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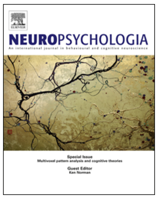

Parcellation of left parietal tool representations by functional connectivity

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ABSTRACT

Manipulating a tool according to its function requires the integration of visual, conceptual, and motor information, a process subserved in part by left parietal cortex. How these different types of information are integrated and how their integration is reflected in neural responses in the parietal lobule remains an open question. Here, participants viewed images of tools and animals during functional magnetic resonance imaging (fMRI). *k*-Means clustering over time series data was used to parcellate left parietal cortex into subregions based on functional connectivity to a whole brain network of regions involved in tool processing. One cluster, in the inferior parietal cortex, expressed privileged functional connectivity to the left ventral premotor cortex. A second cluster, in the vicinity of the anterior intraparietal sulcus, expressed privileged functional connectivity with the left medial fusiform gyrus. A third cluster in the superior parietal lobe expressed privileged functional connectivity with dorsal occipital cortex. Control analyses using Monte Carlo style permutation tests demonstrated that the clustering solutions were outside the range of what would be observed based on chance ‘lumpiness’ in random data, or mere anatomical proximity. Finally, hierarchical clustering analyses were used to formally relate the resulting parcellation scheme of left parietal tool representations to previous work that has parcellated the left parietal lobule on purely anatomical grounds. These findings demonstrate significant heterogeneity in the functional organization of manipulable object representations in left parietal cortex, and outline a framework that generates novel predictions about the causes of some forms of upper limb apraxia.

1. Introduction

1.1. *Manipulable object knowledge*

The ability to use objects according to their function and in the correct context requires the integration of diverse types of information. Consider, for instance, the knowledge and skills involved in the everyday action of picking up a fork and eating some food off of your plate. The target of the initial reaching action must be identified, and a reach-to-grasp action planned and executed. That reach-to-grasp action is based on a prior identification of the particular fork, which is the target of the action (e.g., your fork as opposed to your neighbor’s fork). The reaching action must then take into account various obstacles that may be present (e.g., a glass of wine, your neighbor’s elbow). Furthermore, the reach-to-grasp action ultimately anticipates the way in which the object (fork) will be manipulated, and as such, depends on the integration of identity information and knowledge of the center of mass of that object. For instance, different forks will be picked up at different points along the handle according to their center of mass, but a fork and knife with the same center of mass will also be picked up differently, according to the eventual way the object will be held for use. Then, once the fork is ‘in hand,’ the way in which it is manipulated depends on an understanding of how forks work—you don’t use it to scoop a piece of steak that could be stabbed, and you don’t use it to stab your mashed potatoes but instead scoop them.

When unpacked in this way, it becomes clear that even a simple action like reaching out to pick up fork to begin dinner is a complex process that requires the integration of many different types of information. A range of previous research has demonstrated the involvement of temporal, parietal, occipital and frontal cortex—that is, a whole brain network—in tool processing. For instance, viewing manipulable objects compared to a comparable baseline categories (animals, vehicles) leads to differential neural responses in regions of the inferior and superior parietal lobule, ventral and lateral temporo-occipital regions, dorsal occipital

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cortex, and premotor cortex (e.g., Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Fang & He, 2005; Mahon et al., 2007; Mahon, Kumar, & Almeida, 2013; Martin, Wiggs, Ungerleider, & Haxby, 1996; Noppeney, Price, Penny, & Friston, 2006; Rumiati et al., 2004; for review, see Lewis, 2006). These regions are generally left lateralized, with the exception of the superior/posterior parietal cortex and the fusiform gyrus. We refer to this entire network of regions, which is implicated in the recognition of manipulable objects, as the Tool Processing Network.

Different regions within the Tool Processing Network carry out different aspects of the complex process of object-directed action. For instance, ventral temporal-occipital regions represent visual, visuo-semantic and surface texture information about objects (e.g., see Campanella, D'Agostini, Skrap, & Shallice, 2010; Cant & Goodale, 2011; Capitani, Laiacona, Mahon, & Caramazza, 2003; Gainotti, 1995, 2000; Miceli, Fouch, Capasso, Shelton, Tomaiuolo, & Caramazza, 2001; Rogers, Hocking, Mechelli, Patterson, & Price, 2005). Lateral temporal cortex, in the vicinity of the left posterior middle temporal gyrus and the inferior temporal gyrus, is particularly responsive to mechanical motion associated with tools (Beauchamp, Lee, Haxby, & Martin, 2002, 2003), and is directly anterior and ventral to motion area MT/V5. The left ventral premotor cortex is also involved in processing tool knowledge, and is thought to be important for action planning and sequencing (Chao & Martin, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Passingham, 1985). While the dorsal aspect of premotor cortex has also been associated with the processing of tools (e.g., Grafton et al., 1997), it is typically ventral and not dorsal premotor cortex that is activated during passive viewing of tools or tool naming (cf., Chao & Martin, 2000; Martin et al., 1996).

1.2. The role of left parietal cortex in tool use

It has been known since the pioneering work of Liepmann (1905) that the left parietal lobule plays a particularly central role in supporting complex object directed action. The activation elicited by tool stimuli in the left parietal lobule typically extends in one contiguous cluster from lateral and inferior regions (supramarginal gyrus) dorsally and posteriorly to include the anterior aspect of the IPS, and then caudally along the IPS to dorsal occipital cortex. While there are generally no tool-specific responses in the angular gyrus of the inferior parietal lobule (for review, see Lewis, 2006; Martin, 2007), there is evidence that the angular gyrus may be involved in the grasping phase of tool use (e.g., see Creem-Regehr & Lee, 2005; Johnson-Frey, Newman-Norlund, & Grafton, 2005).

