Research report

# Programming effectors and coordination in bimanual in-phase mirror finger movements

Marie-Pierre Deiber[a,b,*], Vicente Ibañez[c], Roberto Caldara[a],
Carine Andrey[a], Claude-Alain Hauert[a]

[a]*Faculté de Psychologie et des Sciences de l'Education, Université de Genève, UniMail, Boulevard du Pont d'Arve 40, CH-1211 Geneva 4, Switzerland*
[b]*Institut National de la Santé et de la Recherche Médicale, CERMEP, Boulevard Pinel 59, 69003 Lyon, France*
[c]*Unité de Neuroimagerie Psychiatrique, Chemin du Petit Bel-Air 2, CH-1225 Chêne-Bourg, Geneva, Switzerland*

## Abstract

We investigated cerebral activation during programming of in-phase symmetric finger movements in a precued response task. Partial precues provided advance information about either mirror effectors or in-phase coordination of bimanual movements, while full precue specified both response parameters and neutral precue no movement information. Effects of precueing were assessed on reaction time (RT), contingent negative variation (CNV), and alpha and beta event-related desynchronization (ERD). Information on coordination mode induced less efficient preparation than information on effectors, as revealed by longer RT, but paradoxically the CNV was found of larger amplitude for in-phase than for mirror precue. Full and in-phase precues were associated to largest cerebral activation, as reflected by CNV amplitude as well as beta ERD. It is suggested that with in-phase precueing, abstract programming of coordination and concrete preparation of possible effectors overlap, engaging more cerebral resources than when symmetric effectors are pre-specified. Alpha ERD underwent regional modulations dependent on the type of preparation, pointing out the role of the right parietal region in visuomotor transformation with full movement programming, and the preferential implication of the dominant hemisphere and medial brain regions in synchronization of both hand movements. Beta ERD topographical distribution suggested an increased implication of bilateral and medial motor regions in anticipation to the response signal with incomplete movement preparation.
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## 1. Introduction

In actions involving both hands, coordination refers to isomorphic joint movements (e.g., drumming) and contrasts with cooperation, where each hand has a specific and differentiated role and cooperates with the other to produce an unique action (e.g., to peel a fruit) [52,54]. Bimanual coordination has been extensively studied in various behavioral studies devoted to identify the main constraints limiting its efficiency [43]. It is now well established that, in the dynamics of bimanual coordinative mode, two preferred forms of behavior express, during which either homologous or antagonist muscle groups are simultaneously concerned [23]: in the former case, the movements are designed as in-phase and, in the latter case, as anti-phase. The in-phase pattern proves to be the most natural and stable mode of coordination [22], resulting in a strong symmetry tendency in bimanual movements in humans. Little is known about the physiological mechanisms for this tendency. It is

* Corresponding author. Department of Psychology, University of Geneva, Room 5166 40 Bd du Pont d'Arve, Geneva, Switzerland. Fax: +41 22 379 92 29.
*E-mail address:* Marie-Pierre.Deiber@pse.unige.ch (M.-P. Deiber).

generally admitted that the in-phase coordination mode is economical for the motor system since, in this case, a similar motor command can be addressed to both limbs [4]. More, sensory reafferences tend to be temporally intermingled, providing a virtually unique perceptive signal of control for the system [6]. However, the view of a simplified motor command cannot account for the high efficiency of in-phase coordination when functionally different effectors are engaged. Another principle may thus apply for which the direction of movements in the external space (e.g., right hand and foot simultaneously up) constitutes a clear constraint on coordination, affecting a conceptual rather than a sensorimotor level. These observations suggest that, in the bimanual coordinative mode, at least two levels must be distinguished, namely an "abstract" level responsible for the in-phase/anti-phase aspect of the coordination to be produced, irrespective of effectors, and a "concrete" level at which the effectors themselves are specified [43]. The functional properties of bimanual coordination would result from the complex interplay of these abstract and concrete levels [6].

There is growing evidence favoring the view that bimanual coordination is controlled by a widely distributed cerebral network rather than a single anatomical structure [42]. While brain imaging studies have identified the cerebral areas involved [17,20,37,40,47,48], recent EEG studies have provided insights into the functional patterns of activity underlying bimanual coupling [1,9,11]. These studies have been mostly based on comparative assessments, contrasting either bimanual with unimanual movements, or bimanual movements of different effectors and/or complexity. To our knowledge, there is no available data on the neural mechanisms that could subtend the abstract and concrete aspects of bimanual coordination. We intended to address this question by considering the most preferred and stable pattern of bimanual coordination, namely in-phase mirror movements. Because motor execution intermingles recruitment of definite effectors in specific temporal relationships, we focused on the preparation phase of bimanual finger movements. By using the movement-precueing technique and manipulating the information provided in the precue, we intended to disentangle the aspects relative to the recruitment of symmetric effectors from those relative to the preparation of in-phase coordination.

In warned reaction time (RT) tasks, a sustained negativity called contingent negative variation (CNV) develops after the precue during the foreperiod interval [45]. The more movement dimensions are specified in the precue, the more RT decreases and CNV amplitude increases [5,21,25,26,49]. Hence, the CNV potential has been proposed to provide an index of abstract programming at a central level where all movement parameters can be specified in parallel [25,49, 55]. Additionally, a recent study has shown that effector-specific activity also contributed to the CNV potential, in case one motor program controls unilateral movements with different effectors [21]. Thus, conveying information on

both abstract and concrete levels of motor programming, the CNV potential represents a valuable index to characterize the preparation process preceding bimanual movements. Based on the results of Jentzsch's study [21], a particular CNV pattern could be anticipated in association to the precueing of in-phase coordination: while effectors are yet undefined, knowledge of coordination mode (bimanual in-phase movements) would induce concrete programming of potential effectors in addition to abstract motor preparation, resulting in large CNV amplitude. Preparation and execution of movements are also accompanied by an event-related desynchronization (ERD) in alpha and beta EEG frequency bands in regard to the central region, which has been associated to sensorimotor cortex activity [24,31,32,46]. While the extended CNV scalp negativity might be thought as the summation of post-synaptic activities and thus represents a depolarization of cortical cells indicating an increase in their readiness to discharge [14,39], the desynchronization of cortical rhythms, more focally distributed, is interpreted to reflect increased cellular excitability in functionally related groups of neurons [34,38,41]. Hence, CNV and ERD represent different aspects of neural activity, and their coupled analysis is susceptible to give complementary insight into the programming of effectors and coordination mode in preparation of bimanual movements. While a few studies dedicated to motor research have examined simultaneously cortical oscillatory activities and CNV potential [3,15,27,33], none of them have yet investigated how bimanual movements are prepared.

