

Movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS): Motor-imagery duration effects

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ABSTRACT

Objective: To investigate movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS) during two motor-imagery tasks with varying movement duration (brief versus continuous). **Methods:** Twelve subjects performed or kinesthetically imagined the indicated movement (left or right hand movement) for 1 s (brief) or 5 s (continuous) while electroencephalograms (EEGs) were recorded using 16 electrodes covering the sensorimotor cortex of the brain according to the modified 10–20 system.

Results: Significant hemispheric differences were found between contralateral and ipsilateral area in mu ERD, mu ERS and beta ERD during both brief and continuous conditions, showing contralateral dominance of mu and beta ERD and ipsilateral dominance of mu ERS. Beta ERS showed a significant ipsilateral dominance only in the brief condition. Movement imagery duration influenced the lateralization of mu ERD, beta ERD, and beta ERS, but not mu ERS.

Conclusions: The results of this study will aid in clarifying movement-related lateralization in association with imagery tasks under varying movement duration.

Significance: For designing an EEG-based brain–computer interface (BCI) for people with severe neuromuscular impairments, movement imagery-related lateralization can play a key role in utilizing motor-imagery tasks as a control or communication strategy.

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1. Introduction

Electrophysiological studies about human cortical activities in association with sensory processing or motor behavior have produced two general findings: (1) amplitude changes for specific cortical rhythms within various frequency bands (Neuper and Pfurtscheller, 2001a,b; Müller-Putz et al., 2007) and (2) lateralized cortical activities (Leocani et al., 1997; Pfurtscheller and Lopes da Silva, 1999; Serrien, 2008). It is well known that moving certain body parts is preceded by a blocking or desynchronization of 8–13 Hz mu and 14–25 Hz beta rhythms. This pre-movement suppression over sensorimotor areas, also known as event-related desynchronization (ERD), is thought to be related to movement preparation and execution, indicating a state of active cortical processing (Leocani et al., 2001; Szurhaj et al., 2003). The movement termination is then followed by a phasic beta synchronization

(i.e., amplitude increase in the 15–25 Hz beta band) occurring over the precentral region of the brain (Pfurtscheller et al., 1981). It is assumed that this post-movement enhancement, popularly referred to as event-related synchronization (ERS), reflects an idling, deactivated motor cortex (Pfurtscheller et al., 1997b; Alegre et al., 2003). As an indicator of cortical activation/deactivation, event-related (de)synchronization (ERD/ERS) phenomena have widely been reported during various motor tasks of different body parts (Pfurtscheller et al., 1994; Stancák and Pfurtscheller, 1995; Neuper and Pfurtscheller, 1999; 2001a,b; Cassim et al., 2000; Pfurtscheller et al., 2000, 2005; Bai et al., 2007; Erbil and Ungan, 2007; Müller-Putz et al., 2007; Morash et al., 2008), as well as during motor-imagery tasks (Neuper and Pfurtscheller, 1998, 1999; Jeannerod, 2001; Pfurtscheller et al., 2006).

Previous studies also showed that movement-related neural activity is lateralized; a significant ERD over the contralateral side and a significant ERS over the ipsilateral side of the brain for planned and terminated movements, respectively. For example, alpha and beta ERD begin contralaterally about 1.5–2 s before self-paced movement, becoming bilateral during movement execution (Leocani et al., 1997; Pfurtscheller et al., 1997b, 1998; Pfurtscheller and Lopes da Silva, 1999; Taniguchi et al., 2000; Kaiser et al., 2003;

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Serrien, 2008). A significant ipsilateral ERS was found after termination of physical movement (Pfurtscheller et al., 1997b; Stancák et al., 2003; Qin and He, 2005), as well as movement imagination (Pfurtscheller and Lopes da Silva, 1999; Neuper et al., 2006). This movement-related lateralization has been observed through the Bereitschaftspotential (BP, Ikeda and Shibasaki, 1992; Lang et al., 1994), the contingent negative variation (CNV, Kutas and Donchin, 1980), and the lateralized readiness potential (LRP, Wauschkuhn et al., 1997). The results of fMRI brain studies also support the lateralization of brain during movement; the dominant hand (right) is controlled mainly by the contralateral (left) hemisphere (Mattay et al., 1998; Solodkin et al., 2001; Babiloni et al., 2003; Gut et al., 2007).

Despite these research outcomes, more study is still needed to further clarify movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS) for two main reasons. First, it has been well documented that movement-related cortical activity is lateralized, but there are also conflicting results regarding the movement-related lateralization. For example, post-movement beta ERS is rather dominant over the contralateral precentral cortex (Salmelin and Hari, 1994; Pfurtscheller et al., 1996, 1997b; Salenius et al., 1997; Neuper and Pfurtscheller, 2001a,b; Babiloni et al., 2003; Cheyne et al., 2003; Doyle et al., 2005). On the other hand, there are several studies that found post-movement beta ERS both in the contralateral and ipsilateral hemispheres in a number of subjects (e.g., Salmelin and Hari, 1994; Gaetz and Cheyne, 2006). Second, although several studies investigated movement duration effects during physical motor movements (e.g., Cassim et al., 2000; Erbil and Ungan, 2007), there is still a general lack of understanding of the movement-related lateralization associated with various imagery tasks, particularly those with varying movement durations. Furthermore, previous studies regarding movement imagery-related lateralization also found conflicting results. For example, the imagination of right and left hand movements resulted in synchronization of beta rhythms (beta ERS) over the ipsilateral hand area (Pfurtscheller et al., 1997b; Pfurtscheller and Neuper, 1997; Parasuraman and Rizzo, 2008), but Pfurtscheller et al. (2005), who studied beta rebound after three different types of motor-imagery (hand, foot, and tongue), observed a significant beta ERS at the contralateral side of the hemisphere after hand movement imagery.

The main goal of this study is to investigate movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS) during two motor-imagery tasks with varying movement duration (i.e., brief hand movement imagery for 1 s versus continuous hand movement imagery for 5 s). On the basis of earlier findings, three main research questions were tested: (1) would mu and beta ERD/ERS patterns be present during motor-imagery tasks with varying movement durations?; (2) is there significant hemispheric differences in the mu and beta ERD/ERS during brief and continuous hand imagery tasks?; and (3) to what extent does movement duration (brief versus continuous) affect the lateralization of ERD/ERS in the mu and beta bands?

2. Materials and methods

2.1. Subjects

Twelve healthy right-handed participants (10 males and 2 females) volunteered in the study, whose mean age (M) was 20.1 years (standard deviation, $SD = 0.33$). All participants reported being free of any medical or neurological disorders and had normal or corrected vision. Participants gave their written consent after a detailed explanation of the experiment procedure which was approved by the University's Institutional Review Board. Participants were rewarded extra credit for their partaking in this study.

2.2. Task procedures

Before the experiment, each participant was seated in a comfortable chair approximately 80 cm from a 17" computer monitor in a dimly lit room. All participants were instructed to remain relaxed and avoid any unnecessary movement during the experiment. Participants conducted a number of training trials based on the respective tasks that they would perform. For each experimental trial, participants were instructed to direct their attention to the center of the computer monitor responsible for displaying the stimuli (LED lamp).

At second 0, "Ready?" was displayed on the screen (see Fig. 1). At second 5, an indicator appeared on the screen and pointed at one of two different motor-imagery tasks (i.e., left hand or right hand movement) for either 1 s (brief movement imagery) or 5 s (continuous movement imagery). During the brief imagery task condition, for example, the participants imagined the indicated movement for 1 s, until the LED lamp turned off at second 6. In the continuous imagery task condition, they had to perform the indicated motor-imagery for 5 s, until the LED lamp turned off at second 10. Participants were instructed to imagine the kinesthetic experience (Neuper et al., 2005) of movement (e.g., softly clenching a ball with their hand) with their right hand, while their arms rested relaxed on the arm rest. The time between two trials was randomized in a range of 10–15 s in order to detect a reliable power value (Niedermeyer and Lopes da Silva, 2004), while avoiding adaptation. Each task condition was performed separately in a sequence of 20 trials, accounting for both left and right hand imagery. The total experiment time lasted approximately one hour. To overcome the problem of the sequence effect, tasks (i.e., brief or continuous movement imagery) and hands (i.e., left or right hand) were randomized for each participant.

