Two visual systems re-viewed

A.D. Milner [a,*], M.A. Goodale [b]

[a] *Cognitive Neuroscience Research Unit, Wolfson Research Institute, Durham University, Queen's Campus, University Boulevard, Stockton on Tees TS17 6BH, UK*
[b] *CIHR Group on Action and Perception, University of Western Ontario, Canada*

Abstract

The model proposed by the authors of two cortical systems providing 'vision for action' and 'vision for perception', respectively, owed much to the inspiration of Larry Weiskrantz. In the present article some essential concepts inherent in the model are summarized, and certain clarifications and refinements are offered. Some illustrations are given of recent experiments by ourselves and others that have prompted us to sharpen these concepts. Our explicit hope in writing our book in 1995 was to provide a theoretical framework that would stimulate research in the field. Conversely, well-designed empirical contributions conceived within the framework of the model are the only way for us to progress along the route towards a fully fleshed-out specification of its workings.
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1. Introduction

In 1992, we proposed a model of cortical visual processing that made a distinction between vision for perception and vision for action (Goodale & Milner, 1992, 2004; Milner & Goodale, 1993, 1995, 2006). This model was in some ways the culmination of 20 years of scientific collaboration between the two of us. In fact, in 1973 – just a year before Larry Weiskrantz coined the word 'blindsight' – we were lucky enough to be awarded our first research grant by the then Science Research Council (UK). As a condition for receiving the money, we were required to make the journey from St. Andrews to Oxford to talk to Larry, to get both his blessing and his advice about how best to proceed. Needless to say, Larry was gracious in his support and encouragement of the young scientists that we then were—and helped to put us on the right track. It was therefore entirely appropriate, and very pleasing for us, that Larry agreed to write the Foreword to our monograph "The Visual Brain in Action" in 1995.

Our aim in writing that book was to propose a new way of looking at the functional organization of the two broad cortical pathways of visual processing, the ventral and dorsal streams, each of which arise from the same early visual areas (Baizer, Ungerleider, & Desimone, 1991; Morel & Bullier, 1990; Ungerleider & Mishkin, 1982; Young, 1992). The essence of our proposal was that the differences in function between the two streams could be best understood not so much in terms of their visual inputs, but more in terms of the output systems the two streams serve. Both streams process information about the structure of objects and about their spatial locations, and both are subject to the modulatory influences of attention. But the two streams, we argued, process and transmit visual information in quite different ways. The ventral stream transforms visual inputs into perceptual representations that embody the enduring characteristics of objects and their spatial relations. These representations enable us to parse the scene, and to think about objects and events in the visual world. In contrast, the dorsal stream's job is to mediate the visual control of skilled actions, such as reaching and grasping, directed at objects in the world. To do this, the dorsal stream needs to register visual information about the goal object on a moment-to-moment basis, transforming this information into the appropriate coordinates for the effector being used.

The model has developed and steadily crystallized over the 15 years since it was first formulated. At the same time, the formulation has been challenged by a number of authors. In certain instances, these challenges seem to have been predicated

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* Corresponding author. Tel.: +44 191 334 3272; fax: +44 191 334 3241.
E-mail address: a.d.milner@durham.ac.uk (A.D. Milner).

on an imprecise reading of some of the more subtle details of the model. Indeed some comments appear to reflect a misinterpretation of the fundamental distinction we were trying to make between what we called 'vision for perception' and 'vision for action'. Our intention in this paper is to clarify our use of these and other terms, and also to give a fuller account of the processing characteristics for these two kinds of vision. Our concern, in other words, is with clarification and disambiguation. In making our points we will nonetheless touch upon some recent studies by ourselves and others that bear directly on the theoretical and metatheoretical issues raised.

2. Theory and terminology

"Organisms, at one level, are obviously collections of parallel systems that are potentially independent, although normally interactive." (Weiskrantz, 1990, p. 99)

When we first set out our account of the division of labour between the ventral and dorsal visual pathways in the cerebral cortex, our distinction between vision for perception and vision for action was intended to capture the idea that visual information is transformed in different ways for different *purposes*. We fully recognized, however, that the words 'perception' and 'action' are not scientific terms, and can mean different things to different people. Indeed these words have been used by psychologists and philosophers for centuries to convey a range of different ideas and concepts, not all of which are co-extensive with our particular usage. Such differences in usage continue to exist, and have sometimes led to a misunderstanding of exactly what we had in mind when developing our proposal. For this reason we made an effort to spell out as clearly as we could what we meant by vision for perception and vision for action, although we generally did this ostensively, rather than by providing formal definitions. In clarifying here what we were trying to say, we do not wish to imply that our usage is better, just that it is different from that adopted by some other writers.

So, what do we mean by 'perception'? Here we feel that we are close to most experimental psychologists working in the mainstream tradition, as exemplified in the textbooks by Gregory (1997) and Bruce, Green, and Georgeson (2003). What we are primarily referring to is the conscious experience of seeing—that is, the visual experience we have about the current stimulus array. Such a perceptual experience, in most cases, can be translated into a subjective report—at least in principle. This usage of the term 'perception' is standard in the field of psychophysics, where reporting what one sees in visual detection and discrimination tasks forms the usual dependent measure. At the same time, however, we concede that the concept needs to be extended to include 'unconscious' or 'preconscious' perception of objects and events, which refers to mental representations that potentially *could* reach conscious awareness, e.g. with slightly different stimulus parameters (cf. Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). This kind of unconscious perception would be exemplified by cases of masking or inattention (normal or neurological), insofar as the unreportable stimuli can be shown to influence later cognitive operations.

Unconscious perceptual information can have measurable priming effects on subsequent cognitive tasks both in healthy subjects (e.g. Dehaene et al., 1998; Merikle & Joordens, 1997) and in patients with spatial neglect where the information has been presented to the unattended side of the visual field (Berti & Rizzolatti, 1992; Schweinberger & Stief, 2001). Our point here is that this notion of unconscious perception is a natural extension of the normal sense of the word 'perception', even though the word 'perception' gains its everyday meaning from conscious perception. Most psychologists would accept the notion that perceptual processing does not always achieve consciousness, despite the fact that at some level the mental representations of conscious and unconscious percepts, and presumably their neural correlates, are qualitatively similar. There is much theoretical speculation about what distinguishes conscious from unconscious percepts, but for our purposes both can be seen as gaining their content from common mechanisms in the ventral stream.

