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Short Communication

Paradoxical lateralization of brain potentials during imagined foot movements

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Abstract

Though each foot is controlled primarily by the contralateral hemisphere, the event-related brain potentials preceding an overt foot movement are largest over the ipsilateral side of the head. Because such "paradoxical lateralization" results from the spatial organization of the motor homunculus, it can provide a sign of motor-cortex activation. We report paradoxical lateralization in the potentials accompanying imagined foot movements, thereby demonstrating a contribution of cortical areas directly involved in movement execution.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: Motor imagery; Movement-related brain potentials; Paradoxical lateralization; Sensorimotor cortex

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What is wrong with the feet? Like the hands, each foot is controlled primarily by the contralateral hemisphere. As would be expected, the event-related brain potentials (ERPs) preceding a hand movement are largest over the contralateral side of the head. Yet, those preceding a foot movement are largest over the ipsilateral side [3,4]. An explanation is provided in Fig. 1, which displays the classic motor homunculus [19]. Movement of a limb excites its neural representation in the motor homunculus, causing current to flow into nearby cortex. Because the hands of the homunculus are located laterally, each produces an electrical field more negative over its own hemisphere (contralateral to the moved hand). Because the feet of the homunculus are located on the inner surface of the longitudinal fissure, each produces a field more negative over the opposite hemisphere (ipsilateral to the moved foot). The more negative the potentials from the homunculus, the more they augment the (net negative) potentials conducted to the scalp from other brain areas.

Like overt hand movements, imagined hand movements can be accompanied by scalp-recorded ERPs that are larger contralateral to the involved hand [2,15,16]. Because of their good temporal resolution, these lateralized potentials provide the opportunity to monitor motor imagery moment-by-moment. Unfortunately, it is not entirely clear from where in the motor system they arise. Studies employing functional MRI have found motor imagery to activate a number of cortical areas that preferentially control the contralateral hand, including primary motor cortex [13,20,23]. Effects on primary motor cortex have likewise been found using transcranial magnetic stimulation (TMS) [8,11,22]. Though some of these cortical areas could in principle cause the observed lateralization of potentials on the scalp, it remains uncertain which if any is actually responsible.

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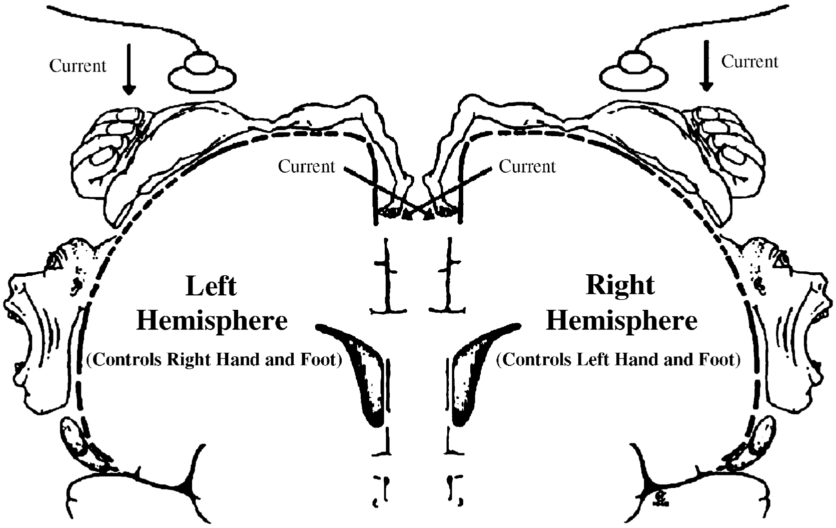

Fig. 1. Motor homunculus (adapted from [19]). Arrows indicate general left–right direction of current flow caused by movement of a hand or foot. Electrodes show scalp locations where normal lateralization during hand movements and paradoxical lateralization during foot movements can be recorded.