2.3. EEG recordings and preprocessing

EEGs were recorded using a EEG cap (g.tec Medical Engineering) embedded with 16 electrodes covering F_3 , F_z , F_4 , T_7 , C_3 , C_z , C_4 , T_8 , CP_3 , CP_z , P_3 , P_z , P_4 , PO_7 , PO_8 , and O_z based on the modified 10–20 system of the International Federation (Sharbrough and Chatrian, 1991). The electrodes were referenced to the right mastoid and grounded to the left mastoid. The electrode impedance was kept less than 5 k Ω . The EEG signal was amplified with a g.USBamp amplifier (g.tec Medical Engineering) and digitized at a sampling rate of 256 Hz by using the BCI2000 system (Schalk et al., 2004). All signal analysis was conducted by a LabVIEW™ program. The recorded EEG trails were band-pass filtered at 8–30 Hz.

2.4. Quantification of ERD/ERS

This study measured the ERD/ERS in the 8–13 Hz mu bands and 14–30 Hz beta bands. By following the standard ERD/ERS calculation (Pfurtscheller and Aranibar, 1979), the quantification of ERD/ERS was carried out in four steps: (1) bandpass filtering for all event-related trials, (2) squaring the amplitude samples to obtain power samples, (3) averaging power samples across all trials, and (4) averaging time samples to smooth data and reduce variability (Pfurtscheller and Lopes da Silva, 1999).

For each trial, ERD/ERS was defined as the percentage power decrease (ERD) or increase (ERS) in relation to a 1 s interval before movement imagery (e.g., defined as seconds 1–2 in the present study as shown in Fig 1). ERD/ERS in this study was determined as the relative amplitude (RA) that can be presented as decrease or increase rates (%) of the differences in movement and reference period:

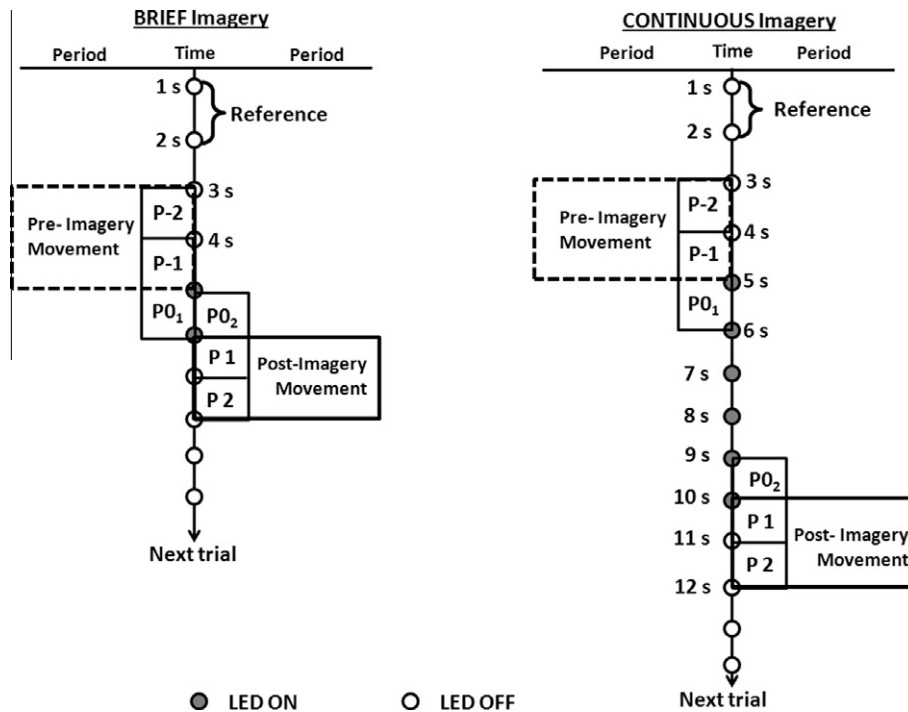


Fig. 1. A task paradigm including trial time sequence: P-i (P + i) indicates i second(s) before (after) movement. P0₁ indicates 1-s time period after movement onset to calculate pre-imagery movement ERD time course and P0₂ indicates 1-s time period before movement offset to calculate post-imagery movement ERS time course. At second 5, a visual stimulus was presented for 1 s in brief condition and 5 s in continuous condition. A 1 s reference interval before the movement (i.e., e.g., 1–2 s in the present study) was used to determine percentage power decrease (ERD) or power increase (ERS).

$$Act_{(j)} = \frac{1}{N} \sum_{i=1}^N y_{ij}^2$$

$$R = \frac{1}{k+1} \sum_{j=r_0}^{r_0+k} Act_{(j)}$$

$$RA_{(j)}(\%) = \left(\frac{Act_{(j)} - R}{R} \right) \times 100(\%)$$

where N is the total number of trials (epochs or sweeps) and y_{ij} is the j th sample of the i th trial of the band-pass filtered data. $Act_{(j)}$ is the averaged power value at the j th sample squared and R is the average power in the reference interval $[r_0, r_0 + k]$, respectively (Graimann and Pfurtscheller, 2006).

2.5. Lateralization Index

Hemispheric lateralization is generally assessed by a lateralization index (LI), commonly used to describe the asymmetry of neural activation intensity. In this study, LI was computed on the basis of the relative power values detected at the two electrode points measured (for more detail see Doyle et al., 2005, pp. 1881–1882). In order to quantify lateralization mathematically, the power value at electrodes, contralateral to the movement side, was subtracted from ipsilateral values for each side. The average of the right and left side differences was obtained using the following Lateralization Index (LI):

$$LI = \frac{[(PowerC3_{Left\ movement} - PowerC4_{Left\ movement}) + (PowerC4_{Right\ movement} - PowerC3_{Right\ movement})]}{2}$$

Movement-related lateralization for a right-side response has a different value compared to lateralization for a left-side response (Gratton et al., 1988; Spencer and Coles, 1999). Asymmetry mea-

sures for both sides were averaged to yield a measure of averaged movement-related asymmetry. A positive LI value indicates contralateral ERD or ipsilateral ERS. Respectively, a negative LI value indicates ipsilateral ERD and contralateral ERS. Essentially, the relative power is indicated by the sign of LI, with a negative sign indicating contralateral ERS dominance and a positive sign indicating contralateral ERD dominance (Doyle et al., 2005). For example, if the contralateral value (i.e., PowerC4_{Left movement} and PowerC3_{Right movement}) is smaller than the ipsilateral value (i.e., PowerC3_{Left movement} and PowerC4_{Right movement}), then LI value is positive, indicating contralaterally desynchronized status in the pre-movement ERD.

2.6. Statistical analysis

For statistical analyses, we used ERD/ERS values and LI values obtained from the right (recording position C4) and left (recording position C3) sensorimotor areas of the brain for three main reasons. First, according to our preliminary data analyses, these two electrode locations were sufficient to detect significant mu and beta ERD/ERS patterns during motor-imagery tasks. Second, previous studies also confirmed that C3 and C4 are the most important electrode locations for discrimination between different motor tasks (Pfurtscheller et al., 1996, 1997b; Ramoser et al., 2000; Parasuraman and Rizzo, 2008; Neuper et al., 2009). Finally, optimizing fewer electrodes is essential to conduct electrophysiological studies about human cortical activities as well as to develop convenient BCI applications, because it can save set-up time and cost.

Movement imagery-related ERD/ERS patterns and hemispheric differences were analyzed using a two-way repeated-measures analysis of variance (ANOVA) with period (three time periods for pre-movement imagery and post-movement imagery) and hemisphere (contralateral versus ipsilateral) as within-subjects factors. Mu and beta bands were separately analyzed. As seen in Fig. 1, an ERD time course was computed for two 1-s time periods before

movement (P-2: seconds 3–4 and P-1: seconds 4–5) as well as the 1-s time period after movement onset (PO₁: brief = seconds 5–6; continuous = seconds 5–6). To calculate an ERS time course, a 1-s time period before movement termination (PO₂: brief = seconds 5–6; continuous = seconds 9–10) as well as two 1-second time periods after movement imagery (brief = P1: seconds 6–7, P2: seconds 7–8; continuous = P1: seconds 10–11, P2: seconds 11–12) were analyzed. The Scheffe's post hoc test known as a more conservative method was used to assess differences among periods (Winer, 1971).

Differences in lateralization index values between brief and continuous motor-imagery tasks were evaluated using a two-way repeated-measure ANOVA with movement duration (brief versus continuous) and period (three pre-movement imagery periods and three post-movement imagery periods) as within-subjects factors. Mu and beta bands were also separately analyzed.

3. Results

To analyze movement imagery-related ERD/ERS patterns, hemispheric differences, and differences in lateralization index values, a series of two-way repeated-measure ANOVAs were conducted. Table 1 shows the overview of significant ANOVA effects. A detailed description of these results is presented.

