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The Beat Goes On: Rhythmic Modulation of Cortical Potentials by Imagined Tapping

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Abstract

A frequency analysis was used to tag cortical activity from imagined rhythmic movements. Participants synchronized overt and imagined taps with brief visual stimuli presented at a constant rate, alternating between left and right index fingers. Brain potentials were recorded from across the scalp and topographic maps made of their power at the alternation frequency between left and right taps. Two prominent power foci occurred in each hemisphere for both overt and imagined taps, one over sensorimotor cortex and the other over posterior parietal cortex, with homologous foci in opposite hemispheres arising from oscillations 180° out of phase. These findings demonstrate temporal isomorphism at a neural level between overt and imagined movements and illustrate a new approach to studying covert actions.

Keywords

covert motor processes; motor imagery; synchronization tapping; movement-related brain potentials; frequency tagging

The present study is concerned with a type of motor-mind reading. We propose a new method for studying *covert motor processes*. The method employs *movement-related brain potentials* to monitor cortical motor areas in the absence of overt movement. Participation of these areas in specific covert acts is revealed by the temporal and spatial pattern of potentials. To illustrate the method, it is applied here to a type of covert motor process known as *motor imagery* or mental simulation. As will be seen, people can drive their cortical motor areas with a pattern quite similar to that during overt movement while producing little or no muscle activity. Moreover, the temporal relations observed between responses from different neural populations suggest that similar motor programs were run during overt and imagined actions.

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To better explain why one would want to engage in motor-mind reading, we will provide some background on covert motor processes in general and motor imagery in particular. Details of the method then will be presented.

Covert Motor Processes

Covert motor processes are motor processes that occur with little or no overt movement or muscle activity. These cognitive processes are motoric in the sense that they are implemented by the same neural machinery involved in overt movement, and perform computations similar to those necessary to produce or control overt movement. Such processes are quite pervasive. For example, motor processes occur without immediate overt consequences when a movement is prepared and then held in readiness until the proper moment (e.g., Leuthold, Sommer, & Ulrich, 1996; Osman, Moore, & Ulrich, 1995, 2003) or inhibited before becoming overt (e.g., De Jong, Coles, Logan, & Gratton, 1990; Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992). Sometimes motor processes are covert because they are not intended to lead to overt movement, for example those occurring when we imagine movements, empathize with the movements of others, or secretly groove to the music.

Covert motor processes of this latter type have been hypothesized to participate in a wide variety of psychological phenomena. The history of psychology is replete with motor theories of perception, cognition, and development. For example, brain processes associated with eye movements have long been thought to influence visual perception (e.g., Helmholtz, 1866/1962), while covert speech has been hypothesized to play a role in speech perception (e.g., Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967) and verbal rehearsal in working memory (e.g., Baddeley, 1983). Recent theories involving embodied cognition (e.g., Barsalou, 1999; Lakoff & Johnson, 2003) posit contributions by brain motor areas to language comprehension and mental representation of concepts. Covert motor processes have a natural place in theories of mind that posit a process of internal simulation to explain our ability to know the states and contents of other minds (Jeannerod, 1994; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Related to mental simulation of others' actions is internalization of one's own. Internalization of actions that were first solely overt has played an important role in developmental theories of cognition, such as enabling inner speech (Vygotsky, 1934/1986) or providing sensorimotor schemas that develop later into more abstract representations (e.g., Piaget, 1952).

What is to be gained by motor-mind reading? If motor processes do play a role in perceptual, cognitive, or developmental phenomena, a full understanding of these phenomena will require an appreciation of that role. A better understanding of covert motor processes might also enhance our understanding of the motor system itself. Because of sensory feedback loops within the motor system, it is difficult during overt movement to separate the endogenous activities that drive the movement from the exogenous sensory consequences of the movement. Monitoring the motor system during motor processes that occur in the absence of overt movement may enable us to study these endogenous activities in isolation (Jeannerod, 1994).

Motor Imagery

The focus here will be on motor imagery, a type of covert motor process involving the mental simulation of actions in the first person. Interest in motor imagery stems in part from the benefits of mental practice on skilled performance in sports and music. There is an extensive literature in Sports Psychology, which generally concludes that mental practice can produce positive effects on learning and performance (e.g., Driskell, Copper, & Moran, 1994; Feltz & Landers, 1983). Recent work suggests that such practice can also be used therapeutically to facilitate motor recovery following stroke (e.g., Jackson, Lafleur, Malouin, Richards, & Doyon, 2001; Stevens & Stoykov, 2003; Weiss et al., 1994). Another clinical application involves the use of imagined movements to convey commands in brain-computer interfaces currently under development for people unable to move or speak (e.g., Pfurtscheller et al., 2003; Wolpaw & McFarland, 2004).

There is little doubt that motor imagery produces effects on the brain and spinal structures responsible for overt movement. Studies using PET or fMRI have found hemodynamic effects throughout the motor system, including the cerebral cortex, basal ganglia, cerebellum, and midbrain autonomic structures (Decety, 1996; Jeannerod, 1994). It has long been known that motor imagery can be accompanied by slight EMG activity from muscles involved in the imagined movements (e.g., Jacobson, 1930; Shaw, 1940). Motor imagery can also influence peripheral motor structures without producing significant EMG activity, as has been shown for the corticospinal tract through transcranial magnetic stimulation (e.g., Hashimoto & Rothwell, 1999; Rossini, Rossi, Pasqualetti, & Tecchio, 1999; Stinear & Byblow, 2003) and spinal reflexes (e.g., Bonnet, Decety, Jeannerod, & Requin, 1997; Li, Kamper, Stevens, & Rymer, 2004).

Some theories of motor imagery emphasize the conscious experience of imagined actions (e.g., Decety, 1996; Jeannerod, 1994), while others emphasize mental operations performed on tacit, procedural representations similar to those that guide overt actions (e.g., Cooper & Shepard, 1975; Parsons, 1987). Yet, despite these differences, both types of theory posit a kind of isomorphism between overt and imagined actions in which timing is fundamental. That is, the temporal relations between elements of an overt action are thought to be preserved between the corresponding elements when the same action is imagined.

It is this temporal isomorphism in combination with its effects on the motor system that make motor imagery especially well suited for our approach to motor mind-reading. These properties suggest that motor system activity during motor imagery might mirror that during overt movement. By mirror it is meant that the same brain areas might become active in the same order and with the same timing. If so, the spatiotemporal pattern of motor-system activity associated with a particular overt movement might serve as a sign revealing when the same movement is imagined. This type of spatiotemporal signature is central to our approach and will be considered below in some detail.

Steady-State Motor Potentials

To detect and monitor covert motor processes, our approach relies on movement-related brain potentials recorded from the scalp. The measures employed are closely related to a negative shift in potential called the Readiness Potential (RP; Kornhuber & Deecke, 1965; Vaughan, Costa, & Ritter, 1968) that occurs just prior to a single voluntary limb movement. The later part of the RP preceding hand movements has three properties relevant to the approach. First, it is largest over the side of the head contralateral to the responding hand (e.g., Boschert & Deeke, 1986). This lateralization of the RP serves as a sign that one hand is more prepared to move than the other. Second, it arises from the motor system. Both intracranial and magnetic recordings indicate that the lateralized portion of the RP arises mainly from primary motor cortex (e.g., Ikeda & Shibasaki, 1992; Lang et al., 1991). Third, it can be observed during covert motor processes. It can occur when one hand is prepared and held in readiness for a delayed response (e.g., Leuthold, Sommer, & Ulrich, 1996; Osman et al., 1995; 2003) or when a hand response is prepared but then inhibited before its overt execution (e.g., De Jong et al., 1990; Miller & Hackley, 1992; Osman et al., 1992). Lateralized motor potentials can also occur during imagined movements of the hand (Beisteiner, Hollinger, Lindinger, Lang, & Berthoz, 1995; Osman, Müller, Syre, & Russ, 2005; Parra et al., 2002), as will be demonstrated here.

The good temporal resolution of ERPs provides a number of avenues by which that portion of brain activity closely linked to a particular cognitive or behavioral event can be isolated from other ongoing activity. One such avenue is to identify, or “tag,” brain activity associated with a rhythmic event by the frequency of the event. *Frequency tagging* can be illustrated most easily in the perceptual domain, where the rhythmic event might, for example, be periodic oscillations in the luminance of a dot projected on an unchanging background. The neural response in an observer would likewise oscillate, as would ERP recordings from the scalp. ERPs in response to such rhythmic events recorded over extended periods of time are referred to as steady-state (reviewed in Regan, 1989). These ERPs are typically represented in the frequency domain, wherein power is plotted as a function of frequency. In the example here, a peak would be expected to occur in the ERP power spectrum at the frequency (and possibly its harmonics) of luminance oscillation. This frequency tags the neural response to the corresponding rhythmic changes in external stimulation. It serves as a kind of carrier frequency whose amplitude and phase convey information about the neural response.

A good illustration of the type of information conveyed by tagging frequencies concerns the effects of selective attention on the neural response to sensory stimulation. The above example concerning visual perception can be extended to include two oscillating dots of light, each oscillating at a different frequency on a constant background and projected to a different location within an observer's visual field. The power spectrum of the observer's ERPs will now contain a peak at each of the two stimulus frequencies. Next, suppose that the observer attends to one dot of light and ignores the other. The result will be to increase the amplitude of the peak at the frequency of the attended stimulus and to decrease the amplitude of the peak at the frequency of the ignored stimulus. In other words, modulation of the neural response to each stimulus by selective attention can be discerned from changes in the amplitude of their respective tagging frequencies. This finding has, in fact, been reported in several studies (e.g., Müller, Teder-Salejarvi, & Hillyard, 1998a; Müller et al., 1998b; Müller & Hillyard, 2000).

Our approach uses frequency tagging to study covert motor processes. In the present study, we used steady-state motor potentials related to the lateralized portion of the RP to detect imagined movements. Unlike the RP, however, which has been studied mostly in connection with single discrete movements, the ERPs used here arose during continuous rhythmic movements, both overt and imagined. Imagined rhythmic hand movements were detected by examining power at a tagging frequency in the steady-state lateralized potential related to their rhythm. To the best of our knowledge, the present study is the first to use frequency tagging to study motor processes. So far, steady-state ERPs have been recorded mostly in response to sensory stimulation, though they have begun to be recorded also during rhythmic finger tapping (e.g., Gerloff et al., 1997; 1998). These latter studies, however, have focused on frequencies other than the rate of tapping and concerned overt movements only.

Frequency Tagging Covert Motor Processes

We now turn to a more detailed description of our general approach and its application in the present study. Central to the approach is the definition of a spatiotemporal ERP signature to serve as a sign for the presence of covert motor processes. This signature involves (a) the presence of power in the steady-state ERP at one or more tagging frequencies, (b) the topographic distribution of this power across the scalp, and (c) phase relations between signals at the same tagging frequency recorded from different scalp locations. These properties are determined by the temporal structure of the experimental task in combination with anatomical considerations. In the present study, the task was to imagine taps that alternated between the left and right index fingers at a constant rate. The spatiotemporal signature we sought as a sign of motor system activity caused by imagined tapping was (a) a signal at the frequency of alternation between the two hands that was (b) maximal over sensorimotor cortex and (c) had a 180° phase relation (like that of the hands) between recordings over opposite hemispheres.

Though the spatial resolution of ERPs is somewhat limited, the spatiotemporal signatures can nevertheless be based on ERP responses from individual cortical motor regions of interest (ROIs). The proximity of cortical motor regions to the skull in combination with spatial filtering helps make this possible. Among the ROIs useful for detecting covert motor activity are primary sensorimotor cortex, premotor cortex, posterior parietal cortex, and the supplementary motor area (SMA). These particular brain areas lie consistently beneath the same standard electrode sites across individuals (Homan, Herman, & Purdy, 1987; Steinmetz, Furst, & Meyer, 1989) and can be identified reliably from cortical landmarks in magnetic resonance images. The role of spatial filtering is to attenuate the contribution of distant electrical sources (via volume conduction) to the recordings at each electrode site, so that the recordings reflect more accurately activity from underlying areas. The type of spatial filtering used in the present study is a standard one involving a Laplacian transform of the electrical recordings (Perrin, Pernier, Bertrand, & Echallier, 1989).

