Quasi-movements: A novel motor–cognitive phenomenon

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Abstract

We introduce quasi-movements and define them as volitional movements which are minimized by the subject to such an extent that finally they become undetectable by objective measures. They are intended as overt movements, but the absence of the measurable motor responses and the subjective experience make quasi-movements similar to motor imagery. We used the amplitude dynamics of electroencephalographic alpha oscillations as a marker of the regional involvement of cortical areas in three experimental tasks: movement execution, kinesthetic motor imagery, and quasi-movements. All three conditions were associated with a significant suppression of alpha oscillations over the sensorimotor hand area of the contralateral hemisphere. This suppression was strongest for executed movements, and stronger for quasi-movements than for motor imagery. The topography of alpha suppression was similar in all three conditions. Proprioceptive sensations related to quasi-movements contribute to the assumption that the "sense of movement" can originate from central efferent processes. Quasi-movements are also congruent with the postulated continuity between motor imagery and movement preparation/execution. We also show that in healthy subjects quasi-movements can be effectively used in brain–computer interface research leading to a significantly smaller classification error (∼47% of relative decrease) in comparison to the errors obtained with conventionally used motor imagery strategies.
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1. Introduction

Executed movements are the only known natural way by which individuals are able to communicate with the environment. This includes a broad repertoire of motor activities such as skilled limb and finger movements, locomotion, eye movements, vocalization, etc. We define movement performance as a sequence of neuronal activations related to carrying out a motor intention, which culminates in the contraction of a muscle. The latter is also referred to as movement execution or motor response. However, there are examples when the activation of neuronal motor structures does not produce a motor response. For instance, patients with neuromuscular impairments intend and try to execute a movement but do not succeed because of damage in the central or peripheral nervous system. Another example is kinesthetic motor imagery, which is defined as mental/neuronal simulation of an action without activation of the effectors (Decety, 1996; Guillot & Collet, 2005; Haggard, 2005; Jeannerod, 1994, 1995, 2001; Lotze & Halsband, 2006; Michelon, Vettel, & Zacks, 2006; Neuper, Scherer, Reiner, & Pfurtscheller, 2005). However, contrary to the pathological examples mentioned above, kinesthetic motor imagery is performed without the intention to execute a movement.

In the present study we provide evidence for a novel type of motor–cognitive activity which is neither movement execution nor motor imagery. We refer to this phenomenon as "quasi-movements" and define them as volitional movements which are minimized by the subject to such an extent that finally they

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become undetectable by objective measures. Performance of quasi-movements requires training: healthy participants learn to make movements so small that ultimately they are indistinguishable from the background electromyographic (EMG) activity at rest. The existence of quasi-movements implies the possibility that the performance of a movement would not necessarily lead to the movement execution.

Our study combines electromyographic, electroencephalographic (EEG), and psychological testing in order to address the multifaceted nature of quasi-movements and to provide methodological details on their performance. On the basis of our results we discuss how quasi-movements are relevant for the understanding of motor imagery and the "sense of movement". Quasi-movements represent a unique paradigm for studying movement organization without contamination by the peripheral proprioceptive activation, which is a confounding factor in neuroimaging studies involving overt movements.

We also propose that in healthy subjects quasi-movements can be effectively used in brain–computer interface (BCI) applications (for an overview: Birbaumer, 2006; Blankertz, Dornhege, Krauledat, Müller, & Curio, 2007; Donoghue, 2002; Wolpaw, Birbaumer, McFarland, Pfurtscheller, & Vaughan, 2002). BCI establishes a human–machine interaction on the basis of brain activity only. It enables the communication with the environment for people with severe neuromuscular/motor impairments like paralysis or amputation. Apart from comparatively rare studies with patients, BCI research often relies on healthy subjects for the refinement and testing of novel algorithms and approaches. In their case motor imagery is mostly used as a substitutional strategy to the so-called "attempted movements" of patients who try but cannot execute a movement. Our results suggest that quasi-movements represent an effective strategy for BCI studies in healthy subjects, since (1) quasi-movements resemble "attempted movements" more closely than motor imagery, and (2) quasi-movements are associated with a pronounced and lateralized modulation of neuronal oscillations over the sensorimotor cortex. Importantly, the single-trial analysis of EEG data shows that quasi-movements reduce the classification error by ∼47% compared to motor imagery.

2. Methods

2.1. Participants

Seventeen healthy volunteers (mean age 29 years, range 19–48 years; 9 males, 8 females) without any history of neurological or psychiatric disorders participated in the present study and gave informed consent. Thirteen of the subjects were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal vision.

2.2. Procedure

During the experiment the subjects were sitting comfortably in a chair in front of a computer screen. The subjects performed three different tasks, which will be referred to as "real", "imagery", and "quasi-movement". In all experimental conditions the subjects were instructed to react in a specific manner (described below) to the visual stimuli presented on the computer screen. The stimuli were the black letters "L" and "R" (visual angle $4.8° \times 3.4°$) on a grey background. These stimuli are referred to as "left" and "right" class and were presented in a random order. The duration of each stimulus was 3 s, and the inter-stimulus interval varied randomly in the range of 3 ± 0.2 s. In the "real" task the subjects were asked to perform a series of approximately six quick abductions with the abductor pollicis brevis (APB) of the left or right thumb, depending on whether the "L" or "R" stimulus was presented, respectively. The APB muscle was chosen in the present study for the following reason: it is a flat, superficially located muscle and therefore even its smallest activations are detectable, since the contracting muscle fibers are close to the recording surface electrode. The subjects were asked to execute weak but visible thumb abductions. In the "imagery" task they were asked to imagine the aforementioned abductions with the same strength and frequency. The subjects were instructed to perform motor imagery from a first person perspective and to concentrate only on the kinesthetic aspects of the movement without its visualization.

The main idea of the "quasi-movement" task was to train subjects to perform the movement from the "real" condition but to minimize its strength to such an extent that it would be practically undetectable with EMG. In this sense the performance of quasi-movements becomes comparable to motor imagery, where motor responses, if present, are usually indistinguishable from the background EMG activity. Minimization of motor responses was achieved with a training period of individually varying length (∼10–20 min) before the data recording. The following instructions were provided for the subjects: "Perform an abduction of your thumb and let this movement be relatively small. Now try to minimize this movement even further making it as small as possible". In the first part of the training the subjects were shown their own EMG traces on the screen. They were asked to reduce the amplitude of motor responses (self-paced) in order to produce EMG activation just above the baseline level. In the second part of the training subjects did not observe their EMG traces, but instead were instructed verbally by the researcher to further reduce the movement strength. This was a crucial moment during the training of the quasi-movements, since the subjects were asked to minimize already minuscule movements so that they become undetectable in EMG (as assessed by the researcher).

Each of the three tasks consisted of two sessions presented in a random order, apart from five subjects where the order of the tasks was fixed in the following manner: "imagery", "quasi-movement", and "real". The duration of one session was ∼12 min including two 30-s breaks. Each session consisted of 54 "L" and 54 "R" stimuli, thus the total number of stimuli for each class was 108 in two sessions. Experimental procedures were approved by the Ethics Committee of Charité University Medicine Berlin, Berlin, Germany.

2.3. Data acquisition

EEG and EMG data were recorded with Ag/AgCl electrodes, using *BrainAmp* amplifiers and *BrainVision Recorder* software (Brain Products GmbH, Munich, Germany). EMG was recorded from the left and right APB with one electrode located over the muscle belly and the other over the proximal base of the phalanx. During data acquisition EEG and EMG signals were band-pass filtered between 0.1 and 250 Hz and digitized at a rate of 1000 Hz. For the offline analysis EMG data was high-pass filtered at 10 Hz.

EEG data was recorded with 120 electrodes placed according to the extended International 10–20 system (Jasper, 1958), the reference electrode being placed on the nose. For the following offline analysis the most anterior, posterior, and temporally located electrodes were excluded from the analysis because of the potential contamination by muscle activity. After this exclusion the total number of channels was reduced to 86.

Control experiments were performed in two subjects with the recordings of additional muscles contributing to the thumb movement. In one subject right and left extensor pollicis brevis and flexor pollicis longus muscles were recorded in addition to APB. In another subject right and left extensor pollicis brevis and flexor pollicis brevis muscles were recorded together with APB. In these two subjects we also recorded the movement of the left thumb with an accelerometer (model BP-BM-40, Brain Products GmbH) with the sensitivity 300 mV/g and the threshold $0.0002g$, where g is 9.8 m/s^2. The accelerometer was a one-dimensional sensor and was positioned on the proximal phalanx of the left thumb with the principal measurement axis being adjusted along the direction of abduction. Although the sensor was one-dimensional it could detect any tangential component of acceleration, which fitted the goal of our measurements—to detect the movement but not to reconstruct its trajectory.

2.4. EEG analysis

2.4.1. Amplitude modulation of spontaneous alpha oscillations

In the first part of the analysis EEG data was re-referenced using the Laplacian method, which is based on the subtraction of the averaged activity of four neighboring electrodes from the activity in a given electrode (Graimann & Pfurtscheller, 2006; Hjorth, 1975). In order to evaluate the degree of the cortical activation related to task performance, we based our analysis on the previous findings showing that alpha oscillations desynchronize when a given cortical area is involved in the perceptual, motor or cognitive processing—a phenomenon referred to as event-related desynchronization or ERD (Berger, 1929; Gastaut & Bert, 1954; Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes da Silva, 1999).