## 2. Materials and methods

### 2.1. Subjects

Twelve normal volunteers participated in the study, including 4 men and 8 women, with a mean age of 23.4 ± 6.5 years. All subjects were right handed as measured by the Edinburgh Inventory [29]. The protocol was approved by the Ethical Committee of the University of Geneva, and all the subjects gave their written informed consent for the study.

### 2.2. Experimental paradigm

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 little finger of each hand could be moved to press one specific key.

A delayed reaction time paradigm was used. Visual stimuli were presented at a constant viewing distance of 1.20 m and consisted of four signals arranged in a 3 cm grey square on a black background. A preparatory stimulus (S1)

characterized by two or four empty signals was presented for 2000 ms, requiring the subject to prepare his movement. An imperative stimulus (S2) characterized by four filled signals was then presented for 2500 ms, prompting the subject to execute the movement within the corresponding response window. A varying time interval (1.5–3 s) elapsed after S2 before a new S1 was presented (Fig. 1). Movements consisted in brisk bimanual in-phase or anti-phase flexion–extension of the index and/or little fingers in different combinations, with maximum flexion leading to keypress. A single flexion–extension cycle was required for each finger concerned. Bimanual in-phase movements corresponded to a simultaneous flexion–extension cycle of right and left fingers, while anti-phase movements presented a 180° phase lag between the cycle of each finger. Four preparation conditions were designed, differing by the information carried out by S1 (Fig. 1): (1) Full: complete movement information, requiring in-phase keypress with both indexes; (2) Mirror: partial information about the fingers to move, requiring keypress with both indexes; (3) In-phase: partial information about the mode of coordination of left and right movements, requiring in-phase keypress; (4) None: no movement information (meaningless signal combination). The four conditions were mixed at random in series of 68 trials. Focusing on the analysis of in-phase mirror movements led to select unique patterns for full as well as for partial precues, with the mere constraint of equalized number of response configurations between the mirror and the in-phase conditions being respected ($n = 3$). As such, our experimental design had two main advantages: first, the limited number of possible configurations contributed to keep the duration of the whole experiment within reasonable limits; second, the absence of the anti-phase configuration

for the coordination precue avoided the bias of a potential preselection of the first hand designed, which could confound the preparation of anti-phase coordination into the preparation of first side effectors. Subjects had an initial practice run, until they got familiar with the patterns and their associated responses. Six series were then acquired within a session, giving a total of 102 trials per condition. Additionally, a baseline condition was designed with the same temporal structure as the preparation conditions, but using meaningless S1 and S2 signals: the subjects were required to watch the stimuli while staying motionless (Rest condition). Two series of the Rest condition were acquired (totaling 102 trials), at the beginning and at the end of the session.

### 2.3. Data acquisition

Continuous EEG was recorded from 61 surface electrodes, mounted on a cap (Quick Cap, NeuroScan Inc.). Data were sampled at 500 Hz, the upper cutoff was 100 Hz and the lower cutoff was set to DC (DC amplifiers and software by NeuroScan Inc., Herndon, Va., USA). Linked earlobes served as reference. The electrooculogram (EOG) was recorded bipolarly from two electrodes placed above and below the right eye. Two bipolar EMG channels were recorded from surface electrodes positioned over the right and left forearm flexors (flexor digitorum communis), electrodes of each pair being located ~15 cm apart. The high pass filter for EMG was set to 10 Hz. Visual stimuli as well as keypresses were automatically documented with markers in the continuous EEG file. Reaction time (RT) corresponded to the time interval between S2 and the first keypress. For each condition, mean RTs were calculated for
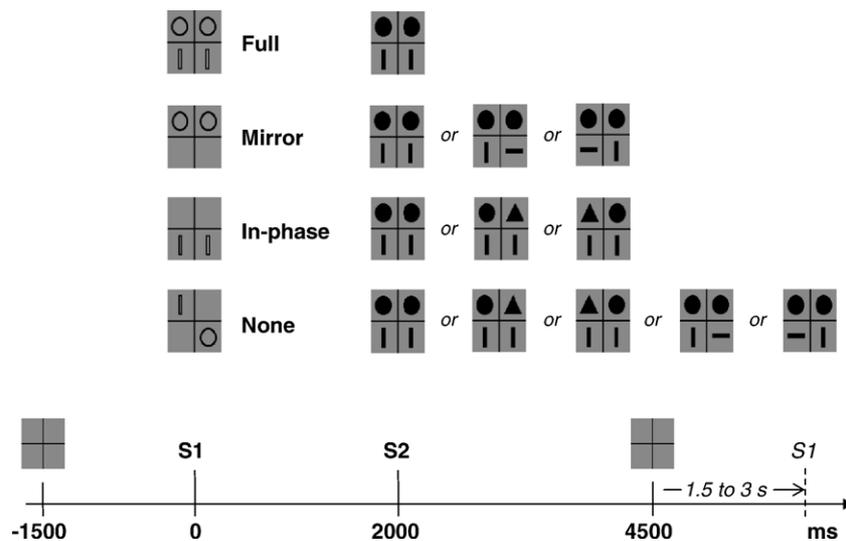


Fig. 1. Visual stimuli for each experimental condition and temporal sequence of events in a single trial. Empty signals for preparation (S1), filled signals for execution (S2). Left panel signals for left hand, right panel signals for right hand. Circle for index, triangle for little finger; two vertical bars for in-phase movements; vertical and horizontal bars for anti-phase movements, starting with the side of the vertical bar. There is a single informative S1 configuration for each of the Full, Mirror, and In-phase conditions: Full: "both indexes, in-phase"; Mirror: "both indexes"; In-phase: "in-phase". S1 is uninformative in None.

all response patterns, as well as for the in-phase mirror response pattern alone. Moreover, the RT to each response pattern was studied in the None condition, in absence of advance information.

