



Research report

Tool manipulation knowledge is retrieved by way of the ventral visual object processing pathway

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ABSTRACT

Using functional Magnetic Resonance Imaging (fMRI), we find that object manipulation knowledge is accessed by way of the ventral object processing pathway. We exploit the fact that parvocellular channels project to the ventral but not the dorsal stream, and show that increased neural responses for tool stimuli are observed in the inferior parietal lobule when those stimuli are visible only to the ventral object processing stream. In a control condition, tool-preferences were observed in a superior and posterior parietal region for stimuli titrated so as to be visible by the dorsal visual pathway. Functional connectivity analyses confirm the dissociation between sub-regions of parietal cortex according to whether their principal afferent input is via the ventral or dorsal visual pathway. These results challenge the ‘Embodied Hypothesis of Tool Recognition’, according to which tool identification critically depends on simulation of object manipulation knowledge. Instead, these data indicate that retrieval of object-associated manipulation knowledge is contingent on accessing the identity of the object, a process that is subserved by the ventral visual pathway.

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1. Introduction

Visual object processing has been argued to be organized at a macroscopic level into two functionally independent visual pathways (e.g., Goodale and Milner, 1992). The ventral visual pathway projects from primary visual cortex (V1) to ventral occipital–temporal cortex, and supports form-based object identification and analysis of surface properties such as color and texture (Cant and Goodale, 2007; Goodale and Milner,

1992; Grill-Spector et al., 2001). Lesions to ventral stream structures classically result in impaired visual object recognition and perceptual decisions (e.g., judging the orientation of a line) but spared reaching and grasping (e.g., Goodale and Milner, 1992). The dorsal visual pathway projects from V1 to dorsal-occipital and posterior parietal cortex. It supports volumetric and spatial analysis of objects in the service of object-directed reaching and grasping. Patients with lesions to dorsal stream structures can have difficulty with reaching

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and/or grasping the same visual stimuli for which they can recognize and about which they can make normal perceptual judgments (e.g., Jeannerod et al., 1994; Perenin and Vighetto, 1988).

A number of functional Magnetic Resonance Imaging (fMRI) studies have shown that viewing common tools leads to differential blood oxygen level-dependent (BOLD) responses in localized regions within the temporal and parietal lobes, compared to a range of baseline categories (e.g., animals, vehicles, places; e.g., Chao et al., 1999; Chao and Martin, 2000; Mahon et al., 2007; Noppeney et al., 2006). Viewing tools elicits differential BOLD contrast in the medial fusiform gyrus, a structure unequivocally within the ventral visual pathway. Tool stimuli also elicit differential BOLD responses in the left posterior middle temporal gyrus, on the lateral surface of the temporal lobe. Whether the left posterior middle temporal gyrus that is tool responsive should be considered a part of the dorsal stream or the ventral stream, or both, is an open issue: it is just anterior to visual motion area MT/V5 which is unequivocally a part of the dorsal stream (Ungerleider and Mishkin, 1982; see also Beauchamp et al., 2002) but lesions to the middle temporal gyrus are associated with lexical semantic and conceptual level impairments for tools (e.g., Damasio et al., 2004). Finally, tool stimuli elicit differential BOLD responses in the left parietal lobule, across a large swath of cortex extending from posterior parietal cortex anteriorly along the intraparietal sulcus (IPS), and inferiorly into the supramarginal gyrus of the inferior parietal lobule (IPL) (e.g., Chao et al., 1999; Chao and Martin, 2000; Mahon et al., 2007; Noppeney et al., 2006).

