

# The Visual Brain in Action

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PSYCHE, 4(12), October 1998

<http://psyche.cs.monash.edu.au/v4/psyche-4-12-milner.html>

**KEYWORDS:** visual consciousness, ventral and dorsal streams, visuomotor action, unconscious perception.

**PRECIS OF:** A. David Milner and Melvyn A. Goodale *The Visual Brain in Action* (Oxford Psychology Series, No. 27). [Oxford University Press](http://www.oxfordup.com), xvii + 248pp. ISBN: 0198524080. Price: \$35.00 pbk.

## 1. The Functions of Vision

Standard accounts of vision implicitly assume that the purpose of the visual system is to construct some sort of internal model of the world outside -- a kind of simulacrum of the real thing, which can then serve as the perceptual foundation for all visually derived thought and action. The association of rich and distinctive conscious experiences with

most of our perceptions gives credence to the idea that they must constitute a vital and necessary prerequisite for all of our visually-based behavior.

But even though the perceptual representation of objects and events in the world is an important function of vision, it should not be forgotten that vision evolved in the first

number of other subcortical vi

findings from a broad range of studies in both humans and monkeys are more consistent with a distinction not between subdomains of perception, but between perception on the one hand and the guidance of action on the other.

One source of evidence for the perception-action distinction comes from the study of the visual properties of neurons in the ventral and dorsal streams. Neurons in ventral stream areas such as IT are tuned to the features of objects, and many of them show remarkable categorical specificity; some of these category-specific cells maintain their selectivity irrespective of viewpoint, retinal image size, and even colour. They are little affected by the monkey's motor behavior, but many are modulated by how often the visual stimulus has been presented and others by whether or not it has been associated with reward. Such observations are consistent with the suggestion that the ventral stream is more concerned with the enduring characteristics and significance of objects than with moment-to-moment changes in the visual array.

Neurons in the dorsal stream show quite different properties from those in the ventral stream. In fact, the visual properties of neurons in this stream were discovered only when methodological advances permitted the experimenter to record from awake monkeys performing visuomotor tasks. Different subsets of neurons in PP cortex turned out to be activated by visual stimuli as a function of the different kinds of responses the monkey makes to those stimuli. For example, some cells respond when the stimulus is the target of an arm reach; others when it is the object of a grasp response; others when it is the target of a saccadic eye movement; others when the stimulus is moving and is followed by a slow pursuit eye movement; and still others when the stimulus is stationary and the object of an ocular fixation. In addition, of course, there are many cells in the dorsal stream, as there are in the ventral stream, that can be activated passively by visual stimuli -- indeed logic requires that the visuomotor neurons must receive their visual inputs from visual cells that are not themselves visuomotor. These purely visual neurons are now known to include some that are selective for the orientation of a stimulus object. One important characteristic of many PP neurons is that they respond better to a visual stimulus when the monkey is attending to it, in readiness to make a saccadic or manual response. This phenomenon is known as neuronal enhancement.