Where we depart from the traditional view of perception is in terms of what happens next. Most people (including most scientists and philosophers) have made the commonsense assumption that the mental representations that underlie perception provide not only the foundations for visual cognition, but also *ipso facto* the visual metrics required for action (an issue eloquently addressed by Clark, 2001). Our model differs from this traditional view in a crucial way. We agree that perception represents our visual experience of the world, but not that it provides the direct foundation for action. This is not to say, of course, that perception cannot influence action. Indeed, perception would never have evolved unless it had some adaptive value. Our point is that the link between perception and action is an indirect and flexible one in which cognitive operations such as memory and planning play a crucial role.

So what do we mean by 'action' and what are the roles of the two streams in the guidance of action? The key contribution of the perceptual mechanisms in the ventral stream is the identification of possible and actual goal objects—and the selection of an appropriate course of action to deal with those objects. But the subsequent *implementation* of that action is the job of the dorsal stream. This stream plays no role in selecting appropriate actions, but is critical for the detailed specification and online control of the constituent movements that form the action, making use of metrical visual information that maps directly onto the action in the 'here and now'. In other words, both streams contribute to action, but in quite different ways.

The role of the ventral stream in action, then, is to provide visual information to enable the identification of a goal object such as a coffee cup, and to enable other cognitive systems to plan the action of picking up that cup. This would include the selection of the class of hand postures appropriate to the particular task at hand (whether that be taking a sip of coffee, for example, or putting the cup in the sink). But action planning of this sort is quite abstract, and the final movements that constitute the action could take many different forms. It is the dorsal stream's job to use the current visual information about the size, shape, and disposition of the object in egocentric coordinates (in the case of the coffee cup, with respect to the hand) to program and control

the skilled movements needed to carry out the action. This then is the specialized meaning we give to "vision for action": not the use of visual information for abstract planning, but rather its use in the detailed programming and real-time control at the level of elementary movements. To achieve this, the dorsal stream does not use the high-level perceptual representations of the object constructed by the ventral stream, but instead relies on current bottom-up information from the retina to specify the required movement parameters such as the trajectory of the reach and the required grip aperture needed to grasp the target object.

Some writers, such as Glover (2004), have convolved action planning with the detailed programming of the constituent movements of an action. As he puts it, "planning is responsible for: selecting the target; for all movement parameters relating to non-spatial target characteristics; for the initial determination of the movement parameters relating to spatial target characteristics. . .; for determining the timing of movements. . .; and for the selection of macroscopic (i.e. postural) aspects of the movement." (Glover, 2004, p. 4). Thus, in terms of our model, Glover has obscured an important distinction. He goes on to argue, along with Rossetti, Pisella, and Vighetto (2003), that the role of the dorsal stream is restricted to the on-line control of movement execution and is not involved in the initial specification of the movement parameters.

There is undeniably good evidence for a dorsal-stream role in on-line control during the course of an action. In particular, this aspect of reaching may be selectively disrupted by transcranial magnetic stimulation administered over the posterior parietal cortex (Desmurget et al., 1999), and is severely impaired in patients with bilateral optic ataxia caused by damage to the dorsal stream (Gréa et al., 2002; Pisella et al., 2000). But separate research has also shown that these very same patients with optic ataxia head off in the wrong direction right from the start of their reaching movements (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003). In addition, when reaching out to grasp objects of different sizes, these patients show deficits in calibrating their grip aperture (Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, Decety, & Michel, 1994), a parameter that is largely determined before movement onset (Jakobson & Goodale, 1991; Jeannerod, 1984; Jeannerod & Biguer, 1982). Complementary evidence comes from the patient D.F., who has bilateral lesions to object recognition areas in the ventral stream (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al., 1991). Despite the fact that D.F. cannot perceive (discriminate or report) the dimensions and orientation of objects, she has no difficulty in calibrating accurate grasping movements, presumably because her intact dorsal stream is engaged when she initiates her actions. In short, the weight of current evidence bears out our working assumption that the dorsal stream plays a central role in the programming of actions (i.e. the pre-specification of movement parameters), as well as in their on-line control.

But while the dorsal stream plays the leading role in motor programming, there is complementary evidence that supports a ventral-stream role in the *planning* of action. For example, van Doorn, van der Kamp, and Savelsbergh (2007) have recently shown that healthy subjects are vulnerable to the Müller-Lyer

illusion not only when making perceptual estimates of the length of a rod, but also when choosing the kind of grip (one-handed versus two-handed) necessary to pick the rod up end-to-end. Yet the same subjects showed no illusion in programming their actual grip size (in agreement with several previous studies—see Section 4 below). These data cannot be explained without making a sharp distinction between the visual processes that guide action selection and those that govern motor programming. van Doorn et al.'s data accord well, of course, with many earlier observations on patient D.F., whose ventral-stream shape-processing system is destroyed (James et al., 2003). For example, D.F. would often make errors in selecting the correct part of an everyday object to grasp, despite then grasping it with perfect skill (Carey, Harvey, & Milner, 1996). In short, the distinction between the planning and programming of actions is a crucial one to preserve. It is forced upon us by the empirical data.

The visual information used by the dorsal stream for programming and on-line control, according to the model, is not *perceptual* in nature. According to our definitions, therefore, it cannot be accessed consciously, even in principle. In other words, although we may be conscious of the *actions* we perform, the visual information used to program and control those actions can never be experienced (for recent empirical evidence, see McIntosh, McClements, Schindler, et al., 2004; Milner, in press; Schenk, Schindler, McIntosh, & Milner, 2005). Larry Weiskrantz once characterized dorsal-stream vision as, "in a sense, blindsight without blindness" (Weiskrantz, 1997, p. 138). We maintain that the nature of both dorsal-stream vision and blindsight stand in sharp contrast with visual processing in the ventral stream, *even when that processing fails to reach awareness*. The processing of vision for perception – conscious or unconscious – is, according to our model, restricted to the ventral stream.

