



Frontal theta activity reflects distinct aspects of mental fatigue

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ABSTRACT

Longer lasting performance in cognitively demanding tasks leads to an exhaustion of cognitive resources and to a state commonly described as mental fatigue. More specifically, the allocation and focusing of attention become less efficient with time on task. Additionally, the selection of even simple responses becomes more error prone. With respect to the recorded EEG, mental fatigue has been reported to be associated with an increase in frontal theta and frontal and occipital alpha activity. The present study focused on the time course of changes in behavior and in the EEG to characterize fatigue-related processes. Participants performed a spatial stimulus–response–compatibility task in eight blocks for an overall duration of 4 h. Error rates increased continuously with time on task. Total alpha power was larger at the end compared to the beginning of the experiment. However, alpha power increased rapidly and reached its maximal amplitude already after 1 h, whereas frontal theta showed a continuous increase with time on task, possibly related to increased effort to keep the performance level high. Time frequency analyses revealed power changes in the theta band induced by task relevant information that might be assigned to a drain of executive control capacities. Thus, frontal theta turned out to be a reliable marker of distinct changes in cognitive processing with increasing fatigue.

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1. Introduction

Prolonged periods of cognitive activity lead to so-called “mental fatigue”, a decline of cognitive performance that is, among other factors, responsible for a large number of severe traffic accidents (Boksem, Kostermaans, Tops, & De Cremer, 2012) and for other potentially adverse incidents. Mental fatigue leads to reduced working memory performance and to a decrease in the ability to focus attention, it causes distractibility and provokes lapses in information processing, which resulting in inadequate behavior (Boksem, Meijman, & Lorist, 2006; Lorist et al., 2000). Mental fatigue has primarily been defined in motivational terms, as the unwillingness of alert, motivated subjects to continue to perform mental work (Grandjean, 1968; Tops & Boksem, 2010). One core property of mental fatigue is assumed to be its gradual and cumulative nature (Lal & Craig, 2001a).

Spectral EEG measures have been proposed to be valid and reliable indicators of mental fatigue (Lal & Craig, 2002). A shift

of EEG power toward low-frequency bands (Delta, Theta Alpha) has repeatedly been reported (Aeschbach et al., 1997; Cajochen, Brunner, Krauchi, Graw, & Wirz-Justice, 1995; Phipps-Nelson, Redman, & Rajaratnam, 2011; Zhao, Zhao, Liu, & Zheng, 2012), while higher frequencies (Beta, Gamma) typically decrease in amplitude (Lal & Craig, 2001b). This shift in spectral distribution might be related to a decrease in the level of arousal (Tops & Boksem, 2010), one core aspect of mental fatigue. However, these effects show a high variability or even reverse effects both across experimental settings and subjects (Lal & Craig, 2001a; Lal & Craig, 2002). For example, Kirov, Warsawskaya, and Voynov (1996) report a global increase in spectral power also including the beta frequency band. For the alpha band, both systematic increases with ongoing time on task and decrease have been reported. In a comprehensive review of the functional meaning of alpha oscillations, Klimesch (1999) points out that alpha activity rather decreases with increasing fatigue. He refers to studies that showed increasing theta but decreasing posterior alpha activity in distinct stages from wake to sleep (Hori, Hayashi, & Morikawa, 1991; Tanaka, Hayashi, & Hori, 1997). Addressing the initially mentioned studies that report increasing alpha activity with increasing fatigue, Klimesch (1999) notes that an increase in lower alpha power occurs before most subjects are close to falling asleep (Akerstedt, Torsvall, & Gillberg, 1987; Phipps-Nelson et al., 2011; Torsvall & Akerstedt, 1987). In

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those cases, an increase in lower alpha power may reflect the increased effort and probably also the difficulty of the subjects to maintain a state of alert wakefulness. Even more closely related to mental fatigue appears to be an anteriorization of alpha activity (e.g. Barwick, Arnett, & Slobounov, 2012).

Some effects on spectral power with time on task appear to depend on task complexity. While Kamzanova, Matthews, Kustubayeva, and Jakupov (2011) found an increase both in alpha and in theta power with time on task that was more pronounced for the more demanding of two vigilance tasks, more effortful tasks such as a Stroop task evoke a power increase in the theta band only (Barwick et al., 2012). Kirroy et al. (1996) found that an increase in alpha power can be seen with an attentional task whereas theta power increased with more demanding ongoing arithmetic calculations.

Nevertheless, EEG measures are capable of predicting behavior (Gevins et al., 1990; Jap, Lal, & Fischer, 2011). Power in the upper alpha band is positively related to good performance in cognitive functions such as memory (Doppelmayr, Klimesch, Stadler, Pöhlhuber, & Heine, 2002; Vogt, Klimesch, & Doppelmayr, 1998) or mental rotation (Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005). Changes in the theta band appear to be directly related to changes in performance with time on task (Paus et al., 1997; Yamamoto, 1993). In particular, direct analyses of lapses and other behavioral errors, e.g. in a visuomotor tracking tasks demonstrate that they go along with increased theta activity (Peiris, Jones, Davidson, Carroll, & Bones, 2006). Furthermore, an increase in pre-stimulus theta activity can predict lapses in stimulus detection (Makeig & Jung, 1996). Accordingly, large alpha power and small power in lower frequency bands characterize the EEG of subjects with good cognitive performance (Klimesch, 1999).

