

Post-movement beta synchronization after kinesthetic illusion, active and passive movements

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Abstract

After the completion of a voluntary movement or in response to somatosensory stimulation, a short-lasting burst of beta oscillations (post movement beta ERS, beta rebound) can be observed. In the present study, we investigated if this is also true for the illusion of movements, induced by a vibration at 80 Hz on the biceps tendon. We compared the post-movement synchronization of EEG beta rhythms induced by active and passive movements and illusion in eight right-handed healthy subjects. As a result, a short-lasting post-movement beta ERS was present over motor areas after both active and passive and also after illusion of movement in all subjects. These results suggested a possible role of MI and the somatosensory cortex in the somatic perception of limb movement in humans.

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1. Introduction

Different cerebral rhythms, which display modality specific modulation, characterize the brain activity of sensory and motor areas during body movements and somatosensory processing. For example, several EEG studies reported that the amplitude of ongoing rhythmic activity in the beta (15–30 Hz) frequency bands can be influenced by active or passive motor activity of distinct body parts. Using the event-related desynchronization/synchronization (ERD/ERS) technique, it has been shown that such movements are preceded by a desynchronization of beta EEG rhythms (Pfurtscheller and Berghold, 1989), beginning over the contralateral central region about 1.5 s before movement onset. After the termination of the movement, beta ERD is followed by a short lasting burst of beta oscillations. Since these bursts of beta oscillations, described as post-movement beta synchronization

(PMBS) or beta rebound (Pfurtscheller et al., 1996, 2005), are most prominent immediately after termination of movement, they have been related to a state of cortical “deactivation” of locally restricted motor networks (Neuper and Pfurtscheller, 2001). Indeed, the beta rebound appears to be maximal over sensorimotor cortical areas involved in movement execution (Salmelin et al., 1995), it has also been suggested to reflect “active inhibition” of motor cortical neurons (Pfurtscheller and Neuper, 1997).

Summarizing the literature the beta rebound was found to have some important features. It shows a somatotopical organization (Salmelin et al., 1995), a frequency-specificity for the hand and foot representation areas (Neuper and Pfurtscheller, 2001) and a maximum which coincides with a reduced excitability of corticospinal neurons (Chen et al., 1998).

For example, Chen et al. (1998) found in several transcranial magnetic stimulation (TMS) studies that cortical activation either by median nerve stimulation or self-paced finger movement is accompanied by a significant decrease of the corticospinal excitability level after termination of the stimulation and the movement, respectively. This phasic post-movement (stimulation) excitability decrease might be associated with the “beta rebound”

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reflecting an active inhibition of motor cortical neurons reported in the EEG (Pfurtscheller et al., 2005; Neuper and Pfurtscheller, 2001) and MEG (Hari, 1995; Hari et al., 2000) as well.

Furthermore, EEG and MEG (magneto-encephalographic) studies have demonstrated that median nerve stimulation or mechanical stimulation of the finger can induce a beta burst (Salmelin and Hari, 1994; Salenius et al., 1997; Pfurtscheller et al., 2002; Stancák et al., 2003). In these studies, a beta rebound could have been observed which showed the same characteristics as the beta rebound induced by voluntary finger movement. This suggests that beta ERS could also reflect cortical processing of sensory inputs from the muscles, that is refferent input from the limbs may at least partly account for the beta ERS (Cassim et al., 2001). On the other hand, there is evidence that mental imagination of movement (Neuper et al., 1999; Pfurtscheller et al., 2005) or even passive movements (Alegre et al., 2002; Müller et al., 2003; Cassim et al., 2001) can also produce a reliable beta ERS.

For example, Pfurtscheller et al. (2005) investigated the beta rebound after four different types of motor imagery (left/right hand, both feet, tongue) at the vertex. They found that only both feet motor imagery elicited a constant beta rebound, whereas hand motor imagery was less consistent and in tongue imagery it was totally absent. Thus, the reported findings do not support the hypothesis that the SMA acts as the main source of the midcentral beta rebound (Ohara et al., 2000). Indeed, if this would be the case, one should expect that also tongue or hand motor imagery would induce beta oscillations in the central area. They concluded that the termination of motor cortex activity, independent of whether it follows the actual execution

or just imagination of a movement, may involve at least two networks, one corresponding to the primary motor area and another one in the SMA.

