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An evolving view of duplex vision: separate but interacting cortical pathways for perception and action

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In 1992, Goodale and Milner proposed a division of labour in the visual pathways of the primate cerebral cortex between a dorsal stream specialised for the visual control of action and a ventral stream dedicated to the perception of the visual world. In the years since this original proposal, support for the perception–action hypothesis has come from neuroimaging experiments, human neuropsychology, monkey neurophysiology, and human psychophysical experiments. Indeed, some of the strongest support for this hypothesis has come from behavioural experiments showing that visually guided actions are largely refractory to perceptual illusions. Although controversial, the findings from this literature both support the original hypothesis and suggest important modifications. The ongoing challenge for neurobiologists is to map these behavioural findings onto their corresponding neural substrates.

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Abbreviations
AIP   anterior intraparietal sulcus
area LO   lateral occipital area
fMRI   functional magnetic resonance imaging
LOC   lateral occipital complex
MRI   magnetic resonance imaging
RF   rod-and-frame
ST   simultaneous tilt
**TMS**   transcranial magnetic stimulation

Introduction

Visual systems first evolved not to enable animals to perceive the world but to provide distal sensory control of their movements. Vision as 'sight' is a relative new-comer on the evolutionary landscape, but its emergence has enabled animals to carry out complex cognitive operations on mental representations of the world — operations that greatly increase the potential for flexible, adaptive behaviour. According to a proposal put forward by Goodale and Milner in 1992 [1], the operating charac-teristics of the more recently evolved 'vision-for-perception' system are quite different from those of the more ancient 'vision-for-action' system. Indeed, according to Goodale and Milner [1,2,3•], it is this duplex nature of vision that drove the emergence of distinct visual pathways in the primate cerebral cortex (Figure 1). They argued that the dorsal 'action' stream, which projects from early visual areas to the posterior parietal cortex, provides flexible control of more ancient subcortical visuomotor modules for the control of motor acts. The ventral 'perceptual' stream, which projects from early visual areas to the temporal lobe, provides the rich and detailed representa-tion of the world required for cognitive operations, such as recognition and identification. The division of labour between the two streams posited by Goodale and Milner has not only helped to organise a broad range of data from monkey neurophysiology to human neuropsychology but it has also stimulated a great deal of research on predicted differences between vision-for-action and vision-for-perception. In this review, we highlight some of this research, particularly studies carried out over the past two years, and show that the perception–action distinc-tion has stood the test of time remarkably well.

Neuropsychology meets functional magnetic resonance imaging

Patients with lesions in the dorsal stream, in the superior regions of the posterior parietal cortex, can have problems using vision to direct a grasp or aiming movement towards objects (optic ataxia) even though many of these patients can describe the orientation or relative position of those objects quite accurately [4]. The opposite pattern of deficits and spared visual abilities has been reported in patients with visual form agnosia, in which the brain damage is assumed to be in the ventral stream [5,6•]. The most compelling example of such a case is patient DF, a young woman who suffered irreversible brain damage in 1988 as a result of anoxia from carbon mon-oxide poisoning [5]. Even though DF is unable to indicate the size, shape, and orientation of an object, either verbally or manually, she shows normal anticipatory open-ing of her hand and rotation of her wrist when reaching out to grasp that object [5,7]. A recent high-resolution structural magnetic resonance imaging (MRI) study [8••] revealed that the lateral occipital complex (LOC), a structure in the ventral stream that has been implicated in object recognition [9,10•], is severely damaged in DF (Figure 2). The damage is largely localised to the lateral occipital area (area LO) [11], in the more lateral aspect of LOC. In addition, functional MRI revealed that none of the LOC, even the regions in the fusiform gyrus outside