Some of the studies outlined above demonstrate that frequency measures, as long as they only consider the power in a particular frequency band, can provide only indirect evidence for changes in information processing. However, total power in a specific frequency band might be taken as the origin for event-related changes. The reactivity in band power is assumed to be correlated with the absolute power at resting state (Klimesch, 1999). Additionally, it appears plausible that event-related changes in particular frequency bands can be assigned to distinct cognitive functions. Lower alpha desynchronization has been assigned to attentional processes, whereas event-related decreases in higher alpha power relate to sensory processing (Klimesch, 1999). Hanslmayr, Gross, Klimesch, and Shapiro (2011) proposed that increases in alpha power are related to changes toward internally oriented brain states that might hamper detection and identification of stimuli. Theta synchronization relates rather to encoding of new information. In more general terms, the close relationship of frontal theta to the recruitment of cognitive control has been shown in numerous studies investigating response monitoring (Cavanagh, Frank, Klein, & Allen, 2010; Luu & Tucker, 2001), control of memory functions (Holz, Glennon, Prendergast, & Sauseng, 2010; Klimesch, Freunberger, & Sauseng, 2010; Onton, Delorme, & Makeig, 2005; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010) as well as error processing (Hoffmann, Labrenz, Themann, Wascher, & Beste, 2013; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Trujillo & Allen, 2007; Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007; Yordanova, Falkenstein, Hohnsbein, & Koley, 2004). Thus, frontal theta power appears to be a reliable correlate for cognitive control.

The fact that frontal theta and an anteriorization of alpha activity seem to be the most reliable measures of mental fatigue fits well into a recent framework of this phenomenon that describes mental fatigue in terms of motivational mechanisms implemented in fronto-cortical structures: mental fatigue can be seen as a discrepancy between energy invested into a task and potential rewards (Boksem & Tops, 2008). This adjustment takes place by

promoting reward-related information to the ACC in order to adjust behavior for getting the maximal reward with the least aversive consequences (Lorist, Boksem, & Ridderinkhof, 2005). According to Sarter, Gehring, and Kozak (2006), mental effort that is assigned to the same neural system is highly capable to uphold stable cognitive functioning even under suboptimal conditions, given that motivation is high. Beside motivation, energy costs are a central determinant within this framework. Energy loss (exhaustion) and motivation loss due to uncertainty about the duration of the task and boredom might add to the overall picture of mental fatigue.

In the present study, the effects of time on task apart from motivational factors and states close to sleep were measured continuously in a long term experiment. Above all, we intended to track the cognitive and physiological changes that go along with time on task continuously. Separate blocks of the same task were run repeatedly, thus making the time course for any measure obtained available for analysis.

Participants had to perform in a situation that was similar to a regular working environment with respect to temporal parameters: they started the experiment in the morning, were continuously informed about the duration of the experiment and were allowed to take a 15 min break after 2 h.

Overall, the subjects performed in a spatial stimulus–response correspondence task (= Simon Effect; Simon, 1969; Simon, Sly, & Vilapakkam, 1981) for 4 h. EEG was measured continuously and evaluated in 8 blocks of 25 min each in which the very same stimuli were processed in different randomized order.

Spectral EEG parameters of mental fatigue were extracted by a Fast Fourier Transformation (FFT). Additionally, time frequency analyses were run on basis of single trials (to recover induced activity) and on basis of the individual average (to recover evoked activity). For the FFT and the time frequency analyses parameters of alpha and theta activity values were extracted.

Assuming that exhaustion is a steadily progressing phenomenon, we specifically looked at the time course of changes throughout the task. Any measure directly reflecting mental fatigue should change continuously and steadily with time on task.

2. Materials and methods

2.1. Participants

14 volunteers (7 female), between 21 and 27 years old (mean age: 23.4 years) participated in the experiment. All participants received 60 € for participation in the entire experimental procedure lasting approximately 6 h. None of the participants reported any neurological or psychiatric disorder. All had normal or corrected to normal vision, reached perfect score in the Ishihara test for color blindness and all were right handed. Participants provided informed written consent prior to entering the experiment. The study was approved by the local ethics committee.

2.2. Task

The stimuli used consisted of two successively presented frames. In the first frame two gray bars (luminance: 30 cd/m²) were presented 1.1° left and right from a fixation cross (see Fig. 1). The bars were 1.35° long and 0.56° wide and each of them was oriented either vertically or horizontally. The bars were presented on a dark gray background (5 cd/m²). The first frame that was not informative for the task itself was presented for 200 ms. Following a blank interval of 50 ms, the second frame was then presented for a duration of 200 ms.

From the display of frame 1 to frame 2 one of the two bars changed its color, either to red or to blue without any luminance

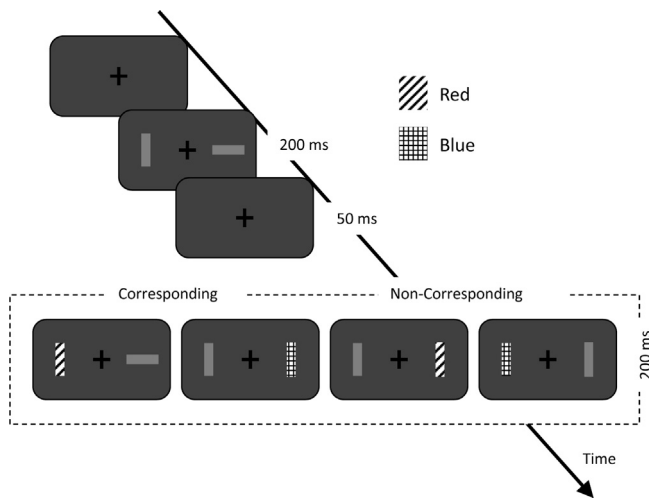


Fig. 1. Set-up and procedure. Participants had to detect changes in a fast sequence of two frames that contained two bars, oriented either vertically or horizontally (randomized). Across the two frames one of the two bars changed its color, either to red or to blue. The color change appeared either alone, accompanied by an orientation change of the same bar or of the bar at the opposite location. Data in all analyses were collapsed across these three conditions. The task of the subjects was to make a choice response based on the identity of the color (press the left key for red and the right key for blue). Accordingly, color change and response could be at the same side (corresponding) or not (non-corresponding).

change (equiluminant). The color of this bar was the imperative information participants had to respond to.

