INTRODUCTION

Human behavior is not stable over time. A decline of performance with increasing time-on-task is a common observation in everyday life. This phenomenon is referred to as mental fatigue. It is a cognitive state which is characterized by a reduced alertness, deteriorated performance (Borghini et al., 2014; Grandjean, 1979), and an aversion to invest further effort into a task (Hockey, 1997). The occurrence of mental fatigue has been found to be more likely in rather monotonous and repetitive tasks (Körber et al., 2015; Thiffault & Bergeron, 2003), as well as in partially automated tasks (Körber et al., 2015; Saxby et al., 2008). This observation renders working environments in which monitoring tasks are...
essential as particularly prone to negative effects of mental fatigue. In many of these work places, like professional driving and air traffic control, for example, human error may lead to a fatal outcome (Bener et al., 2017; Dinges, 1995; Herman et al., 2014; Papadelis et al., 2007). Due to its noninvasive character and the excellent temporal resolution, the EEG has recently been proposed as a tool to detect mental fatigue in order to prevent human error (Orghini et al., 2014; Lal & Craig, 2001, 2002). Consequently, a large amount of research has been conducted aiming at identifying the electrophysiological signature of mental fatigue. Due to the large variety of experimental paradigms and analysis approaches that has been used, the overall result pattern is still unconnected. The present study intents to narrow the gap between recent lines of research.

One of these recent lines of research consists of studies investigating the representation of mental fatigue in the EEG in the spectral domain. Spectral analysis may be performed even when the onset of specific cognitive processes is not controlled for. It is therefore particularly useful for simulation studies and studies conducted in real-world scenarios. Spectral analysis has thus been deployed to investigate mental fatigue in studies investigating real-world car driving (Perrier et al., 2015), real-world train driving (Torsvall & Akerstedt, 1987), in driving simulation studies (Awais et al., 2014; Campagne et al., 2004; Craig et al., 2012; Ghargozlo et al., 2015; Lal & Craig, 2002; Phipps-Nelson et al., 2011; Wascher et al., 2016), in real-world and simulated helicopter flying (Caldwell et al., 2002), as well as in a simulated work place (Wascher, Heppner, et al., 2016). The spectral properties of the EEG associated with mental fatigue were also investigated in highly controlled laboratory studies using a large variety of paradigms like a visual attention task (Boksem et al., 2005), a Stroop task (Barwick et al., 2012), an n-back task (Tanaka et al., 2012), a stimulus–response correspondence task (Wascher et al., 2014), visual search (Fan et al., 2015), arithmetic task (Trejo et al., 2015), and the Simon task (Arnau et al., 2017). A very consistent finding that could be observed in all of these studies to some degree is an increase of spectral power in the lower frequency bands, particularly in the theta and alpha bands, with increasing mental fatigue (for a review and meta-analysis see Lal & Craig, 2001; Tran et al., 2020).

In general, such increases of theta and alpha power with increasing time-on-task were linked to cognitive states of decreased arousal (Klimesch, 1999) or drowsiness (e.g., Torsvall & Akerstedt, 1987). Specifically, the increase of synchronized activity in the alpha range has been related to reduced information processing (Pfurtscheller & Lopes da Silva, 1999) and an increased alpha power at sensory areas has consequently been interpreted as an internally oriented focus of attention (Cooper et al., 2003; Hanslmayr et al., 2011). In the context of mental fatigue, alpha power increases thus seem to indicate that an individual disengages from the actual task and potentially engages in mental imagery or mind wandering instead (cf. Arnau et al., 2020; Compton et al., 2019). Such an interpretation is well in line with recent frameworks on cognitive resource management (Kool & Botvinick, 2014; Kurzban et al., 2013) and frameworks that conceptualize mental fatigue as a signal indicating that current behavior is no longer adaptive (e.g., Boksem & Tops, 2008).

The observed increase of theta band power with mental fatigue, however, is less easily reconcilable with existing theories. Theta activity, in particular frontal midline theta, has been described as a correlate of executive control (Cavanagh & Frank, 2014; Cavanagh et al., 2012; Ithipuripat et al., 2013). It has been suggested that top-down control is being exerted via inter-areal communication in the theta range, which is orchestrated by the prefrontal cortex (Botvinick, 2007; Helfrich & Knight, 2016; Hopfinger et al., 2000). Furthermore, it has been shown that frontal theta power does not only vary as a function of task demands (Gevins et al., 1997; Zakrzewska & Brzezicka, 2014), but also as a function of cognitive effort (Onton et al., 2005; Smit et al., 2005). Against this background, the most straightforward interpretation of increasing theta power with mental fatigue would be an increase of cognitive effort. This, however, diametrically opposes the idea an increasing unwillingness for further task engagement being the core aspect of mental fatigue (Grandjean, 1979; Tops & Boksem, 2010). It also opposes the findings of a rich body of literature that investigated mental fatigue deploying event-related analysis of the EEG signal. These event-related studies represent a second line of research, investigating mental fatigue from a more basic research perspective.

Most of the studies on mental fatigue made use of event-related analysis methods applied in the time domain, so-called event-related potentials (ERP). A vast majority of findings report a decline of ERP amplitudes with increasing time-on-task. A decline of the parietal P3 has been observed over the course of the experiment using an n-back task (Hopstaken et al., 2015), a visual dual-task (Guo et al., 2016), a Simon task (Möckel et al., 2015), and a vigilance task (Haubert et al., 2018). A decline was also observed for the N2 component in a Simon task (Boksem et al., 2006; Möckel et al., 2015) as well as in a Flanker paradigm (Faber et al., 2012). Similar observations were made for ERN/Ne amplitudes (Boksem et al., 2006; Lorist et al., 2005), the CNV (Boksem et al., 2006), and the N1 (Boksem et al., 2005). Very few studies investigating mental fatigue using time–frequency decomposition of the event-related EEG signal. A decline of induced frontal theta activity with time-on-task could be observed by Wascher et al. (2014), indicating reduced exertion of executive control. This fits ERP findings on the N2 and the ERN/Ne, two ERP components that have been related to Theta activity (cf. Cavanagh & Frank, 2014), and on the P3 component that has been described as reflecting the allocation
of cognitive resources (Allison & Polich, 2008). The observations from event-related EEG signal analysis thus strongly suggest that task engagement in general declines with increasing mental fatigue. This deduction is further strengthened by the observation of increasing N2b amplitudes with time-on-task in response to irrelevant stimuli (Boksem et al., 2005) which demonstrates that it is indeed a decline in cognitive control reflected in the signal, rather than an unspecified effect resulting in overall reduced event-related measures.

