Motor Cortex Activation Induced by a Mirror: Evidence From Lateralized Readiness Potentials

Pascale Touzalin-Chretien and André Dufour
Laboratoire d’Imagerie et de Neurosciences Cognitives, Centre National de la Recherche Scientifique, Université Louis Pasteur, Strasbourg, France

Submitted 11 February 2008; accepted in final form 27 April 2008

Touzalin-Chretien P, Dufour A. Motor cortex activation induced by a mirror: evidence from lateralized readiness potentials. J Neurophysiol 100: 19–23, 2008. First published May 14, 2008; doi:10.1152/jn.90260.2008. Similar motor regions are activated during voluntarily executed or observed movements. We investigated whether observing movements of one’s own hand through a mirror will generate activations in the cortical motor regions of both the moving and nonmoving hands. Using the lateralized readiness potential (LRP), an electrophysiological correlate of premotor activation in the primary motor cortex, we recorded evoked responses to movements while subjects were viewing the performing (right) hand through a mirror placed sagittally, giving the impression that the left hand was performing the task. Reliable LRP s were recorded in relation to the seen hand, indicating motor cortex activity in the contralateral hemisphere of the inactive hand while the opposite hand was performing the movement.

INTRODUCTION

Observing an action has been found to lead to cortical activation of some of the same regions activated when performing the action. The existence of this motor resonance mechanism, called the mirror neuron system, suggests a direct link between action and perception and may contribute to the understanding of another person’s actions or intentions. Several functional magnetic resonance imaging (fMRI) studies have focused on identifying brain regions involved in action observation. Observation has been primarily observed in parietal areas in which both visual and kinesthetic information may converge (Buccino et al. 2001; Iacoboni et al. 1999). Other studies have emphasized a modulation of the neuronal activity in the contralateral hand section of the primary somatosensory cortex when visual information of hand actions is provided (Oouchida et al. 2004). The activation of somatosensory areas has been shown to be further modulated by the relative orientation of the observed hand (Jackson et al. 2006) and first-person perspective has been found to lead to significantly greater activation in the somatosensory cortex than third-person perspective. In addition, this motor activity can occur prior to observing someone else’s action (Kilner et al. 2004). Using an electrophysiological technique, the presence of a motor preparation marker was recorded prior to observation of a predicted movement. Moreover, observation of an action has consequences on the peripheral motor system. Using motor-evoked potentials (MEPs) induced by transcranial magnetic stimulations, hand muscle activity has been found to increase significantly when subjects observe a hand movement (Gaggiato et al. 2001). Moreover, facilitation of MEPs seems to be enhanced when the hand presented is viewed from the first-person perspective (Maeda et al. 2002). Together, these findings suggest that observing somebody else’s movement generates the motor program corresponding to that particular movement. Interferences between observed and executed movements have also been observed (Kilner et al. 2003), suggesting interactions within a common neural network that encodes both observed and executed movements. Indeed, behavioral studies have shown decreased movement accuracy when an observed movement is qualitatively different from a simultaneously executed movement. Increased reaction times at the onset of finger movements have also been recorded in response to the presentation of different finger movements (Brass et al. 2001). Thus it is unclear whether observed and executed movements interfere when the observed movement originates from the subject’s own body, as when viewed in a mirror. To test this hypothesis, we carried out experiments in which subjects performed movements with their right hands, which could only be seen through a mirror placed sagittally, giving the impression that the left hand was performing the task. Activation of motor cortices related to the active and observed hands was assessed by analyzing the event-related component called the lateralized readiness potential (LRP), which reflects only movement-related parameters and effectively isolates activities that reflect only lateralized response preparation. Importantly, neuroanatomical evidence from surface and depth electrode recordings has shown that the LRP is generated, at least in part, in the primary motor cortex (Gemba et al. 1990; Okada et al. 1982; Vaughan Jr et al. 1968). In addition, the LRP component reflects response preparation and commences before muscle contraction begins, and therefore can occur in the absence of an overt response (de Jong et al. 1988; Galdo-Alvarez and Carrillo-de-la-Pena 2004; Miller and Hackley 1992; Minelli et al. 2007).

We hypothesized that observing movements of one’s own hand through a mirror, giving the impression of movements of the opposite, nonmoving hand, can generate activations in the cortical motor regions of both the moving and nonmoving hands.