3.1. Brief hand movement imagery

3.1.1. Event-related (de)synchronization patterns during brief motor-imagery task

Fig. 2 displays the grand average mu (Fig. 2A) and beta (Fig. 2B) ERD/ERS power time courses during self-paced brief movement imagery. Table 2 also shows a summary of inter-subject variations in mu and beta ERD/ERS with standard deviation of motor-imagery tasks that 12 participants performed.

3.1.1.1. Pre-movement mu and beta ERD. A significant period effect was found for mu ERD values during brief movement imagery, $F(2, 22) = 3.91$, $p = 0.0353$, indicating a significant mu ERD pattern (Fig. 2A). Post hoc Scheffe's test showed that the average ERD value was significantly smaller at PO₁ (i.e., 1 s after movement onset), compared to other time periods ($p < 0.01$). The period effect was also found to be significant for beta ERD during brief movement,

$F(2, 22) = 3.84$, $p = 0.0371$, indicating a significant pre-movement beta ERD pattern (Fig. 2B). Post hoc Scheffe's test showed that the average ERD value was significantly smaller at P-1 (i.e., 1 s before movement onset), compared to other time periods ($p < 0.01$).

3.1.1.2. Post-movement mu and beta ERS. The repeated-measures ANOVA results showed a significant main effect of period on mu ERS values during brief imagery movement, $F(2, 22) = 21.52$, $p < 0.0001$, indicating a significant post-movement mu ERS pattern (Fig. 2A). The average period values were significantly larger 2 s after movement offset ($p < 0.01$ with Scheffe's post doc test). Results also showed the post-movement power increased in the 14–30 Hz beta bands during brief movement imagery, $F(2, 22) = 5.00$, $p = 0.0162$ (Fig. 2B), indicating a significant post-movement beta ERS pattern. Post hoc Scheffe's test showed that the average value was significantly larger at P1 (i.e., 1 s after movement termination) and P2 (i.e., 2 s after movement termination), compared to PO₂ (i.e., 1 s before movement termination) ($p < 0.01$).

3.1.2. Hemispheric difference during brief motor-imagery task

3.1.2.1. Pre-movement mu and beta ERD. The repeated-measures ANOVA for mu ERD showed a significant main effect for hemisphere in the brief condition, $F(1, 11) = 12.06$, $p = 0.0052$. The relative power value in the contralateral area ($M = -13.27$, $SD = 26.96$) was lower than in the ipsilateral area ($M = 1.63$, $SD = 28.53$), indicating contralateral dominance as well as a more desynchronized status of the contralateral area in pre-movement ERD. Beta ERD showed a significant main effect for hemisphere in the brief condition, $F(1, 11) = 25.79$, $p = 0.0004$. The relative power value in the contralateral area ($M = -14.45$, $SD = 12.24$) was smaller than in the ipsilateral area ($M = -7.56$, $SD = 11.47$), indicating contralateral dominance of ERD in the contralateral area.

3.1.2.2. Post-movement mu and beta ERS. Results showed a significant hemisphere effect on mu ERS during brief movement imagery, $F(1, 11) = 5.63$, $p = 0.0370$. Grand average of the relative power was larger ipsilaterally ($M = -3.43$, $SD = 35.60$) than contralaterally ($M = -12.74$, $SD = 35.12$), indicating ipsilateral dominance and more synchronization of the ipsilateral area in post-movement ERS. On beta ERS, a significant hemispheric difference was also found in the brief condition, $F(1, 11) = 18.59$, $p = 0.0012$. The relative power in the ipsilateral area ($M = 1.33$, $SD = 14.08$) was larger than in the contralateral area ($M = -4.61$, $SD = 14.78$).

Table 1
Significant effects for ERD/ERS and Lateralization Index parameters.

Parameter	Movement duration	Effect	Pre/post-movement (ERD/ERS)	Frequency band	F-value
ERD/ERS power amplitude	Brief movement imagery	Period	ERD	Mu	$F(2, 22) = 3.91^*$
			ERS	Beta	$F(2, 22) = 3.84^*$
		Hemispheric difference	ERD	Mu	$F(2, 22) = 21.52^{**}$
				Beta	$F(2, 22) = 5.00^*$
			ERS	Mu	$F(1, 11) = 12.06^{**}$
				Beta	$F(1, 11) = 25.79^{**}$
	Continuous movement imagery	Period	ERD	Mu	$F(1, 11) = 5.63^*$
				Beta	$F(1, 11) = 18.59^{**}$
		Hemispheric difference	ERD	Mu	$F(2, 22) = 3.94^*$
				Beta	$F(2, 22) = 4.04^*$
			ERS	Mu	$F(2, 22) = 6.10^{**}$
				Beta	$F(2, 22) = 9.16^{**}$
Lateralization Index (LI)	Movement duration	Period	ERD	Mu	$F(1, 11) = 5.36^*$
				Beta	$F(1, 11) = 8.30^*$
		Hemispheric difference	ERD	Mu	$F(1, 11) = 6.03^*$
				Beta	$F(1, 11) = 5.89^*$
			ERS	Mu	$F(1, 11) = 9.03^*$
				Beta	$F(1, 11) = 16.12^{**}$

* Denotes 0.05 level of significance.

** Denotes 0.01 level of significance.

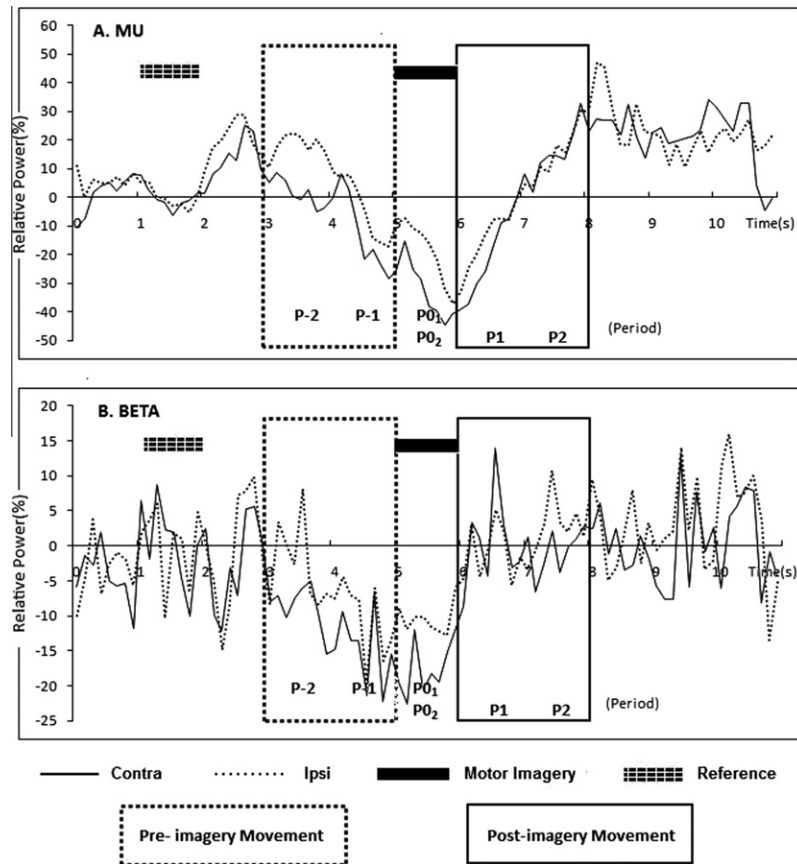


Fig. 2. Mu (A) and beta (B) ERD/ERS patterns of brief movement imagery with respect to contralateral (solid lines) and ipsilateral (dash lines) areas: Thirty-two consecutive points (i.e., 8/s of sampling rate) were averaged in order to reduce the number of power values. All values are relative to the baseline (0) in ERD and ERS patterns. A smaller ERD value denotes more desynchronized status in the pre-movement ERD, while a larger value denotes more synchronized status in the post-movement ERS. The relative powers of contralateral area were smaller than ipsilateral area in the mu and beta pre-movement ERD during brief movement imagery, indicating contralateral dominance. That is, relative powers were larger contralaterally than ipsilaterally in the mu and beta ERD. However, the relative powers of ipsilateral area were larger than contralateral area in the mu and beta post-movement ERS, indicating ipsilateral dominance during brief movement imagery.

Table 2

Summary of inter-subject variation in mu and beta ERD/ERS of motor-imagery tasks that 12 participants performed (standard deviation in parentheses).