To help resolve this ambiguity, we wanted to see if paradoxical lateralization would occur when movement of a foot is merely imagined. If so, it would implicate either primary motor or somatosensory (jointly termed sensorimotor) cortex, since only these areas contain homunculi with the requisite spatial arrangement. In contrast, suppose for example that lateral premotor cortex (an area less directly involved in movement execution than sensorimotor cortex) is solely responsible for ERP lateralization during motor imagery. Because it is located entirely on the outer aspects of the hemispheres, the same non-paradoxical pattern should then be observed for the feet as for the hands. (For a similar analysis of ERPs during advance preparation for a to-be-signaled movement, see [12].)

Nineteen participants providing informed consent were tested in a protocol approved by the University of Pennsylvania Institutional Review Board. Participants alternated between two types of 72-trial blocks. On “hand blocks” they made or imagined taps with their left or right index fingers, and on “foot blocks” they made or imagined taps with their left or right big toes. A single tap was required on each trial. Each block consisted of four trial types defined by whether the tap was overt or imagined and whether it involved the left or right limb. These occurred equally often and in a random order. There were two test sessions, the first of which served as practice. The reported results are based on five hand and five foot blocks from each participant’s second session.

To help control the time at which the imagined movements occurred, both overt and imagined movements were synchronized to the temporally predictable occurrence of a brief visual signal (synch signal). Each trial began with the appearance of a fixation cross in the middle of a computer monitor. After 500 ms, the fixation cross was temporarily replaced for 250 ms by a warning signal (“E” or “I”) that indicated whether the response on that trial should be overtly executed or imagined. One second later, the fixation cross was replaced for 250 ms by a second warning signal (“L” or “R”) that indicated whether the response should involve the left or right limb. Finally, after another second, the fixation cross was replaced for 50 ms by the synch signal (“X”). The trial ended 700 ms later, with the fixation cross vanishing from the screen.

After each block, participants received feedback about their performance and filled out a brief questionnaire. Feedback concerned their overt taps on the preceding block, including the deviation from synchrony with the synch signals and number (if any) on trials requiring imagined taps. The questionnaire asked participants to rate their imagined taps during the preceding block on several dimensions, including sensation of movement, sense of intention or effort, vividness, and absence of muscle activity. Its main purpose was to encourage participants to cultivate their images along these lines. The eight questions comprising the questionnaires are shown in Table 1.

Participants sat facing a monitor across a table with their heads supported by a chinrest, forearms resting on the table, and shoeless feet flat on the floor below. On hand blocks,

Table 1
Questions on the imagery questionnaires

(1) How strong was the “sensation of movement” in the imagined movements?
(2) How strong was the sense of “intention” or “effort” in the imagined movements?
(3) How “concrete” or “vivid” were the imagined movements?
(4) How often did you imagine the signaled movement on imagery trials?
(5) How accurate was the timing of your imagined movements compared with that of your executed movements?
(6) How accurate were your initial choices of response finger or toe for imagined movements compared with those for executed movements?
(7) How often did you move your muscles while imagining movements?
(8) How difficult was it for you to imagine movements?