Definition of the ERP signature used to detect covert motor processes can sometimes be guided by the ERPs observed during overt movements. This is especially true when the overt movements seem likely to involve the same brain structures temporally organized in the same way as the to-be-detected covert motor processes. In the present study, participants made both real and imagined finger taps. To the extent that the ERP response of motor areas during imagined taps resembles that during overt taps, one may conclude that these areas behaved in similar ways during both the overt and imagined movements. In the present study, these similarities included both the presence of and phase relations between steady-state signals at the tapping frequency. While these similarities are germane to often asked questions about the neural and functional equivalence between overt and imagined movements (e.g., Decety, 1996; Jeannerod, 1994; Parsons, 1987), in the present context they served a somewhat different purpose. Overt movement was used here to discover ERP features that if present during imagined movement would indicate task-related activity of the motor system.

In sum, the experiment now to be reported involved overt and imagined tapping at a constant rate. We examined the steady-state motor potentials at a tagging frequency equal to the rate of alternation between left and right taps. The presence of signals at the tagging frequency from motor areas during imagined movement, as well as the phase relations between these signals, served as signs that the motor areas were active in a manner similar to that during overt movement. The experiment is intended to serve as a demonstration of the general approach. Motor imagery was chosen as an initial test case because it seemed likely that covert motor processes would occur and that they would have an ERP signature similar to that observed during overt production of the same movements. The results show the feasibility of using frequency tagging to isolate brain activity arising from rhythmic motor processes and to detect its presence in the absence of overt movement. Besides providing a concrete illustration of the approach, we also will consider how it might be applied to other activities besides motor imagery, where the presence of covert motor processes is less certain.

Method

Participants

Eighteen participants were each tested individually in a single four-and-a-half hour session. All had normal or corrected-to-normal vision, no apparent motor problems, and were able to perform the experimental task well. Each was paid $35 for participation.

Apparatus

Stimulus presentation and data acquisition were controlled by two linked PCs running InstEP software. Visual stimuli were presented on a computer monitor. A response box was constructed from a 9 × 15 cm digit pad by removing all but two horizontally adjacent keys and affixing a thimble to each key. The thimbles were attached lengthwise to the keys and oriented such that the inserted fingers were horizontal and pointing forward. Response registration (microswitch closure) required about 50 g of pressure and key travel of about 1/4 cm. Electrophysiological signals were recorded with tin electrodes and a 64-channel SAI amplifier. EEG was recorded using an ECI electrode cap, and EOG and EMG were recorded from individual loose electrodes. The precise 3-D location of each electrode on the participant's head was determined with a Polhemus Isotrak digitizer. A custom-built RMS converter rectified EMG recordings prior to digitization.

Setup, Stimuli, and Responses

Participants sat facing the monitor across a table, with their elbows resting on the table and their index fingers inserted into the thimbles on the response box. The response box was located on the table directly in front of them at a comfortable distance along the line perpendicular to the midline of the body. The stimuli were individual characters (see below) presented on the monitor against a dark background. The height of each subtended a visual angle of about 1° at a viewing distance of about 75 cm. Responses were alternating flexions of the left and right index fingers (see below). Both stimulus presentation and the point between the adjacent tips of the two response fingers occurred at the participant's midline.

Experimental Task

The task was to synchronize overt and imagined taps to a series of visual stimuli and consisted of individual trials like those shown in Figure 1. On each trial, 20 brief (50 ms) stimuli were presented serially at a constant rate of 1 per 840 ms (1.19 Hz). There were two types of trials, A (top panel) and B (middle panel). On Type A trials, the stimulus series began with a yellow star, followed by a yellow letter L, and then a yellow letter R. The star served as a warning signal, and the letters provided information about the order of the upcoming left and right taps. Next, the numbers 1 through 8 appeared in green. The participants' task was to synchronize taps with the left index finger to the odd green numbers and taps with the right index finger to the even green numbers. Next came the numbers 1 through 8 in red. At this point, participants were supposed to continue tapping, but in their imagination (again, with left taps synchronized to the odd numbers and right taps synchronized to the even numbers). The final two stimuli on Type A trials were a green L followed by a green R, to which an overt left and right tap were to be synchronized. Type B trials differed from Type A trials in two ways. First, the L's and R's were switched, so that R always preceded L. Second, participants began their alternating left and right taps (overt and imagined) with a right finger tap, that is, taps with the right finger were synchronized to odd numbers, and taps with the left finger to were synchronized to even numbers.

Participants alternated between blocks of 20 trials of Type A and 20 trials of Type B. Half began the sequence with Type A, and half began with Type B.

Feedback and Questionnaires

After each block, participants received feedback about their performance and filled out a brief questionnaire. Feedback concerned the overt taps on the preceding block and included (1) their average deviation from synchrony with stimulus onset (constant error), (2) the standard deviation of the tapped intervals (variable error), and (3) the number of overt taps (if any) occurring during the portion of the trials requiring imagined taps. The questionnaire asked subjects to rate their imagined movements of the preceding block on several dimensions, including (1) sensation of movement, (2) sense of intention or effort, (3) vividness, and (4) absence of muscle activity. The main purpose of the questionnaire was to encourage participants to cultivate their motor imagery along these dimensions. The eight questions comprising the questionnaire are shown in Table 1. Participants answered each by circling one of the numbers (integers 0–10) on a rating scale directly below.

Procedure

At the start of each session, prior to performing blocks of the experimental task, each participant was given synchronization practice. Participants learned to synchronize a single key press with the left or right index finger to the second of two brief (50 ms) visual stimuli. The first stimulus was a randomly presented L or R, which signaled the finger to tap with. The second stimulus was a star that appeared 840 ms (the interstimulus interval in the experimental task) after onset of the first. Feedback was provided after each tap about whether it had preceded or followed onset of the second stimulus and by how many ms. Synchronization practice continued until most of the participant's taps occurred within 100 ms of stimulus onset (typically about 35 taps).

Participants next performed four practice blocks in the experimental task. During the first, emphasis was placed on learning to produce well-synchronized overt tap sequences. Imagery instructions were provided between the first and second practice blocks. At this point, the questionnaire was introduced and each scale explained. Participants were told that they would be filling out the questionnaire after each of the remaining blocks. After the third practice block, the electrical sensors (cap and individual electrodes) were applied. The deleterious effects of eye movements on EEG recordings were then explained, and participants were given instructions about where to fix their gaze and when they could blink or move their eyes. A fourth practice block was then administered to refamiliarize participants with the experimental task and to give them practice minimizing blinks and eye movements.

The remainder of the session consisted of 10 blocks in the experimental task, during which the reported data was obtained.

Electrophysiological Recording

EEG was recorded from 59 electrode sites specified in the Extended International 10/20 System (AES, 1991; see Figures 4 and 6), and referenced to the left mastoid. (All ERP measures reported here are independent of choice of reference.) Vertical and horizontal EOG were recorded bipolarly respectively from sites above and below the midpoint of the right eye and 2 cm external to the outer canthus of each eye. EMG was recorded bipolarly from the primary muscles involved in flexion of the index fingers (flexor digitorum of each arm) using standard forearm flexor placements (Lippold, 1967). EEG and EOG were filtered online with a band pass (half-power cutoff) of 0.03 to 30 Hz. EMG was filtered online with a band pass of 0.1 to 500 Hz and then RMS-converted to a DC signal. All signals were digitized at a rate of 100 Hz.

Preliminary Signal Processing

Recordings during the final 10 blocks from each participant were analyzed. The continuous recordings during each block were first divided into segments corresponding to individual trials. Segments during which microswitch closure (a sign of overt tapping) occurred while tapping was to be imagined (less than 2%) were then excluded. All remaining segments were averaged to yield a separate set of averages for each participant's A and B blocks. Each set consisted of average ERP recordings from the 59 scalp electrode sites, EMG recordings from the left and right arms, and vertical and horizontal EOG recordings.

Results

Overview of Behavioral Findings

Observable measures of performance included: 1) the presence or absence of overt taps (hits vs. misses during overt tapping and correct rejections vs. false alarms during imagined tapping), 2) their timing relative to the synchronization signals (constant and variable errors), 3) their timing relative to each other (intertap intervals), and 4) the involved hand (correct or in error). These measures provide an indication of how well participants were able to perform the overt portions of the task and to refrain from making overt responses during imagined tapping.

Overt Taps

Participants seldom missed a tap or tapped with the incorrect hand. The average miss rate per participant was 0.5% (min = 0%; max = 1.05%). The average rate per participant of taps with the wrong hand was 0.19% (min = 0%; max = 0.8%). The participants' success at synchronizing their keypresses to the stimuli is reflected by the magnitude of their constant errors (mean deviation from synchrony) and variable errors (standard deviation of individual taps around the mean interval). The average constant error per participant was −24 ms (min = −4 ms; max = −84 ms), and the average variable error per participant was 74 ms (min = 45 ms; max = 100 ms). This constant error is of the size and direction found typically in synchronization studies for 800 ms tap intervals, while the variable error is somewhat larger (e.g., −34 and about 40 ms, respectively in Peters, 1989).

Further information about the rate of overt tapping is shown in Figure 2, which displays the distribution of intertap intervals (time between successive overt taps) for each participant. The middle line, inner pair of lines, outer pair of lines, and pair of dots represent respectively the median, 25th and 75th percentiles, 10th and 90th percentiles, and 5th and 95th percentiles. The average duration per participant of the intertap intervals was 853 ms (min = 846 ms; max = 861 ms), and the average *SD* was 57 ms (min = 41 ms; max = 70 ms).

Covert Taps

Observable errors during covert tapping are necessarily false alarms. The average rate per participant of false alarms during covert tapping was 0.27% (min = 0%; max = 0.56%). Almost all (97.47%) involved the correct hand. The vast majority of false alarms (88.61%) occurred at the point in the trial when the first covert tap was required, that is, were persevarations of overt tapping. To detect the presence, involved hand, and rhythm of the covert taps, we relied on the ERP measures described below.

Overview of Electrophysiological Findings

Three methods, discussed in more detail below, were used successively to distill the movement-related portion of ERPs arising during the series of stimuli and responses. First applied was a subtraction procedure for isolating the portion of the ERP response that depends solely on whether a response (overt or imagined) is made with the left or right hand. Next, the results of this subtraction were spatially filtered to minimize the contribution of distant (including noncortical) sources to the recordings at each electrode site. Finally, the spatially filtered signals were converted to the frequency domain. This enabled us to examine the response at the left-right tap alternation frequency during both overt and imagined tapping.

Statistical tests were performed on the results from the frequency domain. The tests all employed a jackknife procedure to evaluate reliability (see Mosteller & Tukey, 1977; Robertson, 1986), where replications involved the amplitude spectra of average waveforms. These average waveforms were each based on all but one participant, with a different single participant excluded from the average waveform(s) in each replication. The purpose of averaging waveforms across participants before computing amplitude spectra was to minimize the contribution of noise to the power at each frequency. The statistical tests and standard errors reported below are all based on means of leave-out-one replications and jackknife-estimated sampling distributions of these means (see Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001).