Band	Motor-imagery	Period	Contralateral side	Ipsilateral side
Mu	Brief	P-2	-0.272 (21.496)	16.04 (18.302)
		P-1	-13.08 (16.406)	1.195 (27.167)
		P0	-26.48 (34.743)	-12.32 (32.842)
		P1	-12.75 (28.401)	-5.164 (34.661)
		P2	15.233 (25.941)	18.409 (31.448)
	Continuous	P-2	-0.375 (23.709)	5.213 (25.027)
		P-1	-24.37 (27.311)	-20.65 (25.512)
		P0 ₁	-19.07 (31.114)	-13.07 (29.335)
		P0 ₂	3.44 (18.657)	12.867 (23.435)
		P1	24.73 (30.708)	38.171 (40.008)
		P2	21.061 (24.641)	27.849 (37.951)
Beta	Brief	P-2	-9.320 (10.840)	-3.396 (12.396)
		P-1	-17.908 (10.722)	-12.822 (13.942)
		P0	-15.121 (13.058)	-7.471 (8.307)
		P1	-1.616 (13.406)	4.089 (17.858)
		P2	0.334 (13.038)	6.390 (12.440)
	Continuous	P-2	-2.890 (11.108)	0.586 (17.268)
		P-1	-7.667 (14.595)	-6.353 (13.583)
		P0 ₁	-12.475 (12.936)	-8.728 (12.416)
		P0 ₂	4.615 (17.247)	0.201 (17.948)
		P1	18.133 (22.508)	20.451 (25.942)
		P2	21.618 (21.176)	17.771 (23.205)

3.2. Continuous hand movement imagery

3.2.1. Event-related (de)synchronization patterns during continuous motor-imagery task

Fig. 3 displays the grand average mu (Fig. 3A) and beta (Fig. 3B) ERD/ERS power time courses during self-paced continuous movement imagery.

3.2.1.1. Pre-movement mu and beta ERD. The period effect was found to be significant for mu ERD during continuous movement imagery, $F(2, 22) = 3.94$, $p = 0.0344$, indicating a significant mu ERD pattern (Fig. 3A). A significantly smaller average ERD value was found at P-1 (i.e., 1 s before movement onset) and P0₁ (i.e., 1 s after movement onset), compared to P-2 (i.e., 2 s before movement onset) ($p < 0.01$ with Scheffe's post doc test). The relative power in the beta bands significantly decreased shortly before continuous movement onset, $F(2, 22) = 4.04$, $p = 0.0321$, indicating a significant beta ERD pattern (Fig. 3B). The average ERD value was significantly smaller at P0₁ ($p < 0.01$ with Scheffe's post doc test).

3.2.1.2. Post-movement mu and beta ERS. During continuous movement imagery, a significant period effect was found for mu ERS values, $F(2, 22) = 6.10$, $p = 0.0078$, indicating a significant mu ERS pattern (Fig. 3A). The average period values were significantly larger at P1 (i.e., 1 s after movement offset), compared to other time periods ($p < 0.01$ with Scheffe's post doc test). A significant period effect was found on beta ERS values during continuous movement

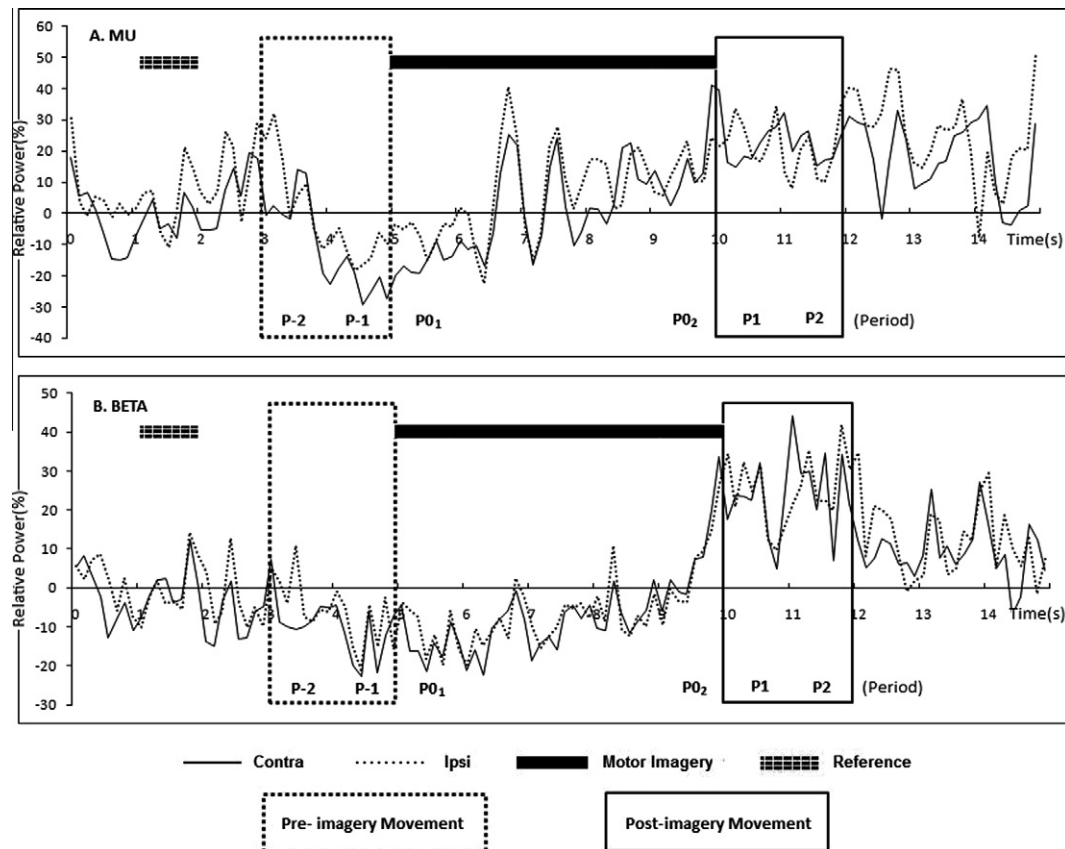


Fig. 3. Mu (A) and beta (B) ERD/ERS patterns of continuous movement imagery with respect to contralateral (solid lines) and ipsilateral (dash lines) areas: Thirty-two consecutive points (i.e., 8/s of sampling rate) were averaged in order to reduce the number of power values. The relative powers of contralateral area were smaller than ipsilateral area in the mu and beta pre-movement ERD during continuous movement imagery, indicating contralateral dominance. In the mu ERS, the relative powers of ipsilateral area were larger than contralateral area, indicating ipsilateral dominance during continuous movement imagery. However, there was no significant difference of relative power in the beta ERS during continuous imagery movement, even though, the relative powers of contralateral area were larger than ipsilateral area.

imagery, $F(2, 22) = 9.16$, $p = 0.0013$, indicating a significant beta ERS pattern (Fig. 3B). Average period values were significantly larger at P1 (i.e., 1 s after movement offset) and P2 (i.e., 2 s after movement offset), compared to P0₂ ($p < 0.01$ with Scheffe's post hoc test).

3.2.2. Hemispheric difference during continuous motor-imagery task

3.2.2.1. Pre-movement mu and beta ERD. A significant hemispheric difference was found between contralateral and ipsilateral area in pre-movement mu ERD during the continuous condition, $F(1, 11) = 5.36$, $p = 0.0409$. The relative power value in the contralateral area ($M = -14.96$, $SD = 29.05$) was smaller than in the ipsilateral area ($M = -8.78$, $SD = 28.21$), indicating contralateral dominance in pre-movement ERD. There was also a significant hemispheric difference of beta ERD during continuous movement, $F(1, 11) = 8.30$, $p = 0.0149$. The relative power grand average in the contralateral area ($M = -7.67$, $SD = 13.19$) was smaller than in the ipsilateral area ($M = -4.83$, $SD = 14.70$), indicating more desynchronized ERD of the contralateral area.

