Research report

Post-switching beta synchronization reveals concomitant sensory reaafferences and active inhibition processes

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HIGHLIGHTS

- Electrical neuroimaging shows beta synchronization after selective inhibition.
- Beta synchronization in a restricted-band (22–26 Hz) within left parietal cortex.
- Beta synchronization in a broad-band (14–30 Hz) within right pre-frontal cortex.
- Beta synchronization is related to active inhibition and sensory reaafferences.

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ABSTRACT

It is known that post-movement beta synchronization (PMBS) is involved both in active inhibition and in sensory reaafferences processes. The aim of this study was examine the temporal and spatial dynamics of the PMBS involved during multi-limb coordination task. We investigated post-switching beta synchronization (assigned PMBS) using time-frequency and source estimations analyzes. Participants (n = 17) initiated an auditory-paced bimanual tapping. After a 1500 ms preparatory period, an imperative stimulus required to either selectively stop the left while maintaining the right unimanual tapping (Switch condition: SWIT or to continue the bimanual tapping (Continued condition: CONT). PMBS significantly increased in SWIT compared to CONT with maximal difference within right central region in broad-band 14–30 Hz and within left central region in restricted-band 22–26 Hz. Source estimations localized these effects within right pre-frontal cortex and left parietal cortex, respectively. A negative correlation showed that participants with a low percentage of errors in SWIT had a large PMBS amplitude within right parietal and frontal cortices. This study shows for the first time simultaneous PMBS with distinct functions in different brain regions and frequency ranges. The left parietal PMBS restricted to 22–26 Hz could reflect the sensory reaafferences of the right hand tapping disrupted by the switching. In contrast, the right pre-frontal PMBS in a broad-band 14–30 Hz is likely reflecting the active inhibition of the left hand stopped. Finally, correlations between behavioral performance and the magnitude of the PMBS suggest that beta oscillations can be viewed as a marker of successful active inhibition.

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1. Introduction

Electro-cortical recordings in normal human adults show that amplitudes of alpha and beta rhythms are modulated over the sensorimotor cortex before, during and following the execution of voluntary movement [1–4]. During unilateral limb movement, these modulations are characterized by a reduction of amplitude during the preparation and execution phases (event-related desynchronization, ERD) followed by an increase of amplitude synchronization once the movement is completed (event-related synchronization, ERS; also called post-movement beta synchronization, PMBS). More specifically, alpha and beta ERD start about 2 s before the voluntary movement over the contralateral sensorimotor areas and extends bilaterally with movement initiation.

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The PMBS occurs approximately 1 s after movement termination over the contralateral sensorimotor areas [2,5–8]. While converging studies confirm that alpha and beta ERD are related to cortical activations [6,9,10], the significance of the PMBS is unclear. It is proposed that the PMBS could reflect cortical inhibition [4,9,11,12] and/or sensory reaffereence processing [1,13–15].

The hypothesis of sensory reaferences processing emerges because large PMBS is observed after median nerve stimulation or tactile stimulations of the finger [13,16,17]. Houdayer et al. [13] used a task in which participants either performed right index finger or on or on the median nerve. A PMBS (13–25 Hz) was observed in all conditions, with more intensity for finger extension and median nerve stimulation than for index finger stimulation. Authors concluded that the PMBS is related to reafference information and depends on the type and quantity of the afferent inputs. The work of Cassem and collaborators [1] illustrated the relation between PMBS and sensory reaferences during active and passive movements (involving no motor cortex activity) as well as during passive movements following deafferentation by ischemic nerve block. They reported similar magnitude of PMBS (13–25 Hz) after active and passive movements and the suppression of PMBS after passive movements with deafferentation. Authors concluded that the PMBS cannot solely be related to pure motor deactivation but may involve the processing of sensory reaferences. However, Alegre and colleagues [18] showed that during a sequence of right hand movements, the PMBS emerged in left central region only once the whole action was finished and not after each sequential movement. This result indicates that the PMBS might be more closely related to the termination of the motor plan (inhibition process) than to the sensory reaferences processes.

