND THE TWO VISUAL STREAMS

Milner and Goodale propose that only the products of ventral stream processing reach visual awareness

(Milner, 1995, 1998; Milner & Goodale, 1995, 2006, 2008). The ventral stream is thus necessary for visual awareness. Here, it may be helpful to adopt Koch's (2004) distinction between necessary neural activity that determines the *specific* contents of awareness, and activity that does not determine specific contents, but creates *enabling* conditions for awareness. For instance, the reticular activating system may enable awareness, but its activity does not predict the specific content of awareness. By contrast, lesions within the ventral stream produce content-specific changes in experience, such as form agnosia and prosopagnosia, and neural activity within this stream covaries with perceptual report, even in the face of unchanging stimulation (for instance, during binocular rivalry, e.g. Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002). Milner and Goodale (2006, epilogue), provide an overview of neurophysiological and neuroimaging evidence that establishes *specific* roles for ventral stream sites in visual awareness.

An important caveat to the above proposal is that ventral stream activity is not sufficient for awareness. This is true in that we are unaware of much of the processing within the ventral stream, and in that further *enabling* conditions are required for us to be visually aware of anything. Disorders such as neglect and extinction implicate parietal and frontal regions in visual awareness. This is consistent with brain imaging results which, alongside ventral stream sites, have often found frontal and parietal activations that correlate with changes in perceptual report (for reviews, see Rees, 2007; Rees, Kreiman, & Koch, 2002). These fronto-parietal activations, including activations within the dorsal stream, might conceivably reflect changes in the specific content of visual awareness. Alternatively, they may be attentional modulations, determining which visual representations enter awareness. This latter interpretation would not challenge Milner and Goodale's proposal. A true challenge would require evidence that activity outside of the ventral stream can determine the specific content of awareness.

In fact, this evidence may already exist. Area MT has all the qualities expected of a specific site for visual awareness. Its stimulation modifies visual awareness of motion (Salzman, Britten, & Newsome, 1990), its lesioning (Schenk & Zihl, 1997; Zihl, von Cramon, & Mai, 1983) or inactivation (Beckers & Hömberg, 1992) induces selective akinetopsia, and its activity correlates with verbal reports of perceived motion, even when that motion is dissociated from afferent stimulation by being apparent (Kaneoke, Bundou, Koyama, Suzuki & Kakigi, 1997), illusory (He, Cohen, & Hu, 1998; Tootell et al., 1995), imagined (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998), or even implied (Kourtzi & Kanwisher, 2000). MT is not within the ventral stream, but is classed by Milner and Goodale as an early visual area, with common feeder status for both visual streams ("Introduction" above). By this reckoning, ventral stream processing does not produce all the contents of visual awareness.

Leaving MT aside, we can approach Milner and Goodale's proposal from another angle, and assess its implication that processing within the dorsal stream cannot reach visual awareness. Some of the most-cited evidence for this view comes from blindsight, in which patients may be able to direct saccadic or reaching movements toward stimuli that they do not report seeing (Weiskrantz, 1986). Remarkable as these abilities are, blindsight does not provide strong or specific evidence to dissociate the dorsal stream from visual awareness. First, although many authors emphasize residual action-abilities, there are numerous reports of residual perceptual discriminations in blindsight, for instance of color, orientation (Weiskrantz, 1986, 1987), and form (Danckert, Maruff, Kinsella, de Graaff, & Currie, 1998; Trevethan, Sahraie, & Weiskrantz, 2007) (for a review, see Danckert & Rossetti, 2005). Second, for actions and discriminations alike, preservation is only relative: above chance but inferior to normal performance. Blindsight does not imply that the normal operation of the dorsal stream is unconscious, since the unconscious abilities are not exclusively visuomotor, and are anyway far from normal.

Stronger evidence is found where more fully preserved abilities are dissociated from visual awareness. For instance, a visual extinction patient has been shown to avoid obstacles (McIntosh et al., 2004) and to use brief visual feedback from the hand (Schenk, Schindler, McIntosh, & Milner, 2005), regardless of whether he could report the relevant stimuli. Crucially, his "unaware" performance was indistinguishable from his "aware" performance, in contrast to the degraded implicit processing of extinguished stimuli typical in the perceptual domain (for a review, see Driver & Vuilleumier, 2001). Perhaps the strongest evidence, however, comes again from visual form agnosia, and patient DF (see also Karnath et al., 2009). DF's visuomotor repertoire is vastly richer than that of any blindsight patient yet studied, as might be expected given the cortical inputs to her dorsal stream. Her ability to act systematically in accordance with visual attributes that she cannot explicitly report (e.g. size, orientation, shape) suggests that successful dorsal stream processing does not evoke, nor require, visual awareness in the normal brain.

However, recent evidence shows that DF is not *entirely* unable to report on the visual features that guide her actions, provided that the question is posed in the right way. Schenk (2006) found that DF's verbal report in a visual distance-matching task was in the normal range if asked to report on *egocentric* distance, which presumably underlies her preserved visuomotor performance. Her visual size discrimination also improved significantly if probed just before or during a grasping movement toward the discrimination target (Schenk & Milner, 2006). These findings suggest that the cognitive system can access the information used in action. Whether or not this should qualify as "visual" awareness is a more difficult matter (Clark, 2009).

Schenk's (2006) experiment raises the intriguing notion that the dorsal stream may contribute a heightened visual awareness of the world in relation to oneself. This egocentric quality, and its absence after dorsal stream damage, might be hard to articulate, making it easy to overlook (for a similar suggestion, see Riddoch et al., 2004). Further possible evidence for this emerged recently, again from patient DF. Although she does not find it easy to describe her visual experiences, it is clear that she is vividly aware of color and texture, and has stereo vision (Milner et al., 1991). Psychophysical investigations show that DF uses absolute binocular disparities to support absolute distance judgments, outperforming many controls, but is selectively impaired in using relative disparities between adjacent surfaces to judge their separation (Read, Phillipson, Milner, & Parker, 2008). The prevailing view is that relative depth between surfaces is processed in the ventral stream, while absolute disparity is processed preferentially in the dorsal stream (e.g. Neri, 2005). One possible interpretation of these data is that DF's experience of absolute depth derives from her dorsal stream, although a critical role for spared parts of her ventral stream cannot yet be ruled out.