Figure 1
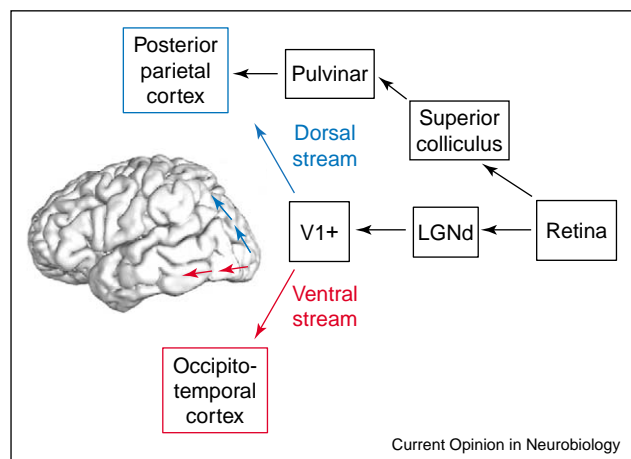
Schematic representation of the two streams of visual processing in human cerebral cortex. The retina sends projections to the dorsal part of the lateral geniculate nucleus in the thalamus (LGNd), which projects in turn to primary visual cortex (V1). Within the cerebral cortex, the ventral stream (red) arises from early visual areas (V1+) and projects to regions in the occipito-temporal cortex. The dorsal stream (blue) also arises from early visual areas but projects instead to the posterior parietal cortex. The posterior parietal cortex also receives visual input from the superior colliculus through the pulvinar. On the left, the approximate locations of the pathways are shown on a 3-D reconstruction of the pial surface of the brain made from an anatomical MRI. The routes indicated by the arrows involve a series of complex interconnections.

the lesion in area LO, was activated when DF was presented with line drawings of common objects, even though healthy participants showed robust activation in the same area (Figure 3). The lack of activation with line drawings mirrors DF's poor performance in identifying the objects in the drawings. With coloured and grey-scale images, stimuli that she identifies more accurately than line drawings, DF did show some ventral-stream activation, particularly in the fusiform gyrus although the activation was more widely distributed than that seen in controls, and did not include area LO (Figure 3).

In DF's dorsal stream, the structural MRI revealed shrinkage of cortical tissue within the intraparietal sulcus (IPS), a region that has been implicated in visuomotor control [12,13,14•,15,16]. Nevertheless, as can be seen in Figure 3, when DF grasped objects that varied in size and orientation, she displayed relatively normal activation in the anterior intraparietal sulcus (AIP), an area that plays a crucial role in the visual control of grasping in both humans [17–20] and monkeys [21–23]. Taken together, these findings provide additional support for the idea that perception and action are mediated by separate visual pathways in the cerebral cortex, and confirm the respective roles of the ventral and dorsal visual streams in these functions.

Figure 2
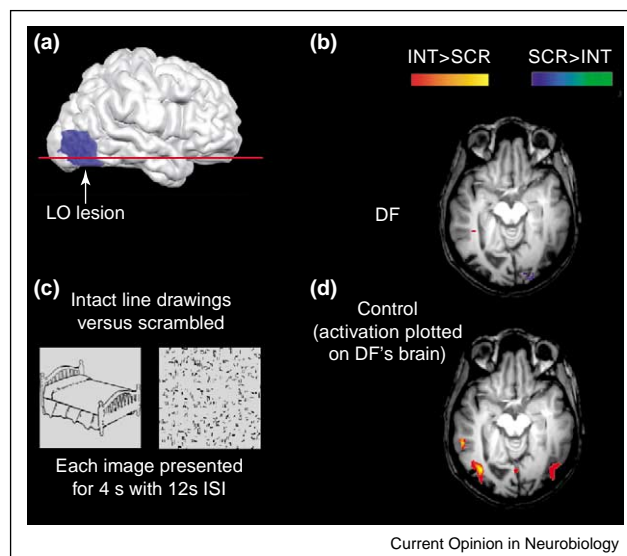
An event-related fMRI study of object recognition in DF [8••]. **(a)** The lesions in DF's brain were reconstructed from high-resolution MRI slices and were then rendered on the pial surface. **(b)** The lesions in the lateral occipital area (LO) were present on both sides of DF's brain and can be seen on the slice depicted here (reference line for slice is shown in red on the 3-D reconstruction in [a]). **(c)** When DF was presented with line drawings and scrambled versions in an fMRI experiment, she showed no differential fMRI activation to the line drawings. The absence of activation is evident in the slice shown in (b). **(d)** In contrast, a control subject showed robust differential activation to the same line drawings. The activation in the brain of the control subject has been stereotactically morphed to fit onto DF's brain. Note that the activation to the line drawings in the control subject falls neatly into the corresponding LO lesions on both sides of DF's brain. Abbreviations: INT, intact drawings; ISI, interstimulus interval; SCR, scrambled drawings.