There is already good evidence from neuropsychology to suggest a coarse parcellation of left parietal tool representations. A deficit in visually-guided reaching in peripersonal space is classically associated with damage to superior/posterior parietal cortex, and/or dorsal occipital cortex (Desmurget & Sirigu, 2009; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Jeannerod, Decety, & Michel, 1994; Karnath & Perenin, 2005; Pisella et al., 2000), and functional neuroimaging studies designed to highlight the reach-to-grasp component of actions have found activation in posterior regions of parietal cortex (Cavina-Pratesi, Goodale, & Culham 2007; Culham et al., 2003; Konen, Mruczek, Montoya, & Kastner, 2013). In contrast, lesions to the anterior intraparietal sulcus (aIPS) tend to disrupt grip scaling of the fingers during reaching but may not affect the reach component of the action itself (Binkofski et al., 1999a, 1999b). Finally, limb apraxia, a deficit in performing skilled action, is classically associated with damage to the supramarginal gyrus of the left inferior parietal lobule (Liepmann, 1905). Patients with limb apraxia can be impaired for gesturing object use from verbal command, pantomiming object use from visual presentation of an object, and imitating actions (see, e.g., Buxbaum & Saffran, 2002; Buxbaum, Veramonti, & Schwartz, 2000; Garcea, Dombovy, & Mahon, 2013; Liepmann, 1905; Negri et al., 2007; Ochipa, Rothi, & Heilman, 1989; Rumiati, Zanini, Vorano, & Shallice, 2001; for reviews, see Binkofski & Buxbaum, 2013; Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Goldenberg, 2009; Johnson-Frey, 2004; Leiguarda & Marsden, 2000; Mahon & Caramazza, 2005; Osiurak, Jarry, & Le Gall, 2009; Rothi, Ochipa, & Heilman, 1991).

It is clear that the computations underlying reach-to-grasp actions are supported by the classically defined dorsal stream, and as such, are computed 'on the fly' on the basis of the current state of the world (Milner & Goodale, 2008). In other words, you don't (typically) reach to grasp a glass on the basis of where you know it is, but on the basis of where you perceive it to be at the moment that the grasp is planned. However, it is not at all clear that complex object-associated manipulations could, in principle, be supported by only a dorsal stream analysis of the visual input. This is because complex object object-associated manipulations are not given by the visual input. For instance, the knowledge of how a pair of pliers, a pair of scissors or a wrench is used once the objects are in hand, is information that is stored. In their influential model of apraxia Rothi, Heilman and colleagues analogized those action representations to lexical representations of words (e.g., Rothi et al., 1991; see also Negri et al., 2007).

Thus, in principle, it should be possible to dissociate tool activation across inferior parietal regions (manipulation component of action) and superior parietal regions (reach-to-grasp component of action) according to whether the provenance of the information is the ventral or dorsal stream, respectively. One way to accomplish this is to capitalize on asymmetries in how different classes of retinal ganglion cells map onto the two visual pathways (see Merigan & Maunsell, 1993)—because the dorsal visual pathway is biased against receiving direct inputs from parvocellular channels, stimulus information that is preferentially processed in parvocellular channels (e.g., color, high spatial frequencies) should not, by hypothesis, be analyzed through the dorsal pathway. Recent functional imaging work with healthy subjects has shown that when visual stimuli are titrated psychophysically so that their processing is biased toward parvocellular channels (hence away from a dorsal visual pathway), tool-stimuli continue to elicit differential activation only in *inferior* regions of left parietal cortex, but not in posterior/superior regions of left parietal cortex (Almeida, Fintzi, & Mahon, 2013; Mahon et al., 2013). Furthermore, those same left inferior parietal regions that are activated for stimuli that are titrated so as to not be visible by the dorsal visual pathway exhibit privileged functional connectivity to regions of the Tool Processing Network in the ventral stream, such as the left medial fusiform gyrus. The reverse dissociation has also been observed: Using continuous flash suppression, Fang and He (2005) showed that suppressed images of tools continue to activate posterior parietal and dorsal occipital regions, even though processing within the ventral stream for the same stimuli was entirely abolished (for behavioral work and discussion, see Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008).

Thus, there is already strong precedent regarding the whole brain neural network that broadly supports object directed action, as well as indications about how to parcellate tool representations in parietal cortex on functional grounds. A largely separate literature has sought to develop a parcellation scheme for left parietal cortex based on cytoarchitecture, anatomical connectivity, and the distribution of neurotransmitter receptors (Borra et al., 2008; Borra, Ichinohe, Sato, Tanifuji, & Rockland, 2010; Caspers et al., 2011, 2006. 2013; Mars, Jbabdi, Sallet, O'Reilly, & Croxson, 2011; Orban, Claeys, Nelissen, Smans, & Sunaert, 2006; Ruschel et al., in press; Rushworth, Behrens, & Johansen-Berg, 2006). Some approaches have explicitly sought to parcellate the inferior parietal lobule (Caspers et al., 2011, 2006, 2013; Ruschel et al., in press; Zhong & Rockland, 2003), or superior parietal lobule (Konen & Kastner, 2008; Zhang, Fan, Zhang, Wang, & Zhu, in press), or the entire parietal lobule (Durand, Nelissen, Joly, Wardak, & Todd, 2007; Konen et al., 2013; Mars et

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