After the Laplacian transformation the activity in each channel was filtered in the 8–13 Hz frequency range. Then the Hilbert transform (Clochon, Fontbonne, Lebrun, & Etevenon, 1996; Graimann & Pfurtscheller, 2006; Rosenblum & Kurths, 1998; Rosenblum et al., 2002) was applied in order to obtain an amplitude envelope of alpha oscillations. EEG activity processed in this way was averaged across epochs separately for each stimulus class ("L" or "R"). Using averaged traces of the amplitude dynamics of alpha oscillations, the ERD was calculated for each channel according to:

$$\text{ERD} = \frac{\text{POST} - \text{PRE}}{\text{PRE}}$$

where POST is the averaged amplitude in the post-stimulus interval (70–3300 ms) and PRE is the averaged activity in the pre-stimulus interval (−500 to 0 ms). For each class an electrode was selected with the strongest ERD in the left and right sensorimotor areas. This analysis was performed for all three conditions.

2.4.2. Classification of single EEG epochs

The following part of the analysis describes the single epoch classification of EEG data for the left and right thumb (quasi-)movement/imagery. This contrast of left versus right movements (also referred to as classes) is crucial for capturing the brain activity produced by motor (imagery) components, while the rest of the activity, related to general factors such as attention or arousal levels, should be similar for both classes.

Below we describe a procedure for the selection of a frequency band, time interval, and spatial EEG structure which optimally discriminate EEG activity between the two classes for each of three conditions. These procedures are also regularly used in the Berlin Brain–Computer Interface project (BBCI; Blankertz, Dornhege, Krauledat, et al., 2006; Blankertz, Dornhege, Lemm, et al., 2006; Shenoy, Krauledat, Blankertz, Rao, & Müller, 2006).

(1) *Selection of frequency band and interval.* First EEG data (after the Laplacian transformation) was filtered in the broad frequency range from 7 to 30 Hz, where one would expect to see a major reactivity in the tasks, and then the amplitude envelope of oscillations was obtained with the Hilbert transform. Subsequently a special procedure was applied to find which post-stimulus interval discriminates best between the "left" and "right" class. For this purpose we used point-biserial correlation which gives a measure of the covariation between a continuous variable (such as the mean amplitude of EEG activity in a specific post-stimulus interval) and a binary variable (−1 and 1 for the "left" and "right" class). The time points with the strongest correlations in the post-stimulus interval were selected with the criteria of encompassing 80% of the total score. The interval determined in this way was then used for the selection of a frequency band discriminating optimally between both classes. For this purpose power spectra (based on Fast Fourier Transform) were computed for each epoch in the calculated time interval, and the point-biserial correlation was calculated between each frequency bin and the binary class variable. The neighboring frequency bins with the strongest correlation were selected to form an optimal frequency band (*band*) for the discrimination between the two classes. The lower and upper limits of *band* were defined on the basis of the point-biserial correlation being not smaller than 1/3 of the highest correlation in the center of *band*. Next, an optimally discriminating time interval (*interval*) was determined again, but this time using *band*.

(2) *Common Spatial Pattern analysis.* The original raw EEG data was band-pass filtered using *band*, and the epochs were created in *interval*. The obtained EEG segments were subjected to Common Spatial Pattern analysis (CSP; Fukunaga, 1990; Graimann & Pfurtscheller, 2006; Koles, Lind, & Soong, 1995; Koles & Soong, 1998; Müller-Gerking, Pfurtscheller, & Flyvbjerg, 1999) using all available channels. The main idea behind CSP analysis is to determine spatial filters W which maximize the variance in one class while simultaneously minimizing the variance in another class. In the case of band-pass filtered EEG signals, variance is equivalent to power in a given frequency range, and thus spatial filters optimize the extraction of ERD or event-related synchronization. The CSP procedure has been successfully applied to the classification of single EEG epochs in the context of online brain–computer interfacing (refer for technical details to Blankertz, Dornhege, Krauledat, Müller, & Curio, 2005; Dornhege, Blankertz, & Curio, 2003). W^{-1} can be seen as common spatial patterns, which represent time-invariant EEG "sources". The relationship between W and W^{-1} is similar to the relationship between mixing and de-mixing matrices in independent component analysis. For the following analysis we selected only four filters (two for each class) with the largest eigenvalues. Increasing the number of filters usually would not lead to an increased discriminability between the classes. Using the obtained filters W, the original EEG recordings X are then projected (spatially filtered) onto

$$Z = WX$$

In this case since there are only four filters (four rows in W) the resulting matrix Z contained only four EEG sources. Then the logarithm of variance was calculated for each epoch in Z in time window *interval*.

(3) *Classification of epochs with linear discriminant analysis.* Linear discriminant analysis was used to classify epochs from the matrix Z as belonging to either "left" or "right" class (Blankertz et al., 2005; Friedman, 1989; Shenoy et al., 2006).

(4) *Cross-validation.* The combination of CSP and linear discriminant analysis was verified with a cross-validation. The main idea of this procedure is to use one part of the data set for the training of the classifier, and another part for verifying how the classifier can be generalized to the data which has not been used in the training procedure. The training consists of finding CSP filters and parameters for linear discriminant analysis on the basis of the training data set while *band* and *interval* remain the same. For the present study we divided our data set of all epochs into eight non-overlapping segments, and the classifier was trained on 7/8 of the total number of epochs and then tested on the remaining 1/8. Thus, altogether eight training data sets were obtained. In each of these iterations the percentage of misclassified epochs has been calculated and averaged across all iterations, leading to the classification error. One has to note that this single-trial classification procedure is not only relevant for the analysis within BCI context, but also represents a powerful tool for the selection of temporal, spectral, and spatial aspects of neuronal activations related to movement execution, motor imagery, and quasi-movements.

2.4.3. Similarity between spatial activation patterns

As mentioned above, the matrix W^{-1} reflects the spatial map of cortical EEG activations. We were interested in quantifying the degree of similarity between the activations maps across different conditions. A "similarity index" was calculated as the absolute value of the cosine of the angle between two CSP maps from two different tasks, e.g., "imagery" and "quasi-movement". The angle was in an E-dimensional space, where E is the total number of channels. The "similarity index" varies from 0 to 1, with 1 corresponding to completely similar patterns and 0 to completely dissimilar patterns.

2.5. EMG analysis

2.5.1. Detection of weak motor responses

One of the main steps in our EMG analysis was the detection of motor responses related to the task performance. Both manual and automatic procedures were utilized. When using the manual procedure, EMG data was segmented into epochs in the time interval from −2000 to 3300 ms with respect

to the stimulus. The detection of motor responses was performed via the visual inspection of each single epoch, separately for the left and right hand. An important point during this inspection was that the researcher did not know whether a given stimulus belonged to the "left" or "right" class. This was necessary in order to avoid a possible bias of knowing that a given EMG epoch corresponded to a specific stimulus. Although a visual inspection is a very demanding and lengthy process, it is used as an important criterion for the absence/presence of motor responses instead of relying only on automatic procedures (Abbink, van der Bilt, & van der Glas, 1998; Hodges & Bui, 1996; Reaz, Hussain, & Mohd-Yasin, 2006).

Left hand EMG traces sometimes contained residuals of electrical heart activity, and in order to remove these artifacts we utilized Independent Component Analysis (FastICA; Hyvärinen & Oja, 2000) with kurtosis as a contrast function. Some EMG epochs contained excessive amounts of background muscle activity and were also excluded from the analysis since they compromised the ability to detect weak motor responses. The number of epochs with detected movements was then translated into a "detection rate". We define a correct motor response when only left movements were detected for the stimulus "L", and only right movements for the stimulus "R". The detection rate is then defined as the ratio of the total number of epochs with correct motor responses to the total number of epochs. For the "real" condition the detection rate should be 1 (or 100%) since each stimulus should be associated with detectable motor responses. For the "imagery" and "quasi-movement" conditions the detection rate should be rather small since none of these tasks implies presence of strong EMG activity.

An automatic classification of EMG epochs was also performed. The EMG epochs were classified on the basis of root-mean square (RMS) values in the post-stimulus interval (70–3300 ms). We used the same classification procedure as described above for EEG, but our feature vectors were post-stimulus RMS values of EMG from the left and right APB. Linear discriminant analysis as well as cross-validation was applied to RMS values in order to obtain the average classification error. Importantly, in the case of manual inspection of EMG the complete absence of motor responses in all trials would correspond to a zero detection rate. In the case of automatic single-trial EMG analysis the classification error of 0.5 corresponds to a random classification of the motor responses.

