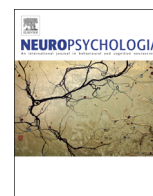




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Review article

Visual motion serves but is not under the purview of the dorsal pathway

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ABSTRACT

Visual motion processing is often attributed to the dorsal visual pathway despite visual motion's involvement in almost all visual functions. Furthermore, some visual motion tasks critically depend on the structural integrity of regions outside the dorsal pathway. Here, based on numerous studies, I propose that visual motion signals are swiftly transmitted via multiple non-hierarchical routes to primary motion-dedicated processing regions (MT/V5 and MST) that are not part of the dorsal pathway, and then propagated to a multiplicity of brain areas according to task demands, reaching these regions earlier than the dorsal/ventral hierarchical flow. This not only places MT/V5 at the same or even earlier visual processing stage as that of V1, but can also elucidate many findings with implications to visual awareness. While the integrity of the non-hierarchical motion pathway is necessary for all visual motion perception, it is insufficient on its own, and the transfer of visual motion signals to additional brain areas is crucial to allow the different motion perception tasks (e.g. optic flow, visuo-vestibular balance, movement observation, dynamic form detection and perception, and even reading). I argue that this lateral visual motion pathway can be distinguished from the dorsal pathway not only based on faster response latencies and distinct anatomical connections, but also based on its full field representation. I also distinguish between this primary lateral visual motion pathway sensitive to all motion in the visual field, and a much less investigated optic flow sensitive medial processing pathway (from V1 to V6 and V6A) that appears to be part of the dorsal pathway. Multiple additional predictions are provided that allow testing this proposal and distinguishing between the visual pathways.

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1. Visual motion is involved in almost all visual functions

Our visual system copes with ongoing visual motion, either induced by our own movements or by the movements of objects or events external to us. While the visual system relies on stabilization mechanisms such as the corollary discharge /efferent copy (Crapse and Sommer, 2008a,b) to counteract the significant visual motion changes induced by our movements (eye, head, or body), visual motion is inherently present even upon fixation (micro-saccades, drift, and tremor (Yarbus, 1967; Martinez-Conde et al., 2004, 2013)). Over and above the optic flow changes we encounter when we move in the world, movements around us introduce additional visual motion (including the movements of our extremities). Put simply, the persistent visual motion encountered by our visual system dictates that visual motion will be inherent to all our visual experiences. These include the involvement of visual motion in visuo-vestibular and body balancing mechanisms (Paulus and Zihl, 1989; Shallo-Hoffmann and Bronstein 2003), in observation of stationary scenes as we scan them, in shape perception (for animated, non-animated, moving or stationary shapes), in smooth pursuit, saccades, hand-eye interaction and coordination, understanding facial expressions or body gestures, and even when we scan, skim and read across texts.

2. Visual motion processing is not under the purview of the dorsal pathway

A seminal theoretical account proposes that the visual system is segregated into two main processing pathways: the dorsal “where”/“how”/“action”/“spatial” pathway associated with aspects related to attention, spatial navigation, and preparation for action, and the ventral “what”/“perception”/“object” pathway associated with the computation of form and shape perception representations, such as edges, textures, surfaces, and colors (Ungerleider and Mishkin, 1982; Vaina, 1990; Goodale and Milner, 1992). However, there is evidence that speaks against the strict two-pathway hypothesis (Franz et al., 2000; McIntosh and Schenk, 2009; Hesse et al., 2012; Himmelbach et al., 2012). Numerous studies indicate involvement of ventral regions in dorsal-associated functions (e.g. depth or motion (Britten et al., 1992; Van Oostende et al., 1997; Grill-Spector et al., 1998; Janssen et al., 1999, 2000a,b; Kourtzi and Kanwisher, 2001; Gilaie-Dotan et al., 2002; Zhuo et al., 2003, 2013b; Li et al., 2013)), or the involvement of dorsal regions in ventral-associated functions (e.g. shape or face (Hasson et al., 2003; Janssen et al., 2008; Konen and Kastner, 2008; Srivastava et al., 2009; Romero et al., 2012, 2014; Freud et al., 2015; Theys et al., 2015)). Furthermore, other studies provide support for distributed processing in the visual cortex (e.g. (Schiller, 1993; DeYoe et al., 1994; Lennie 1998; Haxby et al., 2001)). Therefore the prevailing view is of a more complex and distributed visual cortex rather than the strict two-pathway segregation (Milner and Goodale, 2008; McIntosh and Schenk 2009).