In line with the conclusion of Alegre and colleagues [18], others studies suggest that the PMBS is related to inhibitory processes. Precisely, PMBS has been related to deactivation (also called idling state or resting state) or active inhibition processes. Despite a clear distinctness between these processes, PMBS related to active inhibition has been suggested during motor imagery or execution of coordination tasks [11,19,20] and Go/No-go task [12] while PMBS related to deactivation has been observed during discrete voluntary movements task [3,4,9,21].

The PMBS related to deactivation processes have been observed after movement termination. Pfurtscheller and collaborators [9] showed that the PMBS (around 20 Hz) was maximal over the contralateral hemisphere after voluntary self-paced right manual movements and hypothesized to a deactivation processes. Using transcranial magnetic stimulation (TMS) on hand area, Chen et al. [22] corroborated the deactivation hypothesis by showing a reduction of excitability of the contralateral motor cortex within the first second after termination of a finger movement. A more recent study investigates the PMBS in a Go/No-go task in which participants were required to respond with a brisk foot movement at a Go stimulus or to withhold foot movement at a No-go stimulus [12]. The results reveal a PMBS in both conditions suggesting that the PMBS is not exclusively observed after the termination of movement but also during the withholding of prepared action. In the No-go condition, the PMBS is likely to stand for a more active processing involved in the inhibitory control of human motor behavior.

The PMBS associated to active inhibition processes have been observed during execution of alternated movements between several limbs. Pfurtscheller and collaborators [11] reported simultaneous alpha/beta ERD and PMBS in a task where participants have been invited to perform either a hand or a foot movement in response to visual stimulation. During foot movements, an ERD (10–12 Hz) occurred in the foot area with a concomitant PMBS (around 20 Hz) in the hand area. All occurs as if the PMBS refers to an active inhibition of the effector that does not move. In another study, Pfurtscheller and Neuper [19] instructed the participants to imagine movements with the right or the left hand according to a visual stimuli. Again, these authors found an ipsilateral PMBS (around 20 Hz) during the imagined movement. The ipsilateral PMBS was interpreted as an active inhibition of motor area to prevent any movement from the resting hand. TMS studies also evidenced active inhibition processes during repetitive manual movements [23,24]. In the study from Stinear and Byblow [24], participants performed index movements auditory paced (1 Hz) with the dominant hand while TMS is applied over the ipsilateral primary motor cortex (M1) not involved in the movement. Results showed an increase of intracortical inhibition in the ipsilateral M1 during the unilateral index movements. Authors concluded that the increased intracortical inhibition in the ipsilateral M1 might actively prevent unwanted homologous muscle activation in order to prevent motor interference. More recently, active inhibition was evidenced in a motor switching task [20]. Using task-related spectral power measures, authors showed an increase of beta power (13–30 Hz) over the frontal area during switching from anti-phase to in-phase bimanual coordination, supporting the occurrence of an intentional inhibition of the more complex anti-phase to the less complex in-phase coordination. Finally, in Cremoux et al. [25], decreased PMBS (13–31 Hz) amplitude in participants with spinal cord injury was associated to longer time to inhibit voluntary contractions.

All in all, according to the two inhibitory processes describe above, one can view the neural deactivation as a closed door (we accompany someone to leave the room and we close the door) while active inhibition might refer to a door being kept closed (we accompany someone to leave the room and we stay behind the door to prevent the person to come in again).

Up to now, there are several evidences that the PMBS represents both sensory reaferences and motor inhibition processes. The present study proposes to examine the temporal and spatial dynamics of PMBS associated with sensory reaferences and active inhibition processes during a switching task from a bimanual phase to an unimanual tapping. The switching task involves the selective stopping of one hand’s tapping while maintaining the activation of the tapping of the other hand. The switching signal was presented during the ongoing bimanual tapping movement, ensuring that motor responses were initiated before being selectively inhibited. We hypothesize that sensory reaferences processes may be evidenced after switching by the presence of a PMBS in the sensorimotor region contralateral to the hand continuing the unimanual tapping [4,13] while active inhibition processes may take place in relation to the stopping hand, producing an ipsilateral PMBS in the motor regions [11].