3.2.2.2. Post-movement mu and beta ERS. Results showed a significant main effect of hemisphere on mu ERS values during continuous movement imagery, $F(1, 11) = 6.03$, $p = 0.0319$. That is, the grand average was larger ipsilaterally ($M = 29.72$, $SD = 35.21$) than contralaterally ($M = 21.12$, $SD = 25.73$), indicating ipsilateral dominance in post-movement. However, no significant hemisphere effect was found on beta ERS in the continuous condition, even though the grand average relative power was larger contralaterally

($M = 14.78$, $SD = 21.18$) than ipsilaterally ($M = 12.80$, $SD = 23.76$). Fig. 4 indicates examples of time–frequency maps displaying various ERD/ERS phenomena of 1 selected subject. Overall, desynchronization was located around the beginning of movement imagery; synchronization was located around termination of movement imagery. A decrease in power was observed between 1 s and 2 s before the movement imagery in both hemispheres (C3 and C4). This result showed ERD phenomena that were decreased notably in the symmetrical hemisphere compared with the asymmetrical hemisphere. The minimal power values (maximum ERD) were especially strong in the mu band. Otherwise, the increased power value (maximum ERS) was maintained not only during movement but also after movement imagery. Similar to ERD phenomena, ERS phenomena also showed the symmetrical hemisphere. The maximal power values in the beta band were around 16–18 Hz.

3.3. Lateralization in brief and continuous hand imagery movements

3.3.1. Pre-movement mu and beta ERD

Fig. 5 displays Lateralization Index (LI) values for brief and continuous movements in pre-movement mu and beta ERD. The repeated-measures ANOVA for mu ERD showed a significant main effect of movement duration (brief versus continuous movement) on pre-movement ERD, $F(1, 11) = 5.89$, $p = 0.0335$. That is, the grand average LI value in brief movement imagery ($M = 14.91$, $SD = 18.96$) was larger than in continuous movement imagery ($M = 6.17$, $SD = 14.08$). The grand average LI for brief and continuous movements in mu ERD showed positive values, indicating

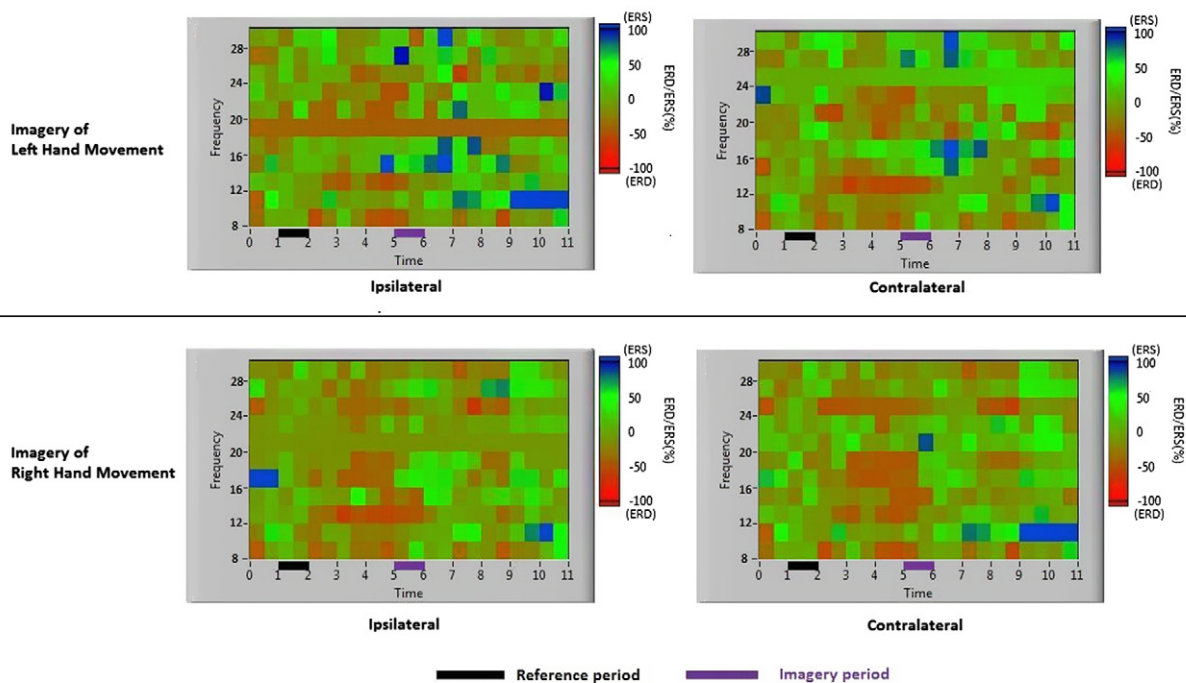
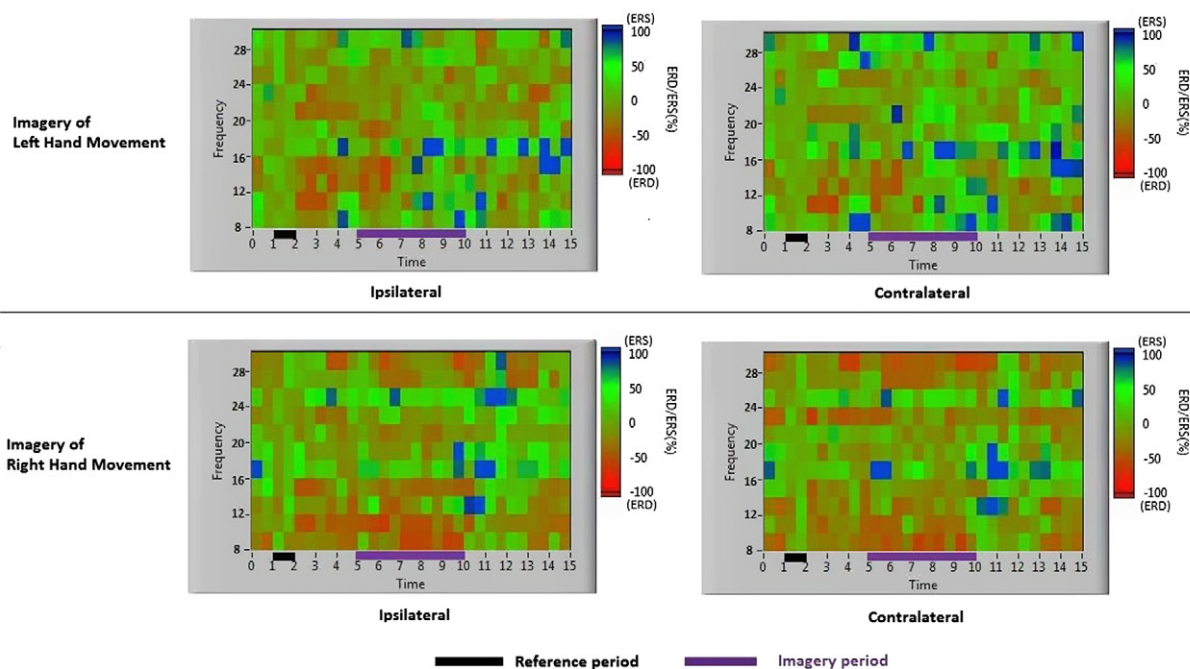
A. BRIEF MOVEMENT**B. CONTINUOUS MOVEMENT**

Fig. 4. Examples of time–frequency domain maps displaying ERD (red) and ERS (blue) in the brief (A) and continuous (B) movement imagery conditions. Digitized EEG signals were analyzed using fast Fourier transform with the 2 Hz point and a 500 ms EEG epoch. The map shows the whole trial (time; x-axis) and the frequency range (μ and β ; y-axis). In order to reduce the number of time-lag, EEG data were calculated for a 0.125 s interval and averaged for 0.5 s within the trial length. Overall, ERD was extensively shown before the movement imagery and ERS was shown after the movement imagery (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

contralaterally dominant ERD. However, there was no significant period effect.

A significant duration effect was also found on the LI values of beta ERD, $F(1, 11) = 9.03$, $p = 0.0120$. The grand average LI value of brief movement ($M = 6.88$, $SD = 8.06$) was larger than the continuous one ($M = 2.84$, $SD = 7.47$) in the beta band. However, no significant period effect was found on the LI values of beta ERD.

