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ABSTRACT

Apraxia, a disorder of higher motor cognition, is a frequent and outcome-relevant sequel of left hemispheric stroke. Deficient pantomiming of object use constitutes a key symptom of apraxia and is assessed when testing for apraxia. To date the neural basis of pantomime remains controversial. We here review the literature and perform a meta-analysis of the relevant structural and functional imaging (fMRI/PET) studies.

Based on a systematic literature search, 10 structural and 12 functional imaging studies were selected. Structural lesion studies associated pantomiming deficits with left frontal, parietal and temporal lesions. In contrast, functional imaging studies associate pantomimes with left parietal activations, with or without concurrent frontal or temporal activations. Functional imaging studies that selectively activated parietal cortex adopted the most stringent controls.

In contrast to previous suggestions, current analyses show that *both* lesion and functional studies support the notion of a left-hemispheric fronto-(temporal)-parietal network underlying pantomiming object use. Furthermore, our review demonstrates that the left parietal cortex plays a key role in pantomime-related processes. More specifically, stringently controlled fMRI-studies suggest that in addition to storing motor schemas, left parietal cortex is also involved in activating these motor schemas in the context of pantomiming object use. In addition to inherent differences between structural and functional imaging studies and consistent with the dedifferentiation hypothesis, the age difference between young healthy subjects (typically included in functional imaging studies) and elderly neurological patients (typically included in structural lesion studies) may well contribute to the finding of a more distributed representation of pantomiming within the motor-dominant left hemisphere in the elderly.

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Contents

1.	Introduction
2.	Methods
3.	Results
	3.1. Structural lesion studies of the neural basis of pantomiming
	3.2. Functional imaging studies on the neural basis of pantomiming
4.	Discussion
5.	Conclusions
Ack	nowledgments & funding source
Refe	rrences

1. Introduction

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Apraxia is a disorder of higher motor cognition and a common sequel of left hemispheric stroke (Goldenberg, 2009). Apraxia significantly impacts upon rehabilitation: after discharge from the rehabilitation unit apraxic stroke patients depend more on their caregivers and return less frequently to work than patients without apraxia (Dovern et al., 2012). Frequently observed clinical symptoms of apraxia are

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deficits of i) imitating abstract/meaningless and symbolic/meaningful gestures, ii) pantomiming the use of objects and tools (Goldenberg et al., 2003), and iii) actual object use, in particular when complex sequential actions including multiple objects are required (Dovern et al., 2011).¹ These deficits are assumed to represent impairments of the structural (for meaningless gestures) and the semantic (for meaningful gestures including pantomime) action processing route (Rumiati et al., 2010a) which may correspond to the dorso-dorsal and ventro-dorsal streams, respectively (Binkofski and Buxbaum, 2013). Accordingly, most studies investigating the ecological relevance of apraxia (e.g., (Hanna-Pladdy et al., 2003)) used both meaningful and meaningless items, items that tap into both the semantic and the structural processing domain (Dovern et al., 2012). To further our insights into the relationship between the two action routes and their relation to the various symptoms of apraxia is likely to result in a deeper understanding of the pathophysiology underlying apraxia. Due to high sensitivity and specificity, tests of pantomiming the use of objects and the imitation of meaningless hand gestures are considered the "gold standard" for detecting apraxic deficits related to the semantic and structural processing route. While there is consensus that the (inferior) parietal cortex is essential for imitation (Mengotti et al., 2013; Rumiati et al., 2009, 2010b), the neural basis of pantomime is debated (Frey, 2008; Goldenberg, 2009; Kroliczak and Frey, 2009; Vingerhoets, 2014). To elucidate the issue, we here perform both a review of the literature and a meta-analysis of the relevant structural and functional studies concerned with the neural basis of pantomime of object use.

