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Actual and mental motor preparation and execution: a spatiotemporal ERP study

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Abstract Studies evaluating the role of the executive motor system in motor imagery came to a general agreement in favour of the activation of the primary motor area (M1) during imagery, although in reduced proportion as compared to motor execution. It is still unclear whether this difference occurs within the preparation period or the execution period of the movement, or both. In the present study, EEG was used to investigate separately the preparation and the execution periods of overt and covert movements in adults. We designed a paradigm that randomly mixed actual and kinaesthetic imagined trials of an externally paced sequence of finger key presses. Sixty channel event-related potentials were recorded to capture the cerebral activations underlying the preparation for motor execution and motor imagery, as well as cerebral activations implied in motor execution and motor imagery. Classical waveform analysis was combined with data-driven spatiotemporal segmentation analysis. In addition, a LAURA source localization algorithm was applied to functionally define brain related motor areas. Our results showed first that the difference between actual and mental motor acts takes place at the late stage of the preparation period and consists of a quantitative

modulation of the activity of common structures in M1. Second, they showed that primary motor structures are involved to the same extent in the actual or imagined execution of a motor act. These findings reinforce and refine the functional equivalence hypothesis between actual and imagined motor acts.

Keywords Motor preparation · Motor execution · Imagined or actual response · Negative contingent variation · EEG segmentation

Introduction

The traditional information processing view of motor behaviour (Theios 1975) distinguishes between preparatory and executive processes in the sequence of operations leading to a motor response. Studies on monkeys related motor preparation to the primary motor area (M1) (Ashe et al. 1993; Georgopoulos et al. 1989; Tanji and Evarts 1976). In human subjects, several studies (EEG or MEG: Deecke 1987; Deecke et al. 1969; event-related desynchronization in the EEG alpha band: Pfurtscheller 1989; implanted subdural recordings: Neshige et al. 1988) showed that M1 exhibits a contralateral maximal activity in the late preparatory period of a self-paced motor response. This activity follows an important, bilateral activity of the supplementary motor area (SMA). Deiber et al. (1996), in a positron emission tomography study, compared different conditions of motor preparation using a pre-cued reaction time paradigm. They identified a network of cerebral structures involved in the motor preparatory processes including the contralateral frontal and parietal cortices, ipsilateral cerebellum, thalamus and contralateral basal ganglia. Of particular interest, the same neuronal network also turned out to be characteristic of motor execution (Catalan et al. 1998). All these findings are from overt movement studies.

One of the most challenging topics, in the motor field of the cognitive neuroscience domain, is the investigation of the mental imagination of a motor act, namely the mental

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representation of a self performing motor act without overt movement. Several studies tried to evaluate the role of the executive motor system, in particular M1, in motor imagery (MI_m). The earliest positron emission tomography work on this issue failed to show an activation of this area during MI_m (Decéty et al. 1988; Roland et al. 1980). However, these studies suffered from a clear procedural limitation due to the fact that the term ‘motor imagery’ was used as equivalent to visual imagination of a motor act. As noted by Jeannerod (1994), MI_m is not equivalent to visual imagination, this latter process implying a visual mental image and not a kinaesthetic internal representation of the action. *Sensu stricto*, MI_m should definitely be understood as the “(...) conscious mental rehearsal of a motor act without performing any overt movement [and implying] that the subject feels himself executing a given action” (Schnitzler et al. 1997, p. 201).

In this framework, recent functional neuroimaging studies showed an activation of M1 during MI_m by instructing subjects to practice kinaesthetic mental imagery (EEG: Beisteiner et al. 1995; Lang et al. 1996; Naito and Matsumura 1994; Pfürtscheller and Neuper 1997; MEG: Lang et al. 1996; Schnitzler et al. 1997; fMRI: Lotze et al. 1999; Porro et al. 1996, 2000; Roth et al. 1996; PET: Lang et al. 1994). In some of these studies (Lotze et al. 1999; Porro et al. 1996, 2000), this activation was weaker compared to the motor execution (ME_x) condition. To date, there is a general agreement (resulting in the ‘functional equivalence hypothesis’, Jeannerod 2001) in favour of the activation of M1 during MI_m, although in reduced proportion as compared to ME_x.

However, it is still unclear whether the difference of activation intensity in M1 between actual or imagined motor acts occurs within the preparation period or the execution period, or both. The aim of the present event-related potential (ERP) study is to examine this issue. Indeed, the ERP technique provides a direct measure of cognitive processes as they occur and thus represents a powerful technique with which to track the time course of the functional processes involved. A first set of ERP data has been provided on this question by Cunnington et al. (1996), who studied motor cerebral potentials associated with the preparation of an actual or imagined externally paced motor sequence. The level of cerebral activity (maximal peak amplitude of the late potential preceding the response—contingent negative variation, CNV) appeared higher in the preparation of an actual motor response than in the preparation for imagining movement. The authors concluded that the two types of motor responses involve similar preparatory processes, most likely related to the SMA. More recently, Jankelowitz and Colebatch (2002) provided comparable results and interpretation. Altogether, these data suggest the involvement of similar processes between the preparation for motor execution and for motor imagination. However, both paradigms used in these ERP studies systematically involved several repetitions of the same type of response within a time period (fixed-blocks design), which does not favour a careful and vivid mental motor realization. In the

same way, no attempt was made in order to control the subject’s engagement in this covert activity. In addition, these studies focused only on the preparation period, and, hence, they cannot provide a direct measure of the cerebral activity underlying the execution processes of covert and overt movements, and its relationship with the preparation period. As a consequence, the question of the origin of the weaker activity observed for M1 in the MI_m compared to the ME_x condition cannot be elucidated by these results.

To avoid these methodological limitations, the temporal resolution of the EEG was used here to investigate separately the preparation and the execution periods of overt or covert finger movements in a paradigm randomly mixing actual and kinaesthetic imagined trials. During the MI_m condition, some intermittent verification trials were randomly introduced in order to control that imagined finger movement sequences were correctly realized. The task consisted of the production of a simple externally paced sequence of key presses involving three fingers of the dominant hand. Before each sequence, a visual signal instructed the subjects on the way, actual or imagined, they must produce their response. It then became possible to compare, in the same experimental design, the cerebral activations implied in the preparation to motor execution (P-ME_x) and the preparation to motor imagery (P-MI_m), as well as to compare the cerebral activations implied in motor execution (ME_x) and motor imagery (MI_m).

Methods

Subjects

Ten healthy, right-handed subjects (five men, aged 21–43 years, laterality index >0.6 according to Bryden’s questionnaire, 1977), students or research assistants, were tested. They did not present any history of neurological or psychiatric disease and took no medication at the time of the recording. All subjects gave their written informed consent and the protocol was approved by the ethics committee of the University of Geneva (Faculty of Psychology and Educational Sciences).

Stimuli and procedure

Subjects were seated in front of a 17” screen located at a distance of 1.20 m. The task consisted of a sequence of finger key presses. The subject’s right forearm was placed on an inclined plane (the side of the hand on the upside) to avoid tactile stimulations that could occur during the motor imagery task from the contact of the fingers with the response keys placed at the front.