Taken together, the findings of applied research-oriented studies deploying spectral analysis of the EEG signal, as well as the results of the basic-research-oriented studies using event-related analysis, are both in line with recent theories on the nature of mental fatigue (e.g., Boksem & Tops, 2008; Kurzban et al., 2013). However, both lines of research cannot be aligned seamlessly since spectral measures show an increase with time-on-task, whereas the event-related measure also in the time-frequency domain exhibit a decline. With respect to alpha oscillations, this contrariety in numbers does not lead to inconsistent interpretations as alpha power is considered to be task negative (Compton et al., 2011; Klimesch, 1999). Increases in theta, moreover, indicate an increase in cognitive engagement, whereas a decline in event-related correlates of executive control indicate the opposite. This leads to the question which aspects of cognitive processing and mental fatigue are reflected in each of these measures? This question cannot easily be answered based on recent research, as studies deploying spectral analysis usually do not specify whether the analyzed signal predominantly reflects task-related or non-task-related activity (in simulation studies it is simply not possible). In studies deploying event-related analysis, moreover, non-task-related activity is mostly lost due to the process of generating the event-related measures relative to a pre-stimulus baseline (ERP, ERS/ERD).

In the present study we address this issue by investigating time-on-task effects via linear regression on single-trial, time-frequency decomposed data. Time–frequency analysis allows for investigating spectral and temporal dynamics at the same time. The segments we use for the analysis cover task-related processing as well as the intertrial interval. By deploying a single-trial baseline approach that preserves time-on-task-related variance even in the baseline period, systematic changes in the signal over the course of the experiment can be analyzed for task-related and non-task-related activity simultaneously. The data analyzed are data of participants performing in a Simon task (Simon, 1969; Simon et al., 1981) that were already investigated in an ERP study (Möckel et al., 2015) as well as in a study using spectral analysis (Arnau et al., 2017). We expect that we will be able to locate the findings of both studies using a single approach and, by doing so, gaining further insight into which aspects of mental fatigue are reflected in the respective measures. For the statistical evaluation a data-driven, cluster-permutation approach will be used in order to minimize the danger of interpreting single frequency band effects in isolation. We expect to replicate recent findings of increases of spectral power in the theta and alpha frequency bands, as well as the observation of a decline in task-related activity. Beside the factor time-on-task, we are also considering stimulus–response correspondence as an experimental factor. This way, we address the question whether time-on-task affects executive functioning rather in a general or a specific way.

2 | METHOD

2.1 | Sample

The sample for this study comprised 21 subjects with an age range from 20 to 30 years. The sample is largely identical to the sample of younger participants from Möckel et al. (2015). Three subjects of this sample had to be excluded from further analysis: Two participants confused the response mapping over the course of the experiment and one data set had to be excluded due to bad data quality. The remaining sample with N = 18 (11 female) had a mean age of 24.33 (SD = 3.34) years. The inclusion criteria were right-handedness, not suffering from any psychiatric or neurologic disorder, being non-smoker, and a normal or corrected to normal vision. The recruitment took place via announcing the study in a Facebook group of the institute. In accordance with the Declaration of Helsinki, all participants participated voluntarily and signed an informed written consent. The study was approved by the ethics committee of the Leibniz Research Centre for Working Environment and Human Factors, Dortmund.

2.2 | Procedure

It was ensured that the participants did not obtain any information about the actual duration of the experiment in order to prevent final spurt phenomena that can counteract fatigue (cf. Bergum & Lehr, 1963). This concerned the announcement of the study, the recruitment of the participants, the preparation of the EEG montage, as well as the pre-experimental briefing. The participants were thus also instructed to hand over any time keeping devices like watches or smartphones to the experimenter for the duration of the experiment. The EEG recording took place in an electrically shielded and sound attenuated cabin. In order to control for circadian effects, each participant had to arrive at 8:30 a.m. at the laboratory. The experiment started immediately after the EEG montage had been finished.

During the experiment, the participants performed a visual Simon task (Simon, 1969; Simon et al., 1981). The target stimuli were presented lateralized with respect to a
fixation cross with an eccentricity of 4.5° visual angle (see Figure 1). The targets could be either a square (diameter 0.41°) or a diamond (diameter 0.61°). The participants had to respond according to the identity of the stimulus (square or diamond) and had to ignore location at which the stimulus is being presented (left or right). This results in two trial types: SR corresponding trials, in which stimulus presentation side and response side are identical, and SR non-corresponding trials, in which the side at which the stimulus is being presented and the response side are opposite. Responses were given by pressing force sensitive keys with the left and right index finger. Whether a square or a diamond was mapped to the left or right response key was counterbalanced across participants. The stimuli were presented for 150 ms. The interstimulus interval was jittered and had a mean duration of 2,800 ms.

The experiment was subdivided into nine blocks of 480 trials each (see Figure 1). Each block had a duration of approximately 22 min. After every block, the participants rated their subjective level of fatigue and motivation on a 1- to 9-Likert scale with negative polarity. After the third and after the sixth block, that is, approximately after having performed for 1 or 2 hr in the experiment, there was a longer break during which the participants left the recording cabin. The duration of these breaks was approximately 12 min. The experiment ended after the participants completed the final block. Overall, the experiment had a duration of approximately 3 hr and 45 min, during which the participants had to wear the electrode cap all the time.

2.3 | EEG recording

The EEG was recorded using a montage of 60 active Ag/AgCl electrodes (ActiCap, Brain Products, Gilching, Germany) which were arranged according to the 10–20 system. AFz was used as ground electrode, P9 was used as online reference. The data were sampled at 1,000 Hz using a BrainAmp DC amplifier (Brain Product, Gilching, Germany). A 250 Hz hardware low-pass filter was applied and impedances were constantly kept below 10 kΩ.