The similarity of observed beta ERS after voluntary movements, median nerve stimulation and imagination provides arguments for the notion that this type of beta oscillation is more likely related to the previous motor cortex activation than to the processing of somatosensory refferences, since the latter are probably not present during motor imagery.

Another kind of motor imagery is the kinesthetic illusion, which is compared to motor imagery less studied in the context of post movement beta synchronization. Kinesthetic illusions, e.g. illusory sensation of limb movement, can be elicited by artificially manipulating proprioceptive pathways through tendon vibration at optimal frequencies at around 80 Hz (Roll and Vedel, 1982; Naito et al., 1999; Goodwin et al., 1972). Subjects experience that the vibrated muscles are being stretched. This kinesthetic illusion is caused because the vibration of the tendon excites the muscle spindles in a manner similar to when the muscle actually stretches (Roll and Vedel, 1982; Roll et al., 1989). The direction of such kinesthetic illusion depends on the anatomical site of the vibrated muscles and corresponds to their lengthening. Naito et al. (1999) and Naito and Ehrsson (2001) found in several positron emission tomography (PET) studies that kinesthetic illusions experienced by the subjects during tendon vibration lead to activation of the contralateral somatosensory cortex as well as the primary motor cortex (MI). Furthermore, they found stronger activation of MI compared to somatosensory cortex. This result together with the findings that MI is also active during passive limb movements

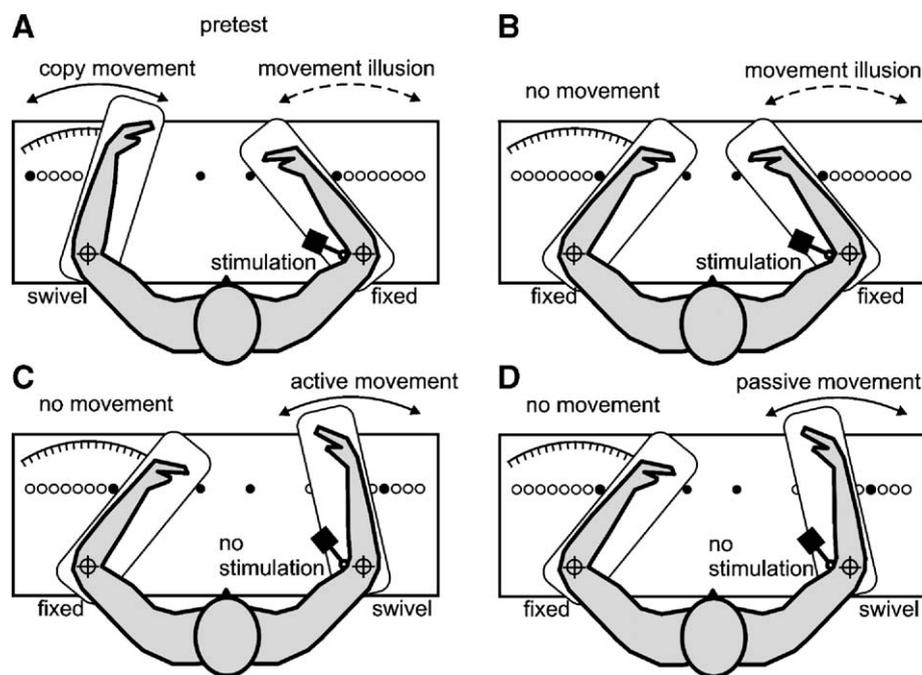


Fig. 1. Experimental setup with three different types of movements. (A) Setup for the pretest. (B) Illusion of movement assembly. Both arms are fixed. (C) Active movement. The right board is movable, whereas the left board is fixed. (D) Passive movement. Passive movement is induced by the investigator by pulling a cord. There is no mechanical stimulation within the active and passive movement condition. Beginning and ending of the movements are indicated by the presentation of noise via a loudspeaker.

(Weiller et al., 1996) suggests that MI has sensory functions in a sense that its neurons receive and process sensory afferent inputs from muscle spindles without generating any actual movements (Naito et al., 2002; Naito, 2004).