2.5.2. Comparison of pre- and post-stimulus EMG activity

One of the main ideas of the present study was to show that in the "quasi-movement" condition it is possible to perform movements with motor responses being indistinguishable from the background EMG at rest. In such a case the amplitude of muscular activity in the pre- and post-stimulus intervals should not be different in the majority of epochs. Furthermore, EMG activity in the post-stimulus intervals of the "quasi-movement" condition should not be significantly different from the values obtained during motor imagery. We clearly realized the fact that if we did not visually detect motor responses in many epochs, this would not be sufficient to exclude the possibility that some slight tonic EMG activity might have been associated with the subject's efforts to respond to the stimuli. Therefore, the analysis of RMS values was performed in order to compare EMG activity from the pre- and post-stimulus intervals. First, we excluded epochs containing motor responses from the analysis (as identified during the visual inspection). Wilcoxon's rank sum test was then applied in order to test for the differences between the pre- and post-stimulus RMS values. The reason for using this non-parametric test was the fact that the RMS values were not normally distributed. The comparison of EMG values in pre- and post-segments was performed individually for each subject and hand.

2.5.3. Statistical analysis across subjects

We used the non-parametric Spearman's rank correlation coefficient (r) for determining the dependency between different variables belonging to psychometric, EMG, and EEG measures. Non-parametric Wilcoxon's sign rank test was utilized for the comparison of two variables and p-values were adjusted with Bonferroni corrections when appropriate. If the analysis required comparison of multiple variables we used repeated measures ANOVA.

2.5.4. Relationship between EEG and EMG activity

One of the important aspects of the current study was to show that quasi-movements can be used as an alternative to motor imagery in BCI experiments with healthy subjects. This might be possible if the "quasi-movement" task provides a more effective modulation of ongoing neuronal oscillations compared to motor imagery, and if the peripheral feedback from occasional motor response is not strong enough by itself to modulate EEG activity. In order to show that the classification procedure is not dependent on the occasional presence of task-related EMG responses in some of the epochs, we performed the following three types of analysis.

(1) As described above, the automatic classification procedure was applied both to EEG and EMG data. Additionally the classification of EEG and EMG epochs was performed after the exclusion of epochs containing visually detected motor responses. Differences between the obtained classification results in EEG and EMG data (based on all available epochs or only on those without detected motor responses) were tested for significance with Wilcoxon's sign rank test.
(2) Furthermore, the expected classification error reduction in the "quasi-movement" condition compared to the "imagery" condition in EEG data (based on all epochs) should not be related to a classification error reduction in EMG data. Spearman's rank correlation was used for determining this dependency.
(3) In the cross-validation procedure one obtains correctly and incorrectly classified epochs. In these two groups the number of epochs with visually detected motor responses was calculated. Then the following ratios were calculated: M_{incorr}/NM_{incorr} and M_{corr}/NM_{corr}, where M_{incorr} and NM_{incorr} are the numbers of trials with and without detected motor responses in incorrectly classified epochs, respectively; and M_{corr} and NM_{corr} are the numbers of trials with and without detected motor responses in correctly classified epochs, respectively. In order to compute the significance that these two ratios are different we used Fisher's exact test. The main idea behind this analysis was to show that the proportion of epochs with the detected motor responses is the same in correctly and incorrectly classified trials, and thus the output of the classifier is not influenced by the presence of EMG activity in some of the epochs.

2.6. Task ratings

The subjects were asked to answer a number of questions related to the nature and performance of the experimental tasks. Prior to the recordings we were interested to comprehend the subjects' understanding of the term "imagination"; they selected three words from a list of expressions related to "imagination", and three words from a list of semantically opposite expressions.

The subjects were asked to evaluate their subjective experience of movement execution, motor imagery, and quasi-movements on two different rating scales. (1) The experienced proprioceptive sensations were assessed using a discrete scale, consisting of five steps with "1" and "5" corresponding to the weakest and the strongest sensations, respectively. (2) The subjects were asked to what extent they evaluate the task belonging to the "real" or "imagery" category, by putting a mark on a solid line connecting these two terms (referred to as "reality index"). These task ratings were given after the completion of the second session of each condition. (3) The subjects sorted the tasks in an ascending order with respect to the required effort and concentration, that is, how demanding tasks were ($n = 12$).

3. Results

3.1. Psychological testing

All subjects understood term "imagination" as a type of mental activity which is not directly associated with the ongoing perceptual processing or motor activity. All subjects could perform motor imagery without any previous training (Jeannerod & Decety, 1995); yet for familiarizing with the task they could perform motor imagery for about 1 min before starting the experimental recordings. Training of the "quasi-movement" task required approximately 10–20 min for reaching the point where

motor responses to the presentation of the stimuli were not distinguishable from the pre-stimulus EMG. Surprisingly, upon the completion of the "quasi-movement" task, 15 out of 17 subjects spontaneously reported that they experienced the performance of quasi-movements similar to the performance of motor imagery. Yet, when being asked whether they were trying to execute real movements, 16 subjects replied positively, only one subject replied negatively and reported to perform motor imagery instead.

The degree of "reality" (subjective quantification of "real" or "imagery" aspects) was measured in all three conditions. The repeated measures ANOVA showed a significant task effect ($F_{2,30} = 116.8, p < 0.001$), and post hoc tests demonstrated that the reality index was strongest in the "real" condition, weakest in the "imagery" condition, and it had an intermediate value in the "quasi-movement" condition (all pair-wise comparisons were significant, $p < 0.001$, Fig. 1A). The reality indices from the "imagery" and "quasi-movement" condition were highly and significantly correlated, as evaluated with the non-parametric Spearman's rank correlation ($r = 0.71, p < 0.002$, Fig. 1B). Proprioceptive sensations also demonstrated a significant condition effect ($F_{2,30} = 33.5, p < 0.001$), with the same relationship between the conditions as for the reality index (Fig. 1C); all pair-wise comparisons of variables were significant ($p < 0.05$). Twelve subjects rated the tasks in the following order "quasi-movement", "imagery", and "real" with respect to the amount of the required effort and concentration (the first five subjects did not perform this rating).

3.2. EMG activity

One subject had to be excluded completely from the EMG analysis because of the excessive amounts of the background muscle activity in all recordings. Additionally one subject had to be excluded from the analysis of the "quasi-movement" condition due to incorrect task performance (as described above). An example of the averaged EMG activity from one subject is presented in Fig. 2. Only epochs without visually detected motor responses were averaged. Note that the RMS values in the pre- and post-stimulus intervals are indistinguishable from each other for "quasi-movement" and "imagery" conditions. Ideally, epochs in both conditions should not contain detectable EMG motor response. Yet a few epochs in both conditions were associated with weak visually detectable motor responses; usually they were very small (the mean amplitude of EMG peaks for "quasi-movement" and "imagery" conditions was ∼30 μV, compared to ∼340 μV in the "real" condition). If occasionally present, the motor responses during the performance of "quasi-movement"/"imagery" tasks were also very transient, lasting only for a few milliseconds, which is quite different from the "real" condition, where EMG bursts lasted for tens of milliseconds.

After the exclusion of the epochs with the detected motor responses, the pre- and post-stimulus RMS values in the "imag" and "quasi" conditions were ∼2 μV (Fig. 3A). Left hand EMG had slightly larger amplitudes for both pre- and post-stimulus intervals (compared to the right hand), because of occasional
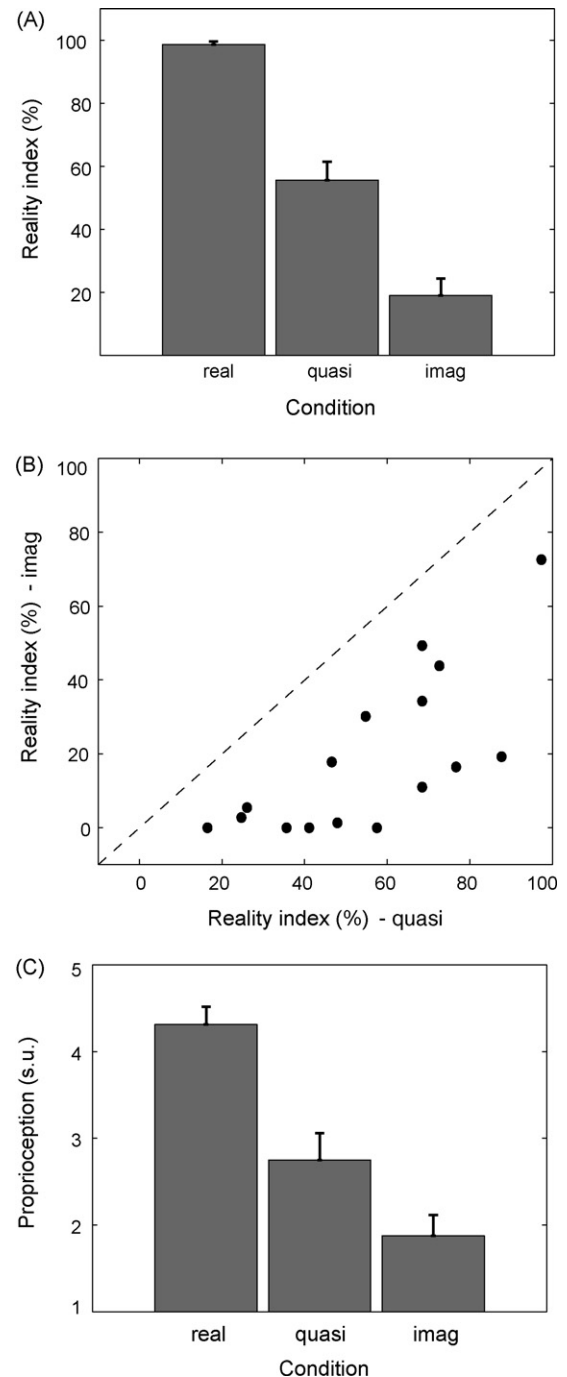