Overall, the exclusive identification of the contents of visual awareness with ventral stream processing is open to debate. A specific role for MT in the awareness of motion may be enough to refute the literal truth of the claim. On the other hand, there is considerable support for the spirit of the proposal, which assumes a prominent role for the ventral stream in furnishing visual awareness. Even so, we should not dismiss the idea that dorsal stream contributions shape the *quality* of visual awareness in ways that are no less real, though they may be less readily reportable. Finally, even if Milner and Goodale's proposal is taken as literally true, it should be noted that we only become aware of the products of ventral stream processing given attentional activity in other areas, including the dorsal stream. This echoes our earlier conclusion (Section 2) that any visual function of significant complexity is likely to require the collaboration of multiple brain systems.

CONCLUSIONS

The ability of the *perception–action* model to give a unifying and plausible account of diverse findings in neurophysiology, neuropsychology, functional imaging and experimental psychology has made it enormously influential over two decades. The conceptual simplicity and counterintuitive appeal of the model have promoted its wide dissemination and discussion within and beyond the field of cognitive neuroscience, and its assumptions and predictions have been targeted by hundreds of empirical papers. This brief review has necessarily been very selective. However, alongside support for the spirit of the model, we have found mixed evidence for its specific claims, especially for the high degree of functional independence assumed between the two visual streams. Milner and Goodale's characterizations of the ventral and dorsal streams (Table 1) may be broadly correct, but the specializations are relative, not absolute.

The ventral stream is necessary for object and scene comprehension, and intimately involved in forging the contents of visual awareness. The dorsal stream is critical for the normal guidance of action. These functional roles are secure, but it is doubtful that they can be parsed into mutually exclusive domains of vision-for-perception and vision-for-action. The "Perception vs. action" section above concluded that ventral stream influences on action guidance are not restricted to higher planning levels but extend even to the spatial programming of simple actions. The subset of visuomotor behaviors that do not benefit from ventral stream participation in the normal brain may be vanishingly small, perhaps restricted to fast online updating and implicit obstacle avoidance. Conversely, the "Awareness and the two visual streams" section proposed that the dorsal stream contributes egocentric spatial aspects to our visual awareness, participating directly in vision-for-perception.

The "Spatial codes for perception and action" and "Temporal properties of perception and action" sections found some evidence to suggest that only the ventral stream can encode allocentric relationships between objects, or support sustained visual representations, consistent with Milner and Goodale's view. On the other hand, the data imply that the dorsal stream can access and employ these ventrally derived representations, again emphasizing extensive inter-stream interactions. This highlights a recurrent theme of the present review: Visual functions of any significant complexity are likely to involve collaboration between the two visual streams, and other brain systems. To take a prominent example, even if we were to accept an *exclusive* role for the ventral stream in providing the contents of visual awareness, awareness of these contents would still require attentional modulation from other brain areas. Some would argue that descriptive labels with such broad connotations as "perception" or "action" should not be applied to the specific contribution of any subdivision of the total participating network (cf. Jeannerod & Jacob, 2003; Pisella et al., in press; Rossetti et al., 2003).

A major mission of the *perception–action* model has been to displace the entrenched classical conception of a unitary, all-purpose, visual representation of the world, so it is perhaps inevitable that the independence of the two streams has been emphasized over their interaction. However, one of the ironies of the model's success is that the classical view has, to some extent, been replaced by the notion that our brains house two separate, unitary visual representations. The reality is much more fluid and task-specific than this. For instance, the various depth cues available in viewing a scene may be extracted in different brain areas, albeit with different latencies, then be generally available to inform any responses for which they are useful. Visuomotor responses tend to weight binocular and extra-retinal cues relatively more, and pictorial cues relatively less heavily than do perceptual responses, but evidence for categorical distinctions between the guiding representations is lacking.

In defining and defending their model, Milner and Goodale's (1995, 2008) stated goal has been to provide a theoretical framework to stimulate research. This goal has been met many times over. More fundamentally, their model has redefined the way that cognitive neuroscience views the functional specialization of sensory systems, by prioritizing the role of behavioral output requirements in determining where in the brain, and how, sensory information is analyzed. The *perception–action* framework encompasses diverse experimental findings, and it would be self-defeating to reject such explanatory scope outright. On the other hand, this review suggests that each of the *specific* claims of the model regarding the specializations of the two visual streams (Table 1) has either been refuted ("Perception vs. action" and "Awareness and the two visual streams" sections above) or found limited empirical support ("Spatial codes for perception and action", "Visual illusions in action", and "Temporal properties of perception and action" sections). Perhaps, then, we should view the model not as a formal hypothesis, but as a set of heuristics to guide experiment and theory. The differing informational requirements of visual recognition and action guidance still offer a compelling explanation for the broad *relative* specializations of dorsal and ventral streams. However, to progress the field, we may need to abandon the idea that these streams work largely independently of one other, and to address the dynamic details of how the many visual brain areas arrange themselves from task to task into novel functional networks.

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Commentaries on Schenk and McIntosh (2010)

Dissociations of perception and action do not automatically imply independent visual processing streams

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Abstract: Since the publication of Milner and Goodale's perception–action model of visual processing, there has been a general tendency to attribute any dissociation in the performance of perceptual and action tasks to a difference in the abilities and limitations of the ventral and dorsal visual streams. However, behavioral dissociations do not necessarily imply different underlying neural systems. In particular, there is a class of illusions, brought about by distortions of the observer's egocentric reference frame, that can cause perception–action dissociations without requiring or implying the existence of separate visual processing streams.

The review of Schenk and McIntosh does an excellent job of detailing evidence that the perception–action model is an oversimplification of the complex relationships that exist between the functional regions of the dorsal and ventral visual cortices. Although the model laid out by Milner and Goodale has provided a theoretical framework for stimulating research, there has been a tendency in the literature to over-rely on the model as a way of accounting for *any* dissociation of perception and action, which has pre-empted attempts to explore other possible causes of these dissociations. One illusion that has been suggested to provide evidence for separate processing streams is the induced Roelofs effect: When a visual target is presented within the context of a large rectangle that is offset left or right from the observer's objective midline, its egocentric location is misperceived as being shifted in the direction opposite that of the rectangle. Despite this perceptual illusion, pointing movements to the target remain accurate (Bridgeman, Peery, & Anand, 1997). A subsequent analysis indicated that the perceptual illusion was caused by a distortion of the observer's egocentric reference frame, with, for example, a rectangle shifted to the observer's left causing the subjective midline to be pulled to the left, which would, in turn, cause the enclosed target to be misperceived as being shifted to the right (Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004).

