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Special issue: Commentary

Two visual pathways – Where have they taken us and where will they lead in future?

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1. Introduction

We are delighted to see the impressive range of empirical and theoretical research that has been inspired directly or indirectly by our Two Visual Systems (TVS) model. The utility of a good theory, after all, lies not so much in its truth (no simple theory can truly describe the complexities of the brain), as in its value as a scientific tool and as an impetus for further research. If, after extensive empirical investigation and scrutiny, a theory can still retain a claim to its essential broad-brush validity, then so much the better: a process of modification, refinement and elaboration may ultimately yield a closer approximation to the truth. But even if it is eventually abandoned, a theory can still claim to carry heuristic value – that is, value in framing useful research questions, in providing pointers to where fruitful inquiry might best be directed, and in stimulating research in areas that might otherwise be neglected. By doing so, the theory will ensure that science moves forward and provides a clearer picture of how the world (and in this case, the brain) truly works. This issue of *Cortex* provides good evidence that if only by these criteria – the stimulation of empirical and theoretical research – the Two Visual Systems model can fairly be judged to have had some appreciable success since its proposal twenty-five years ago.

The research reported in this special issue has stemmed from the specific model that we put forward (Goodale & Milner, 1992; Milner & Goodale, 1995), which recast the original theory of Ungerleider and Mishkin (1982) of two cortical visual systems in the primate brain. Their classic 1982 paper demonstrated through anatomical studies how cortical visual areas in the primate brain are grouped into two broad clusters (the ventral and dorsal pathways or streams), and went on to propose functional correlates for these two systems. According to Ungerleider and Mishkin's *what vs. where* model, the ventral stream is crucially concerned with object recognition, while the dorsal stream mediates visuospatial perception. Ten years later, we re-interpreted the behavioural data available at the time, including their own work on patient D.F., and proposed that the division of labour between the two streams might be better characterized as one between two modes of output, rather than two modes of input (i.e., object vs spatial vision). Specifically, we argued that vision needs to serve two broad functional roles in an animal's life: to provide visual recognition routines for identifying goals and potential threats, and to direct real-time guidance of the animal's movements. Our proposal cuts across the distinction made by Ungerleider and Mishkin, in that *both* visual streams would need to deploy aspects of *both* object and spatial vision in order to fulfil their proposed functional roles.

We are heartened to see that our conceptual framework has also contributed to the development of similar models in the auditory system (Rauschecker, present issue; for review, see Hickok & Poeppel, 2007) and the somatosensory system (Dijkerman & de Haan, 2007). The Rauschecker article, in particular, offers a novel and over-arching account of the functional organization of the dorsal stream in both vision and audition in which 'where, when and how' are combined to produce coordinated actions. We are also encouraged to see that the TVS has inspired machine learning approaches to understanding the division of labour between the two pathways. In this special issue, Scholte, Losch, Ramakrishnan, de

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Haan & Bohte apply cost-functions and deep neural networks to an understanding of how information about objects might be processed and stored in these networks. One of the challenges faced by machine learning approaches, however, is how to model optimal actions. Perceptual discrimination is relatively easy to simulate but modelling goal-directed actions is much more difficult. Machine learning approaches to understanding the functional organization of the brain, however, are an exceptionally promising development.

The majority of the remaining articles in this special issue can be broadly grouped according to the methodologies used to interrogate the TVS model we proposed. We will comment on them under four headings: (a) studies of neurological patients; (b) functional neuroimaging; (c) nonhuman primate studies; (d) studies of visual illusions and psychophysics.

1.1. *Studies of neurological patients*

1.1.1. *Visual form agnosia*

One of the inspirations for our TVS model in the early 1990s was the discovery that a patient with visual form agnosia (D.F.) was able to perform well-calibrated acts (posting and grasping) toward visual stimuli that she was unable describe or discriminate (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). This, of course, was well before the days of functional MRI, at a time when neuropsychological observations like these were the lifeblood of cognitive neuroscience. D.F. provided evidence that visual recognition and visually-guided action could be dissociated, and although the evidence as to D.F.'s brain damage (caused by hypoxia) was less than precise, it was apparent that (a) there was disseminated damage in several parts of the brain, but (b) there was a substantial bilateral region of dense atrophy in the lateral occipital lobes. This latter observation was consistent at least with the idea that the early stages of the ventral stream had suffered major damage. We proposed that, while clearly D.F. could never be described as having focal lesions, nevertheless her likely ventral-stream damage might have caused a disruption of visual perception and recognition while leaving her dorsal stream, if not intact, at least able to function satisfactorily in visuomotor tasks.

