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Parallel and distributed neural models of the ideomotor principle: An investigation of imitative cortical pathways

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Abstract

Humans' capacity to imitate has been extensively investigated through a wide-range of behavioral and developmental studies. Yet, despite the huge amount of phenomenological evidence gathered, we are still unable to relate this behavioral data to any specific neural substrate. In this paper, we investigate how principles from psychology can be the result of neural computations and therefore attempt to bridge the gap between monkey neurophysiology and human behavioral data, and hence between these two complementary disciplines.

Specifically, we address the principle of *ideomotor compatibility*, by which 'observing the movements of others influences the quality of one's own performance' and develop two neural models which account for a set of related behavioral studies [Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial and imitative cues. *Brain and Cognition 44*, 124–143]. We show that the ideomotor effect could be the result of two distinct cognitive pathways, which can be modeled by means of biologically plausible neural architectures. Furthermore, we propose a novel behavioral experiment to confirm or refute either of the two model pathways.

Keywords: Neural mechanisms of imitation; Ideomotor principle; Neural field computation

1. Introduction

Human capacity to imitate has been extensively investigated through a wide range of behavioral and developmental studies (see Billard, 2002 for a review). Yet, despite the huge amount of phenomenological evidence gathered, we are still unable to relate this behavioral data to any specific neural substrate. Particularly informative in the attempt to resolve this issue was the neurological evidence for the existence of a common neural substrate devoted to the recognition and production of movements, the so called *mirror neuron system* (see Decety & Sommerville, 2003; Iacoboni et al., 1999; Rizzolatti et al., 2001 for recent reports on this system in monkeys and humans). While the mirror neuron system offers an exciting line of study, it has yet to be shown how this circuit, in connection with other well-known neural circuits for visual representation of motion and for motor control, may explain the behavioral data on imitation.

Several computational studies using different approaches have already attempted to address the issue of the mirror neuron system. A comprehensive review of these studies can be found in Oztop, Kawato, and Arbib (2006). One of the most influential approaches is based on motor control theory (Billard & Mataric, 2001; Demiris & Hayes, 2002; Oztop et al.; Wolpert, Doya, & Kawato, 2003), which considers the tight link between motor execution and action observation. In this approach, a set of predictive inverse and forward models allows an observed movement to be compared with entries in the observer's motor repertoire. When a sufficiently similar action is found, its execution is facilitated. Our work is more in line with that of Arbib, Billard, Iacoboni and Oztop (2000), which attempts to uncover the neural pathways at the origin of human imitation capabilities. Our approach, however, is strongly multidisciplinary, in that its main sources of inspiration come from both psychological theories and neuroscience. We investigate how the former's principles can be the result of neural computations and therefore attempt to bridge the gap between monkey neurophysiology and human behavioral data, and hence between these two complementary disciplines.

In this paper, we address the principle of *ideomotor compatibility*, by which '*observing the movements of others influences the quality of one's own performance*' (Brass,

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Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschäger, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Kilner, Paulignan, & Blakemore, 2003), and develop two neural models which account for a set of related behavioral studies (Brass et al., 2000). We show that the ideomotor effect could be the result of two distinct cognitive pathways, which can be modeled by means of biologically plausible neural architectures. Furthermore, we propose a novel behavioral experiment to confirm or refute either of the two model pathways. In Section 2, we briefly recall the experiment by Brass et al.

1.1. Brass et al. experiment

In their experiment Brass et al. (2000), used a stimulus–response (SR) paradigm to verify two hypotheses of the ideomotor theory. These two hypotheses are based on the neural correlate that the human brain appears to possess highly specialized neural circuits devoted to the recognition of movements performed by others and that these circuits are likely to be shared by the motor preparation circuits (Decety & Sommerville, 2003; Iacoboni et al., 1999). The first of the hypotheses states that if a subject was requested to respond to the motion of a demonstrator then he would experience a motor facilitation, giving faster reaction times compared to if the subject was asked to make the same movement in response to a spatial cue. The second hypotheses states that the facilitatory effect would be greater if the movements of the demonstrator and subject were very similar (*ideomotor compatible*) than if they were of a different type (*ideomotor incompatible*).