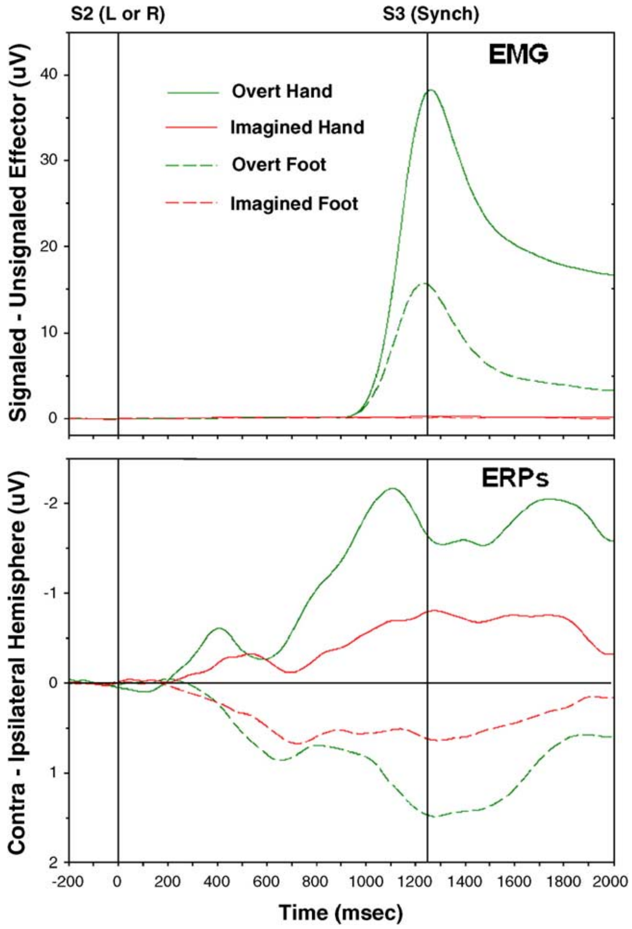

Fig. 2. EMG and ERPs during overt or imagined flexions of a finger or toe. Top panel: difference between rectified EMG recorded from the flexor muscles of the signaled (left or right) and unsignaled limb. S2 = stimulus signaling the finger or toe with which to make (or imagine) the flexion. S3 = signal to which the flexion (overt or imagined) was synchronized. Bottom panel: difference between voltage over the hand areas of primary motor cortex (C3/4 sites, [1]) contralateral and ipsilateral to the signaled limb. Negative and positive values indicate respectively larger ERPs contralateral (normal lateralization) and ipsilateral (paradoxical lateralization).

their index fingers rested on two adjacent response keys directly in front of them. On foot blocks, their big toes rested on two adjacent response keys under the table. Each key was immobile and attached snugly to a finger or toe with a velcro strap. Responses were overt and imagined isometric flexions of the left and right index fingers or big toes. Stimuli were individual characters presented on the monitor against a dark background at the participant's midline.

Continuous recordings were made of key pressure, electroencephalographic activity (EEG), electro-ocular activity (EOG), and electromyographic activity (EMG). Pressure was measured by a stress gauge attached to each key. EEG was recorded from 57 standard sites across the scalp [1] and referenced to the left mastoid (though the measures of ERP lateralization are reference free). Vertical and horizontal EOG were recorded bipolarly from sites above and below the right eye and external to the outer canthus of each eye. EMG was recorded bipolarly with surface electrodes from the Flexor Digitorum Superficialis of each arm and Flexor Hallucis Longus of each leg. EEG and EOG were filtered on-line with a band pass of 0.03 to 30 Hz. EMG was filtered on-line with a band pass of 0.1 to 500 Hz and then RMS-converted to a DC signal. All signals were digitized at 100 Hz and low-pass filtered offline at 4 Hz.

The most important results concern left–right differences in movement-related activity at the muscular (EMG) and cortical (ERP) levels. Differences between EMG activity in the signaled and unsignaled limb are shown in the top panel of Fig. 2. This difference, reflecting muscle activity that depends on which response side is signaled, was significant at synch signal onset for both overt finger taps [$t(18) = 7.67$, $P(\text{one-tailed}) < 0.001$] and overt toe taps [$t(18) = 6.93$, $P(\text{one-tailed}) < 0.001$]. In contrast, it was virtually absent during motor imagery, as reflected in its size for imagined taps relative to that for overt taps at synch signal onset (fingers: $\bar{\chi} = 0.9\%$, SE = 0.4%; toes: $\bar{\chi} = 3.2\%$, SE = 2.5%).

