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The ventral fiber pathway for pantomime of object use

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ABSTRACT

The current concept of a dual loop system of brain organization predicts a domain-general dual-pathway architecture involving dorsal and ventral fiber connections. We investigated if a similar dichotomy of brain network organization applies for pantomime (P) and imitation of meaningless gestures (I). Impairments of these tasks occur after left hemispheric brain lesions causing apraxia. Isolated impairments and double-dissociations point towards an anatomical segregation. Frontal and parietal areas seem to contribute differently. A special role of the inferior frontal gyrus and underlying fiber pathways was suggested recently.

Using a combined fMRI/DTI-approach, we compared the fiber pathway architecture of left hemispheric frontal, temporal and parietal network components of pantomime and imitation. Thereby, we separated object effects from pantomime-specific effects. P and I both engage a fronto-temporo-parietal network of cortical areas interconnected by a dorsal fiber system (superior longitudinal fascicle) for direct sensory–motor interactions. The pantomime-specific effect additionally involved the triangular part of the inferior frontal gyrus, the middle temporal gyrus, the inferior parietal cortex and the intraparietal sulcus, interconnected by ventral fibers of the extreme capsule, likely related to higher-order conceptual and semantic operations. We discuss this finding in the context of the dual loop model and recent anatomical concepts.

Introduction

Praxis is a motor–cognitive faculty associated with gestural expressions, imitation, and skilled manual actions that may involve tools and objects. Apraxia, a "disorder of skilled movement" that cannot be attributed to paresis or attention-, language- or sensory deficits, classically affects domains such as imitation of meaningless gestures, actual or pantomimed use of tools and objects, or action recognition (Liepmann, 1900; Geschwind, 1965, 1975; Heilman et al., 1982; Rothi et al., 1985, 1997; Haaland et al., 2000). These domains are tested routinely during clinical assessment and classification of apraxia subtypes. Distinct error patterns, isolated impairments and double dissociations strongly suggest an anatomical segregation within related brain networks (Barbieri and De Renzi, 1988; Goldenberg and Hagmann, 1998; Rothi et al., 1997; Peigneux et al., 2000; Bartolo et al., 2003; Negri et al., 2007, also see Leiguarda and Marsden, 2000 for a review).

Consequently, neurocognitive models of apraxia (Roy and Square, 1985; Rothi et al., 1991; Cubelli et al., 2000; Rumiati et al., 2004, 2005; Buxbaum et al., 2005; Tessari et al., 2007; Stamenova et al., 2012) share the idea of different processing streams: a non-semantic, direct route for immediate sensory–motor conversions, as in gesture imitation, and an indirect, semantic route that incorporates knowledge about tools and objects for tool use and pantomime, contacting the conceptual level of an action (see Koski et al., 2002 for a review). However, the anatomical implementation remained underspecified.

Growing evidence from lesion and neuroimaging studies suggest that pantomime and imitation are anatomically implemented within a widespread, left-lateralized, fronto-temporo-parietal cortical network (Johnson-Frey, 2004; Johnson-Frey et al., 2005; Beauchamp and Martin, 2007; Hermsdoerfer et al., 2007; Kroliczak and Frey, 2009). Specific

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functional contributions of different network areas remain controversial: fMRI studies of pantomime support a substantial role of the left inferior parietal lobe (IPL) (Moll et al., 2000; Choi et al., 2001; Buxbaum et al., 2007), but lesion studies at single-case and group levels often demonstrate defective imitation, but preserved pantomime after parietal lesions (Heilman et al., 1986; Basso et al., 1987; Mehler, 1987; Goldenberg and Hagmann, 1997; Peigneux et al., 2000; Haaland et al., 2000; Goldenberg et al., 2007). A recent functional–anatomical study using lesion subtraction techniques (Goldenberg et al., 2007) suggested that pantomime of tool use deficits are specifically associated with lesions of the left inferior frontal cortex (IFG), adjacent prefrontal and insular cortex, and subinsular white matter. Goldenberg hypothesized that not only cortical damage, but also disconnection of subcortical fibers could account for isolated pantomime deficits.

A recently developed framework integrates knowledge from these lesion- and functional imaging studies with insights from behavioral models and conceptualizes the praxis network in terms of multiple streams dedicated to the processing of distinct aspects of higher motor functions. Evolving the concept of distinct ventral and dorsal streams for visual processing (Mishkin and Ungerleider, 1982; Goodale and Milner, 1992), this model further divides the dorsal stream into a dorso-dorsal stream, running from visual areas (area V6) to the intraparietal sulcus, superior parietal cortex and dorsal premotor cortex, and a ventro-dorsal stream, connecting medial superior temporal areas with the inferior parietal cortex and the ventral premotor cortex (Rizzolatti and Matelli, 2003; Pisella et al., 2006, see also Binkofski and Buxbaum, 2013 for comprehensive information on the multiple stream model). The dorso-dorsal pathway is related to the "online" sensorimotor control of ongoing actions, whereas the ventro-dorsal pathway is concerned with action semantics (Rizzolatti and Matelli, 2003). The ventral stream, running from visual areas to the temporal cortex, accounts for visual object processing and object semantics. Recently, Binkofski and Buxbaum suggested that the dorso-dorsal stream should be recognized as a "structure system" specialized for automatic visual analysis of spatial object features (*e.g.* shape, size) towards reaching and grasping, whereas the ventro-dorsal "functional-system" or "use-system" supports long-term conceptual representations of skilled actions involving tools and objects, thus touching the domain of action semantics (Buxbaum and Kalénine, 2010; Binkofski and Buxbaum, 2013). Lesions within regions of the ventro-dorsal stream would lead to impairments of tool use *and* pantomime of tool use (Binkofski and Buxbaum, 2013). This model was recently refined on the basis of results from our lab indicating a crucial role of the dorso-dorsal stream also for imitation of meaningless gestures. Moreover, we showed that pantomime of tool use relies not only on regions within the ventro-dorsal stream such as the inferior parietal lobule, but also on temporal areas belonging to the ventral stream (Hoeren et al., 2014).

