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RESEARCH ARTICLE

Effects of longer vs. shorter timed movement sequences on alpha motor inhibition when combining contractions and relaxations

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Abstract

Alpha inhibitory processes reflect motor stimuli by either increasing or decreasing amplitude (i.e., power). However, the functional role and interplay of event-related alpha oscillations remains a regulatory domain that has not been sufficiently addressed, particularly with respect to different muscle activation types and durations in consecutive movement (i.e., motor) tasks. The aim of this study was to investigate alpha-band activity (7–13 Hz) in longer vs. shorter timed isometric muscle activations at distinct torques (20% and 40% of maximum voluntary contraction, MVC) when combined in one motor task sequence. In a randomized and controlled design, 18 healthy males volunteered to perform 40 longer (i.e., 6 s) and 40 shorter (i.e., 3 s) motor task sequences, each comprising isometric contractions (i.e., palmar flexion) from baseline to 20% and 40% MVC subsequent to relaxations from 40% and 20% MVC to baseline. Continuous, synchronized EEG, EMG and torque recordings served to determine alpha-band activity over task-relevant motor areas at distinct torques. Main findings revealed increases in alpha activity during subsequent progressive muscle relaxation (from 20% MVC in long and short: $p < .001$; from 40% MVC in short: $p < .05$), whereas modulations in relevant motor areas were not significant ($p = .84$). It may be suggested that an active task-relevant inhibitory process indicates motor task sequence-related relaxation mirrored by an increasing alpha activity.

Keywords Alpha oscillation · Isometric · EEG · EMG · Torque · Muscle activation

Introduction

In traditional models of neuronal communication, neurons send messages (encoded in action potentials) along their axons to all anatomically connected neurons. Nonetheless, a flexible and effective communication system in addition to fixed anatomical structures is required to enable numerous motor functions that we use in everyday life.

Alpha-band oscillations (7–13 Hz) are due to their high incidence in general background activity, the most investigated oscillations. In particular, alpha oscillations precede and respond to external motor stimuli or tasks either by increasing or decreasing power. Their functional importance as well as the neuronal mechanism during sequential (sports-related) movements, however, remains unclear.

Movement-specific alpha oscillations were examined for the first time in 1979 (Pfurtscheller and Aranibar 1979). Self-paced finger movements showed a significant reduction in alpha-band power both before and during the movement, located bilateral above central regions of the cortex. Event-related desynchronization (ERD) was then evidenced in a variety of studies (Crone et al. 1998; Pfurtscheller et al. 1998; Rau et al. 2003; Alegre et al. 2003; Guger et al. 2005; Neuper et al. 2006; Pfurtscheller 2006; Babiloni et al. 2008). ERD is defined by amplitude attenuation and is assumed to be a correlate of increased neuronal excitability in thalamocortical systems (Steriade 1988; Pfurtscheller 2006). Task-relevant brain regions exhibit ERD, whereas task irrelevant or interfering regions exhibit event-related synchronization (ERS). Regarding the traditional view, an increase in alpha power (i.e., ERS) reflects 'cortical idling',

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while the magnitude of alpha attenuation (i.e., ERD) reflects the degree of cortical activation or the release of inhibition (Pfurtscheller and Lopes da Silva 1999). However, ERS was recently observed in specific tasks (Klimesch et al. 2007). The increase in amplitude (i.e., power) is assumed to represent cognitive processes related to temporal attention and access to the knowledge system. This interpretation relies on the inhibition timing function of alpha-band activity (Klimesch et al. 2007). It enables two attentional functions (suppression and selection) and thereby selective access to relevant memory traces. With respect to alpha as an inhibitory oscillation, it causes rhythmic changes between minimal and maximal inhibition (Klimesch et al. 2007; Klimesch 2012). In turn, this behaviour may be related to the ongoing alternation of muscle contraction/relaxation during all kinds of movements.