Fig. 1. Subjective task ratings in three experimental conditions. (A) Reality index. (B) Relationship between the reality indices in "quasi-movement" and "imagery" conditions. (C) Evaluation of proprioceptive sensations. Error bars: standard error of the mean, s.u.: scale units, dashed line: main diagonal. Data represent the grand average across all subjects.

residuals from the electrical heart activity. Slightly increased values of EMG activity in the post-stimulus interval in the "quasi-movement" condition were observed but were not statistically larger than in the "imagery" condition. Such increase most likely relates to a general tonic EMG activity in the "quasi-movement" condition since a similar tendency was observed for the pre-stimulus EMG activity (Fig. 3A) and for the left and right hands, thus indicating that this increase cannot explain spe-
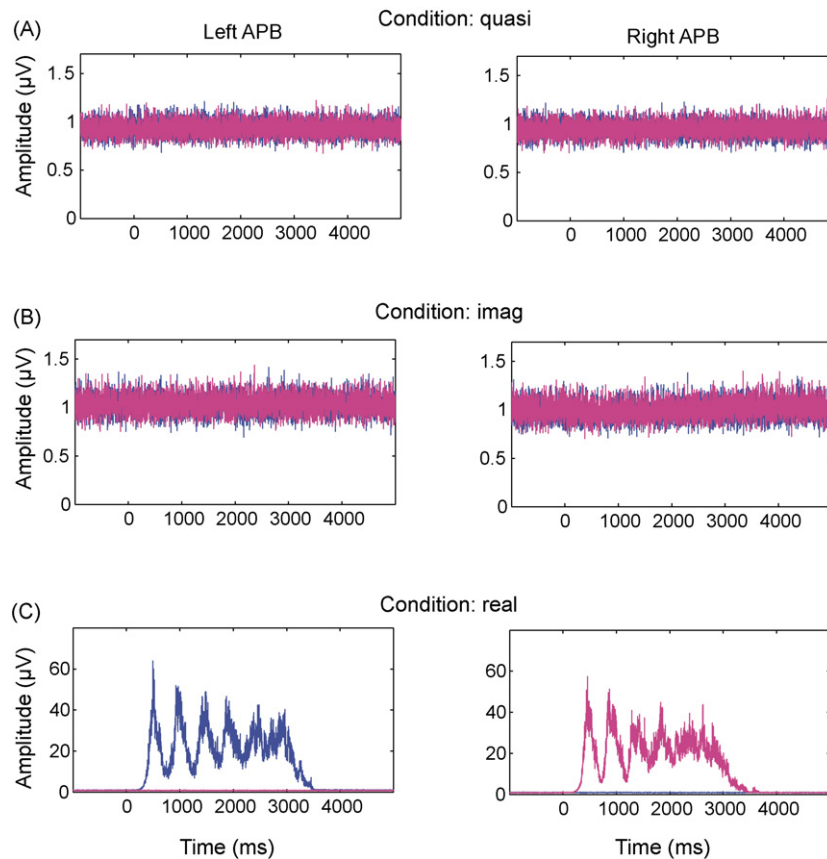
Fig. 2. EMG activity in three experimental conditions from a representative subject (S11). (A and B) Averages of rectified EMG signals across epochs without detected motor responses in quasi-movements and motor imagery, and in executed movements (C). Blue and magenta lines represent EMG activity for the two stimulus classes of the left and right thumb movements, respectively.

cific and transient changes observed in EEG (described below). After the exclusion of epochs with visually detected motor responses, Wilcoxon's rank sum test demonstrated no significant difference (at the threshold level $p < 0.05$) between pre- and post-stimulus RMS values of EMG activity, when each subject and hand were analyzed separately in the "imagery" and "quasi-movement" conditions. We also run a repeated measures ANOVA across subjects in order to compare the EMG activity between "quasi-movement" and "imagery" conditions, the "real" condition being excluded for the obvious reason of always containing strong post-stimulus EMG activity. Neither for left nor right hand ANOVA demonstrated a significant condition effect ("quasi-movement" vs. "imagery": left hand $F_{1,14} = 2.7$, $p = 0.12$, right hand $F_{1,14} = 3.05$, $p = 0.1$) and no significant interval effect ("pre" vs. "post": left hand $F_{1,14} = 0.5$, $p = 0.49$, right hand $F_{1,14} = 0.04$, $p = 0.85$). Also there was no significant interaction between condition and interval (left hand $F_{1,14} = 0.88$, $p = 0.36$, right hand $F_{1,14} = 0.2$, $p = 0.66$). These results indicate that both tasks had similar RMS values during the performance of the tasks.

The detection rate for visually determined motor responses in all conditions is presented in Fig. 3B. The ANOVA demonstrated a significant condition effect ($F_{2,28} = 522.9$, $p < 0.001$). As expected, the detection rate was nearly at unity for the "real" condition, intermediate for "quasi-movement", and smallest for

"imagery" condition. Here it is important to emphasize that a non-zero detection rate can also be associated with some instances where postural or other non-specific EMG activation (e.g., arousal-level) might have coincided with the presentation of the stimuli.

There was no significant correlation between the detection rate and the subjective proprioceptive sensations, neither in the "quasi-movement" ($r = 0.14$, $p = 0.63$) nor "imagery" ($r = 0.18$, $p = 0.52$) conditions.

3.3. Control experiments with the measurement of additional muscles and acceleration

Further control experiments have shown that the classification of EMG signals (between the left and right classes) on the basis of additional muscles is not superior to the classification on the basis of APB. This was the case when the post-stimulus EMG activity was analyzed separately for each muscle and when the activity from all three muscles was combined for the analysis (Table 1). Some deviations from the expected 0.5 value (typical for classification at a chance level) were random, as found on the basis of confidence levels obtained with multiple random permutations of the values belonging to the left and right class. Importantly in the "real" condition the amplitude of EMG responses in the additionally measured muscles
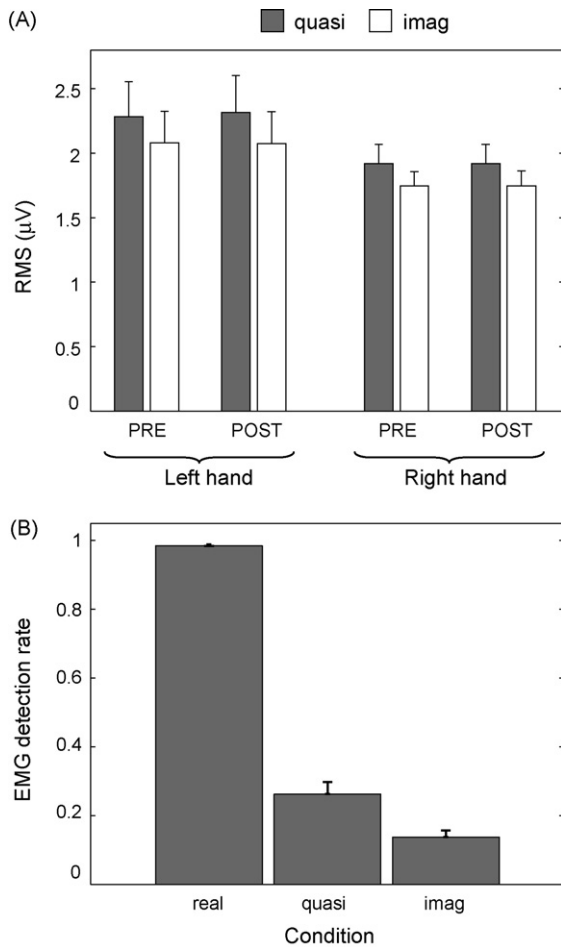
Fig. 3. EMG analysis. (A) EMG activity in pre- and post-stimulus intervals for quasi-movements and motor imagery. (B) Detection rate of motor responses. PRE: pre-stimulus interval (−1000 to 0 ms), POST: post-stimulus interval (70–3300 ms), RMS: root-mean square, error bars: standard error of the mean. Data represent the grand average across all subjects. In "quasi-movement" and "imagery" conditions epochs with visually motor responses were excluded from the average.

was at least two times smaller (range 2.3–14 times) than the amplitude of APB responses, thus indicating both stronger activation and superior recording conditions for the latter one. Automatic classification of the activity from the accelerometer also did not reveal any significant classification of the post-

Table 1
Mean classification error of EMG and movement acceleration in the post-stimulus interval

Condition/muscle	Subject	APB	EPB	FPL	FPB	A/E/F	ACC
Imagery	S16	0.51	0.46	0.44	–	0.48	0.44
	S11	0.57	0.56	–	0.53	0.55	0.55
Quasi-movements	S16	0.49	0.49	0.5	–	0.5	0.49
	S11	0.5	0.48	–	0.51	0.56	0.55