The aim of the present study was to investigate the function and cortical localization of post movement beta synchronizations elicited by kinesthetic illusions compared to active and passive movements. Based on the results of the described previous studies, we expect that kinesthetic illusion will evoke a similar pattern of beta rebound like active or passive movements, primarily present in MI.

2. Methods

2.1. Subjects

Eight right-handed healthy volunteers (five females and three males, mean age 23.5 years, S.D. = 3.2) participated in this study. All subjects gave their informed consent and were paid for their participation. For mu ERD calculation the EEG data of all eight subjects were included in the statistical data analysis. Data of one subject was excluded for beta ERS statistical analysis due to outliers in the illusion condition (max. ERS value above 500%).

2.2. Experimental design

The subjects were sitting in a comfortable semi-reclining armchair in a darkened and electrically shielded room. Both arms were fixed on movable boards. A special mechanical device (Mini Shaker Type 4810, Brüel and Kjær, Denmark) positioned on the right biceps tendon delivered vibration.

The vibration amplitude was adjusted in a pretest to induce optimal kinesthetic illusions at 80 Hz and then kept constant throughout the experiment. The stimulation frequency of 80 Hz was chosen, according to previous studies, where such frequency was found to be optimal eliciting the experience of illusion (Naito et al., 1999). During this pretest, the right arm was fixed in a defined angle and stimulated 10 times for 4 s with a frequency of 80 Hz. Both arms were kept away from vision during the pretest as well as during the three experimental conditions. For the pretest, subjects were instructed to copy the movement they feel on the stimulated right arm with the left arm (Fig. 1A). The extent of the extension/flexion of the left arm was read off a scale on the left board and logged in a list. The mean extent of the movement was calculated. After this pretest, the following main experimental conditions were performed with eyes opened:

1. Induction of illusion of movement of the right forearm by mechanical 80 Hz stimulation (Fig. 1B).
2. Performance of a voluntary active movement of the right forearm with a speed and amplitude comparable to those experienced during the illusion condition (Fig. 1C).
3. Performance of a passive movement of the right forearm with a speed and amplitude comparable to those experienced during the illusion condition (Fig. 1D).

2.3. Procedure

Each subject performed each of the three experimental conditions. Within the first experimental run both boards were fixed in a predefined angle. Illusion of movement was induced 50 times by a 4 s mechanical 80 Hz biceps tendon vibration and an inter-stimulus interval of 6 s. Subjects were asked to concentrate on the right stimulated arm. The task assigned to subjects in the second run was to perform voluntary active right forearm movements so that the performed active movement corresponded with the illusory movement during the first run. During the third experimental condition (third run), the investigator induced passive right forearm movements by pulling a cord. By means of an expander which was fixed on the right board releasing the cord, the arm was brought back to the initial position. During the second and third runs, only the left arm was fixed and there was no mechanical stimulation during these two experimental conditions (active, passive). Instead of the stimulation unit a loudspeaker was connected to keep the noise level constant over the three conditions and to indicate the beginning and the end of the active and passive movement. The active period lasted 4 s and the interval between the movements was 6 s. Active as well as passive movements were performed during the presentation of the noise via the loudspeaker.

In order to analyze the data according to the exact timing of the paradigm, digital trigger signals, indicating the beginning of the vibration, active and passive movement were recorded, respectively. In the illusion condition, trigger signals were automatically generated by the system every time the stimulation started. In the active as well as in the passive condition, the trigger signals were generated by a contact sensor every time the actual movement started.

After the experiment, participants were instructed to complete a short “illusion questionnaire” where they had to rate (1 = not similar at all to 5 = very similar) their subjective feeling of similarity concerning the three different movements.