Trial-Type A-B Subtraction

The average recordings for each trial-type reflect not only overt and imagined tapping, but also other perceptual (e.g., stimulus detection), cognitive (e.g., time estimation) and perhaps nonspecific (e.g., arousal) processes time-locked to each trial. A subtraction procedure was therefore employed to help isolate movement-related responses. The procedure, illustrated in the bottom panel of Figure 1, involved subtracting each of the average waveforms for trial-Type B (ERPs at each scalp electrode site, EMG in each arm, VEOG and HEOG) from the corresponding waveform for trial-Type A. Recall that 1) the portion of the stimulus series containing the red and green numbers was identical for both trial-types, and 2) odd numbers were associated with left taps in Type A trials and right taps in Type B trials, while the opposite was the case for even numbers. The subtraction therefore removed all but that portion of the ERP that depended on whether the tap involved a left- or right-hand movement during that part of the trial on which numbers were presented. The resulting differential motor response was such that left taps minus right taps occurred at odd numbers, and right taps minus left taps occurred at even numbers. A full cycle of this left-right/right-left alternation repeated every two taps (2 × 840 ms = 1680 ms = 0.6 Hz).

Some results of this subtraction can be seen in Figure 3. Rectified EMG recordings for the left and right fingers are shown in Panel A. The cyclic alternations in polarity of each trace result from the alternation between fingers in combination with the A-B subtraction: The left finger is more active (positive value) on A than B trials for odd taps and more active on B than A trials for even taps, while the reverse is true for the right finger. The eight spikes in the left-most portion of the EMG traces correspond to the initial eight overt taps made on each trial, and the final two spikes correspond to the final two overt taps. The flat traces in between the overt taps occurred while participants imagined tapping. If any EMG occurred during this portion of the trial, its magnitude was at most a very small proportion of that produced by overt tapping.

Panel B shows the difference in electrical potential over the left and right cortical hand areas (recording at site C3 minus recording at C4). This ERP trace displays a pattern similar to the EMG during overt taps. There is likewise an oscillation at the rate of alternation between left and right taps, due here to the A-B subtraction in combination with the more negative potential observed over each hemisphere when the tap was made with the contralateral than ipsilateral hand.[1] Unlike the EMG, however, oscillations in the ERP arising from left-right alternation are quite evident, albeit somewhat reduced in magnitude, during the imagined taps. The beat goes on!

The EOG for horizontal eye movements is displayed in Panel C. HEOG is included to demonstrate that the oscillations observed over motor cortex during imagined tapping were not due to participants looking back and forth at their left and right hands. Such an artifact could arise through volume conduction because the back of the eye is more negatively charged

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[1] C3 is over the left motor cortex and C4 is over the right motor cortex. Let Left (C3-C4) and Right (C3-C4) represent the difference between recordings at these electrode sites during left and right-hand taps. Because of the A-B subtraction, the resulting ERP will then correspond to Left (C3-C4) − Right (C3-C4) for odd taps and Right (C3-C4) − Left (C3-C4) for even taps. These values are equal respectively to −2 and 2 times the difference between recordings contralateral and ipsilateral to the responding hand [(Left (C4-C3) + Right (C3-C4))/2].

than the front.[2] Like the ERP trace above, the HEOG is the difference between recordings at two electrode sites, except that these sites are located on the outer canthi (temples, next to the eyes). The HEOG is displayed at a scale 25% that of the ERP, which equals a conservative estimate (high side) of the propagation coefficient relating HEOG recorded from the outer canthi and HEOG recorded from sites over motor cortex (Hillyard & Galambos, 1970). In other words, the HEOG is scaled to equal its effects on recordings of the ERP. As can be seen, there was very little sign of left-right oscillation of the eyes at the tap alternation frequency during either overt or imagined tapping.

Laplacian Derivative of Potential

So that the recordings at each scalp electrode site might better reflect the activity of nearby cortical sources, a Laplacian transform was performed on the ERP difference waves from the trial-Type A-B subtractions.[3] This involved a spherical-spline interpolation procedure (Perrin et al., 1989), in which the measured 3-D locations of the electrodes were used to fit a spline (continuous surface representing voltage across the scalp) individually to each participant's head. The Laplacian derivative of the ERP (LD-ERP) over an electrode site is the second derivative of the spline function at that location. Because it is related to rate of change over space, sharp spatial gradients in voltage contribute most to the LD-ERP while gradual changes contribute little. This amplifies the contribution of nearby electrical sources and diminishes that of distant ones. LD-ERPs over the left and right cortical hand areas (C3 and C4) are displayed separately in Panel D. As in Panel B (C3 minus C4), there is an oscillation at the tap-alternation frequency during imagined tapping. But here it can be seen that the two hemispheres responded in opposite directions to left versus right taps.

The effects on the LD-ERP of left-right alternation of overt and imagined taps can be seen at all 59 scalp recording sites in Figure 4. The vertical line in the middle of each trace divides the period of the initial eight overt taps from the period of the eight imagined taps. The large oscillations evident at the beginning and end of many of the traces arose during overt taps, and the smaller oscillations evident in the middle arose during imagined taps. Because the LD-ERP recordings at a particular electrode site reflect mostly activity from nearby cortical areas, the presence of oscillations at so many sites indicates a response across large areas of the cortex to left-right tap alternation, both overt and imagined. To further isolate this rhythmic response from other possible effects on the LD-ERP and to better characterize its topography, we now turn to analyses in the frequency domain.

Amplitude Spectra of LD-ERPs

Frequency tagging was used to distill yet further that portion of the cortical response most functionally related to the overt and imagined tapping. This involved isolating the frequency component of each LD-ERP wave at the left-right tap alternation rate. The first step was therefore to convert the LD-ERP waves shown in Figure 4 from the time domain to the frequency domain, which was accomplished here by Fast-Fourier Transform (FFT; radix 2, no padding, rectangular window). Separate amplitude spectra were calculated for each of the 59 A-B difference waves during two intervals: 1) the initial eight overt taps, and 2) the imagined taps. These spectra were based on 5.12 sec (512 data-point) intervals, located in the middle of overt and imagined tapping (6.72 sec each) and shown by the gray-hatched areas in Figure 3.

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[2] Looking to the left or right produces greater electrical potential over the hemisphere contralateral than the hemisphere ipsilateral to the direction of gaze. Thus, merely looking at the left or right hand can produces the same pattern of ERP lateralization over motor cortex as moving the hand.

[3] Identical results would have been obtained if the Laplacian transforms of trial Type B waveforms had been subtracted from the Laplacian transforms of the trial Type A waveforms.

The results of the FFTs are shown in Figure 5, with amplitude spectra for overt taps plotted in the top panel and amplitude spectra for imagined taps plotted in the bottom panel. All plots display amplitude as a function of frequency and have a resolution of approximately 0.2 Hz (reciprocal of 5.12 sec). Note that the amplitude scale for the overt taps is twice that for the imagined ones. Each line corresponds to the spectrum of the LD-ERP at an individual electrode site. As can be seen, both panels contain a prominent peak at the 0.6 Hz bin in the spectra for many electrode sites. This indicates that the oscillations shown in Figure 4 during overt and imagined tapping occurred at the tap alternation frequency. Averaged across all 59 electrode sites, amplitude at this frequency was significantly above noise level (as estimated by the mean amplitude of the two surrounding frequencies bins) for both overt movements ($\bar{x} = 8.25$ uV, $t(17) = 8.10$, p(one-tailed) < 0.0001) and imagined movements ($\bar{x} = 2.98$ uV, $t(17) = 3.79$, p(one-tailed) < 0.001).

Tagging Frequency Amplitude

Figure 6 shows the topographic distribution of LD-ERP amplitude at the tap-alternation frequency during overt taps (left panel) and imagined taps (right panel). Color indicates amplitude (red = more), concentric lines indicate regions of equivalent amplitude, and dots indicate electrode positions. The scale for overt taps is approximately twice that for imagined ones. Each panel presents a radial projection of a spherical head model, with the electrodes in their canonical locations (Extended 10–20 System, AES, 1991). The amplitudes at all other locations on the models were interpolated by means of a spherical spline (Perrin et al., 1989) constrained to pass through the values at the electrode locations.

A number of common features can be seen in both panels. First, the LD-ERP at the tap alternation frequency was broadly distributed over both hemispheres, but with little amplitude at the midline between the hemispheres. Second, there are two pairs of prominent amplitude foci, with the members of each pair appearing at homologous locations in the left and right hemispheres. The centrally located pair appears over sensorimotor cortex, while the posterior pair appears over posterior parietal cortex.[4]

The spatial coordinates of the foci (spline-interpolated point of maximum amplitude) are expressed numerically in Table 2, which shows the means and standard errors of their polar coordinates (phi and theta) on the spherical head model. It can be seen here that the locations of the four foci did not differ much between overt and imagined movements. It can also be seen that the left and right members of each homologous pair appeared in locations close to mirror images of one another (equal thetas, phis equidistant from 180°). Finally, examination of the standard errors allows evaluation of how consistent foci locations were across participants and across overt versus imagined movements.

The top panel of Figure 7 displays an estimate of the amplitude at each of the (spline-interpolated) foci in Figure 6. The estimate is the average of the amplitudes at six nearby surrounding electrode sites, shown by circled dots in Figure 6. (Amplitudes at these individual sites can be found in the Appendix.) An ANOVA involving three factors (OI: overt vs. imagined taps, CP: central vs. posterior focus, and LR: left vs. right focus) was performed on these six-electrode estimates. Effects were significant for OI, $F(1, 17) = 38.78$, $p < 0.001$, OI × CP, $F(1, 17) = 8.79$, $p < 0.01$, and OI × CP × LR, $F(1, 17) = 9.95$, $p < 0.01$, marginally significant for CP, $F(1, 17) = 3.21$, $p < 0.1$ and CP × LR, $F(1, 17) = 3.60$, $p < 0.1$, and insignificant for LR, $F(1, 17) = 1.48$ and OI × LR, $F(1, 17) = 0.22$.

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[4] Both sensorimotor and posterior parietal cortices have been found to lie consistently beneath the same standard electrode sites across individuals (Homan et al., 1987; Steinmetz et al., 1989). These sites agree well with those surrounding the central and posterior power foci in the present study (labeled in Figure 4).

More specific information on the pattern of amplitudes in Figure 7 was obtained from a series of post hoc *t* tests, each involving a separate (nonpooled) error term. Two differences between the amplitudes of the foci during overt and imagined movement were apparent. First, amplitude was greater at all foci during overt than imagined tapping. These overt-covert differences were confirmed by four post hoc tests adjusted for simultaneity by Bonferroni correction (left central: $\bar{x}$ = 10.2 uV, $t(17) = 5.31$, p(one-tailed) < 0.0002; right central: $\bar{x}$ = 12.1 uV, $t(17) = 5.14$, p (one-tailed) < 0.0002; left posterior: $\bar{x}$ = 7.5 uV, $t(17) = 6.69$, p(one-tailed) < 0.0001; right posterior: $\bar{x}$ = 4.6 uV, $t(17) = 3.50$, p(one-tailed) < 0.006).

Second, the difference in amplitude between overt and imagined tapping was greater at central than posterior foci. This observation is consistent with a greater effect on sensorimotor than posterior parietal cortex of whether a movement is executed or merely imagined, perhaps due to a greater involvement of sensorimotor cortex in the final efferent commands preceding overt movement or to subsequent kinesthetic feedback. It was evaluated statistically first by examining the ([overt central − covert central] − [overt posterior − covert posterior]) interaction term (OI × CP in above ANOVA), which proved to be significantly greater than zero ($\bar{x}$ = 5.1uV, $t(17) = 2.97$; p(one-tailed) < 0.005). Such a statistical interaction could occur, however, if the topography for imagined tapping was merely an attenuated version (i.e., amplitude at all foci reduced by the same proportion) of the topography for overt tapping (McCarthy & Wood, 1985; Ruchkin, Johnson, & Friedman, 1999; Urbach & Kutas, 2002). To control for this possibility, the foci amplitudes for each (jackknife) replication were converted to z-scores separately for overt and covert movement (thus equating the mean and range of foci amplitudes in each condition). Despite this normalization procedure, the interaction term was again significantly greater than zero ($t(17) = 2.96$; p(one-tailed) < 0.005).