Since pointing movements to the target in the induced Roelofs effect have been shown to be unaffected by the illusion, one might argue that the sensorimotor systems of the brain must be immune to the illusion. However, imagine what would happen to a movement that is guided within the same distorted reference frame in which the location of the target is encoded. In the example above, a left-shifted rectangle pulls the subjective midline to the left, so that a target that is in the observer's midsagittal plane would appear to be located a small distance to the right of the subjective midline. If, now, the sensorimotor systems use the distorted subjective midline as a reference and guide the hand to a spatial location that is a small distance to the right of that reference, the movement would land accurately on target (Dassonville & Bala, 2004). In essence, the error of encoding the target location within the distorted reference frame would be cancelled by the error of guiding the movement within the same distorted reference frame.

A similar cancellation of errors has been shown to allow accurate movements in the face of other illusions that are caused by distortions of the observer's reference frame, including one that is induced by a distortion of subjective eye level (Li & Matin, 2004) and another induced by a distortion of subjective vertical (Li, Matin, Bertz, & Matin, 2008). Undoubtedly there are still other illusions that would lead to perception–action dissociations in a similar manner, without suggesting the existence of two separate visual systems that are differently susceptible to the illusion. Moreover, this should serve as a more general reminder that all behavioral dissociations are not alike, and thus researchers should not fall into the trap of trying to use a single mechanism to explain them all.

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Computation in the dorsal and ventral stream

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Abstract: I argue that the evidence described by Schenk and McIntosh warrants the search for a new approach to the function of the dorsal and ventral visual streams rather than merely recasting the model in terms of relative specialization. In this regard, it may be profitable to think in terms of the computations carried out by the two visual streams. The effects of memory provide one source of information concerning the distinctive nature of these computations.

Schenk and McIntosh provide a compelling review of the empirical and conceptual shortcomings of the perception–action model of Milner and Goodale (e.g., 2006). Despite these shortcomings, though, Schenk and McIntosh suggest that the functional distinction between perception and action still has heuristic value if the assumption of independence is relaxed and if the distinction is understood in terms of relative rather than absolute specialization. While the value of the action–perception model in stimulating research in the past is undeniable, a distinction in terms of relative specialization is likely to be much less helpful. In particular, it is difficult to anticipate what should be predicted on the basis of such a revised distinction, and, as a consequence, the account of the two visual streams becomes difficult to disprove. Instead, it may be more productive to search for other conceptions of the roles played by the two visual streams.

An alternative to specifying the broad functions of the two streams is to identify the nature of the computations they perform. From this perspective, the dorsal stream is important for action because the nature of the computations and representations delivered by the dorsal stream are often used in the control of action, and the ventral stream is similarly important for perception and action planning because of the relevance of the information it provides. The perception–action model provides some clues to the distinct nature of these computations, and a framework cast in such terms provides the potential to make explicit distinctions between the two streams while still allowing for the complexity that the extant data would seem to demand.

The pervasive role of memory provides an important source of evidence concerning these dorsal and ventral computations. Schenk and McIntosh note the importance of memory for the programming of force parameters, but immediately preceding actions also affect other action parameters such as choice of grasp (Dixon & Glover, 2004) and movement trajectory (Jax & Rosenbaum, 2007). Such findings by themselves are problematic for the view that action is determined by modular, *de novo* dorsal-stream calculations. However, it seems likely that memory is used differently in the two streams. For example, Dixon and Glover (2009) found that grip aperture in the course of reaching and grasping a disk was affected by the relative size of the disk on the previous trial in two ways. For most of the reach, previous disk size had a contrastive effect, so that grip aperture was smaller following a large disk and larger following a small disk. However, near the end of the reach, as the hand neared the target disk, the effect of previous disk size reversed (a perseveration effect), so that grip aperture was larger following a large disk and smaller following a small disk. A speculative interpretation is that the dorsal stream uses memory for previous actions to form default values for visually guided reaching and that the use of such information is evident as the hand nears the target. In contrast, the ventral stream may use previous experience as perceptual anchors, leading to size-contrast effects in the planning of grip aperture.

The point of this comment, though, is not to argue for a particular interpretation of the role of the ventral and dorsal streams, but rather to assert that the time is ripe for a large-scale reinterpretation of the evidence marshaled for and against the perception–action model. One possible framework for doing so is to think in terms of the nature of the computations that the visual streams carry out.

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Ventral and dorsal streams as modality-independent phenomena

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Abstract: Interest in ventral and dorsal streams is not limited to vision, and the functionality of similar pathways in other domains has also been considered. Auditory dual pathway models share many conceptual and empirical concerns with those put forward for vision, including the absolute vs. relative, localized vs. distributed, and exact nature of functionality of the two streams. Despite their problems, dual pathway hypotheses provide broad frameworks with which to consider cortical architecture across the senses.

Schenk and McIntosh reject a strong version of visual ventral and dorsal activity, in which perception (ventral) and action (dorsal) are viewed as functionally independent. Dual pathway models of visual processing have had a tremendous impact on cognitive neurosciences and have recently been extended to account for auditory processing (Kaas & Hackett, 1999; also tactile processing, Dijkerman & De Haan, 2007). Given the opportunity for massive cortical interconnectivity, it seems unlikely that spatially distributed and temporally coordinated processing streams covering large areas within the brain will show complete functional independence in any modality. However, weaker versions of auditory ventral and dorsal activity have been considered in which certain processes tend to be carried out along one pathway rather than another.

