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Alpha band power changes in unimanual and bimanual sequential movements, and during motor transitions

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Abstract

Objective: To investigate the cortical activation during execution of unimanual and bimanual synchronous and asynchronous finger sequences, as well as during transitions between those sequences.

Methods: Task-related power (TRPow) analysis of multichannel surface EEG was used to examine the regional oscillatory brain activity in the lower (7.8–9.8 Hz) and upper (10.8–11.8 Hz) alpha band. Unimanual to bimanual, bimanual to unimanual, and unimanual to unimanual transitions, prompted by visual cues, were studied in 10 right handed subjects.

Results: (1) Execution of unimanual and bimanual movements was accompanied by a bilateral activation over the central regions. (2) The 7.8–9.8 Hz TRPow decrease was more prominent for left and bimanual movements, suggesting sensitivity of the lower alpha band to task difficulty. (3) No difference in alpha oscillatory activity was found between bimanual synchronous and asynchronous sequences. (4) Transitions between motor sequences were invariably accompanied by a mesioparietal TRPow decrease in the lower alpha band. (5) This mesioparietal activation was contingent to the change of motor program, and could not be accounted for by the change of visual cue, or related attentional processes.

Conclusion: The 7.8–9.8 Hz mesioparietal activation most likely reflects a posterior parietal motor command initiating transition between motor programs.

Keywords: Bimanual movement; Motor transitions; EEG; Alpha band; Parietal cortex

1. Introduction

Oscillatory brain activity in the alpha band (8–12 Hz) is reduced or suppressed during preparation and execution of movements, a phenomenon first described as 'blocking' of the central mu rhythm (Gastaut et al., 1954; Chatrian et al., 1959), and which has been later referred to as 'event-related desynchronization' (ERD) (Pfurtscheller and Aranibar, 1977; Pfurtscheller and Berghold, 1989; Toro et al., 1994). Desynchronized alpha band activity is interpreted to reflect increased cellular excitability in thalamocortical systems, whereas synchronized alpha band activity occurring immediately after movement execution, or over remote cortical regions, reflects a cortical idling state (Steriade, 1993; Toro et al., 1994; Pfurtscheller et al., 1996; Pfurtscheller and Lopes da Silva, 1999). The alpha ERD is often divided into two subcomponents, namely a lower frequency (8–10 Hz) and a upper frequency (10–12 Hz) component. These two components differ in terms of amplitude and topography, the lower alpha component being smaller and more posterior than the upper component (Toro et al., 1994; Andrew and Pfurtscheller, 1997; Manganotti et al., 1998; Babiloni et al., 1999; Pfurtscheller et al., 2000), but their functional significance remains an object of debate.

There are few EEG and MEG studies devoted to the comparison of brain activity underlying unimanual and bimanual movements. Most of them have examined the activity preceding movement and at initiation of movement, less often during movement performance. Responses related to bimanual movements have been generally reported of larger amplitude than those related to unimanual movements (Kristeva et al., 1990; Lang et al., 1990; Kristeva et al., 1991; Urbano et al., 1998; Cui and Deecke, 1999a). In addition, there is suggestive evidence that the temporal aspect of coordination between the two hands influences the magnitude of movement-related potentials (Lang et

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al., 1988; Cui and Deecke, 1999b). Concerning oscillatory brain activity, execution of unimanual movements are accompanied by a bilateral alpha ERD over the central regions, with predominance over the contralateral hemisphere (Toro et al., 1994; Leocani et al., 1997; Gerloff et al., 1998a; Manganotti et al., 1998; Andres et al., 1999; Babiloni et al., 1999). The alpha ERD associated to bimanual movements has been examined only recently, and is described as bilaterally distributed with mesial posterior extension (Andres et al., 1999). However, no systematic comparison has been performed with unimanual movements.

In the present paper, we investigated changes in the alpha band oscillatory activity during execution of unimanual and bimanual sequences of finger movements. We used a task-related power approach, which relates to continuous task performance rather than to a single event (Gerloff et al., 1998a). Our first objective was to evaluate whether the task-related power changes could differ between unimanual and bimanual sequences. We examined synchronous and asynchronous sequential movements of both hands, in order to explore the relation between the alpha band oscillatory activity and the temporal mode of bimanual coordination. Our second objective concerned the transition between unimanual and bimanual motor programs, and vice versa. Production of movement typically consists of an initiation, followed by an execution phase, and these phases have specific electrophysiological correlates (Deecke et al., 1976; Lang et al., 1988; Gerloff et al., 1998b). Additionally, motor behavior is characterized by constant transitions between movements, which could correspond to the (re)organization of cerebrally encoded motor programs (Kelso, 1984; Buchanan and Kelso, 1993). Our purpose was to further specify the pattern of oscillatory activity associated with transition between movements, as compared to initiation and execution of movement, to evaluate whether motor transition appeared as a simple shift between cerebral activity patterns, or whether it could imply some specific activity, possibly driven by specific brain regions.

Our motor tasks consisted in sequential tapping movements of the index and middle fingers, and were instructed by visual cues, which triggered the initiation of movement as well as the change of motor program. The lower and upper frequency components of the alpha band were analyzed separately, in an attempt to investigate further their functional significance in relation to motor performance and transition between motor programs.

2. Methods

2.1. Subjects

Ten normal volunteers were studied, including 3 men and 7 women, with a mean age of 24.4 ± 3.2 years. All subjects were right handed as measured by the Edinburgh Inventory (Oldfield, 1971). They all gave their written informed consent for the study.

2.2. Experimental design

2.2.1. Main experiment

Subjects sat comfortably in a dimly lit room, with both arms resting on an especially designed table including adjustable armrests. Their hands were positioned palm down on a 4-element keypad (designed by NeuroScan Inc., Herndon, VA, USA), so that the index finger and the middle finger of each hand could be moved to press one specific key. A motor sequence is defined by a successive press of the index finger (1) and the middle finger (2). There were 4 different motor sequences: unimanual right: R1–R2 (Right); unimanual left: L1, L2 (Left); bimanual synchronous: R1–L1, R2–L2 (Syn); bimanual asynchronous: R1, L1, R2, L2 (Asyn).

Visual stimuli were presented at a constant viewing distance of 1.20 m, and consisted of two juxtaposed 1.8 cm gray squares on a black background, filled or not by a black cross to indicate the sequence type (Fig. 1). A trial was designed as follows: a first stimulus (stimulus A) was presented on the screen for a duration of 2.75 s, requiring the repetitive execution of a motor sequence at a regular, self-paced rate (execution A). A second stimulus (stimulus B) was then presented for 2.75 s, prompting the change to another motor sequence to be performed repetitively at a rate similar to the first sequence (execution B). A third stimulus (stop signal), presented for 0.7 s, required immediate cessation of the movements (Fig. 1). Five motor conditions of 40 trials each were tested, defined by the repetitive execution of a first motor sequence (execution A) and a transition to a second motor sequence, to be also executed repetitively (execution B): 1. Right-Bimanual, 2. Left-Bimanual, 3. Syn-Unimanual, 4. Asyn-Unimanual, 5. Unimanual-Unimanual. These 5 motor conditions corresponded to 3 types of transitions: unimanual to bimanual (U–B), bimanual to unimanual (B–U), and unimanual to unimanual (U–U). Conditions 1 and 2 belonged to U–B transitions; in each of these conditions, there was an equal number of transitions to Syn and Asyn sequences, occurring in random order. Conditions 3 and 4 belonged to B–U transitions; in each of these conditions, there was an equal number of transitions to Right and Left sequences, occurring in random order. In condition 5 (U–U transitions), trials starting with right (50%) and left (50%) hand were randomized, and transitions were dictated by the nature of execution A (i.e. if execution A is Right, then execution B is Left, and vice versa). In order to reduce anticipation of stimulus B, 15% of trials were added at random in every condition, in which duration of stimulus A or B was either shortened or increased; these trials were not included in the analysis. A rest condition was also studied in which the subject had to remain still while looking at the stimuli on the screen, all