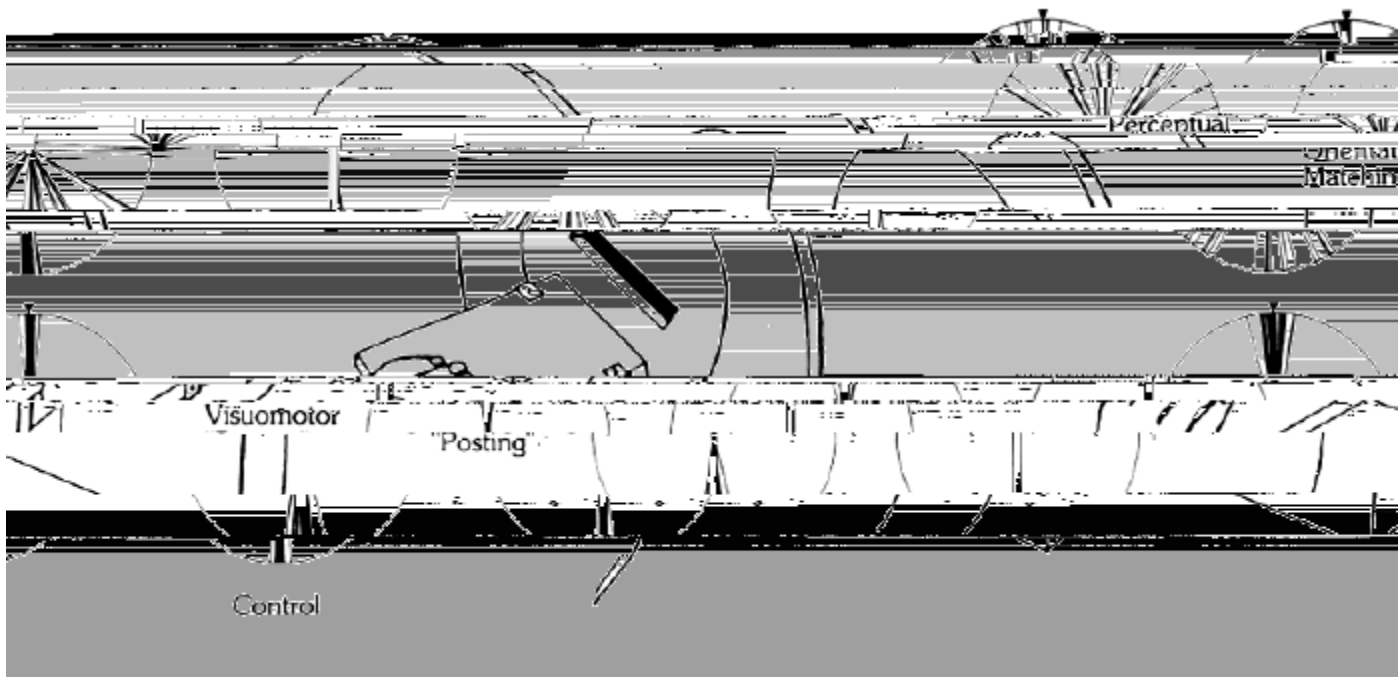
The electrophysiology can readily explain why posterior parietal lesions impair landmark task performance: quite simply, the monkey fails to orient toward the landmark. Recent behavioral studies bear out this interpretation. The electrophysiology also explains one of the most obvious effects of PP lesions, namely the monkeys' inability to reach accurately to grasp a moving or stationary food morsel, and why they fail to shape and orient their hands and fingers appropriately to pick up the morsel. The most recent development in this area has been the elegant experiments of Gallese and his colleagues (1997). They have demonstrated that micro-injections of a drug (muscimol) into a particular part of the PP cortex will cause a temporary impairment in hand shaping when the monkey reaches to grasp objects. This fits well with the recent discovery of visually-responsive cells within that same part of PP cortex, as well as in anatomically linked areas of premotor cortex, which respond selectively during the grasping of particular objects (Sakata et al., 1997; Rizzolatti et al., 1988). Such evidence is consistent with the proposal that visual

networks in the dorsal stream compute more than just spatial location. Indeed, in agreement with the electrophysiology, the behavioral literature is fully consistent with the idea that the dorsal stream has a primary role in mediating the visual control and guidance of a wide range of behavioral acts (Milner & Goodale, 1993). Furthermore, even though the egocentric locations of visual targets are indeed computed within the PP cortex, it has now been clearly shown that this is done separately for guiding movements of the eyes and for movements of the hands, both in the monkey brain (Snyder et al., 1997) and in the human brain (Kawashima et al., 1996).

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little difficulty in giving perceptual reports of the orientation and location of the very objects they fail to grasp.