Analogous differences between ERPs recorded over the signaled and unsignaled hemispheres (contralateral and ipsilateral to the signaled limb) are shown in the bottom

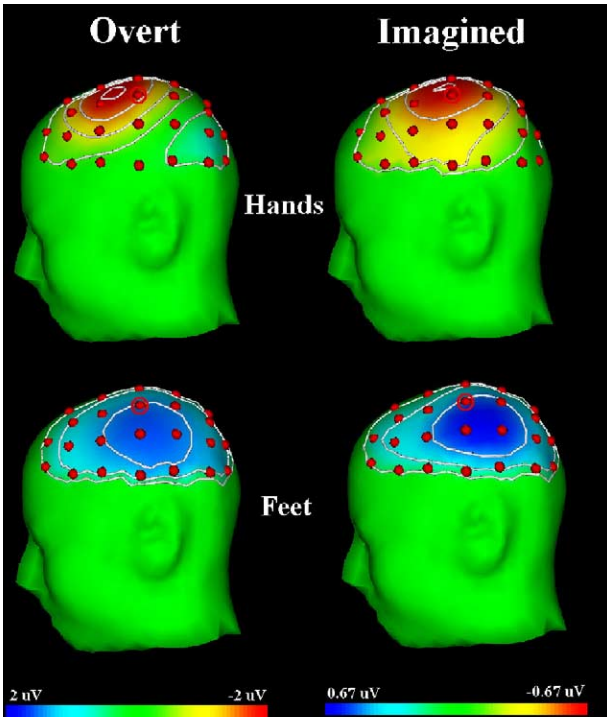

Fig. 3. Topography of ERP lateralization during overt or imagined flexions of a finger or toe at synch signal onset. Differences in voltage between scalp locations contralateral and ipsilateral to the signaled limb are displayed as a map of a single hemisphere. The voltage at each location equals the difference in voltage between homologous locations over the contralateral and ipsilateral hemisphere. Red signifies more negative voltage over the contralateral hemisphere, and blue signifies more negative voltage over the ipsilateral hemisphere. Concentric white (isopotential) lines mark regions of comparable lateralization. Red dots = electrode positions (each representing a homologous pair). Circled dots = C3/4 pair (Fig. 2).

panel of Fig. 2. These were likewise tested statistically at synch signal onset. As expected, a normal pattern of lateralization was observed during overt finger taps [$t(18) = 6.45$, $P(\text{one-tailed}) < 0.001$] and a paradoxical pattern was observed during overt toe taps [$t(18) = 5.41$; $P(\text{one-tailed}) < 0.001$]. ERP lateralization occurred also during imagined taps, despite the lack of EMG. As with overt movements, the pattern was normal for the fingers [$t(18) = 3.48$, $P(\text{one-tailed}) < 0.002$] and paradoxical for the toes [$t(18) = 3.35$, $P(\text{one-tailed}) < 0.002$]. A more complete picture of ERP lateralization at synch signal onset is presented in Fig. 3, which displays its topographic distribution. It can be seen here that lateralization during overt and imagined movements had a similar overall topography, which was normal for the hands and paradoxical for the feet.

In summary, paradoxical lateralization was observed in the ERPs accompanying imagined foot movements without EMG. This finding agrees with functional MRI [13,20,23] and TMS [8,11,22] evidence that motor imagery can activate the primary motor cortex without also producing muscle activity. Motor imagery has been hypothesized to evoke cognitive processes similar to those that prepare and control overt movement [5,10,17]. But, because earlier studies had failed to detect its effects on the primary motor cortex [6,9,18,21], motor imagery was generally believed as late as the mid-1990s to comprise only the more abstract motor functions [5,6,18]. Since then, however, evidence has continued to accumulate that it can engage, not only portions of the motor system involved in action planning, but also those more directly involved in movement execution (but see [7]).

What is new about the present findings is a demonstration that the electrical fields responsible for ERP lateralization during motor imagery do in fact arise from sensorimotor cortex. The time course of this lateralization can thus provide a window on the dynamic state of sensorimotor cortex as motor imagery unfolds. The temporal structure of an overt act is thought to be preserved when it is imagined [5,10,17,18]. Does this temporal isomorphism extend to the sensorimotor cortex? Because of their good temporal resolution, ERPs can help answer this question [15]. Our findings may be relevant as well to situations besides motor imagery where people drive their motor systems without producing overt movement. Simple non-invasive measures like those examined here might, for example, provide stroke victims with feedback, enabling them to activate spared portions of their motor cortices at an earlier stage in the neural reorganization following injury [14].

Acknowledgments

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