Different visual processing for perception and action

According to the Goodale and Milner model, the dorsal and ventral streams both process information about the structure of objects and about their spatial locations, but they transform this information into quite different outputs [1,2,3•,12,24•,25•]. Because the visuomotor systems of the dorsal stream are responsible for the control of highly skilled actions, it is imperative that these systems compute the absolute metrics of target objects in a frame of reference centred on specific effectors (i.e. egocentric coding) [14•,26•]. Visual perception has no such requirement for absolute metrics, or egocentric coding. Indeed, object recognition depends on the ability to see beyond the absolute metrics of a particular visual scene; for example, one must be able to recognise an object independent of its size and its momentary orientation and position [3•,12]. Many recent psychophysical findings support the general notion that perception and action are mediated by independent visual systems that carry out quite different computations on the information present on the retina.

Figure 3
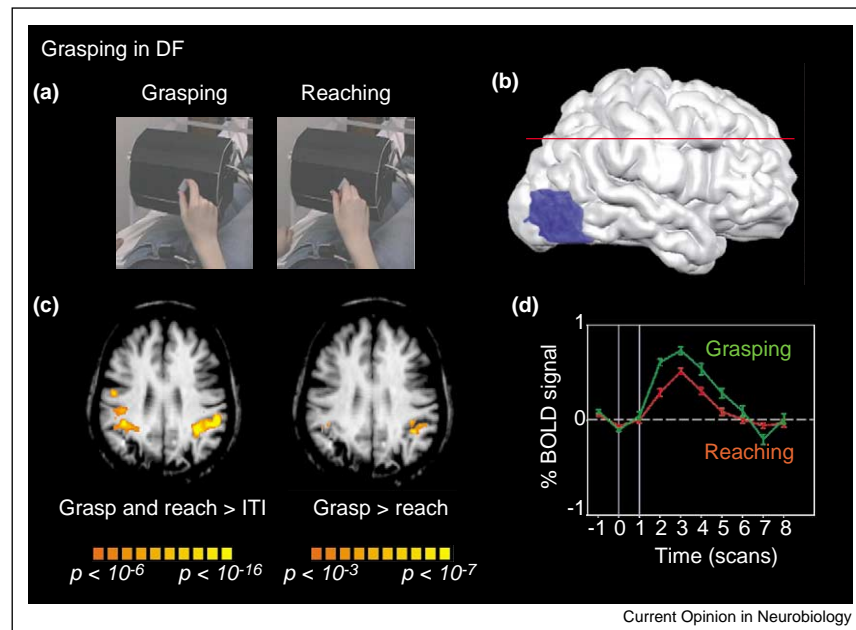
An event-related fMRI study of grasping in DF [8••]. (a) While lying in the darkened scanner, DF was presented with rear-illuminated target objects that she could view directly (i.e. no mirror was used). The orientation and size of the objects varied from trial to trial. Her task was either to reach out and grasp the target shape or, in a control condition, to simply reach out and touch it with her knuckles. (b) The reference line for the slices is shown in red on this pial-surface reconstruction of DF's brain. (c) A slice taken through DF's parietal lobe reveals selective activation in the anterior lateral intraparietal sulcus (area AIP) when she grasps the target object. The activation is similar to that seen in control subjects. (d) The graph shows the time course of AIP activation for grasping and reaching. Abbreviations: ITI, inter-trial interval.