The subjects' task was to press a key based on the identity of the color change. They pressed the left button for a change to blue and a right button for a change to red irrespective of the location of the color change. Accordingly, stimulus and response side could have been the same (corresponding) or different (non-corresponding) meaning.

Color changes could occur alone, accompanied by the change of orientation of the bar that changed the color, or accompanied by a change of orientation of the opposite bar. Differences between these stimulus conditions will not be addressed here, instead all data reported are collapsed for this task condition.

2.3. Procedure

The experiment started at 9 am for every subject to minimize the effect of circadian variance. Participants entered the laboratory, performed Ishihara's Test for color blindness and filled in the Edinburgh Handedness Inventory.

Then the electrode cap was applied and the instruction was read out loud. At about 10 am participants entered the EEG cabin and the experiment was started. Participants were seated in a dimly lit, electrically shielded and sound attenuated EEG cabin equipped with a comfortable armchair with two force keys integrated into the armrests.

Before the main experiment, participants were made familiar with the force sensitive keys. In order to get a representation of the response threshold, they trained force production in a task for a short period, in which they were asked to press the keys after a visual signal. Both the actual force and the criterion for a correct response (200 cN) were displayed on the screen continuously. Participants were asked to produce a force that is comfortable to them even for a longer duration and clearly exceeds the displayed criterion.

In the main experiment, the subjects performed 8 Blocks of 480 trials each (duration approximately 25 min). Before and after each block, they were asked to sit still for 1 min to relax, respectively to

prepare for the task. Between these periods, short resting periods of 3 min were introduced. After the 4th block, a break of 15 min was inserted, in which participants were allowed to go to the toilet and to eat one or two power bars (depending on body mass index). Blood sugar level was measured at the beginning of the experiment during the break and at the end of the experiment using a merchantable blood glucose meter (Bayer Contour® USB). Blood sugar level was not related to behavioral performance, neither intra- nor interindividually.

2.4. Data analysis

2.4.1. Behavioral data

Responses were defined as presses on the force keys that exceeded 200 cN (which is similar to forces required in computer keyboards) between 150 and 1500 ms after the color change. Any trials during which the response force criterion was either not met or during which it was met or exceeded on the other, incorrect force key, were coded as erroneous. Response times of correct responses as well as response accuracy were tested in a repeated measures ANOVA with the factors correspondence (2; corresponding vs. non-corresponding) and block (8).

2.4.2. EEG data

EEG was recorded from 60 Ag/AgCl active electrodes (ActiCap, Brain Products, Gilching, Germany) affixed across the entire scalp according to the extended 10/20 System (Pivik et al., 1993). Eye movements were scanned continuously from two electrode pairs affixed above and below the left eye (vertical EOG) and at the outer canthii of each eye (horizontal EOG). EEG and EOG were sampled on-line with a frequency of 1 kHz using a BrainAmp MRplus DC-amplifier (Brain Products, Gilching, Germany), with a band-pass filter of 0–200 Hz.

All data were filtered with a Butterworth zero-phase low pass filter at 35 Hz @ 48 dB/Octave and were then resampled to 256 Hz using a cardinal spline based resampling method.

For the analysis of the total power, segments with a length of 2 s and with an overlap of 200 ms were extracted from the continuous ongoing EEG in the experimental blocks. The resulting data segments were tapered with a Hanning window with 10% of the total segment length. FFT power spectra with a spectral resolution of 0.5 Hz were calculated for both sides of the spectrum, resulting in FFT segments containing the full spectral information. The resulting FFT segments were averaged to stabilize the spectral content. The power in the FFT was extracted for theta activity (6–7 Hz), the lower alpha band (9–10 Hz) and the upper alpha band (10–11 Hz).

For the calculation of induced and evoked wavelet activity, segments from 1000 ms before to 2000 ms after the first stimulus in the sequence were extracted. Complex Morlet wavelets were calculated with 30 logarithmic scales in a frequency window from 1 to 30 Hz. Morlet c was set to 7. Segments were either submitted to wavelet decomposition individually and only then averaged, resulting in induced wavelet activity, or were first averaged and only then submitted to wavelet decomposition, resulting in evoked wavelet activity being returned. For subsequent analyses, scales 17, 20, 21 were extracted, corresponding to wavelet layers with center frequencies at 6.53 Hz, 9.28 Hz and 10.44 Hz.

Mean voltages from the interval preceding the first (non-informative) frame (–200 to 0 ms) were extracted as baseline measures. Changes in the amplitude of evoked and induced activity were measured between 100 and 300 ms following the onset of the stimulus sequence, reflecting the response to the first non-informative frame, and between 500 and 700 ms, reflecting processing of the imperative information.

