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Specialization of the left supramarginal gyrus for hand-independent praxis representation is not related to hand dominance

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ABSTRACT

Data from focal brain injury and functional neuroimaging studies implicate a distributed network of parieto-fronto-temporal areas in the human left cerebral hemisphere as playing distinct roles in the representation of meaningful actions (praxis). Because these data come primarily from right-handed individuals, the relationship between left cerebral specialization for praxis representation and hand dominance remains unclear. We used functional magnetic resonance imaging (fMRI) to evaluate the hypothesis that strongly left-handed (right hemisphere motor dominant) adults also exhibit this left cerebral specialization. Participants planned familiar actions for subsequent performance with the left or right hand in response to transitive (e.g., "pounding") or intransitive (e.g. "waving") action words. In linguistic control trials, cues denoted non-physical actions (e.g., "believing"). Action planning was associated with significant, exclusively left-lateralized and extensive increases of activity in the supramarginal gyrus (SMg), and more focal modulations in the left caudal middle temporal gyrus (cMTg). This activity was hand- and gesture-independent, i.e., unaffected by the hand involved in subsequent action performance, and the type of gesture (i.e., transitive or intransitive). Compared directly with right-handers, left-handers exhibited greater involvement of the right angular gyrus (ANg) and dorsal premotor cortex (dPMC), which is indicative of a less asymmetric functional architecture for praxis representation. We therefore conclude that the organization of mechanisms involved in planning familiar actions is influenced by one's motor dominance. However, independent of hand dominance, the left SMg and cMTg are specialized for *ideomotor transformations*—the integration of conceptual knowledge and motor representations into meaningful actions. These findings support the view that higher-order praxis representation and lower-level motor dominance rely on dissociable mechanisms.

1. Introduction

Damage to the dominant left cerebral hemisphere has been long associated with ideomotor apraxia (hereafter "apraxia"), an acquired disorder in the representation of skilled actions that cannot be attributed to difficulties in linguistic, sensory or lower-level motor functions (Geschwind and Kaplan, 1962; Heilman and Rothi, 1997; Liepmann, 1900). A classic assessment of praxis at the bedside involves asking patients to pantomime familiar actions involving tools, or other manipulable objects, in response to verbal commands that provide little contextual information for retrieval (Liepmann, 1900). Apraxic patients may perform well with actual object use yet exhibit considerable difficulties with pantomime (Randerath et al., 2011), and sometimes also with intransitive gestures (e.g., waving hello or signaling thumbs-up) that do not involve objects (Cubelli et al., 2000; Pazzaglia et al., 2008; Stamenova et al., 2010). Critically, apraxia affects pantomime (and often imitation) regardless of the hand used, a phenomenon which indicates that it arises from disruptions of action representations at a *hand-independent level* (Leiguarda and Marsden, 2000). Because most apraxic patients have sustained injuries to the left cerebral hemisphere, testing typically involves the non-hemiplegic left hand, which also happens to be the non-dominant side for the vast majority of patients.

There is reasonable, though imperfect, degree of convergence between the neuropsychological literature on right-handed apraxics, and the results of functional neuroimaging studies of pantomime in healthy adults. Overall, neuroimaging investigations

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also find evidence that the motor dominant left hemisphere supports hand-independent representations of praxis skills (Bohlhalter et al., 2009; Choi et al., 2001; Fridman et al., 2006; Johnson-Frey et al., 2005; Kroliczak and Frey, 2009; Moll et al., 2000; Ohgami et al., 2004; Rumiati et al., 2004; Vingerhoets et al., 2011). Despite using different paradigms – and in some cases both transitive pantomime and intransitive gestures (Fridman et al., 2006; Kroliczak and Frey, 2009; Bohlhalter et al., 2009) – these investigations consistently detect involvement of the left posterior parietal cortex, particularly the SMg and adjacent intraparietal sulcus (IPS). These data are therefore compatible with classic theories in neuropsychology that implicate the left SMg as playing a critical role in supporting hand-independent praxis representations (Heilman et al., 1982; Rothi et al., 1985).

Consistent with more recent neuropsychological findings pointing to a wider network of areas that are critical for praxis skills (e.g., Goldenberg, 2003b; including the middle frontal gyrus, MFg, e.g., Haaland et al., 2000, and left inferior frontal gyrus, with adjacent insular and ventral premotor cortices, Goldenberg et al., 2007), neuroimaging studies also report increased hand-independent activity in various regions that lie beyond the left posterior parietal cortex (for a recent neuroimaging meta-analysis see Niessen et al. (2014)). These areas include the left MFg, supplementary motor (SMA) area, premotor, and/or the prefrontal cortices (Choi et al., 2001; Hermsdorfer et al., 2007; Johnson-Frey et al., 2005; Kroliczak and Frey, 2009; Moll et al., 2000; Ohgami et al., 2004; Rumiati et al., 2004). A notable subset of studies also finds greater engagement of the left caudal middle temporal gyrus (cMTg) (Choi et al., 2001; Hermsdorfer et al., 2007; Johnson-Frey et al., 2005; Kroliczak and Frey, 2009), an area implicated in the conceptual representation of familiar manipulable objects and associated actions (Beauchamp et al., 2002; Beauchamp and Martin, 2007; Chao and Martin, 2000; Martin et al., 1996; Kellenbach et al., 2003; Mahon et al., 2007; Weisberg et al., 2007), and/or the visual analysis of tool's features (Vingerhoets, 2008). Indeed, damage in this vicinity impairs performances on tasks that require accessing such knowledge (Tranel et al., 1997; Tranel et al., 2003). The cMTg and neighboring temporal regions are furthermore strongly interconnected with the SMg (Ruschel et al., 2014).