## 2.4. Data analysis

EEG signals were corrected for ocular artifacts using a threshold rejection algorithm (Neuroscan Inc.). The total analysis window was 4500 ms, starting 1500 ms before S1. The 4500 ms EEG trials were digitally filtered off-line (low-pass filter 70 Hz, slope 24 dB/octave) and a baseline correction over 1500 ms prior to S1 was computed. The CNV potential, largely present over the scalp, is a composite waveform made of sub-cortical as well as cortical radial and tangential contributions [3,28]. For this reason, no procedure of re-referencing or spatial filtering was used on the data, which could have noticeably attenuated some CNV components. Moreover, the use of high spatial filtering such as Laplacian transformation on scalp potential as well as on spectral power data can result in complex topographical patterns particularly hard to interpret, mainly due to the difficulty in identifying tangential sources [2,19]. For congruence purposes in parallel analysis of CNV and ERD, the ERD calculation was also performed on the dataset in common reference. Topographic analysis of each electrophysiological index was focused on differential distribution patterns across conditions rather than on anatomical localization of activity for each condition.

The EEG trials were automatically scanned for contamination by muscular or electrode artifacts, and the remaining trials were inspected visually to control for minor artifacts. A minimum of 60 artifact-free trials were averaged per subject and condition, after merging trials from the 6 series (within-subject-averaged waveforms). There was an equal number of trials averaged per condition for each subject. To study electrophysiological indices of cerebral activity, we opted for a region of interest (ROI) approach, which focuses on a restricted number of electrodes on the basis of the regional distribution of the indices under study.

### 2.4.1. Contingent negative variation

As previously reported [9], the CNV in preparation for bimanual movements displayed an extended scalp distribution centered medially on the scalp surface (Fig. 4A). Three ROIs of 3 electrodes each were selected in order to account for a possible lateralization of the CNV potential with the mode of preparation: left hemisphere (F3, C3, P3), medial region (Fz, Cz, Pz), and right hemisphere (F4, C4, P4). Since the onset latency of the CNV was variable between subjects and electrodes, and in order to avoid resulting measurement biases, the CNV amplitude was assessed during its sustained phase, i.e., between 1000 ms and 2000 ms after S1. The 1000 ms analysis period was further subdivided into two segments displaying special

characteristics: the initial CNV [1000;1500 ms] reached a peak of amplitude in the frontocentral region, while the terminal CNV [1500;2000 ms] declined in amplitude and was more posteriorly distributed. In each of these 2 segments, the mean amplitude was calculated for each electrode of interest, and a logarithmic (log) transformation was performed in order to obtain a Gaussian distribution of the values. For statistical assessment of CNV amplitude, a 3-way repeated measures ANOVA was performed on these mean log amplitude values, with Condition (Full, Mirror, In-phase, None), Time ([1000;1500 ms], [1500;2000 ms]), and ROI (Left, Medial, Right) as within-subject factors.

### 2.4.2. Event-related desynchronization/synchronization (ERD/ERS)

In a first step, the reactive frequency ranges were determined on the basis of visual inspection of the grand average power spectra in the 2 s delay period [35]: differences between preparation and rest conditions were most prominent in the alpha (8–12 Hz) and beta ranges (15–25 Hz). In consequence, further analysis of the spectral power time course was focused on these frequency bands, using the standard technique of ERD/ERS [34]. The same trials selected for CNV analysis were used for ERD/ERS calculations. The signal was digitally filtered in the 8–12 Hz and 15–25 Hz bands, respectively, using narrow band-pass filters ($-48$ dB/octave). The filtered signals were then squared and averaged across trials. The spectral power magnitude at each electrode ($P$) was normalized by expressing the change in signal power as a ratio to the average power during the baseline ($B$) using the following formula: $\%(\text{ERD/ERS}) = ((B - P)/B)*100$. The 1500-ms period preceding S1 served as baseline. Thus, positive percentage values correspond to a decrease in power, or desynchronization (ERD), negative percentage values to a power increase, or synchronization (ERS), and null values to an absence of power variation.

In both alpha and beta bands, an ERD was elicited within 0 and 500 ms after S1 and maintained throughout the delay period (Figs. 3B and C). ERD amplitude was assessed during its sustained phase, i.e., between 500 and 2000 ms after S1.This time window was further subdivided within three time segments of 500 ms each, with the two last segments matching those for CNV analysis: [500; 1000 ms], [1000; 1500 ms], and [1500; 2000 ms]. Alpha and beta ERDs were more focally distributed over the central, mesial, and parietal regions than the CNV potential (Figs. 5A and 6A). To account for this distribution, six ROIs of 2 electrodes each were selected, overlying brain structures that have been shown to be involved in motor preparation in a paradigm similar to the present one [10]: sensorimotor cortex, parietal cortex, and mesial motor regions. The choice of the electrodes included in each ROI was also guided by recent motor EEG studies of task-related power and coherence values [1,11,16]. Electrodes known to overlie
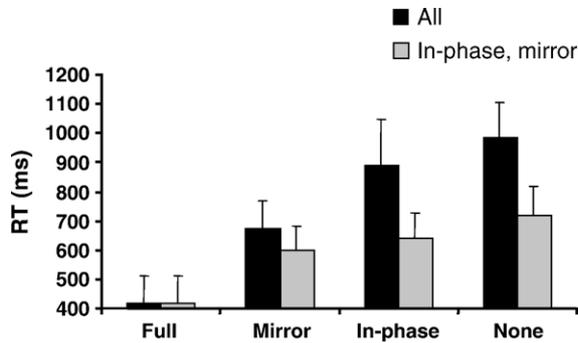
Fig. 2. Mean reaction time (RT) and standard deviation to all patterns confounded and to the in-phase mirror pattern (*n* = 12). For each measure, the RT is significantly different between conditions.

approximately the primary sensorimotor cortex were grouped into two central ROIs, one on each hemisphere: Left Central (LC): C3, CP3; Right Central (RC): C4, CP4. Likewise, electrodes overlying the parietal region were grouped into two parietal ROIs, one on each hemisphere: Left Parietal (LP): P3, PO3; Right Parietal (RP): P4, PO4. Electrodes in the midline were grouped into two mesial ROIs: Anterior mesial, overlying the supplementary motor area (SMA): FCZ, CZ; and Posterior mesial, overlying the precuneus (PCu): CPZ, PZ. The ERD/ERS values for each electrode of interest were averaged within the 6 ROIs. ERD/ERS statistical analysis was performed independently in the alpha and beta frequency bands using 3-way repeated measures ANOVAs with Condition (Full, Mirror, In-phase, None), Time ([500; 1000 ms], [1000; 1500 ms], [1500; 2000 ms]), and ROI (LC, RC, LP, RP, SMA, PCu) as within-subject factors.