Finally, there was little evidence of hemispheric differences in tagging frequency amplitude, at least for the present choice of electrode sites used to estimate foci amplitudes. Differences in amplitude observed between homologous foci in the left and right hemispheres were evaluated by four tests Bonferroni-corrected for simultaneity. The greater amplitude found at the left than at the right posterior focus during overt movement was marginally significant ($\bar{x}$ = 4.2 uV, $t(17) = 2.32$; p(one-tailed) < 0.07). But none of the other differences between homologous left and right foci were significant (covert posterior: $t(17) = 0.79$, overt central: $t(17) = 0.99$, covert central: $t(17) = 0.86$). There were, of course, robust differences in the direction of the response of the two hemispheres to left- versus right-hand taps. These were reflected in tagging frequency phase and are discussed in the next section.

Tagging Frequency Phase

We now turn to the phase of the LD-ERP signals at the tap-alternation frequency. The results to be reported concern recordings at the same 24 (4 × 6) electrode sites (circled dots in Figure 6) used to estimate amplitude at the four foci (Figure 7, top panel). Because amplitude at the tap-alternation frequency was largest at these sites, the observed phase should be the least influenced by noise. The 24 phase values for overt movement were rotated around the average of their locations on the phase circle, as were the 24 phase values for covert movement. This set the average phase during overt and covert movement to zero while preserving the phase differences between electrode sites. Each individual rotated phase value is presented in the Appendix.

The focus here will be on three types of evidence provided by the phase results. The first concerns the phase difference between the two hemispheres. This bears on the connection between the tagging frequency signal and neural populations responsible for overt and covert movements that alternate between the hands. The second type of evidence concerns phase differences between tagging frequency foci within the same hemisphere. This bears on the relative timing of the neural populations responsible for these foci. Finally, we will consider whether the entire pattern of phase differences across all electrode sites was the same for overt and covert movements. This bears on whether the overall pattern of temporal organization, comprising all neural populations that contributed to the tagging frequency signal, was the same for both types of movement.

The bottom panel of Figure 7 provides an indication of the topography and range of phase at the tap-alternation frequency. As in the top panel, an estimate is displayed for each of the foci in Figure 6. Again, each estimate is the average of measures made from six nearby surrounding electrode sites. As can be seen, there was an approximately 180° phase difference between homologous foci in the two hemispheres during both overt and covert movement (Δ overt central: $\bar{x}$ = 179°, *SE* = 5.1°; Δ overt posterior: $\bar{x}$ =188°, *SE* = 4.8°; Δ imagined central: $\bar{x}$ = 192°, *SE* = 10.9°; Δ imagined posterior: $\bar{x}$ = 198°, *SE* = 9.1°). A 180° phase difference indicates opposite electrical polarity at all points in time (>180° indicates oscillations over left foci led oscillations over right foci, and <180° indicates the opposite). Note that the precise values of the phase differences depend on which particular electrode sites are used to calculate phase estimates for the foci. Nevertheless, the results are as would be expected if the two hemispheres exhibited opposite patterns of response to the alternation between left and right taps, both during overt and covert movement.

There were also large differences between the phase estimates for central and posterior foci in the same hemisphere (Δ overt left: $\bar{x}$ = 117°, *SE* = 5.9°; Δ overt right: $\bar{x}$ = 125°, *SE* = 6.8°; Δ covert left: $\bar{x}$ = 103°, *SE* = 8.1°; Δ covert right: $\bar{x}$ = 109°, *SE* = 14.8°). These differences are the combined result of two factors. First, the tap-alternation responses at central and posterior sites were of opposite polarity. Had they been simultaneous, these responses would have been 180° out of phase. Second, there was a temporal shift. Responses recorded at the sites around the posterior foci occurred earlier on the average than those recorded around the central foci.[5] This temporal shift reduced the 180° difference due to polarity by 55–77°. Since 1° is equivalent to about 4.7 ms (1680 ms cycle/360°), this represents a temporal shift of about 257–359 ms.[6]

Figure 8 shows rotated phase at the tap-alternation frequency for each of the 24 individual electrode sites surrounding the foci (see also Appendix). Phases during overt movement are shown along the abscissa, and phases during covert movement are shown along the ordinate. It can be seen here that the phase at each electrode site was quite similar during overt and covert movement. The slope and fit of the best fitting regression line are shown in the left-hand corner. A similar plot was made and linear regression performed for each jackknife replication. Both the mean correlation (0.992, *SE* = 0.006) and mean slope of the regression lines (1.01, *SE* = 0.024) were close to 1. The good fit to a linear function with a slope of 1 implies that the set of phase differences between all electrode sites (276 pairs) is similar during overt and covert movement. The total configuration of phase differences across electrode sites is determined in part by the temporal organization of the different neural populations that contribute to the LD-ERP response at the tap-alternation frequency. The temporal organization of these neural populations during overt movement thus appears to have been well preserved during covert movement.

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[5] Because the overt and imagined tap sequences consisted of a known number of taps that occurred at known times, the waveform oscillations corresponding to each serial position in the sequences could be distinguished (see Figures 3 and 4). This made it possible to determine whether phase differences between recordings from different electrode sites were due to polarity reversal, temporal shifts, or both.

[6] An interesting finding was that there was also a phase shift across the six electrode sites surrounding each of the individual foci (see Appendix). The same pattern occurred at all four foci and during overt and imagined movements: responses at the anterior sites preceded those at posterior sites.

Single-Trial Classification of Phase

The frequency-domain analyses reported so far were based on the combined recordings from 18 participants. Each participant contributed close to 100 Type-A trials (odd tap = left, even tap = right) and 100 Type-B trials (odd tap = right, even tap = left), on which the tapping was 180° out of phase. Each of these trials contained a segment with overt taps and a segment with imagined taps. We report now on our efforts to classify each individual segment as coming from a Type A or B trial. This classification was based solely on the difference between the LD-ERP recorded over the left and right hand areas of motor cortex (C3 - C4), which was used to compute a tagging frequency phase for each segment. Figure 9 shows the tagging frequency phases of the segments from one participant. Type-A segments (closed circles) and Type-B segments (open circles) are shown for overt taps in the left panel and imagined taps in the middle panel. Trial number is represented by distance from center of each polar plot, and phase is represented by angle. As can be seen, the closed circles tend to cluster in one phase region, while the open circles cluster in another at the opposite side of the circle. As might be expected, the A versus B clusters have less overlap for overt than imagined taps.

To classify the segments, a line (boundary) was drawn across each polar plot dividing it into A and B regions. The boundary was rotated to an angle that maximized the number of A segments falling into the A region and B segments falling into the B region (correct classifications). Each individual segment was classified using a new boundary determined by the other (close to 199) segments in the plot. This leave-out-one analysis shows how successful a classification criterion based on training observations is when applied to a completely different set of test observations. For the participant displayed, 99% of the overt-tap segments and 82% of the imagined-tap segments were classified correctly. Each of the 18 participants produced a pair of polar plots containing their overt-tap and imagined-tap segments. The proportion of correct classifications for each participant is shown by a dot in the right panel of Figure 9. As can be seen, it was always lower (below the diagonal line) for imagined-tap segments (ordinate) than overt-tap segments (abscissa). The average correct was 87% and 73% respectively for overt- and imagined-tap segments. Better performance yet could be expected from a classification scheme using a more sophisticated algorithm based on more of the LD-ERPs than just the C3 - C4 difference. Moreover, in the absence of imagery feedback, even the most conscientious participants were unlikely to have imagined tapping on all 200 trials. These results suggest that frequency tagging short segments of EEG to detect and classify covert rhythmic movements might prove useful for brain-computer interfaces, as will be discussed below.

Discussion

The preceding experiment was intended to demonstrate a general approach to motor-mind reading, that is, to detecting the presence and measuring the time-course of covert motor activity. We examined the steady-state motor potentials at a frequency equal to the rate of alternation between left and right taps, both overt and imagined. The presence of signals at this tagging frequency from motor areas during imagined movement, as well as the phase relations between these signals, served as signs that the motor areas were active in a manner similar to that during overt movement. These results demonstrate the feasibility of using the approach to (a) isolate brain activity arising from rhythmic motor processes and (b) to detect its presence during one type of covert motor activity, motor imagery.

Functional Interpretation of ERP Signature

The approach relies on the definition of a spatiotemporal signature to serve as a sign of task-related motor system activity. This signature needs to be based on a signal arising solely from the motor system. The ERP responses recorded during the tap synchronization task, however, were most likely produced by a confluence of perceptual, motor, and other processes. Distillation of a pure motor signal from this complex mix involved the successive application of three operations. First applied was a subtraction procedure for isolating the portion of the ERP that depended solely on whether a response (overt or imagined) was made with the left or right hand. Next, the results of this subtraction were spatially filtered to minimize the contribution of distant sources to the recordings at each electrode site. Finally, the spatially filtered signals at each site were converted to the frequency domain, so that power and phase at the left-right tap-alternation frequency, that is, the tagging frequency, could be obtained.

By definition, the resulting signal arose only from neural populations that (a) responded differently during left and right-hand movements, and (b) produced a cyclic response at the same frequency as the alternation between left and right hands. This spatially filtered signal was found to be largest over cortical motor areas (as discussed below) and was characterized by a 180° phase relation between recordings over the left and right hemispheres that mirrored the 180° phase relation between movements of the left and right hands. Given the correlative nature of ERP measurements, it cannot be established definitively whether the signal arose directly from neural activity in the causal chain that resulted in either overt or imagined movements. For the purpose of motor-mind reading, however, the presence and timing of neural processes producing the signal need only mirror the presence and timing of processes that do play a causal role.

ERP Signature During Overt and Imagined Movements

The spatiotemporal signature we sought as a sign of motor system activity was (a) a signal at the frequency of alternation between the two hands that was (b) maximal over sensorimotor cortex and (c) had a 180° phase relation between recordings over opposite hemispheres. Such a signature was indeed observed during imagined tapping. Moreover, its presence cannot be accounted for by small overt hand movements or eye-movement artifacts, given the lack of EMG and HEOG. Not surprisingly, a similar spatiotemporal signature was observed also during overt movements. To the extent that the ERP responses of motor areas during imagined taps resemble those during overt taps, one may conclude that these areas behaved in similar ways during both.

There were both similarities and differences between overt and imagined movements in tagging frequency topography. Two prominent power foci occurred in each hemisphere during both overt and imagined taps, one over sensorimotor cortex and the other over posterior parietal cortex. The locations of the foci during imagined movement were quite close to those during overt movement. The power of the signal was less during imagined than overt movement, with a disproportionately large reduction over motor cortex. This observation is consistent with a greater role for sensorimotor cortex during overt than during imagined movement, as it could possibly result from the final efferent commands to move and/or from kinesthetic feedback during overt movement.

The similarity between overt and imagined movements in phase relations at the tagging frequency was quite remarkable. There was an approximately 180° phase relation between homologous foci in the left and right hemispheres during both overt and imagined movements, as would be expected if the two hemispheres exhibited opposite patterns of response to the alternation between left and right taps. The total configuration of phase differences across electrode sites, both within and between hemispheres, was quite similar during both overt and imagined movements. These phase differences reflect the temporal organization of different neural populations in producing the tagging frequency signal. The temporal organization of these neural populations during overt movement thus appears to have been preserved during imagination of the same movements.