APB: abductor pollicis brevis, EPB: extensor pollicis brevis, FPL: flexor pollicis longus, FPB: flexor pollicis brevis, A/E/F: classification based on the combination of all three muscles, ACC: accelerometer, (–) the muscle was not measured in this subject. Note that none of the classification errors deviated significantly ($p < 0.05$) from 0.5, as found with the tests based on random permutations of values between the left and right classes.
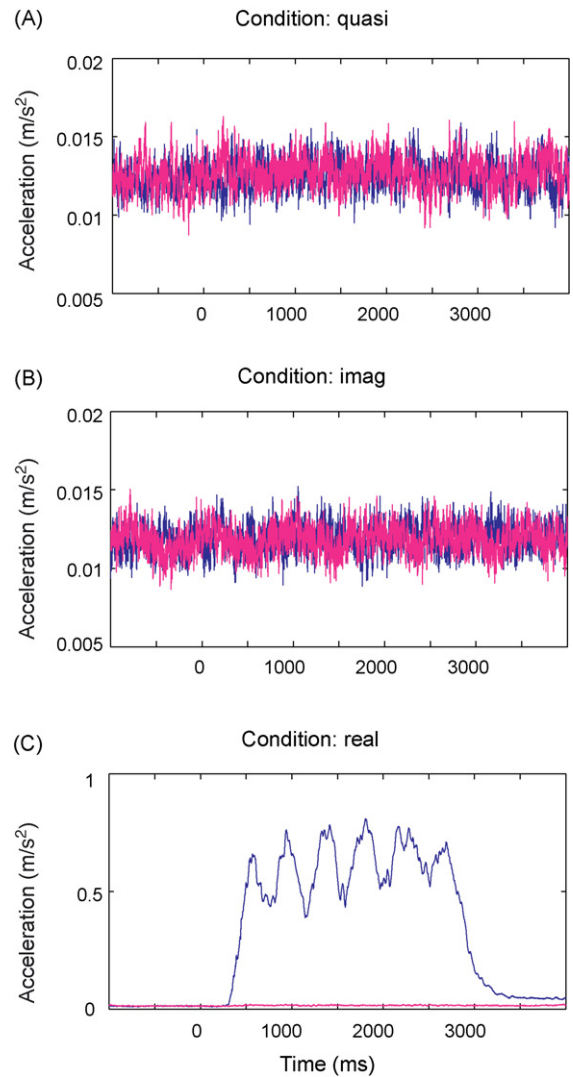

Fig. 4. Recordings of movement acceleration. The data is from one subject (S16, left thumb). (A–C) Averaged activity for quasi-movements, kinesthetic motor imagery, and executed movements, respectively. Blue line: left class (left thumb movement/imagery is required), magenta line: right class (no movement/imagery is required). The data represent averages of rectified acceleration traces for all epochs.

stimulus values belonging to the left and right classes (Table 1). Fig. 4 shows an average activity of acceleration for one subject.

3.4. EEG activity

One subject had to be excluded completely from EEG analysis because of absence of rhythmical activity, which could be modulated. Another subject was excluded because of insufficient amount of recorded data, and the exclusion of a third subject was due to an inappropriate performance of the "quasi-movement" task (see above; $n = 14$ for EEG analysis).

As expected, spontaneous alpha oscillations were decreased in the amplitude over the sensorimotor areas during the performance of all three tasks. Fig. 5 shows a topographic plot of attenuation of alpha oscillations in the three experimen-
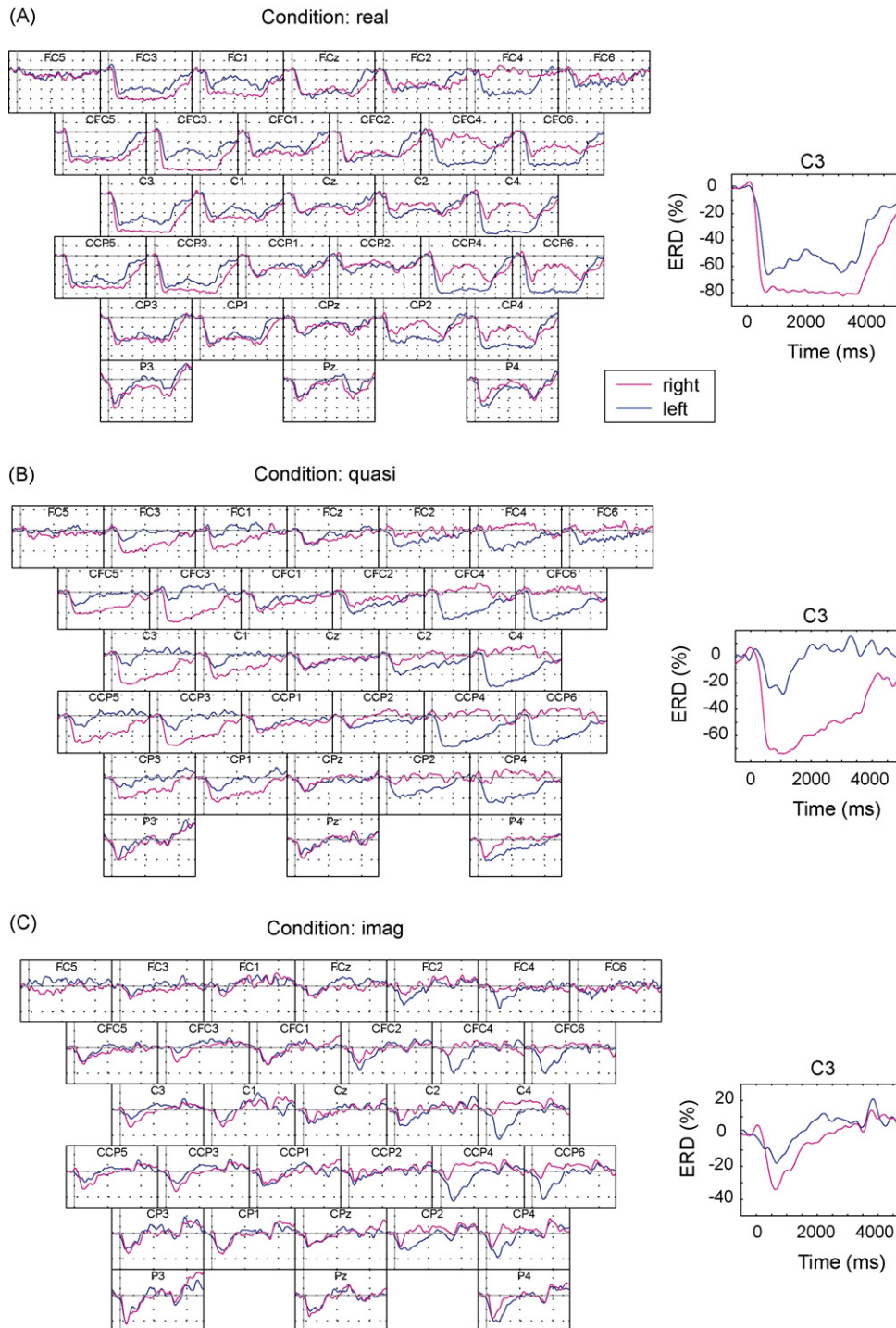
Fig. 5. Topographic plot of attenuation of alpha oscillations (8–13 Hz) in the three experimental conditions from a representative subject (S11). A subset of electrodes (representing Laplacian activity) is shown over the fronto-centro-parietal areas. The activity of C3 electrode is shown at the right side for each of the conditions. ERD: event-related desynchronization. Blue and magenta lines represent EMG activity for the two stimulus-classes of left and right thumb movements, respectively.

tal tasks in a representative subject. The strongest attenuation occurred in channels above the central areas, and the ERD in the contralateral hemisphere was most pronounced. A repeated measures ANOVA with the factors condition (three levels) and hemisphere (two levels) demonstrated a significant effect of the condition for the left ($F_{2,26} = 21.7$, $p < 0.001$) and right hand ($F_{2,26} = 16.5$, $p < 0.001$) reactions. Post hoc analysis revealed that ERD was significantly stronger ($p < 0.05$) in the "real" than in the "quasi-movement" and "imagery" conditions in both hemispheres. ERD was also stronger in the "quasi-movement" than in the "imagery" condition, but only in the contralateral hemisphere (post hoc $p < 0.05$). Fig. 6 shows the strength of ERD in all conditions and hemispheres (grand-average data).
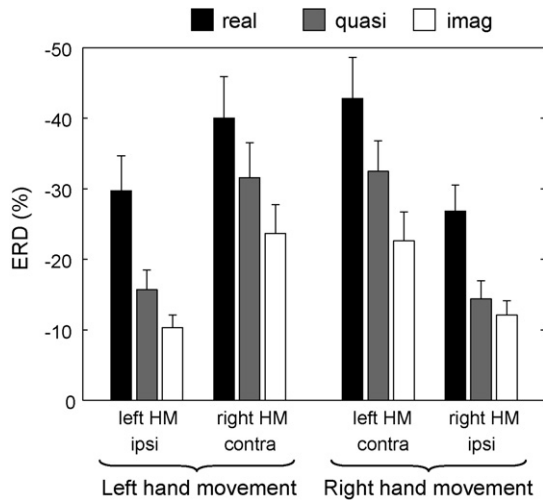
Fig. 6. Modulation of spontaneous neuronal oscillations (8–13 Hz) in three experimental conditions. HM: hemisphere, ipsi: ipsilateral hemisphere, contra: contralateral hemisphere, error bars: standard error of the mean. Data represent the grand average across all subjects.