For the MI_m condition, subjects were instructed to imagine fingers’ movements in a kinaesthetic way, namely to try to feel the sensations that are usually felt in the muscle-tendon complexes when actually executing the movement. Just before the experimental session, the participants were extensively trained to make a kinaes-

thetic image of the activity of their fingers in an imagined thumb-fingers opposition repeated sequence.

1. *Preparation to execution (P-MEx)/Preparation to imagination (P-MIm)*: A preparation period of 1 s was determined by the interval between the onset of a visual preparatory stimulus (PS) and the onset of the first auditory stimulus (S_1), which acts as a go signal for the execution/imagination period (Fig. 1). The PS of 900 ms specifying the mode of realization of the movement (circle = execution; triangle = imagination) were presented at random. The figures were displayed in white on a black background with an approximate size of 1° of visual angle.
2. *Motor execution (MEx)/Motor imagination (MIm)*: The task consisted of the execution/imagination of a fixed sequence of finger presses on response keys. The movements (right hand forefinger—middle finger—third finger) were externally paced by an auditory signal (500 Hz, 80 dB, 500 ms in duration) with an interstimulus interval (ISI) that randomly varied between 1.6 and 2 s; the sequence was repeated three times in a row during a trial (see Fig. 1). A central cross was present during the entire experiment; subjects were instructed to continuously fixate this cross. To maximize attention and compliance with the imagery task, we elaborated verification trials in which subjects, after having heard a sound of a higher frequency (1,000 Hz, 80 dB, 500 ms in duration) that could appear at any point of the finger sequence, had to start to actually execute the movement with the finger following the one they just used for the imagery task. Reaction times in the motor execution period were recorded through a response box with three keys (Neuroscan Inc., Herndon, VA, USA).

Some training trials (3 MEx trials, 1 MIm trial, and 2 MIm verification trials presented in random order) were first administered to the subjects. This training session helped them to become familiar with the task requirements

and to learn the association between the preparatory stimulus and the corresponding mode of realization of the movement.

The experiment comprised 80 MEx and 80 MIm trials, as well as 20 MIm verification trials that were not included in the analysis. The events were equally and randomly distributed within five blocks (16 MEx, 16 MIm and 4 MIm verification trials; total number of events = 36 per block). The order of the blocks was counterbalanced between subjects to control for order effects.

EEG recordings and analysis

EEG was continuously recorded over experimental blocks from 60 Ag/AgCl electrodes mounted on an elastic cap (Easy-Cap, FMS, Munich, Germany) according to the revision of the 10/20 system (American Electroencephalographic Society 1991). The data were digitized at a sampling rate of 1,000 Hz and the band-pass filtering was fixed to 0.15–70 Hz; the impedance of all electrodes was kept under 5 k Ω . Linked ear-lobe electrodes served as reference. A bipolar EOG monitored vertical eye movements. The Neuroscan software (Neuroscan Inc., Herndon, VA, USA) was used for the recording and analysis of the EEG data. EEG signals were corrected for ocular artefacts using an algorithm implemented in the software. They were baseline corrected and band-pass filtered (1–30 Hz, 24 dB/oct). Sweeps with an amplitude exceeding $\pm 40 \mu\text{V}$ in any of the scalp channels were eliminated (on average, approximately 65% of the trials, corresponding to 52 events per condition, were kept for each subject). For the remaining valid trials, and for each subject, the recorded electrophysiological signal was separately averaged across all the electrodes and experimental conditions, resulting in individual ERPs for each condition. Then, ERP signals were averaged across all the subjects in their respective conditions, resulting in the grand mean average per condition. For each grand-mean average separately, the

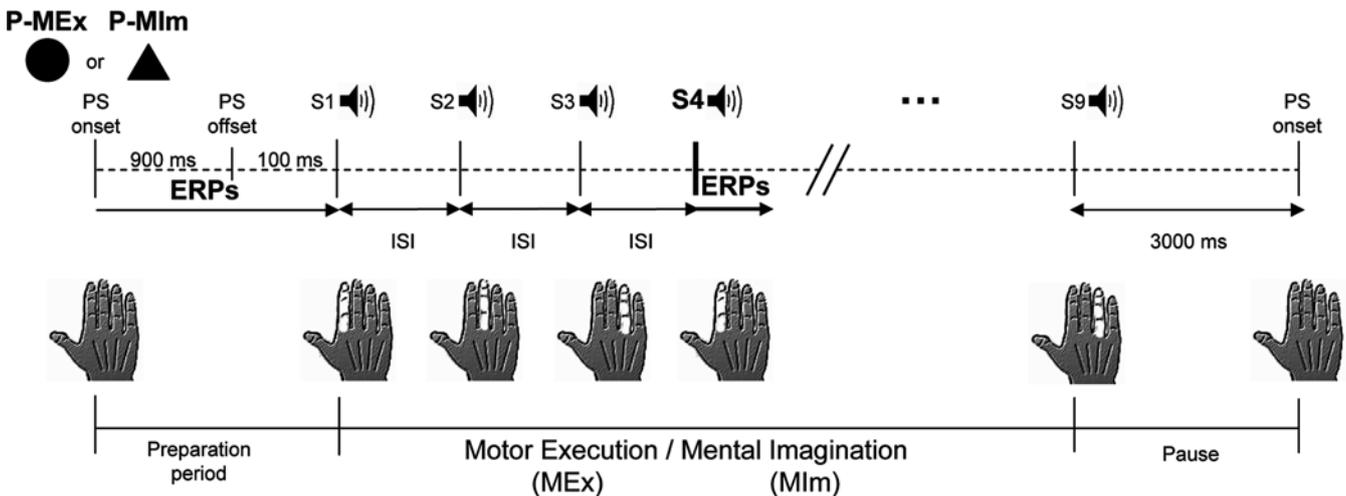


Fig. 1 Experimental paradigm (*P-MEx* preparation to execution, *P-MIm* preparation to imagination, *PS* preparatory signal, S_n auditory stimuli, *ISI* interstimuli interval, randomly varying between 1,600

and 2,000 ms). For the MEx and MIm periods, the analyses were restricted to S_4 (forefinger response, see text)

average reference signal was calculated and obtained off-line by the sum of the activity in all recorded channels divided by the number of channels. Finally, grand-mean ERPs were rescaled against their respective average reference signal.

Due to the experimental design, separate analyses were conducted for the preparation and the execution period.

Preparation period

Data were subjected to two independent analysis procedures consisting of: (1) ERP waveform analysis and (2) analysis of ERP map topography.

First, EEG data were analysed by a waveform analysis of the contingent negative variation (CNV), traditionally associated with the processes preceding motor execution in delayed reaction time paradigm (Walter et al. 1964). Separate ERPs time-locked to the PS onset were obtained for P-MEx and P-MIm over the 1-s preparation period; the baseline correction was set to the 200-ms interval before PS onset. The waveform analysis of the CNV was conducted in both conditions with a repeated measures ANOVA on the mean amplitude of the last 500 ms on electrodes C3, CZ, C4 (where maximum CNV signals are recorded, cf. Bonnet et al. 1998; Jankelowitz and Colebatch 2002).