Neural Sources of ERP Signature

The present findings provide some indication as to the approximate locations in the brain from which the tagging frequency signal arose. Our conclusions rest partly on a process of elimination. Subcortical motor structures, such as the basal ganglia or cerebellum, are unlikely to have contributed to the signal. These areas do not contribute much to electrical potentials recorded at the scalp (Nunez, 1981), and any minimal contribution would have been reduced further by spatial filtering. Likewise, the signal did not originate from any cortical motor areas that produced responses with similar scalp topographies during left- and right-hand movements, such as the (medially located) supplementary motor area. The contribution of these areas would have been removed by the A-B subtraction. Finally, the signal is unlikely to have originated from a single source in each hemisphere, located between the central and posterior foci and oriented in a way that would produce both (dipole tangential to the scalp). Such sources would have produced signals at the central and posterior foci that (a) were 180° out of phase and (b) maintained the same amplitude ratio during overt and imagined movements.[7] Both predictions were disconfirmed by our findings. The sources of the tagging frequency signal are therefore cortical and likely to be in the general vicinity of the power foci in the topographic maps.

Both the central and posterior foci overlie cortical areas known to participate in movement and are close to foci observed in the lateralized potentials for single movements. The central foci are quite close to the scalp locations (electrode sites C3 and C4) where maxima are observed in the lateralized portion of the readiness potential preceding hand movements. The middle of each focus is at a location found consistently across individuals to lie just anterior to the central sulcus (Homan et al., 1987; Steinmetz et al., 1989). Nearby cortical areas that could produce a lateralized signal include primary motor cortex (BA 4), premotor cortex (lateral BA 6), and somatosensory cortex (BA 1–3). In light of the expected response by somatosensory cortex to sensory feedback from overt movement, it is somewhat surprising how similar the central foci during overt and imagined movement are in their locations and the phase differences between surrounding electrodes. Perhaps, sensory feedback from overt movement added little to the tagging frequency signal. Alternatively, participants may have produced internally a somatosensory response similar to that from external feedback as part of their imagined movements (see Table 1 on desired sensory properties of imagined movements).

The centers of the posterior foci are located over the left and right angular gyri (BA 39) in posterior parietal cortex (PPC). The PPC is known to play an important role in movement. Single-cell recordings in monkeys (Andersen & Buneo, 2002) and fMRI studies in humans (e.g., Simon, Mangin, Cohen, Bihan, & Dehaene, 2002) have shown the PPC to be active during pointing, grasping, and eye movements. Damage to the PPC can cause a number of movement-related disorders, including ideomotor apraxia and optic ataxia (Kolb & Whishaw, 1996). Two findings from the present study support the widely held view (e.g., Andersen & Buneo, 2002) that the PPC is involved in a more abstract level of motor organization than primary motor cortex. First, the posterior signals preceded the central signals associated with the same tap. Second, the amplitude of the posterior signals was less influenced than that of the central signals by whether the taps were overtly executed or imagined. A further finding helps to distinguish movement-related signals at posterior foci from another lateralized ERP (N2pc) with similar foci indicating a left or right focus of visual-spatial attention (e.g., Luck & Hillyard, 1994; Woodman & Luck, 2003). The latter ERP signature involves a more negative potential contralateral to the focus of attention, while the potentials observed here over PPC were more positive contralateral to the hand of the upcoming tap (and likely focus of attention). Similarly

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[7] Current from a tangential dipole would flow into the scalp at one focus (sink) and out from the other (source), with sink and source alternating between odd and even taps.

lateralized movement-related potentials over PPC have been reported to precede lateralized potentials over motor cortex in several studies (Leuthold & Jentzsch, 2002; Wauschkuhn, Wascher, & Verleger, 1997).

Implications for Motor Imagery

The implications of our findings for motor imagery depend on the functional interpretation of the ERP tagging frequency signals observed during periods in which participants were supposed to imagine tapping. The correspondence of tagging frequency to the rate of imagined tapping, the phase relations between hemispheres indicative of alternation between hands, and their cortical motor sources all suggest a response highly specific to motor imagery. But before accepting this conclusion, let's first consider ways in which tagging frequency ERPs might have arisen during periods of putative motor imagery regardless of whether such imagery actually occurred. For example, perhaps they were caused by continued reverberation of the motor system following overt taps. One reason to doubt this hypothesis is that their topography resembles that preceding a single imagined tap not immediately following overt ones (Osman, Müller, Syre, & Russ, 2005; Parra et al., 2002). There was also little sign that amplitude at the four foci diminished over the imagery period (e.g., Figure 3D). Another possibility is that presentation of the synch signals during the imagery period induced an automatic motor response resulting from stimulus–response associations established during overt tapping. Contrary to this hypothesis, the ERP lateralization associated with each synch signal began before the signal, as would be expected for the anticipatory responses required by synchronization. The ERP lateralization is also unlikely to have arisen from an automatic response, since similar lateralization during imagined taps in a reaction time paradigm can be voluntarily inhibited (Osman, Russ, & Albert, 2002).

If one grants that it produced the observed tagging frequency signals, the general implication for motor imagery is that people can drive their cortical motor areas with a temporal-anatomical pattern similar to that during overt movement, yet refrain from producing muscle activity. This conclusion is supported also by studies using TMS, which have found changes in motor cortex excitability specific to the identity, role, and timing of muscles involved in imagined movements (e.g., Hashimoto & Rothwell, 1999; Rossini et al., 1999; Stinear & Byblow, 2003). Using noninvasive measures, the present study found a pattern of neural activity during both overt and imagined tapping that consisted of quick dynamic changes related to the timing and finger of individual taps. The similarity between overt and imagined movements extended to temporal relations between movement-related activities of different neural populations. These temporal relations were reflected in phase differences between spatially filtered tagging frequency signals recorded over different scalp locations. One would expect the content and coordination of information-processing operations performed by different neural populations to influence their relative timing. It is therefore of considerable interest that the total configuration of phase differences between electrodes with substantial tagging frequency power (24 sites surrounding four amplitude foci) was so similar for overt and imagined tapping (see Figure 8). It seems unlikely that such a degree of temporal isomorphism could occur at a neural level without a corresponding temporal isomorphism at the information-processing level. In other words, the neural populations that were active during both overt and imagined tapping behaved as if they were running the same motor programs during each.

Methodological Extensions

The frequency tagging approach can be extended beyond the present example in a number of ways. To begin with, it should be possible to overcome an important limitation of the current experiment. The signal at the tagged frequency reflected only the difference between the cortical responses for left and right taps, and thus failed to capture cortical motor activity that occurs equally regardless of the involved hand. One might expect this latter activity to comprise more abstract motor processes performed at more central levels of the motor system. The portion of the motor potential common to both left and right taps was removed by the subtraction of Type B-trials from Type A-trials. But even without subtraction, this response would have been confounded with that to the synch signals. Since the taps (left and right combined) and signals occurred at the same rate (a tap synchronized to each signal), their associated ERPs could not be separated by frequency tagging.

There are several ways in which future work might overcome this limitation. One is to have participants synchronize taps to every other stimulus in the series. As an example, consider an experiment with the same number of alternating left and right taps as the present one, but with twice as many synch signals presented at a constant rate. In pilot studies, we have found that the LD-ERP amplitude spectra under such conditions contain three prominent peaks. One occurs at the left-right alternation frequency and, as in the present experiment, reflects the portion of the tap-related neural response that depends on response hand. A second peak occurs at twice the tap alternation frequency (the rate of individual taps, irrespective of hand). This reflects the tap-related neural response that is invariant across hands. The third peak reflects a response evoked by the synch signal and occurs at the frequency of signal presentation. Though it may seem counterintuitive, motor responses can be isolated from sensory ones by presenting *more* stimuli.

The possibility that each of several frequencies can selectively tag one of several different processes contributing concurrently to the same behavior could prove useful. Many actions, such as speaking or playing a musical instrument, are controlled hierarchically. That is, the processes that produce, time, or sequentially arrange a series of elements operate on elements defined at several levels, some more microscopic and others more macroscopic. For example, the elements controlled while playing a piece of music might involve individual notes at one level and individual measures at another. Frequency tagging might be used to distinguish between and selectively study processes operating at different levels. Because they differ in duration, elements at different levels within the same series progress at different rates. Hence, the processes that operate at each level might be tagged by different frequencies.

Further Applications

One potential application already hinted at concerns brain-computer interfaces (BCIs). These interfaces allow a user to control a computer without overt movement and may provide a useful communication channel for people unable to speak or move (Wolpaw, Birbaumer, McFarland, Pfurtscheller, & Vaughan, 2002). A number of BCIs have employed imagined movements by the left or right hand to produce lateral asymmetries in scalp-recorded EEG (e.g., Pfurtscheller et al., 2003). By repeatedly producing these asymmetries, the user can communicate with the computer in a binary (left-right) code. Imagined rhythmic tapping combined with frequency tagging might likewise enable a user to control features detectable in short segments of EEG. The present experiment found phase (L-R vs. R-L) of imagined tapping to be distinguishable on individual trials (see Figure 9). If tapping hand or rate could be distinguished on individual trials as well, it might even be possible to convey information along several channels concurrently (as in Wolpaw & McFarland, 2004).

Frequency tagging might also be used to study covert actions beyond strictly motoric ones. Indeed, it might prove applicable to many of the voluntary cognitive acts that can be performed repeatedly in synchrony with a rhythmic signal. A natural candidate is covert (inner) speech. Besides its important role in thought, covert speech has proven useful for studying the brain bases of speech production by helping to circumvent electrical and motion artifacts that accompany overt speech (e.g., Rowan et al., 2004). Spatially filtered signals at a tagging frequency over cortical speech areas might be used to monitor their activities during such speech. Related to covert speech is the rehearsal of verbal material in working memory. The cyclic nature of memory rehearsal would seem well suited for frequency tagging. If the items in a short list were rehearsed in synchrony to rhythmic signals, memory rehearsal might yield a signal at a tagging frequency. It might then be possible to ascertain whether some of the cortical areas involved in covert speech are involved also in verbal memory rehearsal. There are many other possible examples. In each case, it would be necessary to separate signals arising from the process of interest from those evoked by the synchronization signal. As mentioned, this might be accomplished by synchronizing the process to alternate signals. Another option would be to alternate between different variants of the process (e.g., different word lengths or types) on each trial. As in the present experiment, Type A and B blocks could involve different orders, and ERP differences between the two could be examined at the alternation frequency.

Finally, frequency tagging might be well suited for examining how different cortical areas coordinate their respective activities to implement cognitive functions. One approach to this problem has been to examine the moment-by-moment relations between electrical signals from these areas (e.g., Gevins et al., 1989; Urbano, Babiloni, Onorati & Babiloni, 1998). Tagging frequency phase might be especially useful in this regard. We have seen in the present study how the phase pattern over different cortical areas can provide information about the relative timing of their task-relevant activities. It is possible also to examine phase coherence at the tagging frequency. The coherence between two signals at a particular frequency is determined largely by how consistent their phase difference remains over time. One might expect increased coherence when cortical areas producing different signals temporally coordinate their respective activities. There has been considerable interest in using ERP phase coherence to study such *functional connectivity* between cortical areas during tasks involving various types of information processing (e.g., Gerloff et al., 1998; Weiss & Rappelsberger, 2000). An important advantage of the frequency tagging approach is that the frequencies at which task-relevant changes in coherence could occur are known and selected in advance. In sum, by examining tagging frequency coherence between spatially filtered signals recorded over different cortical regions, one might be able to examine the functional connectivity between those regions during a variety of cognitive tasks.

Conclusions

Steady-state ERPs have traditionally been used to study sensation and perception. In this paper, we propose and demonstrate an approach in which steady-state ERPs are used to study the production of responses. These responses can be motoric, overt or covert, and might include also higher-level acts of cognition. What is novel about the approach is the definition and application of a tagging frequency signal. Participants are induced to emit this signal by cyclically producing the response of interest at a given rate. The strength of the approach stems in part from the identity relation between production rate of the response and the frequency of the signal that tags it. This identity leads to a signal with good functional specificity, as well as allows its frequency to be known and selected a priori. The amplitude and phase of this signal can be used to detect the activity of different cortical regions and to provide information about the relative timing of these activities. Phase coherence might also be used to study functional connectivity between regions. In the present study, amplitude and phase of the tagging frequency signal over different cortical regions defined a spatiotemporal signature used to detect covert motor activity. The presence of this signature during motor imagery provided a powerful demonstration of functional and neural equivalence between overt and imagined movements. We believe that frequency tagging could likewise yield important insights into other phenomena on the response-related, endogenous side of cognition.

