

# What Neuroimaging Tells Us About the Division of Labour in the Visual System

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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 (1995) propose that the visual system is able to accommodate two distinct functions: vision for action and vision for perception. These functions are proposed to rely respectively on the dorsal and the ventral streams. This functional dissociation emphasizes the output rather than the input side of the visual analysis. Progress in neuroimaging offers various ways to investigate this model. There is now evidence from studies using positron emission tomography on the study of brain activity in the perception of human movement that the roles of the two pathways are more easily understood when considered from the point of view of the output side of visual processing as suggested by Milner and Goodale.

A well established general framework indicates that the visual cortex is organized into two distinct pathways both originating in the primary visual cortex. The ventral stream which reaches the inferotemporal cortex is involved in the identification of objects, whereas the dorsal stream which projects into the parietal cortex is engaged in the visual spatial localization of objects (Ungerleider & Mishkin, 1982). In their book, Milner and Goodale (1995) substantially reinterpreted these functions on the basis of certain neuropsychological dissociations. They postulate that both streams process information about object features and their spatial location, but that the visual information is used

differentially by each stream. The ventral pathway allows the construction of long-term perceptual representations, from object features and their relations. These representations are implicated in the recognition, categorization and signification of objects. In contrast, processes supported by the dorsal pathway are concerned with on-line information about the spatial location of objects. The dorsal stream and associated pathways are responsible for the programming and for the visual control of skilled movements. To summarize, the purpose of the visual processing (perception vs. action) determines the nature of the processing engaged (ventral or dorsal stream).

The bedrock of the model proposed by Milner and Goodale is that vision accommodates two distinct functions. One is concerned with acting on the world and the other with representing it. This distinction is then reformulated as vision for perception and vision for action. It seems clear that such a distinction is based on a top-down approach. Perhaps not surprising since the two authors are cognitive neuropsychologists and despite the fact though they justify these distinctive functions from an evolutionary view-point. However this need not be contradictory. In fact I very much appreciate the scheme of the book, which starts from anatomy, then goes on neurophysiology and then on single case studies in neurological patients.

Most of the evidence used for the model of Milner and Goodale comes from single case studies (RV and DF). This is a good illustration of the power of cognitive neuropsychology. Within cognitive neuropsychology, it is argued that single-patient studies allow valid inferences about normal cognitive processes. Once a process is seen in a clinical setting it can then be further elucidated in studies on normal subjects. While several positron emission tomographic (PET) studies have been performed since the time the book was written, most of them have addressed the dissociation between visuospatial and recognition processes. However a few studies have directly searched for the neural activations associated with the distinction between vision for perception and vision for action. For example, we have performed two PET-activation experiments during perception of human actions.

In the first experiment, subjects were presented with video filmed pantomimes (meaningful and meaningless actions) and were requested to observe the stimuli with two purposes, either to imitate the action or to recognize it after the scanning period (Decety et al., 1997). The scans were taken only during the observation phase and thus we were able to focus on brain activity related to the perception for action or perception for recognition. The results, as predicted by the model of Milner and Goodale, showed that observation of action in order to imitate (vision for action) was specifically associated with bilateral activation of the dorsal pathways, reaching the premotor cortex. Conversely, when the task was to observe in order to recognize, the ventral pathway was involved.

The second PET experiment (Grezes, Costes, & Decety, 1998) was performed in two separate sessions using the very same set of stimuli as those presented above. In the first, subjects were required to look at videofilms without any specific aim. In the second session, subjects were requested to watch the videofilms with the aim to imitate the

actions presented. A reference condition consisted of presentation of stationary hands and was randomly distributed among the two sessions.

Observation of meaningful actions and meaningless actions without any aim was associated with activation of a common set of cortical regions. In both hemispheres, the occipito-temporal junction (Brodmann Area (BA) 37/19) and the superior occipital gyrus (BA 19) were involved. In the left hemisphere, the middle temporal gyrus (BA 21) and the inferior parietal lobe (BA 40) were found to be activated. These regions are interpreted as related to the analysis of hand movements. In addition to this common network, meaningful and meaningless movements engaged specific networks, respectively: meaningful actions were associated with activations mainly located in the left hemisphere in the dorsal precentral gyrus (BA 6), the inferior frontal gyrus (BA 44/45) and the fusiform gyrus (BA 38/20), whereas meaningless actions involved the dorsal pathway (inferior parietal lobe, BA 40 and superior parietal lobule, BA 7) bilaterally and the right cerebellum. In contrast, meaningful and meaningless actions share almost the same network when the aim of the perception is to imitate. Activations were located in the right cerebellum and bilaterally in the dorsal pathway reaching the premotor cortex. Additional bilateral activations were located in the SMA and in the orbitofrontal cortex during observation of meaningful actions.

Thus, when perception has no goal, the pattern of brain activation is dependent on the nature of the movements presented. But when perception has a goal, namely to imitate, the subject's strategy has a top-down effect on the information processing which seems to give priority to the dorsal pathway involved in perception for action. In other words, vision for action does not necessitate access to semantic knowledge of objects, which may explain the brain activations found during perception of pantomimes to imitate. These results provide direct evidence for the model presented by Milner and Goodale.

I agree with Milner and Goodale that the distinction made by Ungerleider and Mishkin (1982) between a dorsal space and a ventral form system is not the best way to characterize the division of labor in the visual system. I think that neuroimaging studies in normal subjects will in the future further clarify this distinction between the two models.

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