

Mu-rhythm changes during the planning of motor and motor imagery actions[☆]

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ABSTRACT

Motor imagery is a mental representation of motor behavior which has been widely used to study the cognitive basis of movement. The assumption that real movements and motor imagery (virtual movements) use the same neurobiological basis has been questioned by functional magnetic resonance data. The functional similarity in the planning of real and virtual movements was studied here by analyzing event-related EEG recordings of the Mu-activity in the sensitive-motor cortex, pre-motor cortex and supplementary motor cortex. A visual stimulus (an arrow) which displayed the information needed for planning a motion (which can be executed or imaged later after the display of a second stimulus) induced a short-lasting phase-locked Mu-response (PLr) which was wider and more widespread when it was used for the motor planning of real or virtual movements than when it was passively watched. The phase-locked Mu-response was accompanied by a persistent decrease of the Mu-rhythms which were not phase-locked to stimuli (NPLr), a response which also was more marked and generalized when stimuli were used for motor planning than when they were passively observed. PLr and NPLr were similar during motor testing and imagery testing, suggesting that both tasks activated the Mu rhythms to a similar degree. This congruency between real and virtual movements was observed in the three cortical areas studied, where the amplitude, latency and duration of the phase-locked and non-phase-locked Mu response was similar in both cases. These noticeable similarities support the idea that the same cortical mechanisms are recruited during the planning of real and virtual movements, a fact that can be analyzed better when an event-related paradigm and a high time-resolution method are used.

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1. Introduction

Motor imagery (MI) is a dynamic mental representation of motor behavior which is not accompanied by real movements (virtual movement). As virtual movements show many similarities with real movements and they are not interfered with by variables involved in the execution of real movements (e.g. somatosensory stimuli) (Sabate, Gonzalez, & Rodriguez, 2007; Sabate, Llanos, & Rodriguez, 2008), MI has been widely used to study the cognitive basis of movement. The similarity of cognitive functions involved in real and virtual movements has been

supported by chronometric studies showing that both movements consume the same execution time and use the same neurobiological basis. The time needed to execute a motor pattern is similar to that needed for its MI (Abbruzzese, Trompetto, & Schieppati, 1996; Crammond, 1997; Sirigu et al., 1996), and this increases in both cases with the complexity and accuracy of the task (Fitts' law) (Decety & Lindgren, 1991; Dominey, Decety, Broussolle, Chazot, & Jeannerod, 1995; Jeannerod & Frak, 1999; Sirigu et al., 1996). This real–virtual congruency has been observed in normal subjects under different conditions (e.g. during ageing) (Morales, Dopico, Sabate, Gonzalez-Hernandez, & Rodriguez, 2007; Sabate, Gonzalez, & Rodriguez, 2004) and in patients with different brain lesions (e.g. stroke and Parkinson disease) (Cramer, Finklestein, Schaechter, Bush, & Rosen, 1999; Dominey et al., 1995; Gonzalez, Rodriguez, Ramirez, & Sabate, 2005; Morales et al., 2007; Sirigu et al., 1996; Thobois et al., 2000). However, this real–virtual congruency decreases in some circumstances. For instance, congruency decreases occurs when

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movements are automatically executed without conscious supervision (Sabate et al., 2004), or when they need an “on line” adjustment during their execution (Rodríguez, Llanos, & Sabate, 2009). In addition, the real–virtual congruency of patients with brain damage may be transiently lost just after acute lesion, requiring a time interval where the motor practice (e.g. 1–2 weeks after stroke) to restore the pre-lesion congruency (Sabate et al., 2007). These data suggest that similarities between real and virtual movements could be the result of an active process (which scans the competence of elements involved in the motor behavior to adjust motor planning and virtual imagery to the real capability of the motor system) (Sabate et al., 2007) more than the result of using the same neuronal basis (the common-basis hypothesis). Thus, the functional similarity between real and virtual movements and the neuronal networks involved in each case are still a matter of debate.