Address for reprint requests and other correspondence: P. Touzalin-Chretien, Laboratoire d’Imagerie et de Neurosciences Cognitives, CNRS, ULP, 21 rue Becquerel, 67087 Strasbourg, France (E-mail: pascale.touzalin@linc.unistra.org.fr).
METHODS

Participants

Eleven healthy paid volunteers (five males, six females; mean age 27.7 yr) were enrolled in the experiment. Nine participants were right-handed and two were left-handed according to self-reports. All subjects provided written informed consent and the study protocol was approved by our local Ethics Committee. Each subject participated in one experimental session, which lasted around 90 min.

Materials and procedures

Subjects performed a forced-choice task unimanually under four different and randomly presented conditions, defined by different views of the responding hand. Participants were seated at a table in the experimental room. Depending on the experimental condition, a mirror was placed either vertically (in the middle of the table and in the midsagittal plane of the subject with the reflective surface facing the right arm; Fig. 1A) or horizontally (with the reflective surface facing the subject’s right hand; Fig. 1B), or was absent (no-mirror condition). Two light-emitting diodes (LEDs) were placed on the table 3 cm apart, 40 cm from the subject, and on the side of the responding hand, with two response keys placed beside the LEDs. The LEDs were switched on randomly for 200 ms, and subjects were asked to press—as quickly as possible—the upper (lower) button when the active (inactive) hand was placed on the table symmetrically to the LEDs. The LEDs were switched on randomly for 200 ms, and subjects were asked to press—as quickly as possible—the upper (lower) button when the upper (lower) LED was switched on under the following four conditions: in condition 1, participants had a direct view of the right (performing) hand. In condition 2, subjects performed the task and were instructed to fixate their performing hand in the mirror which was placed sagittally, giving the impression of a direct view of the left (inactive) hand. In condition 3, the mirror was placed frontally giving visual feedback of the right hand in a frontal view. In condition 4, the task was performed using the left hand as per condition 1 (i.e., with a direct view of the performing hand). An opaque cover was used to prevent direct visualization of the right performing hand in the two conditions involving the mirror (conditions 2 and 3). In all conditions, the inactive hand was placed on the table symmetrically to the responding hand. In all, 150 trials randomly spaced from 2,600 to 3,000 ms were performed under each condition.

EEG recording

Electroencephalographs (EEGs) were recorded using Ag/AgCl Bio-Semi’s active electrodes mounted in an elastic cap. The electrodes were placed at C3 and C4 sites according to the 10/20 system (Klem et al. 1999), above the hand area of the left and right motor cortex, with the left ear lobe (A1) as a common reference, and sampled at a rate of 2,048 Hz (band-pass 0.02 to 500 Hz, with off-line digital smoothing, 10-Hz cutoff). To monitor ocular artifacts, vertical and horizontal electrooculographic (EOG) potentials were recorded from bipolar derivations using Ag/AgCl electrodes. Muscle activity (electromyography, EMG) of both hands was recorded by the means of bipolar derivations placed at ventral forearm sites that roughly intersected the wrist–elbow distance.

Artifact rejection and the duration of the averaging epoch ranged from 200 ms before stimulus onset to 500 ms afterward. After rejection of invalid trials (i.e., those contaminated by artifacts), data analyses were performed on a mean of 134 trials per condition and subject.

RESULTS

Electrophysiological results

To calculate response-specific lateralization according to the viewed hand, event-related potentials (ERPs) were computed separately for each of the four conditions defined by the visual feedback of the performing hand, and were subjected to a two-step subtraction procedure. This double-subtraction method accounted for unilateral motor activity evoked by voluntary movements. First, the difference in waveforms between C3 and C4 was calculated for each trial and condition. Second, the average waveform for condition 2 trials and the average waveform for condition 4 trials were subtracted from the average waveform for condition 1 trials. Using this analytical design, condition 1 versus condition 4 should indicate the classic LRP, that is, response preparation/execution for either the left or the right hand. Condition 1 versus condition 2 should indicate the LRP due to hand visualization through the lateral mirror. An additional subtraction procedure was performed as a control waveform between conditions 1 and 3. No LRP was expected in this latter case since functional imaging studies have shown that activations are observed in the left hemisphere when observing an actor’s left-hand movement presented frontally (Jackson et al. 2006). Thus subtracting a negative waveform induced by the movement of the right hand (condition 1) from a similar negative waveform induced by the movement of the right hand seen in the mirror frontally (condition 3) should result in a baseline waveform, which was termed the control potential.

