Neuropsychologia ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Anatomical and spatial matching in imitation: Evidence from left and right brain-damaged patients

Paola Mengotti [a,*], Enrico Ripamonti [b], Valentina Pesavento [c], Raffaella Ida Rumiati [a]

[a] Neuroscience Area, SISSA, Trieste, Italy
[b] Department of Economics, Management and Statistics, Statistical Section, University of Milan-Bicocca, Milan, Italy
[c] S.C. Medicina Riabilitativa, Azienda Ospedaliero-Universitaria 'Ospedali Riuniti', Trieste, Italy

ARTICLE INFO

Article history:
Received 23 December 2014
Received in revised form
24 June 2015
Accepted 29 June 2015

Keywords:
Ideomotor compatibility
Apraxia
Correspondence problem
Right hemisphere
Gesture imitation

ABSTRACT

Imitation is a sensorimotor process whereby the visual information present in the model's movement has to be coupled with the activation of the motor system in the observer. This also implies that greater the similarity between the seen and the produced movement, the easier it will be to execute the movement, a process also known as ideomotor compatibility. Two components can influence the degree of similarity between two movements: the anatomical and the spatial component. The anatomical component is present when the model and imitator move the same body part (e.g., the right hand) while the spatial component is present when the movement of the model and that of the imitator occur at the same spatial position. Imitation can be achieved by relying on both components, but typically the model's and imitator's movements are matched either anatomically or spatially. The aim of this study was to ascertain the contribution of the left and right hemisphere to the imitation accomplished either with anatomical or spatial matching (or with both). Patients with unilateral left and right brain damage performed an ideomotor task and a gesture imitation task. Lesions in the left and right hemispheres gave rise to different performance deficits. Patients with lesions in the left hemisphere showed impaired imitation when anatomical matching was required, and patients with lesions in the right hemisphere showed impaired imitation when spatial matching was required. Lesion analysis further revealed a differential involvement of left and right hemispheric regions, such as the parietal opercula, in supporting imitation in the ideomotor task. Similarly, gesture imitation seemed to rely on different regions in the left and right hemisphere, such as parietal regions in the left hemisphere and premotor, somatosensory and subcortical regions in the right hemisphere.

1. Introduction

One conceptualization of imitation considers it as an act of copying someone's movements. As such imitation requires an interaction between at least two actors: the model, i.e., the person executing the movement in the first place, and the imitator, i.e., the person copying the movement. To accomplish imitation, the imitator needs to integrate the sensory information coming from the visual system with the motor system in order to reproduce the movement. How this integration is accomplished is known as the *correspondence problem* (Brass and Heyes, 2005) and it is still matter of debate. It is therefore critical to investigate how the observed actions are mapped onto the motor system of the observer.

The production of a simple action has been shown to be facilitated or interfered by the simple concurring vision of a similar or different movement, suggesting that imitation is indeed based on sensorimotor interaction. In one of these studies (Brass et al., 2000), participants were required to move one of two fingers in response to a spatial cue (i.e., a cross placed on the hand stimulus on the screen) while observing a moving hand as task-irrelevant cue. Results showed that when the movement performed by the participants was the same as the one performed by the hand stimulus, their reaction times were smaller than in the opposite condition, that is when the two movements differed. Subsequent studies manipulated this basic paradigm (Brass et al., 2001a, 2003; Bertenthal et al., 2006; Longo et al., 2008; Longo and Bertenthal, 2009; Boyer et al., 2012) and replicated the original observation that action is modulated by perception. According to this view, the integration between perception and action is achieved through a process of *common coding* or *ideomotor compatibility* (Prinz, 1997; Brass et al., 2000, 2001a; Hommel et al., 2001; Massen and Prinz, 2009) between the model and the imitator. This occurs because

* Correspondence to: Cognitive Neuroscience, Institute of Neuroscience and Medicine (INM-3), Research Centre Jülich, Leo-Brandt-Str. 5, 52425 Jülich, Germany.
E-mail address: p.mengotti@fz-juelich.de (P. Mengotti).

http://dx.doi.org/10.1016/j.neuropsychologia.2015.06.038
0028-3932/

percepts and action plans share common properties and it is this similarity that allows imitation to be achieved: the more similar is the perceived movement with the movement to be produced, the easier is the production of the movement (Prinz, 1997; Massen and Prinz, 2009).

Moreover, the degree of similarity or ideomotor compatibility between imitator's and model's movements can be based on two different parameters: the anatomy of the model and the location in space of the model's movements. The anatomical imitation is based on the anatomical matching with the model; for instance, if the model moves his/her left arm, the imitator will move his/her left arm, with movements being performed in different positions of the space. The "mirror" or spatial imitation consists in replicating the movement as if the imitator was in front of a mirror. Thus when the model moves his/her left arm, the imitator will move his/her right arm, to spatially match the model. As the anatomical and spatial components have been teased apart in several studies (Bertenthal et al., 2006; Mengotti et al., 2012; Mengotti et al., 2013b), it is likely that the two processes rely on different cognitive processes (Boyer et al., 2012; but see also Heyes and Ray, 2004 for a different account).