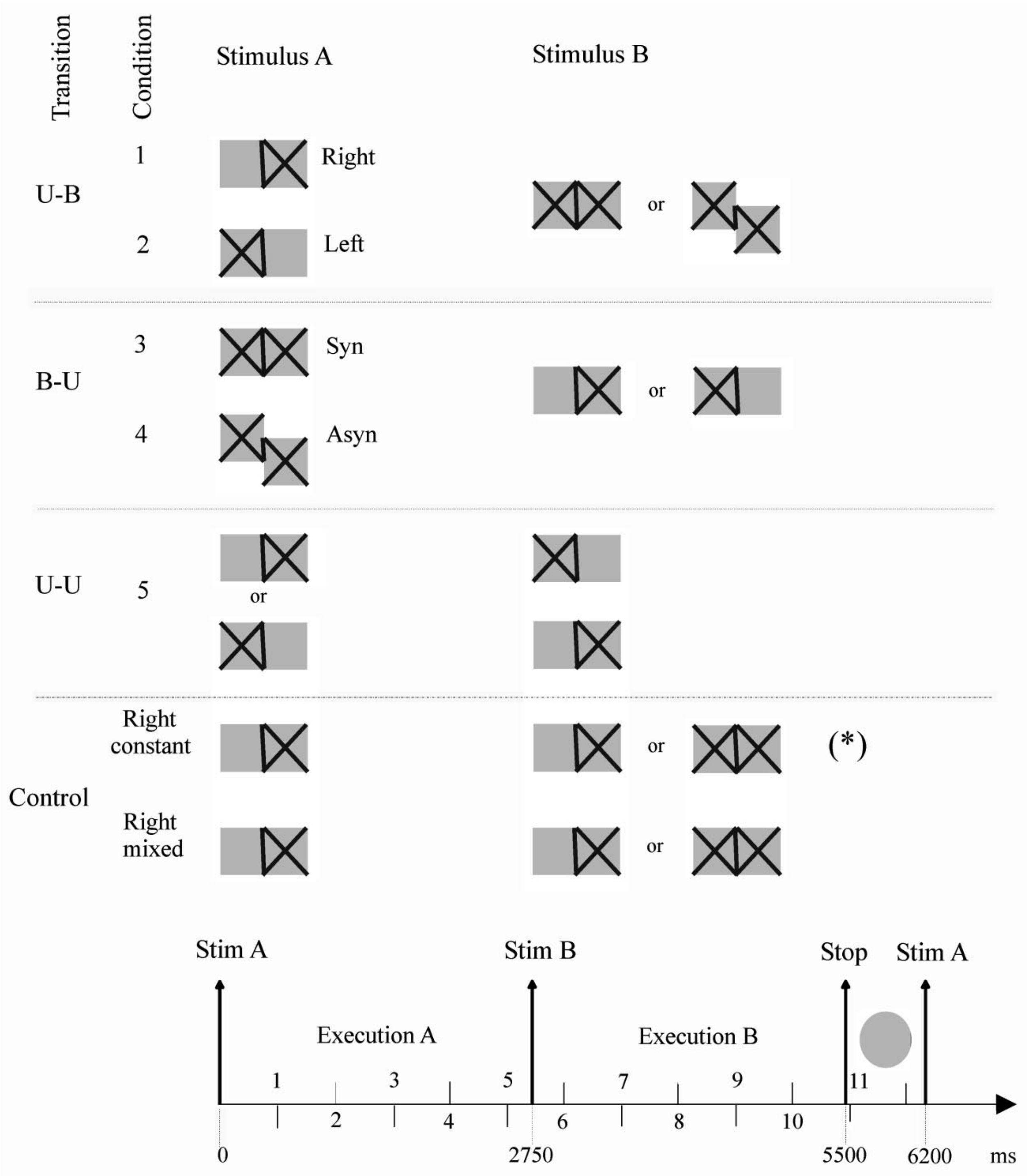

Fig. 1. Experimental paradigm. Transition: U–B, unimanual to bimanual; B–U, bimanual to unimanual; U–U, unimanual to unimanual. Condition: 1, Right-bimanual; 2, Left-bimanual; 3, Syn-unimanual; 4, Asyn-unimanual; 5, Unimanual-unimanual. Unimanual movements are indicated by one square filled with a black cross, the side of which codes movement side. Bimanual movements are indicated by two filled squares; facing squares code for synchronous movements, shifted squares for asynchronous movements. The motor sequence corresponding to each of the visual patterns is indicated in italics. The rest condition is not illustrated. Control: control experiment composed of the ‘Right constant’ and ‘Right mixed’ conditions. (*): no change of motor program required. For conditions 1–4, and both control conditions, stimulus B has a 50% chance to be of one type or another. For condition 5, it is stimulus A which has a 50% chance to be of one type or another, stimulus B being determined by stimulus A. Bottom: temporal axis corresponding to one trial; numbers in italics correspond to the 11 overlapping epochs of 1024 ms duration used for TRPow calculation. The gray circle represents the stop signal.

patterns being presented in random order. A session included two replications of each condition, and was subdivided into two blocks: in the first block, the order of presentation of the conditions was pseudo-randomized between subjects, and in the second block, this order was reversed (e.g. 3, 5, 1, rest, 4, 2; 2, 4, rest, 1, 5, 3).

2.2.2. Control experiment

A control experiment was designed on 8 new right handed normal volunteers (3 men, 5 women, mean age: 30.4 ± 9.4 years) with two objectives: first, to evidence a potential effect of change of visual stimulus, independently of the motor response; second, to test the effect of change of motor program as opposed to no change. In the two control conditions, the 'Right constant' and the 'Right mixed' conditions, stimulus A was always the right pattern and stimulus B was either the right or the bimanual synchronous pattern, both presented in the same proportion (Fig. 1). Temporal parameters were the same as in the main experiment. The first objective was tested by the 'Right constant' condition, in which subjects were required to keep doing the right hand sequence, independently of stimulus B pattern. Thus, the effect of change of visual stimulus could be isolated, the motor response remaining constant. In order to avoid complete ignorance of stimulus B, since no change in motor program was required, the subjects had to count silently left pattern stimuli occurring in 10% of the cases; trials corresponding to these patterns were rejected from analysis. The second objective was tested by the 'Right mixed' condition, in which the subjects were to follow the instruction given by stimulus B, i.e. either keep doing the right hand sequence (Right pattern) or change to the bimanual synchronous sequence (Syn pattern). Thus, the effect of change of motor program could be tested directly in comparison with the absence of change. Each condition was performed twice in a row, starting with the 'Right constant' condition, so that the subjects were not yet aware of the motor significance of the Syn pattern presented at stimulus B, thus avoiding mental association between pattern and movement.

2.3. Data acquisition

Continuous EEG was recorded from 47 surface electrodes, mounted on a cap (Easy-Cap, FMS, München, Germany). Data were sampled at 1000 Hz, the lower cutoff was 0.05 Hz and the upper cutoff 100 Hz (DC amplifiers and software by NeuroScan Inc., Herndon, Va., USA). Linked earlobes served as reference. A potential limitation of such a reference is that it may induce greater alpha power suppression at most distant electrode sites. Computation of a reference-free derivation could theoretically overcome this limitation, but on the other hand such derivation tends to underestimate distributed cortical sources with largely radial generators, which can be a disadvantage for detecting activation of mesial and lateral premotor areas. In any case, the use of a subtractive approach to determine task-related power changes (see below for detailed description) minimized signals common to activation and rest conditions. Two bipolar EMG channels were recorded from surface electrodes positioned over the right and left forearm flexors (flexor digitorum communis), each pair of electrodes being located ~15 cm apart. The high pass filter for EMG was set to 10 Hz. Each visual stimulus as well as each key press were automatically documented with a marker in the continuous EEG file. Temporal occurrence of each key press could thus be retrieved off-line, for calculation of reaction time to stimulus A (RT), reaction time to stimulus B, designed as transition time (TT), and time elapsed between each keypress (tapping interval).

2.4. Data analysis: task-related power (Gerloff et al., 1998a)

Since EEG analysis was performed on ongoing motor performance, a task-related power (TRPow) approach was chosen (Gerloff et al., 1998a), rather than the classical ERD methodology which usually relates to phasic changes of EEG signals associated to single, discrete events. In contrast with classical ERD, TRPow is computed by discrete Fourier transform of fixed time periods, thus reducing temporal resolution but allowing high frequency resolution. EEG signals were corrected for ocular artifacts using a threshold rejection algorithm (Neuroscan Inc.), and digitally filtered off-line (1–40 Hz, slope 24 dB/octave). For each condition, the trials were divided into segments of identical duration on which the spectral power of the signal could be calculated: on every occurrence of stimulus A, the continuous EEG recording was divided into 11 overlapping epochs of 1024 ms (Fig. 1). After removal of slow drifts by linear trend correction, and baseline correction using the entire epoch window, the single epochs were inspected automatically for artifacts, and double-checked manually. Because whole trials in which artifacts occurred were excluded, there was an equal number of replications for each epoch. A minimum of 30 artifact-free trials was obtained per subject for each of the two transition types within a motor condition, after merging trials from the two acquisition blocks. Each single epoch was hamming windowed to control for spectral leakage.

For spectral power analysis, a discrete Fourier transform was computed for each 1024 ms epoch, allowing a frequency resolution of 0.98 Hz. Spectral power was calculated on each epoch for all frequency bins between 1 and 30 Hz, and the power samples per epoch were averaged across all trials within each condition. In order to reduce the effects of inter-subject and inter-electrode variation in absolute spectral power values, as well as to eliminate power oscillations due to visual stimulation, task-related power at an electrode x (TRPow_{x}) was obtained by subtracting rest ($\mathrm{Pow}_{x\ \mathrm{rest}}$) from corresponding activation conditions ($\mathrm{Pow}_{x\ \mathrm{activation}}$), according to Eq. (1)

$$\mathrm{TRPow}_{\mathrm{x}} = \mathrm{Pow}_{\mathrm{x\ activation}} - \mathrm{Pow}_{\mathrm{x\ rest}} \qquad (1)$$

Therefore, task-related power decreases (activation) are expressed as negative values while task-related power increases are expressed as positive values. A potential disadvantage of using a rest condition temporally independent from the motor conditions is that differences in arousal and attention could occur. However, this is mitigated by the fact that these factors fluctuate randomly within and across trials during rest, thus limiting consistent effects on TRPow calculation. For analysis of the lower and upper alpha components, the non-overlapping frequency ranges of 7.8–9.8 and 10.8–11.8 Hz were, respectively, selected. Power changes corresponding to each frequency range were obtained by averaging the power value of the respective frequency bins.

