



The time-course of activation in the dorsal and ventral visual streams during landmark cueing and perceptual discrimination tasks



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ABSTRACT

Different patterns of high density EEG activity were elicited by the same peripheral stimuli, in the context of *Landmark Cueing* and *Perceptual Discrimination* tasks. The C1 component of the visual event-related potential (ERP) at parietal – occipital electrode sites was larger in the *Landmark Cueing* task, and source localisation suggested greater activation in the superior parietal lobule (SPL) in this task, compared to the *Perceptual Discrimination* task, indicating stronger early recruitment of the dorsal visual stream. In the *Perceptual Discrimination* task, source localisation suggested widespread activation of the inferior temporal gyrus (ITG) and fusiform gyrus (FFG), structures associated with the ventral visual stream, during the early phase of the P1 ERP component. Moreover, during a later epoch (171–270 ms after stimulus onset) increased temporal–occipital negativity, and stronger recruitment of ITG and FFG were observed in the *Perceptual Discrimination* task. These findings illuminate the contrasting functions of the dorsal and ventral visual streams, to support rapid shifts of attention in response to contextual landmarks, and conscious discrimination, respectively.

1. Introduction

A striking feature in the neural architecture of vision in primates is that visual processing occurs in two distinct, and relatively independent cortical pathways, known as the dorsal and ventral visual streams (Milner and Goodale, 2006; Ungerleider and Mishkin, 1982). Here, we report an electrophysiological study that illuminates the contrasting roles of the dorsal and ventral streams, for supporting rapid shifts of spatial attention and forming conscious perceptual representations, respectively.

Sensory information from the eyes is conveyed, via the lateral geniculate nucleus (LGN) of the thalamus, to primary visual cortex (V1) in occipital cortex. Cortical visual processing then splits into two parallel streams: The dorsal visual stream follows a route from V1 to posterior parietal cortex, while the ventral visual stream forms a parallel pathway connecting V1 with inferotemporal cortex. The vast majority of fibres in the dorsal stream carry signals that originate from the two magnocellular (M-cell) layers of LGN, while the ventral stream is the main target of fibres originating from the four parvocellular (P-cell) layers of LGN. In addition to its P-cell input, the ventral stream also receives substantial M-cell input (Ferrera et al., 1994). P-cell and M-cell derived fibres have distinct physiological properties. Notably, signal conduction speed is substantially quicker in the latter case (Merigan and Maunsell, 1993), and this property has been linked with

the observation that visually responsive cells in ‘high-level’ structures in the dorsal stream respond with extremely brief latencies, leading some authors to refer to these parietal areas as ‘the fast brain’ (Bullier, 2001).

According to the influential ‘what vs. where’ theory of Ungerleider and Mishkin (1982), the ventral stream is responsible for encoding the identity of objects, while the dorsal stream is responsible for encoding their locations and spatial relationships. Key evidence for this view came from ablation studies carried out with rhesus monkeys. Lesions to the ventral stream, but not those applied to the dorsal stream, impaired *Perceptual Discrimination* (discriminating between familiar and unfamiliar objects). Conversely, lesions to the dorsal stream, but not those applied to the ventral stream, impaired performance of a visual landmark task, where monkeys were rewarded for choosing a covered foodwell that was close to a landmark object, such as a striped cylinder (Ungerleider and Mishkin, 1982).

Milner and Goodale (2006) proposed that rather than being specialised for encoding different stimulus attributes (object identity vs. spatial location), the ventral and dorsal visual streams are specialised for performing distinct visual functions, associated with cognition and motor behaviour respectively. According to this framework, the ventral stream delivers conscious perception of the visual world, and provides representations that participate in memory, planning and executive functions, while processing in the dorsal stream is dedicated to the control of visually guided actions. Milner and Goodale refer to the

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distinct functions associated with the ventral and dorsal visual streams as *vision for perception* and *vision for action*, respectively. Strong evidence for Milner and Goodale's theory has been obtained from human neuropsychology. In patient DF, bilateral damage to area LO, part of the ventral stream, produced a dense visual agnosia, rendering her unable to recognise familiar objects or even perform simple visual discriminations, such as judging the orientation of a slot presented in various orientations. However, visual processing in the dorsal stream appears to have been spared, and she has retained the ability to perform visually guided actions. DF is able to reach for and grasp objects appropriately, and is able to orient her arm and hand correctly, when asked to 'post' her hand through a slot presented in different orientations – even though her ability to consciously report slot orientation is at chance (Milner and Goodale, 2006). In contrast, patient RV, who has sustained damage to the dorsal stream, is able to recognise familiar objects, but exhibits a syndrome known as optic ataxia, where the ability to perform visually guided actions, such as reaching for and grasping an object is severely impaired (Milner and Goodale, 2006). According to (Milner, 2012) evidence from functional neuroimaging, together with neuropsychological observations indicates that visual processing in the dorsal stream is non-conscious. Moreover, visually guided actions, such as reaching for a cup, and visuomotor skills, such as playing tennis or baseball, require rapid visual processing, and the speedy conduction velocity of the M-cell inputs to the dorsal stream is likely to be an important factor for efficient performance of such actions.