Despite the *perception–action* distinction being the current dominant force in the characterization of visual ventral and dorsal activity, the older *what–where* distinction has been the focus of much of the auditory literature. This was recently summarized in a functional neuroimaging meta-analysis examining ventral and dorsal activity across 36 studies (Arnott, Binns, Grady, & Alain, 2004). Equivalent degrees of initial activation for spatial (*where*) and nonspatial (*what*) information were found in the posterior temporal lobe, which then partitioned into a dorsal route to the superior frontal sulcus in which spatial tasks generated greater activity, and a ventral route to the inferior frontal gyrus in which nonspatial tasks generated greater activity. Further evidence for a *what/where* distinction is provided by neurological case studies, in which patients collectively show a double dissociation between lesion profile and performance, namely problems in sound localization and damage to more posterior/parietal areas, and problems in sound identification and damage to more lateral/temporal areas (Clarke, Bellmann, Meuli, Assal & Steck, 2000). Consistent with the weak version of visual ventral and dorsal activity, these paths are best characterized by relative rather than absolute differences in the flow of certain kinds of information and operation.

In a transition similar to that observed in the visual literature, discussion of ventral (*what*) and dorsal (*where*) processing in audition has begun to focus on multiple interpretations of the dorsal stream, while the ventral stream continues to be associated with stimulus identity. Alternative conceptualizations have recast the auditory dorsal stream as a pathway critical for sensory-motor integration and goal-directed (speech) action (*do* pathway; Warren, Wise, & Warren, 2005), and as a pathway critical for the processing of spectral motion: how an auditory signal changes over time (also known as a '*how*' pathway; Belin & Zatorre, 2000). Emphasizing the importance of auditory time rather than space in the dorsal stream may be a reasonable maneuver in terms of the proposed preference for spatial aspects of visual processing, and temporal aspects of auditory processing (e.g., Kubovy & Van Valkenburg, 2001).

Ultimately the degree of localized functionality must be tempered by the acknowledgement that dorsal and ventral streams have numerous opportunities to communicate with one another during both auditory (Hall, 2003) and visual (Milner & Goodale, 1995) processing. Such observations make a weak version of the ventral/dorsal model more likely, highlighting the need to understand where and when interstream communications arise. Despite the attraction of sensory isomorphism, the eventual preferences of such neural trajectories may rest with the architecture of individual sensory systems, the specific task demands (Glover, 2002), and also the eventual need to integrate information across modalities in pursuit of a multisensory environment in which we may operate successfully. Despite its flaws, the ventral/dorsal distinction provides us with a framework with which to explore these issues.

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Two visual streams: Interconnections do not imply duplication of function

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Abstract: Schenk and McIntosh (S&M) provide a useful review of the perception–action model (PAM), highlighting some of the gaps that need to be filled, and counteracting the erroneous belief held by some that the PAM implies two mutually independent streams. Although we agree with S&M's contention that the functional independence of the two streams has been overestimated, we reject their speculation that "the specializations proposed may be relative rather than absolute." We argue that the contributions made by the two streams are quite distinct, and that establishing how they work together is the key to a full understanding of visually guided behavior.

Our colleagues Thomas Schenk and Robert McIntosh (S&M) pose the question "Do we have independent visual streams for perception and action?" Our emphatic answer is "No." Indeed we acknowledged this truth when first framing the perception–action model (PAM), on the basis both of anatomical and physiological evidence for cross-talk between the two streams, and of sheer armchair logic (Goodale & Milner, 1992; Milner & Goodale, 1995). Thus we are in full agreement with the main conclusion offered by S&M—and in fact many of their detailed arguments echo our own published views. S&M do not dispute the basic tenets of PAM—their objective is to take stock of the model's track record, and to propose ways of elaborating on those basic tenets in order to deal with data that have appeared since we first proposed the model.

It seems to us that even the studies reviewed here that are the most critical of the PAM can actually be handled by the model, if reasonable assumptions are made about the nature of the interstream interactions. But of course agreeing that the two streams are highly interactive is not to agree with S&M's further suggestion that "the specializations proposed may be relative rather than absolute." (p. 53). It is crucially important not to conflate these two propositions. Of course, to a large extent the two streams share common inputs from early retinotopic cortical areas (orientation, location, size, etc.), so that processing of these visual features is not the absolute province of one or other stream. But how such inputs are then transformed and used, we suggest, is very different (indeed often complementary) in the two streams. For example, visual information is coded in effector-based ("egocentric") coordinates in the dorsal stream (Milner & Goodale, 2006), while the ventral stream operates principally, though not exclusively, in world-based ("allocentric") coordinates. There is good evidence for this, and indeed Schenk (2006) himself recently reached a similar conclusion on the basis of testing carried out with patient DF.

Our intention, then, is to review (and ultimately question) S&M's proposal that the specializations of the dorsal and ventral streams are only relative. We suggest instead that there are real and substantive differences in the nature of the transformations carried out in the two streams.

PLANNING AND PROGRAMMING

What specialized contribution does the dorsal stream make to the visual guidance of action? Not much, say S&M: "the subset of visuomotor behaviors that do not benefit from ventral stream participation in the normal brain may be vanishingly small, perhaps restricted to fast online updating and implicit obstacle avoidance." (p. 61). But if this is so, how can we explain DF's rather accurate programming of reach and grasp parameters in many laboratory and everyday tasks, despite severe bilateral damage to the shape-processing areas of the ventral stream? Since these residual visuomotor skills allow DF to live a remarkably full life, they can hardly be considered trivial. Moreover we know that they are mediated by her dorsal stream, which shows near-normal fMRI activations during reaching and grasping (James, Culham, Humphrey, Milner, & Goodale, 2003). Thus her grasping is almost certainly guided by an independent analysis of object geometry in the dorsal stream. Indeed, there is good neurophysiological evidence for such processing, which indicates it to be coarser, faster, and more metrically scaled than in the ventral stream (e.g., Srivastava, Orban, De Mazière, & Janssen, 2009).