2.5. Statistical analysis

Subtraction of power values as shown in Eq. (1) may be used to demonstrate task-related changes of the mean values. However, the variance of spectral power values is more variable at higher power level, and therefore a transformation of the power values is necessary prior to further statistical evaluation. Since logarithmic (log) transformation stabilizes the variance of spectral power estimates (Halliday et al., 1995), we used this procedure to give approximately constant residual variance at all levels of the response. Thus, for statistical analysis, Eq. (1) becomes Eq. (2)

$$\mathrm{logTRPow}_x = \log[\mathrm{Pow}_{x\ \mathrm{activation}}] - \log[\mathrm{Pow}_{x\ \mathrm{rest}}] \qquad (2)$$

Electrodes of interest were defined similarly to the region-of-interest approach that has been used in neuroimaging techniques such as PET and fMRI. The choice of electrodes was also guided by recent motor EEG studies of task-related power and coherence values (Gerloff et al., 1998a; Andres et al., 1999). Electrodes known to overlie approximately the primary sensorimotor cortex were grouped into two latero-central regions-of-interest (ROI), one on each hemisphere: ROI 1: C3, CP3 (left hemisphere); ROI 2: C4, CP4 (right hemisphere). Electrodes of interest in the midline were grouped into two mesial ROIs: ROI 3: FCz, Cz (anterior midline); ROI 4: CPz, Pz (posterior midline, or mesioparietal). ROIs 3 and 4 are likely to overlie approximately the supplementary motor area (SMA) and the precuneus, respectively (Steinmetz et al., 1989). Position of the 4 ROIs, each consisting of two electrodes of interest, is detailed in Fig. 5.

Two separate statistical analysis were performed, the first one designed to compare the different types of motor sequences, and the second one aimed at evaluating the TRPow changes accompanying the transition between the different motor sequences. In the first analysis, the steady state execution of the motor sequences was examined within the time period corresponding to execution A: the mean logTRPow values for epoch 2 and 4 were computed for each condition and entered into a two-way repeated measures analysis of variance (ANOVA), with SEQUENCE (Right, Left, Syn, Asyn) and REGION (ROI 1–4) as within-subject factors. In the second analysis, the question was to test whether the transition between motor sequences could be related to a specific pattern of TRPow, that is, distinct from stable execution as well as initiation of a motor sequence. Thus, our working hypothesis could be modeled by 4 consecutive motor states, i.e. initiation, execution A, transition, and execution B. To fit with this model, and to reduce the number of statistical variables, a unique time window was selected to represent each of the motor states, with the constraint that they should not be overlapping. RT and TT ranges were respectively used to assign the initiation and the transition phase to the appropriate epoch (see Section 3), and the epochs contiguous to the transition epoch were selected to represent execution A and B. As a result, the analyzed time data set was composed of epochs 1, 4, 6, and 8, representing each of the 4 motor states respectively. For each of the 3 transition types (U–B, B–U, and U–U), a two-way repeated measures ANOVA was performed on the logTRPow values, with EPOCH (1, 4, 6, 8) and REGION (ROI 1–4) as within-subject factors.

For the control experiment, the statistical analysis was restricted to the time window corresponding to transition (epoch 6; see Section 3). A two-way repeated measures ANOVA (CHANGE, REGION) was performed on each condition: in condition ‘Right-constant’, the effect of *change of visual stimulus* was tested, whereas in condition ‘Right mixed’, the effect of *change of motor program* was tested.

Statistical analysis was performed separately on the lower (7.8–9.8 Hz) and on the upper alpha band (10.8–11.8 Hz). Statistical threshold was set at $P < 0.01$.

3. Results

3.1. Motor performance

Performance is presented in Table 1 for each type of motor sequence. Tapping interval refers to the mean interval between the elements of the sequence (intervals R1–R2 for right sequence, L1–L2 for left sequence, R1/L1–R2/L2 for bimanual synchronous sequence), calculated over the first and second repetitions of the sequence. For bimanual asynchronous sequence, the mean of the 3 within-sequence intervals (R1–L1, L1–R2, R2–L2) is calculated. Since tapping interval was not different in execution A and B in any of the motor sequences, the mean tapping value is presented. The mean tapping interval is of 431 ms, corresponding to a movement rate of 2.3 Hz. It is remarkably constant within each type of sequence (on average, within-subject variability 10.6%, inter-subject variability 27.7%), and is not significantly different between the types of sequence (one-way ANOVA, $F = 3.5$).

3.1.1. Conditions 1–4

RT is of 403 ms on average, and is not significantly different between conditions ($F = 2.2$). TT, of 582 ms on average,

Table 1
Motor performance[a]

Motor sequence	Motor condition	RT	CV	Errors	Motor transition	TT	CV	Errors	Tapping interval	CV	Errors
Right	1	410 ± 117	28.6	0	Syn–right	544 ± 70[b]	12.9	0	431 ± 122	28.2	1
					Asyn–right	637 ± 97[c]	15.2	2		*12.4*	
	5	448 ± 57	12.6	8	Left–right	478 ± 71	14.8	0			
Left	2	417 ± 92	22.1	4	Syn–left	561 ± 76[d]	13.6	1	443 ± 121	27.2	5
					Asyn–left	633 ± 150[e]	23.7	3		*10.5*	
	5	449 ± 65	14.4	7	Right–left	470 ± 84	18.0	0			
Syn	3	376 ± 96	25.6	4	Right–syn	565 ± 102	18.1	6	424 ± 120	28.2	6
					Left–syn	569 ± 57	10.0	9		*9.8*	
Asyn	4	410 ± 123	30.1	5	Right–asyn	563 ± 91	16.1	7	424 ± 116	27.3	19
					Left–asyn	584 ± 62	10.6	12		*9.6*	

[a] Motor conditions 1–5 as described in text and Fig. 1. Syn, synchronous; Asyn, asynchronous; RT, reaction time; TT, transition time; CV, coefficient of variation. Values of RT, TT and tapping interval are mean values over 10 subjects ± standard deviation, in milliseconds. CV values are mean values over 10 subjects, expressed in % (CV = (standard deviation/mean)*100). CV values in italics correspond to mean of within-subject CV (i.e. within-subject variability). Errors represent the total number of keypress errors over 10 subjects.

[b] Repeated-measures ANOVA, contrast analysis: Syn-right vs. Asyn-right, $P < 0.01$.

[c] Asyn-right vs. Left-right, $P < 0.001$.

[d] Syn-left vs. Right-left, $P < 0.001$.

[e] Asyn-left vs. Right-left, $P < 0.001$.

is significantly longer than RT within each condition (Right: $F = 22.8$, $P < 0.001$; Left: $F = 17$, $P < 0.001$; Syn: $F = 46.2$, $P < 0.001$; Asyn: $F = 15.3$, $P < 0.001$). This is an expected observation, for the necessity of changing the motor program at stimulus B without prior knowledge on the new sequence required. TT does not vary according to the preceding motor program, except for the right sequence: it takes longer to switch to a right sequence when the preceding sequence is bimanual asynchronous than when it is bimanual synchronous ($F = 10.5$, $P < 0.01$).

3.1.2. Condition 5

In this condition, in which stimulus A can be either the right or the left pattern, RT is of 448.5 ms on average. RT values are not significantly different from equivalent values in conditions 1 and 2, in which stimulus A is fixed (Right: $F = 4.9$; Left: $F = 2.5$). TT is of 474 ms on average, and does not significantly differ from RT (Right: $F = 0.9$; Left: $F = 0.9$). On the other hand, TT values in condition 5 are significantly shorter than equivalent values in conditions 1 and 2, in which there is an uncertainty on stimulus B (Right: $F = 18.7$, $P < 0.001$; Left: $F = 16.7$, $P < 0.001$).

There was a very low percentage of keypress errors during tapping, with a maximal value of 0.4% for bimanual asynchronous sequence. For the initial keypress, the maximum of errors is of 1.25% for conditions 1–4 (corresponding to condition 4), and of 2% for condition 5. For the transition keypress, a maximum of 6% errors is attained when the preceding sequence is bimanual asynchronous.

