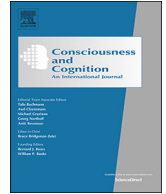




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Review article

Towards a unified perspective of object shape and motion processing in human dorsal cortex

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ABSTRACT

Although object-related areas were discovered in human parietal cortex a decade ago, surprisingly little is known about the nature and purpose of these representations, and how they differ from those in the ventral processing stream. In this article, we review evidence for the unique contribution of object areas of dorsal cortex to three-dimensional (3-D) shape representation, the localization of objects in space, and in guiding reaching and grasping actions. We also highlight the role of dorsal cortex in form-motion interaction and spatiotemporal integration, possible functional relationships between 3-D shape and motion processing, and how these processes operate together in the service of supporting goal-directed actions with objects. Fundamental differences between the nature of object representations in the dorsal versus ventral processing streams are considered, with an emphasis on how and why dorsal cortex supports veridical (rather than invariant) representations of objects to guide goal-directed hand actions in dynamic visual environments.

1. Introduction

A core framework for our understanding of visual cognition is the division of cortical processing into two anatomically and functionally distinct pathways. In an initial conceptualization of the two visual pathways, which was based on lesion studies in monkeys, Mishkin & Ungerleider (1982) described a posterior-to-anterior hierarchical flow of visual information from early visual cortex that bifurcated into a ventral pathway extending anteriorly along lateral and ventral temporal cortex, and a dorsal pathway extending into posterior parietal cortex (PPC). According to this scheme, the ventral pathway is dedicated to processing object shape and identity (i.e., the ‘what’ pathway), and the dorsal stream is dedicated to processing the spatial position of objects (i.e., the ‘where’ pathway). Goodale and Milner (1992, 2018; Milner & Goodale, 1995) argued for a reformulation of this framework in which the emphasis was shifted from distinctions between visual inputs (i.e., cortical processing of visual object properties such as shape, versus object location), to distinctions between how visual information is used: for perception versus goal-directed action. In this framework, the dorsal stream must register accurate, in-the-moment, information about object shape, size and position and transform it into visuospatial coordinates appropriate for acting upon the object with the relevant effectors, such as the arm and hand. For the purpose of the current review, the important point is that in Goodale and Milner’s framework, object properties such as size and shape are computed in dorsal cortex in the service of controlling actions, rather than for guiding perception. For example, in their 1992

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monograph entitled “Separate visual pathways for perception and action”, Goodale and Milner noted that damage to the dorsal stream “can impair the ability of patients to use information about the size, shape and orientation of an object to control the hand and fingers during a grasping movement, even though this same information can still be used to identify and describe the objects” (p. 21). In line with this framework, dissociations between perception- versus action-related processes have been reinforced by over 30 years of convergent evidence from human psychophysics, neuroimaging, and lesion studies. In particular, the existence of object-selective perceptual representations in the ventral processing pathway has been documented extensively, from studies using neuroimaging (Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2000, 2001; Kourtzi, Erb, Grodd, & Bühlhoff, 2003; Malach et al., 1995), to studies of neuropsychological patients with visual agnosia, who, following lesions to ventral cortex, show severe and lasting deficits in their ability to recognize images of objects (Farah, Monheit & Wallace, 1991; Goodale, Milner, Jakobson, & Carey, 1991; Riddoch & Humphreys, 1987). Likewise, there has been widespread support for the notion that dorsal cortex supports vision for action. In addition to neuropsychological evidence (e.g., Bálint, 1909; Holmes, 1918; Jakobson, Archibald, Carey, & Goodale, 1991; Karnath & Perenin, 2005; Perenin & Vighetto, 1988; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Ratcliff & Davies-Jones, 1972; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997), the role of the dorsal pathway in mediating vision for action has been extensively corroborated by neuroimaging (Clower et al., 1996; Culham, Cavina-Pratesi, & Singhal, 2006; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Kawashima et al., 1996) and monkey neurophysiology (Colby, Duhamel, & Goldberg, 1993; Grefkes & Fink, 2005; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997) studies.