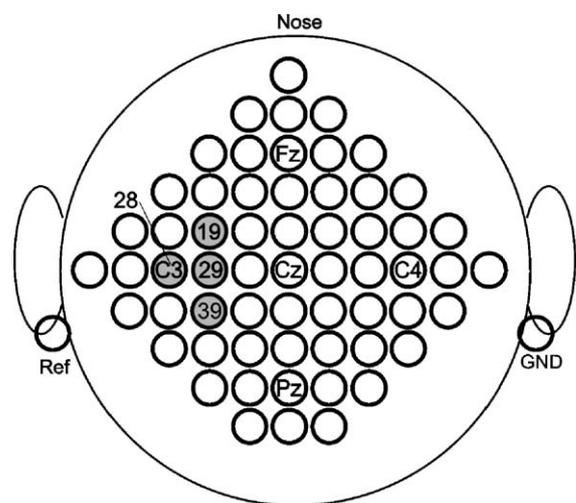


Fig. 2. Electrode positions for monopolar 60-channel recordings, with an inter-electrode distance of approx. 2.5 cm. For ERD/ERS calculation, resulting in time-frequency maps, data of all 60 channels were used. For statistical analysis, data recorded from one of the channels 19, 28, 29 and 39 were used in the present study.

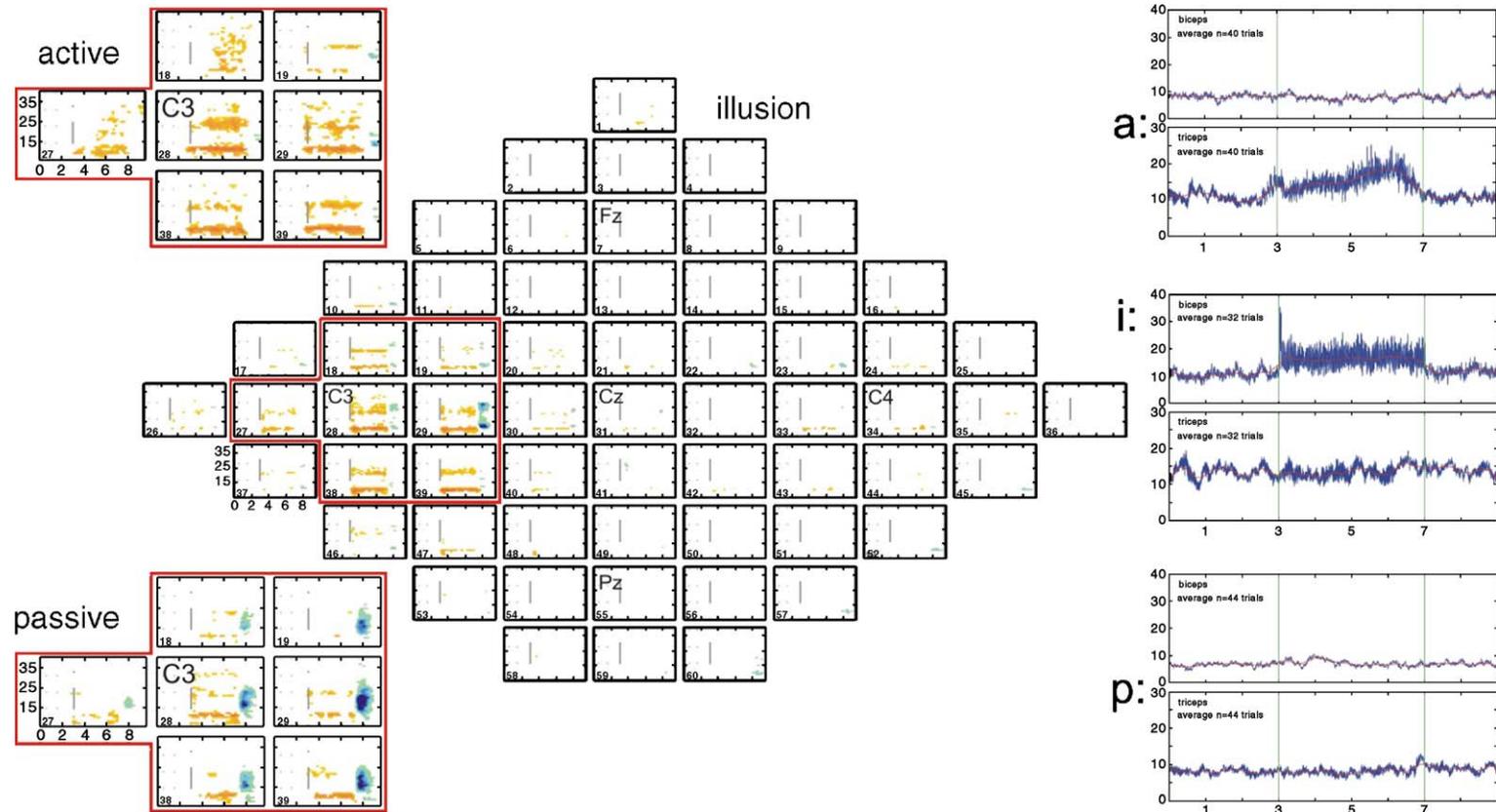


Fig. 3. In the middle of this figure, mean ERD/ERS maps for the illusion condition calculated for all 60 channels are displayed as an example. Left side of the figure shows the mean ERD/ERS maps, averaged over eight subjects separately for each of the three experimental conditions. The red border shows the source derivations which were inspected to define subject-specific reactive beta frequency bands and are enlarged for active and passive movement. EMG, derived from the biceps and triceps, from one subject is displayed on the right side of the figure, separately for each condition (a: active, i: illusion and p: passive), respectively.

2.4. EEG recordings

The EEG was recorded from a grid of 60 Ag/AgCl scalp electrodes referenced to the left mastoid (see Fig. 2) and bandpass filtered between 0.15 and 50 Hz with Notch on. Electrodes were placed with a regular inter-electrode distance of approximately 2.5 cm assuring electrode impedance below 5 k Ω .

The EOG was recorded from two electrodes, one placed above the inner canthi and the other just below the outer canthi of the right eye, in order to detect vertical as well as horizontal eye movements. The surface EMG was recorded bipolarly using disposable ECG electrodes (37 mm diameter). EMG signals were amplified with a time constant of 3.3 s and an upper cut-off frequency of 100 Hz and rectified and full-wave integrated by a contour follower afterwards. The recordings included trigger signals, indicating movement onset and were sampled with 250 Hz. EMG signals from one subject for all three conditions separately are shown on the right side of Fig. 3.

2.5. Data analysis