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Appendix

Appendix

Amplitude (uV) and Phase of Tap-Alternation Frequency at Electrode Sites Surrounding Power Foci

Left central focus					Right central focus				
	Amplitude		Phase			Amplitude		Phase	
Electrode	Overt	Imagined	Overt	Imagined	Electrode	Overt	Imagined	Overt	Imagined
FC3	13.7	4.6	−82.9	−81.2	FC4	16.6	3.0	87.7	84.1
FC1	14.3	5.0	−90.3	−91.3	FC2	16.7	5.4	99.4	97.3
C3	19.4	7.3	−124.4	−122.4	C4	20.4	5.5	54.3	29.9
C1	19.5	7.7	−114.6	−116.0	C2	20.7	7.1	69.4	61.0
CP3	18.1	7.5	−162.9	−167.3	CP4	15.8	6.8	17.0	−8.2
CP1	13.9	5.9	−143.8	−148.8	CP2	16.2	6.2	37.6	17.5
Average	16.5	6.3	−119.8	−121.2	Average	17.8	5.6	60.9	46.9

Left posterior focus					Right posterior focus				
	Amplitude		Phase			Amplitude		Phase	
Electrode	Overt	Imagined	Overt	Imagined	Electrode	Overt	Imagined	Overt	Imagined
P7	13.8	6.6	100.4	121.4	P8	10.7	5.6	−91.1	−82.4
P5	17.8	9.6	126.5	135.9	P6	12.2	7.2	−69.1	−64.3
P3	17.0	8.9	145.5	147.7	P4	11.6	7.2	−37.6	−42.8
P1	10.1	4.6	156.9	159.3	P2	8.7	5.6	−10.1	−27.7
PO7	16.2	8.1	94.7	120.5	P08	11.8	6.1	−100.1	−86.5
PO3	15.8	8.0	116.2	131.1	P04	10.6	6.5	−78.7	−66.6
Average	15.1	7.6	123.4	136.0	Average	10.9	6.4	−64.4	−61.7

Note. The scalp location of each site is shown in Figures 4 and 6.

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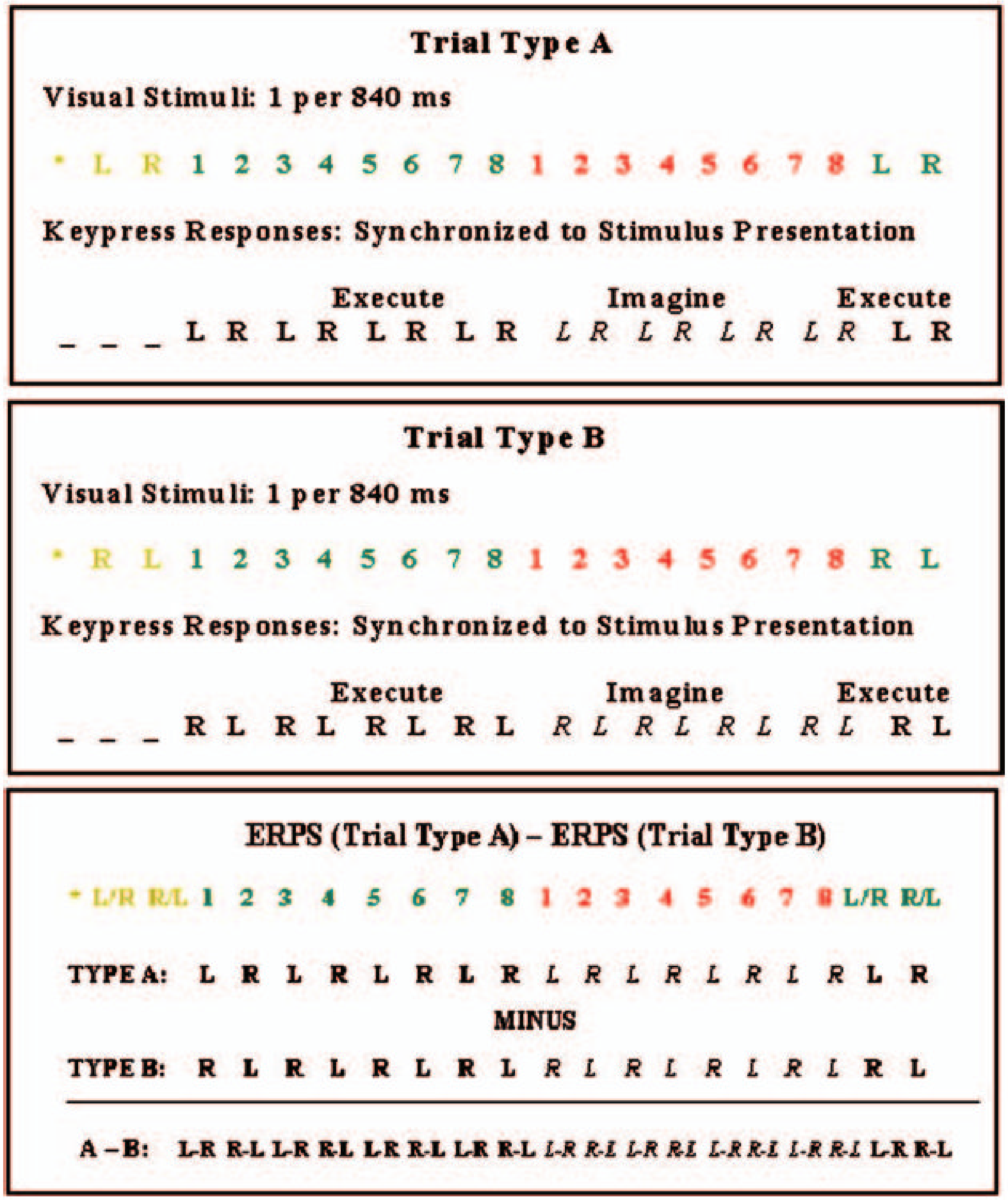

Figure 1.

Trial-Types A and B. The sequence of events on Type A and B trials are shown respectively in the top and middle panels. Alternating taps with the left (L) and right (R) index fingers (real and imagined) were synchronized to stimuli presented every 840 ms. Taps with the same finger (L or R) were thus repeated every 2 × 840 = 1680 ms. The order of L and R taps was reversed in trial Types A and B, while the numeric stimuli remained the same. The bottom panel shows results of subtracting ERPs on trial Type B from those on Type A. Odd taps = L − R. Even taps = R − L. ERPs evoked by the numeric stimuli (same in A and B) cancel, and the remaining movement-related ERPs (L − R and R − L) cycle at 1680 ms = 0.6 Hz.

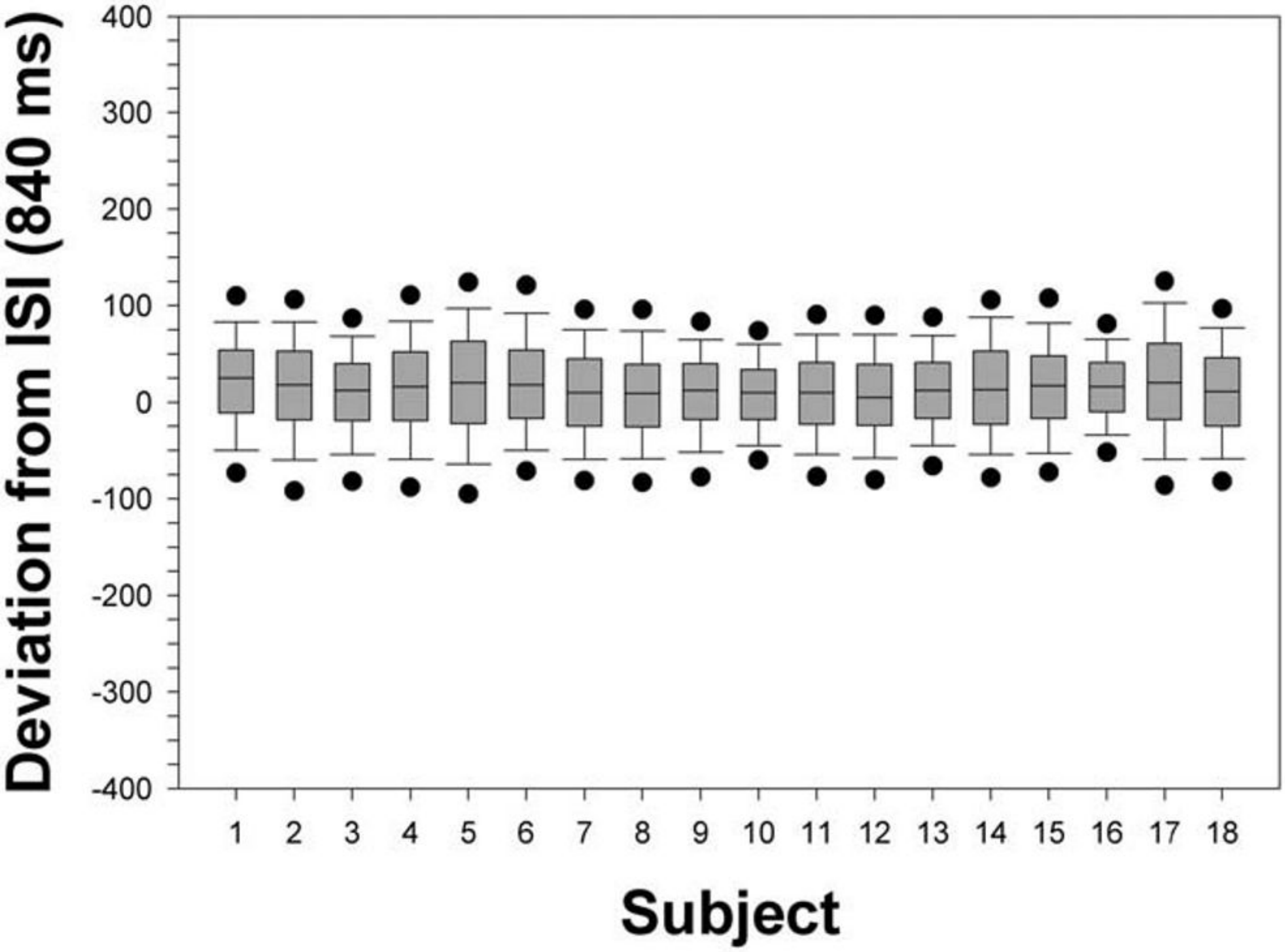

Figure 2.

Distribution of intertap intervals (time between successive overt taps) for each participant. The middle line, inner pair of lines, outer pair of lines, and pair of dots represent respectively the median, 25th and 75th percentiles, 10th and 90th percentiles, and 5th and 95th percentiles. ISI = Interstimulus interval (time between onsets of successive synchronization signals).