When we refer to pantomime of object use, we mean the process of eliciting a meaningful, transitive movement. This can be triggered either by a name of a tool or by showing its picture. A prerequisite for pantomiming object use is the activation of the motor schema that matches the physical affordances of the object. A second important requirement for a correct pantomime of object use is the proper execution of that motor schema without the object being present. While during the actual handling of objects many motor parameters are determined by the structural properties of the object, these motor parameters have to be generated internally in the case of pantomiming object use (i.e., in the absence of the object). For example, the width of the grip holding the pretended glass (grasping component) and the distance between the hand and the mouth (transport component) during the pantomime of drinking from a glass constitute such key motor parameters. Note, however, that Laimgruber and colleagues (Laimgruber et al., 2005) demonstrated by means of kinematic analyses that pantomimes change features of movement execution: Compared to actual drinking, the width of the hand aperture was significantly reduced during pantomime of object use not only in stroke patients but also in healthy control subjects. These changes were, however, most prominent in patients with left brain damage (LBD), in whom the hand aperture was often absent during the pantomime. Taken together, the initiation and proper execution of the appropriate motor schema associated with a given object are the two main aspects of the pantomiming task, the performance of which is specifically disturbed in patients with LBD and apraxia (Goldenberg et al., 2007; Weiss et al., 2008). Accordingly, we here focus on those structural and functional imaging studies which tapped these two key processes underlying pantomiming object use. Consequently, studies in which pantomimes (shown on a video tape or produced by the experimenter) were only imitated were not considered, since the task of imitating a pantomime does not require the (internal) initiation (trigger) of the appropriate motor schema. In contrast, studies that used videotapes of pantomimes to test the subjects' ability to recognize or to evaluate a pantomime were included in the current analysis, since the initiation of the appropriate motor schema is a prerequisite of these tasks: In order to recognize a pantomime as 'hammering' or to judge whether the shown pantomime of 'hammering' is properly executed (i.e., the correct motor parameters are generated in the absence of the object, here: a hammer), subjects have to initiate the appropriate motor schema of hammering so that they can compare it to the pantomime shown. Likewise, studies on pantomime recognition that used videos of gestures with actual objects (Nelissen et al., 2010; Pazzaglia et al., 2008) had to be excluded, because the cognitive processes during the observation of actions with and without corresponding object are essentially different (Weiss et al., 2008). In 1982, Heilman, Rothi and Valenstein proposed a model to explain processes related to gesture execution and discrimination which actually support our current view. According to these authors, visual (when viewing objects) or linguistic (after verbal command) input is transferred to the left parietal cortex, which in turn activates premotor and motor areas for movement execution. The motor schema for a given object-related movement is supposed to be stored in the left IPL. Even though gesture (or pantomime, in our case) execution and discrimination are apparently distinguishable cognitive functions, the processes up to the activation of the appropriate motor schema are likely to be identical (see also (Goldenberg, 1999)). Heilman and colleagues support their model by reporting patient data: Whereas patients with lesions to the IPL are unable both to execute and to discriminate a gesture, patients with anterior lesions sparing the IPL exhibited deficits only in gesture execution, while gesture discrimination was preserved (Rothi et al., 1986). The authors explained this latter pattern of results by a disconnection of parietal and motor areas. Once the motor schema has been activated, the processes related to execution and recognition/discrimination of gestures obviously differ. Therefore, we would like to argue that the execution and the discrimination/recognition of a gesture both rely on the activation of the same motor schema (see also below the discussion of motor schemas for pantomiming object use and actual object use).

After clarifying the motor cognitive processes underlying pantomime of object use, we now turn to the recent debate about the neural basis of pantomiming object use. As stated above, deficits in pantomiming the use of objects and tools are most frequently observed in patients with left brain damage. Traditionally, the left parietal lobe has been considered an important region for pantomiming object use (Rothi et al., 1985, 1986). Consistently, early functional imaging studies of pantomiming tool use following verbal command observed activations within the left parietal lobe (i.e. (Moll et al., 2000; Choi et al., 2001)). Recently, however, it has been argued that these functional imaging data obtained from healthy subjects are at odds with findings in patients (Bohlhalter et al., 2011; Fridman et al., 2006; Goldenberg, 2009; Kroliczak and Frey, 2009). The importance of the parietal cortex for pantomime of object use was questioned based upon the observation that pantomime of object use performance was similar for patients with and without left parietal lesions (Goldenberg et al., 2003). Furthermore, in a lesion study of aphasic patients with left hemispheric stroke Goldenberg and colleagues showed that especially left inferior frontal lesions resulted in deficient pantomime of object use, whereas left parietal lesions did not significantly impair pantomime performance (Goldenberg et al., 2007). Studies using neuromodulation (Bohlhalter et al., 2011) and functional imaging (Bohlhalter et al., 2009; Fridman et al., 2006) further supported the importance of the frontal (and premotor) cortex for transitive actions (and thus pantomiming). On the other hand, there is growing evidence that the parietal cortex integrates representations for complex tool-use skills (e.g., conceptual knowledge about objects and their functional use) that are computed in a distributed network of regions (Frey, 2008; Vingerhoets, 2014). Therefore, both the specific function of the parietal cortex in pantomiming the use of objects and the contribution of the regions participating in the pantomiming network need to be clarified using a meta-analytic approach to resolve the apparent discrepancies between the results of functional neuroimaging studies (in young healthy subjects) and the findings of structural lesion studies (in elderly neurological patients). This approach will also further our understanding of the pathophysiology of apraxia.

¹ Note that we prefer to describe the clinical symptomatology of apraxia and refrain from using terms like ideo-motor apraxia or ideational apraxia, as the different apraxia classifications are currently under debate.

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