3.3.2. Post-movement μ and β ERS

Fig. 6 displays LI values for brief and continuous movements in the post-movement μ and β ERS. Results showed that there were no significant movement duration effect and period effect on the LI values of μ ERS, even though brief movement LI value ($M = 9.31$, $SD = 19.48$) was larger than that of continuous movement ($M = 8.59$, $SD = 19.91$). Grand average LI values for brief and

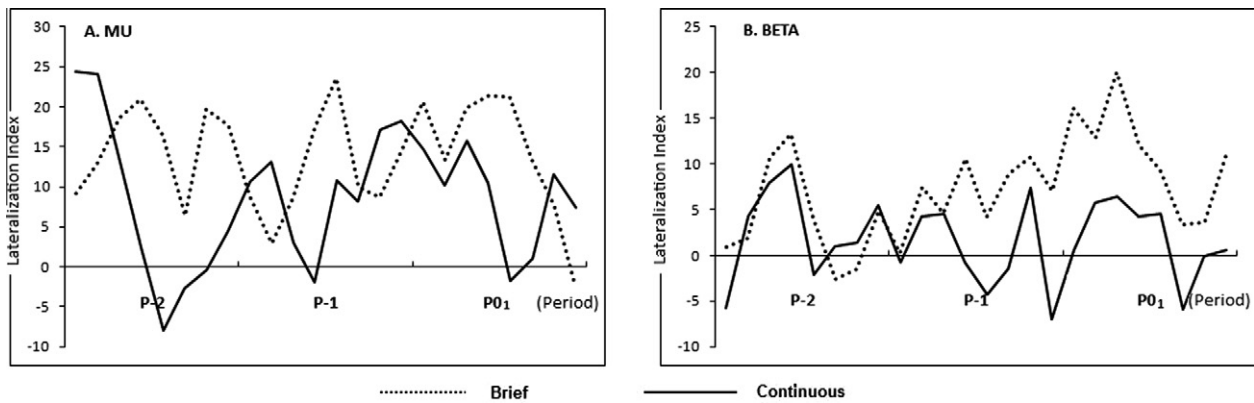


Fig. 5. Lateralization index (LI) on pre-movement ERD in the 8–13 Hz mu band (A) and 14–30 Hz beta band (B).

continuous movement imagery in mu ERS showed positive values, indicating ipsilaterally dominant ERS.

ANOVA results showed a significant movement duration effect on the LI values of beta ERS, $F(1, 11) = 16.22$, $p = 0.0020$. Brief movement imagery LI ($M = 5.94$, $SD = 8.84$) was larger than in continuous movement imagery ($M = -1.97$, $SD = 11.14$). Grand average LI values of brief movement imagery indicated ipsilaterally dominant ERS (positive values). However, grand average LI values for continuous movement imagery showed negative values, indicating contralaterally dominant ERS (see Fig. 6B). There was no significant period effect on the LI values of beta ERS.

4. Discussion and conclusions

The present study investigated (1) the mu and beta ERD/ERS patterns to be elicited by motor-imagery tasks, (2) the hemispheric differences in the mu and beta ERD/ERS during both brief and continuous hand imagery tasks, and (3) the effect of movement imagery duration (brief versus continuous) on the lateralization of ERD/ERS in the mu and beta bands. The results of this study demonstrated several important points. **First, mu and beta ERD/ERS patterns were elicited during hand movement imagery tasks with varying movement duration.** Second, **significant hemispheric differences were found between contralateral and ipsilateral areas for mu ERD, mu ERS and beta ERD during both the brief and continuous conditions, showing contralateral ERD dominance and ipsilateral ERS dominance.** In case of beta ERS, no significant hemisphere difference of the post-movement beta ERS was found in the continuous condition, whereas a significant ipsilateral dominance of post-movement beta ERS was found in the brief condition. Final-

ly, movement imagery duration (brief versus continuous) influenced the lateralization of mu ERD and beta ERD/ERS, but not mu ERS.

4.1. Event-related (de)synchronization (ERD/ERS) patterns during motor-imagery tasks

4.1.1. Pre-movement mu and beta ERD

The results of the present study supported the first research question whether mu and beta ERD/ERS patterns would be elicited during motor-imagery tasks with varying movement duration. That is, both brief and continuous hand movement imageries elicited significant pre-movement suppression and post-movement enhancement in mu and beta rhythms. As seen in Figs. 2 and 3, a power decrease in the present study occurred about 1 s before (P-1) and after movement onset (P0₁). The relative amplitude decrease was larger in brief movement imagery than in continuous movement imagery. Such a mu ERD confirmed the previous observations that mu and beta rhythms can be desynchronized during the preparation and execution of motor-imagery tasks involving the sensorimotor cortex (Pfurtscheller and Lopes da Silva, 1999; Neuper and Pfurtscheller, 2001a,b; Neuper et al., 2005).

4.1.2. Post-movement mu and beta ERS

This study also found significant post-movement enhancements of mu and beta rhythms (ERS) after the termination of hand imagery with varying movement duration, confirming the previous findings that post-movement ERS can be also generated in the supplementary motor area (SMA) during motor-imagery actions (Stancák and Pfurtscheller, 1995; Neuper and Pfurtscheller,

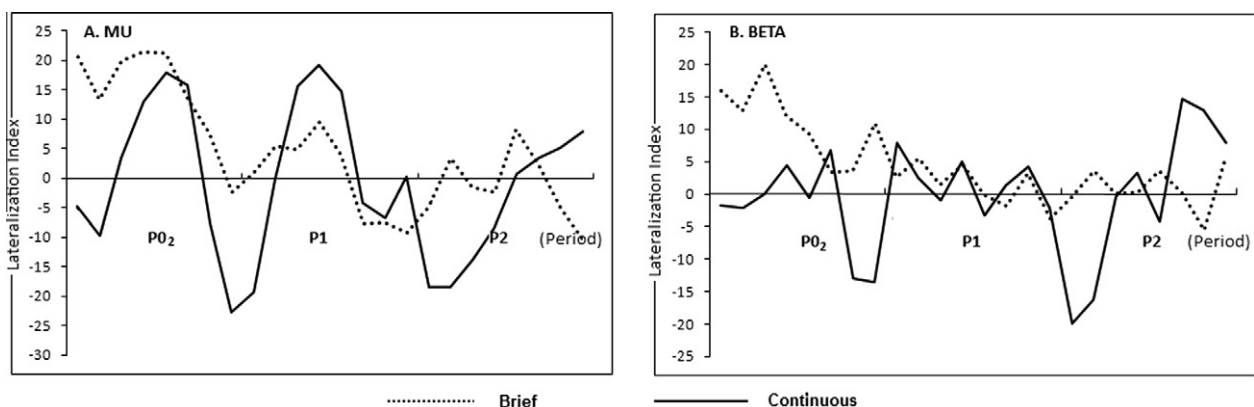


Fig. 6. Lateralization index (LI) on post-movement ERS in the 8–13 Hz mu band (A) and 14–30 Hz beta band (B).

2001a,b; Pfurtscheller et al., 2005). This study observed that mu powers returned to the reference (baseline) values more quickly in continuous motor-imagery (Fig. 3A) than in the brief one (Fig. 2A), whereas beta powers returned more quickly in brief motor-imagery (Fig. 2B) than in the continuous one (Fig. 3B). This finding suggests that patterns of amplitude enhancement or event-related synchronization (ERS) may be affected by movement duration (brief and continuous imagery movements) and frequency bands (mu and beta bands) during movement imagery.

4.2. Lateralization of ERD/ERS during imagery tasks with varying movement durations

4.2.1. Pre-movement mu and beta ERD

Previous studies on the changes in the amplitude of cortical rhythms prior to and after movement demonstrated conflicting results regarding hemispheric differences in the cortical activities within various frequency bands (Stancák and Pfurtscheller, 1996; Pfurtscheller et al., 1997b; Pfurtscheller and Neuper, 1997). This study found significant hemispheric differences in mu and beta ERD during both brief and continuous hand movement imagery tasks. That is, the pre-movement suppression in mu and beta rhythms was contralaterally dominant during hand movement imagery tasks with varying movement durations. This result is consistent with previous findings that showed contralaterally preponderant pre-movement mu and beta rhythm desynchronization when performing motor-imagery tasks (Pfurtscheller et al., 1997b; Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller et al., 2005, 2006; Neuper et al., 2009). For example, Pfurtscheller et al. (1997b), who studied EEG-based discrimination between left and right hand imagery movements, found that imagination triggered a significant contralateral ERD in parallel with the ipsilateral ERS. Pfurtscheller et al. (2005) also found beta ERD in the majority of subjects at electrodes overlaying the contralateral hand representation area.

This study also showed that the lateralization of mu and beta ERD was significantly affected by movement duration. Grand average Lateralization Index (LI) values in the brief condition showed a larger positive value, indicating that the ERD was more contralaterally dominant in the brief condition than in the continuous condition. In the present study, brief movement imagery had a larger impact on the lateralization of mu and beta desynchronization. One possible explanation is because in the present study continuous movement imagery was performed as a task continuously repeated. It is known that neural activity in response to repeated stimuli is accompanied by reduction of cortical neural activity (Grill-Spector et al., 2006). This adaptation phenomenon called “repetition suppression” may occur in the sensorimotor cortex (Erbil and Ugan, 2007). In addition, this study observed that both grand average LI values of brief and continuous movement imagery in the mu and beta rhythms showed the positive values, indicating contralateral dominance. That is, contralateral pre-movement ERD of mu and beta rhythms in brief and continuous conditions was observed. This result is consistent with that of Cassim et al. (2000) and Stancák and Pfurtscheller (1996), who identified contralateral pre-movement ERD without the influence of movement duration. Thus, the contralateral pre-movement ERD can be a good index of cortical activation, not only during physical motor movement, but also imagery motor movement.