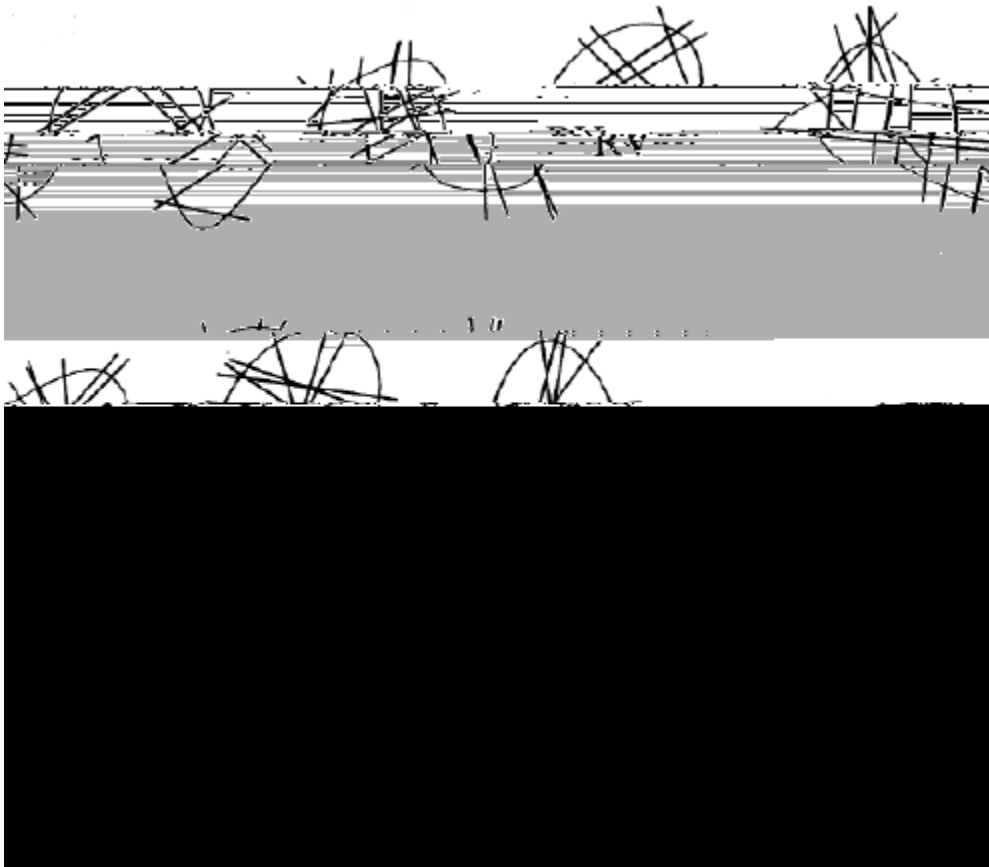
On the other side of the equation, an impairment of ventral stream function seems to occur in humans who suffer from the condition known as visual form agnosia. The classic case of this disorder was described by Benson and Greenberg (1969). Their patient was not only unable to recognize faces or objects, he could not even reliably identify geometric shapes visually, nor distinguish reliably between a square and a rectangle with a 2:1 aspect ratio. Yet the patient was certainly not cortically blind. Recently we have described a very similar patient, D.F. (Milner et al., 1991). We have examined her spared abilities to use visual information in a series of experimental studies. We have found that her attempts to make a perceptual report of the orientation of an oriented slot show little relationship to its actual orientation, whether her reports are made verbally or by manual means (see Figure 2). However, when she was asked to insert her hand or a hand-held card into the slot, she shows no difficulty, moving her hand or the card towards the slot in the correct orientation and inserting it quite accurately (see Figure 2). Videorecordings have shown that her hand begins to rotate in the appropriate direction as soon as it leaves the start position. In short, although she cannot report the orientation of the slot, she can insert her hand or post a card into it with considerable skill.



**been rotated to vertical. Note that although D.F. was unable to match the orientation of the card to that of the slot in the perceptual matching card, she did rotate the card to the correct orientation as she attempted to insert it into the slot on the posting task.**

Similar dissociations between perceptual report and visuomotor control were also observed in D.F. when she was asked to deal with the intrinsic properties of objects such as their size and shape. Thus, she showed excellent visual control of anticipatory hand posture when she was asked to reach out to pick up blocks of different sizes that she could not distinguish perceptually. Just like normal subjects, D.F. adjusted her finger-thumb separation well in advance of her hand's arrival at the object, and scaled her grip size in a perfectly normal and linear fashion in relation to the target width (Goodale et al., 1991). Yet when she was asked to use her finger and thumb to make a perceptual judgement of the object's width on a separate series of trials, D.F.'s responses were unrelated to the actual stimulus dimensions, and showed high variation from trial to trial.

D.F.'s accurate calibration of grip size during reaching to grasp contrasts markedly with



**Figure** **3**  
The 'grasp lines' (joining points where the index finger and the thumb first made contact with the shape) selected by a patient with optic ataxia (R.V.), a patient with visual form agnosia (D.F.), and the control subject when picking up three of twelve shapes that were presented to them. The four different orientations in which each shape was presented have been rotated so that they



Our various studies of D.F. show that she is able to govern many of her actions using visual information of which she has no awareness. But it is clear that this is only true of actions that are targeted directly at the visual stimulus. She cannot successfully use the same visual information to guide an identical but displaced response -- a response using the same distal musculature but at another location. Presumably the difference is that a response displaced in this way is necessarily an arbitrary or symbolic one -- not one that would fall within the natural repertoire of a hard-wired visuomotor control system. Thus D.F. seems to be using a visual processing system dedicated for motor control, which will normally only come into play when she carries out natural goal-directed actions.