The experimental method most frequently used to test the common-basis hypothesis for real vs. virtual movements is functional magnetic resonance (fMRI). This method has provided data showing that areas such as the primary sensorimotor cortex (SMc), pre-motor cortices (PMc), and supplementary motor cortex (SpMc) are recruited by both real movements and their MI (Decety, 1996; Gerardin et al., 2000; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Hanakawa et al., 2003; Lotze et al., 1999; Naito et al., 2002; Porro, Cettolo, Francescato, & Baraldi, 2000; Porro et al., 1996; Sirigu et al., 1996; Stephan et al., 1995), thus supporting the common-basis hypothesis. However, the activation degree (Gerardin et al., 2000; Hanakawa et al., 2003; Michelon, Vettel, & Zacks, 2006) and the spatial distribution of the activation within these areas (Rodríguez, Muniz, Gonzalez, & Sabate, 2004) can be different for real and virtual movements. In addition, there are fMRI studies showing that areas activated during MI and those activated during motor performance of the same action do not always completely overlap (Binkofski et al., 2000; Ruby & Decety, 2001; Sirigu & Duhamel, 2001; Solodkin, Hlustik, Chen, & Small, 2004). This imperfect overlapping could be associated to the differing abilities of subjects for imaging movements (Guillot et al., 2008), but also to the limits of experimental methods used to study the brain activity during real and virtual movements. The fMRI has a high spatial resolution but a low temporal resolution (s), which limits its application to the study of fast motor tasks which, as occurs with MI, can be performed in short time-intervals (ms). Considering that a low time-resolution could produce ambiguous data with puzzling interpretations, the biological basis of real and virtual movements was studied here by using electroencephalography (EEG), a method with a low spatial resolution but an excellent time-resolution (ms). Thus, the aim of this work was to study the electrophysiological behavior of the motor cortex during the planning of real and virtual movements.

The SMc, PMc and SpMc display a typical EEG oscillation known as the Mu rhythm. The Mu rhythm is a short-lasting (0.5–2 s) wave in the alpha range (8–12 Hz) which is recorded at rest (Chatrian, Petersen, & Lazarte, 1959; Gastaut & Bert, 1954; Muthukumaraswamy & Johnson, 2004; Penfield, 1954; Pfurtscheller & Lopes da Silva, 1999; Pineda, 2005) and attenuated by voluntary movements (Babiloni et al., 1999; Leocani, Toro, Zhuang, Gerloff, & Hallett, 2001; Salenius, Schnitzler, Salmelin, Jousmaki, & Hari, 1997; Salmelin & Hari, 1994). These facts initially suggested that the Mu wave is an “idling” rhythm which, in the motor cortex, reflects the same “nil-work” status proposed for the α -wave in the occipital cortex (idling hypothesis) (Kuhlman, 1978; Pfurtscheller, Stancak Jr., & Neuper, 1996). However, a Mu rhythm activation has been also reported during the execution of different tasks (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Krause et al., 2000), thus

suggesting that the Mu wave is a mechanism for improving information processing (processing hypothesis) (Basar, Basar-Eroglu, Karakas, & Schürmann, 2000, 2001; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Palva & Palva, 2007; Sabate, Llanos, Enriquez, & Rodríguez, 2012). In fact, the Mu rhythm could improve data processing when its phase is modified by the task onset, inhibiting the data processing when it is not phase-locked with the task (Sabate et al., 2012). The task sensitivity of the Mu-rhythm has been used here to compare the functional activity of the motor cortex during real movements with that recorded during their motor imagery. The Mu rhythm can change with visual stimuli (Koshino & Niedermeyer, 1975; Pfurtscheller, 1992; Pfurtscheller & Lopes da Silva, 1999), particularly when they are used to trigger the planning of new motor patterns (Sabate et al., 2012). This sensitivity of the Mu rhythm to visual stimuli has been used here to segregate the time interval used to plan movements from the interval used to execute the planned movements (event-related paradigm). Finally, the study was focussed on comparing Mu activity during the planning of real and virtual movements.

2. Material and methods

A total of 11 men ranging between 23 and 58 years of age were studied. All subjects were in good health, had no prior history of cerebral disease or medical treatment which might influence motor performance, and had adequate cognitive and visual-motor functions to perform the test. All subjects were right-handed according to the Edinburgh Inventory of handedness (Oldfield, 1971). The study was approved by the local Research Ethics Committee.

2.1. Procedure

Tests were performed with the right hand in a sound-attenuated and temperature regulated ($22 \pm 1^\circ\text{C}$) room which was lit by homogeneous white light and that provided stable and reproducible environmental conditions. During the experiments, the subjects sat comfortably in a chair in front of a computer screen (60 cm) which showed the visual stimuli (Evoke, ANT Software, Enschede, The Netherlands).