Early evidence that visuomotor control depends on processing distinct from that underlying conscious perception came from a study by Goodale *et al*. [27], in which participants reached to visual targets that changed position during a concurrent saccadic eye movement (i.e. a double-step reaching task). Although participants demonstrated no conscious awareness that the target had changed location, the endpoints of the reaching movements reflected the new rather than original target position [28]. Interestingly, awareness of the target perturbation does not influence the kinematics of manual adjustments [29]. This is consistent with the proposal of Pisella *et al*. [30] that fast corrections to reaching movements are under the guidance of an 'automatic pilot' in the posterior parietal cortex [31–33] that operates on a different time scale than the visual mechanisms underlying conscious perception and volitional motor control. Fast, automatic manual adjustments can be elicited by changes in the target's location but not changes in its colour, which suggests that the visuomotor networks of the dorsal stream do not process colour, but rather receive this input indirectly through the perceptual mechanisms in the ventral stream [34•]. Using a variety of tasks and responses, other investigators [35,36,37••,38–40] have shown important differences between the perception of visual stimuli and the control of actions towards those stimuli, underscoring the view that perception and action engage quite different

visual mechanisms. (At the same time, there is evidence that the machinery our brain uses to understand actions in others is also used to generate those actions in ourselves [41•]. But even in this case, object-based perceptual machinery has to be initially engaged to parse the scene in which the action is embedded.)

Visual illusions: demonstrating a dissociation between perception and action

A particularly intriguing but controversial line of evidence in support of the perception–action hypothesis comes from studies that investigate the influence of perceptual illusions on the control of object-directed actions such as saccades, reaching movements, and manual prehension [42]. Over twenty years ago, it was shown that saccadic endpoints are insensitive to a dot-in-frame illusion in which the perception of a target's location is shifted opposite to the displacement of a large visual frame [43,44]. This suggests that location is processed differently by the visuomotor and perceptual systems. In a widely cited study, Aglioti *et al*. [45] demonstrated that the maximal opening of a grasping hand is insensitive to the robust perceptual illusion that a target disk surrounded by smaller circles is larger than the same disk surrounded by larger circles — despite the fact that grip opening is exquisitely sensitive to real changes in the size of the target disk. Peak grasping aperture is refractory

to a size-contrast illusion even when the hand and target are occluded during the action [46], which indicates that on-line visual feedback during grasping is not required to 'correct' an initial perceptual bias induced by the illusion. These seminal findings implicate different object-processing mechanisms for the perceptual and visuomotor systems, consistent with the perception–action model [1,2,3•,12]. It is important to note, of course, that the model does not depend on these illusion findings, because it was originally derived from extensive neuro-psychological and neurophysiological evidence.

Indeed, several recent findings have challenged the notion that perceptual illusions do not impact the control of object-directed actions. These challenges fall into several categories including, non-replication [47], the contention that early studies did not adequately match action and perception tasks for various input, attention and output demands [48–50], or the idea that action tasks involve multiple stages of processing from purely perceptual to more 'automatic' visuomotor control [51,52]. Most of these challenges can readily be accommodated within the basic framework of the perception–action hypothesis, yet each provides important new insight into the nature of the processing mechanisms underlying perception versus action.

Franz and co-workers [47] have failed to replicate the early results of Aglioti *et al*. [45] and have argued that visually guided actions and perceptual judgements access the same visual processing mechanisms. Such an account, however, cannot explain why the majority of illusion studies find evidence for a dissociation between perception and action [42]. In addition, it cannot explain the dissociations observed in patients with optic ataxia or visual form agnosia — nor for that matter, the extensive neurophysiological and behavioural work on the ventral and dorsal streams in the macaque monkey that support a distinction between vision-for-perception and vision-for-action [1,2,3•,12].