2. Materials and methods

2.1. Participants

Seventeen young adults (9 males; aged 25 ± 3 years, mean ± standard deviation (SD)) participated in the study. All participants had normal or corrected-to-normal vision, were free of medication and none reported a history of major medical disorders, sustained head injury, psychiatric or neurological disorders, alcohol or drug abuse. They were all right-handed (90 ± 8) according to a twelve-items version of the Oldfield Edinburgh handedness inventory [26]. They all provided written, informed consent to participate to the study. The study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki, 18 July 1964) and the Ethics Committee of the canton of Vaud (University of Lausanne) for research on human participants approved all experimental procedures.
2.2. Stimuli

Visual stimuli were presented at the center of the screen with a gray background at 60 cm from the participants. Two loudspeakers placed at 50 cm from the participants delivered the tones of the auditory metronome (2 Hz; high-pitched tones: 4000 Hz) for the whole duration of each trial (10 s). A trial consisted in presentation of a visual start stimulus (white cross fixation) displayed for a random duration between 4500 ms and 6000 ms, followed by the presentation of a visual preparatory stimulus (displayed until the end of the trial, 4000 ms to 5500 ms duration). An imperative auditory stimulus (low-pitched tone 500 Hz; 80 dB), which replaced the high-pitched tones of the metronome, occurred at a fixed interval of 1500 ms after the preparatory stimulus. The preparatory stimulus was either a green cross (Switch condition: “SWIT”; 70 trials) or a red cross (Continue condition: “CONT”; 70 trials). We ensured that each participant was able to easily discriminate the imperative stimulus tone from the metronome beats. Stimulus delivery and response recording were controlled by Presentation 14.4 software (Neurobehavioral System, Albany, CA).

2.3. Procedure and task

The switching paradigm was designed to assess the PMBS during a selective inhibition in a tapping task. At the beginning of each trial, participants produced a bimanual (BM) in-phase index fingers’ tapping on a keyboard in synchronization with the auditory metronome. Each trial engaged BM tapping at the start stimulus following by a preparatory period. During the preparatory period, participants had either to prepare to selectively stop the left index while continuing the tapping with the right index (SWIT condition), or to maintain the bimanual tapping (CONT condition). Thus, participants switched from BM to unimanual (UM) tapping in the SWIT condition, whereas they continued the BM tapping in the CONT condition. The action of switching or continuing had to be executed after the imperative stimulus (Fig. 1).

Participants performed a familiarization block of eight trials (four trials in each condition) before starting the proper experiment, which included 5 blocks of 28 trials (70 trials in each condition). Conditions were randomly assigned. A rest period of approximately 60 s was proposed to the participants between each block. The whole experiment lasted approximately 40 min.

2.4. Electrophysiological recordings and data pre-processing

Continuous EEG was recorded at a sampling rate of 2048 Hz though 64-channels Biosemi ActiveTwo amplifier system (Biosemi, Amsterdam, Netherlands). This system is referenced to the Common Mode Sense (CMS; active electrode) and the Driven Right Leg (DRL; passive electrode) which replace the ground electrodes conventionally used. The CMS-DRL electrodes form a feedback loop which drive the average reference potential of the subject as close as possible to amplifier zero. Electrode impedances were kept below 5 kΩ. Eye blinks were recorded by two electrodes placed above and below the right eye.

Offline analyses were performed with BESA software (MEGIS Software, Inc., Gräfelfing, Munich). Continuous EEG data were corrected for eye blinks and artifacts through an automatic correction of artifacts accounting for EOG activities. Bad electrodes were interpolated using spherical spline interpolation. On average, 8.7% of the 64 electrodes were interpolated. Raw EEG was band pass filtered (0.3–40 Hz with slope 6–24 dB/oct, forward–phase). For each trial in each condition, epochs of interest were time-locked on the imperative stimulus (−2500/+2500 ms) with a baseline from −2500 to −1500 ms. Epochs containing artifacts were rejected (amplitude 120 µV, gradient 75 µV/sample). After transformation to average reference, we performed a time-frequency (TF) analysis of single-trial EEG data using complex demodulation method. The TF analysis was set to a frequency resolution of 1 Hz and temporal resolution of 50 ms in the frequency range 5–30 Hz. The mean power of the −2500 to −1500 ms interval preceding the imperative stimulus was considered as baseline, providing single-trial measure of relative power at each frequency. Using such a TF computation on each single trial and averaging the energy across single trials preserves both evoked and induced activities [27]. The ERD/ERS measures were obtained in a second step by simply averaging the energy across frequency bins of interest (i.e. beta band within 14 and 30 Hz), and contain both evoked and induced information. This approach avoids any a priori hypothesis on the nature of the beta response, which is likely to be a mixture of phase-locked and non phase-locked activities. For more details about the BESA power spectrum analysis, see a previous publication [28].