3. Tasks versus processes

"There is no such creature in psychology as a pure task, nor will there ever be" (Weiskrantz, 1997, p. 42)

It is a perennial problem in psychology that no one task ever provides a pure measure of any given mental or neural process. The brain, and indeed our behaviour, are far too complex for that ever to be possible. There is accordingly no such thing as a pure 'visuomotor task' nor a pure 'perceptual task'. Even when we perform an apparently simple task like reaching or grasping, we cannot help but simultaneously perceive the goal object, and often also our hand reaching out towards it. Indeed as we have indicated above, in most normal circumstances, our actions will be visually co-determined by complementary processing in both dorsal and ventral streams. This of course is an important reason why the kind of dual processing model that we have advocated is difficult to test using healthy subjects and non-invasive experimental paradigms. At first sight, it might be expected that when one system is severely disabled, whether through damage or through temporary interference, then a given task might get closer towards that elusive task-process correspondence, by effectively removing a large subset of alternative processing pos-

sibilities. For example, we can argue that we are seeing a 'purer' form of visuomotor processing, less contaminated by perceptual influences, when our ventral-stream damaged patient D.F. performs a simple act of prehension.

But even here inferences have to be made with great caution. For example, when D.F. is given a "perceptual" task, do the correct responses she sometimes makes necessarily reflect *perception* in the sense we have defined it above? Clearly not. It is notable that her response latencies are invariably very long, and she will often confess that she is "guessing". When supplementary information such as colour or visual texture are absent in such "perceptual" testing, her most successful efforts are often attributable to non-perceptual ways of solving the problem she is faced with. For example, Murphy, Racicot, and Goodale (1996) showed that when D.F. was asked to pick up a square when faced with both an oblong and a square block, she performed above chance, even though in a verbal discrimination she did not. Close examination of video recordings of her grasp revealed that when she was incorrectly reaching towards the rectangle, she would sometimes correct herself midstream and grasp the square instead. It appeared that she was using sensory feedback (or perhaps efference copy) to help her make the correct decision. In other words, she was using information derived from *performing an action* to improve performance on a perceptual task. In this regard, it is interesting to note that D.F. always felt that she was guessing—and that her performance remained far from perfect. A later observation by Dijkerman and Milner (1997) demonstrated another strategy in D.F.: she was able to perform above chance in copying lines of different orientation in a simple drawing task, but only when she was allowed either to draw 'in the air' over the stimulus line first, or at least allowed the time to form a motor image of herself doing so. She was not able to form a *visual* image of the line, but could imagine herself drawing over it with the pencil. In other words, we see here a second example of D.F.'s ability to use *vision for action* in order to help her perform an ostensibly 'perceptual' task. Recent data suggest that D.F. can use internal cross-cueing in the size domain as well (Schenk & Milner, 2006). In this study D.F. did significantly better at guessing whether a shape was a square or a rectangle when performing a concurrent grasping (but not pointing) action towards the shape. A further control condition however showed that the visuomotor cueing benefited only *width* discrimination (that is, not shape discrimination *per se*). Thus the transmitted information was restricted to the dimension determining the calibration of grasping, suggesting again a visuomotor, rather than a visual, source of the signal. Anecdotal observations suggest that D.F. adopts non-perceptual strategies on a regular basis in dealing with the everyday world; sometimes knowingly, but often not. She does this in circumstances where a healthy person would unhesitatingly depend on their perception, and where it is all too easy to assume that D.F. is doing the same.

These observations bear on a recent paper by Schenk (2006) who argues that the dissociations we have reported in D.F. are not ones between vision for perception and vision for action, but rather between what he calls allocentric and egocentric processing. Schenk bases this claim on the results of an experiment that used a 2×2 design in which D.F. was tested for her ability to use
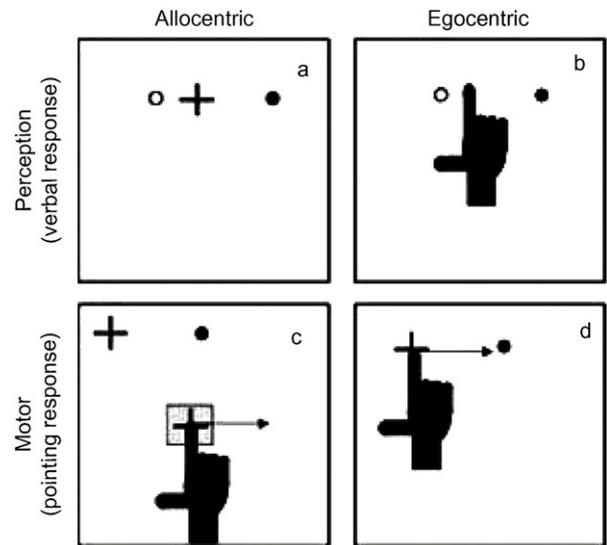

Fig. 1. A diagrammatic representation of the tasks used by Schenk (2006). (a) The 'allocentric perception' task. Patient D.F. was asked to make a verbal judgment as to which of two stimuli was closer to a reference point located between them. (b) The 'egocentric perception' task. Here the patient was asked to make a similar judgement, but this time her forefinger was located at the reference point. (c) The 'allocentric motor' task, in which the patient was asked to make a pointing response from an arbitrary start point to mime the location of the test stimulus with respect to the reference point. (d) The 'egocentric motor' task, in which the patient was asked to make a direct pointing response from a start location to a target stimulus. Figure reproduced in modified form from Schenk (2006), with permission.

allocentric or egocentric spatial processing in both 'perceptual' and 'action' tasks. Not surprisingly, D.F. did poorly on an allocentric perceptual task in which she was asked to report verbally which of two targets was closer to a visual fixation point (see Fig. 1a). Again not surprisingly, she did as well as normal subjects on an egocentric action task in which she was simply asked to point to a target (see Fig. 1d). Both of these cells of the 2×2 design accord with previous studies and conform straightforwardly with our model. But Schenk went on to show that D.F.'s performance on the perceptual task improved when her finger was placed on the fixation point (see Fig. 1b). He argued that this was because the task was now an egocentric one in which she was being asked to judge which of two targets was closer to her finger, rather than which was closer to an external reference point. In the light of the findings by Murphy et al. (1996) and Dijkerman and Milner (1997), however, this result could be equally well explained within the terms of our model. D.F. needed only to imagine making pointing movements to each stimulus in order to help her make a judgement as to which of the two was closer. Thus unlike a healthy control subject, who would have automatically made a perceptual judgement, D.F., on this interpretation, would have used a non-perceptual strategy to solve the task.[1]

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[1] This may explain why, although she did not perform significantly worse than the controls ($p = 0.063$), D.F. did not excel on this task—in striking contrast to her performance on the egocentric action task (Fig. 1d) in which she was as good as the very best control subjects.