Analysis of presubtracted and lateralized waveforms of electrodes C3 and C4 has been shown to be redundant (Miller and Hackley 1992). Consequently, we performed statistical analyses only on the LRP [i.e., for classic LRP (C3 − C4)condition 1 − (C3 − C4)condition 4]. The three waveform outcomes from the four conditions are illustrated in Fig. 2A. As anticipated, right- and left-hand movements under direct view yielded an LRP (condition 1 vs. condition 4). When electrophysiological activity under lateral mirror view condition, giving the impression that the left hand was performing the task, was subtracted from activity under direct view condition (condition 1 vs. condition 2), we observed an LRP, traditionally generated with tasks involving both hands, even though only one hand was involved in the motor task. These results indicate that activation of the left-hand primary motor cortex (right hemisphere) was associated with a right-hand response. Unexpectedly, a lateralized potential was also present with a frontal view of the moving hand (control potential), suggesting activity in the right hemisphere, although it was significantly lower than classic and lateral mirror-induced LPDs. This may be due to the appearance of a right-hand, viewed in a mirror placed frontally, as a left-hand even if subjects recognized their own right hands.

Latency measures

Onset of LRP was estimated for each subject using a segmented regression (SR) method, based on average ERPs (Mordkoff and Gianaros 2000). This method defined the LRP onset as the point of intersection between two straight lines fitted to the LRP waveform, one line fitted to the putative preonset segment of the LRP and the other line fitted to the segment that rose to the peak.

LRPs began at an average of 128 ms following stimulus onset. This latency period was shorter than that for the lateral mirror view [mean: 193 ms; F(1,10) = 8.12, P = 0.017; see Fig. 2D]. Earlier studies have shown that differences in stimulus-locked LRP onset are caused by premotor processes (Mordkoff and Gianaros 2000). The difference observed here...
may indicate incongruence between the motor preparations of the viewed and responding hands. Under the conditions of this study, subjects had to inhibit movement of the real left hand. The observed differences in onset latency may be due to this inhibition process, probably taking place in the premotor cortex.

Amplitude measures

ERP amplitudes were analyzed between LRP onset and the subsequent 200 ms. The mean amplitudes of the two waveforms (LRP and LRP induced by the mirror) were compared with the control potential. Although no clear LRP was visible in the latter condition, a mean amplitude was computed, starting from 160 ms (mean latency between the LRP and the LRP induced by the mirror) and for the subsequent 200 ms. The mean amplitudes for both the direct and lateral mirror view LRPs were found to differ from the control potential ($P < 0.001$ and $P < 0.007$, respectively, post hoc Newman–Keuls test), whereas the difference between the direct and lateral mirror view LRPs was not significant ($P = 0.23$, see Fig. 2C). Importantly, in the two latter conditions, even when motor preparation was observed in the hemisphere contralateral to the viewed hand, no actual movements were executed by this hand (left hand placed behind the mirror), as shown by EMG records (Fig. 2B).

Although we assume that amplitude measures account for an increased ipsilateral activity related to the visual feedback of the performing hand, an alternative explanation is that the LRP in the lateral-mirror condition might be due to a decreased activity in the contralateral hemisphere of the performing hand. However, this hypothesis is not supported by the fact that a reduction of the LRP occurs only in the frontal mirror condition and not in the lateral mirror condition, although both conditions prevented direct view of the performing hand. However, to rule out this hypothesis, we compared the potential of C3 between the direct and lateral mirror view from 100 to 300 ms. No statistical difference in the potential of C3 was recorded between these two conditions [$F(1,10) = 1.41, P = 0.26$], indicating that the presence of the LRP is rather due to an ipsilateral modulation of motor activity.