FFT-power and mean wavelet amplitudes of baseline data and relative changes from the two subsequent time windows were

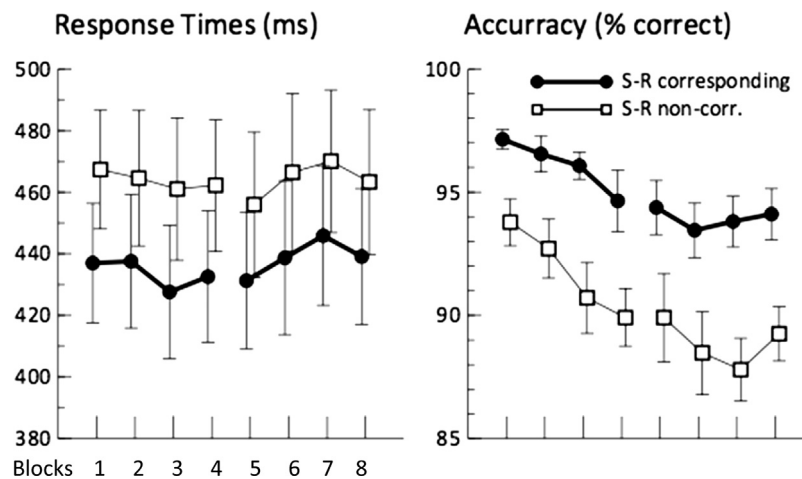


Fig. 2. Behavioral data across the experiment (mean values and standard errors of means are depicted). Response times (left panel) remained rather stable for the entire four hours and showed a constant effect of S-R correspondence. Response accuracy (right panel) was lower for non-corresponding trials across the entire experiment. It additionally decreased with time on task and slightly recovered in the last block.

entered into separate ANOVAs with the factors topography (2; FCz, POz) and time on task (8; ToT Block). Polynomial contrasts for the factor ToT were calculated to evaluate the change of the evaluated measures over time. Based on the fact that the data indicated strong changes in the beginning of the experiment followed by a phase of remarkable stability, additional analyses were run, omitting the first two blocks, thus focusing on the later experimental blocks.

Additionally, in order to demonstrate the contiguity between electrophysiological parameters and behavioral changes over time, correlations between wavelet parameters in the theta band (which showed the most reliable effects of ToT) and error rates were calculated on a single subject basis. For each subject, a correlation across the 8 blocks for all pair-wise combinations was calculated and Fisher- z transformed. The z -Values obtained were averaged and back-transformed into a correlation coefficient. Additionally, pre-stimulus theta level and induced changes were correlated on an intraindividual basis in the same way.

Analyses with more than one degree of freedom were Greenhouse–Geisser corrected (Vasey and Thayer, 1987). In that case, ϵ -values and p -values derived from the corrected degrees of freedom are reported. Partial η^2 (η^2) is reported for behavioral data in the result section. For EEG-data this parameter is listed in the supplementary material.

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biopsycho.2013.11.010>.

3. Results

3.1. Behavioral data

3.1.1. RTs

For response times (see Fig. 2, left panel) no reliable changes were observed across the four hours of the experiment, $F(7,91) = .600$, $p > .2$. A strong effect of S-R correspondence was observed, $F(1,13) = 146.286$, $p < .001$, $\eta^2 = .918$, that did not vary with time on task, $F(7,91) = 1.071$, $p > .2$.

3.1.2. Accuracy

Response accuracy (see Fig. 2, right panel) decreases with increasing time on task, $F(7,91) = 7.704$, $\epsilon = .451$, $p < .001$, $\eta^2 = .372$. The cumulative contrasts (difference of the current block to all preceding ones) indicate a steadily decreasing accuracy with a maximal contrast when block 7 is compared to the preceding

ones, $F(1,14) = 24.428$, $p < .001$, $\eta^2 = .653$. When omitting the first two blocks in order to see the development after an initial adaptation phase, the local contrast remained significant for block 7, $F(1,13) = 8.325$, $p = .013$, $\eta^2 = .390$ and close to significant for the blocks 4, $F(1,13) = 3.675$, $p = .077$, $\eta^2 = .220$, and 6, $F(1,13) = 3.229$, $p = .096$, $\eta^2 = .199$, but not the overall effect of blocks, $F(1,13) = 2.389$, $\epsilon = .423$, $p = .108$, $\eta^2 = .155$. Overall, corresponding trials were responded to more accurately, $F(1,13) = 43.326$, $p < .001$, $\eta^2 = .769$. S-R correspondence did not interact with time on task, $F(7,91) = 1.376$, $p > .2$.

3.2. EEG data¹

3.2.1. Spectral power

Theta activity showed a clear frontal maximum and an increase in amplitude over time, $F(7,91) = 7.884$, $\epsilon = .227$, $p = .005$, which was reflected both in the linear contrast, $F(1,13) = 10.825$, $p = .006$ as well as in the analysis when the first two blocks were omitted, $F(5,65) = 11.337$, $\epsilon = .393$, $p = .007$. An interaction of time on task by topography, $F(7,91) = 5.396$, $\epsilon = .213$, $p = .020$ indicate differential increase at the fronto-central and parieto-occipital lead. However, considering FCz and POz separately, significant increase of theta power with time on task was obtained for both sites (FCz: $F(7,91) = 7.035$, $\epsilon = .217$, $p = .008$; POz: $F(7,91) = 7.033$, $\epsilon = .315$, $p = .001$) (Fig. 3).

The lower alpha band failed to show a significant overall effect of time on task, $F(7,91) = 2.878$, $\epsilon = .147$, $p = .112$, or an interaction of time on task with topography, $F(7,91) = 2.673$, $\epsilon = .191$, $p = .115$. Only for the linear contrast, an interaction of time on task by topography, $F(1,13) = 6.591$, $p = .023$, was observed that indicated an increase in alpha power with time on task restricted to the fronto-central lead, $F(7,91) = 11.704$, $\epsilon = .297$, $p < .001$, where also the linear contrast, $F(1,13) = 7.400$, $p = .018$, and the 6-block analysis reached statistical significance, $F(5,65) = 4.228$, $\epsilon = .541$, $p = .014$.

For the upper alpha band no reliable influence of time on task was observed, $F(7,91) = 2.065$, $\epsilon = .221$, $p = .160$ (Fig. 4).

3.2.2. Induced activity

The slight increase in theta power immediately after stimulus presentation varied with time on task, $F(7,91) = 5.047$, $\epsilon = .599$,

¹ A complete table of all statistical analyses and the effect sizes for spectral analyses is available in the supplementary material.