## 3. Results

### 3.1. Performance

The overall error rate was very low (1.7% of all responses). Incorrect responses (wrong keypresses) were the most common (0.83%), followed by response omissions (0.52%) and early responses (0.15%). Most of the errors

(48%) occurred in the None condition, 29% in the In-phase condition, 13% in the Mirror condition, and 10% in the Full condition.

Fig. 2 presents the mean RT to all patterns confounded and to the in-phase mirror pattern, respectively, and results from statistical analysis are given in Table 1. In both cases, the Full condition was associated with shortest RTs, and the None condition with longest RTs. RTs were longer in the In-phase than in the Mirror condition. There was a significant effect of Condition on RT when confounding all responses as well as when considering the in-phase mirror response only (Table 1). Contrast analysis revealed that in both cases, every condition was significantly different from each other (Table 1). The pattern type has a significant effect on choice RT, as measured in the None condition (one-way ANOVA, $F(4,44) = 31.61$, $P < 0.001$). Contrast analysis showed that the in-phase mirror response pattern was associated to significantly shortest RT ($721 \pm 96$ ms), while the other two in-phase response patterns involving asymmetrical fingers were associated to significantly longest RTs (left index–right little finger: $1170 \pm 264$ ms; right index–left little finger: $1240 \pm 235$ ms). Intermediate RTs were recorded for the two anti-phase mirror patterns (both indexes, starting right: $906 \pm 88$ ms, starting left: $951 \pm 111$ ms).

### 3.2. CNV

For the four preparation conditions, the potential elicited by S1 consisted in a fast event-related response immediately following S1 and a slow rising negativity reaching a maximum at around 1000 ms then decreasing before S2 presentation; at S2, a fast response was observed similar to the one observed after S1 (Fig. 3A). The fast responses evoked by S1 and S2, also present in the Rest condition, merely reflect initial processing of the visual stimuli and will not be considered here. The slow negative potential developing during the delay period corresponds to the contingent negative variation (CNV), it was absent in the Rest condition since no motor preparation was required (Fig. 3A). The CNV was largely distributed over the scalp, with a peak in the central region (Fig. 4A). CNV scalp distribution was similar across all conditions, but amplitude

Table 1
Reaction time (RT) per condition

|  | RT(1) | RT(2) | Main effect for condition | Contrast analysis | $F(1)$ | $F(2)$ |
|---|---|---|---|---|---|---|
| Full | 417 ± 96 | 417 ± 96 |  | Full vs In-phase | 75.3** | 83.1** |
|  |  |  | (1) $F(3, 33) = 96.0$** | Full vs Mirror | 105.3** | 83.0** |
|  |  |  | (2) $F(3, 33) = 94.4$** | Full vs None | 195.2** | 145.5** |
| Mirror | 673 ± 97 | 598 ± 85 |  | Mirror vs None | 158.2** | 160.2** |
| In-phase | 890 ± 158 | 641 ± 88 |  | In-phase vs Mirror | 30.2** | 12.6* |
|  |  |  |  | In-phase vs None | 16.2* | 27.6** |
| None | 985 ± 117 | 721 ± 96 |  |  |  |  |

RT in milliseconds ± standard deviation.
(1) all patterns confounded; (2) in-phase mirror pattern.
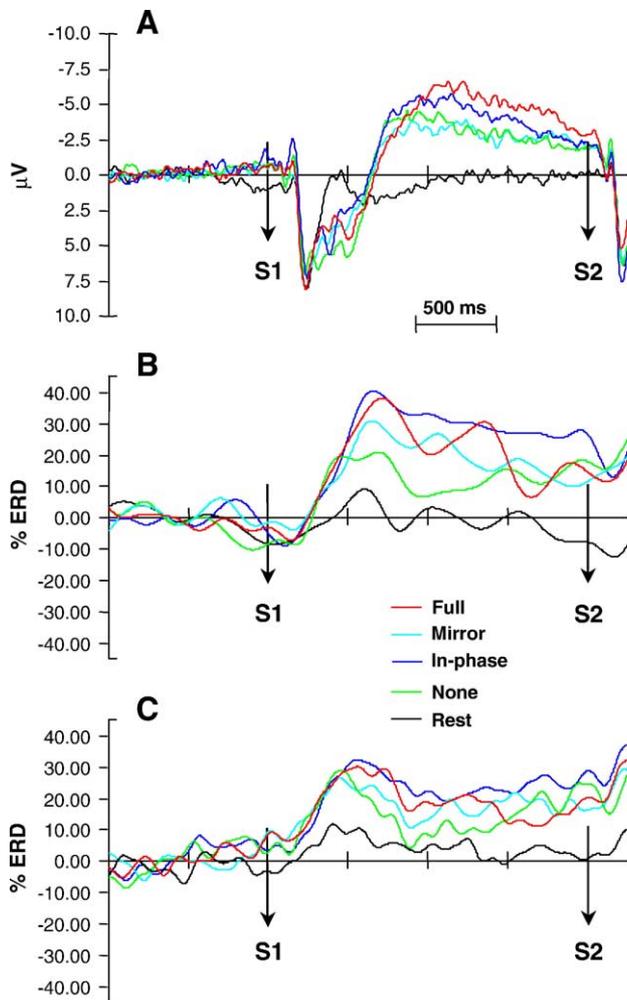*F*: one-way repeated measures ANOVA; *P < 0.01; **P < 0.001.

Fig. 3. Grand average electrophysiological signals on Cz electrode for each condition ($n = 12$). S1 corresponds to time 0 and S2 occurs at 2000 ms. (A) Electrical potentials, revealing the slow negative component (CNV); (B) Alpha ERD/ERS (8–12 Hz); (C) Beta ERD/ERS (15–25 Hz).

differences could be observed between conditions essentially in its initial portion. The 3-way ANOVA (Condition, Time, ROI) revealed significant main effects of Condition ($F(3,33) = 7.19$, $P < 0.001$), Time ($F(1,11) = 15.16$, $P < 0.01$), and ROI ($F(2,22) = 8.44$, $P < 0.01$), but no interactions between factors. The Time effect was due to larger CNV amplitude in the initial as compared to the terminal time period (Fig. 4B). The effect of preparation mode on CNV amplitude was significant in both time periods (Fig. 4B). Contrast analysis revealed that during the initial time period, the CNV amplitude was significantly larger in the Full condition than in the Mirror and None conditions, respectively (Full vs Mirror, $F(1,11) = 12.34$, $P < 0.01$, Full vs None, $F(1,11) = 15.21$, $P < 0.01$). The initial CNV was also larger in the In-phase than in the Mirror and None conditions (In-phase vs Mirror, $F(1,11) = 7.96$, $P < 0.02$, In-phase vs None, $F(1,11) = 5.13$, $P < 0.05$). In the terminal time period, only the Full and the None conditions significantly differed in terms of CNV amplitude

($F(1,11) = 7.98$, $P < 0.02$). The ROI effect resulted from a larger CNV amplitude in the medial leads (Fig. 4C; Contrast analysis, Medial vs Left hemisphere, $F(1,11) = 12.05$, $P < 0.01$; Medial vs Right hemisphere, $F(1,11) = 13.75$, $P < 0.01$).