Only correct trials were considered (mean ± SD: 58 ± 4 in SWIT and 61 ± 5 in CONT condition). On average, the number of epochs included for analysis was 55 ± 5 (rejection: 6.6%) in the SWIT condition and 56 ± 6 (rejection: 8.1%) in the CONT condition. There was
no difference in the percentage of rejection between conditions (\(\chi^2(1) = 1.01, p > 0.3\)). Participants were included when a minimum of 44 trials were accepted by condition, leading to the exclusion of 2 participants. Two more participants were excluded due to abundant EEG artifacts. Seventeen out the 21 recorded participants were thus eventually included in the study.

2.5. Statistical analyses

2.5.1. Behavior

Inter-tap interval (ITI) between each button press of the right index was measured. ITI was considered as correct (1) if the instruction (SWIT/CONT) was respected and (2) if the delay between the left and right button presses did not exceed 50 ms during the bimanual tapping. The non-respect of (1) and/or (2) from 0 to 500 ms after imperative stimulus onset have been recognized as error. Mean, SD and percentage of errors of the ITI from 0 to 500 ms after stimulus imperative onset in SWIT and CONT conditions were compared using paired t-test.

2.5.2. Time-frequency

A paired sampled t-test was performed to compare the time-frequency signals between SWIT and CONT conditions with BESA statistics 1.0. Statistics were performed in beta range 14–30 Hz on a 2500 ms time window time-locked to imperative stimulus onset. Permutation test was fixed at 1000 for a p-value <0.05. Permutation test systematically interchanges the data of subjects and avoids significant effect found by chance. The result of the comparison between SWIT and CONT condition was interpreted in terms of synchronization (PMBS) phenomenon. Thus, PMBS reflects the difference between SWIT and CONT. Using the CONT condition as a control task seems well appropriated to evaluate efficiently the PMBS since it eliminates a large amount of effects attributed to perceptual and attentional processes due to the subtraction between conditions.

2.5.3. Electrical source estimations

Electrical source estimations were computed with Cartool [https://sites.google.com/site/bmlab/cartool; [29]]. We estimated electric sources underlying scalp-recorded data using a distributed linear inverse solution based on a local autoregressive average (LAURA) regularization approach [30–32]. LAURA selects the source configuration that better mimics the biophysical behavior of electric fields (i.e. activity at one point depends on the activity at neighboring points according to electromagnetic laws). The solution space is based on a realistic head model and included 3005 solution points homogeneously distributed within the gray matter of the average brain of the Montreal Neurological Institute (courtesy of R. Grave de Peralta Menendez and S. Gonzalez Andino, University Hospital of Geneva, Geneva, Switzerland). Intracranial sources were estimated for each participant across the whole epoch in a beta frequency-band (14–30 Hz) averaged and then statistically compared using paired-sample t-tests at each time-frame and each node between the SWIT and CONT conditions.

Correction was made for temporal autocorrelation through the application of a >1 contiguous data point temporal criterion (50 ms) for the persistence of significant differential effects [33]. The results of this analysis of source estimations are presented as plot depicting the percentage of solution nodes showing a significant (\(p < 0.01\)) difference as a function of peri-stimulus time [34,35].

2.5.4. Behavioral-brain correlations

The brain activity at each time-frame (from 0 to 2500 ms after imperative stimulus onset) in SWIT was correlated with the percentage of errors in SWIT using Pearson correlation tests. First, solution points significantly different in the paired t-test between SWIT and CONT conditions (\(p < 0.01\)) were used to select the brain activity (\(\mu V/mm^2\)) at each time-frame for each subject. Second, correlations between the brain activities at each time frame in SWIT were correlated with the percentage of errors in SWIT. Finally, all the correlations with a \(p\)-value <0.05 were exported in a 3005 solution points head model.

2.5.5. Global considerations about statistical analyses

The normality of all data was assessed with the Kolmogorov–Smirnov test, ensuring that all variables were normal (all \(p\)-values >0.05) except the percentage of error in the CONT condition \(p\)-value >0.05. Hence, values of the percentage of error in CONT and SWIT condition were normalized using log10 data transformation.