To obtain reference-free EEG data, orthogonal source derivations were calculated by averaging the signal of the four nearest-neighbor electrodes (north, east, south, west) and subtracting it from the center electrode (Hjorth, 1975). From the continuous EEG recordings, time segments with a length of 9.5 s each (3 s before and 6.5 s after movement/trigger-onset) were analyzed. The raw EEG was visually controlled for artifacts. ERD/ERS calculation resulted in time-frequency maps in the range from 6 to 42 Hz (in overlaying 2 Hz bands; $p < 0.05$) of the percentage band power changes, relative to the band power in the reference interval (0.5–1.5 s) separately for each subject, experimental condition and each of the 60 electrode sites (see Fig. 2), respectively (see Fig. 3, middle/left). Significant ($p < 0.05$) band power decrease or increase (ERD/ERS), with respect to the specified reference interval, was determined by using a bootstrap algorithm, as described elsewhere (Graimann et al., 2002). Additionally, EEG data were digitally band pass filtered in the lower (8–10 Hz) and upper mu frequency band (10–14 Hz) to investigate possible differences in movement ERD with respect to the three experimental conditions. Furthermore, visual inspection of the time-frequency maps was carried out for each subject and each condition to define specific individual reactive 5 Hz beta frequency bands, common for all experimental conditions. First inspection showed that highest ERS values could be found contralateral to the movement over electrode positions 19, 20, 28, 29, 30, 39 and 40 (see Fig. 3, middle/left). So within this predefined electrode set the source derivation which displayed the greatest ERS value contralateral to the movement was determined and data of the selected source derivation was used for all statistical analysis (see Fig. 2). The mean latency of the maximum ERS value relative to trigger onset for illusion movement was 4.95 s, for active movement 5.8 s and for passive movement 5.1 s.

A separate analysis of variance (ANOVA) with repeated measurement design was conducted on ERD/ERS values of the

lower and upper mu and beta band, with respect to the three different types of movement (illusion/active/passive). The Greenhouse–Geisser epsilon correction of degrees of freedom was applied if required. In addition to the ERD/ERS values, the corresponding absolute band power in the reference interval (used for ERD/ERS computation) was examined to rule out a priori band power difference between conditions.