Second, ERP map topographies were subjected to spatiotemporal analysis (Lehmann and Skrandeis 1980; Pascual-Marqui et al. 1995), aiming to objectively define stable surface ERP topographies (segments of stable maps) and the time intervals where they rapidly change from one stable configuration into another (segment borders). This procedure is based on findings showing that surface ERP map topographies are not randomly distributed over time, but are rather composed of a sequence of dominant stable scalp topographies (segments) (Lehmann 1987; Michel et al. 1999a), each presumably reflecting different functional stages of information processing at the brain level, the so called *functional microstates* (Brandeis and Lehmann 1986; Lehmann and Skrandeis 1980; Michel et al. 1992; Pascual-Marqui et al. 1995). The map strength over time is represented by the global field power (GFP), which is the spatial standard deviation of the average reference maps' potential distribution, which is mathematically expressed as:

$$\text{GFP} = \sqrt{\frac{\sum_{i=1}^n (x_i - \bar{x})^2}{n}}$$

where \bar{x} represents the average reference, which is $\frac{\sum_{i=1}^n x_i}{n}$ where n = number of electrodes, x_i = voltage at electrode i .

The GFP values are sequentially calculated for each time point over time, and usually periods of map stability

are represented by high values of the GFP. Spatiotemporal segment maps were defined in the grand-mean ERP map series using a clustering procedure that statistically determines, with a cross-validation criterion, the optimal number of segments and their respective time of occurrence (Pascual-Marqui et al. 1995). This technique has been successfully applied to the study of cognitive (Caldara et al. 2003, 2004; Khateb et al. 2000; Michel et al. 1999b; Pegna et al. 1997), sensory (Ducommun et al. 2002) and motor processes (Thut et al. 1999, 2000). This analysis was carried out for P-MEx and P-MIm separately (Cartool software, D. Brunet, HUG, Geneva, Switzerland).

Third, to search for specific processes, i.e. processes present or dominant in one condition when compared to the other, segments of both conditions P-MEx and P-MIm were compared by means of a fitting procedure applied to individual data. This procedure consisted of calculating for each subject the spatial correlation coefficients between a given segment map and the successive ERP maps of each condition in the corresponding time intervals (e.g. Ducommun et al. 2002; for a review, see Michel et al. 2001). This analysis was conducted in order to assess how well a given segment map explains a given condition. The goodness of fit, i.e. the variance explained by this segment in a defined condition, was expressed by the percentage of global explained variance index (GeV). This parameter equals the sum of the explained variances over the time windows of interest, weighted by the strength of the map at each moment in time. In order to identify which maps, if any, distinguish the two conditions, a repeated measures ANOVA with factors Conditions and Maps was calculated on the GeV data. A significant statistical difference would indicate that one condition is significantly better explained by one given map than another; as a consequence, this map is specific to this condition.

Execution period

Stimulus-locked waveform analyses are not appropriate to investigate MEx and MIm conditions. Indeed, any possible difference of amplitude between motor execution and motor imagery could be due to a "latency jitter" in motor-related components (Picton et al. 2000) caused by the fact that people are responding at different times. When response is overt, this effect can be neutralized by using a response-locked waveform analysis, analysis that permits the identification of the best motor activations related to the execution of the movement. Then, for this precise stage of motor execution, a time window and its related electrical scalp topography can be objectively defined by means of the spatiotemporal segmentation analysis. The map topography occurring in this particular time period in motor execution, encapsulating the motor potential, will be referred to as the motor map throughout the article. Finally, by using the fitting procedure, it became possible to assess to what extent this motor map is represented in MEx and MIm conditions respectively.

Concretely, the analysis for the execution period consisted first of a segmentation analysis based on the response-locked signal of the MEx condition. Given its high temporal stability (see “Behavioural results”), movement-related potentials were averaged on the fourth response (S4 in Fig. 1). The period considered was -200 to 400 ms (0 ms = response) with a baseline correction period set -700 to -500 ms before the response. Second, we carried out a fitting of the identified maps in the stimulus-locked signal of MEx and MIm (ERPs averaged separately for MEx and MIm on the S4 auditory stimulus from 0 to 400 ms; baseline period: -200 to 0 ms); this was followed by a two-way repeated measures ANOVA on the GeV values, with Conditions and Maps as factors.

In the same way, the motor map was also fitted backwards into the two types of preparation periods in order to assess the respective involvement of primary motor processes in preparation for actual and imagined movements. A two-tailed paired t -test contrasting conditions was then conducted on the GeV values resulting from this fitting.

Finally, the ERPs map fitting procedure also provides information about when in time a given segment map is best represented (time point of Best explained Variance—BeV). Indeed, this index may be considered as a peak value in terms of the electrical scalp topography distribution and was used to reveal differences in timing, i.e. latencies. These values were compared between conditions using t -tests for the identified motor map.

Source localization

A three-dimensional distributed linear inverse solution called LAURA was used to estimate the brain activity underlying the segment map topography. The LAURA algorithm calculates the local autoregressive average with coefficients that depend on the distances between solution points. This incorporates the known biophysical laws regarding the spatial attenuation of the source strength (Grave de Peralta et al. 2001, 2004; Michel et al. 2001). The lead field applied to this model was calculated on a realistic head model with 4,024 solution points, equally