4.2.2. Post-movement mu and beta ERS

Significant hemispheric differences in mu ERS during brief and continuous hand movement imagery conditions were found. That is, a significant post-movement enhancement in mu rhythms was ipsilaterally dominant during hand movement imagery tasks with varying movement durations. However, the post-movement beta

rhythm synchronization (beta ERS) did not show any hemispheric difference during continuous movement imagery tasks. That is, a significant ipsilateral preponderance of beta rhythm ERS in the post-movement period occurred during the brief movement imagery condition, but no hemispheric difference was found in beta ERS during continuous movement imagery tasks. This finding is consistent with that of Pfurtscheller et al. (1997b), who found a significant ipsilateral ERS of beta band during motor-imagery. Pfurtscheller and Neuper (1997) also reported beta ERS in the several subjects over the ipsilateral area during motor-imagery. It is known that the ipsilateral beta synchronization (beta ERS) can be interpreted as a correlate of deactivation or active inhibition of ipsilateral sensorimotor structure, and this activity is thought to be mediated by thalamocortical systems. (Pfurtscheller et al., 1997b; Wolpaw et al., 2002).

This study also found that movement duration (brief and continuous movements) affected the lateralization of beta synchronization significantly, whereas movement duration did not affect the lateralization of mu synchronization significantly. Similar to mu and beta desynchronization, this study showed that brief movement imagery had a larger impact on the lateralization of mu synchronization even though no significant difference of LI values was found. Grand average Lateralization index (LI) values of mu ERS in the brief condition showed a larger positive sign, indicating that the ERS was more ipsilaterally dominant in the brief condition than in the continuous condition. On the other hand, grand average LI values of beta ERS in the brief condition showed a positive sign, indicating that the ERS was ipsilaterally dominant in the brief condition. Grand average LI values of beta ERS in the continuous condition developed a negative value, indicating that the ERS was contralaterally dominant in the continuous condition. The most persuasive interpretation of this finding is that the lateralization in beta ERS was strongly influenced by the movement duration. Brief movement imagery yielded ipsilateral ERS and continuous movement imagery yielded contralateral ERS, even though there was no significant hemispheric difference in continuous condition. This result differed from Stancák and Pfurtscheller (1996), who found a significant contralateral dominance of beta rebound (ERS) without influence of movement duration during actual motor movement tasks. One possible explanation may be due to a functional difference between actual movement and movement imagery.

4.3. Implications for BCI applications

Basic design and operation of a BCI system has input (i.e., EEG signals), output (i.e., device commands), signal processing to translate input into output, and a protocol (e.g., timing of operation) (Wolpaw et al., 2002). EEG signals from individual cognitive operation are processed to detect specific signal features (e.g., mu and beta ERD/ERS, P300 evoked potentials, etc.). These features are then translated into device commands for operating BCI device. Efficient EEG-based BCI systems require BCI output signals retaining the reliability of apparent correlations between individual cognitive processes (e.g., motor movement imaginary) and accompanying changes in BCI input or output signals. That is, BCI input and out signals are required to be “reliable and significantly related to specific states of the brain” (Pfurtscheller et al., 1997a, p. 643). However, it is important to note that some factors related with individual cognitive process (e.g., movement duration, difficulty of task, etc.) can affect the whole BCI system as well as its performance, because the factors cause the changes in BCI input (i.e., EEG signals) or specific signal features (e.g., ERD/ERS patterns). It is also well known that lateralization of ERD/ERS (e.g., contralateral ERD or ipsilateral ERS) is associated with an increase in the classification accuracy to maximize the separability of classification

between the patterns generated by executing different motor imageries (Parasuraman and Rizzo, 2008).

As we expected, movement imagery duration (brief versus continuous) influenced the lateralization of mu ERD, beta ERD, and beta ERS. Therefore, we suggest that these features can be used when developing effective EEG-based BCI systems, because the changes of ERD/ERS lateralization by movement duration (i.e., brief and continuous movement imagery) can affect not only movement classification but also accuracy (Pfurtscheller et al., 1997a; Morash et al., 2008; Neuper et al., 2009). However, lateralization on mu ERS was not affected by movement duration. In addition, brief movement imagery had a larger impact on the lateralization of mu ERD and beta ERD, and beta ERS. Therefore, we suggest that brief movement imagery-related pre-movement desynchronization (ERD) and post-movement synchronization (ERS) would lead to better accuracy for BCI applications and advantages of BCI's convenience (e.g., user's action and the BCI response) (Morash et al., 2008). The relationship between movement duration and ERD/ERS lateralization has an important implication for both the selection of movement duration (i.e., brief or continuous movement) and types of changes in the electrical activity of the cortex (i.e., ERD or ERS) for the design and development of effective ERD/ERS-based BCI systems.

The results of this study would help us elucidate the movement-related lateralization in association with imagery tasks with varying movement duration. The present empirical study on movement imagery-related lateralization has important implications for designing an EEG-based brain–computer interface (BCI) for people with severe neuromuscular impairments, who cannot control their voluntary muscle movements, to use the motor-imagery tasks as a control or communication strategy (Wolpaw et al., 2002; Morash et al., 2008). The results of this study should also aid in gaining a better understanding of human cortical activity in association with mental imagery of motor actions or behaviors.