Although visual motion is inherent in almost all visual functions, the received view is that visual motion processing and perception are under the purview of the dorsal pathway (e.g. (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992; Gross et al., 1993; Nassi and Callaway, 2009; Kravitz et al., 2011; Markov et al., 2013b, 2014)). The best example for this view is region MT/

V5 (see below) which is (i) sensitive to visual motion across the visual field (Allman and Kaas, 1971; Dubner and Zeki, 1971; Desimone and Ungerleider, 1986; Fiorani et al., 1989; Weiner and Grill-Spector, 2011), (ii) its integrity is critical to visual motion perception as evident from primate (Newsome et al., 1985; Newsome and Pare, 1988; Salzman et al., 1990, 1992; Schiller, 1993; Pasternak and Merigan, 1994; Nichols and Newsome, 2002) and human studies [(Zihl et al., 1983; Marcar et al., 1997; Zihl and Heywood, 2015) and patients 9, 10, 26 in Schenk and Zihl (1997)], and (iii) it has been continually associated with and considered part of the dorsal pathway (e.g. (Shipp and Zeki, 1985; Livingstone and Hubel, 1987; DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988; Regan et al., 1992; Kravitz et al., 2011; Pitzalis et al., 2012a; Markov et al., 2013a,b, 2014)).

But a more scrutinized observation paints a different and more complicated picture. For a start, some types of visual motion perception critically depend on regions *outside* the dorsal pathway. For example, basic motion perception skills, such as detecting visual motion or discriminating the direction of coherent motion when it is embedded in noise, critically depend on the integrity of the right ventral visual cortex (Gilaie-Dotan et al., 2013b). Recent studies also show that biological motion perception, which is the ability to visually perceive human movements, depends on the integrity of regions outside of the dorsal visual pathway, such as the posterior superior temporal sulcus (pSTS) and the ventral premotor cortex (vPMC) (Vaina and Gross, 2004; Saygin 2007; van Kemenade et al., 2012). In addition, the vermis, which is part of the cerebellum, is also critical to visual motion discrimination, irrespective of movement or motor influences (Nawrot and Rizzo, 1995, 1998; Thier et al., 1999; Jokisch et al., 2005; Cattaneo et al., 2014).

Second, visual motion perception loss can adversely affect functions that are associated with regions outside the dorsal pathway. LM, the motion blind patient (Zihl et al., 1983, 1991; Zihl and Heywood, 2015), who has suffered bilateral MT/V5 damage (Zihl et al., 1983; Shipp et al., 1994b), and lost the ability to perceive visual motion, complained that she perceived the visual world in discrete updates (as opposed to the continuous normal perception, see review Zihl and Heywood (2015)). This led to perceptual and functional deficits that went beyond dorsal pathway function. One such example is that she found it hard to maintain her visuo-vestibular body balance – which is not a function associated with dorsal pathway, and upon testing, she was found to be significantly impaired in this domain (Paulus and Zihl, 1989; Zihl and Heywood, 2015). To cope with this deficit, she walked slowly and fixated on fixed locations in the distance to allow her to slowly navigate through the environment. Another non-dorsal visual skill that was adversely affected following her lesion was her reading ability, as her reading was slow and she was unable to read faster (Zihl and Heywood, 2015). This is also consistent with a recent study reporting that transient lesions to MT/V5 induced by transcranial magnetic stimulation (TMS) can impair word recognition, a reading-related skill, in healthy individuals (Laycock et al., 2009).

In addition, some classical dorsal pathway functions can be preserved while visual motion perception is critically impaired. Although this argument, in and of itself, does not rule out the possibility that motion is still processed in parallel to other visual cues within the dorsal pathway, I find it important to highlight these findings. In LM, some dorsal visual functions were preserved

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