3.5. EEG classification of left versus right imagined, executed, and quasi-movements

The selection of *band* (frequency band with the best discriminability between the left and right movement class), *interval*, and CSP filters was performed automatically as described above. Only in three data sets (two "imagery" and one "real" out of 42 sets) we used additional manual adjustment for *band* or *interval*, since the automatic procedure led to an inadequate selection of the limits as revealed via the incongruence between the ERD times courses and the automatically selected frequency/interval values. Importantly, such manual adjustment was not performed blindly but was guided by the inspection of the abovementioned graphs. The classification error in the three conditions is presented in Fig. 7A. The differences between the conditions were significant as revealed by ANOVA ($F_{2,26} = 22.4$, $p < 0.001$) and by all post hoc pair-wise comparisons ($p < 0.05$). The largest classification error was obtained for the "imagery" condition ($\sim$0.23) and the smallest for "real" condition ($\sim$0.08). The error of $\sim$0.08 in the "real" condition indicates that 8% of the epochs were wrongly classified, i.e., left thumb movements were erro-

neously classified as right thumb movement and *vice versa*. The classification error in "quasi-movement" condition was $\sim$0.12. The average relative error decrease (between "imagery" and "quasi-movement" conditions) was $\sim$47%. Fig. 7B shows also individual classification errors for "quasi-movement" and "imagery" conditions. In all but one subjects the classification accuracy has been improved in "quasi" condition.

The grand-average limits for *band* were 9.4–13.9 Hz, 9.1–13.8 Hz, and 8.6–13.4 Hz for the "real", "quasi-movement", and "imagery" conditions, respectively. Grand average of *band* indicates that neuronal oscillations in the alpha frequency range are most sensitive to the discrimination between the left and right hand movements. The grand-average *interval* values were 907–3180 ms, 669–2936 ms, and 562–2572 ms for the same condition order. An example of CSP maps for "quasi-movement" condition is shown in Fig. 8. The spatial activation patterns demonstrated clear topographic differences between the two movement classes, with the largest ERD in *band* being over the contralateral sensorimotor area. When visually inspected, CSP patterns appeared quite similar across the three conditions. Therefore, in order to quantify the differences in spatial topography of EEG we calculated a measure quantifying the similarity between CSP maps across conditions (see Section 2.4). However, neither for left nor right hand movements (imagined, executed, or quasi-performance) we found any systematic tendency (as revealed with insignificant *p*-values in ANOVA) for any of the two condition pairs to be more similar than for other pairs, e.g., the "imagery" versus "quasi-movement" similarity value was not different from "real" versus "quasi-movement" similarity.

3.6. Relationship between EEG and EMG activity

Occasionally, slight EMG activation could be detected (as described above) during the performance of quasi-movements and motor imagery. Therefore, an important question was to investigate whether these rare and weak motor responses might be correlated with the oscillatory neuronal activity, e.g., suppression of EEG activity might have been stronger in epochs with detectable motor responses than without them. Three different approaches were chosen in order to show that the residual EMG activity, even if
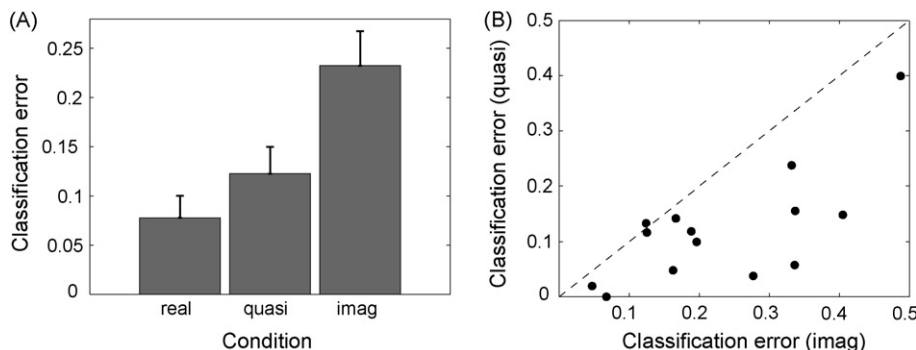

Fig. 7. EEG classification error. (A) Grand-average classification error for quasi-movements and kinesthetic motor imagery. (B) Classification errors for individual subjects in "quasi-movement" and "imagery" conditions. Dashed line: main diagonal.
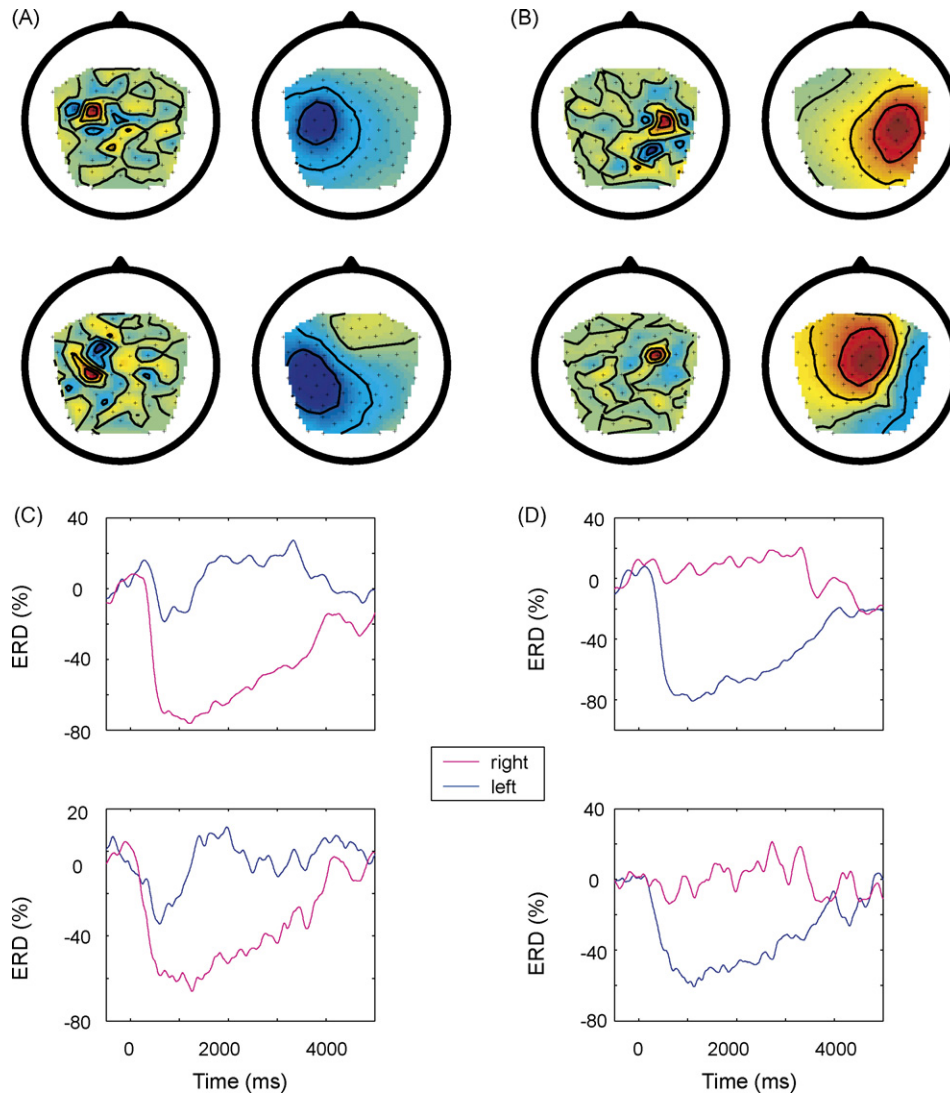
Fig. 8. Common spatial pattern analysis of quasi-movement performance from a representative subject (S11). (A) Topography of demixing (spatial filter) and mixing (activation pattern) matrices for the smallest variance (ERD) in the right movement class. According to CSP analysis, smallest variance in the right class corresponds also to the largest variance in the left class, and *vice versa*. The two rows represent two spatial filters/neuronal activation patterns with the largest eigenvalues for the right thumb movements. (B) The same like in (A), but for the smallest variance in the left movement class. Note that the colors on the maps are not indicative of ERD/ERS, but they reflect the weighting coefficients at a given electrode. The actual decrease or increase in the amplitude of oscillations can be obtained from the time courses shown in the lower part of the figure. (C and D) Time courses of CSP sources depicted in (A and B), respectively. Blue and magenta lines represent EMG activity for the two stimulus-classes of left and right thumb movements, respectively.

present, was not significantly contributing to the reactivity of EEG.