The basic matching mechanisms of imitation have been studied using paradigms of ideomotor compatibility involving very simple finger movements (Brass et al., 2000, 2001a, 2003; Bertenthal et al., 2006; Longo et al., 2008; Longo and Bertenthal, 2009; Boyer et al., 2012; Mengotti et al., 2012, 2013b). However, more often imitation is used, for instance, to learn more complex gestures. After brain damage, this ability to imitate gestures can be impaired; this disorder is known as ideomotor apraxia (see Goldenberg (2009) for an historical review). Patients with ideomotor apraxia show a deficit in imitating actions and/or performing them on verbal command and these deficits cannot be attributed to elementary motor and sensory deficits, aphasia, agnosia or frontal inertia (De Renzi and Faglioni, 1999; Cubelli et al., 2000; see Rumiati et al., 2010, for a review). According to the classical model proposed by Liepmann (1920), action control is achieved in two steps: the generation of the mental image of the intended gesture and the implementation of this mental image into the appropriate motor output. A failure occurring at the first step will give rise to ideational apraxia, clinically characterized by the inability to use objects, whereas a failure at the second step will give rise to ideomotor apraxia.

Cognitive neuropsychological models provided a coherent conceptualization of how imitation comes about, by proposing that the behavior depends on the nature of the input and the output involved in a given task (Rothi et al., 1991; Cubelli et al., 2000; Tessari and Rumiati, 2004). According to these models, imitation is suggested to be accomplished by relying on two main pathways: the semantic pathway, which encompasses the semantic systems and is used for reproducing known gestures, and the direct pathway, used for meaningless gestures, which bypasses the semantic system and allows a direct reproduction of the visual input into motor output. These models allowed generating predictions as to how imitation can break down after brain damage, with selective deficits depending on the particular component of the model that is damaged (see, Rumiati et al., 2010 for a review). Therefore, patients with different lesions will show a deficit in imitation of meaningless or meaningful gestures (Tessari et al., 2007).

Further dissociations are observed in imitation performance depending on the part of the body that it is involved, with lesions differentially affecting the ability to imitate hand postures or finger movements (Goldenberg, 1999). The predominant role of the left hemisphere in supporting the ability to imitate gestures is widely recognized (Liepmann, 1920; De Renzi et al., 1980; Papagno et al., 1993; Goldenberg, 1995; Haaland et al., 2000; Tessari et al., 2007); nonetheless the right hemisphere seems to contribute to imitation (Goldenberg and Karnath, 2006; Goldenberg et al., 2009), in particular when the visuo-spatial analysis of the movement is more important, as for the imitation of meaningless gestures (Tessari et al., 2007; Rumiati et al., 2005). Moreover, right brain-damaged patients' imitation performance is more impaired with meaningless gestures (Tessari et al., 2007) and finger configurations (Goldenberg, 1999, 2009; Della Sala et al., 2006), whereas left brain-damaged patients' imitation performance is more impaired with hand postures (Goldenberg, 1999), suggesting a division of labor between the two hemispheres.

In the present study, we aimed at better understanding the matching processes that sustain imitation by applying a paradigm based on the ideomotor compatibility. This paradigm is particularly useful because it allows studying the effect on patients' performance of the anatomical or spatial matching between the model's and imitator's movements. This has been investigated when both matching processes were present or when the two movements matched at the anatomical or at the spatial level. Participants were asked to reproduce a tapping movement performed by the model in two different ways: in the anatomical subtask, they were instructed to move the finger that matched the model's finger based on the anatomical identity, whereas in the spatial subtask, participants were instructed to move the finger that matched the model's finger based on its location in space. When the model was presented in a mirror perspective, the imitator's and the model's movement matched both for the anatomical identity of the body part moved and for their spatial location in space, whereas when the model was presented in a non-mirror perspective the two movements matched only for one of the two features, either in their anatomical identity or in their spatial location.

Moreover, we analyzed patients' performance on a more complex gesture imitation task, in which they reproduced intransitive gestures performed by a model in a spatial (i.e., mirror) perspective or in an anatomical perspective. This task is a standardized test usually adopted in the neuropsychological assessment to detect deficits in imitation (Tessari et al., 2015).

Indeed, tasks similar to our ideomotor task have been used in neuroimaging studies (Iacoboni et al., 1999; Brass et al., 2001b; Koski et al., 2003; Bien et al., 2009; Mengotti et al., 2012) while gesture imitation tasks are more common in neuropsychological studies (De Renzi et al., 1980; Papagno et al., 1993; Goldenberg, 1995; Haaland et al., 2000; Tessari et al., 2007; Mengotti et al., 2013a). These two lines of research led to different results about the localization of the cognitive processes underlying imitation. Neuroimaging studies with healthy individuals showed consistently bilateral activations of premotor and frontal regions and activations of the parietal operculum (Iacoboni et al., 1999; Brass et al., 2001b; Koski et al., 2003; Bien et al., 2009; Mengotti et al., 2012), whereas in neuropsychological studies lesions to left parietal regions have been more consistently associated with deficits in imitation of gestures (Haaland et al., 2000; Weiss et al., 2001; Tessari et al., 2007; Mengotti et al., 2013a). Only a few studies in which gesture imitation was investigated using neuroimaging with healthy participants (Rumiati et al., 2005; Menz et al., 2009) found bilateral fronto-parietal activations, thus suggesting also some a contribution of the right hemisphere to imitation.

However, no study directly compared ideomotor and gesture imitation tasks in a sample of brain-damaged patients.

Previous evidence allowed scholars to argue in favor of the existence of two distinct mechanisms that can be used to solve the corresponding problem in imitation: a process of spatial compatibility that supports spatial imitation and a process of matching of body parts of model and imitator that supports anatomical imitation. In other words, a mechanism based on the spatial (or