Relationships between the dual-stream models of vision just described and mechanisms of attention-shifting were examined by Lambert et al. (2017). A unified model of vision and attention was presented, in which the focus of attention can shift in response to input from either visual stream. More specifically, it was proposed that non-semantic encoding of *landmark* information by the dorsal stream, elicits rapid shifts in the orientation of attention, while encoding the identity and meaning of environmental cues, via ventral stream encoding, is associated with a slower form of attention-shifting known as endogenous attention (see Chica et al., 2013; Klein, 2004; Klein and Lawrence, 2012). These proposals were tested in a series of experiments investigating attention-shifting in response to landmark and identity cues. In the *Landmark Cueing* procedure participants responded to target stimuli that were preceded by a pair of bilaterally presented cues (e.g. the letters X and T), and the target usually occurred near to one of the cue letters (the landmark). Thus, the location of the target was cued by the *location* of the landmark stimulus. This procedure is conceptually related to the landmark learning task used by Ungerleider and Mishkin (1982) described above: in both cases, an object of interest appears near to a landmark cue. Lambert et al. (2017) also describe a second procedure, termed *Identity Cueing*. As in the landmark cueing procedure, participants responded to targets preceded by a pair of bilaterally presented cue letters, but in this case the two letters were identical. Targets usually appeared on the right of the screen following one pair of letters (e.g. X + X), and on the left following a different letter-pair (e.g. T + T). Hence, in this procedure the location of the target is cued by the *identity* of the cue stimuli, not by their spatial relationship with target location. Across six experiments it was found that visual orienting in response to identity cues collapsed, while orienting in response to landmark cues remained robust under stimulus and task conditions that favoured dorsal stream encoding, namely: peripheral visual presentation, low luminance contrast (see also Lambert and Shin, 2010), brief cue exposure duration, and brief periods between cue and target onset (see also Lambert and Duddy, 2002). Moreover, consistent with characterisations of dorsal stream as non-conscious (Milner and Goodale, 2006; Milner, 2012), landmark cueing effects were observed when participants were aware neither of the presence of low-contrast peripheral landmarks, nor of their predictive utility with respect to target location (Lambert et al., 2017, Experiment 4; see also Lambert et al., 1999, 2000; Shin et al., 2011). Conversely, robust orienting in response

to identity cues was observed when stimulus conditions favoured ventral stream encoding (high luminance contrast, relatively long cue exposure duration, relatively long cue-target delays). Critically, *Identity Cueing* effects were robust and *Landmark Cueing* effects collapsed when cues were rendered with isoluminant borders, which are visible to the ventral stream, but cannot be encoded by the luminance-sensitive, but chromatically insensitive M-cell channels of the dorsal stream (Cavanagh et al., 1992; Livingstone and Hubel, 1988). Accordingly, Lambert et al. (2017) concluded that the behavioural signature of visual orienting in response to landmark cues corresponds well with known characteristics of the dorsal visual stream.

More direct evidence of dorsal stream involvement in *Landmark Cueing* was obtained by Marrett et al. (2011), in a study investigating the ability of patient DF, described above, to shift attention in response to landmark letter cues, and to discriminate consciously between peripheral letters. According to the framework developed by Lambert et al. (2017), the former task should recruit dorsal stream encoding, while performing the conscious discrimination task will require *Vision for Perception*, and recruit ventral stream encoding. Consistent with the damage to her ventral stream and consequent visual agnosia, DF's ability to report consciously whether a particular letter (X or T) had been presented on the left or right was severely impaired (66% correct); the same task was trivially easy for neurologically intact control participants. Nevertheless, and in agreement with our contention that *Landmark Cueing* is mediated by the dorsal stream which remains intact in this individual, the ability of patient DF to perform the *Landmark Cueing* task was essentially normal: she responded more rapidly when a target appeared at the location predicted by visual landmark cues, and her performance was similar to that of four neurologically intact control participants. A second experiment, performed with normal participants, provided preliminary evidence that letter processing in the context of the *Landmark Cueing* and *Perceptual Discrimination* tasks was associated with differential early activation of the dorsal and ventral streams (Marrett et al., 2011). Source localisation of the early phase of the P1 component of the visual event-related potential (ERP) elicited by peripheral letters in the *Landmark Cueing* task, revealed evidence of activation in a dorsal stream structure, the superior parietal lobule (SPL); but when the same stimuli were presented in the *Perceptual Discrimination* task, source localisation during the same time-window indicated activation in two ventral stream structures, the inferior temporal gyrus (ITG) and fusiform gyrus (FFG) (Marrett et al., 2011).

In the current study we used high density EEG to assess activity within the dorsal and ventral visual streams, as participants performed *Landmark Cueing* and *Perceptual Discrimination* tasks. In the *Landmark Cueing* task (see Fig. 1, upper panel), participants were first shown a pair of letters, presented peripherally and bilaterally, and then made a key-press response to indicate the location (left or right) of a target object, a grey circle. On 75% of trials the target appeared on the same side as one of the cue letters (e.g. X). In the *Perceptual Discrimination* task (see Fig. 1, lower panel), participants were also presented with a pair of letters bilaterally, and then made a left or right key-press response. However, in this case the left-right response signalled whether a probe letter presented in central vision had been presented on the left or right. On 75% of trials a particular letter (e.g. X) served as the probe. These features ensured that the stimulus presented initially, the temporal structure, and the probability of making a left or right response were all matched between the two tasks. Behavioural evidence marshalled by Lambert et al. (2017) and described above, together with the neuropsychological and neurophysiological findings of Marrett et al. (2011) led us to predict that the same peripheral letter stimuli would elicit different patterns of neural activation in these two task contexts, with the *Landmark Cueing* task recruiting relatively stronger activation of the dorsal visual stream, and the *Perceptual Discrimination* task recruiting relatively stronger activation in the ventral visual stream.

Presentation of peripheral letter stimuli to the upper visual field in our two task procedures, enabled us to measure and apply source

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