3.2. Time course of TRPow changes

Fig. 2 illustrates the mean TRPow changes during the 11 time epochs, for the 3 transition types. In the lower alpha band, the TRPow values reach a plateau during epochs 2–4, after some variability is observed at initiation of the motor sequences (epoch 1). When the first motor program is unimanual (U–U and U–B transitions), the TRPow values start decreasing during epoch 5; they reach a minimum at epoch 6 for U–U transitions, but continue to decrease during the bimanual motor program for U–B transitions. When the first motor program is bimanual (B–U transitions), the TRPow decrease is of large amplitude, reaching a maximum at epoch 6; TRPow values start increasing right after epoch 6, corresponding to the transition to the unimanual motor program. It is noteworthy that, before and after transition, the TRPow decrease in the lower alpha band is of smaller amplitude in unimanual than in bimanual sequences. In the upper alpha band, the TRPow changes over time are less pronounced than in the lower alpha band.

Steady state execution of the motor sequences was examined during execution A (mean power value over epochs 2 and 4), after it was verified that the TRPow values within each motor sequence were not different during execution A and B (i.e. before and after transition). For the time course model of transition between motor programs (see Section 2), epoch 1 (0–1024 ms) corresponded to motor sequence initiation, since the RT range across all 5 conditions is of 262–716 ms. Epoch 6, starting 190 ms before stimulus B and extending up to 834 ms after it, was identified as corresponding to transition, since the time needed to realize the change of motor program fell between 371 and 770 ms (TT range). Epochs 4 and 8, contiguous to epoch 6, were selected to represent execution A and B, respectively.

3.3. Steady state execution of sequences

Figs. 3 and 4 show, in the lower and upper alpha band respectively, the topographic TRPow maps during the 3 following phases of movement: initiation of motor sequence (row A); steady state execution of motor sequence (row B); and transition between motor sequences (row C). Mean logTRPow values during steady state execution of each motor sequence are presented in Fig. 5. The results of the two-way repeated measures ANOVA (SEQUENCE, REGION) are shown in Table 2.

3.3.1. Lower alpha band (7.8–9.8 Hz)

Fig. 3B shows that the execution of unimanual and bimanual sequences are associated with bilateral TRPow decrease in the central region (i.e. ROI 1 and 2). For bimanual sequences, the TRPow decrease extends to the mesio-parietal region (i.e. ROI 4). The first-order statistical effect of SEQUENCE (Right, Left, Syn, Asyn) is significant (Table 2), and Fig. 5A shows that the logTRPow decrease for all ROIs is less pronounced in the right than in the other sequences (contrast analysis, Right vs. Left: $F = 15.7$, $P < 0.01$, Right vs. Syn: $F = 16.5$, $P < 0.01$, Right vs. Asyn: $F = 8.7$, $P < 0.01$). On the other hand, logTRPow values are not significantly different between left, synchronous and asynchronous sequences. The factor REGION discriminates the data in the following way: the logTRPow decrease is larger in ROI 1 and 2 (laterocentral regions) than in ROI 3 and 4 (mesial regions). There is no significant interaction between SEQUENCE and REGION.

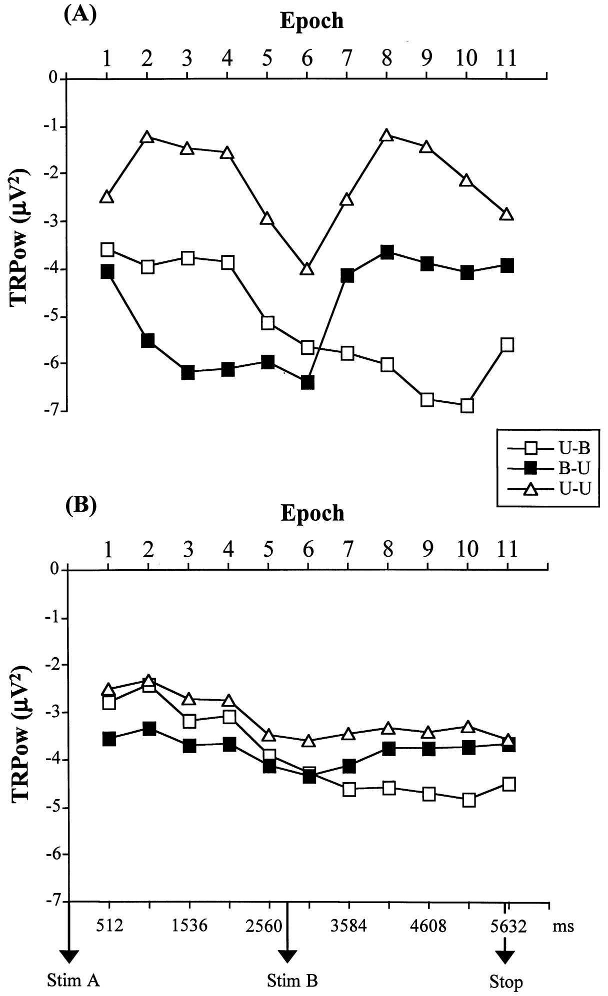

Fig. 2. Time course of task-related power over the 11 epochs of 1024 ms duration. Corresponding scale in milliseconds is given at bottom, with arrows indicating occurrence of stimulus A (0 ms), stimulus B (2750 ms) and stop signal (5500 ms). Each data point represents the average of the 8 electrodes of interest (C3, CP3, C4, CP4, FCz, Cz, CPz, Pz), over conditions 1 and 2 for U–B transitions, conditions 3 and 4 for B–U transitions, and condition 5 for U–U transitions ($n = 10$). (A) Lower alpha band (7.8–9.8 Hz); (B) Upper alpha band (10.8–11.8 Hz).

3.3.2. Upper alpha band (10.8–11.8 Hz)

Fig. 4B shows that the TRPow decrease is focused over the sensorimotor region bilaterally (i.e. ROI 1 and 2) with reduced mesial extension compared to the lower alpha band, especially concerning bimanual sequences. Statistical analysis on logTRPow values does not evidence any significant difference between sequences, but between regions (Fig. 5B, Table 2): as in the lower alpha band, the logTRPow decrease is larger in laterocentral ROI 1 and 2 than in mesial ROI 3 and 4.

3.4. Transition between motor sequences

Time course of mean logTRPow values over epochs 1, 4, 6 and 8 for each transition is shown in Fig. 6. The results of the two-way repeated measures ANOVA (EPOCH, REGION) for each transition type are shown in Table 3.

3.4.1. Lower alpha band (7.8–9.8 Hz)

Transition from one sequence to another, whatever the unimanual or bimanual nature of the first and second sequences, is associated with a mesioparietal TRPow decrease extending to the right hemisphere (ROI 4 and ROI 2) (Fig. 3C). The mesio-posterior distribution of TRPow decrease at transition between motor sequences is distinct from the bilateral laterocentral distribution of TRPow decrease during stable execution of unimanual and bimanual sequences (Fig. 3B). For all 3 transition types, an interaction between EPOCH and REGION is observed, suggesting that the time effect is different according to the region (Table 3). Fig. 6A reveals that the logTRPow decrease is maximum in epoch 6 for all transition types; the interactive effect between EPOCH and REGION is explained by the sharper change of logTRPow values for ROI 4 and ROI 2 across time. A sharper slope is observed in these regions between phases of unimanual sequence execution and phases of transition, i.e. between epochs 4 and 6 for U–B and U–U transitions, and between epochs 6 and 8 for B–U transitions.

3.4.2. Upper alpha band (10.8–11.8 Hz)

The transition epoch is comparable to epochs of steady state execution for all types of transitions, although with slightly more pronounced mesiocentral TRPow decrease