Finally, Schenk showed that D.F. failed on what he characterized as an allocentric 'action' task, in which she was asked to reproduce the position of the target with respect to the reference point by moving her finger a matching distance from a designated start point (Fig. 1c). In our terms, however, this task would not test vision for action, since it is not a task in which the critical visual information maps directly on to the response, guiding it in the 'here and now'. What D.F. was really being asked to do, we would argue, is to reproduce what she perceives, using an arbitrary response (cf. Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). In other words, she was making a *manual report* on her perceptual judgement, similar in essence to the verbal report she used in the allocentric perceptual task. Both 'allocentric' tasks were, in our terms, tests of spatial perception, and thus it is not surprising that D.F. did poorly on them both.

Schenk's (2006) report illustrates starkly the importance of distinguishing carefully between process and task. The fact that a task involves action does not mean that the performance of this task would engage vision for action in the sense that we mean. Conversely, asking D.F. or any other patient with neurological damage to perform a perceptual task does not guarantee that she will use perception to solve it.

4. Metrics and frames of reference for perception and action

"There is an extremely rich neuropsychological harvest to be gathered in the human visual system." (Weiskrantz, 1980, p. 385)

It has always been central to our argument that the two separate streams of visual processing evolved because perception and action require quite different transformations of the visual signals. To be able to grasp an object successfully, for example, it is essential that the brain compute the actual size of the object, and its orientation and position with respect to the observer (i.e. in egocentric coordinates). We also argued that the time at which these computations are performed is equally critical. Observers and goal objects rarely stay in a static relationship with one another and, as a consequence, the egocentric coordinates of a target object can often change radically from moment to moment. For these reasons, it is essential that the required coordinates for action be computed in an egocentric framework at the very moment the movements are to be performed.

Perceptual processing needs to proceed in a quite different way. Vision for perception does not require the absolute size of objects or their egocentric locations to be computed. In fact, such computations would be counter-productive. It would be better to encode the size, orientation, and location of objects relative to the other, preferably larger, objects that are present. Such a scene-based frame of reference permits a perceptual representation of objects that transcends particular viewpoints, while preserving information about spatial relationships (as well as relative size and orientation) as the observer moves around. Indeed, if the perceptual machinery had to deliver the real size and distance of all the objects in the visual array, the computational load

would be prohibitive. The products of perception also need to be available over an indefinite time scale, to allow us to recognize objects (and their relations) from one occasion to the next, by combining current input with stored information. Such perceptual mechanisms allow us to escape the present and to use visual information from the past to inform our actions.

These considerations led us to predict that normal observers would show, under appropriate conditions, clear differences between perceptual reports and object-directed actions when interacting with pictorial illusions, particularly size-contrast illusions. This counter-intuitive prediction was initially based on the simple assumption that the perceptual system could not avoid computing the size of a target object in relation to the size of neighbouring objects, whereas visuomotor networks would need to compute the true size of the object. This prediction was confirmed in a study by Aglioti, Goodale, and DeSouza (1995) which showed that the scaling of grip aperture in-flight was remarkably insensitive to the Ebbinghaus illusion, in which a target disc surrounded by smaller circles appears to be larger than the same disc surrounded by larger circles. In short, maximum grip aperture was scaled to the real not the apparent size of the target disc.

This initial demonstration that grasping is refractory to size-contrast illusions triggered a good deal of interest amongst researchers studying vision and motor control. Many investigators have replicated the dissociation between perception and action, while others have not (for review, see Goodale & Wolf, in press). Of course, the simple fact that actions such as grasping are sometimes sensitive to illusory displays does not refute the idea of two visual systems, which is securely based on a large body of evidence ranging from neuroimaging to neurophysiology. Indeed, in the light of our earlier discussion, one should not be surprised that perception can affect our motor behaviour. The real surprise, at least for monolithic accounts of vision, is that there are a number of unassailable instances in which visually guided action is genuinely unaffected by perceptual illusions.

It is important to note here that not all experiments that appear to show an effect of perceptual illusions on action are truly doing so. Once more a major problem arises from the impurity of the measures that are used in the laboratory, in this case to assay the visual calibration of grasp kinematics during an act of prehension. The hand does indeed open more widely for larger than for smaller objects, other things being equal; but other things are not always equal. One factor that appears to be at work in the case of experiments using the Ebbinghaus display is the very presence of neighbouring stimulus items when grasping movements are made. The problem is that these stimuli (i.e. the annulus of circles that surround the target disc in these experiments) may influence the movements that are made for purely *non-perceptual* reasons. One important factor at work here is that the visuomotor system appears to treat these flanking stimuli as potential obstacles to the grasping movement (Gilster, Kuhtz-Buschbeck, Wiesner, & Ferstl, 2006; Haffenden & Goodale, 2000; Haffenden, Schiff, & Goodale, 2001). Recent experiments by de Grave, Biegstraaten, Smeets, and Brenner (2005), for example, have shown that simply shifting the location of the individual circles within the surrounding annulus can affect maximum grip aperture, pre-

sumably because the fingers would be more likely to 'collide' with the circles in some positions than in others. If the direction of this purely *visuomotor* effect on grip aperture coincides with what would be expected from the perceptual illusion, then the investigator may well erroneously conclude that the action programming is sensitive to the illusion.