Three tests were conducted. The motor test involved the display of two successive visual stimuli, a first stimulus (an arrow) indicating the direction of the finger motion to be performed when a second stimulus (a large dot) gave the signal to execute the movement. In the imagery test, the first stimulus (an arrow) indicated the direction of the finger motion to be performed by MI after the display of the second stimulus (a large dot). The subjects saw the same stimuli without performing any tasks in the passive test. Only the Mu-response to the first stimulus was evaluated (motor response started ≈ 2000 ms after the first stimulus and ≈ 400 ms after the second stimulus). In other words, the active test consisted of preparing to move the thumb in a direction which depended on the instruction given by the first stimulus (a red arrow pointing up-down-right-left). The thumb movement could not be initiated until a large red dot (second stimulus) replaced the first stimulus on the computer screen. The instructions to the subjects used in the active test were as follows: “Please move your thumb (initially placed on a central point of a joystick) to press the button located above, below, to the right or to the left of your thumb (30 mm from the central button), and return your thumb to the initial position as fast as possible. The same task was performed in the imagery test but, in this case, instead of making movements the subjects should perform their motor imagery. Motor imagery consisted of imagining the performance of motor sequences and the kinesthetic sensations associated with it while keeping the finger still. Subjects were informed that “visual imaginations” of the finger movement (an imaginary watching of one’s own hand in motion) and modifications in the muscle tone during the MI task (a simultaneous contraction of the flexor and extensor muscles of the hand) were not permitted. All subjects reported sensations associated with virtual movements but none of them showed evidence of real movements (evaluated with a goniometer for finger movement; Penny and Giles; Christchurch, UK). In each trial, the specific button to be pressed (or imagined to be pressed) was indicated by the direction of the arrow on the screen, but the subjects were not allowed to move their right thumb (or to imagine moving it) until the arrow was replaced by a large red dot”, and a joystick was used for this task. At the beginning of the task, the tip of the right-thumb was touching a button located exactly in the middle of the four surrounding buttons serving as the targets of the movements. The task of the passive test consisted of watching the same stimuli but doing nothing with them (the tip of the right-thumb continued to touch the middle button). In the active and imagery tests, the shape of the first stimulus (an arrow pointing in a

specific direction) identified the direction of the movement to be executed (or to perform its MI) later, whereas the appearance of the second stimulus (a large dot) signaled the execution of the previously prepared movement. Therefore, the subjects needed to identify the direction of the arrow stimulus after the first stimulus, to link the analyzed stimulus with a motor task (visual-motor executive function), and to wait for a second stimulus. In the passive test, the characteristics of the stimuli had no practical consequences on behavior, with the right-thumb remaining motionless after the stimuli observation.

The subjects were instructed, in all the tests, to rest between trials (7 s) looking at the computer screen which was switched off for the first 4 s (spontaneous movements such as those used to prevent weariness or irritation of eyes were then allowed) and the screen was then switched on for the last 3 s and a central white circumference was displayed which was used to fix the eyes before beginning the task. Thus, the time intervals for each test were 4 s for the initial resting period, 3 s for the eye-fixing period, 1.6 s for the arrow stimulus, and 0.6 s for the dot stimulus. All visual stimuli were the same size (20 mm diameter). The study as a whole consisted of 100 event-related trials for each of the three experimental conditions. The real, virtual, and passive trials were completed in blocks which were randomized across subjects and which were separated by rest intervals of 10 min.

2.2. Acquisition and analysis of EEG

EEG data were recorded according to previously reported procedures (Sabate, Llanos, Enriquez, Gonzalez, & Rodriguez, 2011) and an AMP-TRF136AB amplifier and the ASA software were used (both from ANT, Enschede, The Netherlands). EEG data were digitized (at a rate of 512 Hz/channel) from 128 electrodes placed according to the extended International 10–20 system and referenced to the ear (Oostenveld & Praamstra, 2001). Thumb movements were monitored with an accelerometer located in the dorsal portion of the proximal phalanx of the thumb (Model 7290A-2; Microtron, Endeavor; USA) and with a surface electrode which recorded electromyographic activity of the pollicis brevis muscle (digitized at 2000 Hz).

The offline analysis of EEG data began with: (1) a manual rejection of EEG artefacts (all recordings were observed by two trained physiologists who independently switched-off trials disturbed by blinking, eye movements, inadvertent motor acts, instrumental artefacts, etc.), (2) a band-pass filtering for Mu activity (8–12 Hz) performed with a Fast Fourier Transform based filter which does not modify the α -wave phase, and (3) a surface Laplacian (80%) which improved the low spatial resolution of EEG induced by the volume conductive properties of the brain and its covering (Hjorth, 1975; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001; Perrin, Pernier, Bertrand, & Echallier, 1989).

Different data computations were performed after this initial preconditioning of EEG signals to quantify the fast changes of Mu-activity associated with the different task components. The procedure to compute the global response of the Mu rhythm (total response; Tr) and the response of two Mu sub-components (phase-locked response PLr; and non-phase-locked response NPLr) was previously described in detail (Sabate et al., 2011). Briefly, the envelope of signals band-filtered for the Mu rhythm was used as an instantaneous representation of the Mu power (Babiloni et al., 1999; Clochon, Fontbonne, Lebrun, & Etevenon, 1996; Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller & Neuper, 1992; Woertz, Pfurtscheller, & Klimesch, 2004), with the event related average of this envelope being (computed with a Hilbert filter) considered as a representation (Sabate et al., 2011, 2012) of the power of the Mu-response to visual stimuli (total response, Tr). This procedure includes both the phase-locked and non-phase-locked Mu-response to stimuli. The direct event-related averaging of the Mu-wave preserves the PLr of Mu-activity while it progressively deletes the NPLr, with the envelope of PLr then being used to selectively compute the power of the phase-locked response (phase-locked response power; PLr-power). Finally, the power of the Mu-components which did not show a phase-locked response to stimuli was calculated by subtracting PLr from Tr (non-phase-locked response power; NPLr-power).