According to the inhibition timing hypothesis, suggested by Klimesch (2012), three possible physiological mechanisms have been reported: (1) A small amplitude of alpha has no impact on the neuronal firing rate. As soon as the amplitude increases, (2a) the generation of action potentials (APs) is inhibited during the inhibitory phase of alpha. In addition, the firing rate depends on the excitation level of target cells. A further increase in amplitude, (2b) is accompanied by an increase in the inhibitory baseline, meaning that the point of minimal inhibition is shifted, and weakly excited cells are silenced. In task competing networks the highest alpha power is measurable so that (3) all target cells are silenced (for an extensive review cf. Klimesch et al. 2007; Klimesch 2012). With this, it has been suggested that alpha inhibition provides two functions. Firstly, the blocking off of information processing (suppression). This is in line with the finding that alpha hypersynchronization is related to a loss of consciousness (Supp et al. 2011). Secondly, alpha inhibition enables selective neuronal activation (selection). An increase in alpha power (amplitude) induces a pulsed pattern of APs in higher excited cells, while silencing weakly excited cells. Thus, it provides a selective activation of cells that is functionally related to the timing of neuronal activation processes (e.g. movement onsets) (Klimesch 2012).

Considering different states of excitation in cells, excitatory thalamic input from several thalamic nuclei causes an activation of the anterior area by sensory feedback (Brinkofski et al. 2002) or imagination (Sharma et al. 2008). This refers to sensorimotor integration, a dynamic process transforming sensory input into motor output, which is crucial for all movements and environmental interactions (Flanders 2011). During a motor task sequence, the motor system is required to compensate for several issues, such as the delay of sensory feedback, causing an unstable isometric force production, as well as the discrepancies between motor commands and their movement outcomes, causing problems in precisely reaching a certain force level. An exemplary way to compensate for this are forward models. Possibly located in the cerebellum, they receive a copy of the efferent motor command to generate a prediction of the expected body position at very short latency. Forward models provide the ability to adjust motor commands and remain calibrated through motor adaptation: learning driven by sensory prediction errors (Shadmehr et al. 2010).

In terms of voluntary muscle contraction and/or relaxation, neuroimaging studies on motor control suggest the presence of inhibitory neurons as part of the motor cortex. Their activity has been shown to increase in relation to muscle relaxation, indicating that relaxation is not just a withdrawal from contraction (Jankowska et al. 1976; Cheney et al. 1985; Schmidt and McIntosh 1990; Toma et al. 1999; Buccolieri et al. 2004; Li 2013). Functional magnetic resonance imaging (fMRI) revealed a time-locked hemodynamic response to the onset of voluntary muscle contraction and relaxation in contralateral primary motor cortex (M1) and bilateral supplementary motor area (SMA) (Toma et al. 1999). In a recent fMRI study investigating gradual force-controlled gripping tasks, Spraker et al. (2009) found differences in local cerebral activity patterns when comparing force generation with relaxation. The authors also inferred the existence of different mechanisms involved in muscle contraction and relaxation. In addition, findings show the activation of the same cortical areas for both motor modes, suggesting that motor inhibitory neurons are located in close vicinity to their excitatory counterparts (Terada et al. 1995; Toma et al. 1999; Spraker et al. 2009).

By initiating the investigation of central neuronal motor behaviour preceding consecutive motor task sequences, Vogt et al. (2018) revealed larger readiness potentials (RP) depending either on the type of muscle activity or the estimated force level. Contraction vs. relaxation has been shown to be of greater relevance over motor areas, whereas force production and estimation is more relevant over sensorimotor areas. It seems reasonable that central neuronal motor behavioural patterns tend to change given its functional focus (i.e., planning vs. controlling of muscle activation). The present study may be considered as a follow-up investigation using a comparable study design (Vogt et al. 2018) to focus on alpha-band activity. Thus, medium timed motor task sequences (i.e., 3 s) cover important time windows to investigate muscle on-/offsets (Vogt et al. 2018). With respect to frequency band analysis a comparison to longer timed motor task sequences (i.e., 6 s) form a rational for choosing the respective timings in the present study.

The aim is to investigate the effect of continuous voluntary motor task sequences on alpha-band activity in healthy male adults, particularly examining longer (i.e., 6 s) compared to shorter (i.e., 3 s) isometric sequences combining contractions and relaxations. In contrast to a widely shared supposition that ERS reflects idling, it is hypothesized that alpha synchronization is an active inhibitory process that intensifies with progressive muscle relaxation, irrespective of longer or shorter motor task sequences. With this approach, it is aimed to lay the foundation to cover a wider range of realistic human movement characteristics and, thus, further understand underlying neuronal mechanisms.

Materials and methods

Participants

Eighteen healthy, right-handed males, either staff members or students from the German Sport University Cologne, with no neurological or musculoskeletal disorders (27.4 ± 3.98 years, 183.2 ± 7.15 cm, 84.67 ± 7.46 kg) volunteered to participate in this study. All participants provided informed consent and completed the basic gymnastic course at the university, ensuring a decent body perception (i.e., palmar flexion). This study was conducted at Olympic Training Centre Rhineland after approval by the Human Research Ethics Committee of the German Sport University in accordance with the Declaration of Helsinki.