Despite these recent advances, the anatomical basis of the dorsal and ventral streams, particularly with respect to the association fibers connecting different frontal and parietal nodes, have remained uncertain. As the ventral part of the IFG, a crucial structure for pantomime according to Goldenberg et al. (2007), was previously shown to be connected with parietal regions through fibers running along the extreme capsule (EmC) (Vry et al., 2012), we asked whether dissociations of praxic deficits of pantomime and imitation could be interpreted in the light of a recent dual loop model for higher cognitive functions (Weiller et al., 2011; Rijntjes et al., 2012), and whether the predictions made by the multiple-stream-framework outlined above could be integrated into the dual loop model. The dual-loop model combines insights on anatomy and functional imaging to extend the original ventral/dorsal stream hypothesis (Mishkin and Ungerleider, 1982) from visual processing to higher cognitive functions: a ventral pathway, running below the Sylvian fissure along the EmC towards the ventral prefrontal cortex, was anatomically and functionally distinguished from a dorsal pathway along the SLF (superior longitudinal fascicle)/AF (arcuate fascicle)-system coursing above the Sylvian fissure. In the context of the dual-loop model, "dorsal" would represent both "ventro-dorsal" and "dorso-dorsal" pathways of the multiple-stream model. The segregation of distinct cognitive functions along dorsal and ventral pathways was functionally established in the context of language (Saur et al., 2008, 2010; Friederici, 2009; Griffiths et al., 2013; Brauer et al., 2013; Kuemmerer et al., 2013), spatial attention (Umarova et al., 2010), motor imagery (Vry et al., 2012), action semantics (Hoeren et al., 2013) and arithmetic (Klein et al., 2013; Willmes et al., 2014). Consequently, the domain-general dual-loop model was proposed in which time independent cognitive functions (such as semantics and meaning) might rely on processing within the ventral pathway, whereas time dependent processes, as online sensorimotor integration of information, is organized along the dorsal pathway (Weiller et al., 2011; Rijntjes et al., 2012).

Based on the dual-loop model, we predicted a categorical difference of fiber pathway signatures for pantomime and imitation that would render strategic white matter lesions capable of producing isolated impairments. Specifically, we expected that: A. imitation of meaningless gestures predominantly involve the dorsal SLF system for visuomotor transformations (Binkofski and Buxbaum, 2013) and body part coding (Goldenberg, 1995) (functionally assigned to the dorso-dorsal stream in the multiple stream model), and B. pantomime of tool use would both require the dorsal SLF/AF-system for object semantics (assigned to the ventro-dorsal stream within the multiple stream model), and additionally the ventral EmC fiber system related to pantomime-specific conceptual operations (previously not considered in the multiple stream model).

To prove this claim, we applied a combined fMRI- and DTI-based fiber tracking approach. *First*, cortical networks for tool-use pantomiming (condition P), imitation of meaningless hand gestures (condition I) and imitation of meaningless gestures in the visual context of an object (condition IO) were determined by an fMRI experiment. Condition IO was introduced to control for cognitive effects of visual object stimuli (Norman and Shallice, 1980; Grèzes and Decety, 2002) that should activate the ventro-dorsal stream during the pantomime task without being a pantomime-specific cognitive process. By differential analysis of overlapping cortical networks, we intended to disentangle pantomime-specific network components from areas of the dorso-dorsal and ventro-dorsal stream. In a *second* step, the course of fiber pathways between left-hemispheric cortical network components was analyzed and compared between subnetworks.

Material and methods

Subjects

Twenty-four healthy subjects (9 male, 15 female, age 23–42 years, mean 28 years) participated in the study. None had a history of neurological or psychiatric diseases or were treated with psychoactive medication; vision was normal or corrected-to-normal. Right-handedness was assured by the Edinburg Handedness Inventory. All subjects gave written informed consent prior to the study, and the approval of the local ethics committee was obtained.

Experimental design

The study consisted of two experimental parts, the fMRI experiment and the fiber tracking experiment.

fMRI experiment

The goal of the fMRI experiment was to identify brain regions related to tool-use pantomime as opposed to imitation of meaningless gestures, while controlling for visual object stimulus effects. Supplementary Fig. 1