At the end of each of these computations, data were normalized (as changes in μV induced by visual stimuli vs. the pre-stimulus level which in turn was calculated as the mean value of the 200 ms previous to the stimulus onset) and the grand averaging of the mean values obtained for each subject was computed (data shown in Fig. 1 represent the mean value of the group and data shown in Figs. 2 and 3 represent the mean value \pm standard error of the group). Results were spline-interpolated and displayed in 3D using a color-code. This representation was based on a realistic head model computed for each subject by recording the position of each recording electrode (EETRAK, Enschede, The Netherlands) in relation to 3 points which were first identified on the head of the subjects (nasion–left ear–right ear) and then on a magnetic resonance image. The images were previously obtained with a General Electric MR-Signa[®] Excite[™] HD (Milwaukee, USA) equipped with an 8-channel head coil and using a single-shot gradient-echo EPI (TE=1600 ms, TI=650 ms, TR=7600 ms), with in plane resolution of $1 \times 1 \text{ mm}^2$ and 1 mm-thick slices without gaps between the slices, and a field of view of $25 \times 25 \text{ cm}^2$. The position of the electrodes was then normalized to the Talairach coordinates previously computed for each brain, and the recordings

obtained from real electrodes were replaced by others (virtual electrode) located in the same position of the Talairach space which were computed by a spline-interpolation of all the surrounding electrodes.

The statistical analyses (Statsoft; Tulsa, USA) of the stimulus response were performed by comparing the values obtained in the three experimental conditions at the same time-latency (from 200 ms before to 400 ms after the stimulus presentation; 2 ms time-resolution). Thus, an ANOVA which included data of the three experimental conditions (passive test, motor test and imagery test) was initially performed for each time-point of the event related recording. Due to the high number of comparisons, only time-points showing ANOVA differences ($p < 0.05$) of ten or more consecutive time-points ($> 40 \text{ ms}$) were considered as significant. Then, planned (passive test vs. motor test and passive test vs. imagery test) post-hoc comparisons (two-sided t -test; $p < 0.05$) were performed in the time-points which reached these ANOVA criteria. The aim of this procedure was to prevent the simple action of visual stimuli on MU activity being confused with the MU response to motor or MI tasks, but without losing relevant information about the kinematic behavior of MU response.

3. Results

The Mu rhythm displayed a phase-locked response to visual stimuli with a period of $\approx 100 \text{ ms}$ and a different topographical distribution across the scalp. This increase occurred at the same time as a progressive and persistent decrease of non-phase-locked Mu wave power.

3.1. Phase-locked Mu response (PLr)

Visual stimuli induced a phase-locked Mu-rhythm which began $\approx 50 \text{ ms}$ after the stimulus onset and which lasted for about 150–200 ms (Fig. 1). During the passive test, the PLr was evident in the primary sensorimotor cortex (SMc) but not in the premotor cortex (PMc) and supplementary motor cortex (SpMc) (continuous lines show the mean \pm of standard error of the mean value of PLr of the group, dotted lines indicate the confidence interval which includes 95% of pre-stimulus points). The PLr was marked when stimuli were used for motion planning (data of the active test are shown in blue lines) and not when they were passively observed (black lines). The PLr induced by the active test was noticeable in the electrodes located over the SMc, PMc and SpM-C of both brain sides, and particularly in SMc electrodes of the left-brain side. The imagery test also induced a marked PLr which, with the only exception of the left PMc electrode, was similar to that observed during the motor test.

3.2. Power of phase-locked Mu response (PLr-power)

Data of PLr-power agree with those of PLr. Thus, the PLr-power was greater during active or the imagery test than during the passive test in all the recordings, (Fig. 2; continuous lines show the mean value of PLr of the group). In the few areas where the PLr-power reached statistical values during the passive test (see C2, FCC4h and FC4 in Fig. 2 where dotted black lines at the bottom of each graph show statistical differences between the post-stimulus and pre-stimulus data of passive test), the PLr-power was always shorter in time than the PLr-power observed during the motor or imagery tests. Discontinuous lines at the bottom of each graph in Fig. 2 show statistical differences between the PLr-power of passive test vs. motor test (blue) and passive test vs. imagery test (red). Most the areas showing a statistical PLr-power response to motor test showed a PLr-power response to imagery test, and both were of similar amplitude and duration. The PLr-power response started 50–70 ms and disappeared 150–200 ms after visual stimuli in all cases.