In view of the large number and complexity of results obtained in this task, the analysis of the preparatory period will be addressed in another report.

3. Results

3.1. Behavioral data

Mean, SD (516 ± 27 ms and 513 ± 25 ms in SWIT and CONT, respectively) and percentage of errors (9% and 8% in SWIT and CONT, respectively) of the ITI were not different between SWIT and CONT condition (all \(p\)-values >0.1).

3.2. EEG data

3.2.1. Time-frequency analyses

A PMBS is observed in a broad beta frequency-band (14–30 Hz) in medial fronto-central (F2, FCz and Cz), right fronto-central (F2, F4, FC2, FC4, C2, C4 and C6) and right centro-parietal (CP2, CP4, CP6, P4 and P6) regions during the whole post-switching period (from 500 ms to 2500 ms after imperative stimulus onset; duration: 2000 ms). The maximal magnitude of the broad-band PMBS (14–30 Hz) is observed in electrode C4 (Fig. 2). Another PMBS appeared in a restricted beta frequency-band (22–26 Hz) in left fronto-central (F1, FC1 and FC3; from 500 ms to 1500 ms after imperative stimulus onset; duration: ~1000 ms), left central (C1 and C3; duration: ~1500 ms) and left medio-parietal (CPz and CP1; duration: ~1500 ms) regions. The maximal magnitude of the restricted-band PMBS (22–26 Hz) was observed in electrode C1 (Fig. 2). The variability inter-subject was larger in SWIT than CONT for the electrodes C4 (\(\overline{f} = 12.5, p < 0.05; 14–30 Hz\)) and C1 (\(\overline{f} = 6.6, p < 0.05; 22–26 Hz\)).

3.2.2. Electrical source estimation

During the PMBS (14–30 Hz), the time frame-wise analysis of the source estimation revealed periods of widespread significant differences between the SWIT vs. CONT conditions peaking at 750 ms and 1300 ms. The significant solution points are represented on a template brain at the time-frames when the number of solution points showing a significant difference was maximal (Fig. 3).

The first peak of the PMBS (14–30 Hz) showed significant \((p < 0.01)\) difference at 750 ms after imperative stimulus onset within bilateral frontal (pre-central, middle, superior and medial frontal gyri), right frontal (inferior frontal gyrus), right temporal (superior and middle temporal gyri), bilateral parietal (post-central gyrus, inferior and superior parietal lobules) and right parietal (precuneus) cortices. Solution points with maximal difference (SP MAX) were located within right pre-frontal cortex (superior frontal gyrus; Fig. 3). The second peak showed significant \((p < 0.01)\) difference at 1300 ms after imperative stimulus onset within bilateral frontal (pre-central, middle and superior frontal gyri), right temporal (mid and superior temporal gyri), bilateral parietal (post-central
gyrus, superior parietal lobule and precuneus), right parietal (infe-
rrior parietal lobule) and right occipital (cuneus) cortices. Solution
points with maximal difference (SP MAX) were located within right 
parietal cortex (inferior parietal lobule; Fig. 3).

3.2.3. Correlation
The solution points significantly correlated (Pearson p-value
<0.05) with behavioral performance are represented on a template
brain at the time-frames when the number of solution points show-
ing a significant difference was maximal (Fig. 4).
The percentage of errors in SWIT and the solution nodes signifi-
cantly different in SWIT during the PMBS (14–30 Hz) was negatively
correlated (p < 0.05) at 450 ms, 800 ms and 1300 ms after impera-
tive stimulus onset. At 450 ms, brain activity was located within 
right parietal (inferior parietal lobule and post-central gyrus) and 
right frontal (pre-central gyrus) cortices with a maximal correla-
tion within the right parietal cortex (SP MAX: post-central gyrus; 
\( r = -0.67, p < 0.01 \), Fig. 4). At 800 ms, brain activity was located 
within right pre-frontal (superior and middle frontal gyri), right 
parietal (post-central gyrus and superior parietal lobules) and right 
occipital (middle occipital gyrus) cortices with a maximal differ-
ence within right pre-frontal cortex (SP MAX: middle frontal gyrus; 
\( r = -0.69, p < 0.01 \), Fig. 4). At 1300 ms, brain activity was located 
within right pre-frontal (middle frontal gyrus), right parietal (post-
central gyrus, inferior and superior parietal lobules and precuneus) 
and right temporal (superior temporal gyrus) cortices with max-
imal difference within right pre-frontal cortex (SP MAX: middle 
frontal gyrus; \( r = -0.63, p < 0.01 \), Fig. 4).