Their low estimation of the dorsal stream's capacities leads S&M to infer ventral stream involvement "at all levels of action planning and programming." (p. 55). We disagree with this extreme view. We believe that the evidence remains consistent with the dorsal stream's retaining sole responsibility for the programming of kinematic action parameters (Milner & Goodale, 2008). While we accept that under some circumstances a clear ventral stream influence on programming parameters can be demonstrated (e.g., McIntosh & Lashley, 2008), we maintain that this could reflect a modulation of dorsal stream programming mechanisms by high-level ventral stream processing, rather than a ventral stream share in the motor programming itself. But the existence of such semantic influences does not imply that the ventral stream does not contribute in *other* ways to visuomotor processing too: "Perhaps the key to ventral stream involvement in action is not high-level planning, but semantic involvement, exemplified by picking up tools, which must be recognized before an appropriate grasp can be selected." (p. 54). We see no reason why the ventral stream should not play a role in both of these functions, as well as in other aspects of action, such as bridging gaps in time or space. We see no conflict in accepting that DF has difficulty selecting one potential goal for action over another (Murphy, Racicot, & Goodale, 1996), using semantic knowledge to grasp everyday implements (Carey, Harvey, & Milner, 1996), and performing delayed or pantomimed visuomotor acts (Goodale, Jakobson, & Keillor, 1994a). Accordingly we are untroubled by S&M's concern that "No simple criterion based on planning level or semantic involvement predicts the visuomotor tasks with which DF struggles and which, by implication, benefit from ventral stream participation in the normal brain." (p. 54). We freely confess that we cannot always predict such results, which is why our continuing experiments with DF are so valuable. We need the empirical evidence precisely to help us delineate what her quasi-isolated dorsal stream can and can't do.

We have in fact tried to take account of new empirical evidence of all kinds in our progressive refinement of the PAM. S&M seem to be unaware of some of our efforts, and write as if the evidence flatly contradicts the model. For example, they argue that the tuning of initial grip and load forces according to an object's properties shows that not all the parameters of actions can be programmed on the basis of bottom-up input to the dorsal stream. We would not dispute this at all. In fact, we have argued on a number of occasions (e.g., Goodale, 1997; Milner & Goodale, 2006; Cant & Goodale, 2007) that the scaling of these forces relies to a large extent on associative learning between the material properties of the goal object (e.g., its mass/density, compliance, temperature, fragility) and its visual appearance (shape, size, surface cues) and other contextual cues, all of which are processed by the ventral stream. We argue that this reliance on ventral stream processing explains why such forces are often affected by pictorial illusions, such as the Ponzo illusion (Brenner & Smeets, 1996; Jackson & Shaw, 2000), even though the scaling of grip aperture is not.

ILLUSIONS

This brings us to the literature on pictorial illusions and action, which, as S&M point out, has become large and complex, with the arguments becoming increasingly byzantine. Suffice it to mention here that a number of studies do provide remarkably unequivocal support for the PAM. Ganel, Tanzer, & Goodale (2008), for example, have recently demonstrated a double dissociation between perceptual judgements and grip scaling in the context of a Ponzo illusion. Importantly, this dissociation disappeared when a delay was introduced between viewing the display and initiating the action: Now grip aperture reflected the perceived rather than the actual size of the target (presumably because the ventral stream is engaged in delayed actions).

Of course functional MRI cannot detract from such solid findings, though it can (perhaps) shed light on what is going on. It is certainly interesting therefore that Murray, Boyaci, and Kersten (2006) have found that retinotopic coding of targets in V1 is affected by the Ponzo illusion. But we do not agree that the "implications of this finding for the illusions-in-action paradigm are severe." (p. 58). S&M's concern rests on the premise that if V1 codes size incorrectly then this coding should affect both ventral and dorsal stream processing. But the illusory coding of size in V1 has to arise from top-down feedback from ventral stream areas, and of course such feedback takes time (even though this is not reflected in time scale of the BOLD signal). This means that a *veridical* bottom-up signal about target size could be conveyed to visuomotor areas in the dorsal stream from V1 well before any feedback arrives from ventral stream areas via recurrent projections (Lamme, 2001). The notion that action programming often occurs before a full perceptual representation has been constructed is an idea that is increasingly accepted (e.g., de'Sperati & Baud-Bovy, 2008).

VISUAL AWARENESS

A fundamental claim of the PAM is that ventral stream activations determine the phenomenal content of perception. In questioning this, S&M first cite the case of motion perception. While agreeing with Milner & Goodale (1995, 2006) that area MT may well belong to neither stream, they proceed to argue that MT's close correlation with motion perception in many studies must imply that it, an area outside the ventral stream, "can determine the specific content of awareness." (p. 60). There are several fMRI studies, however, indicating that neural activity in MT correlates more with the physical motion of a stimulus than with subjective motion perception (e.g., Itoh, Fujii, Kwee, & Nakada, 2005; Moutoussis & Zeki, 2008). We therefore feel justified in sticking to our view that although MT certainly does play an essential role in motion perception, it is likely that it does this via its well-known projections to the ventral stream.

S&M have themselves provided experimental data that argue strongly against the view that dorsal stream visuomotor processing contributes to the contents of perceptual experience (McIntosh et al., 2004; Schenk, Schindler, McIntosh, & Milner, 2005: see Milner, 2008, for a fuller discussion). Even stronger evidence for a sharp dissociation between visuomotor performance and awareness comes from a recent paper by Striemer, Chapman, and Goodale (2009) showing that a patient with a dense hemianopia following an occipital lesion could avoid obstacles placed in his blind field in a reaching task, even though he never reported seeing those obstacles. Given the demonstrated role of dorsal stream mechanisms in the control of obstacle avoidance (Rice et al., 2006; Schindler et al., 2006), this new work further suggests that those mechanisms can make use of visual inputs that bypass the geniculo-striate pathway.

Are there any other reasons to suppose that the dorsal stream may contribute to the contents of our visual phenomenology? We are unconvinced by Schenk's (2006) finding that DF's judgements of the relative distance of two visual stimuli from her finger (his "egocentric distance" task) was not (quite) significantly impaired. As we have argued elsewhere (Milner & Goodale, 2008), such above-chance performance can be explained within the PAM if DF used a strategy of monitoring her own incipient hand movements to each stimulus (Murphy et al., 1996), or of *imagining* making pointing movements (Dijkerman & Milner, 1997), in order to guess which of the two was closer. These ideas could be easily tested. We are also unconvinced that Schenk and Milner's (2006) finding that DF was able to perform above chance at visual size discrimination when probed just before or during a grasping movement toward the stimulus demonstrates any dorsal stream mediation of perceptual content (though it presumably does reflect a dorsal-to-ventral influence on perception).