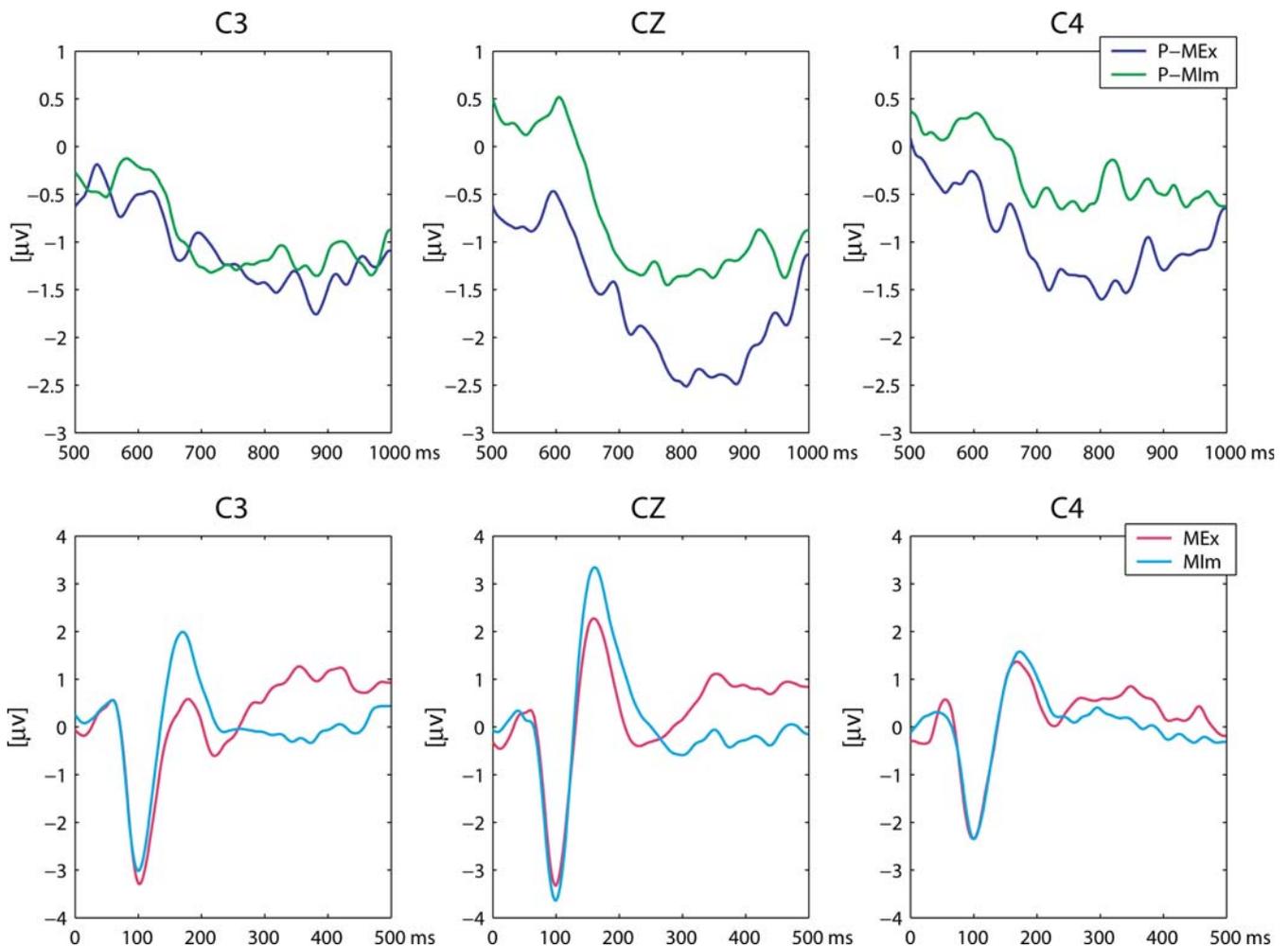


Fig. 2 Average reference ERP waveforms recorded over electrodes C3, CZ and C4 for the P-MEx and P-MIm on the top. Note that CNV was larger for the hemisphere ipsilateral to the finger

movement. On the bottom are reported for illustrative purposes the average reference ERP waveforms for the MEx and MIm conditions. Positive values are up

distributed in the grey matter of the average brain provided by the Montreal Neurological Institute (MNI, Montreal, Canada). Several simulation and application studies showed that this localization procedure reveals meaningful estimates of the 3D distribution of the intracerebral sources (e.g. Itier and Taylor 2004; Michel et al. 2001; Murray et al. 2004; Ortigue et al. 2004; Schnider 2003).

EMG

In order to verify that the participants correctly adapted to the tasks, EMG activity of the right flexor digitorum communis was recorded for all the conditions on the right flexor digitorum communis using bipolar surface derivation. EMG was transformed in absolute value and analysed. For the preparation period the last 500 ms was taken into account, and an early (500–750 ms) and a later pre-stimulus window (750–1,000 ms) was defined. For the

Execution/Imagination period, an early (0–250 ms) and a later poststimulus window (250–500 ms) was defined. Separate repeated measures ANOVAs on mean values of EMG signals, with the Window and the Condition as factors, were used to assess significant differences in the preparation and the Execution/Imagination periods.

Results

Preparation period

Waveform analysis

The waveform analysis of the CNV shows maximal values of the signal on electrodes C3, CZ and C4 (see Fig. 2, top part). The Conditions (2) × Electrodes (3) repeated measures ANOVA performed on the data during the late CNV (500–1,000 ms) indicated that only the factor

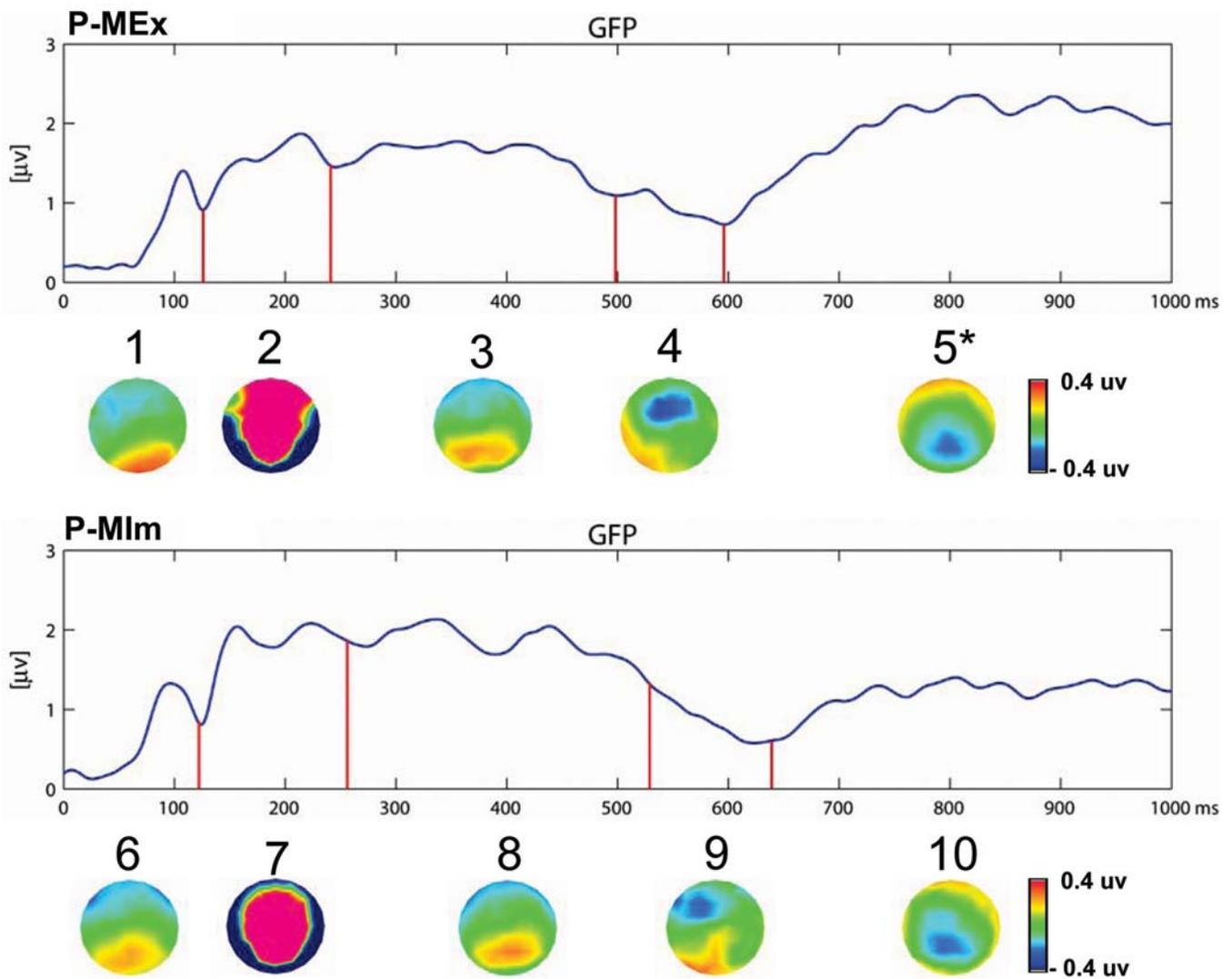


Fig. 3 Global field power (*GFP*), segmentation maps of P-MEx and P-Mim, and corresponding scalp topographies. The maps are viewed from the top, with the nose up and the left ear left. The GFP

represents the spatial standard deviation of the average reference maps' potential distribution. The *star* indicates a significant difference for map 5 between the two experimental conditions

conditions is significant, the mean amplitude of the signal being greater for P-MEx than for P-MIm ($F_{(1,9)}=13.51, p=.005$).