Smeets and co-workers [49,53] have argued that the control of grasping is formed on the basis of the computed locations of points on the object's surface, whereas judgements of object size are formed on the basis of a computation of extent. According to this view, dissociations between judgement and action occur because pictorial size illusions affect the perception of extent but not location (e.g. [54]). Although reasonable, this argument is difficult to separate from Goodale and Milner's original proposal [1,2,3•,12] that the visuomotor system computes absolute (i.e. Euclidean) object metrics, whereas the perceptual system utilizes scene-based (i.e. non-Euclidean) metrics.

Glover and co-workers [51,52] have reported that visual illusions have a larger effect on the early rather than late stages of action, which suggests that on-line movement control is refractory to perception, whereas movement planning is not. Recent attempts to replicate these findings using conventional tasks and data analyses have failed [55], and neuropsychological evidence does not support the contention that the early and late stages of actions access different visual processing systems [56•]. Nevertheless, as we will argue later, there is good reason to believe that perceptual mechanisms are important for the guidance of action in clearly circumscribed situations; Glover's notion of 'action-planning' can be easily subsumed under this framework.

Visual illusions: refining the perception–action hypothesis

Two recent lines of evidence have helped to clarify the relation between object perception and object-directed action in the context of visual illusions. Dyde and Milner [57•,58] have shown that the orientation of the grasping hand is sensitive to a simultaneous tilt (ST) illusion — similar to that used by Glover and co-workers [51] — but not a rod-and-frame (RF) illusion, even though the two visual displays have equivalent effects on judgements of target orientation. Dyde and Milner [57•,58] argue that the sensitivity of action to a perceptual illusion can be understood in terms of the illusion's presumed neural origins. Illusions that presumably arise from 'early' (i.e. area V1, area V2) stages of visual processing, such as the ST illusion, should affect both action and perception as the dorsal and ventral visual pathways share this input. Illusions like the RF that presumably arise from later stages of processing (i.e. in inferotemporal cortex) should not affect action, as the dorsal stream does not have direct access to this processing. Similar accounts have been put forward to explain the fact that there are reliable directional anisotropies in the perception of the direction of motion even though such anisotropies are not present in smooth pursuit eye movements [37••], and the observation that fast reaching movements are sensitive to target mislocalisation errors induced by distant visual motion signals [40].

Several recent studies have highlighted the importance of timing in dissociations between perception and action [59]. Thus, in normal observers, perceptual illusions influence the control of action when the programming of those actions was formed on the basis of a memory of the target stimuli [44,60–65]. These findings suggest that the control of action after a delay depends upon a memory trace of the target object that was originally delivered by the perceptual mechanisms in the ventral stream. Recently, Westwood and Goodale [66•] found that a size-contrast illusion influenced the peak opening of the grasp when vision of the target was occluded at the same time the response was cued, even though the illusion had no effect on grip aperture in trials in which target vision was occluded at the moment of movement