Grip aperture may be affected by such 'obstacle avoidance' behaviour in the case of the Müller-Lyer illusion as well (Biegstraaten, de Grave, Brenner, & Smeets, 2007). These authors contrasted peak grip aperture, the standard measure of visual guidance in size-illusion experiments, with an alternative measure of size processing, namely the velocity of grip closure just before contact. Biegstraaten and her colleagues suggest that the latter measure may provide a purer assay of vision for action in the size domain than grip aperture. They found that when subjects grasped a bar placed on the shaft of a Müller-Lyer figure, the figure influenced peak grip aperture to some degree (as others have found), but did not influence the velocity of grip closure as one would expect if size processing was truly affected by the illusion. The authors conclude that there is no reason to believe that perceived size guides the way that we reach and grasp an object.

Independent studies have confirmed that the proximity of potential obstacles has a systematic effect on grip size during reaching, not only in healthy subjects (Mon-Williams, Tresilian, Coppard, & Carson, 2001) but in patient D.F. as well (Rice et al., 2006). This latter fact suggests that the dorsal stream, which is functionally intact in D.F. (James et al., 2003) governs these obstacle-avoidance behaviours. This inference is strongly supported by the observation by Schindler et al. (2004) that patients with dorsal-stream damage fail completely to take into account the positions of potential obstacles in programming the trajectory of target-directed movements (Schindler et al., 2004). It is worth noting that in other pictorial illusions, such as the Ponzo or Diagonal illusions, where the presence of potential 'obstacles' is less of a problem, investigators have typically found that grip aperture is quite immune to the effects of the illusory display (e.g. Brenner & Smeets, 1996; Jackson & Shaw, 2000; Stöttinger & Perner, 2006).

According to our two visual systems model, vision for action works only in real time and is not normally engaged unless the target object is visible during the programming phase, that is when bottom-up visual information is being converted into the appropriate motor commands. When there is a delay between stimulus offset and the initiation of the grasping movement, the programming of the grip would be driven by a memory of the target object that was originally derived from a perceptual representation of the scene, created moments earlier by mechanisms in the ventral stream (Fischer, 2001; Goodale, Jakobson, & Keillor, 1994; Hu, Eagleson, & Goodale, 1999). Thus, we would predict that memory-guided grasping would be affected by the illusory display, because the stored information about the target's dimensions would reflect the earlier perception of the illusion. In fact, a range of studies has shown that this is exactly the case (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000; Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2000). These findings not only confirm the dissociation

between perception and action, but also provide strong support for the idea that the dorsal 'action' stream operates only in real time (while actions that are driven by remembered targets are dependent on earlier ventral-stream processing). It is worth noting that these results could not have been predicted, nor are they easily explained, by alternative accounts that are predicated on a single visual representation that drives both perception and action.

Less obviously, perhaps, our model does not predict that actions demonstrably driven by the dorsal stream will be immune to *all* visual illusions. Dyde and Milner (2002) pointed out that illusions which arise from early visual cortical areas, before the two streams diverge, should affect both perceptual judgements and the calibration of actions, whereas illusions that arise during later stages of processing within the ventral stream should affect only perception. To test this idea, they selected two illusions of orientation: the simultaneous tilt illusion, which is thought to be generated in areas V1 and/or V2, and the rod-and-frame illusion, which is thought to arise much later, in the ventral stream, because of the obligatory comparison between the orientation of the large frame and the orientation of the rod. As predicted, Dyde and Milner found that the former illusion affected action and perception equally, whereas the latter affected only perception. This again illustrates the potential pitfalls that can beset investigators attempting to demonstrate (or not) a dissociation between perception and action using visual illusions. One first has to consider where in the brain a given illusion is likely to arise.

Another less obvious potential pitfall is related not to the selection of the display but rather to the nature of the actual movements that are required to perform the task. Not all movements will be mediated by the 'encapsulated' visuomotor networks in the dorsal stream. The more unpractised and novel the action, the more likely it is to require a good deal of cognitive supervision and thereby to be influenced by perceptual processing. The first time you use chopsticks, for example, you are vividly aware of what you are doing and you monitor your movements quite consciously, something you do not do when using your fingers, or even a fork, to pick up food. Presumably, this conscious monitoring of unpractised movements depends upon information provided by the perceptual networks in the ventral stream. As a consequence, ventral-stream processing can intrude into the visual guidance of these movements (for related discussions, see Milner & Goodale, in press; van der Kamp et al., in press). Once the action is well-practised and becomes automatized, however, it seems that control of the constituent movements is passed to visuomotor networks in the dorsal stream, which then play the dominant visual role. One might predict therefore that if awkward or unfamiliar hand postures are used to grasp a target object, grip aperture would now be sensitive to pictorial illusions. Gonzalez, Ganel, Whitwell, Morrissey, and Goodale (2007) explored this possibility by directly comparing the sensitivity of skilled versus awkward grasping movements, directed at the same targets presented against the same backdrop of a Ponzo illusion, predicting that the skilled but not the unskilled actions would escape the effects of the illusion. Some subjects were required to use a normal precision grip (with the

thumb and index finger), while other subjects used a much more awkward grip (with the thumb and ring finger). The results were clear and unambiguous. Even though the illusion had no effect on grip scaling in subjects who used a precision grasp, it had a large and significant effect on grip scaling in the subjects who used an awkward grasp. This result provides some confirmation of the idea that awkward actions, which require the use of more deliberate cognitive control, are more likely to rely on the same perceptual processing participants use to make conscious judgments about the size of objects in illusory displays. Interestingly, after 3 days of practice with the awkward grasp, grip scaling became no longer sensitive to the illusion, presumably because the action had become more automatized and thus controlled by the dorsal stream.

These results strongly suggest that in experiments designed to investigate possible differences between vision for action and vision for perception, one should be careful to ensure that the recording methods used to measure the actions do not interfere with the 'automaticity' of the constituent movements. It may be no accident that those laboratories where effects of pictorial illusions on grip scaling have been regularly reported have used quite intrusive recording devices to measure grip aperture (e.g. Franz, Bülthoff, & Fahle, 2003; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; cf. also Radoeva, Cohen, Corballis, Lukovits, & Koleva, 2005). It is notable that the interpretations favoured by Franz and colleagues, which infer a common visual foundation for both perception and action, are quite unable to accommodate the results of Gonzalez et al. (2007). Further experiments by Gonzalez, Ganel, and Goodale (2006) have shown that precision grasping with the right hand is much more resistant to the effects of pictorial illusions such as the Ebbinghaus and Ponzo than precision grasping with the left hand. This again suggests that skill is a major factor in determining whether or not an action will escape the influence of perceptual illusions.[2]

Taken together, these findings highlight the importance of paying close attention to the nature of the task and the nature of the required response when using visual illusions to tease apart the workings of vision for action and vision for perception. Only highly practiced actions with the right hand operating in real time and directed at visible targets presented in the context of high-level illusions are likely to escape the intrusion of ventral-stream perceptual control. Only under these conditions will the specialized role of the dorsal stream in visuomotor control be fully revealed.