2.4 | EEG preprocessing

Preprocessing of the EEG data was performed using EEGLab (Delorme & Makeig, 2004) with MATLAB 2019b (The Math Works Inc., Natick, Massachusetts). Data were band-pass filtered from 1 to 30 Hz. Subsequently, bad channels were detected and removed using kurtosis and probability criteria using EEGLab’s pop_rejchan function (threshold = 10, norm = on for the kurtosis criterium and threshold = 5, norm = on for the probability criterium). A total of 0.78 (SD = 1) channels were removed on average. After re-referencing the data using the common average as reference, the continuous data were segmented into epochs ranging from −2,500 to 1,500 ms with respect to the stimulus onset (see Figure 1). Epochs containing artifacts were automatically detected and rejected using the pop_autorej function with the default parameters. An independent

FIGURE 1 The upper panel of this figure (a) displays the temporal structure of the experiment. The lower panel (b) illustrates the stimuli used for the Simon task.
components analysis (ICA) was performed on the remaining segments and ICs representing artifacts were identified using ICLabel (Pion-Tonachini et al., 2019) and subsequently removed when classified with a probability of less than .5 as reflecting brain activity. On average, 29.22 ICs ($SD = 4.89$) were rejected. Again, epochs with remaining artifacts were rejected automatically. Finally, previously rejected channels were interpolated in order to ensure the same dimensionality in the data for all participants to conduct a cluster-based permutation test. Overall, the average rejection rate for epochs was 7.78% ($SD = 4.59$).

2.5 | EEG signal processing

Time–frequency analysis of the signal was performed by convolving the segmented data with complex Morlet wavelets, which were defined as complex sine waves tapered by a Gaussian. We used 50 wavelets with frequencies ranging from 2 to 25 Hz with linear spacing. The widths of the tapering Gaussians were chosen in a way that the corresponding full widths at half maximum of the wavelets ranged from 1.75 to 8.75 Hz in the frequency domain and from 400 to 100 ms in the temporal domain (cf. Cohen, 2019).

For the exploratory analysis in time × frequency × sensor space the segments were pruned to −1,500 to 1,000 ms relative to the stimulus onset in order to remove the edge artifacts. To make the data suitable for single-trial analysis, we applied a trial-specific baseline normalization. This is usually done by z-normalizing each time–frequency point using the mean and the standard deviation of a frequency-specific baseline period of the respective trial (Grandchamp & Delorme, 2011). This approach, however, would eliminate all time-on-task-related variance in the baseline period and would shift this variance to non-baseline time points instead. Without defining a baseline period, it would be difficult to observe systematic variance related to the stimulus onset. We, therefore, chose the approach of calculating the mean and standard deviation for z-normalizing the single-trial data based on the concatenated baseline periods of all trials. This way, we created a trial-general baseline suited for single-trial analysis. The baseline period used ranged from −1,500 to −200 ms relative to stimulus onset. After normalization, we calculated a linear regression via the normal equation to single-trial data for each point in time × frequency × sensor space using the trial number as predictor. The resulting matrices of regression coefficients entered the statistical analysis to test for systematic time-on-task effects. To test for the effects of stimulus–response correspondence, trials were averaged within each correspondence condition and the averaged normalized power matrices entered the statistical analysis. To test for interaction effects of time-on-task and stimulus–response correspondence, we calculated the linear regression using trial number as predictor separately for corresponding and non-corresponding trials.

In a second analysis, we optimized our methodological approach for event-related frontal theta activity. The segments we used in this analysis ranged from −500 to 1,000 ms relative to the onset of the stimulus. Given that the response times observed in the present study are faster 600 ms on average, these segments cover the relevant task-related variance. A single-trial and trial-specific Z-normalization were applied, with a baseline period ranging from −200 to 0 ms. We furthermore applied a spatial filter to the data that maximizes task-related variance in the theta range. These spatial filters were constructed in a way to maximally distinguish theta band from broadband activity in a time window covering task-related processes. In this multivariate approach, spatial filters are identified based on channel covariance matrices (Cohen, 2017; de Cheveigné & Arzounian, 2015; Duprez et al., 2020; Nikulin et al., 2011). On the one hand, this approach is theory-guided, resulting in an optimized signal-to-noise ratio for the variance of interest. On the other hand, the construction of the filters is also data-driven. This has the advantage of individual differences in topographies being accounted for. The first step is to calculate a signal covariance matrix (S) and a reference covariance matrix (R). For computing the S covariance matrix, we filtered the signal via Morlet wavelet convolution using a 5.5 Hz wavelet with a full width at half maximum in the frequency domain of 5 Hz (cf. Cohen, 2019) and used segments of data covering the period from 300 to 700 ms relative to the stimulus onset. The R covariance matrix was computed using the broadband signal from the same time period. The spatial filters are then identified by finding channel weights ($w$) that maximize $\lambda$ in the equation $\lambda = w^T S w / w^T R w$, which can be done by generalized eigenvalue decomposition (GED, Cohen, 2017; Nikulin et al., 2011). Each of the constructed filters is associated with an eigenvalue that indicates the degree to which the filter is able to distinguish between the S and the R covariance matrices. Since we wanted to focus our analysis on frontal theta activity (cf. Duprez et al., 2020), we selected the spatial filter accordingly in a purely data-driven way: First, we excluded all spatial filters representing eye blinks, defined as filters with higher activation in the most frontal line of electrodes (Fp1, Afz, and Fp2) compared to the second line of electrodes (FC1, FCz, and FC2). We also excluded all spatial filters associated with an eigenvalue of below one standard deviation above the median of all eigenvalues. Of the remaining filters, we selected the one that correlated most with a template activation topography, representing frontal midline activity. This template topography was defined based on the distances of the electrodes to the focus electrode FCz. The distances were normalized to a range from 0 to 1 and then
inverted, so that FCz had a value of 1 and all other values are decreased based on the distance to FCz. The template topography, as well as all selected filter topographies are depicted in Figure 5. After applying the selected filter to the data, time–frequency decomposition, linear regression, and cluster-based permutation statistics were computed equally as it was done for the sensor-space data.