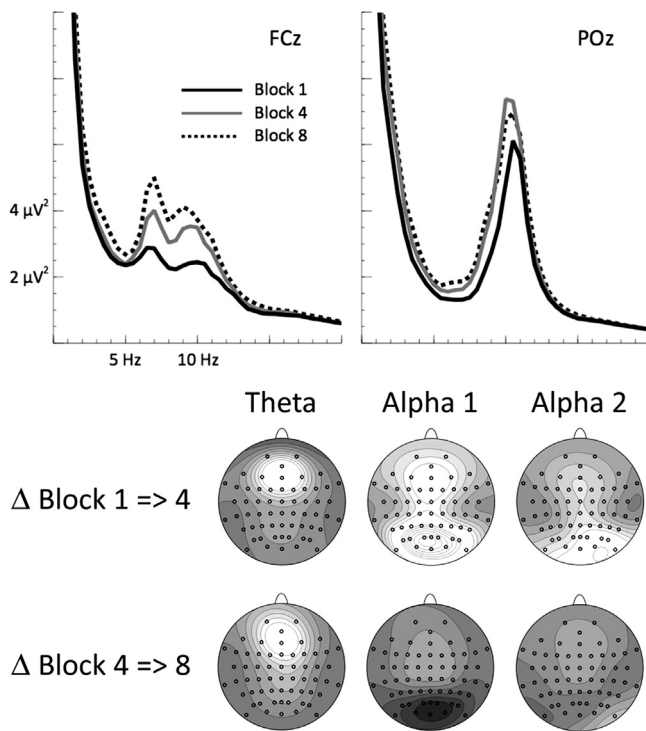


Fig. 3. In the upper half, power spectra for the electrodes FCz and POz are depicted for the first (bold black), fourth (last before a short break; gray) and eighth block (dotted line) of the experiment. Continuous changes were observed only at frontal leads. This becomes even more evident when the change in power from block 1 to 4 and from block 4 to 8 is depicted as topographical map (lower half). From the beginning of the experiment to the last block in the first session, frontal theta, the lower alpha over posterior and frontal electrodes and the upper alpha at occipital sites increased. From the end of the first session to the end of the experiment, power increase was restricted to the frontal theta.

$p = .001$, with largest values in the first block ($0.309 \mu V^2$) and a subsequent decline. This effect of time on task was also significant as a linear contrast, $F(1,13) = 13.550$, $p = .003$, and after omission of the first two blocks, $F(5,65) = 3.484$, $\epsilon = .555$, $p = .020$.

In the second time window (500–700 ms, triggered by the presentation of the second frame) the induced power in the theta band decreased with time on task, $F(7,91) = 5.837$, $\epsilon = .352$, $p = .004$. However, this effect developed during the first two blocks and remained constant thereafter, $F(5,65) = 2.089$, $\epsilon = .467$, $p = .135$. The effect of time on task was more pronounced over frontal than over posterior leads, $F(7,91) = 3.050$, $\epsilon = .473$, $p = .034$. In this second time window a marked effect of S-R correspondence was found for induced theta activity, $F(1,13) = 20.511$, $p = .001$, with

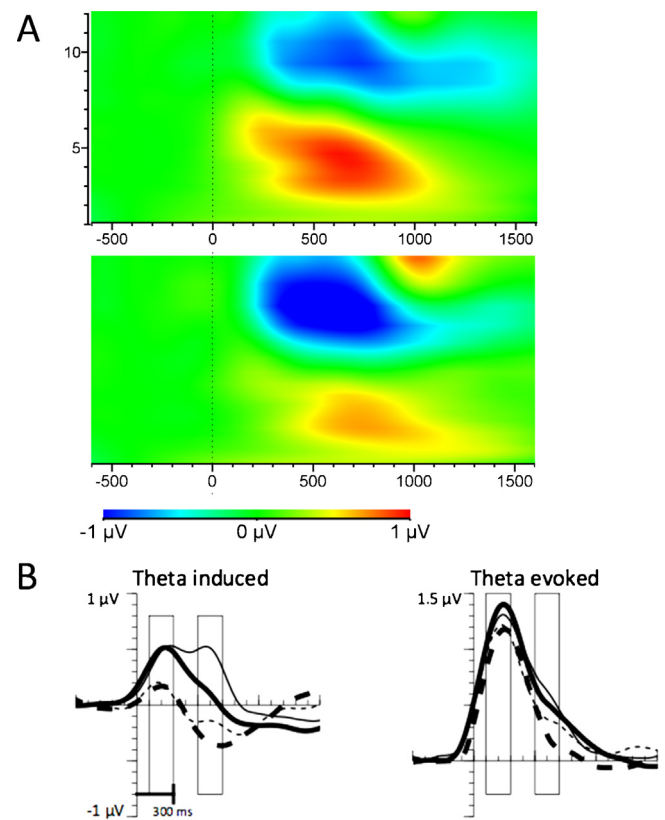


Fig. 5. In the upper half (A), time frequency plots of induced activity are depicted time locked to the onset of the first frame. Results from the first block (upper plot) and the last block (lower plot) are depicted. An increase in alpha suppression with time on task and a decrease of theta activity is demonstrated. In the lower part (B) the time course of the theta power separately for corresponding (bold lines) and non-corresponding trials is depicted. Data from the first block (solid lines) are overlaid with data from the last block (dashed lines). Time zero denotes the onset of the first frame. For induced theta activity (left panel), a clear decrease in power with time on task and a strong effect of S-R correspondence is visible. For evoked theta activity, no systematic effects with experimental factors were observed.

enhanced power for non-corresponding trials over fronto-central leads, $F(1,13) = 14.098$, $p = .002$. No interaction of S-R correspondence with time on task was observed (Figs. 5 and 6).

