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Frontal brain areas are more involved during motor imagery than during motor execution/preparation of a response sequence

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ABSTRACT

Results of several neuroimaging studies support the functional equivalence model, which states that motor imagery (MI) and motor execution (ME) involve the same processes, except for the final execution component. In contrast, the motor-cognitive model implies that MI additionally involves frontal executive control processes. However, according to some authors MI may actually be more comparable to motor preparation (MP). In the current electroencephalographic study, a version of the discrete sequence production paradigm was employed in which human participants initially had to prepare a sequence of five finger movements that subsequently had to be executed, imagined, or withheld. MI, ME, and MP were compared by computing event-related (de)-synchronization in the theta, alpha/mu, and beta bands. Results revealed a major increase in frontal theta power during MI as compared to ME and MP. At the end of the examined intervals, a posterior reduction in alpha power was present during ME and MP, but not during MI. Finally, above sensorimotor areas a decrease in beta power was observed that was most pronounced in the case of ME. The increase of frontal theta activity during MI may reflect increased effort, while the absence of a reduction in posterior alpha power suggests no major involvement of visuospatial attention and/or visual imagery. The present findings favor the motor-cognitive model, as it predicts extra involvement of frontal executive processes during MI.

1. Introduction

Motor imagery (MI) may be defined as the cognitive ability that enables human individuals to perform and experience motor actions in the mind without actually executing these actions by activating corresponding muscles (e.g., see Jeannerod, 2001). MI allows for the practicing of movements without having to execute them, which seems highly relevant for the learning process of musicians, the training of athletes, but also for the rehabilitation of patients with motor disorders (e.g., see Adams et al., 2018). In several papers (e.g., see Krüger et al., 2020; Nyberg et al., 2006; Sobierajewicz et al., 2016, 2017a, 2017b, 2018, 2019), MI was shown to be beneficial for the learning of a sequential hand motor skill. For example, in the studies of Sobierajewicz et al. various discrete sequences of button presses by fingers of either the left or the right hand had to be mentally simulated during a practice phase but executed during a test phase. Results of the ensuing test phase indeed revealed a benefit for the mentally simulated over novel sequences. Several authors have argued that MI and motor execution (ME) activate nearly identical processes (the functional equivalence model; e.g., see Decety, 1996; Jeannerod, 2001, 2006), but recently, it has been proposed that MI differs from ME, as MI may especially rely on executive control processes (the motor-cognitive model; Glover and Baran, 2017; Glover et al., 2020) and/or inhibition (Kasess et al., 2008; Angelini et al., 2015, 2016). According to some authors there may also be quite some similarities between motor preparation (MP) and MI (Lopes da Silva and Pfurtscheller, 1999; Pfurtscheller and Neuper, 1997; Sobierajewicz et al., 2016), but MP might also depend on whether the prepared action (s) subsequently has to be executed or imagined (Angelini et al., 2016). Spatiotemporal characteristics of brain activity during MI, ME, and MP can very well be studied by using the electroencephalogram (EEG) within Go/NoGo discrete sequence production (DSP) tasks as employed by Sobierajewicz et al. (2016, 2017a, 2017b, 2018, 2019) and

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computing event-related synchronization or desynchronization (ERS/ERD) in different frequency bands (for a review, see Neuper and Pfurtscheller, 2010). This approach was followed in the current high density EEG study to determine to what extent MP, and the subsequent MI or ME, while learning a fine hand motor skill during a practice phase, actually are alike.

A distinction has been made between different forms of imagery in relation to motor actions. In some studies, the focus is on visualization of the action or visual imagery (e.g., see Kosslyn, 2005), which relates to visual attention. In the current study the focus is on kinesthetic MI, which requires the participant to "feel the movement and perceive muscle contractions mentally" (Guillot et al., 2009, p. 2159), or to sense one's own motions and experiencing realistic kinesthetic sensations (e.g., see Ridderinkhof and Brass, 2015). Thus, the participant takes a first-person perspective and imagines performing the action him/herself. Apart from the recruitment of motoric processes, it has been argued that kinesthetic MI involves the anticipation of sensory consequences of the action effects (i.e., forward modeling; see Ridderinkhof and Brass, 2015; Kosslyn et al., 2010; Wolpert and Flanagan, 2001; Davidson and Wolpert, 2005). A recent study indeed revealed that imagined self-generated touch produces reduced sensitivity of real tactile sensations (Kilteni et al., 2018), thus, kinesthetic MI seems to imply forward modeling.

Like the functional equivalence model (Decety, 1996; Jeannerod, 2001, 2006), the motor-cognitive model (Glover and Baran, 2017; Glover et al., 2020) assumes functional similarity between MI and ME. Glover and Baran (2017) argued that the preparation stage for MI and ME can be considered to be the same (which relates to ideas dating back to Woodworth, 1899, see the reviews of Elliott et al., 2001, 2010; but see Angelini et al., 2016), as in both cases a motor image is generated based on existing representations. However, the execution stage was proposed to differ between MI and ME as execution automatically relies on sensory feedback together with forward modeling, while these processes are probably not automatically activated in the case of MI. Instead, according to the motor-cognitive model MI requires conscious control processes as the unfolding motor image needs to be monitored, and attention additionally needs to be switched between the motor image and the action being simulated. This may be relatively easy for a well-known often practiced simple action, but the more novel and complex a to-be-simulated action is, the more control may be required (Glover and Baran, 2017), which in that case is assumed to lead to major differences between MI and ME.

Recent quantitative meta-analyses of fMRI (functional magnetic resonance imaging) and PET (positron emission tomography) data confirmed the similarities in brain activity between MI and ME (Hardwick et al., 2018; see also Hétu et al., 2013; Lotze and Halsband, 2006; Ridderinkhof and Brass, 2015). Conjunction analyses revealed activity in primary sensorimotor areas (S_1 and M_1), the premotor cortex (PMC), the pre-supplementary motor area (pre-SMA) and SMA-proper, together with the basal ganglia (BG) and cerebellum (CB). However, contrast analyses also revealed clear differences between MI and ME (Hardwick et al., 2018). In the case of MI, more activity was observed in PMC, pre-SMA, and the posterior parietal cortex (PPC). Although left-lateralized activity of the dorsolateral prefrontal cortex (DLPFC) was only identified in the case of MI, the contrast analyses did not confirm its specificity for MI. During ME as compared to MI, more activity in S_1 and M_1, SMA-proper, cingulate motor areas, and areas within the BG and CB was observed. Based on these results, Hardwick et al. (2018) concluded that the similarities between MI and ME, which support the functional equivalence model, may have been overestimated. Furthermore, they suggested that the observed activity of the DLPFC in the case of MI better fits with the motor-cognitive model. Nevertheless, they concluded that there is no strong support for the motor-cognitive model yet, as the extra activity of DLPFC during MI was not fully confirmed. A possible reason why this effect did not emerge in their contrast analysis may be related to the variety of tasks included in their meta-analyses, as increased control reflected in DLPFC activity may only be pronounced in more complex and novel tasks (see Glover and Baran, 2017).

According to the motor-cognitive model, there may be extra involvement of control processes in the case of MI relative to ME, which may be reflected in increased activity of DLPFC. However, another reason why MI may not be equivalent to ME is that more inhibitory control is needed during MI as the simulated action should be withheld (Kasess et al., 2008; Angelini et al., 2015, 2016). Kasess et al. argued that their results, which were based on the outcome of dynamic causal modeling of fMRI data during ME and MI, point to a strong suppressive influence of the SMA on the M_1. Importantly, different types of inhibition have been distinguished that may be differentially involved during MI, MP, and also ME. Angelini et al. (2015, 2016) pointed to the distinction between pro-active and reactive inhibition. Pro-active inhibition refers to the inhibition that may be required while preparing an action that subsequently may have to be executed after a Go stimulus. Reactive inhibition instead, refers to the inhibition required when a prepared action should be cancelled. Thus, pro-active inhibition may especially be involved during MP and also during MI. Reactive inhibition might be involved during MI when it was initially unclear whether a certain action had to be executed or imagined, which will depend on the experimental design of the study. The EEG analyses of Angelini et al. (2015) pointed to an inhibitory mechanism during MI of a single button press that involves the right inferior frontal gyrus (rIFG) and the pre-SMA (see also the fMRI results of Macuga and Frey, 2012), which are cortical areas known to be involved during both pro-active and reactive inhibition (e.g., see Swann et al., 2012). Another type of inhibition, in which MI and ME could differ is surround inhibition. The execution of a specific action with for example the index finger at a specific moment in time also requires the inhibition of actions of the other fingers. This type of inhibition manifests itself for example at the level of M_1 during ME, and is denoted as surround inhibition (Beck and Hallett, 2011). Aoyama et al. (2016) examined with transcranial magnetic stimulation (TMS) whether MI also involves this type of inhibition, and found support that the self-reported vividness of MI was related with the amount of surround inhibition. Thus, there is some support that surround inhibition is present both in the case of MI and ME.

Most of the studies contrasting MI and ME used relatively simple tasks that implied a single and often quite simple action. The relevance of MI for the learning of a fine hand motor skill, which may be considered as a rather complex task, was examined by Lacourse et al. (2005). They used fMRI to examine changes in neural activity when executing or imagining to execute a seven-element motor sequence with the dominant right hand before (pre) and after (post) a learning phase of several days. In the pre-learning phase, ME especially activated contralateral sensorimotor areas, PMC, SMA, PPC, BG, the cingulate gyrus, and the thalamus. MI implied comparable foci of activation, although in general activation was reduced to about 36% of the activity observed during ME. However, activation in the BG during MI was stronger, which led Lacourse et al. to suggest that they play an inhibitory role by reducing overall activation. In the post-learning phase overall activity during ME decreased as compared to the pre-learning phase, especially with regard to the ipsilateral activation. However, activation in the frontal and especially the parietal cortex increased in the case of imagery, which may be related to increased sensorimotor mapping and/or increased attention or effort in the case of imagery, which partially fits with the motor-cognitive model. In general, the BG became more active during both ME and MI in the post-learning phase, which confirms the well-known relevance of these structures for skilled sequence execution.

As indicated above, some authors argued that there actually may be quite some similarities between MI and MP. Sobierajewicz et al. (2016) revealed comparable learning effects for a group of participants that only prepared executing specific sequences and subsequently withheld their execution (the inhibition group), and another group that prepared and also imagined executing specific sequences (the imagery group). These results could imply that motor preparation (MP) shares relevant aspects with MI (see also Lopes da Silva and Pfurtscheller, 1999;