2.6 Statistical analysis

In order to test for the statistical significance of the factors time-on-task and S–R correspondence, as well as of the interaction linear mixed models were fitted to the behavioral data on single-trial level. Response times and accuracy entered the models as dependent variables and the experimental factors time-on-task and stimulus–response correspondence entered the model as fixed effects. Time-on-task was operationalized as the number of each trial in the experiment in ascending order. A random intercept was modeled for each participant (dv ~ time-on-task * correspondence + (1|subject)). Similar models were fitted to the self-report data on subjective fatigue and motivation, with data from all 12 assessments (see Figure 1a) entering the model.

For the electrophysiological measures in sensor space, cluster-based permutation tests were performed on time × frequency × sensor data. For the spatially filtered data, these tests were performed on two-dimensional (time × frequency) data. Cluster-based permutation tests control for Type I error rates when dealing with multiple comparisons in high-dimensional data (Maris & Oostenveld, 2007). First, t-statistics were computed for each data point in time × frequency × sensor space. A clustering algorithm then identified clusters of neighboring data points below the threshold of a t-value corresponding to p < .1. The sum of t-values of all data points in the cluster then constitutes the test statistic. This test statistic is then evaluated under a H0 distribution of the largest cluster-level statistics obtained from running a randomization procedure 1,000 times. For each iteration the largest test statistic was determined based on data with randomized factor–level assignments. Finally, the observed test statistics is compared against this H0 distribution in a two-sided test and clusters with p < .05 were regarded as significant. For the factor time-on-task, the regression coefficients were compared to null hypothesis regression coefficients obtained from calculating a linear regression with permuted trial numbers. Cluster-based permutation statistics in time × frequency × sensor space were calculated using the FieldTrip toolbox (Oostenveld et al., 2011). All effect sizes were estimated as bias-corrected partial η² (Mordkoff, 2019; subsequently referred to as η²).

3 Results

3.1 Behavior

The behavioral data for four time windows are illustrated in Figure 2 and Table 1 contains the corresponding test statistics which were calculated based on single-trial data. Regarding response times, the performance of the participants declined significantly over the course of the experiment (see Figure 2 and Table 1). A significant Simon effect could be observed, with slower responses for non–corresponding compared to corresponding trials (M = 552.19 ms, SD = 159.51 vs. M = 581.44 ms, SD = 153.65). There was no significant interaction between the factors time-on-task and stimulus–response-correspondence for response times. Like response speed, response accuracy also declined with time-on-task.

FIGURE 2 This figure depicts the behavioral measures response time (left panel) and accuracy (right panel) for four time windows (the statistical analysis was performed on single-trial level). The time windows comprise the first 200 trials, the last 200 trials of the first third, of the second third, and the last 200 trials of the experiment. The error bars are representing the standard deviation.
Response accuracy was overall higher in corresponding compared to non-corresponding trials ($M = 90.14\%$, $SD = 6.39$ vs. $M = 85.77\%$, $SD = 6.76$). Here, a significant interaction between the factors time-on-task and stimulus-response-correspondence could be observed, with the decline of accuracy over time being more pronounced for non-corresponding compared to corresponding trials.

### 3.2 Subjective data

The subjective fatigue increased significantly with increasing time-on-task from $M = 3.94$ ($SD = 1.8$) at the beginning of the experiment to $M = 6.56$ ($SD = 2.2$) at the end. Motivation significantly declined over the course of the experiment from $M = 7.22$ ($SD = 1.59$) at the beginning to $M = 3.39$ ($SD = 1.72$) at the end. The corresponding test statistics are reported in Table 2.

### 3.3 EEG data in sensor space

Cluster-based permutation tests in time $\times$ frequency $\times$ sensor space were calculated for the factors time-on-task, stimulus-response-correspondence, as well as for the interaction. A descriptive overview of the data in time $\times$ frequency space, averaged across all channels, is depicted in Figure 3. For the factor time-on-task, the test was performed on regression coefficients obtained from a linear regression model fitted to single-trial data. A null hypothesis data set was generated by fitting the linear regression model on data using permuted trial numbers. One significant cluster for the factor time-on-task was identified (see upper row of Figure 4). It covers all electrodes and it is spectrally located in the alpha range and the neighboring theta and beta bands. The associated effect sizes are largest at fronto-central electrodes, in the alpha range, as well as during the intertrial interval. The fact that this cluster comprises positive regression coefficients indicates a positive relationship of time-on-task and spectral power.

For the factor S–R correspondence, a significant cluster could be identified as well. This cluster is located in the theta range during the poststimulus onset period (starting at 165 ms) and has the largest associated effect sizes at mid-frontal electrodes (see lower row of Figure 4). The direction of the effect indicates a higher frontal theta power in non-corresponding compared to corresponding trials. No significant interaction between the factors time-on-task and stimulus-response-correspondence could be observed.

### 3.4 Interim discussion

The results reported above are clearly in line with our initial hypothesis. Theta and alpha power significantly increased with increasing time-on-task. The results also indicate a decline of task-related theta activity with increasing time-on-task. Negative regression coefficients can be observed in the theta band in a time window ranging from approximately 0 to 500 ms (see Figure 4). This effect, however, is not significant. It might be the case that this time-on-task effect is too localized in time $\times$ frequency $\times$ sensor space to exceed the $p = .05$ threshold of the H0 distribution generated from permuted data in the exploratory analysis deployed here. Another methodological aspect that possibly reduced the observed task-related decline of theta reactivity is that the increase of theta and alpha power in the baseline period in combination with the trial-general baseline normalization may have led to an underestimation of the