Statistical analyses concerning the movement ERD were performed for a 1500 ms interval starting 500 ms after movement/trigger onset (3.5–5.0 s). Statistical analysis concerning the post-movement ERS were performed for a 1500 ms interval starting after movement at second 7.5, with respect to the three different types of movements.

3. Results

3.1. Band power in the reference interval for mu and beta bands

Separate ANOVAs with repeated measurement design were performed in mu and beta bands and the corresponding reference period (0.5 to 1.5 s) for all of the three movements. There was no significant difference regarding power values in the lower ($F_{(2,14)} = 2.941$, $p = 0.086$) and upper mu band ($F_{(2,14)} = 3.352$, $p = 0.065$) between illusion of movement, active and passive movement, indicating similar means of absolute power values for the three different movements.

The power values in the beta band revealed significant differences between illusion of movement, active and passive movement ($F_{(2,12)} = 7.151$, $p = 0.009$). A post hoc t -test for paired samples showed significant differences between active and passive movement ($t_{(6)} = 3.383$, $p = 0.015$) and illusion and active movement ($t_{(6)} = -2.611$, $p = 0.040$). No significant

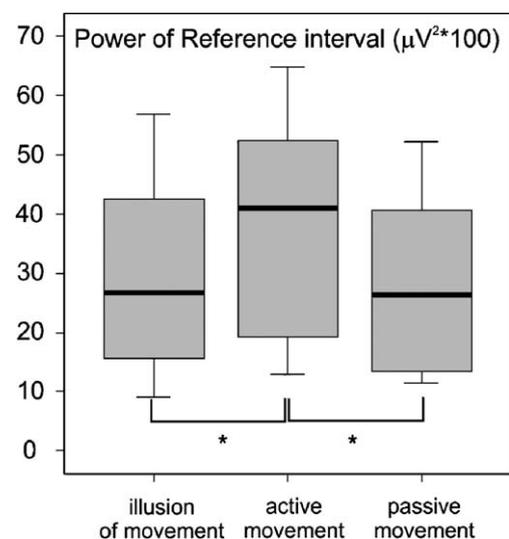


Fig. 4. Results of power of the reference interval within the individual beta band for each condition. The yellow boxes contain all the values between the lower and the upper quartile. The dark line inside the boxes is representing the median values. Lines outside of the boxes represent the lowest and the greatest value. The asterisk shows statistically significant post-hoc differences ($p < 0.05$).

difference was found for condition illusion and passive movement ($t_{(6)} = -0.778$, $p = 0.466$) (Fig. 4).

3.2. Mu frequency–mu ERD during movement

The results of separate ANOVAs with repeated measurement design of the different movement conditions showed neither significant differences in ERD values in the lower (8–10 Hz) mu band ($F_{(2,14)} = 1.237$, $p = 0.320$) nor in the upper (10–14 Hz) mu band ($F_{(2,14)} = 0.963$, $p = 0.406$).

3.3. Beta frequency–beta ERS after movement

The statistical analyses was performed with subject specific center frequencies in the range of 18 to 27 Hz. Individual beta frequencies were held constant for each subject over the experimental conditions. The results of the ANOVA with repeated measurement design showed significant differences in ERS values for the three types of movements ($F_{(2,12)} = 14.929$, $p = 0.001$). Post hoc paired samples t -tests showed a significant difference between active and passive movement ($t_{(6)} = -5.147$, $p = 0.002$). Furthermore, a significant difference was found for beta activity between illusion and passive ($t_{(6)} = -3.922$, $p = 0.008$) movement which is particularly important to the rebound hypotheses, while the difference between illusion and active movement was not significant ($t_{(6)} = 0.777$, $p = 0.941$) (Fig. 5).

3.4. Illusion questionnaire

Whereas significant electrophysiological differences for the three types of movements were obtained, the results of the ‘illusion-questionnaire’, where subjects had to rate their subjective feeling of similarity concerning the different movements revealed no significant differences ($X^2 = 2.174$, $p = 0.337$).