Segmentation analysis

The segmentation analysis returned five different stable map configurations in each condition respectively (P-MEx: Fig. 3, maps 1–5; P-MIm: Fig. 3, maps 6–10). The values of the GeV of each map were then calculated. The repeated measures ANOVA computed on GeV with the design Conditions (2) \times Maps (10) indicated a significant effect compared to the factor Maps ($F_{(9)}=3.69; p=.001$) and an interaction effect ($F_{(1,9)}=12.91; p<.001$, see Fig. 4). The GeV value associated with map 5 is significantly different across the conditions as confirmed by post hoc contrasts ($p=.016$). Maps 1, 2, 3 and 4, identified in P-MEx segmentation, appear as representative in the P-MIm condition. Reciprocally, maps 6, 7, 8, 9 and 10, resulting from P-MIm segmentation, are also representative of P-MEx. The differences between P-MEx and P-MIm revealed by the segmentation analysis take place during the late phase of the preparation period (map 5), in accordance with the CNV results.

Motor execution/Motor imagery period

Behavioural results

The analyses were processed on the responses to the fourth auditory stimulus which presented the highest temporal stability (mean reaction time: 233 ± 8 ms, i.e. a coefficient of variation of 3.4%).

Response-locked ERP in MEx

The segmentation analysis revealed four stable map configurations (Fig. 5). On the basis of previous data in

the literature (Deecke et al. 1976), map segment 2 can be considered as reflecting the presence of the motor potential. Additional objective arguments in favour of this interpretation are: (a) the temporal location starting around the response onset and ending 80 ms after, (b) its temporal correspondence with a burst of EMG activity and (c) its spatial location on the central region of the left hemisphere as located with the algorithm LAURA (see Fig. 5); the LAURA inverse solution identified the maximum activity within the Broadman area 4 on the pre-central gyrus with the Talairach coordinates $x=-41, y=-10, z=44$.

Stimulus-locked ERP

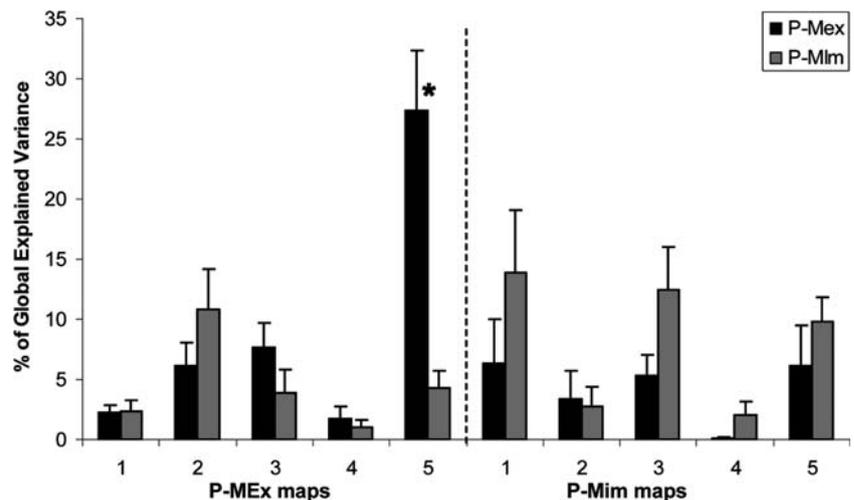
The maps identified by the segmentation analysis in the response-locked ERP in MEx were fitted in the MEx and MIm conditions respectively. The results are reported in Table 1.

A Conditions (2) \times Maps (4) repeated measures ANOVA on GeV values obtained with the fitting procedure of the four response-locked MEx maps in the stimulus-locked signal revealed only a significant effect for the factor Maps ($F_{(3)}=7.825; p=.001$). Furthermore, the time points of the BeV of map 2 in MEx (mean = 200 ms) and in MIm (mean = 222 ms) did not differ (t -test, $t=.30, p=.076$). Likewise, ERP waveforms in the central part of the scalp were not different between these conditions (see Fig. 2, bottom part). To sum up, the

Table 1 Globally explained variance indexes (%) and their standard errors (\pm) resulting from the fitting procedure of the four maps identified in the Response-locked ERP MEx condition, within the MEx and MIm conditions. Only a significant effect for the maps as a factor was observed

	Maps			
	1	2	3	4
MEx	6.90 (2.03)	12.96 (2.51)	6.00 (2.44)	14.80 (2.66)
MIm	8.04 (1.96)	13.30 (1.98)	1.80 (0.83)	19.88 (2.41)

Fig. 4 Mean and standard error of GeV for each map in the P-MEx and P-MIm conditions (significant differences between conditions: * $p<.05$)



