

Two Visual Brains in Action

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COMMENTARY ON: A. David Milner & Melvyn A. Goodale. (1995) *The Visual Brain in Action*. (Oxford Psychology Series, No. 27). Oxford: Oxford University Press. xvii + 248pp. ISBN: 0198524080. Price: \$35 pbk.

ABSTRACT: Milner and Goodale review a wealth of evidence, much of it from their own research, showing that visually guided behavior and perception are controlled by two separate and quasi-independent 'visual brains'. Early evidence showed that motor ability was sometimes preserved despite simultaneous perceptual illusions, and work with patients has differentiated the two systems neurologically. Of the two visual systems, the motor system is less well known: it has a body-based frame of reference, but no memory and limited pattern-recognition capacity.

Though vision seems to its users to be a single sense, we now know that visually guided behavior and perception are controlled by two separate and quasi-independent 'visual brains'. Perception depends upon a pathway from the primary visual cortex through several intermediates to the inferotemporal (IT) cortex, identified by Pribram (1971) as a seat of pattern recognition and necessary to solve problems involving visual choice. If one asks people what they see, they report the contents of this system.

The motor system is more difficult to uncover, because its representations of visual space are not perceived; in Milner and Goodale's definition, this means that they also are not conscious, and the separate motor representation remains inaccessible to verbal report, communication and memory. This is why it was only recently discovered, and why much

less is known about its functions than is known about the perceptual path. Another reason for the recency of discovery of the motor system is that most of its cells, beginning in the posterior parietal cortex and moving anteriorly, are silent when an animal is anesthetized; the cells respond only when the animal is preparing a movement. Uncovering the properties of the cells in the parietal motor pathways could not begin until techniques for recording from active, unanesthetized animals were developed.

Why should we have two visual brains, instead of just one? Wouldn't the brain do better to concentrate all of its resources on one really good visual representation? The answers lie partly in evolution and partly in the variety of jobs that vision is called upon to do. To control visually guided behavior we need a representation that is stable, egocentrically calibrated, and fast, but it need not have high resolution -- I won't know the difference if I'm off by a quarter of a degree in grasping for something, but a whole human face in a crowd may cover only a quarter of a degree, and I would want to know who is there. The motor system needs only to know what is in the environment NOW, and would only be disturbed by memories of what was there before. But perception depends upon matching current input against knowledge from the past (bottom-up and top-down respectively). Thus memory is intimately involved with perception, but is not needed in controlling visually guided behavior.

If this contrast is correct, why should we have a perceptual system at all? The motor representation seems perfectly capable of controlling behavior, and the frog at a simpler stage of evolution seems to get along quite well with just a motor system. The answer might be that both systems control behavior, but the motor system controls behavior in real time while the cognitive system stores up information for use in controlling future behavior. It is involved in decisions, and in events with symbolic importance, while the motor system is the workhorse. Of course this means that the two neurological systems controlling perception and action must interact with each other, and indeed Milner and Goodale document extensive crosstalk between them.

Despite the need for communication, however, the two systems hold distinct representations of visual space. Lesions in neurological patients or in experimental monkeys can damage one system while leaving the other largely unaffected. Blindsight, occurring both in humans and monkeys, is a partial absence of the perceptual branch. Patients with blindsight have no visual experience in part of their visual fields, yet can reach to targets in those fields fairly well (Weiskrantz, 1997).

Blindsight was one of the first bits of evidence that visual capabilities might be divided into separable neurological systems. Other work showed motor ability despite perceptual illusions. A conflict between experiments involving symbolic responses and those involving motor responses was resolved when two types of report, labeled "cognitive" and "sensorimotor," were combined in a single experiment (Bridgeman, Lewis, Heit, & Nagle, 1979). Saccadic suppression of displacement, the failure to perceive a target motion that takes place during a saccade, was contrasted with accurate motor behavior by asking subjects to point to the position of a target that had been displaced and then extinguished (Bridgeman, Lewis, Heit & Nagle, 1979). Subjects were also asked whether

the target had been displaced. Preventing the subjects from viewing their hands (open-loop pointing) guaranteed that only internally stored spatial information could be used for pointing. The displacement was detected on some trials, while on others it went undetected, but pointing accuracy was similar whether or not the displacement was detected perceptually.

Other early evidence came from experiments on induced motion. A fixed target and a background frame were projected on a screen (Bridgeman, Kirch & Sperling, 1981). When the background frame was displaced left or right, subjects experienced stroboscopic induced motion -- the target appeared to jump in the opposite direction. After the target and background were extinguished, the subjects pointed to the last target position. Despite the induced motion, they pointed to the same location whether the target had appeared to jump left or right. This leads to the conclusion that the displacement signal was present only in the cognitive system.

In another condition we inserted displacement information selectively into the motor system by nulling the perceived displacement. Each subject adjusted the real target motion until the target appeared stationary, so that the real motion, in phase with the background, exactly matched the induced motion, out of phase with the background. Thus perception specified a stable target. Nevertheless, subjects pointed in different directions when the target was extinguished in the left or the right positions, showing that the difference in real target positions was still represented in the sensorimotor pathway. This is a double dissociation: in the first condition the apparent target displacement affected only the cognitive measure, while in the second condition the real displacement affected only the sensorimotor measure.

In recent years the empirical base supporting a two-visual-systems interpretation has expanded greatly. Subtle lesions reveal a perceptual system missing just those capabilities presumably needed to control action, yet an intact capability for action. Milner and Goodale describe in detail their famous patient DF, who has severe damage to the perceptual system but an intact motor system. The damage is selective -- DF can recognize the color or size of an object, but cannot identify it despite normal sensory thresholds. If presented with a slit in a card, she cannot identify the orientation of the slit. When asked to put her hand through the slit, though, she orients her fingers in the proper orientation and slips through without contacting the card. She can pick up an object precisely, without knowing its shape. Her motor system is intact even though her perceptual system has no information about the visual information needed for performing the task.

It is interesting that DF is no longer so easy to test. Having had visual agnosia for so long, she can often solve perceptual problems, not because her brain has recovered, but because she has learned ways around her handicaps. She has learned to make physical movements, sometimes very subtle ones, because she knows that she can perform the correct movements 'automatically' and do better than her perception would lead her to expect. Then she simply observes the movements, and reports them as a substitute for perceptual experience. For the slit problem DF rotates her hand into the position

appropriate for penetrating the slit, without actually approaching it, then reports on what has happened to her hand (her proprioception is normal).

The Visual Brain in Action is a joy to read, so well written that it carries the reader along almost like a novel, nailing down a huge variety of phenomena and integrating them smoothly into the two-systems view. Clinical, psychophysical and neurophysiological data are interwoven so seamlessly that the reader is more aware of the problem than the technique, an example of what cognitive neuroscience can become.

Some parts of the story remain incomplete. We don't yet know enough about the interactions of the two systems, for example. Apparently the cognitive branch can inform the motor branch under some conditions, but information cannot flow the other way. It is not clear how the cognitive system identifies a particular object as a target, to a system that cannot recognize different targets. And the temporal lobe/parietal lobe dichotomy is not quite as clean as one would like; the lobes are more convention than anatomical reality in this part of the brain in any case, and nature has not segregated the systems neatly into dorsal and ventral components; things get a bit tangled in the posterior and inferior parietal regions. The distinction between what and how, though, as already proved an enormous step in defining the workings of the visual brain.

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