There are temporal as well as spatial limits on D.F.'s ability to drive her motor behavior visually. After showing her a rectangular block, Goodale et al. (1994a) asked D.F. to delay for either 2 or 30 seconds with eyes closed, before allowing her to reach out as if to grasp it. Even after a 30 second delay, the preparatory grip size of normal subjects still correlated well with object width. In D.F., however, all evidence of grip scaling during her reaches had evaporated after a delay of even 2 seconds. This failure was not due to a general impairment in short-term memory. Instead, it seems that a delayed reach is no longer a natural movement, and indeed this is so even for normal subjects. A detailed

One of the ways in which the visual information used by the motor system can be shown to be quite different from that which we experience perceptually is through the study of visual illusions. Gregory (1997) has argued over many years that higher-level visual illusions, including geometric illusions, deceive the perceptual system because the system makes (false) assumptions about the structure of the world based on stored knowledge. These include, for example, assumptions about perceptual stability and spatial constancy. It seems that the dorsal system, by and large, is not deceived by such spatial illusions (Bridgeman et al., 1979, 1981; Wong & Mack, 1981; Goodale et al., 1986), perhaps because evolution has taught it that a little 'knowledge' can be quite literally a dangerous thing. Instead, the dorsal stream directs our saccadic eye movements and our hand movements to where a target really is, which is not always where our perceptual system tells us it is. Similarly, under appropriate circumstances geometric illusions can be seen to affect visually-guided reaching (Gentilucci et al., 1996) and grasping (Aglioti et al., 1995; Brenner & Smeets, 1996; Haffenden & Goodale, 1998) far less than they affect our perceptual judgements. Thus, we may perceive an object as bigger than it really is, but we open our finger-thumb grip veridically when reaching for it.

We propose that the processing accomplished by the ventral stream both generates and is informed by stored abstract visual knowledge about objects and their spatial relationships. We further surmise that the particular kinds of coding that are necessary to achieve these ends coincide with those that render the representations accessible to our awareness. This would fit with the idea that coded descriptions of enduring object properties, rather than transitory egocentric views, are precisely what we need for mental manipulations such as those required for the planning of action sequences and the mental rehearsal of alternative courses of action.

But of course, the mere fact that processing occurs in this generalized way in the ventral stream could not be a sufficient condition for its reaching visual awareness. For example, there are generally many items processed in parallel at any given time, most of which will be filtered out of awareness by the operation of selective attention. We have therefore proposed that it is only those items that receive more than a certain threshold level of relative activation, for example through the sharpening effects of spatial gating processes known to be active during selective attention (e.g., Moran and Desimone, 1985; Chelazzi et al., 1993), that will reach awareness. That is, we are proposing a conjoint requirement for an item to attain visual awareness: (a) a certain kind of coding (one that is object-based and abstracted from the viewer-centred and egocentric particulars of the visual stimulation that gives rise to it) and (b) a certain level of activation of these coding circuits above the background level of neighbouring circuits.

We do not deny, then, that perception can proceed unconsciously under some circumstances, e.g., when the stimuli are degra

fact that there is insufficient focussing of the activation above the noise of the surrounding assemblies. If this notion is correct, we would predict that such subconscious stimulation, although able to prime certain kinds of semantic decision tasks, would not provide usable inputs to the visuomotor system. Conversely, visual form information that can successfully guide action in a patient like D.F. should not be expected to have significant priming effects on semantic tasks - precisely because that visual processing is never available to conscious experience, even in the normal observer. In short, it may be the case that for an 'undetected' visual stimulus to be able to prime decision tasks, it must at least in principle be accessible to consciousness.

## **4. The Visual Brain in Action**

Although we have emphasized the separation of the dorsal and ventral streams, there are of course multiple connections between them, and indeed adaptive goal-directed behavior in humans and other primates must depend on a successful integration of their complementary contributions. Thus, the execution of a goal-directed action might depend on dedicated control systems in the dorsal stream, but the selection of appropriate goal objects and the action to be performed depends on the perceptual machinery of the ventral stream. One of the important questions that remains to be answered is how the two streams interact both with each other and with other brain regions in the production of purposive behavior.

At the level of visual processing, however, the visuomotor modules in the primate parietal lobe function quite independently from the occipitotemporal mechanisms generating perception-based knowledge of the world. Only this latter, perceptual, system can provide suitable raw materials for our thought processes to act upon. In contrast, the other is designed to guide actions purely in the 'here and now', and its products are consequently useless for later reference. To put it another way, it is only through knowledge gained via the ventral stream that we can exercise insight, hindsight and foresight about the visual world. The visuomotor system may be able to give us 'blindsight', but in doing so can offer no dib in

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