A Dichotomous Visual Brain?

Marc Jeannerod
Institut des Sciences Cognitives
67 Boulevard Pinel, 69675, Bron
FRANCE

jeannerod@isc.cnrs.fr

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ABSTRACT: Recent experiments in normal subjects using neuroimaging demonstrate that the dorsal cortico-cortical pathway is involved during purely perceptual activities. Pathological cases with right posterior parietal lesions show deficits in visuospatial perception. It is argued that the radical dichotomy between perception and action pathways, as heralded in Milner and Goodale's book should be reexamined. The idea of distributed networks using resources in both visual pathways and recruited as a function of task demands is presented.

The Milner and Goodale model of the visual functions of cerebral cortex is based on binary reasoning. Accordingly, the model puts forward the case that the output of the visual cortex is chanelled into two anatomical pathways which account for two modalities of functioning and so ends up with two distinct outcomes: activation of the dorsal cortical pathway generates automatic, unconscious action; whereas activation of the ventral pathway generates conscious perception (see Milner & Goodale, 1995). My point will be that such dichotomies may represent oversimplifications and may even be revealled to be fallacious.

First, perception and action are loose terms which require qualification. My interpretation of the role of Milner and Goodale's "perception" is the creation of a modality-specific (in this case, visual) internal representation of a stimulus viewed by the subject. By contrast, they consider "action" as a direct transformation of the visual stimulus into motor

commands. The ventral pathway, responsible for perception, would be a "cognitive" pathway, enabling the subject to give conscious responses to questions concerning sensory events, and to build a conscious experience from these events. The dorsal pathway, reponsible for visuomotor transformation, would be a "Gibsonian" pathway used for directly mapping sensory events into movements. Action and perception would therefore be fundamentally different ways of dealing with the external world. The problem with this conception is twofold: First, the fact is that a subject is rarely acting *or* perceiving, and that he is mostly using both modalities at the same time. Second, perception involves a great deal of unconscious functioning and does not always lead to immediate conscious experience, while actions are far from being always automatic (they involve representations to the same extent as perception does).

The main argument of Milner and Goodale for matching the perception/action and the ventral/dorsal dichotomies upon each other is based on evidence from lesions. According to the classical double dissociation paradigm, they argue that ventral lesions alter perception, not action, and that dorsal lesions alter action, not perception. If we rely on the above definitions, it is true that patients with ventral lesions may retain accurate visuomotor transformations. By contrast, however, it is not true that perception is unaltered following dorsal lesions (see Warrington & Taylor, 1973). People with dorsal lesions may be unable to copy objects by drawing (the so-called constructive apraxia). They have great difficulties recognising on a photograph objects displayed in a non-canonical orientation (Warrington & James, 1986). They cannot resolve, either motorically or perceptually, the 3-D orientation of objects or their spatial relations with respect to other objects.

Arguments drawn from lesioned brains may not always be valid for understanding normal brain function. Results obtained in normal subjects give a different picture of interactions between perception and action. In a recent study using PET Faillenot et al. (1997) have compared the patterns of cortical activation during two different tasks, an action task (grasping objects of different sizes and shapes by hand), and a perceptual task (matching these objects with each other). In the first task, the main activation focus was in the inferior parietal lobule contralateral to the hand and in the right posterior part of the intraparietal sulcus. In the second task, two foci were found, one in the left inferotemporal cortex, and one in the right posterior parietal cortex: this latter focus partly, but clearly, overlapped with the parietal focus of activation for grasping. This result means that perceptual analysis, even when no action is to occur, uses resources that pertain to the dorsal pathway. Following up this result, Faillenot et al (1999) compared cortical activation during perceptual discrimination of shape orientation when shapes were presented with different degrees of slant in the frontal plane (a 2-D orientation task) or in the sagittal plane (a 3-D orientation task). These tasks, where no action was ever required, did produce activation in areas located in the posterior part of the intraparietal sulcus, as well as at the occipito-temporal junction and in the inferior temporal gyrus (area 37).

At variance with object oriented action, where the visual stimulus is coded in egocentric co-ordinates (i.e., centred on the acting subject), perceptual activity as tested in this type

of experiment implies using an allocentric frame of reference (i.e., centred on the external objects). Indeed, this was the point of the original model of the cortico-cortical visual pathways, where Ungerleider and Mishkin (1982) distinguished between two perceptual channels, one for objects, the other one for space. The effects of occipito-parietal lesions in monkeys were tested using a typical allocentric task where the animal had to determine the mutual spatial relationships between objects. I may be talking here of a "different" sort of perception, oriented, not toward analysis of objects for identification, but toward analysis of their spatial lay out. Whether the latter analysis is more often used in the context of generating an action than in the context of building a perceptual experience is a matter of discussion. By using this type of argument, I simply want to stress the fact that a conscious perceptual activity can be mediated by cortical zones supposed to pertain to the "action pathway" (see Jeannerod, 1997).

Another relevant point in this discussion is visual imagery. The relations of visual imagery to visual perception have been the object of vigorous debate, one of the better supported hypotheses being that visual imagery corresponds to "seeing with the mind's eye" to the same extent as perception corresponds to seeing with the real eye. Accordingly, PET studies in normal subjects have revealed that visual imagery activates cortical areas closely related to visual perception. According to Kosslyn et al (1993), imagery tasks (e.g., mentally representing letters) activate not only primary visual cortex and middle and inferior temporal gyri, but also the angular gyrus and areas in the superior and inferior parietal lobules on both sides.

The above recent studies of normal brain functioning therefore do not support the notion of a clear boundary between regions and mechanisms devoted to action and perception, respectively. This is precisely, perhaps, because the two functions do not work in isolation. As a consequence, it becomes difficult to assign conscious processes, like perception, and automatic processes, like goal-oriented actions, to separate pathways. It is no longer possible to hold that consciousness is a top-down attribute of activities processed in the ventral pathway and, conversely, that the functioning of the dorsal pathway has to be bottom-up and non-conscious. Ventral and dorsal cortico-cortical pathways do not seem to present sufficiently different structural organisations to warrant such a radical functional dichotomy. Recent data demonstrate that semantic processing (a likely ventral function) can prime the motor cortex within extremely short delays and without conscious awareness (Dehaene et al, 1999), two characteristics that Milner and Goodale would consider as pertaining to the dorsal pathway.

My own view on this problem is that processing of visual information is task-dependent. Neural subsystems for analysis of visuospatial cues, object identification, estimation of context, visuomotor transformation, generation of the proper movement, etc., are assembled with each other according to the needs of the task, using resources from ventral and dorsal pathways in both hemispheres. The resulting distributed neural representations revealed by neuroimaging studies are endowed with predominantly "pragmatic" or "semantic" functions, with "pure" action or "pure" perception at the two extremities of the spectrum.

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