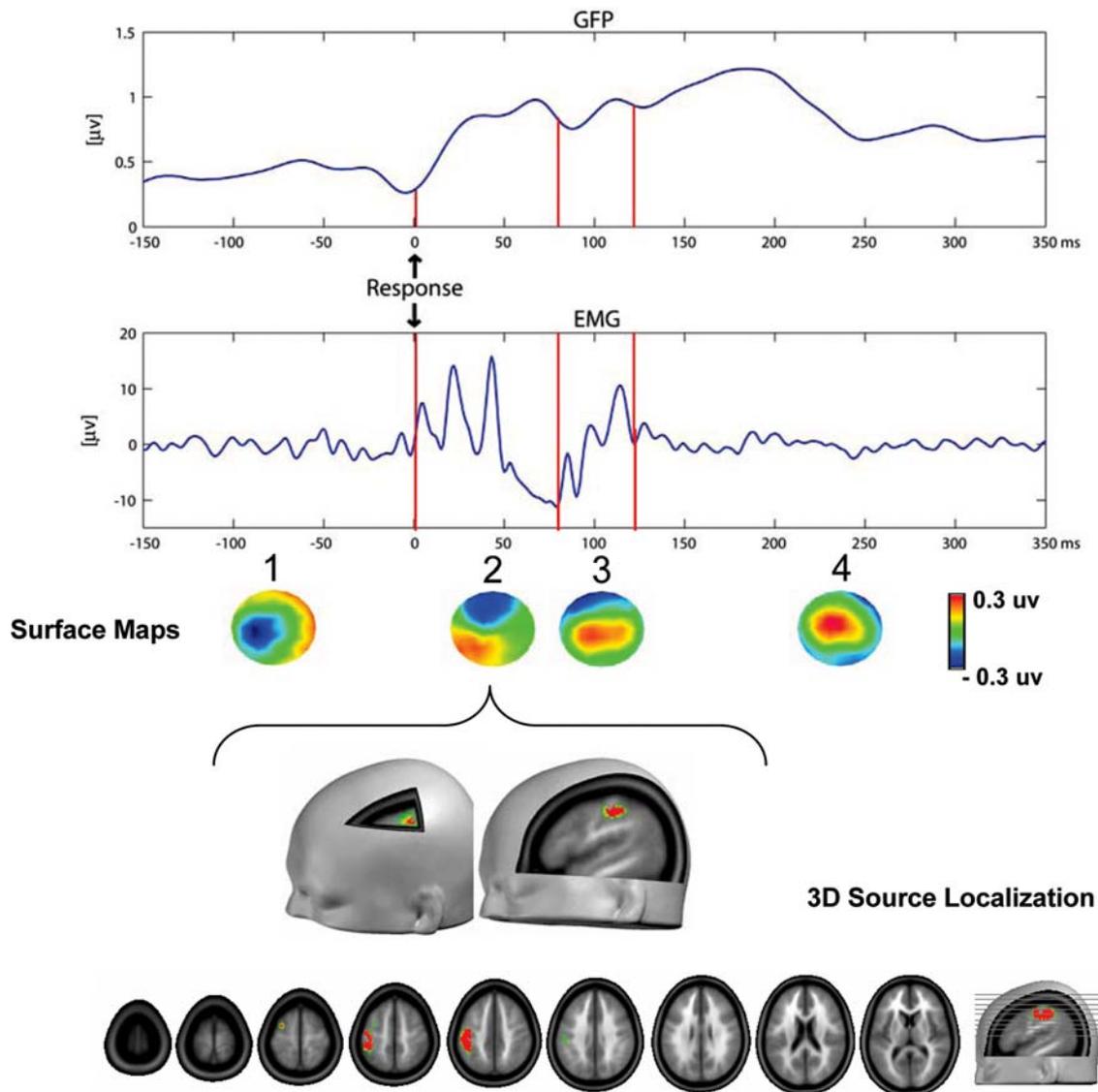


Fig. 5 From the top: *GFP*, mean EMG of the right flexor digitorum communis, the four segmentation maps identified in the response-locked MEx and their respective topographies. The maps are viewed from the top, with the nose up and the left ear left. LAURA inverse

motor map was equally present in both conditions and occurred in a similar time period.

Motor map in preparatory period

Lastly, the motor map was fitted into the preparatory period (between 500 and 1,000 ms) for P-MEx and P-MIm. The *t*-test conducted on the GeV data resulting from this fitting revealed a significant effect ($t_{(9)}=2.308$, $p=.023$) according to condition: GeV was higher in the preparation of effective as compared to imagined execution (22% and 17%, respectively).

solution of the identified motor component (map 2); maximum corresponds to Brodmann area 4 on the pre-central gyrus with the Talairach coordinates $x=-41$, $y=-10$, $z=44$

EMG activity

EMG activity for all the conditions is reported in Fig. 6. Separate repeated measures ANOVAs on mean values of EMG signals, with Window and Condition as factors, were used to assess significant differences in the preparation and the Execution/Imagination periods. Low residual muscular activities were observed during P-MEm and P-MIm, and no significant differences were found between these conditions. In the Execution/Imagination period the repeated measures ANOVA revealed only a significant effect ($F_{(1,9)}=53.792$, $p=.00004$) for the Condition factor, the EMG activity was greater in the MEx ($m=2.24 \mu\text{v}$) compared to the MIm ($m=0.39 \mu\text{v}$) condition, and post hoc *t*-tests significantly identified this effect in both time windows ($p<.001$). Altogether, these results show that the participants correctly adapt to task demands.

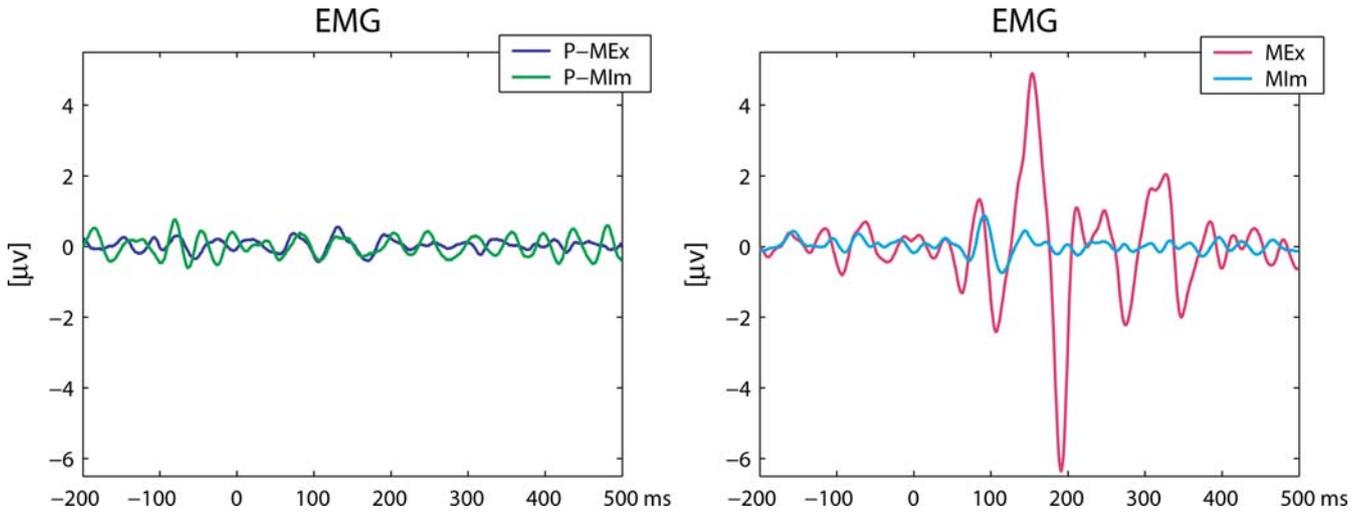


Fig. 6 EMG activity for the P-MEx and P-MIm on the left; MEx and MIm, on the right. Note, as expected, the presence of an EMG burst uniquely in the MEx condition

Discussion

Two main findings were established in the present ERP study: (1) motor imagery and motor execution differ in the late stages of the preparatory period, and (2) motor imagery and motor execution are characterized by the presence of motor maps to the same extent in the execution periods.

Preparation

Direct evidence for cerebral activity preceding a motor response comes from single-cell studies in monkeys (Alexander and Crutcher 1990) and intracranial recordings in humans (Ikeda et al. 1992; Neshige et al. 1988). This activity, generally considered to reflect processes of movement preparation, is described in these studies as bilaterally symmetrical. The waveform analysis on our data showed a difference of signal amplitude between P-MEx and P-MIm on the CNV, the activation being more important during P-MEx, which is in line with previous results (Bonnet et al. 1998; Cunnington et al. 1996; Jankelowitz and Colebatch 2002). The difference between P-MEx and P-MIm is marked during the last 500 ms prior to the go signal. This finding suggests a recruitment of similar neural processes in the P-MIm and P-MEx conditions except in the final stage period related to the execution of the movement.

