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Two action systems in the human brain

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ABSTRACT

The distinction between dorsal and ventral visual processing streams, first proposed by Ungerleider and Mishkin (1982) and later refined by Milner and Goodale (1995) has been elaborated substantially in recent years, spurred by two developments. The first was proposed in large part by Rizzolatti and Matelli (2003) and is a more detailed description of the multiple neural circuits connecting the frontal, temporal, and parietal cortices. Secondly, there are a number of behavioral observations that the classic "two visual systems" hypothesis is unable to accommodate without additional assumptions. The notion that the Dorsal stream is specialized for "where" or "how" actions and the Ventral stream for "What" knowledge cannot account for two prominent disorders of action, limb apraxia and optic ataxia, that represent a double dissociation in terms of the types of actions that are preserved and impaired. A growing body of evidence, instead, suggests that there are at least two distinct Dorsal routes in the human brain, referred to as the "Grasp" and "Use" systems. Both of these may be differentiated from the Ventral route in terms of neuroanatomic localization, representational specificity, and time course of information processing.

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1. Ventro-dorsal and dorso-dorsal substreams

Anatomical studies indicate that extrastriate cortex is composed of at least two segregated but interacting parallel processing streams. Traditionally, the outputs from the primary and secondary visual cortex (V1 and V2) to MT and visual area 4 (V4) are assumed to initiate two anatomically and functionally distinct channels of visual information processing named the dorsal and ventral streams. While MT is specialized for processing motion and depth, V4 is specialized for processing form and possibly color. Newer findings emphasize the role of area V3a in motion processing and its role in the dorsal stream. In general terms, the role of the dorsal stream is to mediate navigation and the visual control of skilled actions directed at objects in the visual world, whereas the goal of the ventral stream is to transform visual inputs into representations that embody the enduring characteristics of objects and their spatial relationships (Milner & Goodale, 2008).

In the monkey, downstream of MT and V3a a large number of interconnected extrastriate cortical areas in the parietal cortex, including medial superior temporal (MST), fundus of the superior temporal (FST), superior temporal polysensory (STP), ventral intraparietal (VIP), lateral intraparietal (LIP), mesial intraparietal area (MIP), anterior intraparietal (AIP) and inferioparietal area PF constitute the dorsal stream. Neuronal processing along the dorsal stream is best characterized by direction of motion and binocular disparity selectivity in MT, more complex motion analysis related to locomotion and pursuit/tracking in areas downstream from MT in the STS (superior temporal sulcus) (MST, FST, and STP), and computations informing target selection for arm and eye movements, object manipulation and visuospatial attention in areas of the intraparietal sulcus (IPS), which divides the IPL and SPL (AIP, MIP, LIP, VIP, and V6a).

There is, however, growing evidence that within the dorsal stream a further anatomical and functional subdivision exists. One of the sources of evidence for the subdivision of the dorsal stream are lesions with numerous neuropsychological consequences affecting visuo-motor function. Dorsal stream lesions affect smooth pursuit eye movements, accuracy of goal directed arm movements, speed discriminations, complex motion perception and the accurate encoding of visual space. The modularity of visuo-motor functions in the posterior parietal cortex (PPC) is also evidenced by the existence of several dorsal sub-streams achieving different visuo-motor transformations (Rizzolatti, Luppino, & Matelli, 1998). The idea of multiple visuo-motor occipito–parieto-frontal pathways has emerged from at least two different backgrounds. First, the theory of independent visuo-motor channels hypothesized that reach-to-grasp movements require independent coding of different object properties (location, size, orientation and shape) (Jeannerod, 1997). Second, anatomical studies have lent support to the idea that the transformation of these properties into appropriate movements of arm, finger and wrist is achieved by separated parieto-frontal pathways controlling the different body

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segments. For instance, anatomical studies have tended to confirm the existence of separate pathways within the dorsal system (Tanne-Gariepy, Rouiller, & Boussaoud, 2002), especially for reaching (V6a → PMd: Galletti, Fattori, Gamberini, & Kutz, 2004) and for grasping (CIP → AIP → PMv). There have also been neuropsychological reports consistent with this hypothesis. For instance, Binkofski et al. (1998) have reported patients with specific grasping-related impairments after a lesion of the anterior intraparietal sulcus.

Rizzolatti and Matelli (2003) have further detailed the anatomy behind the idea of multiple parallel parieto-premotor circuits, suggesting that parieto-frontal circuits are organized in a dorso-dorsal pathway, running from V3a to V6 to V6a and MIP in the superior parietal lobule (SPL), and from here to the dorsal pre-motor areas (F2vr and F7-non-SEF1); and a ventro-dorsal pathway, running from medial superior temporal area (MT/MST) to the inferior parietal lobule (IPL), and from here to the ventral premotor cortex (AIP – F5 and VIP – F4) (see Fig. 1).

Human neuroimaging data appear consistent with a modular architecture of the parietal lobes (for example Grefkes & Fink, 2005; Rushworth, Behrens, & Johansen-Berg, 2006; Seitz & Binkofski, 2003). The apparent absence of substantial crosstalk between a dorso-dorsal pathway through visual area 6 (V6) and the superior parietal lobule (SPL) and a ventral–dorsal pathway through MT and the inferior parietal lobule (IPL) indicates that the dorsal stream may actually consist of two relatively segregated subcircuits. It has been suggested that these parallel dorsal and ventral pathways maintain segregation all the way into motor-related frontal cortical areas such as the frontal eye field (FEF). Likewise, within the dorsal stream, segregated inputs linking the SPL to dorsal premotor area (PMd) and the IPL to ventral premotor area (PMv) have been shown to exist. Rizzolatti and Matelli (2003) proposed that the two anatomically segregated subcircuits of the dorsal stream might mediate different behavioral goals as well: the dorso-dorsal pathway concerned with the control of action 'online' (while the action is ongoing) and the ventral–dorsal pathway for space perception and 'action understanding' (the recognition of actions made by others).