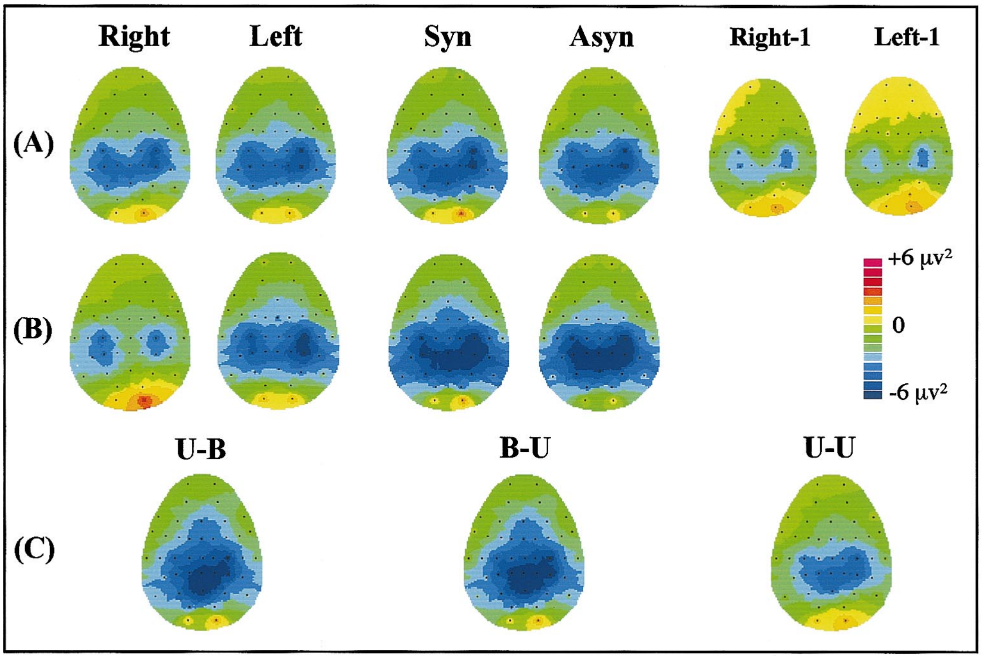

Fig. 3. Grand average of topographic task-related power maps ($n = 10$) in the lower alpha band (7.8–9.8 Hz). The dots indicate electrode positions. TRPow decreases (area of 'activation', negative TRPow values) are coded in blue/green and TRPow increases (positive TRPow values) are coded in red/orange. (A) Initiation of motor sequences, corresponding to epoch 1. Right-1 and Left-1 correspond to condition 5, initiation of right and left hand sequences, respectively. (B) Steady state execution of motor sequences, corresponding to average of epochs 2 and 4. Maps corresponding to steady state execution of unimanual sequences for Right-1 and Left-1 are similar to the maps illustrated in row B for Right and Left, respectively, and are not illustrated for simplification. (C) Transition between motor sequences, corresponding to epoch 6. TRPow maps have been averaged over conditions 1 and 2 for U–B transitions, and conditions 3 and 4 for B–U transitions. Note the bilateral distribution of TRPow decrease at initiation and stable execution of the sequences, contrasting with the mesioparietal distribution at transition between motor sequences. When stimulus B is predictable, transition between unimanual sequences (row C, U–U) is also distinct from initiation (row A, Right-1 and Left-1).

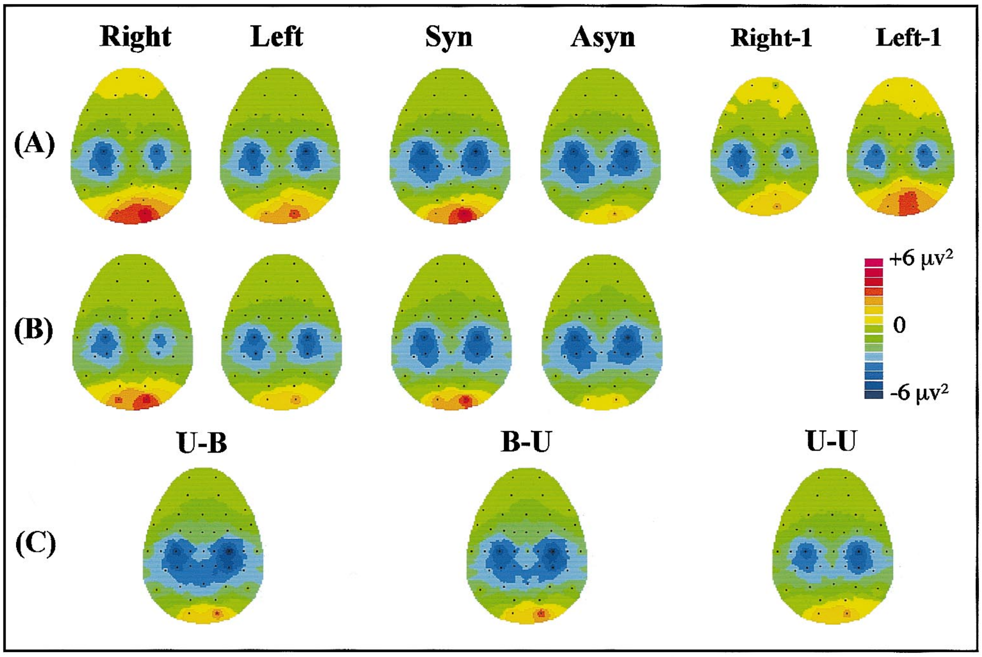

Fig. 4. Grand average of topographic task-related power maps ($n = 10$) in the upper alpha band (10.8–11.8 Hz). Same conventions as in Fig. 3. Note that the bilateral distribution of TRPow decrease is predominant during the 3 phases of movement (A–C).

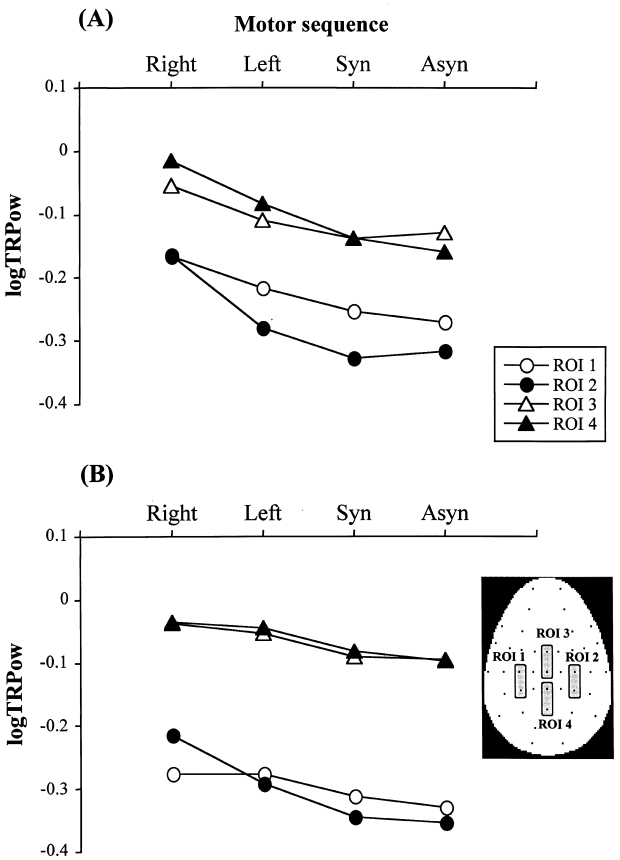

Fig. 5. Grand average of the logTRPow values ($n = 10$) during steady state execution of each condition, illustrated for each ROI. (A) Lower alpha band (7.8–9.8 Hz); (B) Upper alpha band (10.8–11.8 Hz). Electrode placement and position of the ROIs are indicated on the view of the top of the head. ROI 1: left central (C3, CP3); ROI 2: right central (C4, CP4); ROI 3: mesiofrontal (FCz, Cz); ROI 4: mesioparietal (CPz, Pz). Note the enhanced TRPow decrease for left and bimanual sequences, particularly in the lower alpha band.

(Fig. 4C). In contrast with the lower alpha band, an interaction between EPOCH and REGION is observed only in U–B transitions, and refers merely to a sharper effect of transition in the right laterocentral region (ROI 2; Fig. 6B). In B–U transitions, there are independent effects of EPOCH and REGION, whereas in U–U transitions, only REGION has a significant effect (Table 3).

Table 2
Statistical results in steady state sequence execution[a]

		Lower alpha		Upper alpha	
	d.f.	*F*	*P*	*F*	*P*
SEQUENCE (Right, Left, Syn, Asyn)	3	6.5	*	3.6	NS
REGION (ROI 1–4)	3	21.8	**	18.4	**
SEQUENCE × REGION	9	4.2	NS	4.4	NS

[a] Repeated-measures ANOVA on task-related power, log-transformed data: $*P < 0.01$; $**P < 0.001$; NS, non-significant.

3.5. Transition epoch

In the lower alpha band, the passage from one motor sequence to another is characterized by a mesioparietal TRPow decrease similar among all transitions, as illustrated in Fig. 7. A two-way ANOVA (TRANSITION, REGION) does not show any significant effect of the transition type upon the logTRPow values in epoch 6 ($F = 4$), only a significant effect of REGION ($F = 12.7$, $P < 0.001$), with maximal logTRPow decrease in ROI 2.

3.6. Control experiment

Fig. 8 shows the topographic TRPow maps corresponding to stimulus change and to motor program change, in the lower and upper alpha frequency bands. The map of stimulus change is obtained from the 'Right constant' condition by subtracting the map at epoch 6 when the stimulus remains constant from the map at epoch 6 when the stimulus is changing. This difference map does not show any consistent residual TRPow, suggesting that the change of stimulus has no effect on the TRPow. This observation is confirmed by a two-way ANOVA performed on the log TRPow values in the 'Right constant' condition, with STIMULUS CHANGE (change, no change) and REGION (ROI 1–4) as within-subject factors: no significant effect is evidenced, in any of the frequency bands.

The map of motor program change is obtained from the 'Right mixed' condition by subtracting the map at epoch 6 when the motor program is not changing from the same map when the motor program is changing. This difference map reveals mainly in the lower alpha band a TRPow decrease centered in the mesioposterior region, similar to the one observed at transition between motor programs (Figs. 3C and 7). In the lower alpha band, a two-way ANOVA performed on the log TRPow values in the 'Right mixed' condition confirms a significant interaction between MOTOR CHANGE (change, no change) and REGION (ROI 1–4), which suggests that the effect of change in motor program is different according to the region (Table 4). This effect is significantly more pronounced for ROI 4 compared to ROI 1 and ROI 3, but not compared to ROI 2 (contrast analysis, change motor program vs. no change, ROI 1 vs. ROI 4, $F = 39.9$, $P < 0.001$; ROI 3 vs. ROI 4, $F = 13.7$, $P < 0.01$; ROI 2 vs. ROI 4, $F = 1.74$). In the upper alpha band, there is no significant effect of MOTOR CHANGE, nor interaction between MOTOR CHANGE and REGION, but only an effect of REGION (Table 4).