A more general point implicit in the above discussions merits explicit consideration here: the question as to what parts of the visual array are analysed by each system. In our initial writings we over-simplified the contrast between the two systems by implying that the dorsal stream is concerned only with processing the target of an action, while arguing that the ventral

stream takes obligatory account of the spatial context in which the target is embedded. Even a brief reflection on the nature of visuomotor control, however, suffices to establish that this cannot be correct. First, we know from the long history of the topic that online visual feedback from the hand is an important factor in the control of reaching and grasping (Jeannerod, 1988, 1997). This visual information has to be processed somewhere, with the dorsal stream being the obvious candidate. Second, our actions typically do not take place in an empty space, where the only visible external object (other than perhaps a fixation point) is the target of our action. (A Martian might be excused for thinking that this was the case, given the impoverished arrays used in 99% of experimental studies on reaching and grasping in psychology and neuroscience.) Our actions need to take other, non-target, objects into account, and again the dorsal stream is the obvious candidate to take on this role.

As already mentioned, there is good empirical evidence now for the role of the dorsal stream in the guidance of our reaches with respect to non-target objects in the immediate environment. Thus the patients I.G. and A.T. with bilateral optic ataxia both show a total abolition of the normal lawful shifts in reach trajectory that are associated with shifts in location of a left or right non-target object that could pose the risk of collision (Schindler et al., 2004). In a recent study we tested a patient with unilateral left parietal damage (M.H.), who shows a rare pattern of optic ataxia in which only pointing with his right arm to targets in the right visual field is impaired. Strikingly, M.H. shows a highly selective deficit on Schindler et al.'s task—only ignoring potential obstacles on his right, and only doing that when he is reaching with his right hand (Rice, Edwards, Schindler, Punt, McIntosh, Humphreys, et al., submitted). This identical pattern of deficits in pointing and obstacle avoidance suggests that the two may both be mediated by the same dorsal-stream subsystem. A nice further parallel with the processing of visual target information for pointing is provided by the observation that patient M.H. shows quite normal obstacle avoidance behaviour with respect to the right-side object when tested in a delayed version of the reaching task (Rice et al., under revision). Presumably, just as in delayed pointing or grasping, the ventral stream is recruited to code the spatial array in readiness for making the delayed reach (see Section 5 below), enabling M.H. to perform normally.

In contrast to these deficits after dorsal-stream damage, most spatial neglect patients tested in a similar obstacle avoidance task show no impairment at all, despite failing to take account of the left object when asked to make an explicit bisection response between the two objects (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004). Likewise patients D.F. and S.B. with visual form agnosia both show obstacle avoidance behaviour within the normal range (Rice et al., 2006). Taken together, this body of data argues strongly that the processing of non-target objects that might pose a threat of collision depends heavily on dorsal-stream circuitry. At the same time however, it must be recognized that just as in the processing of visuomotor *targets*, the ventral stream can play a role as well, and not only when a delayed response is being made. The ventral stream's role may assume particular importance when the potential obstacles need to be analysed for their semantic or material properties, such

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[2] It should be mentioned, however, that there are other factors at work as well. It turns out that left-handers show a similar right hand advantage. That is, their right but not their left hand grasping movements are immune to the effects of illusions. This latter finding suggests that there may be a special relationship between the left hemisphere and the right hand for the visuomotor control of precision grasping (Gonzalez, Ganel, & Goodale (2006)).

as their fragility or noxiousness. Under such circumstances, the subtle adjustments to reach and grasp parameters that appear to be mediated by the dorsal stream are overshadowed by gross diversions of the reaching hand and a slowing of the movements made (Mon-Williams et al., 2001).

On-line visual processing of hand location during manual reaching and grasping is also likely to depend on dorsal-stream mechanisms, though direct evidence for this is not yet available from patients with optic ataxia. Nonetheless, neurons have been found in the reach-related region of the dorsal stream that code this feedback information in monkeys (Battaglia-Mayer et al., 2001). It will be of some interest to examine using fMRI whether in humans too the homologous reach-related region mediates the use of visual feedback from the hand during reaching. This could be done by comparing closed-loop reaching (i.e. under conditions when the hand is in view during reaching) with open-loop (when the hand is not visible).

In summary, then, although both streams need to focus on a selected target object in performing their primary visual roles, neither does this to the exclusion of other visual information present on the retina. The ways in which non-target information is dealt with, however, are qualitatively different in the two cases. In the case of the ventral stream, the visual coding of the target object is *itself* inherently scene-based—that is its metrics are fundamentally determined by the surrounding array. In the case of the dorsal stream this is not so: indeed the coding of the target has to be as far as possible absolute, and needs to be referred to an egocentric rather than a scene-based framework. Non-target visual information needs to impact dorsal-stream processing dynamically, thereby influencing the moment-to-moment kinematics of the action. It seems likely that this happens without the visual coding of target information being itself modulated: in other words that both target and non-target information each modulate motor control directly and quasi-independently.

5. Double dissociations

"Double dissociations are powerful and useful but not omnipotent" (Weiskrantz, 1997, p. 258).