PLr of MU activity

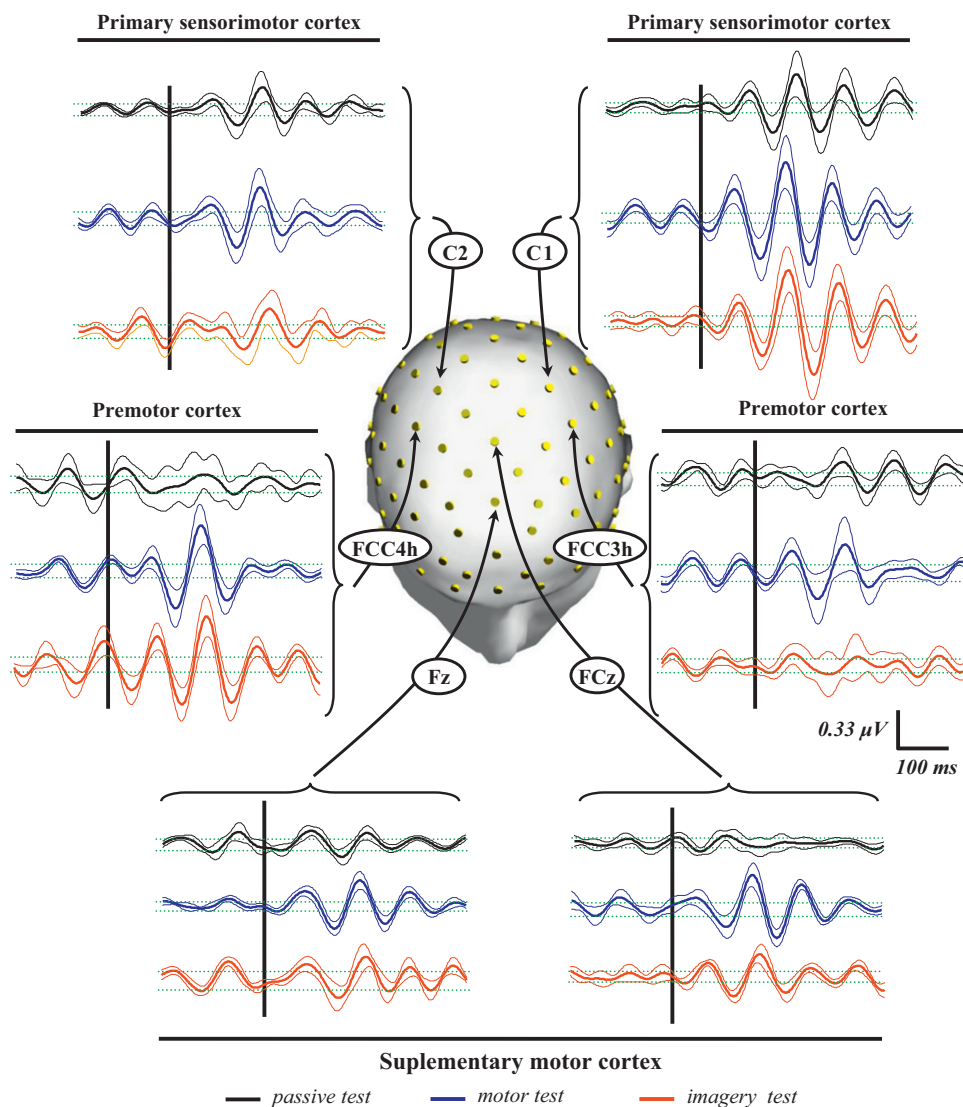


Fig. 1. Phase-locked Mu response (PLr) to visual stimuli (vertical black lines); differences between passive test (horizontal black lines), motor test (blue lines) and imagery test (red lines). Values are mean \pm standard error of the group for representative examples of electrodes located over the sensitive motor-cortex (C1 and C2), pre-motor cortex (FCC3 and FCC4) and supplementary motor cortex (FCz and Fz). Dotted lines indicate the confidence interval which includes 95% of pre-stimulus points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Power of non-phase-locked Mu response (NPLr-power)

The motor test induced a progressive decrease of the NPLr-power which started 100–150 ms after stimuli and persisted during the 300 ms post-stimulus studied (Fig. 3; continuous lines show the mean value of NPLr of the group; blue lines for the motor test and red lines for the imagery test). Discontinuous lines at the top of each graph in Fig. 3 show statistical differences between the NPLr-power of the passive test vs. the motor test (blue) and of the passive test vs. the imagery test (red). The motor test and imagery test showed a similar inhibitory response to stimuli in most electrodes.

4. Discussion

Visual stimuli induced a short-lasting phase-locked Mu-rhythm which was wider and more widespread when they were

used for the motor planning of real or virtual movements. The phase-locked Mu-response was followed by a persistent decrease of the Mu-rhythms which were not phase-locked to stimuli, a response which also was more marked and generalized when stimuli were used for motor planning. PLr and NPLr were similar during motor testing and imagery testing, data suggesting that both tasks activated the Mu rhythms to a similar degree. This congruency between real movements and virtual movements was observed in the electrodes located over the SMC, PMc and SpMc.