Never in our numerous articles about D.F. then or during the 25 years since then, have we claimed that her dorsal stream was *completely* spared. Indeed it would have been a miracle if D.F.'s hypoxic brain damage had not affected the areas of her dorsal stream to some degree. So it was no great surprise when some years ago, in our first MRI study of D.F., James et al. (2003) explicitly reported atrophy in her intraparietal sulcus, even though they were also able to show grasp-related activation in the same region (thereby supporting our original interpretation of D.F.'s surviving visuomotor capacities). In addition, James et al. also described a lesion in the left superior occipito-parietal cortex, another area within the dorsal stream. We now know from high-resolution structural MRI scans that D.F. has cortical thinning in the superior occipito-parietal region in both hemispheres (Bridge et al., 2013). In a recent review, Whitwell, Milner, and Goodale (2014) discussed D.F.'s dorsal-stream damage, and noted explicitly that "*DF's visuomotor performance, even centrally, is not completely normal in all situations*". The article by Rossit et al. in the present issue provides further evidence of the effects of this partial dorsal stream damage.

Rossit et al. show clearly that D.F. is impaired at reaching for peripheral visual targets. The only previous systematic study of D.F.'s reaching, reported by Milner, Dijkerman, and Carey (1999), did not indicate a reaching impairment, but those results do not contradict the findings of Rossit et al., for two reasons. Firstly, Milner et al.'s study was not designed to study far-peripheral reaching – the aim of the study was purely to compare D.F.'s immediate and delayed pointing. The stimuli were in fact presented in locations that averaged only 6.5° lateral to fixation (range 4.2–11.1°). This contrasts with Rossit et al.'s study, where the stimuli were presented at peripheral locations averaging 15° laterally (range 10–20°). Their data show a clear increase in D.F.'s errors with increasing eccentricity across this range, but at the locations (averaging 6.5°) used by Milner et al., it is clear that D.F.'s errors would have fallen within the normal range. Secondly, as Rossit et al. mention, it is possible that D.F.'s parietal damage has become more extensive over time (see Whitwell et al., 2014), so that any mis-reaching that may have been present in 1996 when Milner and colleagues did their testing, could well have deteriorated further by the time of Rossit et al.'s testing 14 years later.

Do their findings imply, as Rossit et al. conclude, that "*patient DF can no longer be considered as an appropriate single-case model for testing the neural basis of perception and action dissociations*"? We believe, on the contrary, that D.F.'s grasping and perceptual reports can continue to throw light on the coding of object geometry in the two visual streams, just as they always have; and that none of our published arguments are compromised by the new data. Even within the visuospatial domain, contrasts between her behaviour and that of optic ataxic patients have proved instructive, both in studies of delayed pointing (Milner, Dijkerman & Carey 1999, 2001) and of obstacle avoidance, where D.F.'s performance is relatively well preserved (Rice et al., 2006), unlike patients with optic ataxia (Schindler et al., 2004). Of course, it would be wonderful if we could do as Rossit et al. recommend, and contrast "*further, more pure cases, of visual form agnosia with optic ataxia*". Unfortunately, however, D.F. is the purest case of visual form agnosia ever yet described, and even impure cases are rare. For a detailed discussion of D.F.'s continuing relevance, we refer the reader to the recent opinion piece by Ganel and Goodale (2017).

In one instructive early study, Goodale Jakobson & Keillor (1994) showed that D.F. was quite unable, after a short delay, to correctly simulate grasping an object (of varying width) that she had been shown earlier. This observation chimed well with the TVS model's conjecture that the dorsal stream acts in the "here and now" and thus has no visual memory. Schenk and Hesse in this issue, argue at length against this idea. They provide a critical review in which they argue that all the evidence supporting the notion that the dorsal stream works in real time has flaws or alternative explanations. Even an unbiased reader, however, might conclude that the parsimony of a single model that accounts for all the data (and predicts most of it) is preferable to a series of ad-hoc alternative accounts of each finding that are not guided by any overall theoretical framework. Schenk and Hesse claim in particular that their finding that D.F. retains good posting performance even after a 3-sec delay (Hesse & Schenk, 2014) provides a definitive

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