Recent work has shown that there is significant interaction between the ventral and dorsal streams, and that rather than the two streams being entirely independent, they are principally dissociated by their afferent inputs. For instance, the ventral stream has been shown to be able to support some visuomotor behavior, and visuomotor performance in the context of ventral stream lesions may not be completely spared, even in simple tasks, particularly when these visuomotor actions are not under online guidance (e.g., Goodale et al., 1994; Karnath et al., 2009; for a review see Himmelbach et al., 2012; Schenk and McIntosh, 2009). In addition, the dorsal stream is not a monolithic entity, and should certainly not be 'equated' with parietal cortex (Goodale and Milner, 1992). Rizzolatti and Matelli (2003) argued that the dorsal stream can be subdivided into a dorso-dorsal pathway, comprising (among other areas) area V6 and the superior parietal lobule (SPL), and dedicated to the online control of visuomotor behavior, and a ventro-dorsal pathway, corresponding (among other areas) to the IPL, and concerned with object-directed actions (left hemisphere), action understanding, and spatial analysis (right hemisphere). Finally, it has been shown that there is strong interconnectivity between the dorsal and ventral visual streams (e.g., Binkofski et al., 2007; Nelissen and Vanduffell, 2011; Pisella et al., 2006; Rushworth et al., 2006; Zhong and Rockland, 2003). For instance, the IPL has connections with aspects of the ventral temporal cortex (Binkofski et al., 2007; Borra et al., 2008; Nelissen and Vanduffell, 2011), and the IPL is increasingly being thought of as the locus of integration of abstract (potentially 'semantic') information about object use that arrives from ventral and lateral temporal

cortices, and visuomotor information coming from dorsal stream regions (V6, SPL), into a coherent object-specific action plan (e.g., Binkofski and Buxbaum, 2013; Frey, 2007; Grafton, 2010; Randerath et al., 2010). Overall, these data and arguments suggest that while the general distinction between a dorsal and a ventral stream holds, there is some overlap in their functions and there is certainly ample interactivity between the two streams.

One way to address the distinction between ventral and dorsal visual streams, the cross-talk between them, and their relation to the organization of semantic memory is by studying how information about manipulable objects such as tools and utensils is represented and organized. Functionally appropriate tool use depends on specific motor information being brought into register with specific visual information. Broadly speaking, object-directed actions can be separated into a reach-to-grasp component, and complex object-associated manipulations. Reach-to-grasp actions are visuomotor acts that are largely constrained by the physical characteristics of the objects; by the current location of the hands, intervening obstacles, and target objects: but do not draw on stored 'semantic' knowledge.¹ Thus, all of the positional and volumetric information necessary to reach toward and grasp an object (albeit not necessarily in a functionally appropriate way) is provided by the visual input. By contrast, complex object-associated manipulations describe the way that objects are manipulated in order for the object to be used in a functionally appropriate way (e.g., the hammering action when using a hammer). It is important to note, however, that object function and object manipulation knowledge doubly dissociate, and are known to be subserved by functionally and neuroanatomically separate systems. This double dissociation has been shown in neuropsychological patients (Buxbaum and Saffran, 2002; Negri et al., 2007; Garcea et al., 2013; Sirigu et al., 1991), fMRI (Boronat et al., 2005; Canessa et al., 2008; Kellenbach et al., 2003), behavioral responses in normal subjects (Tucker and Ellis, 1998; Garcea and Mahon, 2012), and with transcranial magnetic stimulation (Ishibashi et al., 2011; Pelgrims et al., 2011; Pobric et al., 2010).

As noted above, viewing tool stimuli leads to fMRI activation in a large swath of left hemisphere parietal regions, from posterior parietal/dorsal occipital cortex (~V6), through IPS, including the SPL, and the supramarginal gyrus of the IPL in the left hemisphere. Recent data suggest that the parietal regions that comprise this tool network may be assigned to different tool-related functions (e.g., Buxbaum et al., 2006, 2007; Vingerhoets, 2008; Vingerhoets et al., 2009). For instance, Vingerhoets et al. (2009) suggested that different parts of the inferior parietal cortex are responsible for different aspects of gesture planning and coordination necessary for tool use. This complex mosaic of functions and the associated integrative nature of tool-related parietal cortex fits well with the diverse profiles often found in limb apraxia after left parietal lobe

¹ This is not to say that such actions do not draw on any stored information; they draw on a repertoire of skills that have been practiced (i.e., reaching and grasping); rather, they do not seem to require information that is elaborated and generalized to the 'type' of object that is being grasped (for discussion, see Wu, 2008).

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