4.1. Phase-locked and non-phase-locked Mu-rhythms depend on motor task linked to visual stimuli

In agreement with a recent study (Sabate et al., 2012), visual stimuli induced a double action on the Mu rhythm, inhibiting some of its sub-components (NPLr) and activating others (PLr). The decrease of the Mu rhythm power observed in the NPLr shows that the Mu inhibition generally observed during motion

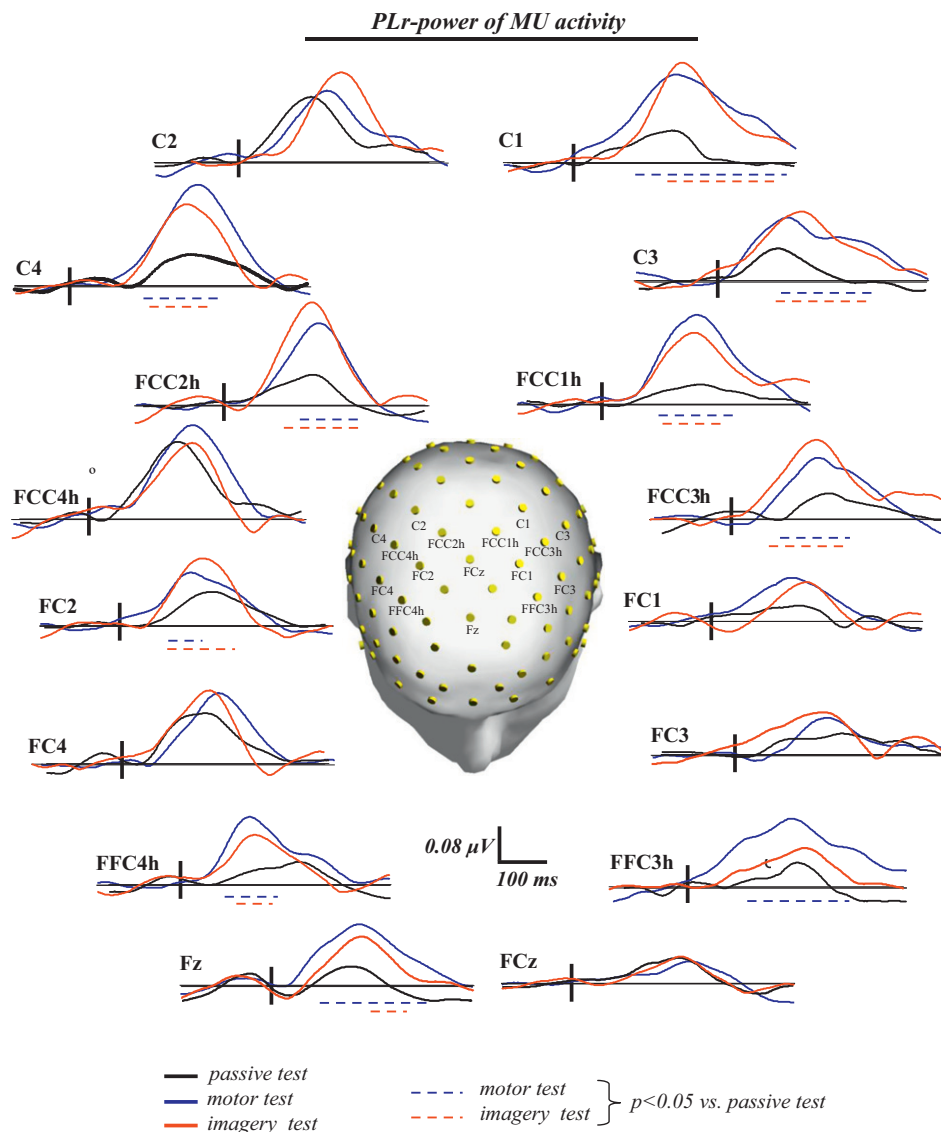


Fig. 2. Power of phase-locked Mu response (PLr-power) to visual stimuli (vertical black lines). Values are the mean of the group for the passive test (black lines), motor test (blue lines) and imagery test (red lines). The discontinuous lines at the bottom of each of the graphs show statistical differences between the passive test and motor test (blue) and between the passive test and imagery test (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Babiloni et al., 1999; Salenius et al., 1997) can also be induced by visual stimuli when they are linked to a motor task. These data agree with previous studies which report a Mu-suppression in subjects observing the behavior of other people (Cheng, Yang, Lin, Lee, & Decety, 2008; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004). The NPLr was more marked when stimuli were used to plan the following behavior than when they were passively observed, suggesting that the visually-induced Mu inhibition is associated to tasks linked to the visual stimulus more than to the stimulus itself.