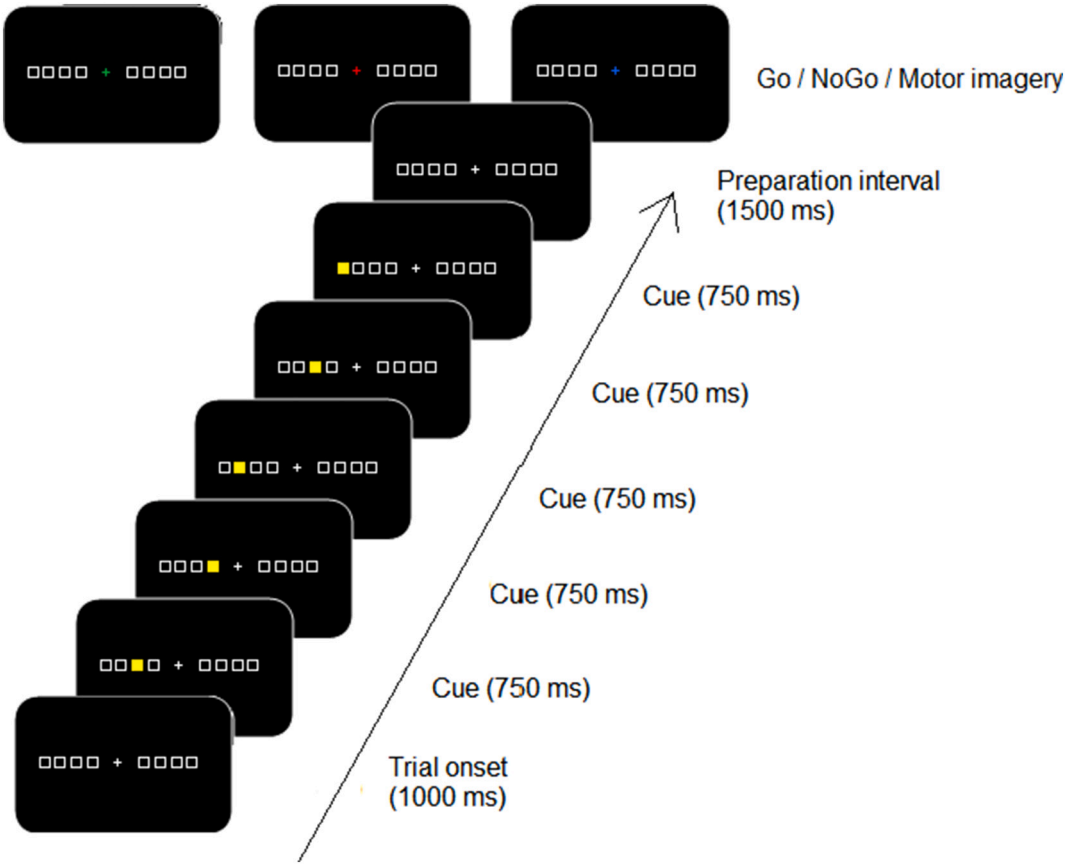

Fig. 1. An example of the sequence of events on a trial in the practice phase. The onset of a trial was signaled with a beep and the appearance of the unfilled grey squares together with the central fixation cross. After 1000 ms, the cues, yellow squares, were presented successively, thereby indicating what response sequence had to be prepared with the different fingers of the left or right hand during the motor preparation (MP) interval. The fixation cross either turned green, blue, or red, which implied that the motor sequence either had to be executed (Motor Execution [ME]; 41.7% of the trials), had to be mentally simulated (Motor Imagery [MI]; 41.7% of the trials), or was to be cancelled (NoGo; 16.6% of the trials). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Pfurtscheller and Neuper, 1997). One could argue that (kinesthetic) MI and MP are nearly the same as they are both covert actions that may involve forward modeling. Furthermore, both might imply proactive inhibition. Nevertheless, MI is characterized by the explicit instruction to mentally simulate executing an action, while MP refers to preparing an action without any suggestion about mental simulation or feeling the movement. MP might also depend on whether the prepared action subsequently has to be executed or inhibited, or to be imagined or inhibited. This issue was examined in a blocked design by Angelini et al. (2016). They observed reduced activity of pre-SMA during MP in the blocks requiring MI as compared to the blocks requiring ME, which they interpreted as a change in strategy that implied less involvement of a decisional stage as no decision has to be made to cancel an action in the MI blocks.

Studies using EEG during MI to determine changes in power in specific frequency bands relative to a baseline period (ERS/ERD; reviewed in Neuper and Pfurtscheller, 2010) revealed that the suppression of the posterior alpha rhythm (~8–13 Hz), which has been related to visual attention (e.g., see Klimesch, 2012), is stronger when people are instructed to use visual imagery than when they are instructed to perform kinesthetic MI. Pfurtscheller and Neuper (1997) revealed that when a participant imagines to perform a lateral hand movement a locally restricted ERD above the contralateral hand area can be observed (i.e., blocking of the central alpha or mu rhythm, also ~8–13 Hz but now with a topography above sensorimotor areas). This blocking of the mu rhythm has also been observed when participants prepare a real movement. Similar results were observed for the beta band (~13–24 Hz; Pfurtscheller and Neuper, 1997). According to Lopes da Silva and Lopes da Silva and Pfurtscheller (1999) the ERDs observed during MP and MI reflect similar types of readiness or presetting of neural networks in sensory and motor areas, which might indicate that MI and MP are indeed more alike than ME.

Later EEG studies made a distinction between ERD in the upper (~10–12 Hz) and lower alpha/mu bands (~8–10 Hz). ERD in the upper band seems more focal and more dependent on the relevant effector, while ERD in the lower band appears to reflect more general preparation processes as it is topographically widespread (see Neuper and Pfurtscheller, 2010). On the basis of their (intracranial) electrocorticographic (ECoG) study, Crone et al. (1998) concluded that alpha/mu and beta ERD relate to the same cortical activation while beta ERD would have both a higher specificity and a lower sensitivity. Stolk et al. (2019) argued on the basis of their ECoG results that alpha and beta bands differ in their anatomical and functional properties as they travel along opposite directions across the sensory and motor cortex. Alpha/mu activity seemed to propagate from posterior to anterior areas while beta activity appeared to move from anterior to posterior areas. Increased ipsilateral alpha power was related to spatially-unspecific inhibition while decreased beta power over contralateral motor cortex was interpreted as a shift from inhibition to excitation.

One could argue that the lack of clear differences in EEG activity between MI and MP in the aforementioned studies (Lopes da Silva and

Pfurtscheller, 1999) relates to the selective focus on the alpha/mu and beta bands. For example, on the basis of Buzsáki's (2006) arguments,[1] it may be proposed that local inhibitory interactions are related to high frequency oscillations while more global inhibitory interactions concern the lower theta (~4–8 Hz) or even delta (~1–4 Hz) bands. Additionally, beta band activity may be more specifically related to motor preparation, while activity within the alpha band has been argued to be less differentiated (e.g., see Tzagarakis et al., 2015; Stolk et al., 2019).

In the current EEG study, interest is focused on what actually happens during MP and during the subsequent MI/ME phase while learning a fine sequential hand motor skill. We chose to use the Go/NoGo version of the DSP paradigm (De Kleine and Van der Lubbe, 2011), which is a variant of the DSP paradigm that has been extensively explored by Verwey and coworkers (e.g., see Abrahamse et al., 2013). A first important advantage of the Go/NoGo variant is the presence of a separate MP stage, which implies the possibility to compare MI not only with ME, but also with MP. Secondly, no visual cues are displayed during the critical time intervals, which avoids possible differences between conditions due to visual stimulation. Thirdly, the paradigm implies that the to-be-simulated action is quite complex, so more control may be required (Glover and Baran, 2017), which may boost possible differences between MI and ME. An earlier study by De Kleine and Van der Lubbe (2011) with this paradigm suggests that during MP of an unfamiliar movement sequence, visuospatial processes are involved to keep the to-be-remembered sequence active in visual working memory, thus, one could also argue that MI/MP of a movement sequence differs from ME in that there is a higher load on visual working memory.

As the involved processes might be reflected in different patterns of oscillations, we focused not only on the alpha/mu and beta bands, but also on changes in the theta band. Instead of bandpass filtering, we employed wavelet analyses with complex Morlet wavelets, which should improve the extraction of relevant oscillatory patterns. Furthermore, we employed a mass univariate approach (e.g., see Groppe et al., 2011), thereby decreasing the chance of missing relevant effects. Finally, MP might differ when participants become aware that a specific motor sequence is either always to be imagined or to be executed (see Angelini et al., 2016), therefore, we also compared MP preceding MI (MPi) and MP preceding ME (MPe).

2. Methods

2.1. Participants

Twenty-four participants took part in this experiment. Due to technical problems (with 1 participant), the inability to properly follow the instructions (as indicated by electromyographic [EMG] activity and horizontal eye movements during critical time intervals, especially during MP in 7 participants), and low quality of several of the EEG measurements (2 participants), only fourteen participants were used in the present analyses ($M_{age} = 22.9$ years, SD = 1.5; 10 female, 4 male, all right-handed, assessed with Annett's Handedness Inventory, Annett, 1970).[2] All participants were recruited from the local student population of the Adam Mickiewicz University in Poznań, Poland. Participants reported to have normal or corrected-to-normal vision, were healthy, had no history of neurological or psychiatric disorder, and used no medication. Participants gave their informed consent before the start of the experiment. The followed procedures were approved by the local ethics committee of the Adam Mickiewicz University and are in line with the Declaration of Helsinki.

2.2. Stimuli and task

The sequence of events on an experimental trial in the practice phase is displayed in Fig. 1. The experiment was programmed with PsychoPy software. A trial started with a beep of 300 Hz (~60 dB for 300 ms), the presentation of a grey fixation cross (1.3°) in the center of a black screen, and the display of four unfilled grey squares (2.5°) on the left and the right from the fixation cross. The eight squares were horizontally aligned and covered a visual angle of 26.5°. One thousand ms after onset of the beep, one of the squares turned yellow for a duration of 750 ms, directly followed by a second square turning yellow, up to a total stimulus sequence of five squares. The stimulus sequence within a trial (details about the different sequences are indicated below) was always restricted to either the left or the right side from the fixation cross. After offset of the fifth square, the display with eight unfilled squares remained present, and after 1500 ms, the fixation cross turned either green, red, or blue, which signaled the end of the MP interval.

Participants had to place their little, ring, middle, and index fingers of the left hand on the **a**, **s**, **d**, and **f** keys of a QWERTY keyboard, and their index, middle, ring, and little finger of the right hand on the **j**, **k**, **l**, and **;** keys. The finger positions corresponded with the positions of the squares. The left-most square related to the left little finger placed at the **a** key, etc. A fixation cross turning green at the end of the motor preparation interval signaled that the presented stimulus sequence had to be executed as fast but also as accurately as possible by pressing the corresponding keys in the proper order (i.e., an ME trial). In the case of a blue fixation cross, participants were instructed to imagine executing the relevant response sequence (i.e., an MI trial, for further details, see below). Finally, after a red fixation cross nothing was to be done and the prepared action had to be cancelled (i.e., a NoGo trial). Participants were asked not to move their fingers or contract their muscles during the preparation phase and during MI trials, which was checked by measuring and examining the EMG (see below). To avoid interference from lateral eye movements, participants were additionally instructed to keep their eyes directed at the fixation cross until the end of a trial.

The experiment consisted of a practice phase of about 80 min and a test phase of about 20 min. During the practice phase, every participant had to learn eight different types of sequences that were presented in a randomized order. Four five-element sequences were related to the left hand, and the mirrored versions of those sequences were related to the right hand. Two of the selected sequences plus their mirrored versions were consistently used as ME trials (40 trials per block). Two other sequences plus their mirrored versions were selected as MI trials (40 trials per block). Finally, all eight types of sequences were also employed as NoGo trials (every sequence was presented twice: 16 trials per block). Each practice block thus contained 96 sequences in total. After four blocks in the practice phase the test phase started.

In the test phase, the sequences employed in the practice phase were accompanied by new sequences that were unfamiliar (not practiced before) but of equal complexity (see below). Now, all sequence types (familiar ME, familiar MI, and unfamiliar sequences) required a response on 83.3% of the trials (20 trials per type of sequence; every sequence was repeated five times), while responses had to be withheld (NoGo) on 16.7% of the trials. The test phase consisted of 72 sequences in total. The test phase was carried out to examine whether there was a benefit of ME and/or MI during the practice phase on sequence learning. No EEG was measured during this phase.

The employed sequences per sequence type were counterbalanced across participants and across fingers. Six different sequence structures were used (1-2-4-3-2, 1-3-4-2-3, 1-4-2-1-3, 1-3-2-4-1, 1-4-3-1-2, 2-1-4-3-1) and four counterbalanced versions of each sequence structure were

[1] "… the cycle lengths (i.e., periods) of the oscillation limit how far information gets transferred in one step. Fast oscillations, therefore, favor local decisions, whereas the involvement of distant neuronal groups in distinct structures in obtaining a global consensus requires more time." (Buzsáki, 2006; p. 116).

[2] Earlier analyses of the current experiment with event-related potentials, event-related lateralizations, and lateralized power spectra examined fewer EEG channels, smaller segments, and used more liberal inclusion criteria (Sobierajewicz et al., 2017a; Van der Lubbe et al., 2017).

created by assigning different keys to the numbers, which eliminates finger-specific effects. This procedure implied that all employed sequences in our experiment had the same level of complexity.

2.3. Procedure

Participants were seated in a darkened room before a desk in front of a CRT screen (display frequency 60 Hz) located at a distance of 70 cm. They were instructed to sit relaxed in a comfortable way and were asked to reduce any movements apart from the requested button presses. Before the start of the experimental session verbal instructions were given and several practice trials were presented to assure that the participants correctly understood the task. They additionally received descriptions of MI relative to visual imagery and were explicitly instructed to use MI only on the trials that MI had to be applied. They were told to simulate the movement sequence from a first person's perspective (Solodkin et al., 2004). The difference between MI and visual imagery was explained by the example: "imagine yourself walking on the street-you can see yourself walking" (visual imagery) vs. "imagine as if you are walking-you imagine your movements during walking" (MI). In the latter case they were also instructed to imagine the somatosensory sensations of executing the movement.

Feedback about correctness of the executed response sequence was given only after a false sequence response or when a premature response was made. At the end of each block and during each break, participants received feedback with information about their mean response times and the percentage of incorrectly executed response sequences.