Experimental procedure

Participants were strapped into an isokinetic dynamometer in an upright sitting position. To standardize the position, the upper arm to torso angle was adjusted to 90°, the respective shoulder was strapped to the back of the chair, and the hand position was predetermined by marks. The experimental procedure was arranged in a randomized and controlled design. After familiarisation with the dynamometer and two maximal voluntary contractions (MVCs), 40 consecutive repetitions of longer and 40 consecutive repetitions of shorter timed motor task sequences were conducted, respectively, each allowing for an approximate 2 min break after each 10th motor task sequence (10 repetitions = 1 block).

To standardize the effect of continuous motor task sequences on alpha activity, predefined individual torque levels were calculated from the two MVC's prior to testing and marked on the screen. Real-time visual feedback of the resultant torques and a high number of repetitive motor task sequences ensured a controlled and reliable study design. Synchronized EEG, EMG and torque recordings throughout the sequences served to determine muscle activation onset (i.e. according to torque levels) and the respective alpha-band activity. After 40 repetitions of either long or short motor task sequences, MVCs were performed to detect fatiguing effects. All motor task sequences were performed unilateral with the dominant hand. The overall test duration for one subject was approximately two hours.

Motor task sequence

An IsoMed 2000 (D&R GmbH, Germany) isokinetic dynamometer was used to display and record resultant torques induced by m. flexor carpi radialis (FCR). Torque was defined as the cross product of the distance vector (i.e., point of force application to wrist joint) and the force vector, which tends to produce a rotational motion.

The experimental motor task sequence consists of four isometric palmar flexion tasks according to a standardized step protocol (Vogt et al. 2018). In each sequence, participants had to voluntarily activate to 20% MVC (20% in), increase to 40% percent MVC (40% in), relax back to 20% MVC (40% out) and completely relax (20% out) (Fig. 1). Each torque level should be held isometrically for three (shorter timings) or six seconds (longer timings) depending on the preconditioned duration of the sequence. Ten seconds of rest were allowed between each sequence, to avoid muscle fatiguing effects.

Participants were instructed to switch between contraction/relaxation levels as quickly and accurately as possible. The duration of each isometric motor task sequence was self-estimated to ensure voluntarism, but supported by visual guidance (i.e., individual screen scaling to approximately meet the long and short sequence duration and predefined torque levels). Further, participants were instructed to avoid neck or facial muscle activation (i.e., teeth grinding, eye blinking) to reduce EEG muscle artifacts. Explicit instructions and feedback helped to avoid movement-related EEG artifacts, improved the participants sense of time and ensured the correct execution of the motor task tasks. To avoid any order effects, participants were randomly assigned to commence the test with the short block followed by the long block or vice versa.

Data collection

EEG recordings

To record EEG signals, BrainVision Recorder 1.21 and EEG actiCAP (Brain Products GmbH, Germany) was used and mounted prior to testing. The EEG-cap consisted of 32 Ag-AgCl electrodes, arranged in the international 10–20 system (Jasper 1958) at positions Fp1, Fp2, F3, F4, F7, F8, Fz, FC1, FC2, FC5, FC6, C3, C4, Cz, CP1, CP2, CP5, CP6, P3, P4, P7, P8, Pz, PO9, PO10, T7, T8, TP9, TP10, O1, O2 and Oz, each referenced to FCz. AFz served as ground electrode. Horizontal electrooculogram (EOG) was recorded by an electrode placed at the outer canthus of the right eye. Electrodes were filled with SuperVisc™ electrode gel (EasyCap, Germany) for optimal signal transduction. The analogue EEG signal was amplified and digitally converted using BrainVision amplifier (BrainProducts GmbH, Germany).