| Table 1 | For response time and accuracy, this table shows $t$-statistics ($t$) with the corresponding regression coefficients ($\beta$) and the 95\% confidence interval (CI) for the fixed effects time-on-task (TOT), S–R correspondence (SRC), that is corresponding vs. non-corresponding trials), and their interaction |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Response time** | | | | | | | | | | | | | | | |
| &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; |
| TOT | 7.77** | 0.007 | 0.005, 0.009 | | | | | | | | | | | |
| SRC | 7.61** | 24.88 | 18.47, 31.29 | | | | | | | | | | | |
| TOT $\times$ SRC | 1.58 | 0.002 | $-$0.001, 0.005 | | | | | | | | | | | |
| **Accuracy** | | | | | | | | | | | | | | | |
| &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; |
| TOT | 2.65* | 3.7e$-$6 | 9.6e$-$7, 6.4e$-$6 | | | | | | | | | | | |
| SRC | $-$5.7** | $-$0.028 | $-$0.038, $-$0.018 | | | | | | | | | | | |
| TOT $\times$ SRC | $-$3.51** | $-$6.8e$-$6 | $-$1.1e$-$5, $-$3e$-$6 | | | | | | | | | | | |
| **Note:** Test statistics corresponding to $p < .05$, or $p < .001$ are marked with one and two asterisks, respectively. |

| Table 2 | For the subjective ratings of fatigue and motivation, this table shows $t$-statistics ($t$), the corresponding regression coefficients ($\beta$), and the 95\% confidence interval (CI) for the fixed effects time-on-task (TOT) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Fatigue** | | | | | | | | | | | | | | | |
| &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; |
| TOT | 6.42** | 0.185 | 0.128, 0.242 | | | | | | | | | | | |
| **Motivation** | | | | | | | | | | | | | | | |
| &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; | &nbsp; |
| TOT | $-$10.83** | $-$0.258 | $-$0.305, $-$0.211 | | | | | | | | | | | |
| **Note:** Test statistics corresponding to $p < .001$ are marked with two asterisks. |
reduction of theta reactivity. We thus decided to perform a second analysis optimized for capturing the task-related theta decline with increasing time-on-task. We did this by (a) dropping the sensor dimension entirely by applying a spatial filter to the data that maximizes for task-related theta variance in the signal (see method section), (b) reducing time–frequency space in the temporal domain using epochs that cover less of the intertrial interval, and (c) applying a trial-specific baseline normalization of the data in order to offset the time-on-task-related increases in the theta and alpha band during the baseline.

3.5 | Spatially filtered EEG data

Data were spatially filtered using filters optimizing the signal-to-noise ratio in the theta range at frontal midline recording sites (see filter topographies in Figure 5). The resulting time series in time x frequency space are illustrated descriptively in Figure 6. Again, cluster-based permutation tests in time x frequency space were calculated for the factors time-on-task, stimulus-response-correspondence, as well as for the interaction. The results of these tests are shown in Figure 7. The test for time-on-task effects revealed a significant negative cluster in the theta range after the onset of the stimulus, ranging from 130 to 665 ms. This indicates a significant decline of task-related frontal theta activity with time-on-task. There was also a positive cluster in the beta range, starting at 770 ms.

For the factor stimulus-response-correspondence, a significant cluster could be observed in the theta band ranging from 75 to 830 ms (see lower panel of Figure 7). No significant interaction between the factors time-on-task and stimulus-response-correspondence could be observed in the spatially filtered data.
In the present study, we investigated the effects of time-on-task on task-related and non-task-related properties of the EEG of individuals performing a Simon-task (Simon, 1969; Simon et al., 1981). We deployed a mostly data-driven analysis of time–frequency decomposed data. The behavioral results clearly indicate, that the participants mentally fatigued. Performance in terms of response speed as well as in terms of response accuracy significantly decreased with increasing time-on-task. For response accuracy, the time-on-task effect was even more pronounced in non-corresponding compared to corresponding trials, which could be interpreted as a more severe impact of mental fatigue on cognitive processing when the need for control is higher. The reported levels of subjective fatigue and motivation are in line with the behavioral findings, as subjective fatigue significantly increases and motivation significantly decreases over the course of the experiment.

Our main motivation for this study was to narrow the gap between two recent lines of research investigating mental fatigue by means of the EEG. Studies conducted in the field of applied cognitive science often investigated mental fatigue in simulated (e.g., Wascher, Getzmann, et al., 2016) or real-world environments (e.g., Perrier et al., 2015). In these experimental settings, the onset and offset of task relevant processing often cannot be controlled for. This means that (a) the investigated signal reflects a mixture of task-specific and non-task-related variance and (b) the signal analysis is restricted to non-event-related methods like spectral analysis. These studies consistently observed an increase of spectral power in the theta and alpha frequency band. A second line of research investigated mental fatigue in highly controlled experimental settings (e.g., Boksem et al., 2006) where the onset latencies of task-relevant stimuli are known and the analysis is tailored toward task-related variance. Here, a consistent finding is a decrease of event-related EEG measures with increasing time-on-task. Our goal was to locate the findings from both lines of research in stimulus locked time–frequency space. Our analysis clearly replicated both observations. Spectral power in the theta and alpha band increased with increasing time-on-task. This increase was most pronounced during the intertrial interval (see Figures 3 and 4). Theta activity in response to the imperative stimulus of the Simon-task, however, actually decreased over the course of the experiment.

4 | DISCUSSION

FIGURE 4 The upper row depicts the significant cluster identified for the factor time-on-task. The left panel shows the regression coefficients obtained from fitting a linear regression model using the trial number as predictor, averaged across all channels. The right panel as well as the topographic map show the corresponding effect sizes, averaged across channels and time–frequency points, respectively. The lower row shows the significant cluster identified for the factor trial-type. Here, the left panel shows the normalized power differences as non-corresponding trials—corresponding trials. Again, the right panel and the topographic map depict the effect sizes. The black contour lines indicate the identified clusters and the black asterisks indicate channels with significant effects of the respective cluster.
FIGURE 5  This figure depicts the template activation used for the selection of the spatial filters obtained from GED in the upper left corner. The remaining topographies illustrate the selected individual spatial filters for each participant.

FIGURE 6  The upper panel illustrates time–frequency decomposed data for corresponding trials and the lower panel the data for non-corresponding trials. As for the sensor space data, four 200 trials wide time windows distributed over the course of the experiment are depicted. Here, Z-normalization was applied on a single-trial basis using a trial-specific baseline.
It thus seems that time-on-task effects are opposite for task-related versus non-task-related oscillatory theta activity.