Despite these comments, we agree wholeheartedly with S&M that the dorsal stream does play a role in determining perceptual experience, insofar as areas within the dorsal stream (notably LIP) are crucial for the control of visuospatial attention. Indeed we have long argued (Milner & Goodale, 1995; Milner, 1995) that such "attentional" enhancement of ventral stream activations is necessary for those activations to reach awareness. But this influence is almost certainly of a content-unspecific modulatory nature.

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Is the visual dorsal stream really very visual after all?

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Abstract: The *perception–action* model (PAM) provides a misleading account of the core function of the dorsal stream: which is the integration of sensory signals to create dynamic representations of corporeal and extrapersonal space. Recent evidence suggests that the parietal-occipital cortex plays a key role in integrating multimodal spatial signals that relate to the direction of gaze and the direction of reaching movements. I suggest that a core deficit of the 'dorsal' stream—optic ataxia—arises because of an inability to *simultaneously* represent different multimodal spatial representations.

Within the PAM the function of the dorsal stream has most often been inferred from neuropsychological studies of the reaching movements of patients with optic ataxia. A recent MRI lesion-overlap study revealed that key regions of the parietal-occipital cortex most strongly associated with optic ataxia included the precuneus (BA7) on the medial surface of the superior parietal lobule (SPL) (Karnath & Perenin, 2005). This area corresponds closely to a region of the monkey SPL termed the 'parietal reach region' (PRR) (Batista, Buneo, Snyder, & Andersen, 1999); and brain imaging (fMRI) studies in humans have confirmed that the parietal-occipital junction (POJ) is activated during memory-guided reaching movements (e.g., Connolly, Andersen, & Goodale, 2003). This region also combines sensory signals (e.g., visual, somatosensory, proprioceptive) to form dynamic, multimodal, task-dependent spatial representations, termed "global tuning fields," that integrate retinal, eye, and hand information, and provide the basis for *eye–hand coordination* (e.g., Battaglia-Mayer & Caminiti, 2002). Optic ataxia has been viewed as a resulting from dysfunction in these global-tuning fields, and in this context it should be noted that: Human fMRI studies show that the POJ is specifically activated for reaching movements to *extra-foveal* visual targets (Prado et al., 2005); most optic ataxic patients only make directional errors when reaching toward extra-foveal visual targets (i.e., where direction of gaze is different from reach direction); in such cases errors are *not* random but instead err in the direction of gaze (Jackson, Newport, Mort, & Husain, 2005); optic ataxic patients may be unable to learn to perform tasks in which reach direction must be decoupled from direction of gaze (Newport & Jackson, 2006).

IS THE POJ REALLY PRIMARILY CONCERNED WITH "VISUAL" PROCESSING?

A recent fMRI study investigated reaching movements made *without vision* from novel, posturally defined, starting positions (Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006). The key finding of this study was that reaches from novel start positions were associated only with increased BOLD activation bilaterally in the POJ (corresponding to the region associated with optic ataxia, identified as the human PRR, and associated with reaching to *extra-foveal* visual targets). This finding is consistent with the SPL maintaining a dynamically updated representation of current body posture (the "body schema").

IS THE DEFICIT OBSERVED IN OPTIC ATAXIC PATIENTS REALLY A DEFICIT OF HIGH-LEVEL VISION?

Recent studies have investigated whether optic ataxic patients reach accurately to nonvisual targets (e.g., Jackson et al., 2009) and demonstrate that patients who can reach accurately to foveated visual targets, and to target locations that are defined posturally *without vision*, nevertheless misreach to extra-foveal targets irrespective of whether these targets are defined visually or proprioceptively.

We have suggested that it is the ability to *simultaneously* represent two different spatial representations that must be directly *compared* that is impaired in non-foveal optic ataxia (Jackson, Newport, Mort, &

Husain, 2005). This is the case when reaching for extra-foveal targets but not for foveated targets (see Jackson et al., 2009). Furthermore, the "dorsal stream" should not be viewed as "visual" but instead as a brain region in which different sensory signals are dynamically integrated to produce multimodal task-dependent spatial representations. In the case of the POJ, it appears to play a role in integrating spatial signals within a "global tuning field" network that relate to the direction of gaze and the direction of reaching movements, and may compute an error or displacement vector based on the angular difference between gaze direction and reach direction that may be particularly important when executing movements away from the direction of gaze (Jackson et al., 2009).

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Vision for action is not veridical

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Abstract: We agree with Schenk and McIntosh that the human brain can better be described in terms of task-specific functional networks than in terms of a division between (dorsal) egocentric vision for action and (ventral) viewpoint-independent vision for perception. However, by concentrating on the lack of experimental support for the latter division, the authors neglect an important reason for postulating that there is a separate vision-for-action system: needing veridical metric information to guide one's actions. We argue that considering this reason would support the authors' conclusion because the visual information that guides our actions does not have to be veridical.

The notion of task-to-task functional networks that Schenk and McIntosh propose is a very likely neural implementation of the behavioral view of task-dependent use of spatial attributes (Smeets, Brenner, de Grave, & Cuijpers, 2002). In this view, the reliability of information determines which information will be used for the task at hand. Aiming for a high reliability can also explain why we use positions and not size for shaping our hand during grasping (Smeets & Brenner, 2008), and why one shifts from using egocentric toward allocentric information after a delay if the target is removed from view.

The idea that we rely on the most *reliable* information seems to imply that we need *veridical* metric information to control our actions (Aglioti, DeSouza, & Goodale, 1995). However, it is clear that not all aspects of vision that are used to control our actions are veridical: Illusions of size, orientation, and speed have all been shown to influence certain aspects of movements (Smeets, et al., 2002). One might even argue that the only aspect of vision for action that needs to be veridical is the information about the target's location.

A target's position can be determined based on extraretinal information about eye-orientation, but often also from other sources, such as pictorial cues. We know that pictorial depth illusions can affect the manual tracking of a moving target with one's invisible hand to the same extent as perception of depth (López-Moliner, Smeets, & Brenner, 2003). Schenk and McIntosh correctly mention that the reliability of information for online control depends on the latency at which it is available: The shorter the latency, the more reliable it is. We have recently shown that pictorial depth cues can be used at a latency that is 40 ms shorter than that for binocular depth cues (van Mierlo, Louw, Smeets, & Brenner, 2009). This means that a cue that need not provide veridical information can be the most important for the online control of actions.