2.4. Electrophysiological recordings

EEG was registered from 128 active channels with a sample rate of 1000 Hz with a QuickAmp128 (Brainproducts, GmbH) amplifier, which has a built-in average reference.[3] An online lowpass filter of 200 Hz was applied. Electrodes were located on positions in an actiCap according to the 10–5 system (Oostenveld and Praamstra, 2001). A ground electrode was located at the Fpz position. During data acquisition electrode impedance was kept below 5 kΩ. Vertical and horizontal eye movements were recorded by measuring the electrooculogram (EOG) with two additional bipolar channels located above and below the right eye and on the outer canthi of each eye. Electromyographic (EMG) activity was measured from electrodes attached above the musculus flexor digitorum superficalis and the processus styloideus ulnae of the left and right forearms. All the electrophysiological data (EEG, EOG, and EMG) and markers signaling relevant stimuli and responses were recorded and stored online with Brain Vision Recorder (Brain Products, version 2.0.3).

2.5. Analyses of the behavioral data

A sequence of five key presses was considered incorrect in the case of a premature response (i.e., before the ME/MI/NoGo signal was presented) and when a false button was pressed. Response time (RT) was defined as the time interval between the onset of the Go signal indicating the requirement of ME and the first key press, and as the time intervals between consecutive key presses. RTs were only determined for correctly executed response sequences. Results were averaged across both hands. RTs in the practice phase were analyzed with a repeated measures analysis of variance (ANOVA) with the factors Block (4) and Key (5). RTs in the test phase were analyzed with the factors Sequence (3; Familiar ME, Familiar MI, Unfamiliar) and Key.

Proportions of correctly executed sequences (PCs) were transformed (arcsine) before carrying out the statistical analyses. The data of the practice phase were analyzed with the factor Block, while the data of the test phase were analyzed with the factor Sequence. Greenhouse-Geisser epsilon correction was applied whenever appropriate. We additionally reported effect sizes (η_p^2), which can be used to compare effects across comparable experimental designs (Lakens, 2013). All statistical analyses were performed with IBM SPSS 25 (IBM Corporation).

2.6. Electrophysiological preprocessing

Analyses of the electrophysiological data during the practice phase were performed offline with Brain Vision Analyzer software (version 2.1.2.327). Relevant segments indicating the start of the trials including the stimulus presentation, the subsequent MP phase, and the final ME/MI/NoGo phase were selected (from −500 to 8000 ms). ME trials with erroneous responses were not excluded to avoid additional artificial differences between ME, MP, and MI (e.g., see Van Rullen, 2011). EEG data were first visually inspected to correct for major artefacts like flat lines, or major long-lasting distortions in the EEG. After application of a baseline from −100 to 0 ms, segments were checked for very large artefacts (min/max: ±500 μV, low activity: 0.1 μV for 100 ms). Next, Independent Component Analysis was carried out to remove components that appeared to have a non-cortical origin. On average 9.3 components (SD 6.3) out of 126 components were excluded. After resetting the baseline, the EEG data were filtered (TC = 5.0 s; lowpass filter 30 Hz; 50 Hz notch filter), while EMG was filtered with a bandpass filter of 20–50 Hz. After application of a new baseline from −100 to 0 ms, the EEG was checked for residual artefacts (min/max: ±150 μV). EMG activity was rectified, and markers were set at moments when EMG and horizontal EOG activity overstepped individually determined criterion values (~60–80 μV).

2.7. Analysis of the EEG data

After preprocessing the EEG data, analyses were performed on data acquired in the practice phase. For each of four conditions (motor preparation of to be executed response sequences [MPe], motor preparation of to be imagined response sequences [MPi], motor imagery of the response sequence [MI], and motor execution of the response sequence [ME]) data was extracted from −500 to 1500 ms relative to the start of the MP phase (offset of the 5th response cue), MI phase (onset of the blue fixation cross), and ME phase (onset of the green fixation cross). We also determined a baseline interval [BASE] from −500 to 1000 ms relative to trial onset (i.e., when the beep and grey squares was presented). Wavelet analyses were performed on the raw EEG data. A complex Morlet wavelet ($c = 5$) was chosen with Gabor normalization. Power (in μV^2) was extracted from the following frequency bands: θ_1 (theta-1; 3.2–4.8 Hz), θ_2 (theta-2, 4.2–6.3 Hz), θ_3 (theta-3, 5.5–8.2 Hz), α_1 (alpha/mu-1, 7.2–10.7 Hz), α_2 (alpha/mu-2, 9.4–14.0 Hz), β_1 (beta-1, 12.2–18.4 Hz), and β_2 (beta-2, 16.0–24.0 Hz). These bands were determined on the basis of a logarithmic separation applied in previous papers (see Van der Lubbe and Utzerath, 2013; Van der Lubbe et al., 2014, 2019).

Averages were computed across trials per individual for each condition and each frequency band. Conditions were compared for 100 ms time windows from 0 to 1200 ms. The average power in the time interval from −300 to −100 ms from BASE, so relative to the start of motor preparation for the trials requiring motor execution (for MPe and ME) or the same time interval relative to the start of motor preparation for the trials requiring motor imagery (for MPi and MI) was taken as baseline. These baselines were used to determine the percentages of increase (ERS) or decrease in power (ERD). For the statistical analyses, we focused on the following 35 electrodes as they overlay nearly all relevant brain areas: F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, PO9, O1, Oz, O2, PO10. We performed separate analyses for each of the theta bands (θ_1, θ_2, θ_3), the alpha bands (α_1, α_2) and the beta bands (β_1, β_2). In line with previous studies that employed a mass univariate

[3] The acquired EEG and behavioral data has been archived and made freely available at DANS (Data Archiving and Networking Services) through the following link: https://doi.org/10.17026/dans-xvr-ngsj.

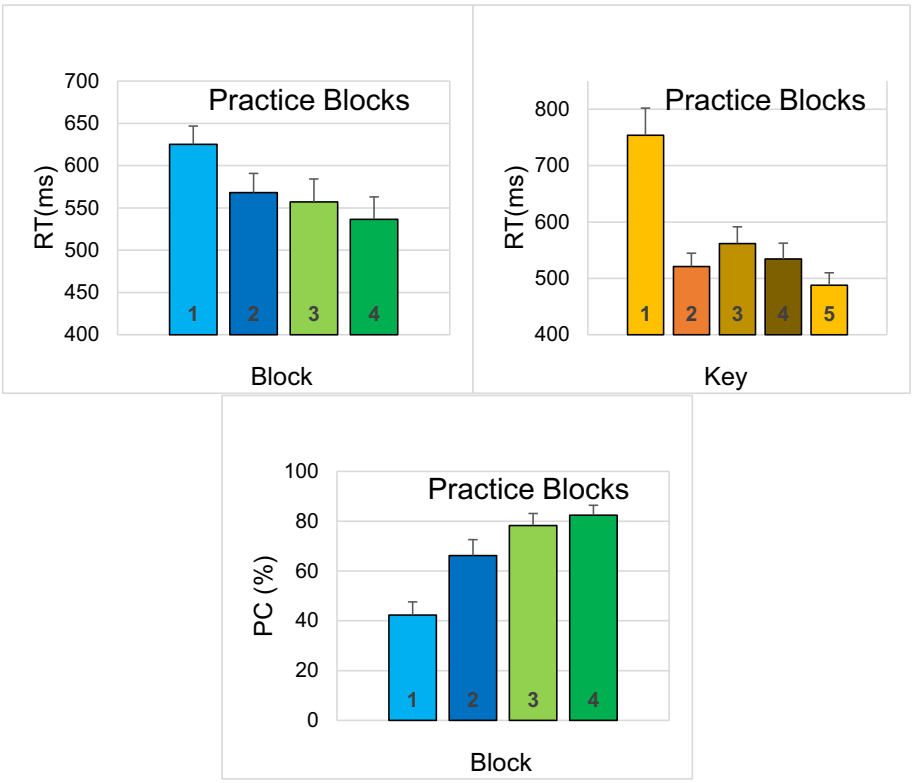

Fig. 2. Mean reaction times (RT) and proportions of correct responses (PC) as a function of Block and Key in the practice phase. The displayed vertical lines on top of the rectangles represent standard error bars.

approach, we employed a criterion of significance for two consecutive time intervals to avoid Type I errors (e.g., see Van der Lubbe et al., 2014, 2019). This approach implies here 35 (electrodes) * 7 (bands) * 4 tests per time window to determine an effect of Condition (MPe/MPi/ME/MI), Hand (left hand [LH]/ right hand [RH]), an interaction between Hand and Condition, and a deviation from power observed in the baseline interval (the intercept). Consequently, the critical *p*-value for two successive time windows was estimated at 0.002 ($p_{crit} < \sqrt{(0.05 / ([\text{nr. of time windows-1}] * [\text{nr. of electrodes}] * [\text{nr. of bands}] * [\text{nr. of tests}]))} < \sqrt{(0.05 / (11 * 35 * 7 * 4))} < 0.00215$). In the case of an effect of condition for two successive time windows, contrast analyses were carried out to clarify the origin of the observed effects. In that case a new critical *p*-value was assessed at 0.05/3 = 0.016, as three comparisons (MPe vs. MPi, MPi vs. MI, MI vs. ME) were made. In other respects, the statistical approach was comparable with the approach employed for our behavioral measures.

3. Results

3.1. Behavioral data

Mean RTs and PCs for the practice phase are displayed in Fig. 2. ANOVAs on RT with the factors Block and Key revealed a main effect of Block ($F(3,39) = 11.5$, $p < 0.001$, $\varepsilon = 0.55$, $\eta_p^2 = 0.47$) and a main effect of Key ($F(4,52) = 17.7$, $p < 0.001$, $\varepsilon = 0.34$, $\eta_p^2 = 0.58$), but no interaction between Block and Key. Contrast analyses indicated that the effect of Block can be described as a linear decrease in RT over time ($F(1,13) = 15.9$, $p = 0.002$, $\eta_p^2 = 0.55$).[4]

Analyses of the arcsine-transformed PCs for the practice phase revealed a main effect of Block ($F(3,39) = 33.2$, $p < 0.001$, $\eta_p^2 = 0.72$). Contrast analyses indicated that the effect of Block can be described as a linear ($F(1,13) = 95.4$, $p < 0.001$, $\eta_p^2 = 0.88$) and a quadratic increase in the proportion of correctly executed sequences ($F(1,13) = 10.0$, $p = 0.007$, $\eta_p^2 = 0.44$). Inspection of Fig. 2 (not-transformed data) shows an improvement in accuracy of about 24% from the first to the second block (block 1: 42.3 [SE: 5.3] %; block 2: 66.2 [6.4] %), a smaller improvement of about 12% from the second to the third block (block 3: 78.3 [4.8] %), and an even smaller improvement of 4% from the third to the fourth block (block 4: 82.4 [4.0] %).

Behavioral data of the test phase are displayed in Fig. 3. The analysis of RT revealed main effects of Sequence ($F(2,26) = 9.4$, $p = 0.001$, $\eta_p^2 = 0.42$) and Key ($F(4,52) = 18.1$, $p < 0.001$, $\varepsilon = 0.44$, $\eta_p^2 = 0.58$). Contrasts analyses revealed that RTs were longer for Unfamiliar sequences (577 [20] ms) than for Familiar ME sequences (489 [21] ms; $F(1,13) = 19.9$, $p = 0.001$, $\eta_p^2 = 0.61$), and also longer for Familiar MI sequences (532 [25] ms) than for Familiar ME sequences ($F(1,13) = 8.3$, $p = 0.013$, $\eta_p^2 =$

[4] Additional contrast analyses showed that the first key press was slower than the second key press ($F(1,13) = 19.1$, $p < 0.001$, $\eta_p^2 = 0.60$; key 1: 754 [SE: 48] ms; key 2: 521 [24] ms), the third key press was slower than the second key press ($F(1,13) = 6.4$, $p = 0.025$, $\eta_p^2 = 0.33$; key 3: 562 [30] ms), and the third key press also tended to be slower than the fourth key press ($F(1,13) = 4.5$, $p = 0.054$, $\eta_p^2 = 0.26$; key 4: 534 [28] ms), while the fourth key press was slower than the fifth key press ($F(1,13) = 13.5$, $p = 0.003$, $\eta_p^2 = 0.51$; key 5: 488 [22] ms).