The marked reduction in the induced power of the lower alpha band occurring already in the initial time window, $F(1,13) = 10.250$, $p = .007$, did not vary with any experimental factor. In the second time window, lower alpha power remained below baseline, $F(1,13) = 22.933$, $p < .001$. For this second time window an effect of time on task was observed, $F(7,91) = 4.315$, $\epsilon = .572$, $p = .038$, that

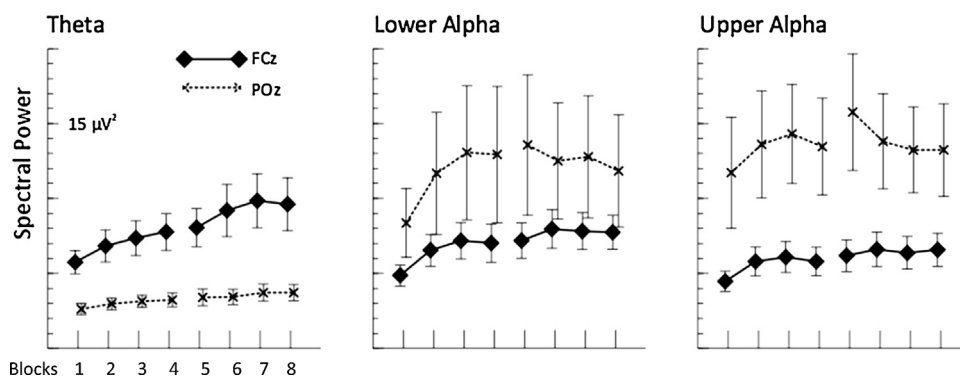


Fig. 4. Means (with standard errors of means) for the theta (6–7 Hz), lower alpha (9–10 Hz), and upper alpha band (10–11 Hz). Separately for FCz (diamonds) and POz (cross; dotted lines). A continuous change in power is only obvious for the frontal theta activity.

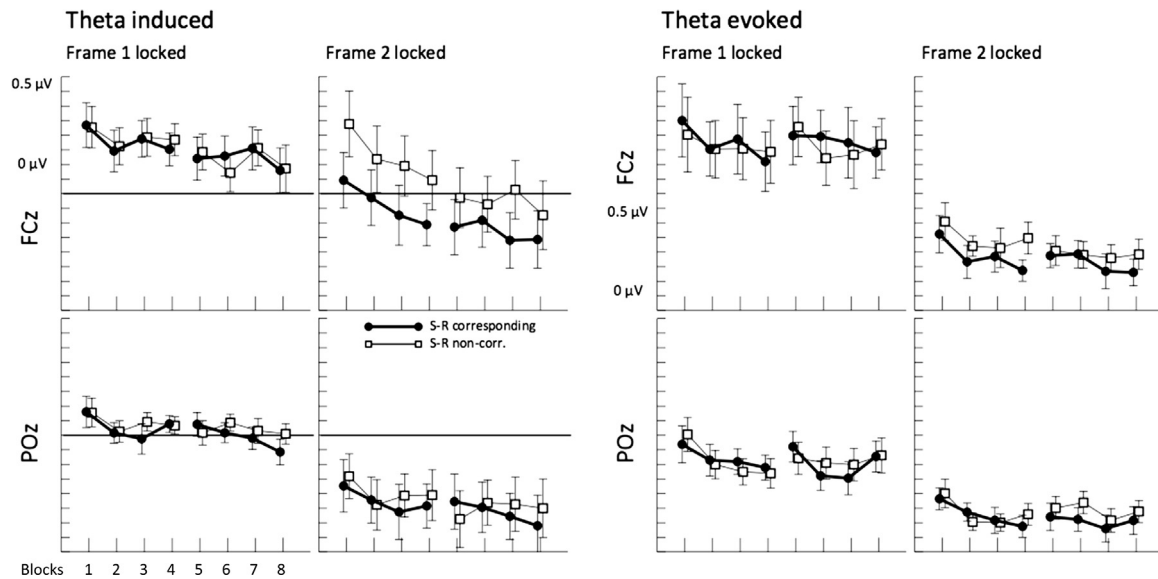


Fig. 6. Means (with standard errors of means) for induced (left panel) and evoked (right panel) theta activity as derived from the time–frequency analyses. A continuous decrease in power is most evident for the induced frontal activity. Additionally, the effect of S-R correspondence is clearly restricted to this measure and remains constant throughout the experiment.

did not completely vanish when the first two blocks were omitted, $F(5,65) = 2.167$, $\varepsilon = .676$, $p = .098$. The decrease in induced power was restricted to posterior electrodes, $F(1,13) = 10.446$, $p = .007$. As for the theta band, an increase at frontal positions in induced power and in non-corresponding trials was observed, which was accompanied by a posterior decrease, $F(1,13) = 10.499$, $p = .006$.

Also for the upper alpha band a power reduction induced by stimulus presentation was observed, $F(1,13) = 21.141$, $p < .001$, that did not vary with experimental conditions. This effect continued after the presentation of the second frame, $F(1,13) = 28.457$, $p < .001$. A reliable time on task effect found was a maximal alpha reduction

in the middle of the experiment, $F(7,91) = 2.869$, $\varepsilon = .508$, $p = .038$. Thus, the effect was still visible when only the last 6 blocks were considered, $F(5,65) = 2.619$, $\varepsilon = .704$, $p = .053$. Decrease of upper alpha power was larger over POz compared to FCz, $F(1,13) = 4.588$, $p = .052$.