The increase of low-frequency spectral power during the intertrial interval with time-on-task is clearly in line with recent studies (cf. Tran et al., 2020). The location of the effect in the intertrial interval indicates that the increase of spectral power with mental fatigue predominantly reflects a change in the cognitive state of the individual rather than a change in task-related cognitive processing.

Time-on-task-related changes in the spectral power of the alpha band can be interpreted as an increasingly stronger internally oriented focus of attention (Cooper et al., 2003; Hanslmayr et al., 2011). A similar increase of spectral power in the alpha band in the intertrial interval has been described in the context of mind-wandering (Arnau et al., 2020; Compton et al., 2019), suggesting that disengaging from the actual task and engaging in alternative activities is a relevant aspect of mental fatigue. A recent fMRI study also identified a decreasing activity of regions associated with external attention with time-on-task, whereas off-task activity increased (Turnbull et al., 2020).

An interesting question emerging from these observations is whether the increase of theta power, that also has been associated with mental fatigue (cf. Tran et al., 2020), is functionally distinct from the alpha power increase. A proposed point of view that affirms this question is that the theta power increase reflects an increase in cognitive effort in order to compensate the detrimental effects of mental fatigue (e.g., Barwick et al., 2012). Some results from studies deploying event-related EEG analysis have indeed been interpreted as reflecting increases in compensatory neural activity with increasing time-on-task. Haubert and colleagues (2018) observed an increase of N1 amplitudes with time-on-task in individuals performing in a visual attention task. Samuel et al. (2019), moreover, found early ERP components to decrease over time, but late ERP components at frontal recording sites to increase. Similarly, Wang et al. (2016) observed increases of late ERP amplitudes (640–1,272 ms) at frontal leads during the first 80 min of a 160-min Stroop task experiment. However, these findings seem to represent very specific effects, as a large number of studies report declining amplitudes of ERP components that reflect various aspects of cognitive control with increasing time-on-task (e.g., Boksem et al., 2005; Hopstaken et al., 2015; Möckel et al., 2015). Additionally, the presumed electrophysiological correlates of compensatory effort were observed in task-related EEG activity. The results of the present study, moreover, clearly show increasing theta power in the intertrial interval, whereas task-related theta decreases. Furthermore, recent frameworks on mental fatigue conceptualize a decrease of task engagement as a central aspect of mental fatigue (e.g., Boksem & Tops, 2017).
2008; Kurzban et al., 2013) and a decrease in motivation with mental fatigue has also been shown empirically (Boksem et al., 2006; Herlambang et al., 2019). Taken together, it appears unlikely that the theta power increase observed in mentally fatigued individuals during the intertrial interval reflects an increase in (compensatory) cognitive effort. Trejo et al. (2015) hypothesized that the increased spectral power in the theta band might be due to an idling of cognitive control networks, resulting from task disengagement. This interpretation is in line with theories on mental fatigue, while still conceptualizing the observed theta power increases as functionally distinct from alpha power modulations.

An alternative explanation for the theta increase would be to assume that the power increases in the alpha and in the theta band are actually the same effect. Surprisingly, power spectra are rarely reported in studies on mental fatigue deploying spectral analyses and frequency bands of interest are often analyzed in isolation. In some studies, a distinct peak in the theta range is observable in the reported power spectrum, in particular at frontal recording sites (e.g., Trejo et al., 2015). More often, however, theta power increases appear to be driven by larger increases in the alpha range (e.g., Craig et al., 2012; Fan et al., 2015). The results from the present study also suggest the latter (see Figure 4). A potential reason for this covariation of alpha and in particular theta power could be that the alpha peak frequency systematically slows down with increasing time-on-task (Arnau et al., 2017; Benwell et al., 2019). The location of alpha oscillatory activity in frequency space thus shifts toward the lower frequencies when individuals mentally fatigue, eventually leading to power increases in frequencies that are traditionally referred to as theta band (4–8 Hz). A potential pitfall related to this issue is that increases in alpha power with time-on-task are often largest at frontal recording sites (Barwick et al., 2012; Wascher et al., 2014), which is observable in the present study as well (see Figure 4). Given that this alpha anteriorization may lead to increases in the neighboring theta band, such an alpha anteriorization can easily be confused with increases in frontal midline theta. This is particularly the case when single electrodes and specific frequency bands are evaluated in isolation.

5 | CONCLUSION

To sum up, in the present study, we investigated in how far results from two lines of research on mental fatigue can be aligned. (Frontal) theta power has been linked to the exertion of executive control but was also found to increase with time-on-task, particularly in studies from the field of applied sciences. Theoretical frameworks on mental fatigue proposed a decline of task-engagement as the factor causing the decline in performance observed in mentally fatigue individuals. This hypothesis is also supported by the results of event-related EEG studies. Using single-trial regression on time–frequency decomposed data, we could replicate both findings in a single analysis. Task-unrelated spectral power during the intertrial interval increases with time-on-task, whereas task-related theta activity decreases. The latter effect was only descriptively observable and not significant in the analysis of sensor space data, possibly due to its comparably small size in time × frequency space. Using an approach tailored toward task-related theta variance, we could show that the observed task-related theta decrease is indeed significant. The results indicate that the increase in spectral power in the lower frequency bands is possibly not discrete. It is possible that an increase of alpha power with time-on-task spreads to the neighboring frequencies as well. This process is particularly pronounced in the theta range due to a slowing of alpha peak frequency over time. This non-task-related modulation of spectral power with time-on-task may be interpreted as an increasingly internally oriented focus of attention, whereas the decline of task-related theta activity possibly reflects a decreased allocation of attentional resources toward task processing. The alternative explanation for increasing theta power with time-on-task of idling theta networks proposed by Trejo et al. (2015) could also explain the findings of the present study.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Stefan Arnau: Conceptualization; Formal analysis; Methodology; Visualization; Writing-original draft; Writing-review & editing. Tina Brümmer: Conceptualization; Investigation; Methodology; Writing-review & editing. Nathalie Liegel: Methodology; Writing-review & editing. Edmund Wascher: Conceptualization; Methodology; Writing-review & editing.