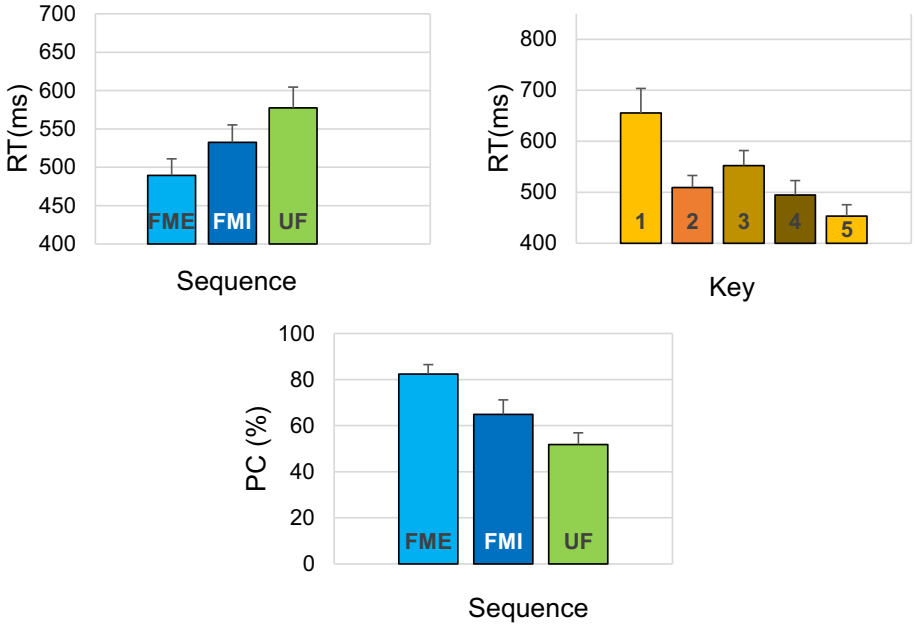

Fig. 3. Mean reaction times (RT) and proportions of correct responses (PC) as a function of Sequence (FME: Familiar Motor Execution; FMI: Familiar Motor Imagery; UF: Unfamiliar) and Key in the test phase. The displayed vertical lines on top of the rectangles represent standard error bars.

0.39). RTs tended to be shorter only for MI sequences than for Unfamiliar sequences ($F(1,13) = 3.2$, $p = 0.096$, $\eta_p^2 = 0.20$).[5]

Analyses of the arcsine-transformed PCs for the test phase revealed a major effect of Sequence ($F(2,26) = 13.6$, $p < 0.001$, $\eta_p^2 = 0.51$). The proportion of correctly produced sequences was larger for Familiar ME than for Familiar MI sequences ($F(1,13) = 10.3$, $p = 0.007$, $\eta_p^2 = 0.44$), tended to be larger for Familiar MI than for Unfamiliar sequences ($F(1,13) = 3.3$, $p = 0.095$, $\eta_p^2 = 0.20$), and was larger for Familiar ME than for Unfamiliar sequences ($F(1,13) = 32.0$, $p < 0.001$, $\eta_p^2 = 0.71$). This result is also visible before data transformation (Familiar ME: 82.4 [4.1] %; Familiar MI: 64.9 [6.3]; Unfamiliar: 51.8 [5.1]%; see Fig. 2).

3.2. ERS/ERD

The outcome of the analyses on the intercept, which demonstrates if there is an overall change in power as compared to the baseline, are reported as Supplementary results in Appendix A. These results are not crucial for addressing the issues indicated in the introduction.

3.2.1. Theta

3.2.1.1. Lower theta (θ_1). A frontal ERS (an increase in power relative to the baseline) was modulated by Condition (see Fig. 4), which was most pronounced at Fz from 400 to 500 ms ($F(3,39) = 36.9$, $p < 0.0001$, $\eta_p^2 = 0.74$). Contrast analyses showed no differences ($p = 0.28$) in ERS between the two preparation conditions (MPe: 10.6% [SE: 3.2] and MPi: 17.0% [5.1]), while a major increase ($p < 0.0001$) in ERS was observed in the MI condition (112.0% [12.7]), that was again smaller ($p < 0.0002$) in the ME condition (45.1% [8.0]).

Above centro-parietal sites we also observed an effect of Condition, being most significant at CP4 from 300 to 400 ms ($F(3,39) = 43.2$, $p < 0.0001$, $\eta_p^2 = 0.77$; see Fig. 5). No ERS was visible in both preparation conditions (MPe: −1.3% [4.0] and MPi: 2.7% [5.4]), while a major increase in power ($p < 0.0002$) was observed in the MI condition (58.2% [9.7]), which tended to be larger ($p = 0.019$) in the ME condition (83.8% [9.7]). Above right occipital sites we also observed an effect of Condition that was most significant at PO8 from 400 to 500 ms ($F(3,39) = 24.3$, $p < 0.0001$, $\eta_p^2 = 0.65$; see Fig. 5). No ERS was visible in the preparation conditions (MPe: 3.1% [4.5] and MPi: 5.8% [3.9]), while a major increase in power ($p < 0.0001$) was observed in the MI condition (60.6% [9.6]) and relative to the MI condition a decrease in ERS ($p < 0.0015$) was present in the ME condition (29.9% [8.3]).

A main effect of Hand (not displayed) was present above left posterior sites from 400 to 700 ms, most significant at PO3 from 500 to 600 ms ($F(1,13) = 30.1$, $p < 0.0002$, $\eta_p^2 = 0.70$), which reflected ERS for left hand trials and no such effect for right hand trials (LH: 6.6% [3.7], RH: 0.5% [3.2]). From 1000 to 1200 ms, a main effect of Hand was present above central and centro-parietal sites that was most significant at C4 from 1100 to 1200 ms ($F(1,13) = 29.4$, $p < 0.0002$, $\eta_p^2 = 0.69$). The latter effect reflected a decrease in power relative to the baseline (ERD) that was present for right hand trials and small (or absent) for left hand trials (LH: −3.7% [2.4], RH: −14.9% [1.7]). No interactions were observed between Hand and Condition that satisfied our significance criteria.

3.2.1.2. Middle theta (θ_2). Major conditional differences were observed (not displayed, but results were highly comparable to those presented in Fig. 4), being most significant from 400 to 500 ms above FCz ($F(3,39) = 26.3$, $p < 0.0001$, $\eta_p^2 = 0.67$). The ERS was comparable in both preparation conditions (MPe: 20.7% [8.4] and MPi: 28.9% [13.0]), while a major increase ($p < 0.0001$) in ERS was observed in the MI condition (132.3% [18.9]), that was smaller ($p < 0.001$) in the ME condition (75.7% [12.0]). Conditional differences were also present above centro-parietal, parietal, and occipito-parietal sites, being most significant from 300 to 400 ms at CPz ($F(3,39) = 19.6$, $p < 0.0001$, $\eta_p^2 = 0.60$). Again, the ERS in both preparation conditions was small and comparable (MPe: 13.5% [3.2] and MPi: 7.6% [2.9]), clearly larger ($p < 0.0003$) in the MI condition (67.1% [13.2]), but now comparable in the ME condition (57.1% [10.2]). Finally, major conditional differences were also present above occipital sites, being most significant at PO10 from 400 to 500 ms ($F(3,39) = 18.2$, $p < 0.0001$, $\eta_p^2 = 0.58$). The ERS in both preparation

[5] Contrast analyses additionally revealed that the first key press was slower than the second key press ($F(1,13) = 19.5$, $p = 0.001$, $\eta_p^2 = 0.60$; key 1: 655 [28] ms; key 2: 509 [22] ms), the second key press was faster than the third key press ($F(1,13) = 5.4$, $p = 0.037$, $\eta_p^2 = 0.29$; key 3: 552 [20] ms), the third key press was slower than the fourth key press ($F(1,13) = 6.4$, $p = 0.025$, $\eta_p^2 = 0.33$; key 4: 495 [28] ms), and the fourth key press was slower than the fifth key press ($F(1,13) = 5.3$, $p = 0.039$, $\eta_p^2 = 0.29$; key 5: 453 [25] ms).

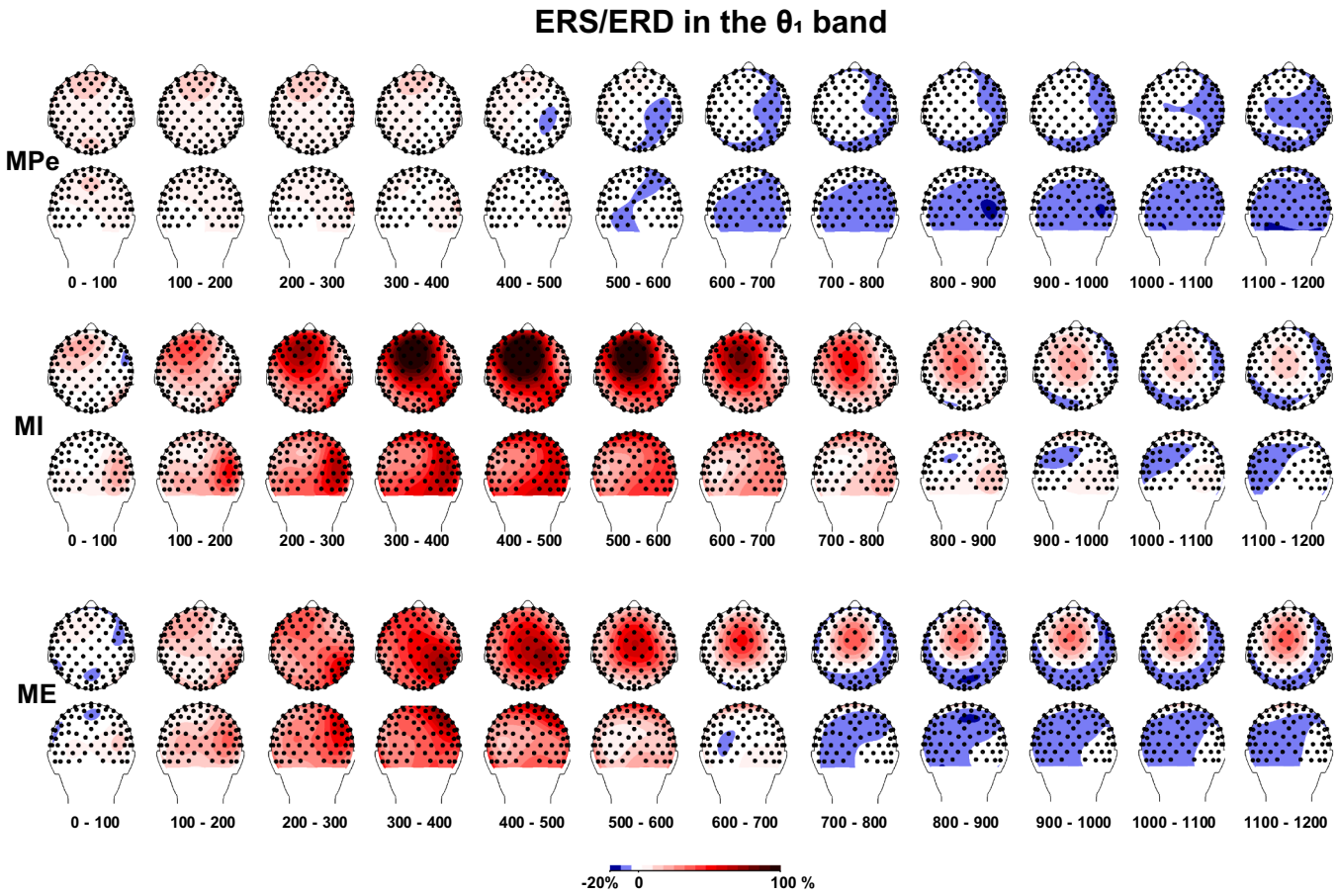

Fig. 4. Topographies (based on interpolation of spherical splines, 4th order) of event-related synchronization (ERS, red) and desynchronization (ERD, blue) in percentages during motor preparation for to be executed sequences (MPe), during motor imagery (MI), and during motor execution (ME) in the lower theta (θ_1) band. The data during motor preparation of to be imagined sequences (MPi) was very similar to the MPe data, and to avoid redundancy we decided not to display them. Percentage of increase (red) or decrease (blue) of power in 100 ms time intervals was determined relative to a baseline period (−300 to −100 ms before the start of motor preparation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

conditions was small and comparable (MPe: 13.2% [5.8] and MPi: 9.4% [6.1]), clearly larger ($p < 0.0001$) in the MI condition (66.9% [10.7]), and comparable with MI in the ME condition (50.3% [8.9]).

An effect of Hand was present at CP4 from 900 to 1200 ms, being most significant from 1000 to 1100 ms ($F(1,13) = 19.0$, $p < 0.0008$, $\eta_p^2 = 0.59$). An ERS was observed for left hand movements (LH: 6.6% [4.4]) while an ERD was observed for right hand movements (RH: −6.6% [2.2]). No interactions were observed between Hand and Condition that met our significance criteria.