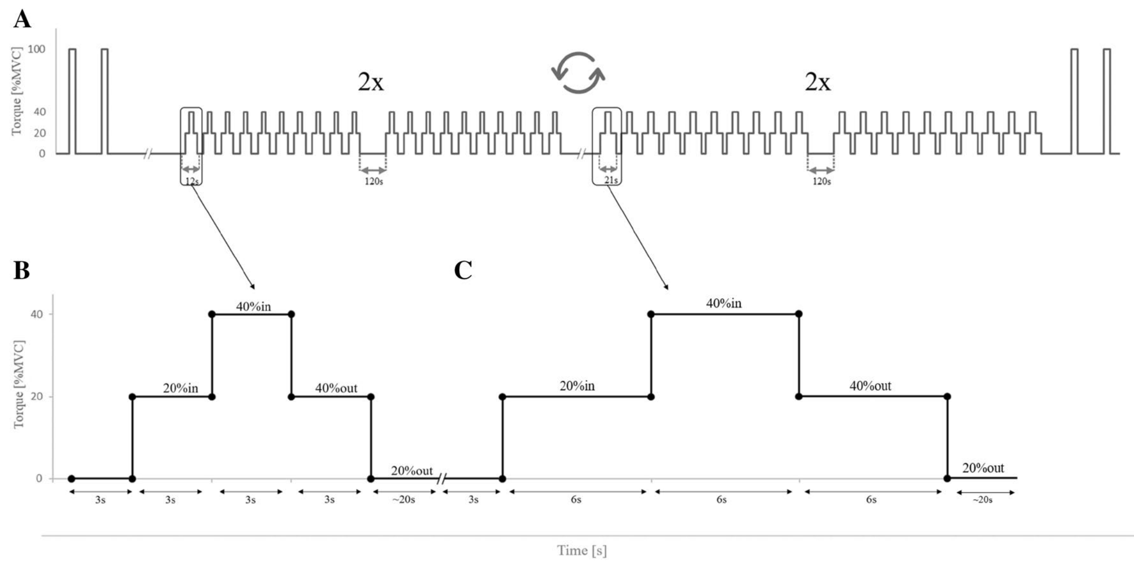

Fig. 1 Illustrative example of the experimental protocol (**a**) including two initial maximum voluntary contractions (MVC) as well as 40 short (**b**) and long (**c**) continuous motor task sequences, respectively. According to previous research and a comparable study design (Vogt et al. 2018), participants were asked to voluntarily activate to twenty percent MVC (20% in), increase to forty percent MVC (40% in), relax back to twenty percent MVC (40% out) and completely relax (20% out). Each torque level should be held isometrically for 3 (shorter timings) or 6 s (longer timings). Random assignment to commence the test with the short block followed by the long block or vice versa

EMG recordings

Surface electromyographic activity (EMG) at the forearm was recorded from m. flexor carpi radialis (FCR; i.e. agonist) and m. extensor carpi radialis (ECR; i.e. antagonist) via Ag-AgCl electrodes centred on the muscle belly. To obtain a good EMG signal with low signal-to-noise ratio (SNR), electrodes were attached according to SENIAM guidelines (Hermens et al. 1999). The EMG signal was recorded at 1000 Hz and converted into digital data via A/D converter system (Brain Products GmbH, Germany). EEG and EMG data as well as the torque values were synchronized to determine muscle on- and offsets during the motor task sequence. All recordings were conducted following the same standardized testing protocol and supervised by carefully instructed and experienced investigators.

Data analysis

EEG analysis

EEG data were analysed offline using Brain Vision Analyzer 2.1.1 (Brain Products, Germany). EEG signals were bandpass filtered between 7 and 30 Hz (time constant 0.023 s, 48 dB/octave). To avoid exclusion, electrode impedance exceeding 10 kΩ was topographically interpolated (up to a maximum of 4 electrodes). Gratton's standard ocular correction (Gratton et al. 1983) was applied to minimize eye-movement artifacts. Based on motor task onset, data were segmented in pre ($t_1 \in [-1000,0]$) and post ($t_2 \in [0,1000]$) referring to previously gathered insights on oscillatory reactivity (Woertz et al. 2004). After automatic artifact rejection (gradient < 100 µV min/max amplitudes ± 200 µV), a minimum of 30 1-s baseline corrected segments (0–100 ms) were used for Fast Fourier Transformation (spectral analysis: resolution at 0.98 Hz, Hanning window 10%). Averaged segments were pooled according to relevant motor areas into premotor cortex (PMC: F3, F4, FC1, FC2 and Fz), primary motor cortex (M1: C3, C4 and Cz), somatosensory cortex (SSC: CP1 and CP2) and posterior parietal cortex (PPC: P3, P4 and Pz; Vogt et al. 2018). Alpha frequency domain (7–13 Hz) was exported according to muscle onset as mean activity in µV and converted into relative alpha activity changes [%] for statistical analysis $\left(\frac{\bar{x}(t_1)}{\bar{x}(t_2)} \times 100\right)$, with $\bar{x}$ being mean alpha activity (µV).