DATA AVAILABILITY STATEMENT

We uploaded the raw EEG data analyzed in the present study, the Matlab code used for the analysis, an event-coding table, a table containing basic demographic data of the participants, and a schematic illustration of the channel layout to the following OSF repository: Arnau, S., Brümmer, T., Liegel, N., & Wascher, E. (2020, December 16). Inverse effects of time-on-task in task-related and task-unrelated theta activity. https://doi.org/10.17605/OSF.IO/CHMKJ

The Matlab code can also be found at the following GitHub repository: https://github.com/fischmech/theta_time_on_task
REFERENCES
Allison, B. Z., & Polich, J. (2008). Workload assessment of computer gaming using a single-stimulus event-related potential paradigm. *Biological Psychology, 77*(3), 277–283. doi:10.1016/j.biopsycho.2007.10.014

Arnau, S., Löffler, C., Rummel, J., Hagemann, D., Wascher, E., & Schubert, A. L. (2020). Inter-trial alpha power indicates mind wondering. *Psychophysiology, 57*(6), 1–14. doi:10.1111/psyp.13581

Arnau, S., Möckel, T., Rinkenauer, G., & Wascher, E. (2017). The interconnection of mental fatigue and aging: An EEG study. *International Journal of Psychophysiology, 117*, 17–25. doi:10.1016/j.ijpsycho.2017.04.003

Awais, M., Badruddin, N., & Drieberg, M. (2014). Driver drowsiness detection using EEG power spectrum analysis. *IEEE Region 10 Symposium*. https://doi.org/10.1109/TENCONSpri ng.2014.6863035

Barwick, F., Arnett, P., & Slabounov, S. (2012). EEG correlates of fatigue during administration of a neuropsychological test battery. *Clinical Neurophysiology, 123*(2), 278–284. doi:10.1016/j.clinph.2011.06.027

Bener, A., Yildirim, E., Özkan, T., & Lajunen, T. (2017). Driver sleepiness, fatigue, careless behavior and risk of motor vehicle crash and injury: Population based case and control study. *Journal of Traffic and Transportation Engineering (English Edition), 4*(5), 496–502. doi:10.1016/j.jtte.2017.07.005

Benwell, C. S. Y., London, R. E., Tagliabue, C. F., Veniero, D., Gross, J., Keitel, C., & Thut, G. (2019). Frequency and power of human alpha oscillations drift systematically with time-on-task. *NeuroImage, 192*(March), 101–114. doi:10.1016/j.neuroimage.2019.02.067

Bergum, B. O., & Lehr, D. J. (1963). End spurt in vigilance. *Journal of Experimental Psychology, 66*(4), 383–385. doi:10.1037/h0048685.

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2005). Effects of mental fatigue on attention: An ERP study. *Cognitive Brain Research, 25*(1), 107–116. doi:10.1016/j.cogbrbrainres.2005.04.011

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2006). Mental fatigue, motivation and action monitoring. *Biological Psychology, 72*(2), 123–132. doi:10.1016/j.biopsycho.2005.08.007

Boksem, M. A. S., & Tops, M. (2008). Mental fatigue: Costs and benefits. *Brain Research Reviews, 59*(1), 125–139. doi:10.1016/j.brainresrev.2008.07.001

Borghini, G., Astolfi, L., Vecchiato, G., Mattia, D., & Babiloni, F. (2014). Measuring neurophysiological signals in aircraft pilots and car drivers for the assessment of mental workload, fatigue and drowsiness. *Neuroscience & Biobehavioral Reviews, 44*, 58–75. doi:10.1016/j.neubiorev.2012.10.003

Botvinick, M. M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience, 7*(4), 356–366. doi:10.1037/075/4CABN.7.4.356

Caldwell, J. A., Hall, K. K., & Erickson, B. S. (2002). EEG data collected from helicopter pilots in flight are sufficiently sensitive to detect increased fatigue from sleep deprivation. *International Journal of Aviation Psychology, 12*(1), 19–32. doi:10.1207/s15327108iap1201_3

Campainge, A., Pebayle, T., & Muzet, A. (2004). Correlation between driving errors and vigilance level: Influence of the driver’s age. *Physiology & Behavior, 80*(4), 515–524. https://doi.org/10.1016/j.physbeh.2003.10.004

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences, 18*(8), 414–421. https://doi.org/10.1016/j.tics.2014.04.012

Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. B. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology, 49*(2), 220–238. https://doi.org/10.1111/j.1469-8986.2011.01293.x

Cohen, M. X. (2017). Multivariate cross-frequency coupling via generalalyzed eigencomposition. *Elife, 6*, 1–26. https://doi.org/10.7554/eLife.21792

Cohen, M. X. (2019). A better way to define and describe Morlet wavelets for time-frequency analysis. *NeuroImage, 199*(May), 81–88. https://doi.org/10.1016/j.neuroimage.2019.05.048

Compton, R. J., Armstein, D., Freedman, G., Dainer-Best, J., & Liss, A. (2011). Cognitive control in the intertrial interval: Evidence from EEG alpha power. *Psychophysiology, 48*(5), 583–590. https://doi.org/10.1111/j.1469-8986.2010.01124.x

Compton, R. J., Gearinger, D., & Wild, H. (2019). The wandering mind oscillates: EEG alpha power is enhanced during moments of mind-wandering. *Cognitive, Affective and Behavioral Neuroscience, 19*(5), 1184–1191. https://doi.org/10.3758/s13415-019-00745-9

Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology, 47*(1), 65–74. https://doi.org/10.1016/S0167-8600(02)00107-1

Craig, A., Tran, Y., Wijesuriya, N., & Nguyen, H. (2012). Regional brain wave activity changes associated with fatigue. *Psychophysiology, 49*(4), 574–582. https://doi.org/10.1111/j.1469-8986.2011.01329.x

de Cheveigné, A., & Arzoumanian, D. (2015). Scanning for oscillations. *Journal of Neural Engineering, 12*(6), 066020. https://doi.org/10.1088/1741-2560/12/6/066020

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source tool-box for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Dinges, D. F. (1995). An overview of sleepiness and accidents. *Journal of Sleep Research, 4*, 4–14. https://doi.org/10.1111/j.1365-2869.1995.tb00220.x