(1) As described above, the classification of EEG and EMG epochs was also run after the exclusion of the epochs with visually detected EMG responses, in order to show that the error differences in EEG classification ("quasi-movement" and "imagery") are not due to the reafferent feedback from the occasional motor responses. After the exclusion of such epochs the "quasi-movement" condition still had significantly smaller classification error in EEG compared to the "imagery" condition ($p < 0.01$, Wilcoxon's sign rank test, Fig. 9A). Some small increase of the classification error in the "quasi-movement" condition relates to the fact

that the classification was based on a smaller number of epochs because of the exclusion of the epochs with detected motor responses. The automatic classification procedure for all EMG epochs demonstrated that the classification error for the "quasi-movement" condition was significantly smaller than for the "imagery" condition ($p < 0.002$, Wilxocon's sign rank test), although on average both errors were above 0.4 (Fig. 9A). Importantly, after the exclusion of the epochs with visually detected motor responses, EMG classification errors increased and were no longer statistically distinguishable ($p = 0.45$) between the "quasi-movement" and "imagery" conditions. Yet the exclusion of the same epochs from EEG data did not eliminate differences in EEG classification errors between two conditions.
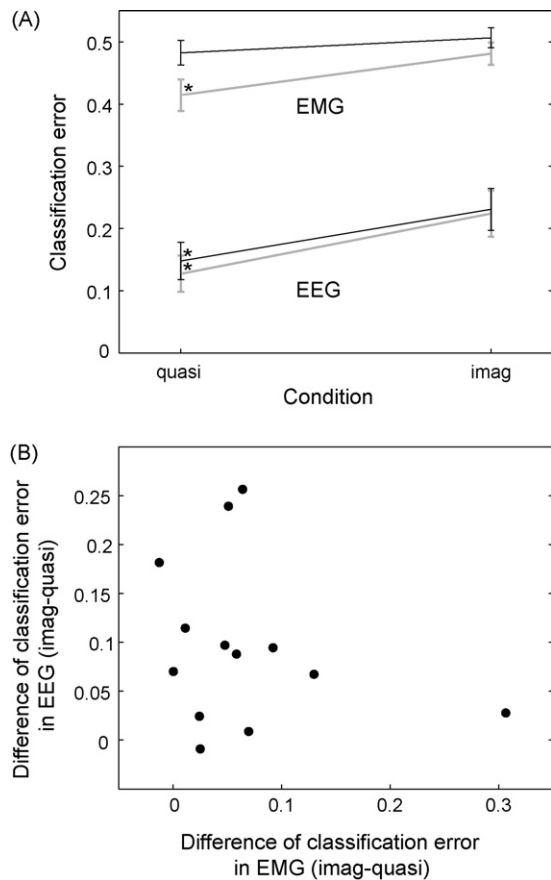
Fig. 9. Relationship between EEG and EMG parameters. (A) Classification errors for EEG and EMG. Black: for all epochs, gray: epochs without visually detected motor responses. Asterisks indicate significant difference (Wilcoxon's sign rank test, $p < 0.01$) between classification accuracy of imagined and quasi-movements. Data represent the grand average across all subjects. (B) Relation between the differences of classification errors from two experimental conditions in EEG and EMG.

(2) The classification error of EEG data was decreased for the "quasi-movement" compared to "imagery" condition. Importantly, if this decrease was related to the respective decrease in EMG classification error, both decreases must have been correlated across subjects. However, this was not the case ($r = -0.2$, $p = 0.5$, Fig. 9B).

(3) Fisher's exact test showed that the proportion of the epochs with detected movements was not different in correctly and incorrectly classified epochs, when tested individually for each subject and condition.

4. Discussion

The present study provides multiple lines of evidence for the performance of a movement with motor responses indistinguishable from the background EMG. Below we discuss our results with respect to the quasi-movement performance (1), neurophysiological aspects of quasi-movements (2) and elaborate on their relevance for studies related to sense of movement/agency (3), motor imagery (4), and brain–computer interface research (5).

4.1. Performance of quasi-movements

4.1.1. Evidence for quasi-movements

When discussing quasi-movements it is essential to show that subjects were trying to perform movements instead of simply imagining them (thus doing a "mental simulation"), since in both cases EMG responses were absent. The following arguments serve as evidence that subjects indeed were trying to perform quasi-movements and not motor imagery: (1) all but one subject reported that they were intending to execute overt thumb movements. (2) It took subjects up to 20 min to learn to perform quasi-movements, while motor imagery could be performed without any training. (3) The detection rate for EMG responses was significantly higher in the "quasi-movement" compared to the "imagery" condition. (4) Alpha ERD was stronger and the classification error was smaller in the "quasi-movement" than in the "imagery" condition.

4.1.2. Absence of EMG responses during quasi-movement performance

The absence of motor responses is a prerequisite for the mental simulation of a movement in case of motor imagery. Similarly detectable EMG responses were absent in the majority of epochs during the quasi-movement performance. Moreover, we showed that after the exclusion of epochs with visually detected EMG responses, muscle activity in the "quasi-movement" condition was not statistically distinguishable between the pre- and post-stimulus intervals. Also there was no significant difference in the post-stimulus values of EMG activity between the "quasi-movement" and "imagery" conditions. Still the question remains whether there were some motor responses left undetected. However, the following considerations show why it is unlikely. Contrary to a vast majority of studies addressing motor imagery with complex movements and a rather large number of muscles, we have chosen a very simple movement of thumb abduction, which is performed primarily with APB muscle. APB is a thin and superficially located muscle, thus making it an ideal candidate for the detection of even the smallest muscle activations. RMS values of muscular activity at rest (pre-stimulus interval) in the "quasi-movement" and "imagery" conditions were ∼2 μV, which is smaller or equal to the reported EMG amplitudes of APB at rest (Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006; Zoghi & Nordstrom, 2007). In additional control experiments we also tested three other muscles for their contribution to the performed task. The results of such testing showed that the discriminability of left and right classes on the basis of EMG was at a chance level both for "quasi-movement" and "imagery" conditions. This indicated that the information from additional EMGs did not improve the detection of the possible motor responses in the "imagery" and "quasi-movement" conditions.

An alternative way to study muscle activity would be to use needle electrodes to record EMG from the individual APB motor units. Yet it would not be beneficial since in the case of absent surface EMG it is highly unlikely to find spiking muscle fibers. Advantageously surface EMG can collect the activity of many spiking motor units, and with spatial filtering procedures one

can even detect the activity of individual fibers (Reucher, Rau, & Silny, 1987; Roeleveld & Stegeman, 2002), especially in flat superficial muscles. Another important point is that since quasi-movements usually are not associated with any muscle contraction, the detection of infrequent activation of motor units should not be difficult since phase cancellations and interference patterns are pronounced only for high levels of muscle contraction (Reucher et al., 1987). In case of quasi-movements surface EMG is also preferable to the registration of mechanical displacements, since electrical muscle activity precedes any mechanical movement due to biomechanical constraints such as muscle stiffness and viscosity. In our additional control experiments we recorded mechanical movement of the thumb with an accelerometer and showed that the detection of possible motor responses is at a chance level in both "quasi-movement" and "imagery" tasks. This finding demonstrated that the classification of thumb movements on the basis of acceleration is not superior to the recording of EMG.

Moreover, it appears that the EMG techniques/procedures used in the present study were adequately sensitive, since they even allowed a detection of significant EMG responses during motor imagery, which is often associated with almost complete muscular quiescence (Guillot & Collet, 2005; Jeannerod, 1994, 1995; Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004; Yue & Cole, 1992). Importantly, the main finding in the present study pertains to the fact that the EMG amplitude in the post-stimulus interval during the performance of quasi-movements is as low as during motor imagery.

4.2. Neurophysiological aspects of quasi-movements

Interestingly, we show that motor imagery and quasi-movements are associated with the specific contralateral neuronal activation, similar to other EEG and functional magnetic resonance imaging studies showing the lateralization of neuronal activity during motor imagery (Blankertz, Dornhege, Lemm, et al., 2006; Michelon et al., 2006; Pfurtscheller & Neuper, 1997). This fact implies that motor imagery and quasi-movements are associated with effector-specific neuronal activation and not necessarily with a very high-level abstract representation of the movement goals, which are often coded unilaterally in the premotor and parietal cortices (Andersen & Buneo, 2002; Buneo, Jarvis, Batista, & Andersen, 2002; Cisek, Crammond, & Kalaska, 2003). Lateralized neuronal activity in the primary motor cortex has been shown to be correlated with the produced movement force (Ashe, 1997; Evarts, 1968; Gribble & Scott, 2002). A number of EEG studies showed also that the movement related potentials, generated in sensorimotor cortex, are correlated with the force production (Kutas & Donchin, 1974; Slobounov, Ray, & Simon, 1998). Importantly, the neuronal activity in the primary motor cortex is also correlated (and to a very large extent) with other parameters of the task such as movement direction or hand position (Kakei, Hoffman, & Strick, 1999; Sergio & Kalaska, 2003)—the parameters which still can be coded in quasi-movements and are likely to be associated with the strong modulation of EEG activity as observed in the present study. The generation of quasi-movements can

also involve inhibitory mechanisms, restraining central neuronal commands to produce supra-threshold activation of alpha-motor neurons in the spinal cord. Stronger ERD in quasi-movements compared to motor imagery can also be explained by the fact that learning to successfully perform quasi-movements is a process similar to the execution of skilled movements which are usually associated with particularly strong engagement of motor structures (Karni et al., 1995).