Along with this Mu inhibition (NPLr), visual stimuli induced a transient activation of a Mu sub-component (PLr) which started soon after the stimuli and disappeared during the progression of the NPLr. This excitatory response was more marked when stimuli were used for planning the subsequent movements than when they were passively watched, thus suggesting that PLr may be enhanced by motor tasks linked to the stimulus presentation. These data agree with previous studies showing a Mu rhythm activation during the execution of movements (Pfurtscheller, 1992; Salmelin & Hari, 1994).

Thus, two opposite Mu rhythm responses were simultaneously induced by the visual-motor task, showing that there are Mu sub-components which can be depressed by a task which simultaneously enhances other sub-components. This segregation could explain the apparent contradictions of previous studies mentioned above. This selective modulation makes the coexistence of a facilitation of the Mu sub-component (PLr) involved in the planning of a particular motor task and an inhibition of other Mu sub-components (NPLr) which could interfere with its computation possible. This possibility agrees with previous data suggesting that neuronal synchrony (Fries, 2005; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Varela, Lachaux, Rodriguez, & Martinerie, 2001) observed during the negative peaks of the cortical waves facilitates information processing (Klimesch, Sauseng, & Hanslmayr, 2007). Thus, both the transient phase-locked Mu-increase (by improving the local interaction of neurons) and the long-lasting non-phase-locked Mu-decrease (by preventing spurious neuronal synchronization associated with other tasks or with cortical regions not involved in the ongoing task) could promote the execution of the visual-motor task studied here.