3.2.3. Evoked activity

There was a trend toward significance of the variation of evoked theta activity across blocks, $F(1,13) = 2.446$, $\varepsilon = .594$, $p = .055$. However, neither a linear contrast was observed, nor did the effect

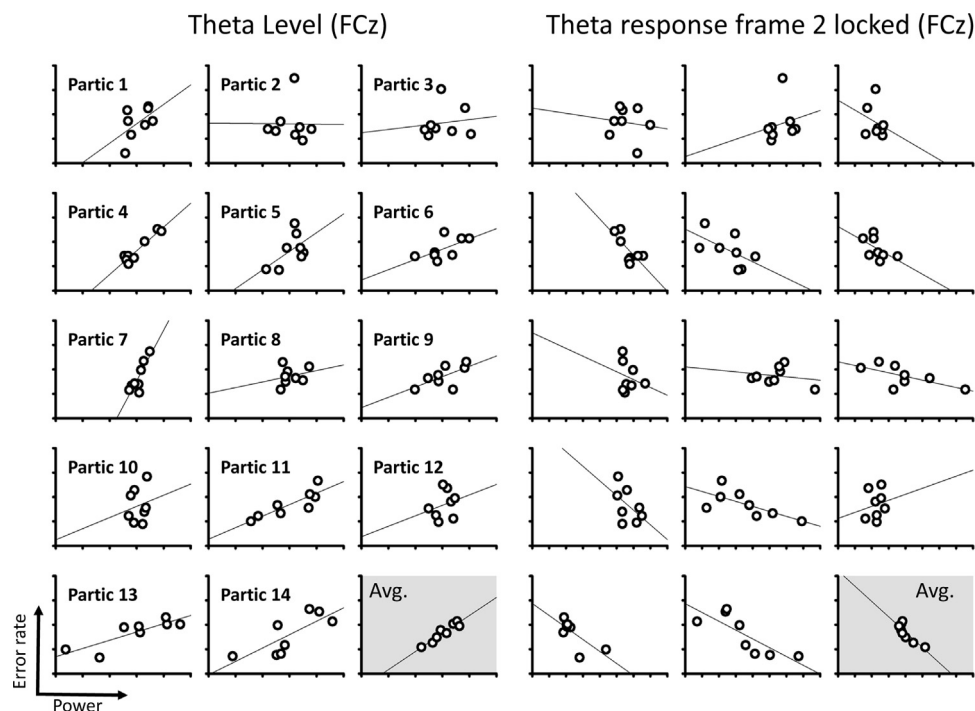


Fig. 7. Error rates in the 8 experimental blocks plotted against the level of frontal theta in the baseline of the time–frequency analyses (left panel) and against the modulation of induced theta activity after the presentation of the imperative signal (right panel), separately for each subject. While a positive correlation is evident for the former, this relation inverts for the latter.

remain when an analysis of only the first 6-Blocks was run, $F(5,65) = 1.629$, $\varepsilon = .737$, $p = .186$.

The same pattern was observed in the second time window (time on task: $F(7,91) = 3.186$, $\varepsilon = .554$, $p = .022$, 6-blocks: $F(5,65) = .657$, $p > .2$). Additionally, a slight, but not significant increase of evoked theta power with non-corresponding trials, $F(1,13) = 3.263$, $p = .094$, $\eta^2 = .201$, was observed.

Evoked activity in the lower alpha band also varied slightly across blocks for the first time window, $F(7,91) = 2.183$, $\varepsilon = .594$, $p = .091$, with largest amplitudes in the first and the fifth block, after the break. No effects were observed after presentation of the second frame.

In the upper alpha band, a strong initial evoked alpha activity peak varied systematically with the factor block, $F(7,91) = 4.405$, $\varepsilon = .492$, $p = .006$. However, as for the lower alpha band, evoked activity was high at the beginning and during block 5, immediately after the break. Evoked alpha power in the second time window varied with experimental blocks in the same way as for the previously described measures, $F(7,91) = 3.001$, $\varepsilon = .377$, $p = .050$, $\eta^2 = .188$.

3.2.4. Correlation analyses

The intraindividual correlations (see Fig. 7) between error rates and the level of induced theta activity before stimulus presentation ranged from $r = -.01$ (Participant 2) to $r = .95$ (Participant 4). Average correlation across all subjects was $r = .62$, $p < .01$. Subsequent induced changes did not strongly co-vary with error rates, neither in the first time window, $r = .39$, $p < .2$, nor when frame 2 related changes were considered, $r = -.46$, $p < .1$. The relation between base level and induced activity was only marginal for the first time window, $r = .46$, $p < .2$, but highly significant for the second time window, $r = .78$, $p < .01$.

4. Discussion

Performing for four hours in a spatial S-R correspondence task led to only marginal effects in behavior. RTs remained stable but accuracy slightly decreased with time on task. Effects of spatial S-R correspondence were stable all through the 4 hours of the experiment for both measures.

In the spectral measures, which have repeatedly been reported in the literature to be reliable correlates of mental fatigue (Aeschbach et al., 1997; Cheng & Hsu, 2011; Lal & Craig, 2001a, 2001b, 2002), there is an obvious increase both in frontal theta and in occipital alpha when comparing the beginning and the end of the experiment. The design of the present study, however, allowed not only the comparison of initial and terminal states in these measures but also to track them across all eight blocks during which the same task was performed throughout. While frontal theta increased steadily, occipital alpha reached its maximum already in the third block and stayed stable for the following 2½ h. Only over frontal leads a continuous increase in the lower alpha band was observed, which is in accord with the notion of alpha anteriorization accompanying mental fatigue (Barwick et al., 2012). Effects on spectral power were more or less equivalent to the outcome of pre-stimulus time–frequency analyses.