EMG and torque analysis

To determine torque onsets of each contraction and relaxation performance (20% in, 40% in, 40% out and 20% out) for short and long tasks, experimenters visually identified the point of maximal slope. Then, for each trial, EMG activity of each muscle (FCR, ECR) was rectified and calculated over a period from − 1 to 1 s based upon torque onset. Mean EMG values were normalized according to MVC and subsequently, EMG values were averaged over all participants (Fig. 3).

Statistics

Statistica 7.2 (StatSoft, USA) and Microsoft Excel 14.3.7 (Microsoft Inc., USA) were used for all statistical analyses. Repeated measures analysis of variance (ANOVA) was used to display interaction and main effects for alpha activity within the factors duration (long vs. short), type (20% in vs. 40% in vs. 40% out vs. 20% out) and motor area (PMC vs. M1 vs. SSC vs. PPC). Fisher's least significant difference (LSD) was applied for post hoc analyses. Due to technical reasons data of 3 participants had to be excluded from the analyses, leaving data of $n = 15$ participants in the Figures, presented as mean ± confidence intervals (0.95), in the text as mean ± standard deviation (SD) and in the tables as mean ± SD. The level of significance was set at $p < .05$, and if applicable at $p < .001$.

Results

Alpha activity

Repeated measures ANOVA for alpha activity showed no interaction effects between duration, type and motor areas ($F_{(9, 168)} = 0.54$, $p = .84$; Fig. 1). Main effects, however, revealed significant differences between duration and type ($F_{(3, 168)} = 3.08$, $p < .05$) over combined motor areas. Post hoc tests revealed an increase in alpha activity (in 20% out) over both relaxation durations ($p < .001$; Fig. 2). Further, alpha activity increased at 40% out in the short duration compared to the long duration ($p < .05$) (Table 1).

Alpha activity and standard deviation (SD) as relative (%) changes from pre/post-comparison according to muscle onset ($t_1 \in [-1000,0]$; $t_2 \in [0,1000]$) of each relevant motor

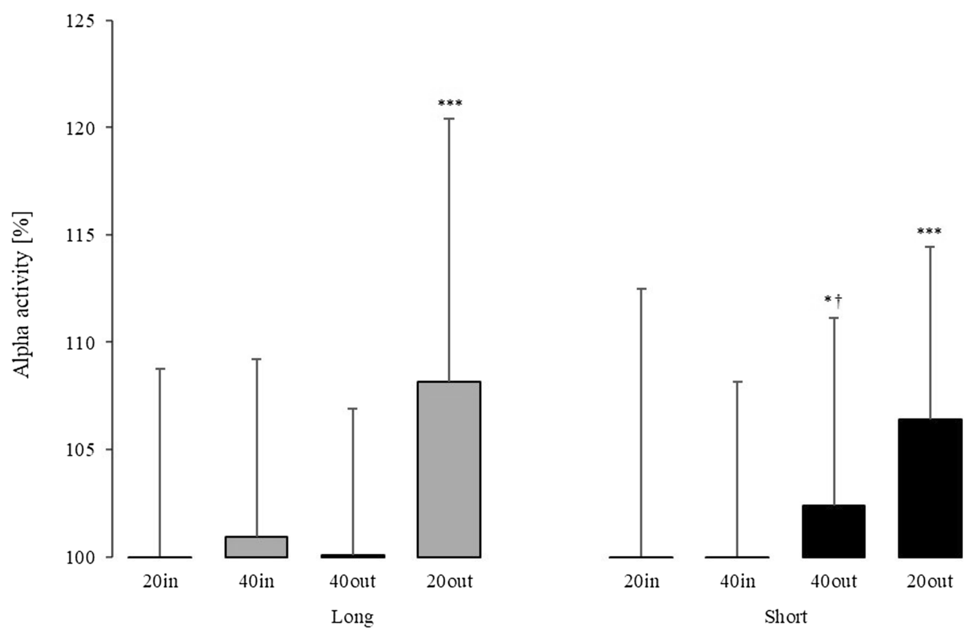

Fig. 2 Relative alpha activity (%) and confidence interval (0.95) from pre/post-comparison for continuous motor task sequence tasks with long (grey) and short isometric contraction durations (black). Alpha activity was measured over all motor areas according to muscle onset. ***Indicates highly significant differences compared to alpha activity changes in previous tasks ($p < .001$). *Indicates significant differences compared to alpha activity changes in previous tasks ($p < .05$). †Indicates differences between long and short contraction durations ($p < .05$). Significances are only displayed within duration and type, respectively