The whole idea that veridical information is available is probably wrong. Even extraretinal information about the position of a fixated target is not veridical: Subjects show biases that remain stable across days when moving their invisible hand to isolated visual targets (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). A careful analysis of the way in which information is used shows why this bias is not a problem: We combine all information optimally, both for the hand and for the target (Smeets et al., 2006). For locating our hand, we combine several visual cues with proprioception; for locating the target we combine visual cues with *extended proprioception*. This term refers to allocentric (visual) information about the target's position relative to the hand, converted into an egocentric judgment by combining it with the proprioceptive location of the hand. In this way, non-veridical visual or proprioceptive information affects the perceived location of the hand and that of the target in the same way, which makes the scheme robust for errors in either modality.

Our conclusion is that there is neither experimental evidence nor a theoretical need for veridical vision-for-action. This makes the absence of a separate vision-for-action stream (as proposed by Schenk & McIntosh) easy to accept.

* * *

Dorsal stream areas process action semantics

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Abstract: Evidence from recent studies investigating the functional and neural mechanisms supporting action semantics, i.e., the knowledge of how to use objects in a functionally appropriate manner, suggests that semantic processing for action is not restricted to high-level perceptual processing in the ventral stream but is directly associated with activation in dorsal areas, i.e., the motor system, and motor performance. These findings argue for a distributed and interactive account of action semantics and against functionally independent processing in dorsal and ventral stream areas.

In their comprehensive review, Schenk and McIntosh argue that the functional division between the dorsal and ventral visual stream is not absolute, but relative, by discussing the different possible ways in which the functional division between dorsal and ventral could be characterized. On p. 54, the authors discuss the possibility that “the key to ventral stream involvement in actions is … semantic involvement, exemplified by picking up tools, which must be recognized before an appropriate grasp can be selected.” However, as the authors argue, damage to ventral stream areas, as evidenced by patient DF for instance, does not result exclusively in action semantic impairments, but in more general action planning deficits as well. Accordingly, semantic involvement cannot be a defining criterion for distinguishing ventral from dorsal stream activity.

In agreement with this conclusion we would like to add that semantic processing for action is not limited to processing in the ventral stream. At a behavioral level many language studies have shown close interactions between semantics and actions (Fischer & Zwaan, 2008). Furthermore, neuroimaging studies suggest that action semantic knowledge activated by words is not stored in high-level association areas, but is actually represented in motor-related brain areas (Pulvermuller, 2005).

In addition to the available language research on action semantics, we recently investigated the involvement of semantics in several (non-linguistic) action conditions, i.e., during the classification of tools and execution of object-directed actions. In a first study, it was found that the classification of tools was accompanied by functional activation of the motor system reflecting the typical use of the object (van Elk, van Schie, & Bekkering, 2009). A second study indicated differential activation of motor areas when subjects performed meaningful as compared to meaningless actions with objects (van Elk, van Schie, & Bekkering, 2010). These studies support the notion that action semantic knowledge may influence motor-related processes and modulate activation in the motor system.

A question that is still open is whether semantics for action are actually represented in the motor system or whether these effects reflect an influence from higher level (e.g., ventral) association areas on the (dorsal) motor system. If action semantics are truly represented in motor-related areas, one should expect a preserved ability to use objects in case of damage to the ventral stream. Interestingly, although patient DF often grasped objects at the incorrect part, she was able to display the appropriate action required for using the object (i.e., performing the right pantomime with the object; Carey, Harvey, & Milner, 1996), suggesting preserved action semantic knowledge about the object. Future research will need to address how dorsal and ventral stream areas differentially contribute to action semantic processing. One possibility, for instance, is that ventral stream areas may be involved in the visual analysis required for grasping the object at the appropriate side (Carey et al., 1996; Valyear & Culham, 2009), whereas dorsal stream areas may be more strongly involved in performing the gesture associated with using the perceived object (van Elk et al., 2010), thereby stressing the necessary involvement of both streams in planning an upcoming goal-directed action. Irrespective of this hypothesis, the available evidence of interactions between semantic and motor processes in dorsal stream areas goes well with the authors’ suggestion that the distinction between dorsal and ventral stream areas is a relative one.

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Reply to Commentaries

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In our review, we argued that the ubiquity and extent of inter-stream interactions suggests that the ventral and dorsal visual streams are not functionally independent processing pathways. Most commentaries agreed with our conclusions. However, the notion that the specializations of the two streams are relative, not absolute, was criticised. We address this and other challenges. We conclude that, while the perception–action model works well as a high-level description of the functional organization of the visual cortex, it does not account for the complex interplay between perception and sensorimotor control revealed by a finer-grain analysis.

Most commentaries seemed to agree with our conclusions, adding valuable extensions and qualifications. Understandably, Goodale and Milner were less enthusiastic, and a significant part of this reply will consider their concerns.

ABSOLUTE OR RELATIVE SPECIALIZATION

Goodale and Milner accept that the functional independence of the two streams has been overestimated, but reject the idea that the specializations of the ventral and dorsal streams are relative rather than absolute. They argue that this is contradicted by absolute differences in the computational properties associated with the two streams. To be clear, when we invoked the idea of relative specialization, we meant relative with respect to the proposed behavioral categories of “perception” and “action”: the specializations of the two streams cannot be mapped one-to-one onto these categories. We do not deny that areas within the two streams have different computational properties (though differences also exist between areas within each stream). Dixon argues that characterizing the two streams in terms of their computational properties would be preferable to specifying broad functions. For instance, the dorsal stream prioritizes egocentric coding to a greater extent than does the ventral stream. However, as we noted in the third section of our paper, there is physiological evidence for allocentric coding in the dorsal stream, so we would caution against assuming that an absolute distinction between perception and action can be replaced by an absolute distinction between spatial coding strategies. While we agree with Dixon’s general point, we doubt whether any computational dichotomy could be sufficiently consistent and important to justify the bifurcation of cortical vision. In our estimation, the *perception–action* model already captures the broad distinction between dorsal and ventral streams, in both functional and computational terms. But the level of description at which the model aims is a very high one, and its boundaries break down at a finer grain of analysis, partly because of the depth and extent of interstream interaction.