References

- Alegre M, Gurtubay IG, Labarga A, Iriarte J, Malanda A, Artieda J. Alpha and beta oscillatory changes during stimulus-induced movement paradigms: effect of stimulus predictability. *Neuroreport* 2003;14:381–5.
- Babiloni C, Carducci F, Del Gratta C, Demartin M, Romani GL, Babiloni F, Rossini PM. Hemispherical asymmetry in human SMA during voluntary simple unilateral movements: an fMRI study. *Cortex* 2003;39:293–305.
- Bai O, Lin P, Vorbach S, Li J, Furlani S, Hallett M. Exploration of computational methods for classification of movement intention during human voluntary movement from single trial EEG. *Clin Neurophysiol* 2007;118:2637–55.
- Cassim F, Szurhaj W, Haouaria S, Devos D, Bourriez JL, Poirat I, Derambure P, Defebvre L, Guieu JD. Brief and sustained movements: differences in event-related (de)synchronization (ERD/ERS) patterns. *Clin Neurophysiol* 2000;111:2032–9.
- Cheyne D, Gaetz W, Garnero L, Lachaux J-P, Ducorps A, Schwartz D, Varela FJ. Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Brain Res Cognit Brain Res* 2003;17:599–611.
- Doyle L, Yarrow K, Brown P. Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks. *Clin Neurophysiol* 2005;116:1879–88.
- Erbil N, Unger P. Changes in the alpha and beta amplitudes of the central EEG during the onset, continuation, and offset of long-duration repetitive hand movements. *Brain Res* 2007;1169:44–56.
- Gaetz W, Cheyne D. Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage* 2006;30:899–908.
- Graimann B, Pfurtscheller G. Quantification and visualisation of event-related changes in oscillatory brain activity in the time–frequency domain. *Prog Brain Res* 2006;159:79–97.
- Gratton G, Coles MGH, Sirevaag EJ, Eriksen CW, Donchin E. Pre- and post-stimulus activation of response channels: A psychophysiological analysis. *J Exp Psychol Hum Percept Performance* 1988;14:331–44.
- Grill-Spector K, Huggins JE, Levine SP, Pfurtscheller G. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cognit Sci* 2006;10:14–23.
- Gut M, Urbanik A, Forsberg L, Binder M, Rymarczyk K, Sobiecka B, Kozub J, Grabowska A. Brain correlates of right-handedness. *Acta Neurobiol Exp* 2007;67:43–51.
- Ikeda A, Shibasaki H. Invasive recording of movement-related cortical potentials in human. *J Clin Neurophysiol* 1992;9:509–20.
- Jeannerod M. Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 2001;14:103–9.
- Kaiser J, Ulrich R, Lutzenberger W. Dynamics of sensorimotor cortex activation to spatial sounds preceding ipsi- versus contralateral manual responses. *Cognit Brain Res* 2003;17:573–83.
- Kutas M, Donchin E. Preparation to respond as manifested by movement-related potentials. *Brain Res* 1980;202:95–115.
- Lang W, Höllinger P, Eghker A, Lindinger G. Functional localization of motor processes in the primary and supplementary areas. *J Clin Neurophysiol* 1994;11:397–419.
- Leocani L, Toro C, Manganotti P, Zhuang P, Hallett M. Event-related coherence and event-related desynchronization/synchronization in the 10 Hz and 20 Hz EEG during self-paced movements. *Electroencephalogr Clin Neurophysiol* 1997;104:199–206.
- Leocani L, Toro C, Zhuang P, Gerloff C, Hallett M. Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. *Clin Neurophysiol* 2001;112:923–30.
- Mattay VS, Callicott JH, Bertolino A, Santha AKS, Van Horn JD, Tallent KA, Frank JA, Weinberger DR. Hemispheric control of motor function: a whole brain echo planar fMRI study. *Psychiatry Res* 1998;83:7–22.
- Morash V, Bai O, Furlani S, Lin P, Hallett M. Classifying EEG signals preceding right hand, left hand, tongue, and right foot movements and motor imageries. *Clin Neurophysiol* 2008;119:2570–8.
- Müller-Putz GR, Zimmermann D, Graimann B, Nestinger K, Korisek G, Pfurtscheller G. Event-related beta EEG-changes during passive and attempted foot movements in paraplegic patients. *Brain Res* 2007;1137:84–91.
- Neuper C, Pfurtscheller G. ERD/ERS based brain computer interface (BCI): Effects of motor imagery on sensorimotor rhythms. *Int J Psychophysiol* 1998;30:53–4.
- Neuper C, Pfurtscheller G. Motor imagery and ERD. In: Pfurtscheller G, Lopes da Silva FH, editors. *Event-Related Desynchronization and Related Oscillatory Phenomena of the Brain. Handbook of Electroencephalography and Clinical Neurophysiology. Revised ed., vol. 6.* Amsterdam: Elsevier; 1999. p. 303–25.
- Neuper C, Pfurtscheller G. Evidence for distinct beta resonance frequencies in human EEG related to specific sensorimotor cortical areas. *Clin Neurophysiol* 2001a;112:2084–97.
- Neuper C, Pfurtscheller G. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *Int J Psychophysiol* 2001b;43:41–58.
- Neuper C, Scherer R, Reiner M, Pfurtscheller G. Imagery of motor actions: Differential effects of kinesthetic and visual-motor mode of imagery in single-trial EEG. *Cognit Brain Res* 2005;25:668–77.
- Neuper C, Wortz M, Pfurtscheller G. ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog Brain Res* 2006;159:211–22.
- Neuper C, Scherer R, Wriessnegger S, Pfurtscheller G. Motor imagery and action observation: Modulation of sensorimotor brain rhythms during mental control of a brain–computer interface. *Clin Neurophysiol* 2009;120:239–47.
- Niedermeyer E, Lopes da Silva F. *Electroencephalography: basic principles, clinical applications, and related fields.* Philadelphia: Lippincott Williams and Wilkins; 2004.
- Parasuraman R, Rizzo M. *Neuroergonomic: the brain at work.* New York: Oxford University Press; 2008.
- Pfurtscheller G, Aranibar A. Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalogr Clin Neurophysiol* 1979;46:138–46.
- Pfurtscheller G, Lopes da Silva F. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 1999;110:1842–57.
- Pfurtscheller G, Neuper C. Motor imagery activates primary sensorimotor area in humans. *Neurosci Lett* 1997a;239:65–8.
- Pfurtscheller G, Sager W, Wege W. Correlations between CT scan and sensorimotor EEG rhythms in patients with cerebrovascular disorders. *Electroencephalogr Clin Neurophysiol* 1981;52:473–85.
- Pfurtscheller G, Flotzinger D, Neuper C. Differentiation between finger, toe and tongue movement in man based on 40 Hz EEG. *Electroencephalogr Clin Neurophysiol* 1994;90:456–60.
- Pfurtscheller G, Stancák A, Neuper C. Post-movement beta synchronization. A correlate of an idling motor area? *Electroencephalogr Clin Neurophysiol* 1996;98:281–93.
- Pfurtscheller G, Neuper C, Flotzinger D, Pergenzer M. EEG-based discrimination between imagination of right and left hand movement. *Electroencephalogr Clin Neurophysiol* 1997a;103:642–51.
- Pfurtscheller G, Stancák A, Edlinger G. On the existence of different types of central beta rhythms below 30 Hz. *Clin Neurophysiol* 1997b;102:316–25.
- Pfurtscheller G, Zalaudek K, Neuper C. Event-related beta synchronization after wrist, finger and thumb movement. *Electroencephalogr Clin Neurophysiol* 1998;109:154–60.
- Pfurtscheller G, Neuper C, Pichler-Zalaudek K, Edlinger G, Lopes da Silva F. Do brain oscillations of different frequencies indicate interaction between cortical areas in humans? *Neuroscience Lett* 2000;286:66–8.
- Pfurtscheller G, Neuper C, Brunner C, Lopes da Silva F. Beta rebound after different types of motor imagery in man. *Neurosci Lett* 2005;378:156–9.
- Pfurtscheller G, Brunner C, Schlögl A, Lopes da Silva F. Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage* 2006;31:153–9.
- Qin L, He B. A wavelet-based time–frequency analysis approach for classification of motor imagery for brain–computer interface applications. *J Neural Eng* 2005;2:65–72.

- Ramoser H, Müller-Gerking J, Pfurtscheller G. Optimal spatial filtering of single trial EEG during imagined hand movement. *IEEE Trans Rehabil Eng* 2000;8:441–6.
- Salenius S, Portin K, Kajola M, Salmelin R, Hari R. Cortical control of human motoneuron firing during isometric contraction. *J Neurophysiol* 1997;77:3401–5.
- Salmelin R, Hari R. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 1994;60:537–50.
- Schalk G, McFarland DJ, Hinterberger T, Birbaumer N, Wolpaw JR. BCI2000: a general-purpose brain–computer interface (BCI) system. *IEEE Trans Biomed Eng* 2004;51:1034–43.
- Serrien DJ. Coordination constraints during bimanual versus unimanual performance conditions. *Neuropsychologia* 2008;46:419–25.
- Sharbrough F, Chatrian GE. American electroencephalographic society guidelines for standard electrode position nomenclature. *J Clin Neurophysiol* 1991;8:200–2.
- Solodkin A, Hlustik P, Noll DC, Small SL. Lateralization of motor circuits and handedness during finger movements. *Eur J Neurol* 2001;8:425–34.
- Spencer KM, Coles MG. The lateralized readiness potential: relationship between human data and response activation in a connectionist model. *Psychophysiology* 1999;36(3):364–70.
- Stancák Jr A, Pfurtscheller G. Desynchronization and recovery of β rhythms during brisk and slow self-paced finger movements in man. *Neurosci Lett* 1995;196:21–4.
- Stancák Jr A, Pfurtscheller G. Event-related desynchronization of central beta-rhythms during brisk and slow self-paced finger movements of dominant and nondominant hand. *Cognit Brain Res* 1996;4:171–83.
- Stancák A, Svoboda J, Rachmanova R, Vrana J, Kralik J, Tintera J. Desynchronization of cortical rhythms following cutaneous stimulation: effects of stimulus repetition and intensity, and of the size of corpus callosum. *Clin Neurophysiol* 2003;114:1936–47.
- Szurhaj W, Derambure P, Labyt E, Cassim F, Bourriez JL, Isnard J, Guieu JD, Mauguire F. Basic mechanisms of central rhythms reactivity to preparation and execution of a voluntary movement: a stereoencephalographic study. *Clin Neurophysiol* 2003;114:107–19.
- Taniguchi M, Kato A, Fujita N, Hirata M, Tanaka H, Kihara T, Ninomiya H, Hirabuki N, Nakamura H, Robinson SE, Cheyne D, Yoshimine T. Movement-related desynchronization of the cerebral cortex studied with spatially filtered magnetoencephalography. *NeuroImage* 2000;12:298–306.
- Wauschkuhn B, Wascher E, Verleger R. Lateralised cortical activity due to preparation of saccades and finger movements: a comparative study. *Electroencephalogr Clin Neurophysiol* 1997;102:114–24.
- Winer BJ. Statistical principles in experimental design. New York: McGraw-Hill; 1971.
- Wolpaw JR, Birbaumer N, McFarland DJ, Pfurtscheller G, Vaughan TM. Brain-computer interface for communication and control. *Clin Neurophysiol* 2002;113:767–91.