The model we have developed was inspired by, and to some extent depends on, a set of partial or complete double dissociations that have been observed between patients like D.F., who has ventral-stream damage, and patients with optic ataxia, who have damage to the dorsal stream. Such evidence, admittedly, is necessarily imperfect, due to such factors as imprecise correspondences between lesion locations and functional brain systems, and the effects of neural and behavioural compensation following brain damage. An example of the former difficulty is that one of the patients most studied in recent research on optic ataxia has lesions that extend into neighbouring territory well beyond the dorsal stream, including large parts of area 39 in the inferior parietal lobule (patient A.T.: Jeannerod et al., 1994). The ventral-stream lesion of patient D.F., on the other hand, is very clearly subtotal, though there does seem to be a functionally complete destruction of the area most concerned with object form perception, area LO (James et al., 2003). The evidence sug-

gests, however, that areas concerned with spatial processing in the ventral stream, including the parahippocampal place area, are partially spared in D.F. (Steeves et al., 2004). Clearly, this being so, there are only restricted possibilities for observing dissociations in the spatial domain between patient D.F. and patients with optic ataxia, in whom the primary diagnostic criterion is a failure to point or reach accurately in space towards visual targets. But of course dorsal-stream damage disrupts visuomotor processing not only in the spatial domain. As mentioned earlier, problems in orienting and shaping the hand during grasping have been documented in several patients with optic ataxia (Jakobson et al., 1991; Jeannerod et al., 1994; Milner et al., 2001; Perenin & Vighetto, 1988), presumably due to damage affecting dorsal-stream areas concerned with the processing of shape for the control of grasping (Binkofski et al., 1998).

Given these considerations one would not expect that strict and absolute double dissociations would be easy to establish—a point made forcefully by Rossetti et al. (2003) and Pisella, Binkofski, Lasek, Toni, and Rossetti (2006). More surprisingly, however, these authors made the much stronger claim that *no* clear double dissociations have yet been established between visual form agnosia and optic ataxia. Indeed they have suggested that until additional testing is carried out one cannot exclude the possibility that the division of labour between the ventral and dorsal streams might be better characterized as a difference between central and peripheral vision rather than as a difference between vision for perception and vision for action. We maintain, however, that the neuropsychological evidence is much stronger than Rossetti and his colleagues have presented it to be, and moreover that it strongly favours the perception-action model. The fact is that despite the difficulties, several convincing examples do exist of double dissociations between visual form agnosia and optic ataxia. In the following paragraphs we summarize just two of them: first one in the spatial domain, and then one in the non-spatial domain. These dissociations co-exist with the undeniable difference in the emphasis on central versus peripheral coding between the two streams, and are perfectly consistent with it. We would contend, in fact, that this difference in coding makes a great deal of sense within our perception-action framework.

Rossetti and colleagues are correct, of course, in pointing out that the reaching deficits in most, though not all, optic ataxia patients are clearest for stimuli in the visual periphery. When these patients are tested in central vision, they often do much better, though even here they are not entirely normal. A critical point, however, is that when a delay is interposed between the presentation of the stimulus and the signal to respond, optic ataxic patients show a significant improvement in their pointing accuracy (Himmelbach & Karnath, 2005; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Revol et al., 2003). Milner, Paulignan, et al. (1999) argued that this improvement occurred because the patient would now use a memory of the stimulus location, based on perceptual processing carried out at the time of stimulation by her relatively intact ventral stream. In support of this interpretation, they explicitly cited experimental data on patient D.F., which demonstrated a directly opposite pattern of results (Milner, Dijkerman, & Carey, 1999). When
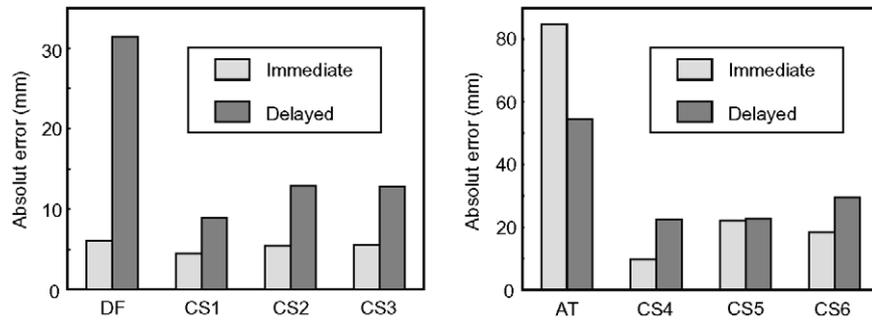
Fig. 2. Pointing to a peripheral visual target in a patient with visual form agnosia (D.F.), as contrasted with the performance of a patient with optic ataxia (patient A.T.). Data are presented in both an immediate pointing condition (light grey bars) and a delayed testing condition, in which the patient had to wait several seconds before responding (dark grey bars). The two graphs are taken from two separate experiments, each of which included three age-matched healthy controls (who were therefore rather younger in the D.F. experiment). The *y*-axis shows the resultant absolute errors in millimetres in both studies. The data are re-plotted from Milner, Dijkerman, and Carey (1999) and Milner, Paulignan, et al. (1999), respectively, with permission.

D.F. was asked to point toward peripheral targets in real time, her accuracy was excellent. But the dependence of that preserved ability on dorsal-stream processing was revealed by the fact that when a delay was introduced between the stimulus and response, D.F.'s pointing became highly inaccurate, with errors now more than twice as large as those of control subjects. Milner, Paulignan, et al. (1999) concluded that the delayed task required participation of ventral-stream systems, which are compromised in D.F. but largely spared in the patients with optic ataxia. In other words, despite the contrary picture painted by Pisella et al. (2006), these data show a very clear double dissociation of abilities and deficits following damage to the dorsal and ventral stream. The contrasting patterns of performance in the two patients are shown in Fig. 2, re-plotted for purposes of direct comparison.