Table 1 Alpha activity [%]

	Total	PMC	M1	SSC	PPC
Long					
20% in	99.24 ± 9.55	103.15 ± 6.50	100.18 ± 8.31	96.74 ± 11.51	96.89 ± 10.51
40% in	100.91 ± 8.33	103.94 ± 5.26	101.19 ± 7.79	99.10 ± 9.21	99.41 ± 10.16
40% out	100.10 ± 6.81	100.19 ± 7.24	100.98 ± 8.14	99.45 ± 6.30	99.78 ± 5.98
20% out	108.15 ± 12.29	107.73 ± 8.66	105.73 ± 11.65	110.06 ± 15.27	109.10 ± 13.45
Short					
20% in	99.83 ± 12.68	104.27 ± 7.22	100.63 ± 11.60	97.79 ± 15.52	96.64 ± 14.58
40% in	99.65 ± 8.52	101.52 ± 5.66	98.41 ± 6.92	99.11 ± 10.50	99.55 ± 10.48
40% out	102.39 ± 8.75	104.04 ± 7.47	104.40 ± 7.31	99.92 ± 10.04	101.09 ± 9.86
20% out	106.41 ± 8.01	108.33 ± 7.48	104.32 ± 7.39	106.99 ± 8.75	105.99 ± 8.61

area for long and short continuous motor task sequences $\left(\frac{\bar{x}(t_1)}{\bar{x}(t_2)} \times 100\right)$, with $\bar{x}$ being mean alpha activity (µV).

EMG and torque activity

Participants were able to accurately maintain the prescribed motor task sequences, according to torque outputs and the steadiness of muscle contracting and relaxing activation of FCR, referenced to ECR (Fig. 3). Mean values of FCR muscle activity revealed no signs of fatigue ($p > .05$) in short or long motor task sequences.

Discussion

The objective of this study was to investigate movement-specific alpha oscillations during repetitive voluntary isometric palmar flexion sequences in healthy male adults. Motor task sequences were divided into longer and shorter timed muscle activation durations, consisting of two torque-related contraction and relaxation tasks, respectively. The main finding was that alpha activity increases at the end of the motor task sequence (i.e., 20% out) regardless of shorter or longer timed muscle activation; however, alpha activity increased when relaxing from greater torques (i.e., 40% out) in shorter compared to longer timed muscle activation. Modulations in alpha activity did not differ between motor areas.

In traditional research, ERD is assumed to be a correlate of increased neuronal excitability so that task-relevant areas exhibit ERD and task irrelevant regions exhibit ERS (Steriade 1988; Pfurtscheller and Lopes da Silva 1999; Pfurtscheller 2006). Thus, previous research considered ERD as the ‘typical’ event-related alpha response, while ERS reflects ‘cortical idling’ (Pfurtscheller et al. 1996). However, the present study reveals that in relaxation tasks an increased alpha power (instead of decreased) can be observed. It may be suggested that increased alpha activity reflects an active task-relevant inhibitory process with numerous functions concerning suppression, selective activation, attentional filtering and semantic orientation (Pfurtscheller and Lopes da Silva 1999; Fries 2005; Klimesch et al. 2007; Jensen and Mazaheri 2010; Zanto et al. 2011; Klimesch 2012). In contrast, ERD is obtained in response to almost any type of preparation task (Pfurtscheller and Lopes da Silva 1999) which is why alpha is already decreased before muscle onset.

The present study strongly suggest that alpha activity is associated with selective activation. The alpha activity we measured in short and long contraction durations remained low at 20% in and 40% in, but gradually increased with muscle relaxation (i.e., 40% out and 20% out). Therefore, during the short contraction blocks at 40% out, alpha activity was significantly higher compared to the previous task (i.e., 40% in), but lower compared to the next one (i.e., 20% out). This underlines the progression mentioned in the inhibition timing hypothesis (i.e., 2a/b) and may be interpreted as follows: Considering alpha oscillations as rhythmic changes between minimal and maximal inhibition, a slight increase in amplitude (i.e., baseline) would silence weakly excited