4. Discussion

4.1. Motor performance

Keypress rate was remarkably constant in all sequences, despite the self-paced mode of tapping. This stability excludes movement rate as a confounding variable in the

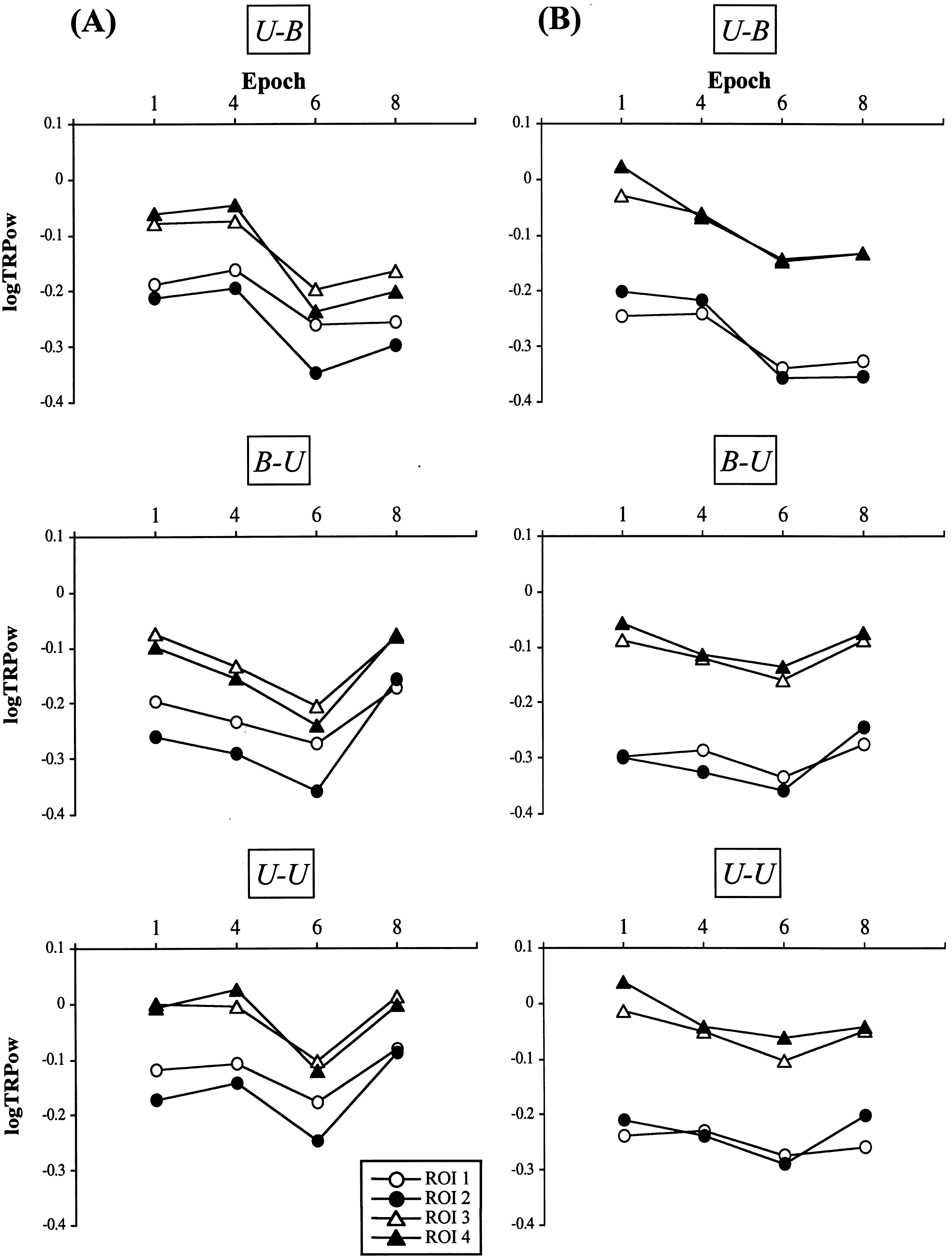

Fig. 6. Time course of logTRPow values over epochs 1, 4, 6, 8 for each type of transition, illustrated for each ROI ($n = 10$). (A) Lower alpha band (7.8–9.8 Hz); (B) Upper alpha band (10.8–11.8 Hz). The logTRPow are averaged over conditions 1 and 2 for U–B transitions, and over conditions 3 and 4 for B–U transitions. Changes of logTRPow over time are prominent in the lower alpha band. Note that in every transition type, logTRPow values are minimal during epoch 6.

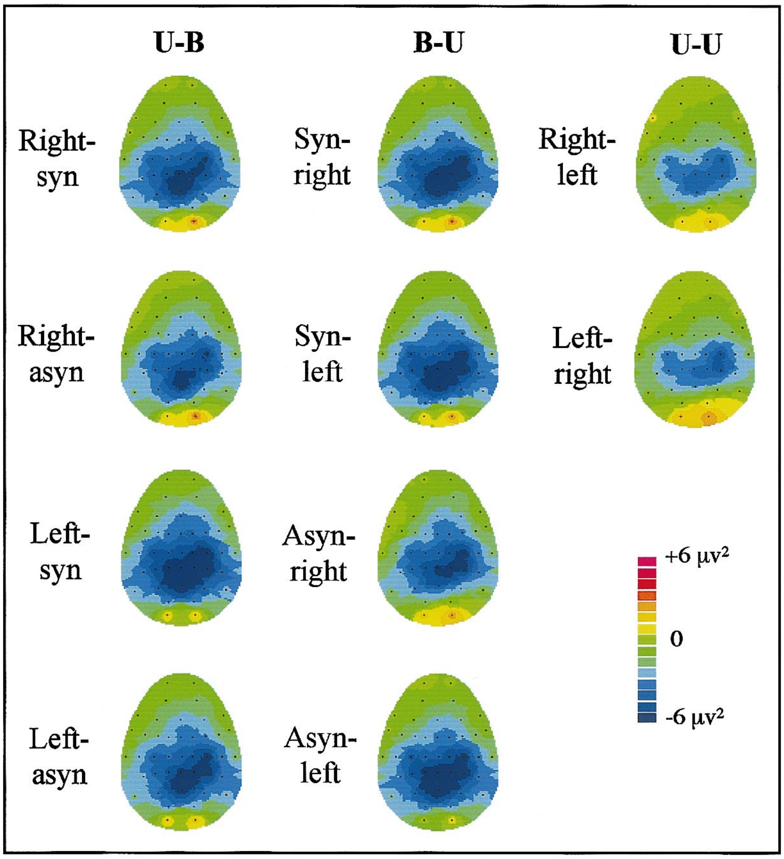

Fig. 7. Grand average of topographic task-related power maps ($n = 10$) in the lower alpha band (7.8–9.8 Hz) for each transition during epoch 6. Same conventions as in Fig. 3. Note the reproducibility of the mesioparietal TRPow decrease for each transition type.

comparison between sequences. The finding that reaction time was not different between unimanual and bimanual sequences is consistent with recent observation (Foltys et al., 2001). In U–B and B–U transitions, the transition time between motor sequences exceeded the simple reaction time, which could result from at least 3 factors: (1) the longer time

Table 3
Statistical results within each transition type[a]

	d.f.	Lower alpha		Upper alpha	
		F	*P*	*F*	*P*
U–B transitions					
EPOCH (1, 4, 6, 8)	3	16.9	**	20.9	**
REGION (ROI 1–4)	3	57.2	**	51.2	**
EPOCH × REGION	9	5.4	**	4.2	**
B–U transitions					
EPOCH (1, 4, 6, 8)	3	13.9	**	5.2	*
REGION (ROI 1–4)	3	67.3	**	57.0	**
EPOCH × REGION	9	7.2	**	2.6	NS
U–U transitions					
EPOCH (1, 4, 6, 8)	3	3.5	NS	1.9	NS
REGION (ROI 1–4)	3	25.5	**	28.4	**
EPOCH REGION	9	2.5	*	1.5	NS

[a] Same conventions as in Table 2.