VENTRAL STREAM INFLUENCES ON ACTION

Goodale and Milner admit that no simple criterion predicts which aspects of visuomotor behavior require ventral stream involvement, but they do not share our worry that pure dorsal action is an endangered species. They point to DF’s visuomotor repertoire as evidence for the wide range of actions mediated by the dorsal stream. We agree that DF’s actions show that much can be accomplished without a fully functioning ventral stream, but this does not mean that the ventral stream does not contribute to such actions in the healthy brain. In the second section of our paper, we cited evidence for ventral stream involvement in even such basic actions as reaching. Goodale and Milner accept this evidence but dispute its meaning, arguing that the ventral stream may exert a high-level influence, but is not involved in action programming itself. To be clear, we have not argued that the ventral stream is directly responsible for programming actions, simply that action programming is routinely informed by ventral stream vision. On this key point, Goodale and Milner seek to preserve the integrity of the perception–action model by arguing that ventral stream influences reflect only a "modulation" of action programming. We cannot rule out a possible distinction between visual information informing action programming, and visual information modulating those programs. However, to be able to apply the distinction we would require a clear criterion by which direct and modulatory influences could be disentangled. At present, we prefer the more parsimonious interpretation that ventral stream visual processing, like dorsal stream visual processing, informs action programming.

An intriguing further qualification is suggested by Van Elk et al., who argue that semantic processing for action may not be limited to the ventral stream. They describe two studies that suggest a role for the dorsal stream in semantically appropriate action planning, though the precise nature of this role is as yet unclear.

ILLUSIONS-IN-ACTION

In the fourth section of our review, we argued that the perception–action model does not reliably predict when actions will resist visual illusions and when they will not. Moreover, the model's predictions are predicated on problematic assumptions, including the idea that contextual illusions affect ventral stream representations only. Our analysis receives support from Dassonville, and Smeets and Brenner. Dassonville points out that dissociations between perception and action do not necessitate distinct visual representations. He cites three illusions that induce subjective shifts of the reference system within which both target and effector positions are coded. In these cases, the illusory shift in target position is matched by the illusory shift in effector position, so that the movement vector remains veridical and the motor output is unaffected. Smeets and Brenner argue that such sharing of sensory influences for target and effector localization is one key strategy by which the action system can achieve robust performance even when working with nonveridical information. They thus deny the assumption, inherent to the perception–action model, that the action system is shielded from nonveridical cues. Instead, it has sophisticated strategies of weighting cues according to their reliability, and combining them in ways that often, though not always, yield accurate performance. In the face of these and other criticisms, Goodale and Milner cite a study that reported a dissociation between perceptual matching and grip scaling for a Ponzo size-illusion (Ganel et al., 2008). It is not clear how this result addresses our concerns. We have not disputed that such dissociations exist, but we maintain that the perception–action model does not provide a satisfactory account of them.

Goodale and Milner also dismiss the relevance of the fact that V1-activity is affected by a Ponzo size-illusion (Murray et al., 2006). They argue that such a modulation "has to arise from top-down feedback from ventral stream areas," and that this will often arrive too late to bias the dorsal stream programming of action. In support of this, they cite a recent finding that short-latency saccades (<250 ms) were less affected by a motion-illusion than long-latency saccades (de'Sperati & Baud-Bovy, 2008). This seems to concede our claim that the most relevant constraints governing which visual cues inform action programming are imposed by the latencies with which they become available. The top-down modulation of early visual representations may be one important general mechanism by which information is shared between dorsal and ventral streams. But it is hard to imagine that such effects would be so sluggish that they would not influence grasping responses initiated more than 1500 ms after stimulus presentation (e.g., the above-cited study by Ganel et al., 2008).

VISUAL AWARENESS

One of the main claims of the perception–action model is that only ventral stream representations can reach visual awareness, and our review sought to question this. We proposed that cases of action blindsight do not provide strong or specific evidence that dorsal stream processing is always unconscious. Comparable abilities may be found in the perceptual domain, without the corresponding inference that perceptual processing is always unconscious. Goodale and Milner responded by citing another example of action—blindsight (Striemer, Chapman, & Goodale, 2009). While undeniably impressive, this case does not affect our original argument. We suggest that it is more critical to evaluate possible instances where extraventral activity does influence visual awareness. We offered the example of area MT, which we hoped was uncontroversial. It is widely held that this extraventral area houses specific neural correlates of motion perception. Goodale and Milner do not share this view, because some studies have found MT activity to be more tightly related to physical than to perceptual aspects of the stimulus (Itoh, Fujii, Kwee, & Nakada, 2005; Moutoussis & Zeki, 2008). Notably, however, Moutoussis and Zeki proposed that the motion percept may be identified with specific subclusters of MT neurons, rather than with higher ventral activity as Goodale and Milner suggest. Given the intense research interest in the neural correlates of awareness, a more definitive answer may not be far away.

We also offered three examples of dorsal stream influences on perception from the responses of patient DF, two of which were addressed in Goodale and Milner's commentary. Goodale and Milner suggest that DF's ability to report egocentric distance (Schenk, 2006) relies on motor imagery, while her improved size-discrimination during grasping (Schenk & Milner, 2006) reflects a dorsal-to-ventral influence on perception rather than any direct awareness of dorsal stream content. The latter interpretation depends on the very assumption at stake: that only the ventral stream can support awareness of visual content. At the very least, however, it concedes that dorsal stream processing may inform perceptual experience. It is interesting therefore to consider what the perceptual correlates of dorsal stream activity might be. Jackson's commentary emphasizes that this stream is not just visual, but generally concerned with multimodal coding for action, so perhaps its associated phenomenology should have a more multimodal egocentric character.

BEYOND PERCEPTION AND ACTION

Dyson et al. argue that weakly held dual-pathway models have guiding value in several sensory modalities. However, in vision, and doubtless in other modalities, the low-level interplay between perception and sensorimotor control is too complex and fluent to be represented adequately by any dichotomy. The perception–action model is a useful high-level description of primate vision, and we do not seek to suggest an alternative. It is now more apt to explore in detail how the many visual areas cooperate to control behavior.

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