### 3.3. Alpha ERD

A weak initial ERS starting before S1 onset was elicited in all conditions including Rest, rapidly followed by a sharply increasing ERD in the four preparation conditions only. The ERD culminated between 500 and 1000 ms, then decreased (Fig. 3B). It disclosed a centroparietal distribution and appeared of larger amplitude in the Full and In-phase conditions, reaching 40% of baseline level (Figs. 3B and 5A). The 3-way ANOVA (Condition, Time, ROI) revealed no significant main effects, but only an interaction Condition × ROI ($F(15,165) = 3.52$, $P < 0.001$). Two features were mainly responsible for this interaction (Fig. 5B): (1) in RP and to a smaller extent in RC, the ERD tended to be larger in the Full as compared to the In-phase condition, whereas in all other ROIs it was higher in the In-phase condition; (2) the ERD over SMA was low in the None condition relative to the other ROIs and conditions.

### 3.4. Beta ERD

The four preparation conditions disclosed a sharp beta ERD increase within 500 ms after S1 onset, comparable to the alpha ERD increase although of less amplitude (~30% of baseline level). The beta ERD reached a peak in the 500–1000 ms time window, followed by a decrease, followed by a second increase culminating after S2 onset (Fig. 3C). Beta ERD was more centrally distributed as compared to alpha ERD and appeared of higher amplitude in the Full and In-phase conditions (Figs. 3C and 6A). The 3-way ANOVA (Condition, Time, ROI) revealed significant main effects (Condition, $F(3,33) = 4.03$, $P < 0.02$, Time, $F(2,22) = 5.09$, $P < 0.02$, ROI, $F(5,55) = 3.73$, $P < 0.02$) as well as an interaction Condition × Time ($F(6,66) = 3.99$, $P < 0.01$). The Condition effect pointed out higher ERD values in the Full and In-phase conditions (Fig. 6B), and contrast analysis revealed significant differences between Full and None conditions ($F(1,11) = 5.03$, $P < 0.05$) and between In-phase and None conditions ($F(1,11) = 7.85$, $P < 0.02$). The time curve was U-shaped (Fig. 6B), and contrast analysis established that the ERD amplitude was significantly smaller in the second time window (1000–1500 ms) as compared to the first (500–1000 ms; $F(1,11) = 7.65$, $P < 0.02$) and last time windows (1500–2000 ms; $F(1,11) = 11.35$, $P < 0.01$). The ROI effect was issued from the contrast between large ERD amplitude in the central ROIs (LC, RC, and SMA) and reduced ERD amplitude in the parietal leads (LP, RP, Pcu; Fig. 6C). The interaction between Condition and Time was largely explained by the ERD pattern in the last time window, which showed an
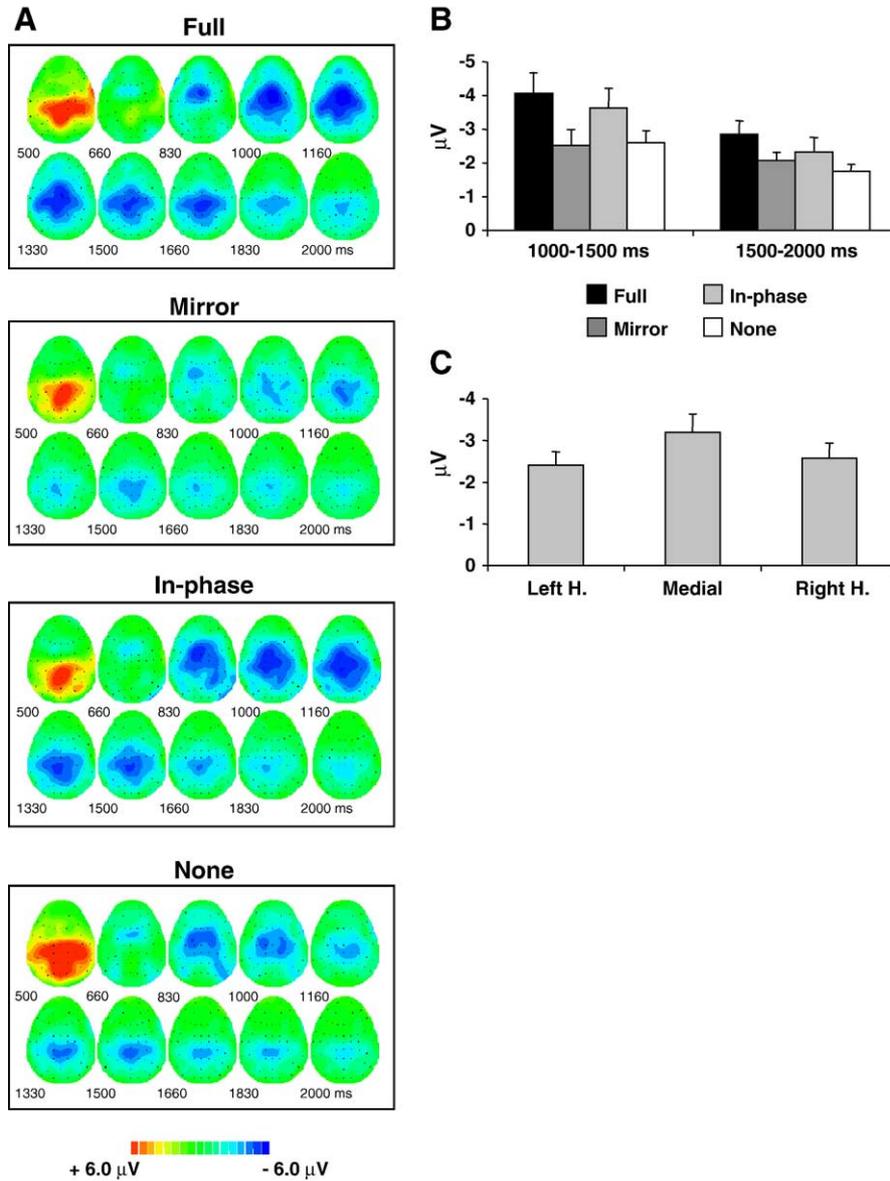
Fig. 4. CNV results. (A) Grand average topographic potential maps in the delay period between 500 and 2000 ms after S1 ($n = 12$). Top views of the head, dots indicate electrode positions. Blue colors for negative, red colors for positive potential values. (B) Mean CNV amplitude ($\pm$standard error) within each time window and condition across all ROIs ($n = 12$). (C) Mean CNV amplitude ($\pm$standard error) for each ROI across time windows and conditions ($n = 12$).

increase in all conditions except in the Full condition (Fig. 6B).