Thus, most measures that cannot be assigned to information processing, both from the spectral and the time–frequency analyses, showed remarkable stability across the task with strong deviations only at the very beginning of the experiment. The lack of continuous changes might have been due to the task used in the present study, which, however, was comparable to previous studies on mental fatigue (Boksem, Meijman, & Lorist, 2005; Boksem et al., 2006) and required continuous and demanding control of irrelevant and behaviorally distracting information, functions that have been repeatedly reported to be strongly affected by mental

fatigue. One possible factor for this stability might be that participants were continuously informed about the remaining time to be spent in the laboratory. This information was given to minimize motivational decline but should not be able to prevent the exhaustion of mental resources. However, as has repeatedly been shown, performance can be kept high for remarkable long durations. Kirov et al. (1996) discuss some Russian studies in which participants were able to perform tasks successfully even across 30 hours in an operator simulation task. Cognitive (attentional) effort (Sarter et al., 2006) might thus be sufficient to overcome the decline in performance. In some cases, mentally fatigued participants may change their response strategy toward a low effort – high risk behavior (Schellekens, Sijtsma, Vegter, & Meijman, 2000). However, the fact that performance may restore substantially even after long lasting cognitive work when incentives are given (Boksem et al., 2006) indicates that a decline in motivation may be the core factor for decreasing performance with time on task.

Also in the present study, participants reported to be severely fatigued but obviously still able to compensate declining capacities by increasing effort afforded to the task. This is what most people experience when they have to perform a particular task for a longer period of time. No matter whether they drive a long distance by car or type in endless lines of numbers, they will try to keep their performance at an acceptable level as long as their motivation does not decline. Accordingly, performance recovered after the short breaks and improved in the last block when the end of the experiment was announced.

Such secondary factors make an unequivocal assignment of EEG changes to fatigue-related mechanisms almost impossible. Considering the measure that shows the most reliable and most continuous change with time on task, namely frontal theta, one might argue that, given also the evidence from previous studies, it reflects exhausting resources with increasing fatigue. Within subjects correlations across the eight blocks of the task showed that error rates increased with increasing pre-stimulus theta. This finding is well in accordance with studies mentioned in the introduction, indicating a relation between pre-stimulus theta level and performance (Makeig & Jung, 1996). On the other hand, such tonic aspects of frontal theta activity might also be discussed in the context of the so-called default mode network (Greicius, Krasnow, Reiss, & Menon, 2003; Scheeringa et al., 2008), an intrinsically correlated network of brain regions that becomes active when no active information processing takes place. Mason (Mason et al., 2007) assigned stimulus independent thoughts to the activation of this network that might occur when a rather boring task has to be performed. Along the same lines, as another tonic measure of the attentional state, pre-stimulus alpha level can be considered. As pointed out by Macdonald and co-workers (Macdonald, Mathan, & Yeung, 2011) this measure is negatively correlated to attentional state and confidence ratings. As the task was rather simple and boring, participants might have accepted the decline in alertness in the beginning up to a point where they encountered obvious problems to perform adequately. In other words, due to the boring task participants might have changed toward an internally oriented brain state that has negative consequences for task performance (Hanslmayr et al., 2011). Thus, both changes in theta and in alpha power can potentially be assigned to decreasing engagement in the task. However, the increase in frontal theta might also be related to invested mental effort, which contradicts both previous explanations. In particular, the correlation with task evoked changes in the theta band and the dependency on task complexity (S-R correspondence) of the latter indicates that the pre-stimulus level might reflect a prerequisite for efficient cognitive control processes. One might argue that theta level reflects resources that are necessary to hold performance at a high level but are not sufficient to avoid any decline.

More specifically for information processing, also induced theta power steadily decreased with time on task, both time locked to the first non-informative frame of the stimulus sequence and to the change that defined the target stimulus. Induced power of the frontal theta has been related to stimulus related executive control functions like attention (Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007) and response monitoring (Luu, Tucker, & Makeig, 2004). Accordingly, in the present study, markedly increased theta activity is observed in non-corresponding trials, which require the control of an inadequate response tendency. This component decreases with time on task. According to the correlation analyses, this might reflect the decline of resources on executive control responsible for increasing error rates.

A second phenomenon induced by the presentation of stimuli is the alpha suppression that has been related to task engagement (Sauseng, Klimesch, Doppelmayr, et al., 2005; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). It has been reported that suppression in the lower alpha band reflects alertness whereas changes in the upper alpha band are related to target processing (Klimesch, Doppelmayr, Russeger, Pachinger, & Schwaiger, 1998). In both sub-bands of the alpha rhythm, the amount of suppression declined with time on task. However, while the alpha suppression evoked by the first frame showed a similar pattern as the overall alpha power, with an initial decrease that remained stable from block three to block eight, at least the upper alpha band suppression evoked by the target continued to decrease with the ongoing experiment, indicating declining efficiency of stimulus processing.

Thus, different measures in the frequency bands investigated reflect distinct changes in mental state and cognitive performance in a longer lasting experiment. Both, increasing and decreasing power might reflect ongoing drain of mental resources. Therefore it has to be questioned, whether spectral EEG measures, such as the spectral power are truly suitable for the measurement of mental fatigue. These measures have repeatedly been discussed as the potential basis for a countermeasure to fatigue in work-related environments. However, as demonstrated above, they might also reflect compensatory mechanisms. Additionally, spectral power cannot reflect altered information processing, which is essential when performance in work related situations should be estimated. The present study demonstrates that the continuous evaluation of various measures throughout an experiment is a necessary prerequisite for the evaluation of mental fatigue. Pre-post measurements, as commonly employed in this field, may well be driven by initial effects related to the adjustment to the experimental situation and can give no indication of the time course of ongoing changes. If one considers the continuous change of a measure as a criterion in order to assign it to the development of mental fatigue, only parameters of the frontal theta activity can validly be considered for this study. However, even here their assignment to fatigue related mechanisms remain rather disputable.

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