4.3. Subjective evaluation of quasi-movements: sense of movement/agency

The results of the present study show that the movement sensations were stronger during quasi-movements than during motor imagery. Importantly there was no significant correlation between this subjective evaluation of proprioception and the EMG detection rate (determining the amount of epochs containing motor responses), thus indicating that the presence of rare and weak motor responses in the "quasi-movement" condition was not crucial for the subjective judgment. Also the strength of alpha ERD did not correlate with the detection rate of EMG, thus suggesting that the occasional residual peripheral activity was not associated with the significant modulation of the cortical activity. So what then might be the reason for the experienced proprioceptive sensations during the quasi-movement performance?

It has been debated for a long time that the "sense of movement" is related not only to the peripheral feedback but also to the central generation of a motor command itself (Amassian, Cracco, & Maccabee, 1989; Bestmann et al., 2006; Melzack, 1990; Willoch et al., 2000). Partly the sense of movement can be related to the efference copy of the motor command which is used for the predictions concerning the reafferent information expected from the planned movements (Sperry, 1950; von Holst, 1954). Efference copy strongly affects the internal evaluation of executed movements, as shown in psychophysical experiments (Farrer, Franck, Paillard, & Jeannerod, 2003; Haggard, 2005; McCloskey, Colebatch, Potter, & Burke, 1983; Tsakiris & Haggard, 2003). The results of these studies also suggest that it is not the efference copy *per se* that modulates the sense of movement, but rather a complex interplay between the sensory predictions of the upcoming movements and the actual sensory feedback (Haggard, 2005; Tsakiris & Haggard, 2003; Wolpert & Ghahramani, 2000). In the case of quasi-movements the forward model would expect "zero" movement feedback which would be congruent with the absent sensory signals during successful quasi-movement performance; this correspondence might also contribute to a sense of agency (Farrer et al., 2003; Haggard, 2005).

4.4. Quasi-movements and motor imagery

In general, motor imagery is defined as a mental rehearsal/ simulation of a movement (Decety, 1996; Feltz & Landers, 1983; Guillot & Collet, 2005; Jeannerod, 1994, 1995, 2001; Michelon et al., 2006; Neuper et al., 2005; Stinear et al., 2006). It has been suggested that there might exist a continuum between

the motor preparation/execution and motor imagery (Jeannerod, 1995); and a functional equivalence between these states has been suggested (Annett, 1996; Jeannerod, 1994; in the sense of Finke, 1980). Motor images are hypothesized to be motor actions with subthreshold activation (Jeannerod, 1995, 2001). Neurophysiological and psychometric studies are in agreement with the above mentioned continuum hypothesis—a great number of studies showed also that the same brain structures are activated in a similar manner during motor imagery and overt movements, e.g., primary and secondary motor areas, parietal and prefrontal cortex, basal ganglia, or cerebellum (Decety, 1996; Guillot & Collet, 2005; Li, Kamper, Stevens, & Rymer, 2004; Lotze & Halsband, 2006; Michelon et al., 2006; Porro et al., 1996; Sharma, Pomeroy, & Baron, 2006; Solodkin, Hlustik, Chen, & Small, 2004). In agreement with these observations we show that the spatial topography of neuronal activation patterns was not significantly different between the three experimental conditions.

What are the similarities between quasi-movements and motor imagery? (1) The majority of subjects spontaneously reported that they experienced the performance of quasi-movements similar to performance of motor imagery. The correlation between the reality indices (the subjectively evaluated degree of "reality", whether the task belonged to the "real" or "imagery" category) indicates that the performance of quasi-movements and motor imagery was perceived similarly. It is conceivable that the major part in the experience of motor imagery is related to the absence of proprioceptive feedback, and most likely this is the reason why subjects tended to perceive quasi-movements similar to motor imagery. (2) Spatial neuronal activation (CSP maps) was similar in all three conditions. (3) Both in motor imagery and quasi-movements there is no motor responses produced in the majority of epochs. The small proportion of epochs with detected EMG responses is congruent with studies showing that motor imagery is associated with some subliminal muscle activity, specific to the target muscles (Guillot & Collet, 2005; Jacobson, 1932; James, 1890; Shaw, 1938; Stock & Stock, 2004).

"Motor imagery is the ability to imagine performing a movement without executing it" (Michelon et al., 2006, p. 811). But interestingly, "performing a movement without executing it" describes exactly the nature of quasi-movements. So what are the differences between quasi-movements and motor imagery? (1) The main distinction is that quasi-movements are intended and performed as "real" movements, while in the case of motor imagery subjects do not intend to perform movements but only to mentally simulate them. (2) The strength of ERD was larger for quasi-movements than for motor imagery.

We hypothesize that the procedure of learning how to perform quasi-movements (by the successive reduction of movement strength to a complete muscular quiescence) might represent a transition process between motor execution and motor imagery, if the latter is operationalized by the absence of motor responses. It seems plausible that in evolution motor imagery was developed after the organisms acquired the possibility to perform overt movements (Currie & Ravenscroft, 1997). And since the neuronal activity in the motor systems during motor imagery

resembles movement performance in many aspects but the production of a motor response, motor imagery might have been acquired through some mechanism which accentuated the uncoupling of motor planning/preparation from the executive functions—the process which our subjects learned during the training to successfully perform quasi-movements. It might even be that the inhibitory neuronal mechanisms, which lead to this uncoupling in quasi-movements, are equivalent to those in motor imagery.

4.5. Quasi-movements and brain–computer interfacing

BCI research aims at the development of human–machine interaction via the use of brain activity as a control signal in a program interface, thus bypassing usual communication channels based on motor activity like keyboard, mouse or speech. Therefore, BCI-driven devices (neuroprostheses or wheelchairs) are of essential interest for persons with severe motor disabilities, such as peripheral or spinal paralysis, stroke or amputation (Birbaumer, 2006; Birbaumer et al., 1999; Blankertz et al., 2007; Dornhege, del Millán, Hinterberger, McFarland, & Müller, 2007; Kübler, Kotchoubey, Kaiser, Wolpaw, & Birbaumer, 2001; Müller-Putz, Scherer, Pfurtscheller, & Rupp, 2005; Neuper et al., 2005; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Pfurtscheller, Leeb, et al., 2006; Wolpaw et al., 2002). The main idea in BCI research is to use neuronal signals which relate to the user's intention. Those must not be based on the afferent input from the periphery (e.g., from the contracting muscles).

Despite considerable advances in implementing novel instrumentation and state-of-the-art signal processing techniques, the introduction of novel behavioral concepts for the strong endogenous modification of brain activity remains a challenging issue. Such paradigms are the main prerequisite for a successful BCI, since even the most advanced techniques are only useful when there is a detectable neuronal signal. So far, motor imagery has been the main strategy in BCI research which is not driven by external stimulation—thus enabling the endogenous modulation of neuronal activity without significant effects due to peripheral feedback from contracting muscles.

Quasi-movements represent an effective alternative to the motor imagery approach in BCI research. In the present study, quasi-movements proved to be the advantageous strategy, since the classification error for the "quasi-movement" condition was ∼47% smaller compared to motor imagery. In this respect an important point is the demonstration that the smaller classification error in the "quasi-movement" condition is not associated with the occasional weak EMG activity. This will be discussed below.

(1) The strongest evidence originates from the fact that the exclusion of the epochs with visually detected motor responses resulted in statistically indistinguishable classification errors of EMG in the "imagery" and "quasi-movement" conditions, whereas the EEG classification error for the "quasi-movement" condition was still significantly smaller in the "imagery" condition. (2) If the decrease of the classification error in EEG between the "quasi-movement" and "imagery" condition was caused by the similar decrease in EMG classification between

both conditions, then one would expect to see a significant correlation between these two types of differences. This was not the case in the present study. (3) Fisher's exact test demonstrated that the proportion of epochs with the detected EMG responses was the same in correctly and incorrectly classified epochs, thus ruling out any dominant role of rare task-related, subliminal motor activity for the reduction of the classification error in "quasi-movement" condition.

Taken together, these results indicate that quasi-movements represent a reliable way to obtain strong and reproducible modulation of ongoing neuronal oscillations without afferent influences from the periphery.

One of the reasons for quasi-movements being more effective in BCI than motor imagery might be due to the fact that quasi-movements do not require specific imagery abilities, which show large inter-individual variability (Galton, 1880; Hall & Pongrac, 1983; Isaac, Marks, & Russell, 1986; Martin, Moritz, & Hall, 1999; Moran, 1993; Richardson, 1994). Instead, the performance of quasi-movements is learned from the overt movement execution, an activity which is familiar to healthy subjects. Importantly, quasi-movements are not aimed at investigating subjects with neuromuscular impairments, but they are used for studying healthy subjects. The performance of quasi-movements more closely resembles the situation with the so-called "attempted movements" in paralyzed patients than motor imagery. This is due to intentional component of movement performance: paralyzed patients try to perform movements (not to imagine/mentally simulate them), but movement execution is impossible due to neuronal lesions.

The motor–cognitive phenomenon of quasi-movements, which are neither motor imagery nor movement execution, is of practical relevance for neurophysiology, neurocognitive psychology, and computational neuroscience, and it can only be adequately studied with the interdisciplinary combination of these fields.

Acknowledgements

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