Segmentation analysis refined this result and also demonstrated the presence of differences between the two types of preparation. One map differed significantly between P-MEx and P-MIm, and was more representative of P-MEx. This observation confirms that a functional difference is present in the process involved when a subject prepares to execute or prepares to imagine a motor act, and that this difference is temporally located at the end of the preparation period. fMRI studies showing reduced activation in M1 during MIm (Lotze et al. 1999; Porro et

al. 1996, 2000; Roth et al. 1996) lead to the assumption that the difference, located in our data at the preparation level, concerns M1. This assumption is supported by the results of the fitting procedure of the motor map into the preparatory period: the motor map was significantly better accounted for in the P-MEx than in the P-MIm condition. This result suggests that the functional difference between the preparatory periods of each condition is restricted to primary motor processes. Interestingly, as expected, weak EMG activity was present to the same extent in both conditions. This observation demonstrates that subjects adapted to the task and indicates that the observed differences cannot be related to a real execution of a movement.

Concluding on this point, our data suggest that the origin of the functional difference between an actual or a mental motor act would initially be situated in the late stages of the preparation level and mainly consists of quantitative modulations of the activity of primary motor structures. This conclusion is in line with Cunnington et al.'s results (1996).

Execution

A map corresponding to the motor component of the response was identified in the response-locked signal of the MEx condition. In agreement with recent fMRI data (Lotze et al. 1999; Porro et al. 1996, 2000; Roth et al. 1996), the LAURA inverse solution identified the activations of this scalp topography in the Talairach coordinates corresponding to the left M1 area.

As showed by the segmentation analysis, the motor map was explained to the same extent in the motor imagery and execution conditions, indicating a comparable activation of this brain structure on both conditions. It is worth noting that this similar pattern of activity occurs despite an expected difference in the EMG activity between the conditions (an EMG burst was observed for the MEx

condition), demonstrating independence between the EMG signal and the activity in M1. The presence of a comparable amount of activity in M1 in MEx and MIm conditions is not in line with fMRI studies that showed a weaker activation of M1 during MIm (Lotze et al. 1999; Porro et al. 1996, 2000). The reasons for such a discrepancy remain unclear. Some procedural aspects differentiate these studies from the present one. First, they did not separate the preparation and execution periods. Second, the task requirements and the procedure adopted in our experiment favoured the involvement of kinaesthetic mental imagery. This point was not specified by Lotze et al. (1999). Now, it is well known that, in the absence of explicit instructions, the preferred mode of mental imagery in adult subjects is visual (Hall and Martin 1995). However, Porro et al. (1996, 2000) explicitly required from their subjects, during motor imagery, that they “imagine (...) feeling the sensations associated with finger-tapping, while keeping the hand still” (Porro et al. 1996, p. 7,689). The only noticeable difference with the procedure used in our study is the introduction of verification trials in the present experiment. It cannot be excluded that the random introduction of these trials, amongst the experimental trials, could have influenced the subjects to adopt a strategy of imagery favouring a high level of activation in primary motor structures. As a consequence, the absence of differences between the amount of variance explained by the motor map in motor imagery and motor execution might be explained by the procedural choices adopted in the present study.

Conclusion

The realization of actual and mental motor acts is differentiated by a modulation of the activity within the same neuronal network, which takes place at the late stages of the preparation period. This network includes primary motor areas in the execution, actual or imagined, of a movement. These findings provide supplementary evidence in favour of the functional equivalence hypothesis and suggest that common structures, including M1, are necessary in the actual or kinaesthetically imagined execution of a motor act.

References

- Alexander GA, Crutcher MD (1990) Preparation for movement: neural representations of intended direction in three motor areas of the monkey. *J Neurophysiol* 64:133–162
- American Electroencephalographic Society (1991) Guidelines for standard electrode position nomenclature. *J Clin Neurophysiol* 79:227–240
- Ashe J, Taira M, Smyrns N, Pellizzer G, Georgopoulos T, Lurito, JT, Georgopoulos AP (1993) Motor cortical activity preceding a memorized movement trajectory with an orthogonal bend. *Exp Brain Res* 95:118–130
- Beisteiner R, Höllinger P, Lindinger G, Lang W, Berthoz A (1995) Mental representations of movements. Brain potentials associated with imagination of hand movements. *Electroencephalogr Clin Neurophysiol* 96:183–193
- Bonnet M, Chiambretto M, Decéty J, Vidal F (1998) Laplacian ERPs for preparation to imagine a learned motor sequence. *Cahiers de Psychologie Cognitive/Curr Psychol Cogn* 17(4–5):685–698
- Brandeis D, Lehmann D (1986) Event-related potentials of the brain and cognitive processes: Approaches and applications. *Neuropsychologia* 24:151–168
- Bryden MP (1977) Measuring handedness with questionnaires. *Neuropsychol* 15:617–624
- Caldara R, Thut G, Servoir P, Michel CM, Bovet P, Renault B (2003). Face versus non-face object perception and the ‘other-race’ effect: a spatio-temporal event-related potential study. *Clin Neurophysiol* 114:515–528
- Caldara R, Rossion B, Bovet P, Hauert CA (2004) Event-related potentials and time course of the ‘other-race’ face classification advantage. *NeuroReport* 15:905–910
- Catalan MJ, Honda M, Weeks RA, Cohen LG, Hallett M (1998) The functional neuroanatomy of simple and complex finger movements: a PET study. *Brain* 121:253–264
- Cunnington R, Iansak R, Bradshaw JL, Phillips JG (1996) Movement-related potentials associated with movement preparation and motor imagery. *Exp Brain Res* 111:429–436
- Decéty J, Philippon B, Ingvar DH (1988) rCBF landscapes during motor performance and motor ideation of a graphic gesture. *Eur Arch Psychiat Neurol Sci* 238:33–38
- Deecke L (1987) Bereitschaftspotential as an indicator of movement preparation in supplementary motor area and motor cortex. *Ciba Found Symp* 132:231–250
- Deecke L, Scheid P, Kornhuber HH (1969) Distribution of readiness potential, premotion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Exp Brain Res* 7:158–168
- Deecke L, Grözinger B, Kornhuber HH (1976) Voluntary finger movement in man: cerebral potentials and theory. *Biol Cybern* 23:99–119
- Deiber MP, Ibanez V, Sadato N, Hallett M (1996) Cerebral structures participating in motor preparation in humans: a positron emission tomography study. *J Neurophysiol* 75(1):233–247
- Ducommun CY, Murray MM, Thut G, Bellmann A, Viaud-Delmon I, Clarke S, Michel CM (2002) Segregated processing of auditory motion and auditory location: an ERP mapping study. *Neuroimage* 16(1):76–88
- Georgopoulos AP, Kalaska J, Caminiti R, Massey J (1982) On the relations between the direction of two-directional arm movements and cell discharge in primate motor cortex. *J Neurosci* 2:1527–1537
- Georgopoulos AP, Crutcher MD, Schwartz AB (1989) Cognitive spatial-motor processes. 3. Motor cortical prediction of movement direction during an instructed delay period. *Exp Brain Res* 75:183–194
- Grave de Peralta R, Gonzalez S, Lantz G, Michel CM, Landis T (2001) Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations. *Brain Topogr* 14:131–137
- Grave de Peralta R, Murray MM, Michel CM, Martuzzi R, Gonzalez Andino S (2004) Electrical neuroimaging based on biophysical constraints. *Neuroimage* 21:527–539.
- Hall CR, Martin KA (1995) Measuring movement imagery abilities: a revision of the Movement Imagery Questionnaire. *Journal of Mental Imag* 21(1&2): 143–154
- Ikeda A, Luders HO, Burgess RC, Shibasaki H (1992) Movement-related potentials recorded from supplementary motor area and primary motor area: role of supplementary motor area in voluntary movements. *Brain* 115:1017–1043
- Itier RJ, Taylor MJ (2004) Source analysis of the N170 to faces and objects. *Neuroreport* 15:1261–1265