3.2.1.3. Upper theta (θ_3). Conditional differences (see Fig. 6) were observed above fronto-central and central sites, being most significant at Cz from 300 to 400 ms ($F(3,39) = 28.2$, $p < 0.0001$, $\eta_p^2 = 0.68$). No ERS was present in both preparation conditions (MPe: −1.8% [5.5] and MPi: 0.4% [5.7]), while a major increase ($p < 0.0002$) in power was observed in the MI condition (69.1% [10.7]), that tended to be smaller ($p = 0.043$) in the ME condition (55.3% [7.2]).

Differences were simultaneously observed above parietal, and especially left and right occipital sites (PO9 and PO10; $F(3,39) > 19.5$, $p < 0.0001$, $\eta_p^2 = 0.60$). At PO9 no ERS was present in the preparation conditions (MPe: −0.5% [7.2] and MPi: −2.5% [3.8]), a clear ERS ($p < 0.0002$) was present in the MI condition (42.4% [7.0]), and this increase in power tended to be larger ($p < 0.027$) in the ME condition (65.8% [12.7]). At PO10, no ERS was present in the preparation conditions (MPe: 4.5% [6.6] and MPi: −4.3% [3.2]), a clear ERS ($p < 0.0001$) was present in the MI condition (50.3% [7.7]) that was comparable ($p = 0.193$) in the ME condition (61.9% [11.3]). Slightly later, conditional differences were present at F7, being most significant from 600 to 700 ms ($F(3,39) = 10.4$, $p < 0.0007$, $\eta_p^2 = 0.44$). Now, ERS was present in both preparation conditions (MPe: 17.7% [5.7] and MPi: 21.2% [6.7]), it tended to be smaller (but $p = 0.149$) in the MI condition (7.8% [5.7]), and turned into an ERD ($p < 0.0004$) in the ME condition (−15.0% [3.5]). No hand-related effects were observed, and no interactions were observed between Hand and Condition that satisfied our significance criteria.

3.2.1.4. Summary and comparison of the effects observed in the theta bands (θ_1, θ_2, θ_3). Results for the θ_1 and θ_2 bands showed a very strong ERS above frontal/fronto-central sites (Fz, FCz, most significant from ~200 to 600 ms) that was most pronounced (and significant) in the MI condition, clearly reduced in the ME condition, and small in the MP conditions. Simultaneously, a centro-parietal ERS was observed that was most pronounced above the right hemisphere (P4 and CP4) that again differed between conditions. This ERS was relatively small (θ_2) or absent (θ_1) in the case of MP, while it was much larger in the case of MI and ME. Furthermore, for the θ_1 band the ERS at CP4 was larger on ME than on MI trials. For the θ_1 band, a posterior ERS at PO8 differed between conditions, which was largest from 400 to 500 ms in the MI condition, reduced in the ME condition, and absent in the case of MP. A comparable effect, now most pronounced at PO10 was observed in the θ_2 band, although in that case, no difference was observed between MI and ME. Quite comparable effects were observed at the PO9 and PO10 sites for

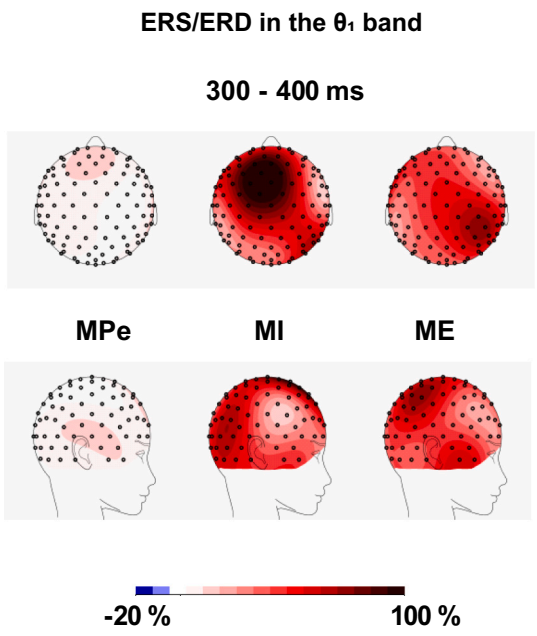

Fig. 5. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the lower theta (θ_1) band from 300 to 400 ms (for more details see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the θ_3 band being most pronounced from 300 to 400 ms. No ERS seemed present in the case of MP, but an ERS was present in the MI condition that tended to be larger in the ME condition (at PO9). A general posterior ERD was observed in later time intervals (~900 to 1200 ms). Results for the θ_3 band suggest that the early frontal ERS, which was largest in the MI condition, became later (600–700 ms) larger in the MP condition and turned into an ERD in the ME condition. Hand-related effects were observed above left posterior (θ_1, ERS for left hand trials from 400 to 700 ms) and right centro-parietal (θ_1 and θ_2, ERD for right hand trials ~1000–1200 ms) sites.

3.2.2. Alpha/mu

3.2.2.1. Lower alpha (α_1). Conditional differences (see Fig. 7) were observed above fronto-central and central sites that were most significant at Cz from 400 to 500 ms ($F(3,39) = 22.7$, $p < 0.0001$, $\eta_p^2 = 0.64$). ERDs were present in both preparation conditions (MPe: −25.4% [4.7] and MPi: −23.2% [4.0]). No such effect ($p < 0.0002$), but an ERS was present in the MI condition (11.9% [8.9]), while again an ERD was present ($p < 0.0003$) in the ME condition (−15.6% [6.7]). At the end of the interval, conditional differences were observed, being most significant at O2 from 1100 to 1200 ms ($F(3,39) = 9.3$, $p < 0.001$, $\eta_p^2 = 0.42$). Again ERDs were present in both preparation conditions (MPe: −27.2% [5.6] and MPi: −23.4% [4.9]), absent ($p < 0.001$) in the case of MI (4.8% [7.3]), and again present ($p < 0.014$) in the case of ME (−21.3% [8.7]).

An effect of Hand was present at PO8 (not displayed) being most significant from 800 to 900 ms ($F(1,13) = 17.1$, $p < 0.002$, $\eta_p^2 = 0.57$). The ERD was larger for left hand than for right hand trials (LH: −29.8% [3.8] and RH: −16.0% [5.2]). No interactions were observed between Hand and Condition that met our significance criterion.

3.2.2.2. Upper alpha (α_2). Conditional differences were present at Fz (see Fig. 8), being most significant from 500 to 600 ms ($F(3,39) = 7.9$, $p < 0.0003$, $\eta_p^2 = 0.38$). No differences were observed between the two preparation conditions (MPe: −20.6% [5.9] and MPi: −21.6% [5.1]), and between MP and MI (−12.8% [6.8]), but for the comparison between MI and ME, the decrease was larger ($p < 0.0004$) in the ME condition (−36.1% [6.2]). Above occipital sites, we also observed conditional differences from 700 to 1000 ms that were most significant at O1 from 900 to 1000 ms ($F(3,39) = 13.0$, $p < 0.0007$, $\eta_p^2 = 0.50$).

In both preparation conditions, there was a comparable reduction in power (MPe: −36.0% [3.8] and MPi: −31.7% [4.0]), but not ($p < 0.0004$) in the MI condition (0.9% [8.8]), while again a clear reduction in power ($p < 0.008$) was observed in the ME condition (−31.9% [6.7]). An early effect of Hand (not displayed) was present above right parietal and centro-parietal areas, being most significant from 200 to 300 ms at CP4 ($F(1,13) = 30.1$, $p < 0.0002$, $\eta_p^2 = 0.70$). A stronger ERD was observed for left hand as compared to right hand trials (LH: −29.4% [6.3] and RH: −15.5% [6.0]). An effect of Hand was also observed later above left posterior sites from 700 to 1000 ms, that was most significant at O1 from 800 to 900 ms ($F(1,13) = 27.3$, $p < 0.0002$, $\eta_p^2 = 0.68$). Here we observed a stronger ERD for right hand as compared to left hand trials (LH: −16.4% [5.4] and RH: −35.9% [4.3]). No interactions were observed between Hand and Condition that met our significance criterion.

3.2.2.3. Summary and comparison of the effects observed in the alpha/mu bands (α_1, α_2). Conditional differences above frontal and central areas seem to be clearer in the lower than in the upper alpha band from 400 to 500 ms. Here we observed comparable (ERD) results in the case of MP and ME, while ERS seems present in the case of MI. Above occipital sites comparable results were observed in both bands at the end of the examined interval (900–1000 ms), although effects seem a bit more pronounced in the upper alpha band. Clear ERDs were present in the case of MP and ME, but not in the case of MI.

An early ERD above right parietal areas (200–300 ms) was observed in the upper alpha band that was larger for left hand trials. A later ERD (800–900 ms) in the lower alpha band above right occipital areas was also larger for left hand than for right hand trials, while in the higher alpha band the ERD above left occipital areas was larger for right hand as compared to left hand trials.

3.2.3. Beta

3.2.3.1. Lower beta (β_1). Conditional differences (see Fig. 9) were observed above left centro-parietal areas (CP3) from 400 to 600 ms, being most significant from 500 to 600 ms ($F(3,39) = 7.5$, $p < 0.0005$, $\eta_p^2 = 0.37$). No differences were observed between the two preparation conditions (MPe: −39.8% [4.0] and MPi: −35.6% [3.9]), and between MP and MI (−37.0% [4.0]), but for the comparison between MI and ME, the decrease was larger ($p < 0.002$) in the case of ME (−49.4% [3.7]). We additionally observed conditional differences above left occipital areas from 400 to 600 ms, being most significant at PO9 from 400 to 500 ms ($F(3,39) = 11.6$, $p < 0.0005$, $\eta_p^2 = 0.47$). No differences were observed between the two preparation conditions (MPe: −21.5% [4.0] and MPi: −18.8% [3.4]), while a further decrease was observed in the MI condition ($p < 0.0001$) that was not different from the decrease in the ME condition (MI: −34.5% [3.7] and ME: −38.0% [4.0]).

An effect of Hand was observed above right parietal areas (P4) from 300 to 500 ms, being most significant from 300 to 400 ms ($F(1,13) = 26.2$, $p < 0.0002$, $\eta_p^2 = 0.67$), which reflected a stronger reduction in power for left hand than for right hand sequences (LH: −40.1% [3.4] and RH: −32.7% [4.1]). Slightly later, we found an effect of Hand at PO8 from 600 to 800 ms, being most significant from 700 to 800 ms ($F(1,13) = 26.2$, $p < 0.0002$, $\eta_p^2 = 0.67$). Again, an ERD was present for left hand trials but not for right hand trials (LH: −19.2% [3.9] and RH: 2.2% [5.8]). No interactions were observed between Hand and Condition that met our significance criterion.