## 4. Discussion

### 4.1. Experimental remarks

The present study investigated the functional organization associated to the preparation of in-phase mirror movements, analyzing the cerebral activity subtending the programming of symmetric effectors and in-phase coordination, respectively. While our full precue designed only in-phase movements of both indexes, our partial precues signaled either the two indexes as mirror effectors or

informed on the in-phase synchronization of bimanual movements. Such a design introduced two principal limitations to be evaluated. The first one concerns the fact that the in-phase movement of both indexes occurred more frequently within a run, and an advantage of this response over the others could be discussed in terms of practice as well as programming bias. In-phase mirror movements correspond to a privileged mode of bimanual coordination, and they are largely documented as being more stable, and thus easier, than any other bimanual movements [22,23,42]. We confirmed this fact when analyzing the RT to the five different response patterns in the None condition and showing that in-phase movements of both indexes were the fastest. Therefore, an unavoidable bias was definitely present in favor of in-phase mirror movements, primarily
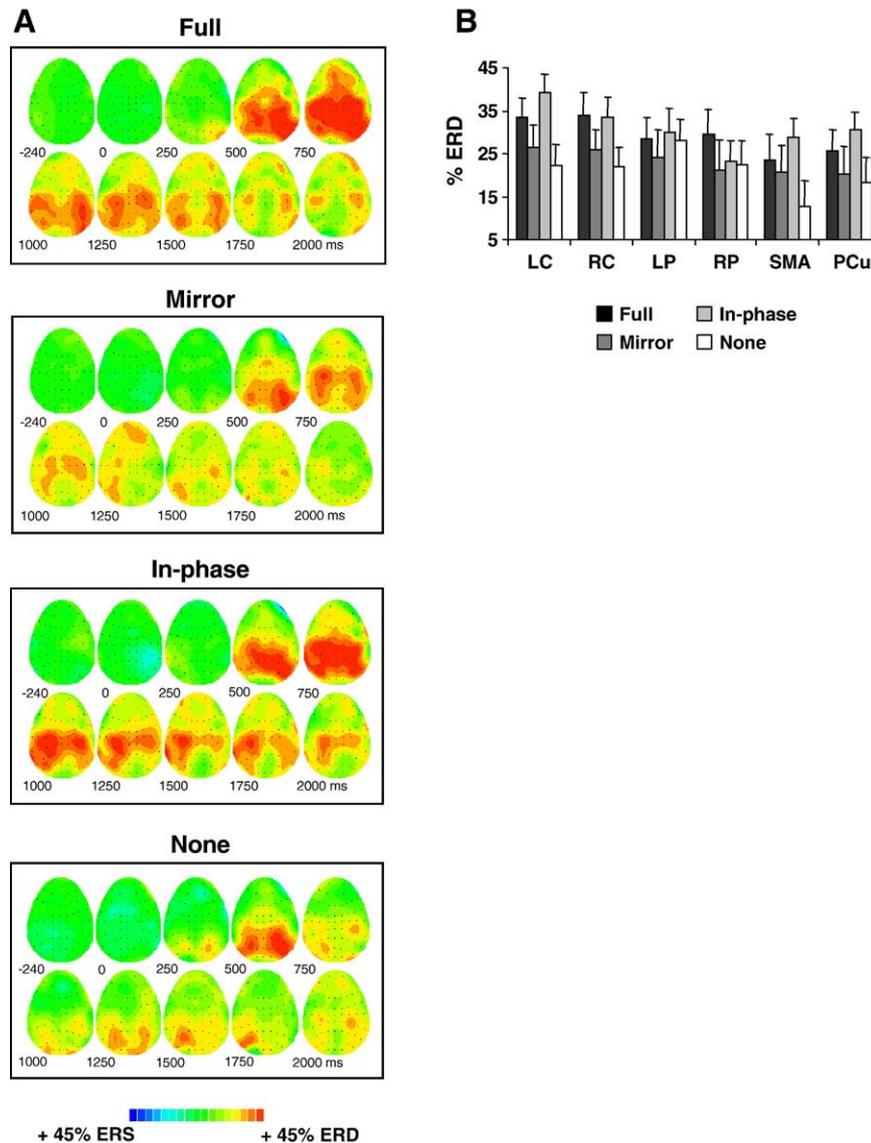
Fig. 5. Alpha ERD/ERS results. (A) Grand average topographic alpha ERD/ERS maps ($n$ = 12) from −240 ms to 2000 ms relative to S1. Red colors for ERD, blue colors for ERS. (B) Mean alpha ERD value (±standard error) for each ROI and condition across the three time windows (500–2000 ms; $n$ = 12). LC: Left Central; RC: Right Central; LP: Left Parietal; RP: Right Parietal; SMA: Supplementary Motor Area; PCu: Precuneus.