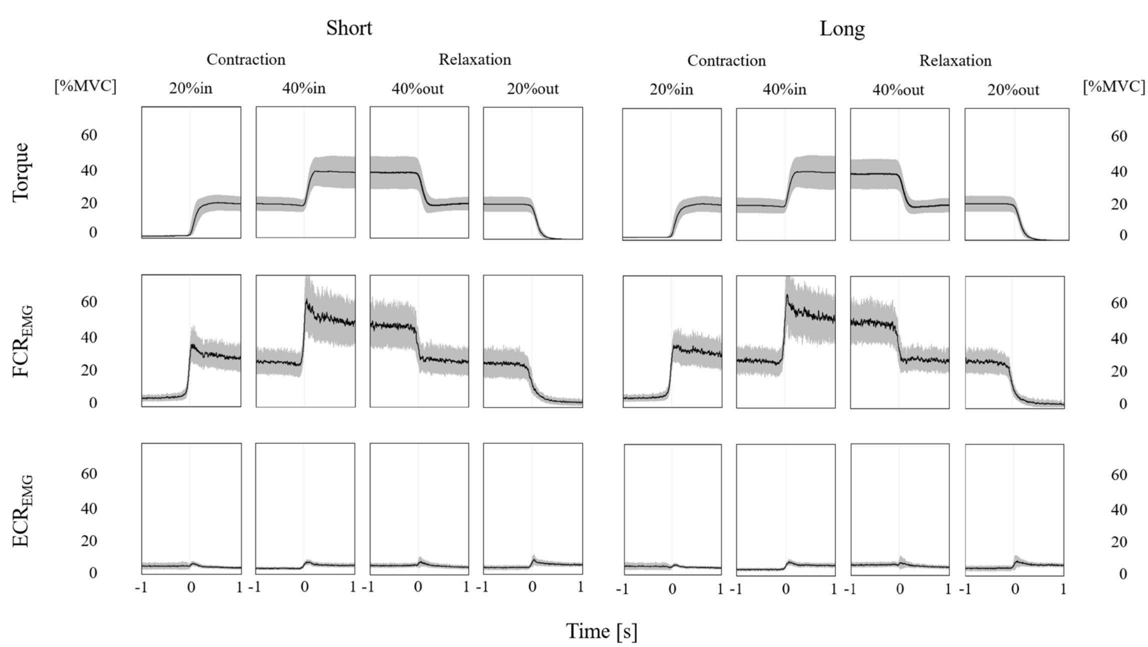

Fig. 3 Displayed are mean performances (black line) ± standard deviation (light grey) from − 1 to 1 s of the prescribed motor task sequences based upon torque onsets (each at 0 s) and including flexor carpi radialis (FCR) and extensor carpi radialis (ECR) with the respective muscle contracting (20% in, 40% in) or relaxing (40% out, 20% out) activation

cells and induce a pulsed pattern of APs in cells with higher excitation levels (Klimesch 2012). Thus, the generation of APs is confined to task-relevant cells, as the amount of forwarded (motor-) stimuli can be decreased if the amplitude is further increased.

In a sense, the measured alpha activity change is an active phenomenon conducting time and quantity of neuronal information processing. Transferring this to the progression of the present study's motor task sequence, the inhibition timing hypothesis can provide a possible explanation. As for the relaxation (i.e., 40% out and 20% out) an increasing alpha activity may be related to an inhibitory baseline shift (2b, 3), resulting in the progressive silencing of target cells. As soon as their cellular excitation level is below the minimal inhibition of alpha, the generation of APs as well as interfering cell communication, is prohibited. Irrespective of shorter or longer muscle activation we found that alpha activity was significantly increased after dropping from 20% MVC back to rest (20% out), reflecting the inhibition of irrelevant (motor-) areas (Pfurtscheller and Lopes da Silva 1999; Klimesch et al. 2007; Jensen and Mazaheri 2010; Klimesch 2012).

In terms of motor control, the present study's findings suggest that muscle relaxation further increases alpha activity. We could not observe significant differences within task-relevant motor areas, possibly as a resulting disadvantage of the comprehensive approach. The complexity of the movement sequence may have caused simultaneous activation of a region of interest at any time. However, there is evidence that voluntary muscle relaxation may be considered as an active process requiring cortical processing and input (Li 2013; Kato et al. 2016). This process might be initiated by the excitation of intracortical inhibitory interneurons in M1 and SMA (Toma et al. 1999). Moreover, evidence is provided by Porter et al. (2001), investigating the neocortical activity of inhibitory neurons in mice. They observed five-fold larger thalamocortical input in firing inhibitory neurons compared to nonfiring neurons, assuming different classes of interneurons serving in the processing of incoming sensory information. Therefore, it can be suggested that inhibition is generated by diverse classes of interneurons, possibly serving different roles in the processing of incoming sensory information and motor control (Porter et al. 2001; Spraker et al. 2009).