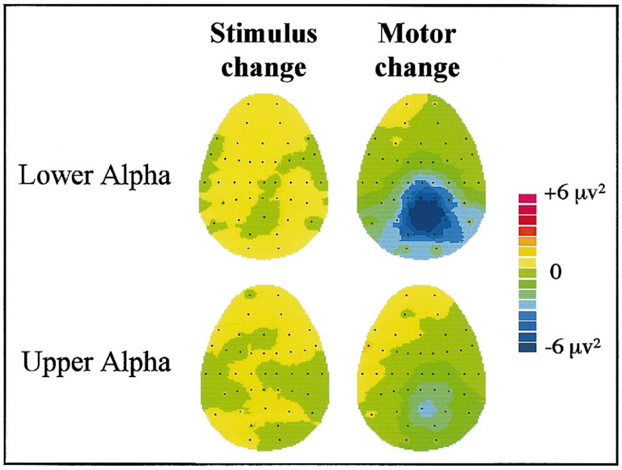

Fig. 8. Grand average of topographic task-related power maps ($n = 10$) in the lower and upper alpha band during epoch 6 for the control experiment. Maps corresponding to 'Stimulus change' are obtained from the 'Right constant' condition, by subtracting trials without change of stimulus B from trials with change. Maps corresponding to 'Motor change' are obtained from the 'Right mixed' condition, by subtracting trials without change of motor program from trials with change. Note that the mesioparietal TRPow decrease is associated exclusively to the change of motor program, and is prominent in the lower alpha band.

presumably needed to program a new sequence when the motor system is already engaged in performance; (2) the inhibition of the first sequence; and (3) the unpredictability of the forthcoming transition signal, which prevented anticipatory behavior. The influence of the third factor appears particularly strong, since transition time was significantly shorter in the U–U transitions in which the transition signal was predictable. The transition time was similar among U–B and B–U transitions, and remained independent on the motor sequence preceding the change. Only transitions from asynchronous bimanual movements tended to take more time, especially those to right sequences. This observation can be explained by a natural tendency to complete the asynchronous sequences before the change, completion which takes theoretically twice the time of the other two-element sequences. Overall, the data suggest that the performance of unimanual and bimanual sequential movements was comparable, as were the transitions between those movements. The present observations are compatible with the behavioral literature (Rosenbaum, 1991).

4.2. TRPow during steady state execution of finger sequences

In both lower and upper alpha bands, TRPow decreases were prominent over the central, and secondarily, mesial regions. Differences of TRPow amplitude between central and mesial regions tended to be larger in the upper alpha band. During execution of unimanual movements, a bilateral TRPow decrease was observed, in accordance with previous topographic ERD studies (Toro et al., 1994; Leocani et al., 1997; Crone et al., 1998; Gerloff et al., 1998a; Andres et al., 1999; Babiloni et al., 1999). In EEG and MEG studies, more data is available in the interval preceding movement than during movement performance, but yet bilateral response to unimanual movements is described (Toro et al., 1993; Salmelin et al., 1995; Urbano et al., 1998). In contrast, in functional imaging studies of finger movements, there is a general consensus for sensorimotor cortex (SMC) activation lateralized contralaterally (Deiber et al., 1996; Catalan et al., 1998; Jäncke et al., 1998; Toyokura et al., 1999). Some descriptions of ipsilateral SMC activation have been made in relation to movements of the non-preferred hand (Kawashima et al., 1993; Kim et al., 1993), as well as to the complexity of hand movements (Rao et al., 1993; Shibasaki et al., 1993; Kawashima et al., 1998). However, the absence of ipsilateral activation in most studies using metabolic measures remains difficult to conciliate with data on oscillatory brain activity. The neurophysiological mechanisms underlying alpha reactivity remain largely unknown, and a common idea is that alpha suppression could reflect activation of a distributed cortical network system capable of supporting motor function. Within this function, and because of the connections existing between neurons of a same functional system, activation of a subset of the network could result in widespread alpha suppression (Crone et al., 1998; Pfurtscheller et al., 2000), in contrast with the circumscribed foci of activation detected with neuroimaging techniques. A contralateral predominance of ERD has generally been described in unimanual movements, although statistical testing was not always performed (Leocani et al., 1997; Crone et al., 1998; Gerloff et al., 1998a; Manganotti et al., 1998; Babiloni et al., 1999). Our own data did not evidence statistically significant larger TRPow decrease over the hemisphere contralateral to movements, although a trend was observed in both lower and upper alpha bands.

Table 4
Statistical results in epoch 6 of the 'Right mixed' condition[a]

		Lower alpha		Upper alpha	
	d.f.	*F*	*P*	*F*	*P*
MOTOR CHANGE (yes, no)	1	11.1	NS	9.8	NS
REGION (ROI 1–4)	3	4.1	NS	7.6	*
MOTOR CHANGE × REGION	3	7.0	*	4.1	NS

[a] Same conventions as in Table 2.

During execution of bimanual finger sequences, the activation reflected by the TRPow decrease reached a maximum of amplitude in the 4 scalp regions examined. In the 7.8–9.8 Hz range, the distribution of the TRPow decrease extended to the mesial region of the scalp, in accordance with earlier observation (Andres et al., 1999). However, the amplitude of the TRPow decrease for bimanual movements remained higher in the central region. On the other hand, we did not confirm neuroimaging findings suggesting a predominant activation of the left hemisphere in bimanual movements performed by right handers (Jäncke et al., 1998; Viviani et al., 1998). Absence of lateralized hemispheric control for simple bimanual movements has also been reported recently in a study of reaction time involving transcranial magnetic stimulation (Foltys et al., 2001).

Comparison between finger sequences revealed that in the lower alpha band, the type of sequence has a significant effect on the TRPow decrease, but that this effect is independent on scalp location: for right sequences, the TRPow decrease was smaller than for left and bimanual sequences. In contrast, Toro and co-workers (Toro et al., 1994) did not observe any difference of the ERD response to movements of the right and left hand, but they tested single digit movements as opposed to two-digit sequential movements in the present study. A possible explanation for the largest TRPow decrease observed in left and bimanual sequences would be that for right handed subjects, these sequences are more demanding than sequences performed with the right hand. The relative proportion of keypress errors between the sequences tends to support this hypothesis, since right hand sequences constantly counted the smallest number of errors, at initiation and during execution of movements. Considering right and left hand movements, this notion of task difficulty, i.e. requirement of a greater effort to perform with the non-preferred hand, has already been proposed to explain a tendency for less asymmetric hemispheric responses to left than right hand movements (Lang et al., 1990; Kawashima et al., 1993; Kim et al., 1993; Urbano et al., 1998; Stephan et al., 1999). Interpretation of the greater sensitivity of the lower alpha band to the nature of the motor sequence can only be speculative. Andrew and Pfurtscheller (1997) have proposed that, although both lower and upper alpha components are probably generated in the underlying neocortical circuitry, the lower alpha component centered around 9 Hz is related to a global generation-mechanism (corticocortical interactions), in contrast with the 12 Hz component related to local circuitry (intracortical interactions). Lower alpha desynchronization could reflect general task demands, and be non-task specific (Klimesch et al., 1998; Pfurtscheller et al., 2000). In this context, one could speculate that an enhanced global mobilization related to task difficulty could be influencing the extensive connections linking the motor system, resulting in a desynchronization preferentially centered in the lower alpha frequency band. Our observation on the absence of regional specificity in the differences between unimanual and bimanual finger sequences is concordant with most findings from ERD, movement-related activity, and functional imaging studies. Concerning the SMC, there is a consensus about the similarity of activation in each hemisphere during bimanual synchronous movements, activation which is not significantly larger than in the hemisphere contralateral to unimanual movements (Urbano et al., 1998; Andres et al., 1999; Toyokura et al., 1999; Jäncke et al., 2000). On the other hand, mesiofrontal activation is reported either of the same order (Andres et al., 1999; Toyokura et al., 1999) or larger in bimanual synchronous than in unimanual movements (Lang et al., 1990; Kristeva et al., 1991; Urbano et al., 1998; Cui and Deecke, 1999a; Jäncke et al., 2000). However, a larger mesiofrontal response in bimanual movements could result from the overlap of the SMA activity in each hemisphere (Urbano et al., 1998), and thus would not necessarily indicate that the SMA contributes preferentially to bimanual movements.

Overall, the two following findings: (1) that the TRPow decreases are not only enhanced during bimanual movements, but also during left hand movements; and (2) that this enhancement does not show any significant regional specificity, support the hypothesis that the notion of energy requirement to perform a task could be more influent on the magnitude of spectral power decrease than the notion of bimanuality, especially in the lower alpha band. In other words, our results in the 7.8–9.8 Hz frequency range suggest that the TRPow decreases can be larger for bimanual than for unimanual movements, but that this effect is consecutive to enhanced task difficulty rather than to the bimanual nature of the movements.