4. Discussion
Using a switching motor task, our results distinguish for the 
first time the temporal dynamics and spatial localization of PMBS 
associated with (i) sensory reafferences and (ii) active inhibition 
processes. Behavioral variables (mean, variability and percent-
age of errors) showed no difference between the switch and 
continue conditions. This suggested that in a context of auditory 
paced tapping (2 Hz), selective stopping of a movement is as easy 
as continued bimanual tapping movements when the participants know beforehand the stopping hand. These results 
showed that both conditions were performed in the same way and 
allowed to match precisely the movements between conditions 
for a better comparison at an electrical level. Electrophysiolog-
ically, we observed large PMBS in SWIT compared to CONT in
a broad-band (14–30 Hz) in right fronto-centro-parietal regions with maximal difference within right central region (sensorimotor regions) during the whole post-switching period. A concomitant PMBS appeared in a more restricted-band (22–26 Hz), limited to left fronto-centro-parietal regions with maximal difference within left central region (sensorimotor regions) during most part of the post-switching period. Electrical source analyses localized the broad-band PMBS (14–30 Hz) within bilateral frontal and parietal and right temporal cortices at 750 ms and within bilateral frontal and parietal, right temporal and right occipital cortices at 1300 ms. Solution points with maximal difference were located within right pre-frontal cortex (superior frontal gyrus) at 750 ms and within right parietal cortex (inferior parietal lobule) at 1300 ms. Finally, we evidenced negative correlations between the percentage of errors in SWIT and the magnitude of the PMBS (14–30 Hz) in SWIT within right parietal and frontal cortices.

To note that the PMBS modulations might be affected by cognitive processes. Indeed, the behavioral response is determined by bottom up factors (i.e. preparatory and imperative stimuli) that might induce an elevation of beta band activity (i.e. amplitude increase [36]). We suppose, however, that cognitive processes related to beta ERS modulations are light because the large part of the cognitive processing takes place during the preparatory period. In addition, the fact that the SWIT and CONT conditions were compared should cancel the residual cognitive processes evoked by the imperative stimulus.

4.1. Active inhibition processes.

At the sensor level, we observed a broad-band 14–30 Hz PMBS during the whole post-switching period (from 500 ms to 2500 ms: duration 2000 ms) within the right hemisphere with a dominance in the right motor region. We suggest that the broad-band and the continuous duration of the ipsilateral PMBS is related to active inhibition processes (top–down control) involved in the stopping of the left index movement during the whole post-switching tapping. Our results corroborate previous studies supporting that PMBS relates to an active inhibition involved discrete hand-foot movement [11] and motor imagery of right–left hand movement [19]. Because TMS studies evidenced active inhibition after repetitive thumb [23] or index movements [24] auditory-paced (1 Hz) in the brain area not involved in the movement, we suggest that, after the switching, the active inhibition set up in the regions representation of the irrelevant movement (i.e. left index selectively stopped) allowing to prevent any unwanted movement of this index previously involved in the task. We provide here additional information about the PMBS duration. Indeed, it was evidenced that PMBS triggering was related to the end of the whole motor process, and not to the end of each motor program [18]. Our results allow to precise that PMBS triggering is related to the end of a partial part of the motor process (i.e. when a part of the movement is selectively stopped while other part of the movement continue the action).

Source estimation analyses further support the assumption of active inhibition within the right hemisphere. Brain activity
difference indeed stemmed within regions involved in selective inhibition, including the right pre-frontal (superior frontal gyrus) and the right parietal (inferior parietal lobule) cortices [37, 38]. Converging evidences support that inhibition processes of a selective movement involves a wide network including the pre-frontal cortex (inferior and superior frontal gyri), the supplementary motor area (SMA), the pre-SMA and the inferior parietal cortex [39–41]. These regions were shown responsible of selective inhibition during reactive paradigm such as stop signal or Go/No-go tasks. Because the selective stopping in reactive paradigm requires a discrete response, the inhibitory processes should be activated during a short period. In our study, where the subject prepared (proactive control) a selective stopping of the left index while maintaining movements with the right index, we show that the same cortical regions are actively inhibited that in the reactive paradigm and that this network stays inhibited during the whole stopping of the left index movement.