While dorsal and ventral streams clearly make up two relatively separate circuits, the anatomical segregation between the two streams is by no means absolute. There is clear evidence of crosstalk between streams, such as the reported connections between V4 and areas MT and LIP, as well as between anterior inferotemporal cortex and inferior parietal area AIP was recently demonstrated in monkey by Borra et al. (2008) and functionally described by Pisella, Binkofski, Lasek, Toni, and Rossetti (2006), Binkofski, Reetz, and Blangero (2007) and Nelissen and Vanduffel1 (2011) (see Fig. 2).

Thus, most connections from the ventral stream reach the ventral part of the dorsal stream, the ventro-dorsal substream. The ventro-dorsal substream seems therefore to constitute an interface between the ventral and the dorsal streams of visual information processing. This way of information exchange between the streams is especially interesting in the context of interaction with objects. It is very likely that both the dorsal and ventral streams are likely to process the same set of visual attributes, but for different behavioral goals. Fig. 3 presents a schematic location of the two dorsal sub-streams and the ventral stream in humans.

2. Object processing in the dorso-dorsal stream

The dorso-dorsal stream is the most direct (immediate) visual pathway for action. A PET imaging study showed that reaching towards targets with various locations in space and presented through a mirror preferentially engages areas in the dorso-dorsal stream (especiallyV6a, see Binkofski et al., 2003). The cardinal deficit associated with lesions in the dorso-dorsal stream is optic ataxia (OA), as characterized by misreaching to visual targets that is most flagrant in the peripheral visual field (Balint, 1909; Garcin et al., 1967; Ratcliff, 1990). Indeed, deficits in on-line motor control demonstrated for reaching (Buxbaum & Coslett, 1997; Buxbaum & Coslett, 1998; Grea et al., 2002; Milner et al., 2001; Pisella et al., 2000; Rossetti, Goldenberg, & Rode, 2005; Rossetti, Revol et al., 2005) and more recently for grasping (Tunik, Frey, & Grafton, 2005) in patients with OA highlights the specificity of the superior parietal region and the parieto-occipital junction for direct goal-directed visuo-motor transformations involving short-lived processes (Milner & Goodale, 1995; but see Kroliczak, McAdam, Quinlan, & Culham, 2007). The usual lesion causing OA includes the superior parietal lobule (SPL), the intraparietal sulcus (IPS) and the parieto-occipital sulcus (POS) (Karnath & Perenin, 2005; Perenin & Vighetto, 1988).

The reach and grasp components constitute a first possible factor of dissociation between the dorso-dorsal and ventro-dorsal streams. Two studies have converged toward the anterior part of the IPS (aIPS) as the lesion site causing the distal grasping deficit (Binkofski et al., 1998; Tunik et al., 2005). Conversely, a recent neuro-anatomical study has proposed a more posterior and ventral site as a minimal lesion site causing the misreaching (Karnath & Perenin, 2005): The junction of the two sulci (IPS and POS), designated in another study as the parieto-occipital junction (POJ, Prado et al., 2005). The common zone of lesion overlap in the Karnath and Perenin (2005) study includes the white matter around this area, suggesting that all connections from occipital to parietal are disrupted and the visuo-motor functions therefore markedly disturbed. How-

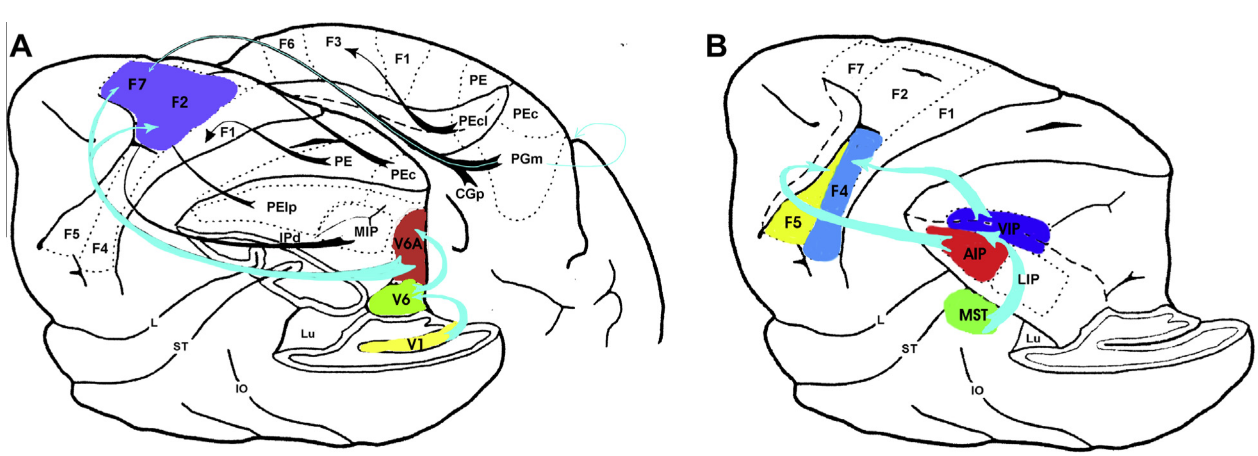

Fig. 1. Dorso-dorsal stream (A) and ventro-dorsal stream (B) in macaque (adopted from Rizzolatti et al. (1998) and Rizzolatti and Matelli (2003)).

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