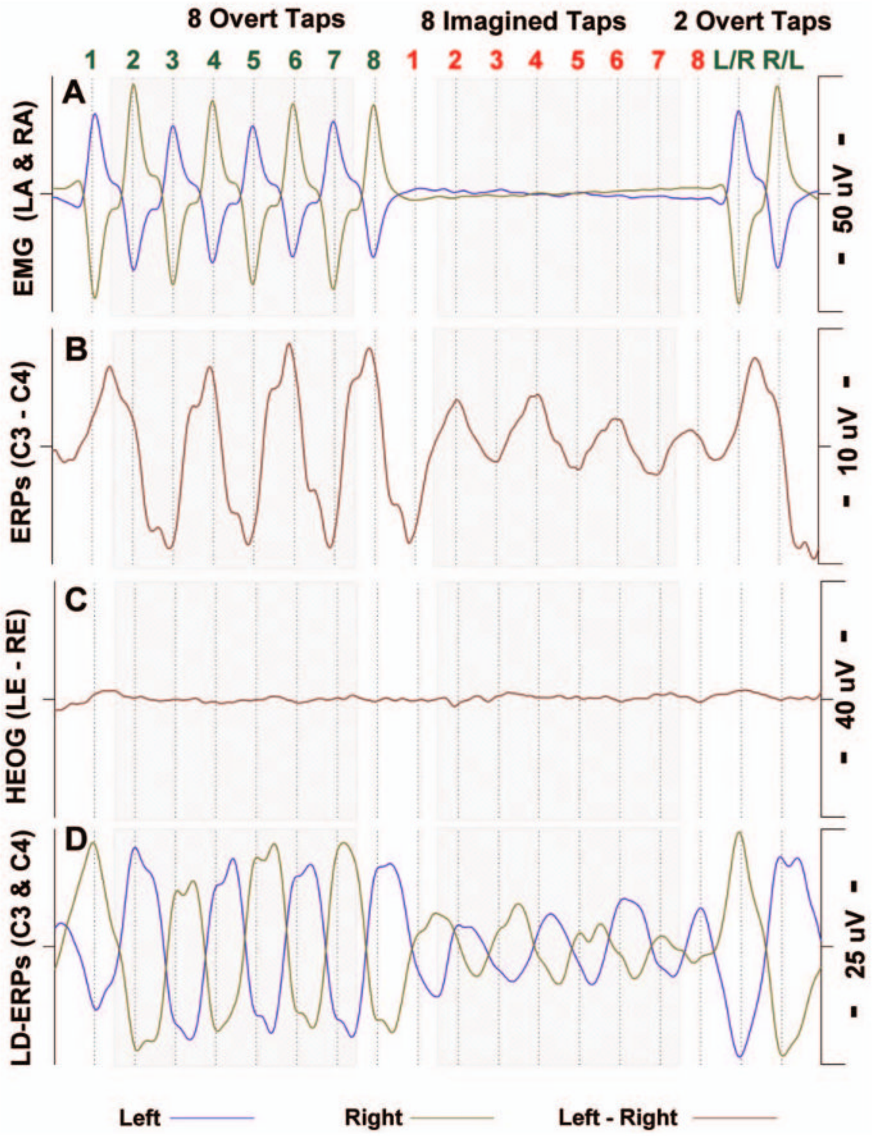

Figure 3.

Responses to overt and imagined taps at the cortical and muscular levels. Each panel shows results of the trial-Type A-B subtraction. Timing and identity of the synchronization signals presented on each trial are shown at the top. Panel A = EMG recorded from the left (LA) and right (RA) arms. Panel B = Lateral asymmetry in ERP at electrode sites over the left (C3) and right (C4) cortical hand areas (C3 − C4). Panel C = Difference between HEOG recorded near the left (LE) and right (RE) eyes (LE − RE). Panel D = Laplacian derivative of ERP recordings (LD-ERPs) from sites over the left (C3) and right (C4) cortical hand areas. Gray-hatched areas indicate intervals used to calculate amplitude spectra (see Figure 5). See text for further description of the measures.

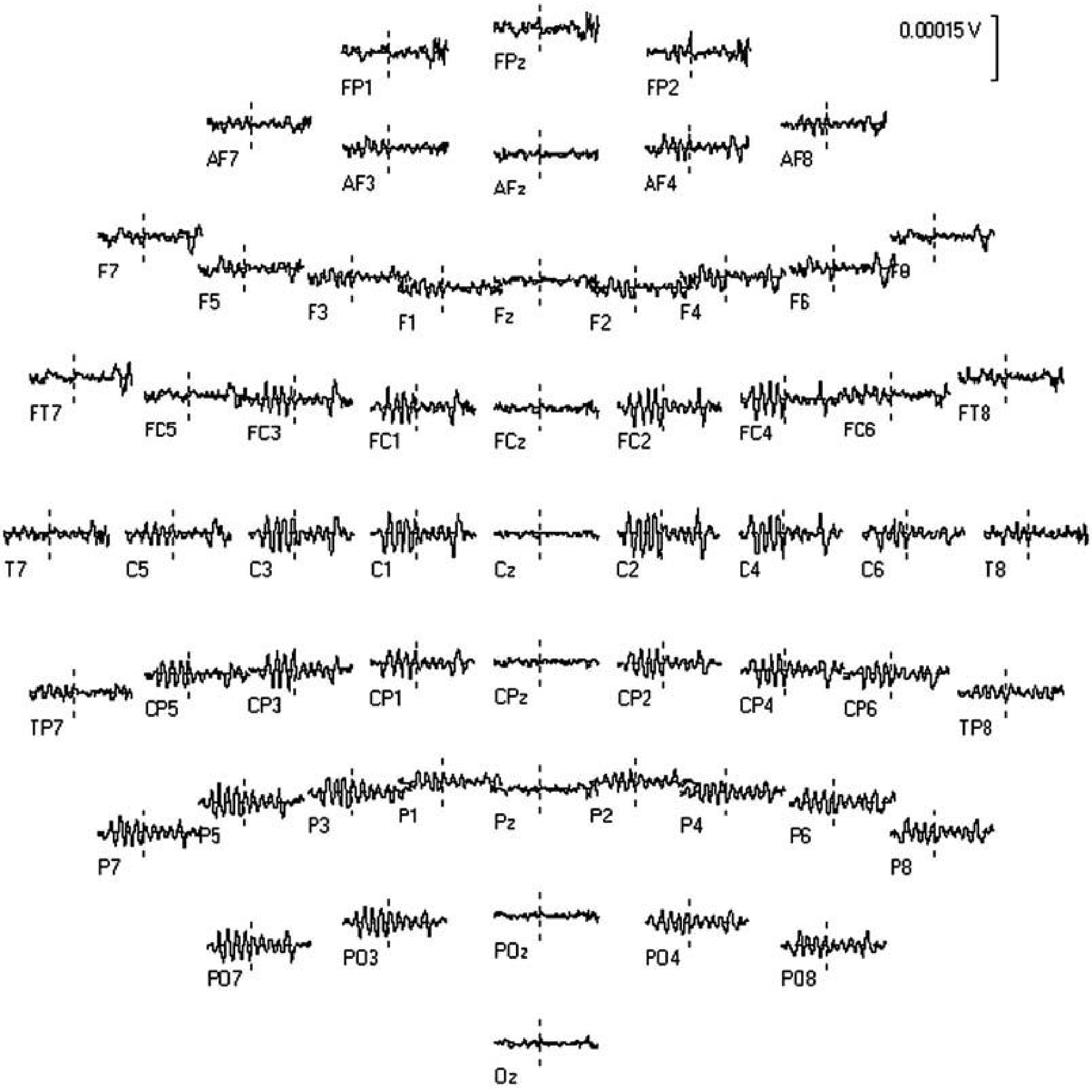

Figure 4.

LD-ERP at each electrode site. The traces were obtained by performing a Laplacian transform (see text) on the ERP difference waves resulting from the trial Type A - trial Type B subtraction.

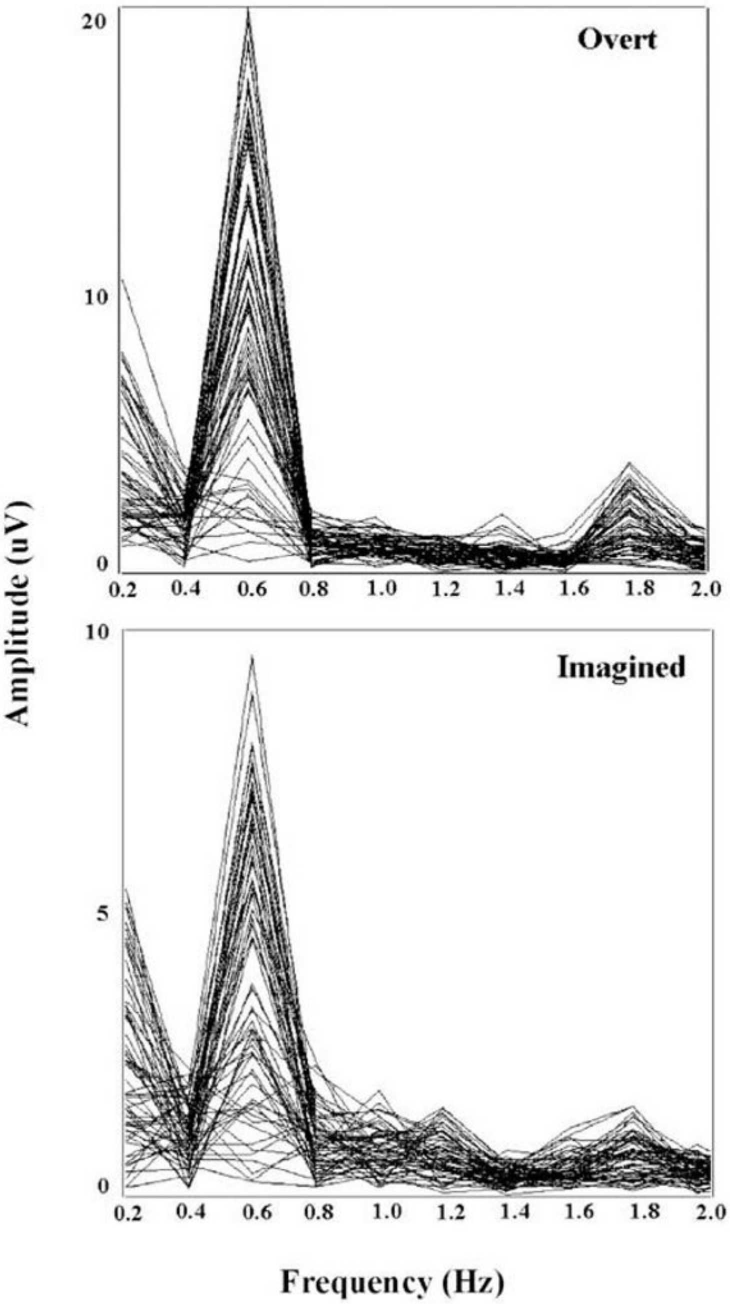

Figure 5.

Amplitude spectra of the LD-ERP at each electrode site during overt taps (top panel) and imagined taps (bottom panel). Each line shows the spectrum at an individual electrode site. 0.6 Hz = frequency of alternation between left and right taps. Note that the scale (uV) is twice as large for overt as for imagined movements.

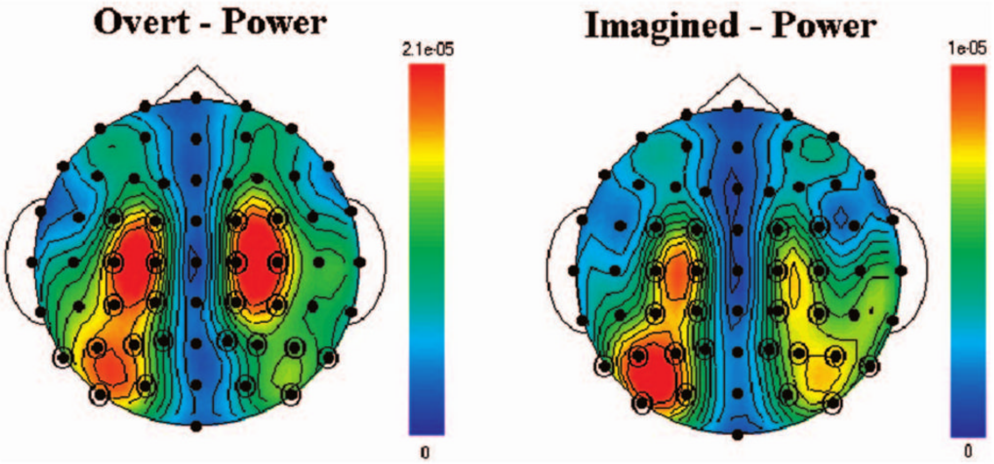

Figure 6.