3.2.3.2. Upper beta (β_2). Conditional differences (see Fig. 10) were

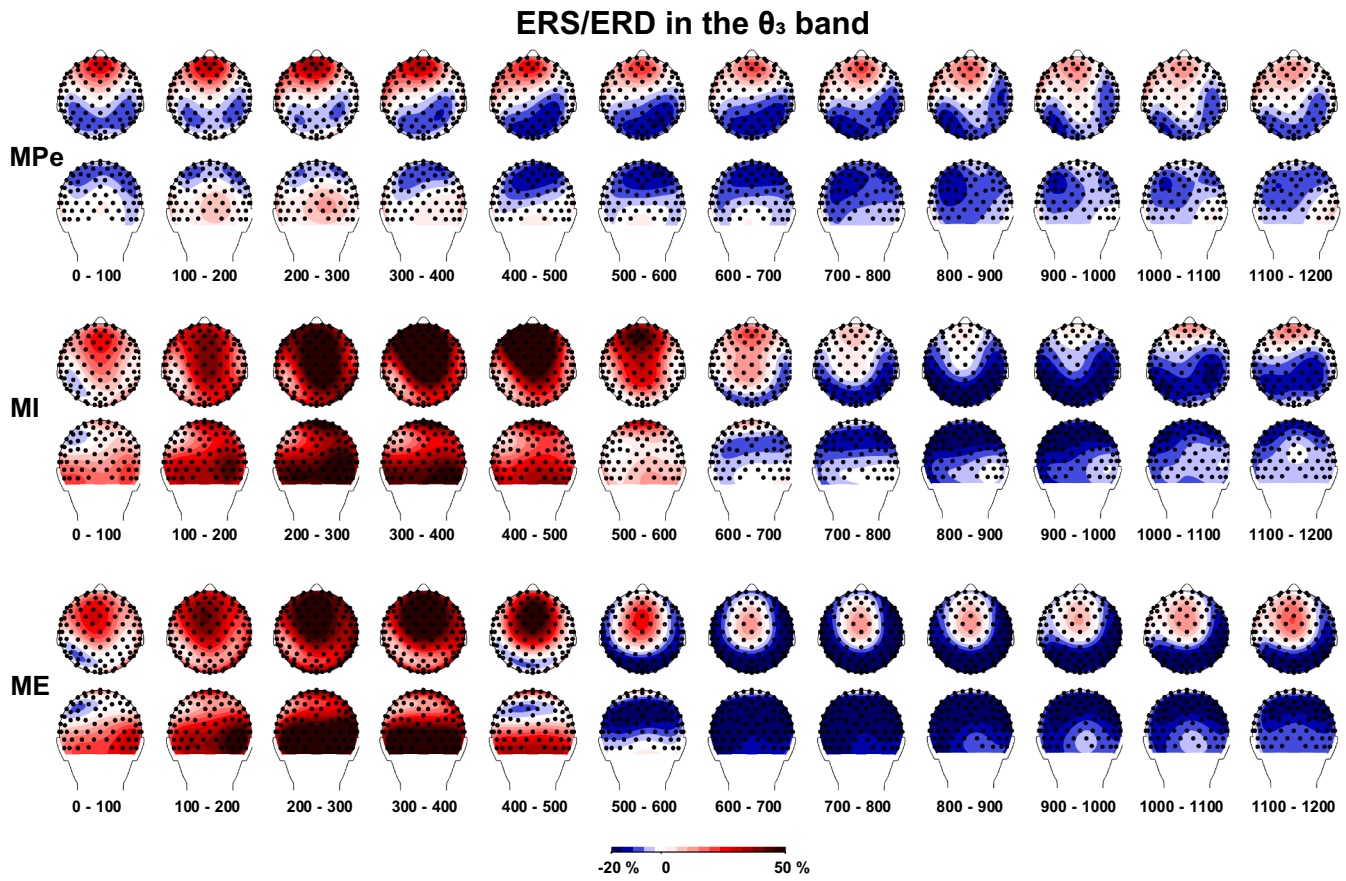

Fig. 6. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the upper theta (θ_3) band (for details, see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

present at Cz from 900 to 1100 ms, being most significant from 900 to 1000 ms ($F(3,39) = 7.1$, $p < 0.001$, $\eta_p^2 = 0.35$). Highly comparable reductions in power were observed in the case of motor preparation (MPe: −27.3% [3.5] and MPi: −27.8% [2.6]) and also MI (−28.7% [4.2]), while a stronger ERD ($p < 0.007$) was observed in the case of ME (−39.2% [3.0]). Conditional differences at CP4 were observed from 500 to 700 ms and 1000 to 1200 ms. The effect of Condition was most significant from 600 to 700 ms ($F(3,39) = 8.6$, $p < 0.0002$, $\eta_p^2 = 0.40$). Again, comparable reductions in power were observed in the preparation conditions (MPe: −36.1% [2.6] and MPi: −36.1% [3.4]) while a trend ($p = 0.055$) to a smaller ERD was present in the MI condition (−28.5% [4.4]), but compared to that condition, a stronger ERD was present in the ME condition (−44.5% [3.4]). Finally, conditional differences were present at Pz from 900 to 1200 ms, being most significant from 1100 to 1200 ms ($F(3,39) = 7.5$, $p < 0.0005$, $\eta_p^2 = 0.37$). A tendency to a smaller ERD seems present ($p = 0.041$) in one of the motor preparation conditions (MPe: −24.1% [3.9] and MPi: −30.5% [3.4]), no difference was found between the latter condition and MI (−26.7% [4.8]), while a larger ERD was observed ($p < 0.003$) in the case of ME (−37.8% [3.8]). Neither an effect of Hand nor an interaction between Hand and Condition was observed that crossed the significance criterion for two successive time windows.

3.2.3.3. Summary and comparison of the effects observed in the beta bands (β_1, β_2). Both in the lower and upper beta bands major reductions in power were observed across the whole scalp. The largest reductions in power were observed above central and centro-parietal sites from 400 to 500 ms. This centro-parietal reduction in beta power was most pronounced in the case of ME. Above posterior areas reductions in beta power (β_1) were observed that were comparable for ME and MI, while smaller ERDs were observed in the case of MP.

4. Discussion

The general idea that the mental simulation of actions by means of MI is beneficial for both patients suffering from motor disorders and for experts in sports or music appears to be well accepted, although behavioral support for the improvement after MI relative to a control condition may not always be that clear (e.g., see below, but see Sheahan et al., 2018). However, what precisely happens during mental simulation of actions and to what extent it differs from real execution (ME) or from just preparing the action (MP) remains a matter of debate. The recent meta-analyses of fMRI and PET data in the study of Hardwick et al. (2018) indicated that the support for the functional equivalence model (Decety, 1996; Jeannerod, 2001, 2006) may have been overstated as there were some indications that activity of DLPFC may be larger in the case of MI, which accords with the motor-cognitive model (Glover and Baran, 2017; Glover et al., 2020). We argued in our introduction that the use of more complex tasks like the Go/NoGo version of the DSP paradigm with different sequences of real or imagined finger movements in the current study might enlarge possible differences between MI and ME. The use of this paradigm has the additional advantage that it allows for a comparison between MP and MI. We focused on ERS/ERD of EEG activity in not only the alpha and beta bands, but also the theta band, as the latter band may be more informative about changes in global inhibitory interactions.

Results for the lower and middle theta bands (θ_1 and θ_2) indicated that a specific process reflected in an anterior ERS (i.e., an increase in

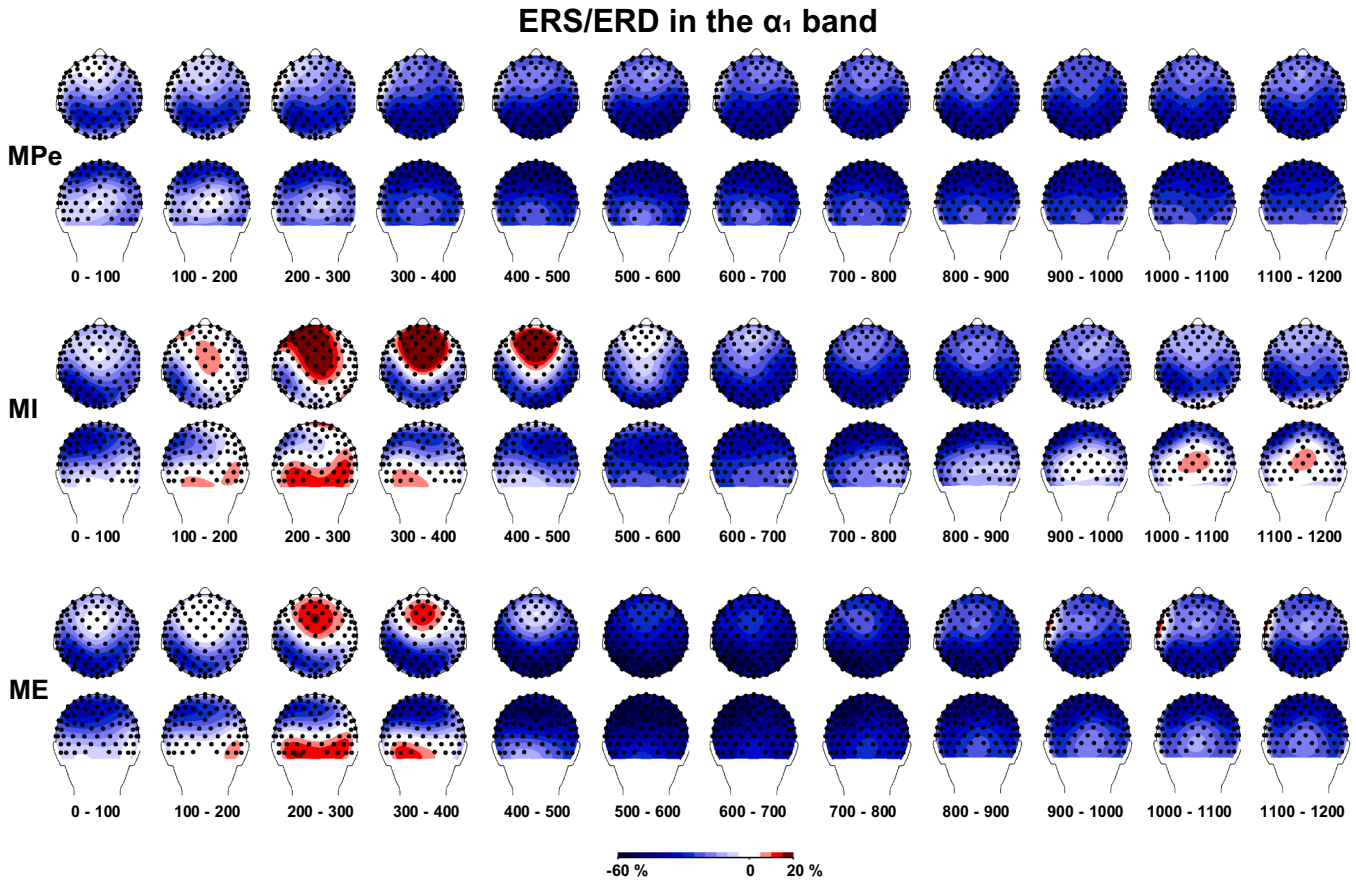

Fig. 7. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the lower alpha (α_1) band (for details, see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

power relative to baseline) was more active during MI, less active in the case of ME, and to a much smaller extent active in the case of MP. The topography of the observed ERS suggests a frontal or fronto-central origin. As the ERS concerns the theta band it may be argued that this increase in power relates to global inhibitory interactions (Buzsáki, 2006). These observations may point to increased activity of DLPFC (in line with the motor-cognitive model) but may also relate to the extra involvement of inhibition related to pre-SMA (Angelini et al., 2015) or SMA-proper (Kasess et al., 2008). Additional analyses of our data with the beamformer source technique could provide more clarity about the source of this effect, although a combined fMRI-EEG approach with the current paradigm would be most convincing. The increase in frontal theta in the case of ME and especially MI may very well be related to the effects on theta observed in the Sternberg task, which may not only reflect an increase in memory load but also increased effort (e.g., see Zakrzewska and Brzezicka, 2014). The still relative large ERS in the case of ME as compared to MP may more easily be interpreted as increased effort than as an increase in the different types of inhibition considered in our introduction. First, pro-active inhibition would especially be involved during MP, and therefore provides no explanation for the clear ERS in the case of ME relative to MP. Secondly, reactive inhibition should not occur in the case of ME, and thirdly, surround inhibition is more likely present within sensorimotor areas (Aoyama et al., 2016). Based on these considerations, we think that our observed anterior ERS in the lower and middle theta bands better fits with the motor-cognitive model.

Another observation in the theta band was a strong ERS above right parietal sites. For the θ_1 band the ERS was larger on motor execution than on motor imagery trials while it was small in the case of MP. Again, one might think of global inhibitory interactions and given its topography and its maximum during ME, this might relate to the anticipation of sensory consequences of the action effects (Ridderinkhof and Brass, 2015; Wolpert and Flanagan, 2001; Davidson and Wolpert, 2005) resulting in reduced sensitivity for tactile stimuli, which is not only present during ME but also during MI (Kilteni et al., 2018). It is, however, not directly clear why this effect would be maximal above right-parietal brain areas (but see below).