Together, these various sources of evidence are consistent with the hypothesis that a distributed parieto-fronto-temporal set of regions within the left hemisphere are critical nodes for *ideomotor transformation*, the integration of conceptual and motor representations in service of familiar, meaningful actions (Johnson-Frey, 2004). The question of whether this left cerebral asymmetry for hand-independent praxis representation depends on hand dominance, however, persists.

Due in part to the preponderance of dominant hand hemiplegia in apraxia, the relationship between cerebral dominance for sensorimotor control of the hand vs. for the representation of praxis remains unclear. One account is that right-handedness is a direct reflection of the left-lateralized system for representing manual praxis (Geschwind and Galaburda, 1985; Heilman, 1997; Kimura and Archibald, 1974; Liepmann, 1908; for a discussion see Goldenberg, 2013b). Indeed, of the small number of left-handed cases of apraxia that have been investigated, some do show signs of apraxia following right hemisphere lesions (Dobato et al., 2001; Poeck and Kerschensteiner, 1971; Valenstein and Heilman, 1979). However, this can also be said for a minority of right-handed patients (Marchetti and Della Sala, 1997; Raymer et al., 1999), which is inconsistent with this speculation. Alternatively, praxis representation and hand dominance might depend on *relatively independent* mechanisms, with most left-handers also representing praxis skills in their left (motor non-dominant) hemispheres. Data from left-handed individuals that have undergone surgical transections of, or sustained injuries to, the *corpus callosum* support this view (Frey, Funnell, Gerry, and Gazzaniga, 2005; Lausberg, Gottert, Munssinger, Boegner, and Marx, 1999). Evidence for a potential dissociation between motor dominance and praxis mechanisms can also be found. A recent comprehensive report on 50 left-handed patients with unilateral brain injuries (Goldenberg, 2013a; for a discussion see also Goldenberg, 2013b) identified three cases with apraxia and aphasia following injuries to the left hemisphere, demonstrating clear dissociations between handedness and apraxia. Yet, three cases with apraxia and no aphasia subsequent to right (motor dominant) hemisphere injury have been also found, demonstrating at least the importance of some low level mechanisms linking handedness and praxis skills.

As these various sources indicate, resolving the relationship between mechanisms responsible for hand dominance and/or praxis representation on the basis of patient data alone has proven very challenging. Yet, apart from inferences based on these studies, remarkably little is known about the organization of praxis in healthy left-handed adults who constitute approximately 10% of the population (Coren and Porac, 1977; Porac and Coren, 1981; Willems, Van der Haegen, Fisher, and Francks, 2014). As a consequence of excluding left-handed participants, functional neuroimaging studies have done little to clarify the relationship between cerebral asymmetries for praxis and motor dominance. An exception is a report on strongly left-handed participants who pantomimed unilateral or bimanual actions in response to familiar visually presented objects (Vingerhoets et al., 2012). Yet, the absence of a control for linguistic functions (see Martin et al. (1996), Chao and Martin (2000), Kroliczak and Frey (2009)), and the lack of a distinction between action planning vs. execution (Johnson-Frey et al., 2005) calls for additional studies on the relationships between the left hemisphere specialization for praxis representation and motor dominance in the healthy adult brain.

In our previous research on strongly left-handed individuals, we focused on the organization of language and praxis in selected regions of interest, and motor dominance was less of an issue (Kroliczak et al., 2011). Here we revisit these same data using whole-brain statistical parametric mapping to test whether, similarly to right-handed adults (Kroliczak and Frey, 2009), these left-handers exhibit evidence for left lateralized parieto-fronto-temporal praxis representation network. Our primary focus is on hand-independent activity during gesture planning. As in our earlier work (Kroliczak and Frey, 2009), we did not expect to find evidence of dissociable mechanisms specialized for the representation of tool use pantomimes (transitive) vs. communicative (intransitive) gestures involving no objects. To the extent that the organization of praxis representation is independent of hand dominance, we predicted that left-handers would also exhibit increases within a left-lateralized, parieto-fronto-temporal network when planning gestures for subsequent production with either hand. Finally, we expected that direct statistical comparisons with the data from right-handers (Kroliczak and Frey, 2009) would also fail to detect significant differences in activity related to hand dominance within the supramarginal gyrus and caudal middle temporal gyrus.

2. Methods

The local Ethics Committee for Research Involving Human Subjects at the University of Oregon approved the experimental protocols, which conformed to the WMA Declaration of Helsinki.

2.1. Participants

Healthy adult, self-identified left-handers (N=51) were invited to visit the laboratory for additional screening. To verify