due to the inherent properties of bimanual coordination. Mixing the different precue conditions within a run contributed to limit a potential strategic bias to prepare for in-phase mirror responses. It is also noticeable that while responses involving the little fingers were the slowest, and proportionally more abundant in the In-phase than in the None condition, the RT difference between these two tasks was in favor of the In-phase condition. Such an observation supports the dominant influence of precueing over the type of finger involved in the response. The second limitation concerns the potential confounding factor relative to the prediction of upcoming response difficulty. Indeed, the in-phase and mirror precues pre-specified partly different responses that were associated to different levels of difficulty, as reflected in their RTs in the absence of advance information (None condition): in-phase movements of

heterogeneous effectors present in the In-phase condition were slower than anti-phase index movements present in the Mirror condition. Again, those differences in difficulty level were unavoidable since they refer to inherent properties of bimanual movements, characterized by preferential modes of coordination. However, facing these potential design confounds essentially deriving from bimanual coordination constraints, it was essential to ensure that the task effects observed on RT were effectively due to the nature of advance information, rather than to any other motor parameter. To this purpose, we performed an independent analysis on the responses to the in-phase mirror pattern, which was present in all conditions. This analysis provided the same results as the analysis involving all responses, confirming the effect of the preparation mode on RT. We can thus affirm that in our paradigm, the RT to S2
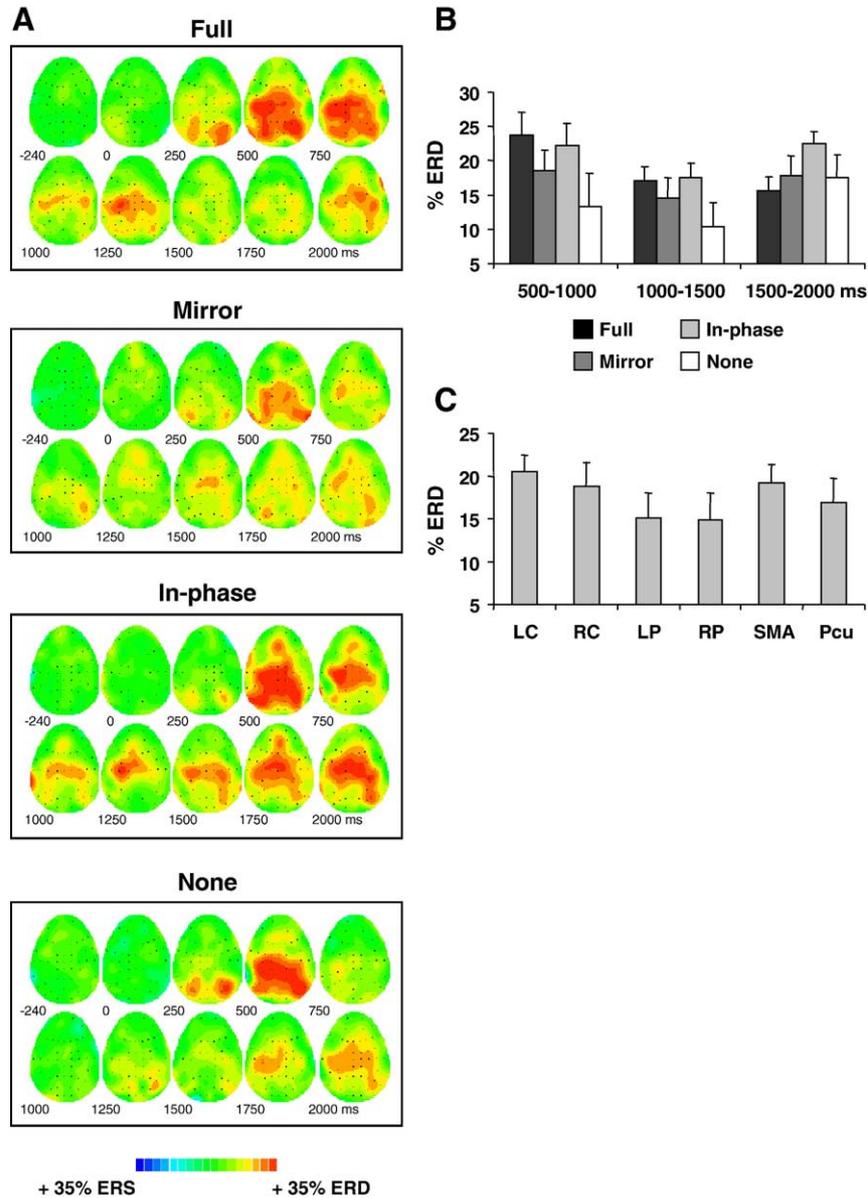
Fig. 6. Beta ERD/ERS results. (A) Grand average topographic beta ERD/ERS maps ($n$ = 12) from −240 ms to 2000 ms relative to S1. Red colors for ERD, blue colors for ERS. (B) Mean beta ERD value (±standard error) within each time window and condition across all ROIs ($n$ = 12). (C) Mean beta ERD value (±standard error) for each ROI across time windows and conditions ($n$ = 12). LC: Left Central; RC: Right Central; LP: Left Parietal; RP: Right Parietal; SMA: Supplementary Motor Area; PCu: Precuneus.

imperative stimulus is indeed dominantly affected by the mode of preparation, independent of motoric aspects linked to bimanual coordination, or potential predictions relative to the difficulty of the upcoming response.

### 4.2. Mode of preparation and response performance

In accordance with previous literature [5,10,13,49], the shortest RTs were observed when the bimanual movement was fully specified, i.e., when both the effectors and the mode of coordination were predetermined. In addition, our RT data showed that specifying the effectors was more efficient on motor performance than the specification of movement coordination. In other words, as far as homolo-

gous effectors and in-phase coordination are concerned, the control system for bimanual movement appeared to take greater advantage of a cue specifying the effectors to be moved than the coordinative mode. These RT results are compatible with the classical model of motor programming, which suggests that not all precues are equally beneficial and that movement effectors are the first parameters to be specified [36].

### 4.3. Mode of preparation and cerebral activity

CNV as well as alpha and beta ERD recorded during the preparation of bimanual movements displayed partially distinct reactivity to the type of advance information. While

both CNV and beta ERD results suggested that the magnitude of cerebral activation was globally influenced by the preparation mode, beta ERD underwent additional temporal modulations that were dependent on the type of precue. On the other hand, alpha ERD showed regional modulations according to the preparation process. An interesting finding concerned the large activation associated to in-phase programming as reflected by CNV and beta ERD amplitudes, which, in contrast to full preparation, was associated to poor motor performance.