The above double dissociation between damage to the two streams refers to spatial processing in peripheral vision. But similar dissociations are just as evident in central vision, and in the domain of object processing. Thus, several patients with optic ataxia have been reported to show clear deficits in scaling their grip aperture to objects presented directly in central vision, even though whenever they were tested for their ability to perceive the dimensions of the same objects they did quite well (Binkofski et al., 1998; Goodale & Wolf, in press; Jakobson et al., 1991; Jeannerod, 1986; Jeannerod et al., 1994). In addition, Goodale, Meenan, et al. (1994) showed that a patient with optic ataxia was unable to use vision to guide her fingers to stable grasp points on the circumference of irregularly shaped objects placed in central vision – even though she was well able to distinguish between them. Quite the opposite pattern of results was evident in the visual form agnosia patient D.F., who could grasp accurately but could not discriminate between the different target objects nor estimate their size manually (Carey et al., 1996; Goodale et al., 1991; Goodale, Meenan, et al., 1994). It is particularly surprising that this second strong double dissociation (see Fig. 3 for illustrative data), like that described above for pointing to peripheral targets, was overlooked in the recent paper by Pisella et al. (2006). Those authors actually entitle their article "No double dissociation between optic ataxia and visual agnosia". The existence
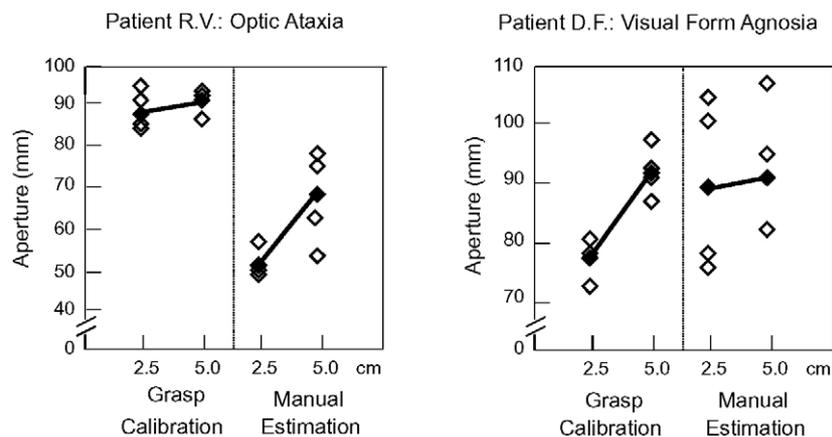

Fig. 3. Grip calibration in a patient with visual form agnosia (D.F.) as contrasted with the performance of a patient with optic ataxia (patient R.V.). For both experiments, the stimuli were presented centrally, and the patient was asked either to reach out and pick up the object using a finger-thumb precision grip (left panel in each case), or to mime its width using finger and thumb (right panel in each case). The *y*-axis shows the maximum separation of markers attached to the tips of forefinger and thumb during reaching to grasp, or at asymptote when the patient had arrived at her judgement, respectively. Data are plotted in each graph for rectangular blocks of 2.5 and 5.0 cm width, respectively. Open shapes show data points from individual trials, and closed shapes the mean of these individual scores. The data for D.F. are re-plotted from Goodale et al. (1991), with permission.

of these two clear instances in the published literature belies that assertion.

These double dissociations from neuropsychology provide strong evidence in support of our proposal that the two visual streams are specialized for different ends, namely for perception and for action. But this proposed division of labour is entirely compatible with the known differences in the extent to which the visual fields are represented in the two streams. In fact, these differences in coding can be regarded as an integral part of the functional specialization of the streams. Already at the level of primary visual cortex, there is a pronounced cortical magnification of central vision. This becomes further exaggerated in the ventral stream, but if anything somewhat reduced in the dorsal stream (for review, see Brown, Halpert, & Goodale, 2005). This over-emphasis on central vision in the ventral stream is just what one might expect in a system whose job it is to construct a rich and detailed representation of the world. The ventral stream exploits the high resolution and wavelength selectivity that characterize processing in the fovea, and is much less interested in the low-resolution information from the periphery. The ventral stream's need for a constant updating of such detailed information entails that gaze must constantly move from one part of the world to another, bringing the processing power of the fovea to bear on the stimulus array (Findlay & Gilchrist, 2003). Thus the role of peripheral stimuli in the ventral stream is a supporting one, helping only to provide a coarse contextual framework for perception. Matters are quite different in the dorsal stream, where the peripheral field is relatively well represented. Indeed some dorsal-stream areas, such as the parieto-occipital area (PO), show almost no cortical magnification at all, with a large amount of neural tissue devoted to processing inputs from the peripheral visual fields (Colby, Gattas, Olson, & Gross, 1988). This broad representation of the visual field in the dorsal pathway is presumably necessary for the efficient visual control of behaviour in which the effector (such as the hand) and the controlling stimuli (such as potential obstacles) are often present in the visual periphery.

As mentioned earlier in this section, optic ataxia patients show an improvement in reaching when a delay is imposed, suggesting that they are able to make use of a relatively intact ventral stream. Over time, these patients may well learn to rely more on the cognitive control offered by the ventral stream than on the depleted automatic control available from the impaired dorsal stream—even when acting in real time. In other words, in order to perform what used to be a skilled act, they may revert to the kind of unskilled strategy that we all use when beginning to master a novel visuomotor act (like using chopsticks: see Section 4). Indeed, in a limiting case, if the dorsal stream were totally destroyed, the patient would have to rely entirely on whatever control the ventral stream could provide. But this kind of compensation would necessarily be far more effective in central vision, since that enjoys a much stronger representation in the ventral than in the dorsal stream. This reasoning thus provides a possible explanation for some cases of central 'sparing' during real-time reaching in optic ataxia patients (e.g. Milner, Paulignan, et al., 1999). Of course, when a delay is imposed on the response, so that the damaged dorsal stream can no longer

be engaged at all, the ventral stream must necessarily deal with signals from the periphery as well. Despite its not being well-equipped to do this, the ventral stream may still be able to guide reaching to peripheral targets better than a badly damaged dorsal stream, thereby causing the typical improvement in pointing accuracy seen with delay. If, on the other hand, the ventral stream is already dealing with central targets even during real-time pointing, then we would not expect a delay to have any beneficial effect on accuracy; and indeed a slight deterioration has been reported (Milner, Paulignan, et al., 1999).

6. Concluding comments

Our intention in writing this paper was to revisit some of the issues and concepts that may not have been made fully clear in our original exposition of the model, or which have developed to some degree in subsequent versions of it. We hope that in doing so we have made our ideas more explicit, and thereby cast light upon some recent controversies in the area. At the same time, by specifying the ideas behind the model in more detail, we hope that we have helped to clear the way for more definitive experiments to be designed that will extend, and undoubtedly modify, the model in the future.

Acknowledgements

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