Behavioral results

Reaction times (RTs) of conditions 1, 2, and 3 were analyzed in correspondence to the classic LRP, the LRP induced by the lateral mirror, and the control potential (frontal mirror), respectively. Subjects responded faster to the direct view condition (mean = 660.5 ms, SD = 105) than to the sagittal (mean = 763.4 ms, SD = 144.9) and frontal (mean = 847.2 ms, SD = 113.8) mirror views. The difference was statistically significant [$F(2,20) = 20.177, P < 0.001$] and the post hoc analysis (Newman–Keuls paired comparisons) indicated a significant difference among all three conditions. These differences could reflect levels of difficulty linked to the spatial uncertainty of the positions of the response keys under mirror conditions, whereas movement onset was similar for all three conditions (Fig. 2B). Although EMG waveforms appear different for the three conditions, despite an identical motor task, we suggest that this was merely due to a greater uncertainty in motor programming under indirect (mirror) views of the performing hand. Identical EMG onsets for the three conditions might indicate that these conditions had no effect on reaction time (movement onset), but only on response time, which reflects visuospatial movement coordination (key press).

DISCUSSION

This study was designed to determine whether observing movements of one’s own hand through a mirror, giving the impression of movements of the opposite hand, could generate activations in the cortical motor regions of both the moving and nonmoving hands. Using an electrophysiological correlate of premotor activation in the primary motor cortex (i.e., the LRP), we found that observing an image of one’s own hand is sufficient to generate cortical motor preparation related to that hand, even if the opposite hand performs the movement. Based on studies showing that the LRP is an on-line measure of
response preparation (Coles 1989), the presence of this component in the contralateral hemisphere of the inactive hand indicates neural activity in the primary motor cortex with respect to this hand while the other hand is active.

The recording of an LRP in the lateral mirror condition also confirms the hypothesis that the visual and motor systems in humans are tightly related. These results are consistent with previous electrophysiological studies in healthy subjects, showing that observing a predicted movement leads to motor activation (Kilner et al. 2004). The current results also indicate that this motor activation is lateralized depending on the visual feedback. Moreover, these findings are in accordance with physiological studies showing that observing an action is sufficient to induce changes in the sensorimotor cortex. Indeed, lateralized activity is observed in fMRI images on the contralateral side to the observed movement (Oouchida et al. 2004). Furthermore, cortical activity depends on hand orientation, with significant lateralized activation of the precentral gyrus when the observed movement is in the first-person perspective (Jackson et al. 2006).

Interestingly, we observed a significant difference in LRP onset between the direct view and the lateral mirror view conditions. This difference may reflect incongruence between the motor preparations of the viewed and responding hands. Under the conditions of this study, subjects had to inhibit movement of their real left hands. This inhibition process, which probably occurs in the premotor cortex, may explain the differences in observed onset latency.

Unexpectedly, we observed activity, although to a lesser degree, in the right motor cortex when subjects were viewing the right hand in the frontal mirror. The right hand, viewed frontally in the mirror, may be coded correctly as a left hand in the CNS, even if subjects recognized their right hands. This hypothesis suggests a relative automatic coding of handedness and is in agreement with the model for the process of handedness recognition (Parsons 1994). According to this model, a preattentive step of handedness recognition could play a role in recognition of actions performed by other individuals.

Under the framework of the mirror system, our data are in line with the existence of an action/observation matching system in the human brain, involving the primary motor cortex.
However, the mirror system was proposed following recordings in monkeys to describe neurons in area F5 (supposed to be situated in the Broca’s region in human) that discharge both when the monkey actively performs an action and when it observes a similar action by another individual (Rizzolatti et al. 1996). Present results do not directly indicate an activation in human premotor cortex (Broca), but may account for the presence of neurons within the primary motor cortex that are activated when observing one’s own movement, in accordance with studies that have shown greater facilitation of MEPs when observing hands in a natural orientation to one’s own (Maeda et al. 2002). Our results are also in line with previous works that have used hands in a mirror configuration to investigate observation processes (Iacoboni et al. 1999), since we observed an LRP in the frontal mirror condition, although to a lesser degree.

The cerebral network through which visual feedback of upper limbs modulates cortical activity in primary motor cortices remains an open question. Such cross-modal modulations might be generated through the visual system via parietal areas, where both visual and kinesthetic information converge, or through facilitation of bilateral motor cross-connections, since one hand is performing the activity. Further studies are being designed to investigate these questions.

REFERENCES