Figure 4
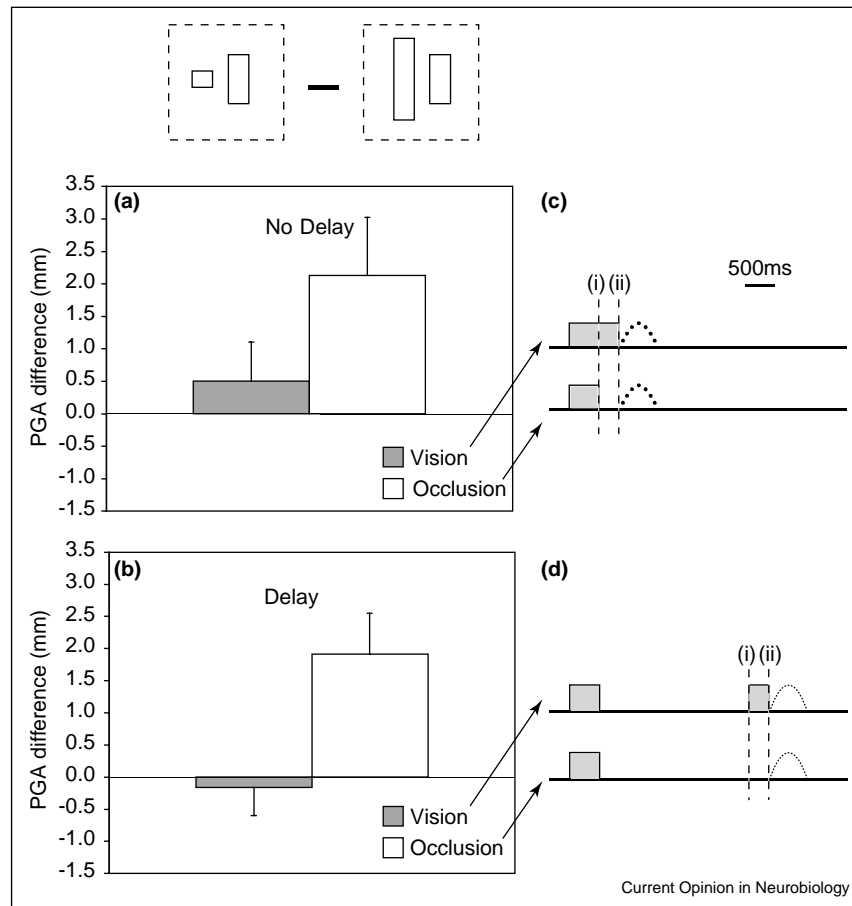
The effects of a size-contrast illusion on visually guided and memory-guided grasping [66•]. Results from Westwood and Goodale [66•]. Illustrated are the difference scores for peak grip aperture for targets presented with smaller minus larger flankers (error bars are SEM). **(a)** No delay group, in which grasping responses were cued immediately after the initial 500 ms target viewing phase. **(b)** Delay group, in which grasping responses were cued 2500 ms after the initial 500 ms target viewing phase. **(c,d)** In the event sequences grey bars represent availability of target and limb vision, (i) denotes auditory response cueing, (ii) denotes onset of hand movement, dashed curves represent movement unfolding. Vision and occlusion trials were randomly intermixed for both groups. For both the no-delay and the delay groups, significant illusion effects were seen in occlusion but not vision trials, indicating that target and limb vision between response cueing and movement onset are crucial for the resistance of grasping to size-contrast illusions. Abbreviations: PGA, peak grip aperture.

initiation (Figure 4). This finding strongly suggests that the visuomotor networks in the dorsal stream operate in 'real time': these networks appear not to be engaged unless the target object is visible at the exact moment the response is required. In other situations (e.g. memory-driven actions or advance movement preparation), the control of action passes to other systems that access a representation of the target object laid down by the perceptual mechanisms of the ventral stream.

Neuropsychological evidence from visual form agnosia [67] and optic ataxia [68,69,70•,71•] provides important converging support for the contention that there are two distinct modes of control for object-directed action: a real-time mode of control that depends on the visuomotor networks in the dorsal stream, and an off-line mode of control that depends, at least in part, on the perceptual mechanisms in the ventral stream. Presumably, such interactions between the ventral and dorsal streams are also responsible for the results of several neurophysiological experiments that have found parietal neurons that are sensitive to stimulus features such as colour [34•], shape [72], duration [73], or motion [74] when these are arbitrarily mapped to object-directed actions.

Conclusions
In summary, there is a wealth of psychophysical evidence that is consistent with the general view that in specific situations, particularly where rapid responses to visible targets are required, visuomotor control engages processing mechanisms that are quite different from those that underlie our conscious visual experience of the world.