The experimental setup comprised of three independent binary variables, leading to eight conditions plus four baseline conditions. The experimental stimuli consisted of a combination of a finger-lifting movement (either index or middle finger) and of a spatial cue consisting of a cross painted on the corresponding or opposite fingernail (see Fig. 1). The subjects reaction times (RTs) were measured while they were asked to respond to the various stimuli by moving the finger that was the closest to either cue (e.g. by moving their index finger for a demonstration of the index finger or for the presentation of a cross on the demonstrator's index fingernail).

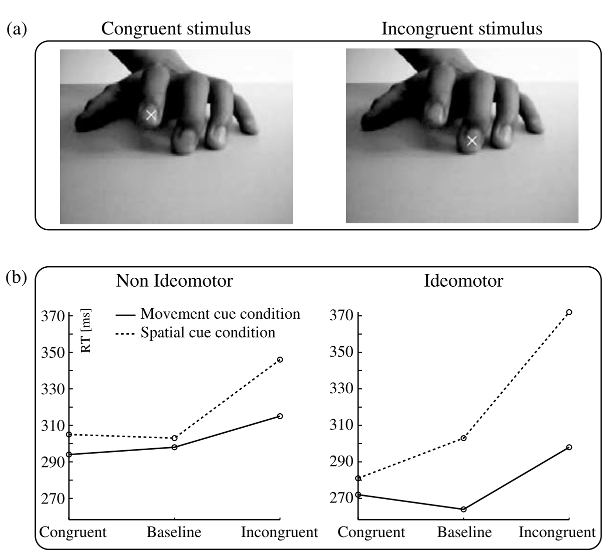

Fig. 1. (a) Examples of congruent and incongruent stimuli used by (Brass et al., 2000) in their experiment; (b) reaction times observed in the original experiment.

These instructions determined the first experimental variable, the relevant stimulus dimension. Furthermore, an interfere paradigm was used in order to examine the effect of the presentation of congruent or incongruent[1] stimuli against a baseline condition in which only the relevant stimulus was presented to the subject. Finally, the experiment was varied in order to examine the effect of ideomotor similarity between observed and executed movements. In one case, the subjects were asked to lift their finger (*ideomotor compatible*) and in the second they were asked to produce a finger-tapping movement (*ideomotor incompatible*).

The results, shown[2] in Fig. 1, were in agreement with the hypotheses. Indeed, responses to finger movements were faster than responses to spatial cues, and ideomotor compatible pairs of observed/executed movements generally produced better RTs. Moreover, typical facilitatory and interference effects were observed between congruent and incongruent conditions, respectively. Next, we present two neural models, which account for these results.

2. Models

Our modeling approach starts with the well-accepted hypothesis that the brain uses parallel pathways to process multimodal information. This so called *parallel distributed processing* (PDP) framework has been successfully applied in explaining a variety of effects observed during stimulus–stimulus and stimulus–response compatibility experiments (Erlhagen & Schöner, 2002; Hasbroucq & Guiard, 1991; Kornblum, 1994; Zhang et al., 1999). In these models, the information passes through a layered network organization, usually consisting of the perceptual, decisional and motor preparatory stages of computation. Generally, multimodal perceptual information is processed separately and simultaneously in a first stage and is then combined within the other layers depending on the nature of the information. This fusion of information within a common layer has sometimes been referred to as the *dimensional overlap* (Kornblum, 1994), which gives a measure of the degree to which sets of items are perceptually, structurally or conceptually similar. This principle allows perceptually similar information to be merged into a common neural substrate and such a mechanism has proved useful in explaining a wide range of human behaviors (Erlhagen & Schöner, 2002; Hasbroucq & Guiard, 1991; Kornblum, 1994; Zhang, Zhang, & Kornblum, 1999). In this

[1] Congruent condition: a left (right) finger movement with a cross on the left (right) fingernail. Incongruent condition: a left (right) finger movement with a cross on the right (left) fingernail.

[2] As the ideomotor variable was tested among two distinct groups of subjects, we shifted the reaction times to make the baseline condition in the spatial cue task coincide in both experiments, since this is the only case in which both experimental conditions are identical.