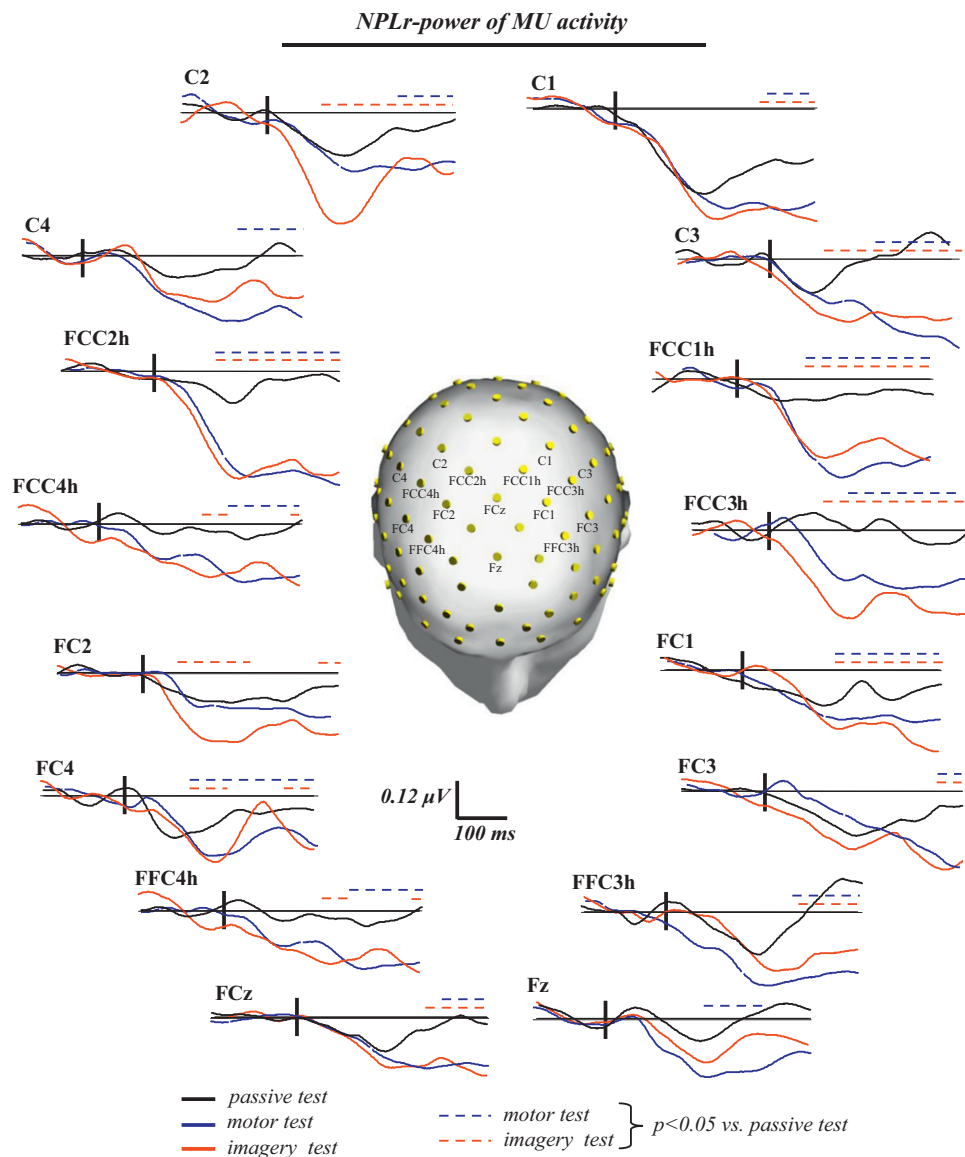


Fig. 3. Power of non-phase-locked Mu response (NPLr-power) to visual stimuli (vertical black lines). Values are the mean of the group for the passive test (black lines), motor test (blue lines) and imagery test (red lines). The discontinuous lines at the top of each graph show statistical differences between the passive test and motor test (blue) and between the passive test and imagery test (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Motor imagery induces phase-locked and non-phase-locked Mu-responses similar to those induced by motor tasks

Motor imagery modified the Mu activity, a finding that, as far as we know, has never been reported. As MI was not accompanied by real movements, it is likely that the Mu-rhythm changes induced by MI may be associated to the non-motor components of the action which are necessary for the movement execution (such as the selection of a motor pattern or the estimation of the probability of reaching the motor goal) (Clark, Tremblay, & Ste-Marie, 2004; Jeannerod, 2001, 2003; Sabate et al., 2004, 2007, 2008; Toni, Thoenissen, & Zilles, 2001), and which are also involved in MI. However, at present one cannot rule out the possibility that a more unspecific task (such as reacting to visual cues by doing “anything” and not necessarily a movement) could be at the basis of MU changes observed here in the motor cortex during both the motor tasks and the MI task. The action of virtual movements on the PLr and NPLr was very similar to that induced

by real movements, suggesting that the Mu wave could perform the same role in both cases. The PLr was observed 50–150 ms after the visual presentation of the instruction for the subsequent real or virtual movement. Thus, the mental task executed during the short time interval where the Mu activity showed the phase-locked response could be associated to the first steps of the visual-motor task. Immediately after the stimulus onset, the arrow stimulus indicating the direction of the finger motion probably activated a mental representation of the goal to be reached before triggering the elaboration of the specific motor pattern needed to reach the identified goal. In any case, neither the execution of movements nor the execution of their MI could be involved in the PLr, which disappeared hundreds of milliseconds before the motion or MI onset.

In a similar way to that observed for real movements, MI induced a simultaneous activation of PLr and NPLr, thus suggesting that while the PLr facilitates the execution of a virtual movement, the NPLr inhibits other imagery tasks able to interfere with the ongoing MI.

4.3. The similarity between real and virtual movements: incorporating Mu rhythm data

All the recordings showing a phase-locked activation of Mu activity during the planning of real movements showed a similar activation during the planning of their MI. The same was observed for the NPLr, which showed similar decreases of the Mu-wave power during the planning of real and virtual movements. These similarities were observed in the SMC, PMc and SpMc, where the amplitude, latency and duration of the PLr and NPLr were similar for the planning of movements and for the planning of their MI. In our opinion, this marked similarity was dependent on the fact that the planning and execution of movements were performed at different times, a fact that occurred when real and virtual tasks were being executed. This time segregation was possible because of the event-related paradigm and the high time-resolution method (EEG) used.

Previous functional magnetic resonance (fMRI) studies have involved the SMC, PMc, and SpMc in both real and virtual movements (Decety, 1996; Gerardin et al., 2000; Grafton et al., 1996; Hanakawa et al., 2003; Lotze et al., 1999; Naito et al., 2002; Porro et al., 1996, 2000; Sirigu et al., 1996; Stephan et al., 1995), but the activation degree of these areas (Gerardin et al., 2000; Hanakawa et al., 2003; Michelon et al., 2006) and the spatial distribution of the activation within each area (Rodriguez et al., 2004) can be partially different in both cases. The time-resolution of fMRI is low (> 1 s) and, even in the case of using an event-related paradigm, fMRI images always include both the movement execution and its previous motor planning. Because MI is not accompanied by real movements, factors such as the proprioceptive stimulation which accompanies the movement execution are not present during MI. On the other hand, the repetitive real movements often used in these studies are planned before the beginning of the motor sequence, and are then executed in an automatic way which does not need new motor plans or conscience supervision. This possibility cannot be used for virtual movements which are necessarily accompanied by their conscious perception (Rodriguez et al., 2009; Sabate et al., 2008). Thus, in these studies the comparison between real and virtual movements is necessarily affected by variables that are more linked to one of them than to the other. A suitable procedure to prevent this fact is to study MI with a high time-resolution method and with an experimental paradigm which separates the time interval used for motor planning and the interval used for the movement (or the MI) execution. Present data suggest that these experimental cautions should be considered when using MI to study the planning strategies of real motion.

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