- Jankelowitz SK, Colebatch JG (2002) Movement-related potentials associated with self-paced, cued and imagined arm movements. *Exp Brain Res* 147:98–107
- Jeannerod M (1994) The representing brain: neural correlates of motor intention and imagery. *Behav Brain Sci* 17(2):187–245
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14:S103–109
- Khateb A, Michel CM, Pegna AJ, Landis T, Annoni JM (2000) New insights into the Stroop effect: a spatio-temporal analysis of electric brain activity. *Neuroreport* 11(9):1849–1855
- Lang W, Petit L, Höllinger P, Pietrzyk U, Tzourio N, Mazoyer B, Berthoz A (1994) A position emission tomography study of oculomotor imagery. *Neuroreport* 5:921–924
- Lang W, Cheyne D, Höllinger P, Gerschlagel W, Lindinger G (1996) Electric and magnetic fields of the brain accompanying internal simulation of movement. *Brain Res Cogn Brain Res* 3:125–129
- Lehmann D (1987) Principles of spatial analysis. In: Gevins AS, Remond A (eds) *Handbook of Electroencephalography and Clinical Neurophysiology, Methods of analysis of brain electrical and magnetic signals*, vol. 1. Elsevier, Amsterdam, pp 309–354
- Lehmann D, Skrandeis W (1980) Reference-free identification of components of checkerboard multichannel potential fields. *Electroenceph Clin Neurophysiol* 48:609–621
- Lotze M, Montoya P, Erb M, Hülsmann E, Flor H, Klose U, Birbaumer N, Grodd W (1999) Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *J Cogn Neurosci* 11(5):491–501
- Michel CM, Henggeler B, Lehmann D (1992) 42-channel potential map series to visual contrast and stereo stimuli: perceptual and cognitive event-related segments. *Int J Psychophysiol* 12:133–145
- Michel CM, Grave de Peralta R, Lantz G, Gonzalez Andino S, Spinelli L, Blanke O, Landis T, Seeck M (1999a) Spatiotemporal EEG analysis and distributed source estimation in presurgical epilepsy evaluation. *J Clin Neurophysiol* 16:239–266
- Michel CM, Seeck M, Landis T (1999b) Spatiotemporal dynamics of human cognition. *News Physiol Sci* 14:206–214
- Michel CM, Thut G, Morand S, Khateb A, Pegna AJ, Grave de Peralta R, Gonzales S, Seeck M, Landis T (2001) Electric source imaging of human cognitive brain functions. *Brain Res Rev* 36:108–118
- Michel CM, Murray M, Lantz G, Gonzalez S, Grave de Peralta R (2004) EEG source imaging. *Clinical Neurophysiology* (in press)
- Murray MM, Michel CM, Grave de Peralta R, Ortigue S, Brunet D, Gonzalez Andino S, Schnider A (2004) The sound and the memory: rapid, incidental discrimination of visual and multi-sensory memories. *Neuroimage* 21:125–135
- Naito E, Matsumura M (1994) Movement-related slow potentials during motor imagery and motor suppression in humans. *Brain Res Cogn Brain Res* 2:131–137
- Neshige R, Luders H, Shibasaki H (1988) Recording of movement-related potentials from scalp and cortex in man. *Brain* 111:719–736
- Ortigue S, Michel CM, Murray MM, Mohr C, Carbonnel S, Landis T (2004) Electrical neuroimaging reveals early generator modulation to emotional words. *Neuroimage* 21:1242–1251
- Pascual-Marqui RD, Michel CM, Lehmann D (1995) Segmentation of brain electrical activity into microstates: model estimation and validation. *IEEE Trans Biomed Eng* 7:658–665
- Pegna A, Khateb A, Spinelli L, Seeck M, Landis T, Michel C (1997) Unraveling the cerebral dynamics of mental imagery. *Hum Brain Mapp* 5:1–12
- Pfurtscheller G (1989) Functional topography during sensorimotor activation studied with event-related desynchronization mapping. *J Clin Neurophysiol* 6(1):75–84
- Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. *Neurosci Lett* 239(2–3):65–68
- Picton TW, Bentin S, Berg P, Donchin E, Hillyard SA, Johnson R, Miller GA, Ritter W, Ruchkin DS, Rugg MD, Taylor MJ (2000) Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiol* 37:127–152
- Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, di Prampero PE (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance study. *J Neurosci* 16(23):7688–7698
- Porro CA, Cettolo V, Francescato MP, Baraldi P (2000) Ipsilateral involvement of primary motor cortex during motor imagery. *Eur J Neurosci* 12:3059–3063
- Roland PE, Larsen B, Lassen NA, Skinhoj E (1980) Supplementary motor area and other cortical areas in organisation of voluntary movement in man. *J Neurophysiol* 43:118–136
- Roth M, Decety J, Raybaudi M, Massarelli R, Delon-Martin C, Segebarth C, Morand S, Gemignani A, Decors M, Jeannerod M. (1996) Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. *Neuroreport*. 7(7):1280–1284.
- Schnider A (2003) Spontaneous confabulation and the adaptation of thought to ongoing reality. *Nat Rev Neurosci* 4:662–671
- Schnitzler A, Salenius S, Salmelin R, Jousmäki V, Hari, R (1997) Involvement of primary motor cortex in motor imagery: a neuromagnetic study. *Neuroimage* 6:201–208
- Tanji J, Evarts EV (1976) Anticipatory activity of motor cortex neurons in relation to direction of an intended movement. *J Neurophysiol* 39:1062–1068
- Theios J (1975) The components of response latency in simple human information processing tasks. In: Rabbit PMA, Dornic S (eds.) *Attention and Performance V*. Academic Press, London, pp 418–440
- Thut G, Hauert CA, Morand S, Seeck M, Landis T, Michel CM (1999) Evidence for interhemispheric motor-level transfer in a simple reaction time task: an EEG study. *Exp Brain Res* 128:256–261
- Thut G, Hauert CA, Viviani P, Morand S, Spinelli L, Blanke O, Landis T, Michel CM (2000) Internally driven vs. externally cued movement selection: a study on the timing of brain activity. *Brain Res Cogn Brain Res* 9:261–269
- Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AI (1964) Contingent negative variation: an electric sign of sensori-motor association and expectancy in the human brain. *Nature* 203:380–384