Our study addressed another important issue, the comparison between bimanual synchronous and asynchronous sequences of movements. The synchronous and asynchronous functional modes refer to the phase relationship between the movements of each hand, and can also be designed as in-phase and anti-phase patterns. These patterns have been shown to represent the most stable temporal couplings, with maximal stability for the in-phase mode of coordination (Kelso, 1984; Tuller and Kelso, 1989). Few studies have examined the cerebral correlates of the two modes of bimanual coordination. Negative cortical DC shifts have been shown of larger amplitude over the mesiofrontal region during execution of alternate compared to simultaneous index finger movements, but no difference was found between simultaneous flexion-flexion (in-phase) and flexion-extension (anti-phase) movements (Lang et al., 1988). In a more recent study, the Bereitschaftpotential has been reported of larger amplitude for spatially congruent (i.e. anti-phase) than for anatomically congruent (i.e. in-phase) bimanual index finger movements (Cui and Deecke, 1999b). Similarly, fMRI data suggest that SMC and mesial wall activation is higher during anti-phase as compared to in-phase finger or fist movements (Stephan et al., 1999; Toyokura et al., 1999). Our own data did not reveal any difference in the alpha oscillatory activity between the synchronous and asynchronous modes of coupling for sequential movements. This negative finding could again be interpreted in relation to the large distributed cortical network system that may subtend alpha suppression in relation to motor function (see above), which would not be sensitive to certain specific parameters of movements. An alternative hypothesis is that the timing commands generating the different modes of bimanual coupling are not reflected in the alpha frequency band. Lastly, there is a possibility that the sequential nature of our tasks is responsible for specific activity patterns that would mask potential differences related to the mode of temporal coupling between the two hands.

4.3. TRPow during transition between finger sequences

A main purpose of the present study was to analyze the pattern of cerebral oscillatory activity associated with motor transition, by contrast with motor initiation and execution. A major finding is that the transition between motor sequences is accompanied by a TRPow decrease localized over the mesioparietal region in the 7.8–9.8 Hz frequency band. This topography is distinct from the bilateral distribution present at initiation or stable execution of motor sequences. We will refer to this phenomenon as mesioparietal activation, since it is postulated that a TRPow decrease reflects the interruption of synchronized activity in functionally related groups of cortical neurons, which can be seen as a correlate of increased cellular excitability (Pfurtscheller and Lopes da Silva, 1999). In the 10.8–11.8 Hz frequency band, there is a tendency for a mesial TRPow decrease at transition, but the distribution remains essentially bilateral and does not focus over the mesioposterior region, as observed in the lower alpha band. The different hypothesis about the nature of the 7.8–9.8 Hz mesioparietal activation are discussed in the following sections.

4.3.1. Visual stimulation

In our paradigm, motor sequences were instructed via visual signals. Stimulus A instructed the first motor program until occurrence of the transition signal, stimulus B, which instructed the second motor program. Thus, the change from stimulus A to stimulus B was an obliged experimental feature, and the question can be raised whether the mesioparietal effect at transition could simply result from this change. It must first be noticed that calculation of TRPow is based on subtraction of a passive viewing task temporally matching the motor tasks, which should ensure the cancellation of effects related to the presentation of visual stimuli. To further test the effect of change of visual stimulus, the ‘Right constant’ condition was designed in which subjects performed the same motor sequence during the whole trial, although the visual signal changed at stimulus B in half of the cases. The absence of remaining activation when subtracting trials with no change at stimulus B from trials with change at stimulus B confirms that the change of stimulus cannot by itself be responsible for the mesioparietal activation.

Considering the unpredictability of the transition signal, there is a possibility that the mesioparietal activation could relate to the absence of knowledge about the forthcoming transition. However, we have an argument that invalidates this hypothesis: the mesioparietal activation was present at transition between unimanual sequences, in which the forthcoming transition stimulus was always predictable. On the other hand, in these U–U transitions the mesioparietal activation was absent at initiation of motor program (stimulus A), and yet the left or right hand side of the first motor sequence could not be predicted (Figs. 3A and 4A). Consequently, the mesioparietal activation appears independent on the predictability of the visual signal.

4.3.2. Visual attention

The motor responses required in our paradigm were conditioned by visual stimuli, and thus they were intrinsically dependent on visual attention. We attempt to clarify this issue in the interpretation of our results, aware of the existence of data suggesting that the alpha ERD is sensitive to attention. In a word recognition task, Dujardin and coworkers have observed a widespread desynchronization in the alpha band with high attentional load, reaching its maximum just before motor response (Dujardin et al., 1993). In an oddball paradigm with targets and non-targets, slower alpha frequencies (6.4–10.4 Hz) have been shown to desynchronize in relation to attentional demands such as alertness and expectancy (Klimesch et al., 1998). However, contradictory findings have been reported, showing that oscillations in the 7–13 Hz frequency range are disrupted by movement but not affected by attention (Nashmi et al., 1994). In relation to the visual modality, a decrease of the parieto-occipital 10 Hz activity has been reported when visual stimuli are selectively attended (Foxe et al., 1998). This observation is consistent with the presence of a 10–12 Hz ERD in the occipital region in the period preceding a visual stimulus providing knowledge of results (Bastiaansen et al., 1999, 2001). Together, these findings suggest that the alpha desynchronization in the parieto-occipital region could reflect active engagement of the visual areas in the anticipatory period of a relevant visual stimulus.

In our tasks, attention to the transition signal merely includes a sustained attention component, present when two patterns are attended with equal probability, and a selective attention component, occurring in case attentional priority has to be given to one pattern in favor of the other (Coull, 1998). Combined examination of the results from main and control experiments provide some clues on the potential role of these attentional processes in the mesioparietal activation reported in our study. In the main experiment, sustained attention is necessarily higher in the motor tasks as compared to the rest condition, and thus could play some role in the TRPow changes observed. In the ‘Right mixed condition’, the two possible patterns for stimulus B are attended equally. Yet, the mesioparietal activation survives the subtraction between two types of trials involving the same level of sustained attention, suggesting that the activation is independent on the sustained attention component. On the other hand, the tasks in the main experiment are not supposed to require selective attention, since both possible patterns of stimulus B must be equally attended: the presence of the mesioparietal activation in these tasks thus suggests that it is independent on selective attention. In summary, although a definite assessment of attentional effects remains beyond the scope of the paper, the present observations support the hypothesis that the mesioparietal activation evidenced at transition between motor programs does not primarily depend on sustained or selective attentional processes to the instruction stimulus.

4.3.3. Motor transitions

The preceding arguments suggest that the mesioparietal activation is not due to the sensory input instructing the change, nor to attentional processes related to it. This activation occurs at transition between motor programs, and thus it is likely to be associated with the motor output aspect of the change. Since bimanual execution of movements was associated with marked increase in mesial activation, an initial question would be whether the mesioparietal activation could reflect a simple transitional state from unimanual to bimanual motor performance. This hypothesis can be discarded for two reasons: (1) transitions from bimanual to unimanual movements also elicited mesioparietal activation, although unimanual movements are characterized by a reduced mesial activation compared to bimanual movements; (2) the mesioparietal activation was also elicited at transition between unimanual movements. A decisive test to ensure that the mesioparietal activation is due to the motor aspect of the change is to show that it remains when comparing a situation involving a motor change with a situation of constant motor production. The 'Right mixed' condition tested this hypothesis in contrasting trials requiring a change of motor sequence with trials in which the initial sequence had to be pursued. The results clearly showed that the mesioparietal activation was present when a transition occurred as compared to a situation without transition, indicating that it is contemporary to the change of motor program.

The mesioposterior distribution of the TRPow decrease at transition is compatible with the involvement of the posterior parietal cortex in the change between motor programs. Our data further suggest that this implication is specifically related to the transition from one motor plan to another, and not to motor initiation from a rest state, since in the latter situation no parietal activity comparable to the one observed at motor transition was elicited. Recently, a PET study examining the brain activity related to the change between in-phase and anti-phase bimanual movements has evidenced a unique focus of activation in the posterior border of the left angular gyrus, and has concluded to a key role of the posterior parietal cortex in commanding the change between two bimanual motor programs (de Jong et al., 1999). The anatomical location found by these authors appears distinct from the mesioparietal activation evidenced in the present work, but procedural differences between the two studies have to be underlined: first, the group of de Jong et al. (1999) focused on transitions between bimanual motor programs, which were not studied here, and second, the anatomical generators responsible for the lower alpha parietal oscillatory activity cannot be definitely resolved by our method. Nevertheless, both studies demonstrate a role of parietal cortex in the change between motor programs, and our own data further suggest that mesioparietal activation occurs independently on the unimanual or bimanual nature of these programs.

Several animal studies have demonstrated that the posterior parietal cortex is concerned with the intention about the movement to make (Andersen et al., 1997). In particular, the activity of the lateral intraparietal area has been shown to be altered by changes in the monkey's intentions with regard to eye movements, independently of overt behavior (Bracewell et al., 1996). Intention-related signals have been described in the posterior parietal cortex, that are independent of attentional processes (Snyder et al., 1997). Our data do suggest that, when the motor system is engaged in task performance, the posterior parietal cortex might subserve a command function to change the motor program on external instruction. The respective contribution of intention and action in this command function remains beyond the experimental reach. The finding of a mesioparietal activation centered in the lower alpha band, discussed as reflecting corticocortical connections (Andrew and Pfurtscheller, 1997), is consistent with the representation of the parietal cortex as a key structure for sensorimotor transformations, through the integration of cognitive functions such as intention, attention, and selection of targets (Andersen et al., 1997). Our data further suggest that the intervention of the parietal cortex in changing the motor program, as reflected by the mesioparietal TRPow decrease in the lower alpha band, concerns more specifically the processes related to motor production rather than visual processing.

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