Since Goodale and Milner’s original work, object-selective representations were discovered in PPC of the dorsal processing pathway, first in non-human primates (Denys et al., 2004; Lehky & Sereno, 2007; Murata et al., 2000; Sereno & Maunsell, 1998; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990), and later in humans (Denys et al., 2004; Fang & He, 2005; Konen & Kastner, 2008; Mruczek, von Loga, & Kastner, 2013). Interestingly, these dorsal visual object areas appear to be recruited independently of attention, and irrespective of whether a grasping movement was planned or initiated by the observer. In one of the first detailed studies of object representations in human dorsal cortex, Konen and Kastner (2008) used an fMRI-adaptation paradigm to measure the selectivity profile of different regions of human cortex to object shape, as well as to object size and viewpoint. Observers passively viewed black-and-white computerized images of objects, such as silhouettes of basic geometric shapes, line-drawings of everyday familiar objects and tools, and images of objects whose 3-D shape was defined by monocular depth cues such as shading, specular highlights and occlusion. Within the ventral stream, neural populations selective for shape included intermediate (e.g., V4) and higher-level areas such as the lateral occipital complex (LOC). Importantly, object-selective responses were also observed within topographically-defined areas along the dorsal pathway, including V3A, MT, and V7, as well as in ventral regions of PPC in the intraparietal sulcus (IPS), in IPS1 and IPS2. Moreover, both LOC and IPS1 and IPS2, responded similarly, despite changes in the size and orientation of the images, suggesting that object areas in inferotemporal cortex and PPC share a pattern of increasing invariance (or generalization) across changes in viewing conditions. Based on these results, Konen and Kastner (2008) argued that basic information about object shape, size and viewpoint, are represented in the ventral and dorsal pathways, and that the representations in each stream appear to be strikingly similar.

Since these early reports of shape processing in the dorsal stream, research into the nature of object-related processing in dorsal cortex has been burgeoning. There has been a rapid increase in studies documenting the cortical organization of object-related representations using fMRI (Chandrasekaran, Canon, Dahmen, Kourtzi, & Welchman, 2007; Erlikhman, Gurariy, Mruczek, & Caplovitz, 2016; Ludwig, Kathmann, Sterzer, & Hesselmann, 2015) and the temporal aspects of dorsal object processing using EEG (Wolke, Scholte, & Lamme, 2014; Zaretskaya & Bartels, 2015; Zaretskaya, Anstis, & Bartels, 2013). Others have emphasized the involvement of dorsal cortex (in addition to ventral stream areas) in processing particular classes of objects, such as man-made tools (e.g., Chao and Martin, 2000; Lewis, 2006; Macdonald and Culham, 2015). However, the extent to which these dorsal object representations reflect ‘toolness’ versus other attributes of the stimuli, such as their elongation, is still a subject of debate (Almeida et al., 2014; Chen, Snow, Goodale, & Culham, 2017; Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012). These recent neuroimaging studies have been complimented by case studies in neuropsychological patients, for whom aspects of object processing remain intact despite the fact that contributions to object processing from the ventral stream are reduced or eliminated due to brain damage (Freud, Rosenthal, Ganel, & Avidan, 2015). The data from these neuropsychological patients suggest that dorsal cortex may process shape during perception, in addition to action-related tasks (Milner et al., 1991; Goodale et al., 1991). Nevertheless, in line with Goodale and Milner’s (1992) two visual systems model, this shape processing was insufficient to support conscious awareness because the agnosia patients in Freud et al.’s (2015) study were unable to perform explicit shape-related judgments above-chance. A recent study using the continuous flash suppression approach, which effectively suppresses object processing in the ventral- but not the dorsal pathway, further supports these earlier patient findings by demonstrating that 3-D shape representations computed in the dorsal pathway can contribute to perceptual decisions (Fang & He, 2005; Freud, Robinson, & Behrmann, 2018).

Although much has been learned about dorsal cortex over the past 20 years, there remain a number of outstanding questions and controversies. The functional significance of dorsal stream object representations is unclear, and a detailed account of object processing in dorsal cortex is lacking (Freud, Plaut, & Behrmann, 2016; Kravitz, Saleem, Baker, & Mishkin, 2011). Important unresolved questions include whether object information is computed directly within neural populations in parietal cortex (or is relayed to dorsal cortex, perhaps via areas V3 and/or V4), what types of object properties are processed along the dorsal pathway, and the extent to which the dorsal and ventral pathways represent redundant or unique object information (Konen and Kastner, 2008). Despite Milner and Goodale’s (1992) emphasis on the fact that the output requirements for visually-guided actions with objects requires constant in-the-moment updating of object properties and spatial position in egocentric space, research in the domain of 3-D shape processing, and spatiotemporal integration, in dorsal cortex has unfolded largely in parallel. For example, with respect to what types of object

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