With regards to the lower and upper alpha/mu bands (α_1 and α_2), overall reductions in power (ERD) were observed, being most pronounced above sensorimotor areas and especially right parietal cortex. Reductions in alpha power, especially the upper alpha band, were also observed above occipital areas. These results confirm the idea that sensorimotor areas are involved in the case of ME, MP and MI. The reduction above right parietal areas may be related with increased involvement of spatial attention that may link different modalities (visual, somatosensory, hand-motor; e.g., see Verwey et al., 2020), while the reduction in the alpha power above occipital areas can be interpreted as the more specific involvement of visuospatial attention (Klimesch, 1999; Deiber et al., 2012). Some differences were observed between MI, ME, and MP. No ERD in the lower alpha/mu band was present above central areas in the case of MI, and also no posterior reduction was observed at the end of the examined interval. The latter findings suggest that motor-related activity was reduced in the case of MI, and also that the involvement of visual attention was less during MI than during ME and MP (see also Van der Lubbe et al., 2017). The absence of a posterior reduction in alpha power, which may be expected in the case of visual attention additionally corresponds with the idea that the participants in our tasks performed kinesthetic MI, and not visual

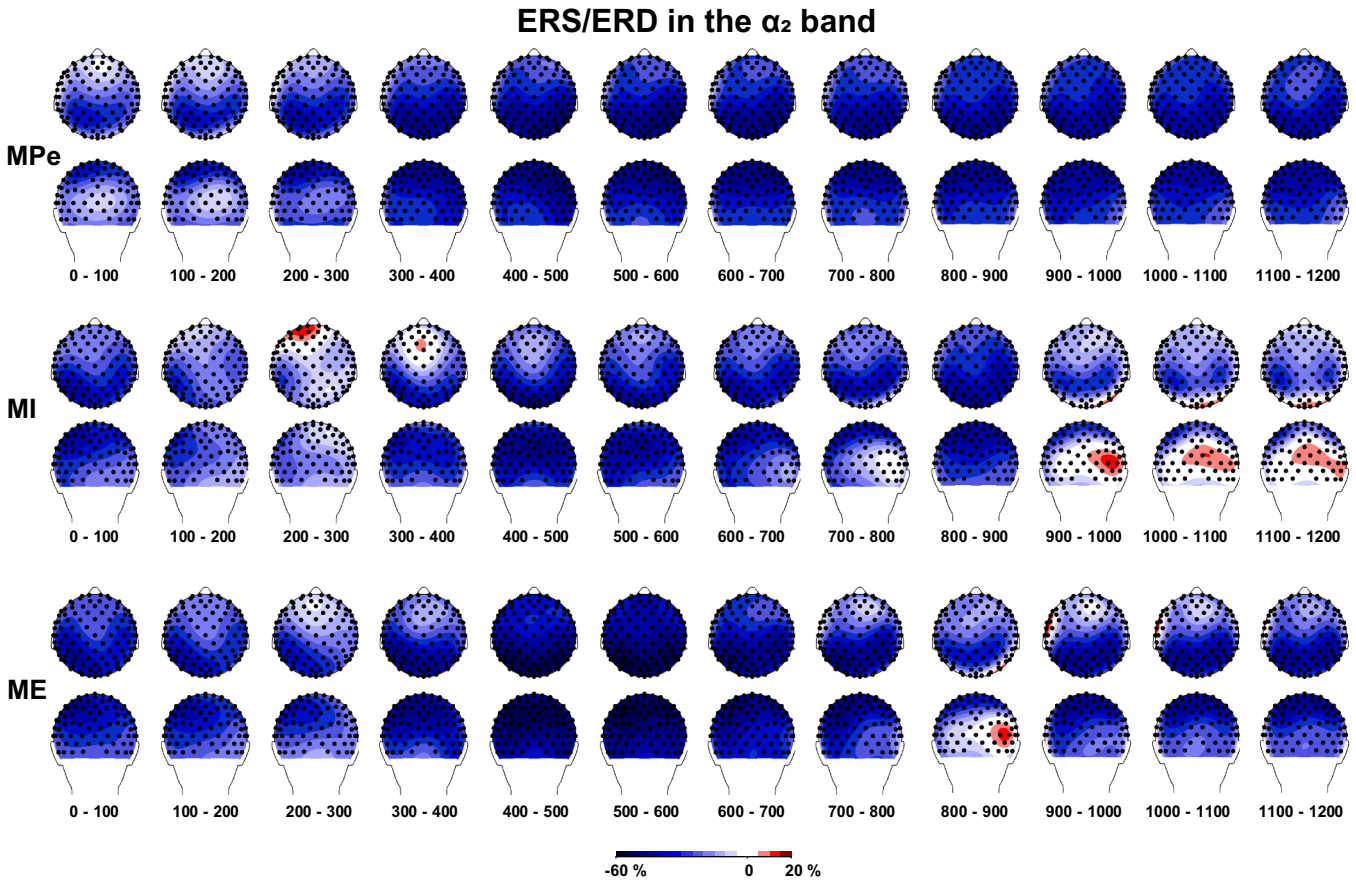

Fig. 8. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the upper alpha (α_2) band (for details, see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

imagery.

In the lower and upper beta bands (β_1 and β_2), a major reduction of power (ERD) was observed but strongest reductions were observed above the centro-parietal areas, which seems related to activity in sensorimotor areas. A comparison between conditions showed that the ERD was largest in the case of ME for both beta bands, while reductions in power were comparable for MP and MI. In the lower beta band, we additionally observed left posterior ERDs after about 400 ms that were larger for ME and MI than for MP. These findings seem in line with the idea that the reduction of power in the beta bands is more specifically related to motor activation (see Stolk et al., 2019).

Altogether the EEG results in our tasks seem to indicate that MI differs in several aspects from ME, which we interpret as 1) increased mental effort reflected in ERS in the lower and middle theta bands, which may originate from DLPFC, in line with the motor-cognitive model; 2) more involvement of visuospatial attention in the case of ME as compared to MI at the end of the relevant time interval; 3) increased activity of sensorimotor areas in the case of ME as compared to MI and MP. The first two interpretations do not accord with the functional equivalence model, while the third interpretation corresponds with the observations of Lacourse et al. (2005). Our observations additionally indicate that MI does not equal MP, as again, more effort and a reduction in visuospatial attention seem present in the case of MI. Nevertheless, there is also some overlap between MI and MP as in both cases reductions were present in the beta bands, which partially replicates the findings from Pfurtscheller and Neuper (1997). A possible reason why earlier studies did not reveal clear differences between ME and MI may be related to the more demanding task that we employed, which may boost effects, and our decision to focus on changes in the theta bands. The current Go/NoGo version of the DSP tasks requires multiple actions that have to be carried out sequentially. This implies an increase in required effort. Furthermore, quite some visually presented information has to be remembered during preparation, which suggests an increased load on visual working memory (see De Kleine and Van der Lubbe, 2011). Finally, proper execution of the task requires fine hand motor control that may benefit from the help of visuospatial attention. Thus, the functional equivalence model may hold under relatively easy task settings, but more demanding tasks reveal that MI does not equal ME, in line with the motor-cognitive model.

If we focus on our behavioral data, it also becomes clear that MI is not as efficient for learning as ME of a sequence of button presses. We observed that sequences that required MI only tended to be executed

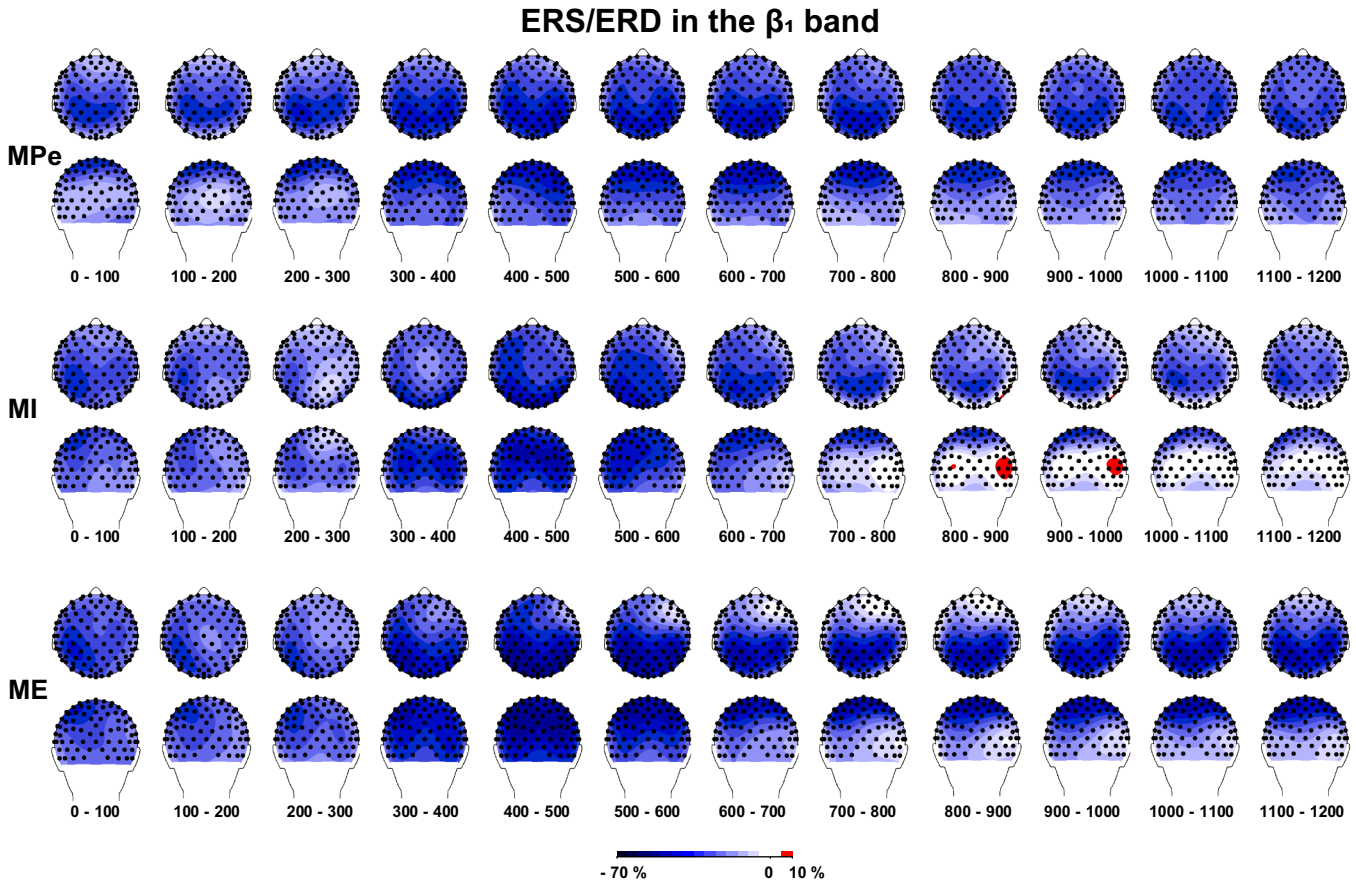

Fig. 9. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the lower beta (β_1) band for the 400–500 ms and the 500–600 ms time windows. Percentage of increase (red; not present) or decrease (blue) was determined relative to a baseline period (−300 to −100 ms before the start of motor preparation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

faster and more accurately than sequences that were not yet learned, whereas a clear benefit was observed for sequences that required ME. These findings correspond with our observations that a substantial amount of physical practice in combination with MI is needed to reach a comparable level as full physical practice (see Sobierajewicz et al., 2016). Thus, it should be realized that the use of MI to learn a certain movement sequence cannot substitute the learning by ME.

Partially inspired by the findings of Angelini et al. (2016), we also explored whether there were differences between MP of sequences that always had to be mentally simulated (MPi) and sequences that subsequently required button presses (MPe). No clear differences were observed. These findings, however, do not discredit the observations of Angelini et al. (2016) with regard to reduced activity of pre-SMA during MP preceding MI. In our study, participants may not have been aware that some sequences were never executed while some other sequences within the same block of trials never required motor imagery. As Angelini et al. (2016) employed a blocked design, it was in their experiment always clear when the movement to be prepared had subsequently to be executed or imagined.

Although we cannot fully exclude that the clear increase in frontal theta during MI reflects reactive inhibition, it seems quite relevant for future studies to incorporate a condition with a larger number of trials in which a prepared motor sequence explicitly has to be inhibited. By comparing results in this condition during inhibition with MI, more support can be obtained that MI implies increased effort and not an increase in reactive inhibition. Additionally, it may very well be the case that inhibition is also reflected in the delta band (~0.1–4 Hz). To examine this possibility, the length of the intervals during which MP, MI, and MI takes place needs to be enlarged to enable a proper estimation of power in this frequency band. Another relevant manipulation is varying the length of the sequence of the to be executed or imagined response sequence. If the observed effects in the theta band during MI and ME are related to an increase in memory load and/or increased effort then we may expect an influence of varying the sequence length on the magnitude of ERS, while such a manipulation seems unlikely to affect reactive inhibition.