Further, from an attentional perspective, it has been suggested that alpha phase synchronization coordinates access to memory traces to support top-down processing (Klimesch et al. 2010; Zanto et al. 2011). Although the responsible areas of the prefrontal cortex are not part of this analysis, the present motor task sequence is dependent on cognitive processing of sensory information (i.e., ensure constant force production, estimate time, coordinate activation/relaxation, etc.), and thus involving sensorimotor integration. If alpha activity is indeed inhibitory, one of its functions might be to block (motor-) neurons outside the attentional focus to operate more accurately and efficiently. This ability provides selective access to pre-activated (learned) information that classifies the meaning of sensory information or 'higher order information' – representing alpha activity as temporal attention providing semantic orientation (Klimesch 2012). This is in line with the strong increase in alpha activity immediately after the offset (i.e., 20% out), when stimulus processing and the previously active motor areas become irrelevant.

Further, lateralized alpha activity has shown, in previous research, that when covert attention is focused on one hemifield, alpha increases in the ipsilateral, but decreases in the contralateral hemisphere (Worden et al. 2000; Pfurtscheller et al. 2000; Rihs et al. 2007; van Gerven and Jensen 2009; Handel et al. 2011; Klimesch 2012). In principle, this may be linked to the present results, as alpha lateralization describes selective access to brain areas (e.g., motor areas) depending on the inhibition of task-irrelevant area entries. However, findings showed neither hemispherical differences nor significant interaction effects between relevant motor areas. This might be an indication for a lack of spatial resolution or varying information processing under certain task demands accomplished by a highly complex communication system.

Limitations and outlook

In the present study, EEG was used due to its high time resolution and the non-invasive, portable set up. However, this approach requires a high number of task repetitions and it is lacking spatial resolution. This lack of spatial resolution might be one reason for the absence of hemispherical differences that we found. The muscle that we are referring to is rather small and so is the respective area in the brain with respect to the Homunculus. A larger sample size or the use of localization methods might be suitable to detect significant differences. In addition, EMG activity of the non-dominant hand might be useful to control co-contraction and should be considered for future investigations. EEG is limited to oscillatory activity occurring in extended sensory and motor regions (Hari and Salmelin 1997) making reliable forecasting of intracranial (travelling) relationships difficult. Similar problems may be considered for the investigation of isolated alpha activity without reference to other frequency bands. It is of crucial importance to understand cross-frequency interactions (e.g., between gamma and alpha activity) and the working brain as a network (Jensen and Mazaheri 2010).

With respect to increasing alpha activity in relation to muscle relaxation, we are aware that there are significant discrepancies within long and short contraction durations (i.e., at 40% out). Although we did not observe indicators of fatigue ($p > .05$), a temporary decrease in isometric strength due to the long sequence duration may diminish the difference between 40% out and 20% out, so that alpha inhibition only occurs with full relaxation. The resulting impact on gradual muscle relaxation remains to be confirmed.

Other remaining questions are the functional interplay between sensorimotor integration and suppressive alpha activity, the role of the thalamus during cognitive and motor tasks, and the exact physiological mechanisms of alpha in detail. A promising approach to address above mentioned problems is to apply intracranial recordings in humans performing cognitive and motor tasks. For example, it would be interesting to examine different setups (self-reliant counting or different contraction velocities) in combination with additional cognitive tasks (life-kinetic exercises, memory and retention or distraction tasks, etc.). However, from an ethical perspective, the implementation of these invasive approaches is rather difficult.

Conclusion

Voluntary isometric motor task sequences (palmar-flexion) in combination with EEG revealed significant increases in alpha activity during subsequent progressive muscle relaxation, whereas no differences between task-relevant motor areas could be observed. It may be suggested that an active task-relevant inhibitory process indicates motor task sequence-related relaxation mirrored by an increasing alpha activity. Bilateral information processing throughout the motor task sequence is proposed to represent similar information processing between relevant motor areas. Although discussed from different functional perspectives, future research on alpha activity is necessary to investigate this highly complex oscillatory system, in particular according to motor behaviour in continuous movement sequences.

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Compliance with ethical standards

Conflict of interest All authors declare no actual or potential conflict of interest, including any financial, personal or other relationships with other people or organisations that could inappropriately influence, or be perceived to influence, the publication of this work.

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