### 4.3.1. CNV

CNV amplitude was sensitive to the preparation type, essentially in its initial 500 ms portion. The CNV potential has been classically subdivided into an early wave, supposed to reflect principally orienting reaction to the precue, and a late wave, which was thought to be associated to motor preparation as well as other non-motoric processes such as response signal expectancy [45,50]. However, since every study uses a specific time interval between the precue and response signal, and differs in terms of task parameters and complexity, there is a tremendous disparity in the literature about CNV measurements, and no consensus exists on the exact duration of the underlying processes. A recent study using a unimanual forewarned RT task has shown that the initial CNV was accompanied by an early lateralized alpha ERD over the sensorimotor cortex, suggesting that task-specific motor processing already occurs in relation to the warning stimulus [3]. This result is supported by our own findings of alpha and beta ERD arising early after S1. More importantly, it is compatible with our observation that the initial CNV is significantly influenced by the precue as a tool for motor preparation. The precueing effects observed on initial CNV remained on terminal CNV, but of less amplitude. Thus, the present data suggest that the programming of effectors and coordination for bimanual movements would take place relatively early during the instructed foreperiod and that a trace of it would remain until the occurrence of the response signal. The antero-posterior topographic differences between the initial and terminal CNV likely result from the interplay of distinct functional processes during the preparatory period: frontal, mesiofrontal, and central activity related to orienting attention, selection of motor action, and task-specific motor processing would contribute to the frontocentral distribution of the initial CNV, while central muscle programming as well as posterior sensory-related anticipatory attention for S2 would participate to the centroparietal topography of the terminal CNV [9,18].

The CNV was of similar amplitude in the Full and In-phase conditions, a result that contrasts with the performance data, RT in the In-phase condition being much longer than in the Full condition. Earlier reports have generally demonstrated a positive correlation between CNV amplitude and informative content of the preparatory stimulus, in parallel with a negative correlation between CNV ampli-

tude and RT [5,13,15,26,49,51]. However, Jentzsch and colleagues also found that CNV amplitude with partial precue specifying side only was similar than with full precue specifying effectors and side, and they suggested that a motor program could be activated at an abstract level even when the effectors were not known [21]. They reached the conclusion that a common motor program could control for the movements of functionally close effectors and that when side only is known, both abstract and effector preparation could occur. Such parallel process would account for comparable or even larger CNV amplitude in the partial condition specifying side compared to the full precue condition, due to overlapping abstract and effector-specific motor activity. Our own findings are compatible with this view, suggesting that when only the in-phase mode of coordination is known for finger movements, abstract programming and concrete effector preparation are taking place, resulting in large CNV amplitude. Additionally, the fact that CNV amplitude was larger in the In-phase than in the Mirror condition further supports the hypothesis that overlapping programming processes are involved in the former condition vs single preparation of symmetric effectors in the latter condition. Concerning CNV topographic distribution, our data revealed a peak of amplitude over the midline, in accordance with a previous study on bimanual finger sequence preparation [9]. Such localization is compatible with the implication of bilateral and medial motor structures in bimanual programming [42], regions that are also implicated in CNV generation [3,28].

### 4.3.2. Alpha ERD

In spite of a tendency for higher alpha ERD in Full and In-phase conditions, our data did not evidence main effects of preparation mode on alpha activity. Accordingly, we had previously reported the lack of sensitivity of alpha activity to the precise nature of the task by showing that alpha oscillations did not differentiate bimanual in-phase and anti-phase sequences [11]. In confirmation of a recent study [15], the absence of global alpha reactivity to specific task attribute contrasts with the reactivity of the CNV potential, which would better reflect the relevance of task parameters to action performance. However, the present results evidenced differences in alpha scalp topography according to advance information, suggesting that modulations of alpha oscillations indeed occur during bimanual motor preparation and that they reflect regionally specific processes. These differences concerned the Full and In-phase conditions on one hand and the None condition on the other hand. Regions of interest located in the right hemisphere, more specifically parietal regions, showed comparatively higher alpha activity in the Full than in the In-phase condition, while left hemispheric and medial regions presented the converse pattern. A right parietal activation in the Full condition would be concordant with the completion of the stimulus–response transformation

process in the presence of all movement parameters [7,51]. Programming in-phase coordination engaged predominantly left hemispheric and medial regions, an observation compatible with the hypothesis that temporal coupling in bimanual movements may depend on a pace-keeping mechanism preferentially controlled by the dominant hemisphere [12,53]. Enhanced activity observed for electrodes located over the midline structures additionally suggests the participation of higher-level sensorimotor areas (SMA, cingulate motor area, precuneus) in programming in-phase coordination. This observation is consistent with dipole source analysis [21,25] and further supports the hypothesis that medial activity could be related to abstract motor programming. The None condition contrasted with the others essentially for the reduced activation in electrodes overlying the SMA region, as reflected by low alpha ERD. This observation in a condition where no specific motor preparation of any sort could be achieved is consistent with the commonly accepted role of SMA both in preparation of movements [30] and bimanual coordination [43].

### 4.3.3. Beta ERD

The beta oscillations underwent modulations in the 2-s preparation period, which is compatible with their fast rebound properties [8]. In the last period of the delay, within 500 ms before S2, the beta ERD tended to accentuate in all conditions except in Full. The resulting interaction between time and condition factors could reveal a special sensitivity of beta oscillations to expectancy, since the system had to get ready for processing additional information at S2 in the Mirror, In-phase, and None conditions. The overall larger beta ERD with in-phase and full precues paralleled the result on CNV amplitude, suggesting more intense cerebral activation during these information conditions. However, beta ERD appeared less sensitive than initial CNV, since it differentiated only the Full and In-phase conditions from the None condition. This is consistent with the view that beta oscillations correspond to large-scale processes tuning cortical excitability and that finer task-dependent modulations occur at cortical level, as revealed by modifications of post-synaptic responses reflected in the CNV. Bilateral central and mesiofrontal distribution of beta ERD is compatible with the activation of the motor-related neuronal network [44].

### 4.4. Towards an understanding of bimanual motor preparation

In-phase mirror movements represent a privileged mode of bimanual coordination, as confirmed by the present performance results for various combinations of coordinative modes and hand effectors. Focusing on motor programming, we have shown that performance gained more when the precue specified mirror effectors rather than the in-phase coordinative mode. Such finding is compatible

with the view that in bimanual coordination, a concrete level that concerns the effectors can be distinguished from an abstract level relative to the coordinative mode, the former being associated with faster response execution than the latter. A remarkable observation concerns the fact that cerebral activity associated to bimanual motor programming could not be simply predicted by the behavioral results. Our data showed that programming in-phase coordination necessitated more cerebral resources than programming symmetric effectors. In line with a previous motor preparation study contrasting partial programming of side with complete, side and effector preparation [21], these findings support the hypothesis that intermingled brain processes could be engaged in the preparation phase for bimanual movements. In particular, large cerebral activity associated to in-phase coordination programming could result from the overlap of abstract motor programming, putatively located in the higher-level mesial motor regions, and effector-specific activity originating in corresponding primary motor areas.

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