Hypothesis of active inhibition during the post-switching period was strengthened by the negative correlation between behavioral and neurophysiological data. Maximal correlation was located within right parietal (post-central gyrus) and right pre-frontal (middle frontal gyrus) cortices. This result indicates that the larger the PMBS, the lower the level of error rate, suggesting that the magnitude of the PMBS is related to the selective inhibition efficiency. Relationship between beta synchronization and behavioral performance has been recently reported during a visuomotor task [42]. These authors showed a negative correlation between the amplitude of the PMBS and the size of the preceding angular error. We suggest here that the PMBS could be an electrocortical marker of the efficiency of active inhibition processes during selective hand movement.

Taken together, these observations point out the involvement of the active inhibition processes within right pre-frontal and right parietal network during selective inhibition and raise the possibility that this is mediated, at least in part, by the dynamic modulation of the degree of beta synchronization.

4.2. Sensory reafferences processes

Time-frequency analysis at the sensor level revealed a contralateral (left) PMBS concomitant to the ipsilateral (right) PMBS. This contralateral PMBS appeared in a more restricted beta frequency-band (22–26 Hz) with a dominance in the left sensorimotor regions during a shorter time period (from 500 ms to 2000 ms after imperative stimulus onset; duration: 1500 ms). The link between PMBS and motor inhibitory processes cannot be evoked here since the right index is engaged in both conditions. Instead of the inhibitory hypothesis, the contralateral PMBS could emerge to the large ipsilateral PMBS (i.e. overflow) due to massive transcallosal connections of both hemispheres. It is of interest, however, that the
magnitudes of the contralateral PMBS is less large and that its duration is shorter than in the ipsilateral hemisphere. This result corroborates with previous studies showing that PMBS induced by the movement had a greater magnitude and lasted longer than PMBS related to cutaneous stimulation [8, 13, 43]. Another hypothesis concerns the involvement of sensory reafference processes (i.e., bottom-up control) related to the right index tapping movement. Supporting this hypothesis, previous studies showed a PMBS within sensorimotor regions after nerve stimulation on thumb and finger movement [13, 17]. In our task, once the switching to unilateral right tapping was performed, we assume that sensory reafferences coming from the right index finger are sent to the sensorimotor regions. We suggest that the duration of the left PMBS could be related to the need to stabilize the regularity of the tapping with the contralateral brain in the post-switching phase. These results could confirm our hypothesis about the existence of reafferences processes in the contralateral hemisphere in relation to continuing tapping of the right hand.

The contralateral PMBS found in a restricted band (22–26 Hz) at the sensor level was localized within the left parietal cortex (superior and inferior parietal lobules) at the brain space level. This brain activation was reduced in magnitude and time duration compared to the ipsilateral brain activity. This result is in accordance with the hypothesis of sensory reafferences processes involved in continuous hand tapping since the parietal lobe is known to play a major role in the integration of sensorimotor information in motor skill during grip force task [44] or bimanual coordination task [45]. More precisely, the inferior and superior parietal lobules were shown to be activated when subjects covertly prepares movements or switch intended movements [see also [46]]. Finally, we suggested that sensory reafferences contribute an important source of information in our switching paradigm in order to produce efficient regular tapping movements.

5. Conclusion

This study shows for the first time simultaneous PMBS within distinct brain regions, latencies and frequency ranges during a motor switching task. We suggest that the PMBS correspond to concomitant active inhibition and sensory reafferences processes. The PMBS within left parietal cortex might reflect the sensory reafferences (bottom–up control) of the right hand tapping disrupted by the switching in order to maintain a regular rhythm. The PMBS within right frontal and right parietal cortices might reflect the continued active inhibition (top–down control) of the recently stopped left hand in order to prevent interference with the right hand tapping. Furthermore, we evidenced a marker of active inhibition through the magnitude of the PMBS. Overall, we conclude that a bimanual switching task is a suitable paradigm to reveal distinct functional aspects of post-movement beta synchronization.

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References