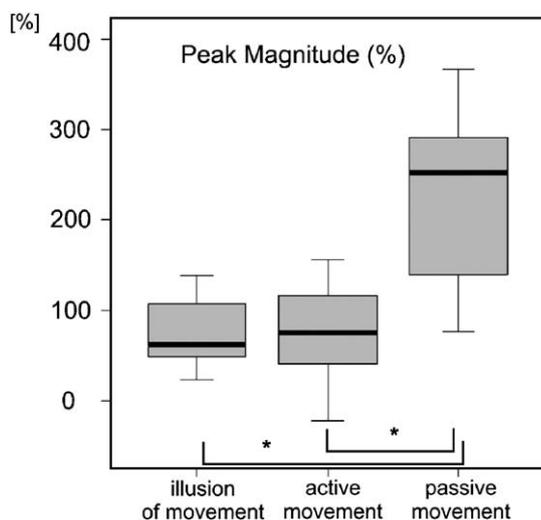


Fig. 5. Results of peak magnitude (ERS) after the movement within the individual beta band for each condition. The yellow boxes contain all the values between the lower and the upper quartile. The dark line inside the boxes is representing the median values. Lines outside of the boxes represent the lowest and the greatest value. The asterisk shows statistically significant post-hoc differences ($p < 0.05$).

4. Discussion

The present study investigated the function and cortical localization of post movement beta synchronizations elicited by kinesthetic illusions compared to active and passive movements.

When cortical activation during illusion of movement was compared with active and passive movement, a mu ERD contralateral to the movement was found in all three conditions. This might suggest an association of all three motor tasks with activation in primary and somatosensory areas. Additionally, the results of the illusion questionnaire where no differences between the subjective feeling of similarity concerning the different movements were found might indicate the similar activation patterns in the upper and lower mu frequency bands.

According to our hypothesis, we found that kinesthetic illusion also induced a beta rebound like active or passive movements. However, the spatial localization of the beta ERS in all conditions elicited in somatosensory and primary motor areas, its amplitude size varied significantly. The highest amplitude was found in the passive movement, which could be explained by the relationship between cortical activation and excitability of neurons. That is, if the magnitude of the beta rebound is negatively correlated with the excitability level of motor cortex neurons, a larger beta rebound is expected with passive as compared to active movement (Chen et al., 1998; Schnitzler et al., 1997; Pfurtscheller et al., 2005). Furthermore, an active movement resulted in both, an efferent flow to the muscles and in proprioceptive afferences, whereas passive movement was accompanied by an afferent flow only. Another explanation for the higher beta ERS in the passive condition compared to the active condition could be due to the different performance of execution. Whereas the active movement and its ending was a continuous slow process, the passive movement, on the other hand, stopped abruptly when the movable board reached the starting position causing a massive afferent flow. The observation of a suppressed beta rebound during movement illusion can be interpreted that illusion is accompanied with an increased level of motor cortex excitability similar as found during active movement. It is known that kinesthetic illusions can be elicited by artificially manipulating proprioceptive pathways through tendon vibration (Naito et al., 1999; Goodwin et al., 1972) because the vibration excites the muscle spindles in a manner similar to when the muscle actually stretches (Roll and Vedel, 1982; Roll et al., 1989). That is active movement and illusion of movement share similar neural circuitry in motor areas and result both in an activation of motor cortex neurons. The results of the present study further support this assumption and it is in line with the results of several brain imaging studies which have shown an activation of motor cortex neurons not only during motor execution but also during illusion of movement (Naito et al., 1999; Lotze et al., 2000; Naito and Ehrsson, 2001).

The results of the beta ERS after different movements could be explained by the assumptions made above, however, there are some discrepancies concerning the corresponding values in the reference interval. Against our expectations of similar cortical activation during the reference intervals in all three conditions, the results revealed significant differences. Whereas the high power values in the active movement condition could be

explained by a kind of cortical pre-activation of the required movement, the lower power in the two other conditions is mainly unclear. One possible reason could be the contribution of different cortical networks in the motor area concerning different movements, e.g. active, passive or illusion. Taking these assumptions and the results of the presented study into account, a direct relationship between beta ERS and corresponding power of reference interval cannot be made and needs further investigation.

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