The ongoing challenge for neurobiologists is to map these behavioural findings onto the brain and reconcile them with what we already know about the dorsal and ventral streams from primate neurophysiology and human neuropsychology. Preliminary efforts have been made in this regard in primate neurophysiology [75] and human transcranial magnetic stimulation (TMS) [76•], but much more work remains to be done. In particular, we anticipate that important advances in understanding the interactions between the dorsal and the ventral streams will be made using TMS to disrupt neural processing at precise points in a temporal sequence [77]. For example, recent findings from TMS studies point to the importance of recurrent projections from extrastriate to striate cortex in conscious perceptual experience [78••,79]. The role of such recurrent projections in the visuomotor networks of the dorsal pathway is much less clear, and might represent a fundamental difference between perception and action systems.

Update

Two recent papers provide additional evidence to the debate about the differential effects of visual illusions on perception and action. Stone and Krauzlis [80••] showed that, on a trial-by-trial basis, there was a close correspondence between the perceived direction of motion and the control of pursuit eye movements. This result supports the idea that the differences between perception and action in motion processing that have been previously demonstrated [37••] could arise after common processing in early motion areas. A second paper by McCarley *et al.* [81•] found that voluntary but not reflexive saccades were sensitive to the Müller-Lyer illusion, supporting the idea that perceptually driven responses are more likely to be affected by scene-based relational cues than are more automatic reflexive responses [66•]. Finally, the search for the neural substrates of perception–action differences continues. In a recent paper, Schwartz and co-workers [82•] provide evidence from single-unit work in the monkey that activity in primary motor cortex reflects the actual trajectory of a monkey's hand movement, whereas activity in the ventral premotor cortex codes the perceived trajectory of that movement.

Acknowledgements

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coordinates for different kinds of motor acts. They argue convincingly for a common eye-centred reference frame that is modulated by eye-, head-, body- or limb-position signals. Such a reference frame would facilitate communication between different areas that are involved in coordinating the movements of different effectors and might also permit sensory targets in different modalities to share the same spatial coordinates.

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pointing kinematics, but only TMS over dorsal regions disrupted the effect
of real object size on the movement. These findings suggest that the
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sought evidence for a common representation of visual motion that is
accessed for motion perception and control of eye movements. Results
indicated a high correspondence between judgements and motor
responses even when performance was near chance levels, strongly
implicating a shared motion input for perception and action. These

findings are consistent with other work by Churchland *et al*. [37••] cited
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segregation between vision-for-action and vision-for-perception occurs
downstream of motion processing regions.

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at the vertex of the illusion cued the response) and voluntary (i.e. a
saccade to the vertex of the illusion was cued by a verbal instruction)
conditions. Illusory biases were observed only in the voluntary condition,
suggesting that the generation of voluntary (i.e. endogenous control) but
not reflexive (i.e. exogenous control) responses accesses a perceptual
representation of the intended target. These results are consistent with
our real-time model of sensorimotor function. This model suggests that
advance movement preparation (i.e. endogenous control) accesses a
perceptual representation of the environment, whereas real-time move-
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Using a virtual manual-tracking task in which the mapping between actual
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trajectory of the limb in both humans and monkeys. Humans reported no
awareness of the illusion, suggesting that the visual feedback of their
virtual limb dominated conscious perception of action. Using the same
task, single-unit recordings in monkey ventral premotor cortex (PMv) and
primary motor cortex (M1) were used to explore neural representations of
the hand's trajectory. Activity in M1 reflected more closely the actual
trajectory, whereas activity in PMv was more closely linked to the
perceived trajectory. The authors suggested that a sub-population of
neurons in PMv play a leading role in 'vision-for-perception', at least in the
context of perceiving and monitoring one's own actions. Although it is not
yet clear how these findings relate to the perception–action model (which
focuses on the visual processing of objects rather than actions), this study
is noteworthy for attempting to identify the neurobiological basis for
differences between conscious perception and control of action.