Topography of LD-ERP amplitude at the frequency of alternation between left and right taps (0.6 Hz). Color indicates amplitude (red = more), concentric lines indicate regions of equivalent amplitude, and dots indicate electrode positions. (See text for explanation of circles around dots.) The central sulcus is slightly posterior to the central row of electrodes. Note that the scale (uV) is approximately twice as large for overt as for imagined movements.

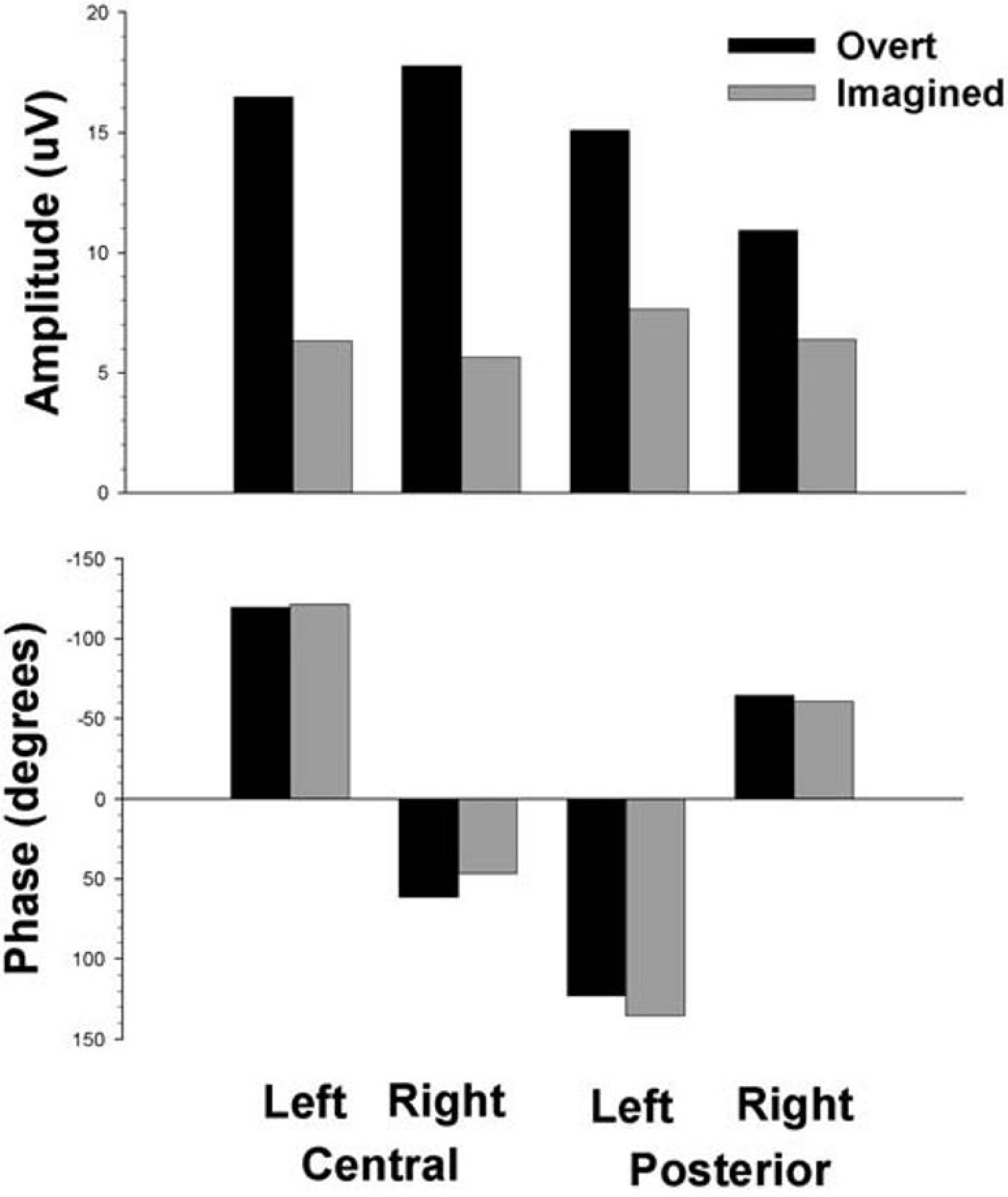

Figure 7.

Amplitude (top panel) and phase (bottom panel) of the tap-alternation frequency during overt and imagined movement. Each bar shows an average based on the six electrode sites surrounding one of the four power foci (circled dots in Figure 6). The values at individual electrode sites can be found in the Appendix.

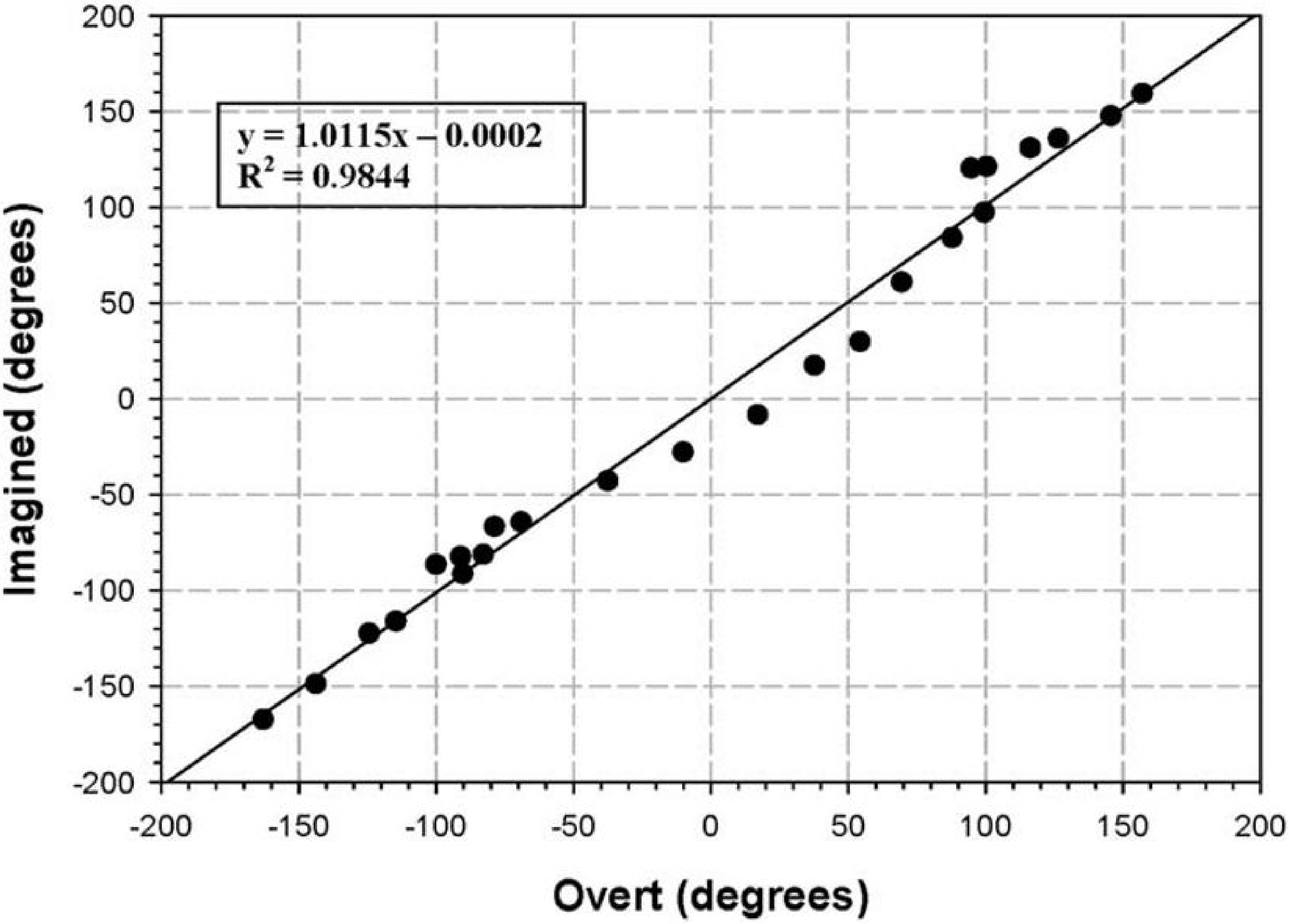

Figure 8.

Phase of the tap-alternation frequency at individual electrode sites during overt (abscissa) and imagined (ordinate) movements. Each point corresponds to one of the 24 (4 × 6) electrode sites surrounding the four power foci (circled dots in Figure 6). The numerical values can be found in the Appendix.

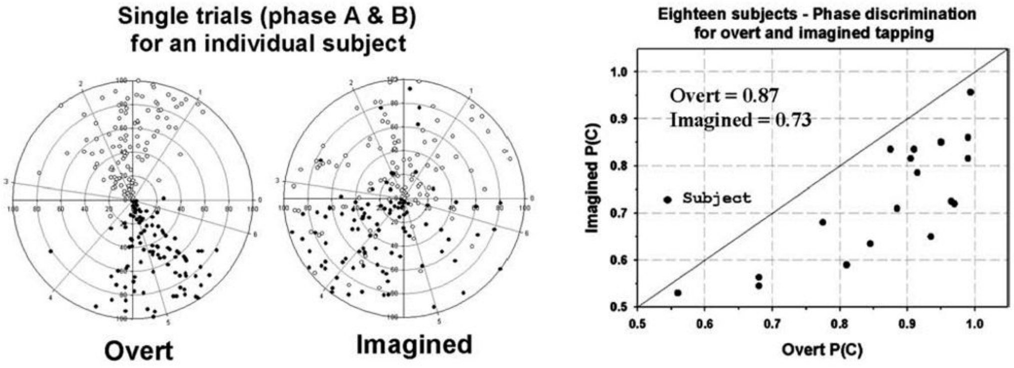

Figure 9.

Single-trial classification of overt and imagined tap segments. Left and middle panels: Type-A (closed circles) and Type-B (open circles) segments for an individual participant; Phase = angle on plot; Trial # = distance from center. Right panel: Classification accuracy (PC) for each of the 18 participants (dot).

Table 1
Questions on the Imagery Questionnaire

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 left and right taps during imagery sequences?
5. How accurate was the timing of your imagined movements compared with that of your executed movements?
6. How accurate were your choices of response finger 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?

Note. Participants answered each question by circling one of the numbers (integers 0–10) on a rating scale directly below.

Table 2
Polar Coordinates of Amplitude Foci at the Tap-Alternation Frequency

	Central foci				Posterior foci			
	Left hemisphere		Right hemisphere		Left hemisphere		Right hemisphere	
	Phi	**Theta**	**Phi**	**Theta**	**Phi**	**Theta**	**Phi**	**Theta**
Overt	89.55	33.93	272.44	32.92	140.85	76.21	218.68	80.00
	(6.89)	(1.47)	(13.11)	(1.88)	(1.73)	(3.95)	(3.34)	(3.89)
Imagined	93.12	33.30	254.85	32.76	140.66	75.35	218.36	73.09
	(12.18)	(2.45)	(30.29)	(7.96)	(1.86)	(3.08)	(4.29)	(8.89)
Difference	−3.56	0.62	17.59	0.16	0.19	0.87	0.32	6.91
	(11.08)	(2.04)	(31.38)	(7.79)	(2.44)	(2.99)	(3.58)	(7.43)

Note. Mean coordinates appear above their standard errors, which are shown in parentheses.