In sum, on the basis of our findings in the theta bands (ERS) it can be argued that MI differs from ME due to the extra recruitment of frontal brain areas during MI that reflects increased effort. Furthermore, MI is clearly not identical to MP. Our results in the alpha band (ERD) suggest that the load on visuospatial attention is reduced in the case of MI relative to ME and MP, which supports the view that participants

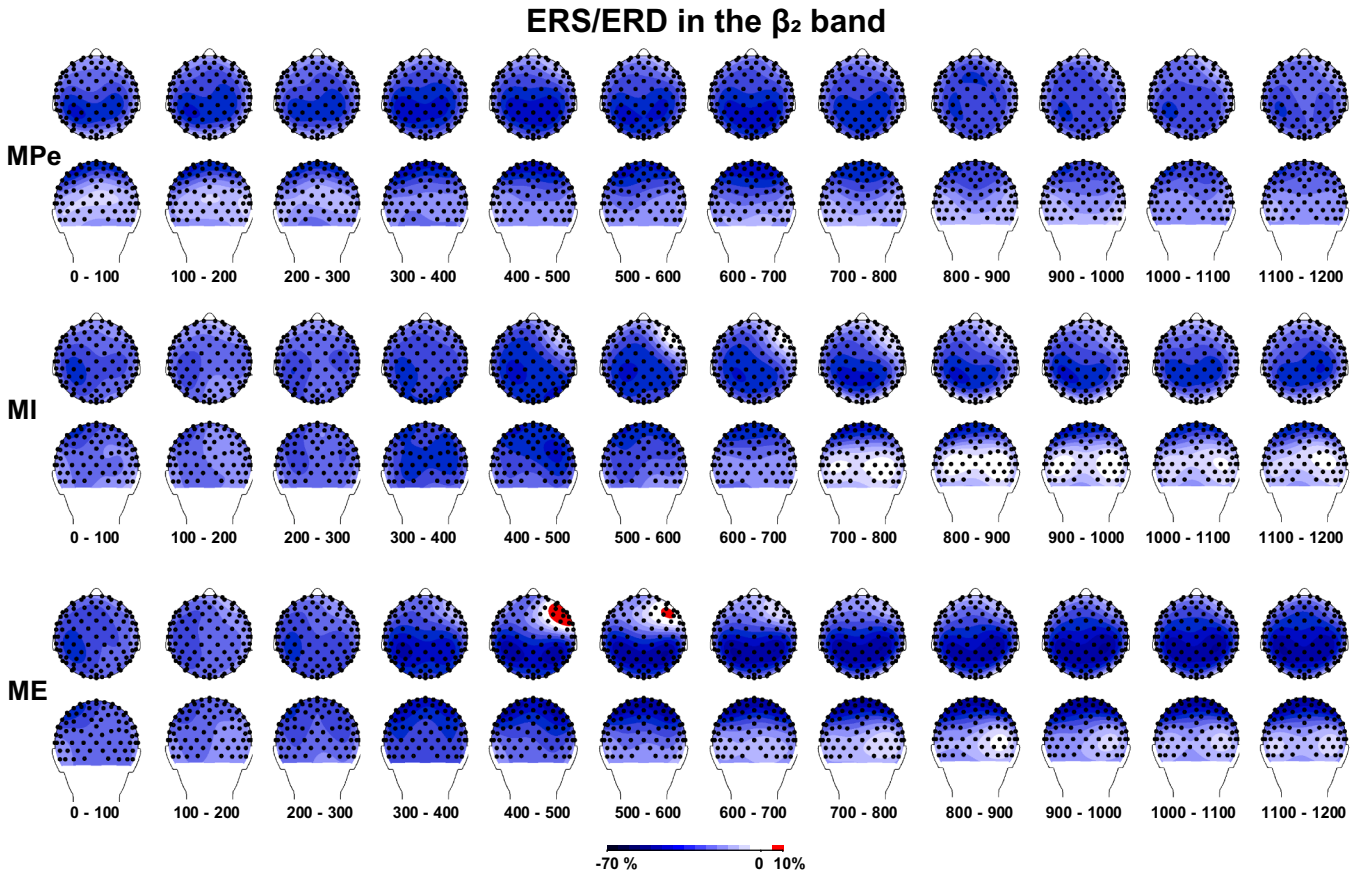

Fig. 10. Topographies of event-related synchronization (ERS, red) and desynchronization (ERD, blue) during motor preparation for to be executed sequences (MPe), motor imagery (MI) and motor execution (ME) in the upper beta (β_2) band for the 600–700 ms and the 900–1000 ms time windows. Percentage of increase (red; not present) or decrease (blue) was determined relative to a baseline period (−300 to −100 ms before the start of motor preparation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

employed kinesthetic MI in our study. Finally, our observations in the beta bands (ERD) are in line with the idea that this band is especially sensitive to ME. Altogether, our results seem to favor the motor-cognitive model.

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Appendix A. Supplementary ERD/ERS results

Lower theta (θ_1)

Analyses revealed an overall increase in power relative to the baseline (ERS) that initially (300–400 ms) was most significant at F7 (37.4% [3.9]; $F(1,13) = 91.7$, $p < 0.0001$, $\eta_p^2 = 0.88$), then (400–500 ms) at Fz (46.2% [4.6]; $F(1,13) = 100.5$, $p < 0.0001$, $\eta_p^2 = 0.89$), and for a longer duration (500–800 ms) at Cz ($F(1,13) > 34.6$, $p < 0.0001$, $\eta_p^2 = 0.73$). The ERS at Fz was present from 0 to 1200 ms ($F(1,13) > 17.0$, $p < 0.0013$, $\eta_p^2 = 0.57$). From 100 to 500 ms, there was additionally a right posterior ERS that was most significant at P4 from 300 to 400 ms (32.4% [5.5]; $F(1,13) = 35.1$, $p < 0.0001$, $\eta_p^2 = 0.73$). Finally, a left posterior decrease in power (ERD) was most significant at PO3 from 1100 to 1200 ms (−10.3% [1.6]; $F(1,13) = 40.3$, $p < 0.0001$, $\eta_p^2 = 0.76$).

Middle theta (θ_1)

The overall analyses revealed an ERS that was initially most significant at F3 from 300 to 400 ms (45.7% [5.8]; $F(1,13) = 62.7$, $p < 0.0001$, $\eta_p^2 = 0.83$), and subsequently (400–600 ms) at Fz ($F(1,13) > 57.4$, $p < 0.0001$, $\eta_p^2 > 0.82$). At the same time, ERS was also present above central, centro-parietal, and parietal sites, which was most significant at CP4 from 300 to 400 ms (34.1% [3.7]; $F(1,13) = 86.8$, $p < 0.0001$, $\eta_p^2 = 0.87$), and above occipito-parietal and occipital sites, which was most significant at PO10 from 400 to 500 ms (35.0% [5.8]; $F(1,13) = 36.4$, $p < 0.0001$, $\eta_p^2 = 0.74$). The ERS above Fz and Cz was present for all examined time windows ($F(1,13) > 17.0$, $p < 0.0013$, $\eta_p^2 > 0.57$).

Upper theta (θ_3)

Analyses showed ERS above frontal, fronto-central and central sites. Initially, this effect was most significant above F7 from 200 to 300 ms (29.5% [4.1]; $F(1,13) = 53.2$, $p < 0.0001$, $\eta_p^2 = 0.80$), and next above FCz from 300 to 400 ms (42.7% [4.4]; $F(1,13) = 94.1$, $p < 0.0001$, $\eta_p^2 = 0.88$). The ERS above FCz was present from 0 to 600 ms ($F(1,13) > 18.6$, $p < 0.0009$, $\eta_p^2 = 0.59$). We also observed ERS above occipital sites, which were most significant from 200 to 300 ms at PO9 (28.1% [4.2]) and PO10 (32.2% [5.8]; $F(1,13) > 31.1$, $p < 0.0001$, $\eta_p^2 = 0.71$). A reduction in power relative to the baseline (ERD) was later observed from 700 to 1100 ms at centroparietal, parietal, and occipito-parietal sites, which was most significant at P4 from 900 to 1000 ms (−14.3% [2.9]; $F(1,13) = 24.2$, $p < 0.0003$, $\eta_p^2 = 0.65$).

Lower alpha (α_1)

Overall, a frontal reduction in power relative to the baseline (ERD; not displayed) was most significant at FCz from 900 to 1000 ms (−21.4% [3.9]; $F(1,13) = 29.2$, $p < 0.0002$, $\eta_p^2 = 0.69$). Above central sites this reduction occurred earlier and was most significant at Cz from 700 to 800 ms (−23.7% [3.9]; $F(1,13) = 36.5$, $p < 0.0001$, $\eta_p^2 = 0.74$). We also observed a right parietal reduction in power. This was initially most significant at TP8 from 500 to 600 ms (−32.6% [4.2]; $F(1,13) = 58.9$, $p < 0.0001$, $\eta_p^2 = 0.82$), then at CP4 from 700 to 800 ms (−43.7% [6.3]; $F(1,13) = 48.6$, $p < 0.0001$, $\eta_p^2 = 0.79$), and at P4 from 800 to 900 ms (−39.9% [5.9]; $F(1,13) = 45.7$, $p < 0.0001$, $\eta_p^2 = 0.78$). Finally, we observed an occipital reduction in power that was most significant from 600 to 700 ms at PO8 (−29.3% [4.1]; $F(1,13) = 50.0$, $p < 0.0001$, $\eta_p^2 = 0.79$) and PO10 (−28.3% [4.6]; $F(1,13) = 38.5$, $p < 0.0001$, $\eta_p^2 = 0.75$).

Upper alpha (α_2)

Above frontal and fronto-central brain areas the most significant reduction in power (not displayed) was observed at FCz from 500 to 600 ms (−26.5% [3.4]; $F(1,13) = 59.5$, $p < 0.0001$, $\eta_p^2 = 0.82$). Above central brain areas, these effects were most significant at C3 from 400 to 500 ms (−31.7% [4.2]; $F(1,13) = 57.6$, $p < 0.0001$, $\eta_p^2 = 0.82$) and at C4 from 500 to 600 ms (−40.6% [4.5]; $F(1,13) = 81.1$, $p < 0.0001$, $\eta_p^2 = 0.86$). Even stronger reductions in power were observed at centroparietal and parietal sites being most significant from 400 to 500 ms at CP4 (−45.3% [4.0]; $F(1,13) = 129.7$, $p < 0.0001$, $\eta_p^2 = 0.91$) and P4 (−47.4% [4.3]; $F(1,13) = 124.1$, $p < 0.0001$, $\eta_p^2 = 0.91$). Significant reductions were also observed above occipito-parietal and occipital brain areas, being most significant at PO8 from 400 to 500 ms (−40.2% [4.1]; $F(1,13) = 96.4$, $p < 0.0001$, $\eta_p^2 = 0.88$) and O1 from 500 to 600 ms (−36.8% [3.5]; $F(1,13) = 108.3$, $p < 0.0001$, $\eta_p^2 = 0.89$).

Lower beta (β_1)

A frontal ERD was initially most significant at FC3 from 400 to 500 ms (−30.3% [3.7]; $F(1,13) = 67.2$, $p < 0.0001$, $\eta_p^2 = 0.84$) but at the end of the examined interval (1000–1100 ms) became most significant at FCz (−24.6% [2.3]; $F(1,13) = 115.0$, $p < 0.0001$, $\eta_p^2 = 0.90$). Even more significant reductions were observed above central and centro-parietal areas for the whole examined interval, being initially most significant at CP3 (−42.1% [2.9]) and CP4 (−39.5% [3.2]) from 400 to 500 ms ($F(1,13) > 151.4$, $p < 0.0001$, $\eta_p^2 > 0.92$), and finally at CP3 from 1000 to 1100 ms (−37.3% [3.1]; $F(1,13) > 141.7$, $p < 0.0001$, $\eta_p^2 = 0.92$). Above occipital areas, ERDs were most significant from 400 to 500 ms at PO8 (−36.3% [3.0]; $F(1,13) = 148.5$, $p < 0.0001$, $\eta_p^2 = 0.92$).

Upper beta (β_2)

An overall reduction (not displayed) in frontal β_2 power (−23.7% [2.7]) was most significant from 800 to 900 ms at Fz ($F(1,13) = 26.2$, $p < 0.0001$, $\eta_p^2 = 0.86$). This ERD was even stronger above fronto-central areas, being most significant at FCz from 800 to 900 ms (−29.1% [2.2]; $F(1,13) = 173.8$, $p < 0.0001$, $\eta_p^2 = 0.93$). Comparable effects were present above central brain areas, being most significant at Cz from 1100 to 1200 ms (−30.0% [2.4]; $F(1,13) = 160.2$, $p < 0.0001$, $\eta_p^2 = 0.93$). Major reductions were also present above centro-parietal areas, being most significant at CP4 from 400 to 500 ms (−37.3% [2.7]; $F(1,13) = 185.9$, $p < 0.0001$, $\eta_p^2 = 0.94$), and above parietal areas being most significant at P3 from 300 to 400 ms (−31.6% [2.4]; $F(1,13) = 170.3$, $p < 0.0001$, $\eta_p^2 = 0.93$). Above occipito-parietal and parietal areas, most significant reductions were observed at PO4 from 300 to 400 ms (−27.2% [2.8]; $F(1,13) = 94.2$, $p < 0.0001$, $\eta_p^2 = 0.88$), and at PO10 from 400 to 500 ms (−25.2% [2.4]; $F(1,13) = 111.7$, $p < 0.0001$, $\eta_p^2 = 0.90$).

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