Duprez, J., Gulbinaite, R., & Cohen, M. X. (2020). Midfrontal theta phase coordinates behaviorally relevant brain computations during cognitive control. *NeuroImage, 207*, 116340. https://doi.org/10.1016/j.neuroimage.2019.116340

Faber, L. G., Maurits, N. M., & Lorist, M. M. (2012). Mental fatigue affects visual selective attention. *PLOS ONE, 7*(10), e48073. https://doi.org/10.1371/journal.pone.0048073

Fan, X., Zhou, Q., Liu, Z., & Xie, F. (2015). Electrocencephalogram assessment of mental fatigue in visual search. *Bio-Medical Materials and Engineering, 26*(s1), S1455–S1463. https://doi.org/10.3233/BME-151444

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory:
Effects of task difficulty, type of processing, and practice. *Cerebral Cortex, 7*(4), 374–385. https://doi.org/10.1093/cercor/7.4.374

Gharagozlou, F., Saraji, G. N., Mazloumi, A., Nahvi, A., Nasrabadi, A. M., Foroushani, A. R., Kheradmand, A. A., Ashouri, M., & Samavati, M. (2015). Detecting driver mental fatigue based on EEG alpha power changes during simulated driving. *Iran Journal of Public Health, 44*(12), 1693–1700.

Grandchamp, R., & Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology, 2*(September), 1–14. https://doi.org/10.3389/fpsyg.2011.00236

Grandjean, E. (1979). Fatigue in industry. *Occupational and Environmental Medicine, 36*(3), 175–186. https://doi.org/10.1136/oem.36.3.175

Guo, Z., Chen, R., Zhang, K., Pan, Y., & Wu, J. (2016). The impairing effect of mental fatigue on visual sustained attention under monotonous multi-object visual attention task in long durations: An event-related potential based study. *PLoS ONE, 11*(9), e0163360. https://doi.org/10.1371/journal.pone.0163360

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews, 67*(1–2), 331–343. https://doi.org/10.1016/j.brainresrev.2011.04.002

Haubert, A., Walsh, M., Boyd, R., Morris, M., Wiedbusch, M., Krusmark, M., & Gunzelmann, G. (2018). Relationship of event-related potentials to the vigilance decrement. *Frontiers in Psychology, 9*(March), 1–11. https://doi.org/10.3389/fpsyg.2018.00237

Helfrich, R. F., & Knight, R. T. (2016). Oscillatory dynamics of prefrontal cognitive control. *Trends in Cognitive Sciences, 20*(12), 916–930. https://doi.org/10.1016/j.tics.2016.09.007

Herlambang, M. B., Taatgen, N. A., & Cnossen, F. (2019). The role of motivation as a factor in mental fatigue. *Human Factors, 61*(7), 1171–1185. https://doi.org/10.1177/0018720819828569

Herman, J., Kafoa, B., Wainiqolo, I., Robinson, E., McCaig, E., Connor, J., Jackson, R., & Ameratunga, S. (2014). Driver sleepiness and risk of motor vehicle crash injuries: A population-based case control study in Fiji (TRIP 12). *Injury, 45*(3), 586–591. https://doi.org/10.1016/j.injury.2013.06.007

Hockey, G. R. J. (1997). Compensatory control in the regulation of human performance under stress and high workload: A cognitive-energetical framework. *Biological Psychology, 45*(1–3), 73–93. https://doi.org/10.1016/S0301-0511(96)00522-4

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience, 3*(3), 284–291. https://doi.org/10.1038/72999

Hopstaken, J. F., van der Linden, D., Bakker, A. B., & Komppier, M. A. J. (2015). A multifaceted investigation of the link between mental fatigue and task disengagement. *Psychophysiology, 52*(3), 305–315. https://doi.org/10.1111/psyp.12339

Ithipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Experimental Brain Research, 222*(4), 255–262. https://doi.org/10.1007/s00221-012-3305-3

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews, 29*(2–3), 169–195. https://doi.org/10.1016/S0165-0173(98)00056-3

Kool, W., & Botvinick, M. M. (2014). A labor-leisure tradeoff in cognitive control Wouter. *Journal of Experimental Psychological General, 143*(1), 131–141. https://doi.org/10.1037/a0031048A

Körber, M., Cingel, A., Zimmermann, M., & Bengler, K. (2015). Vigilance decrement and passive fatigue caused by monotony in automated driving. *Procedia Manufacturing, 3*, 2403–2409. https://doi.org/10.1016/j.promfg.2015.07.499

Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences, 36*(6), 661–679. https://doi.org/10.1017/S0140525X12003196

Lal, S. K. L., & Craig, A. (2001). A critical review of the psychophysiology of driver fatigue. *Biological Psychology, 53*(3), 173–194. https://doi.org/10.1016/S0301-0511(00)00085-5

Lal, S. K. L., & Craig, A. (2002). Driver fatigue: Electroencephalography and psychological assessment. *Psychophysiology, 39*(3), 313–321. https://doi.org/10.1111/1469-8986.36.3.175

Lorist, M. M., Boksem, M. A. S., & Ridderinkhof, K. R. (2005). Impaired cognitive control and reduced cingulate activity during mental fatigue. *Cognitive Brain Research, 24*(2), 199–205. https://doi.org/10.1016/j.cogbrainres.2005.01.018

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods, 164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Möckel, T., Beste, C., & Wascher, E. (2015). The Effects of time on task in response selection—An ERP study of mental fatigue. *Scientific Reports, 5*(1), 1–9. https://doi.org/10.1038/srep10113

Mordkoff, J. T. (2019). A simple method for removing bias from a popular measure of standardized effect size: Adjusted partial eta squared. *Advances in Methods and Practices in Psychological Science, 2*(3), 228–232. https://doi.org/10.1177/2515245919855053

Nikulin, V. V., Nolte, G., & Curio, G. (2011). A novel method for reliable and fast extraction of neuronal EEG/MEG oscillations on the basis of spatio-spectral decomposition. *NeuroImage, 55*(4), 1528–1535. https://doi.org/10.1016/j.neuroimage.2011.01.057

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *NeuroImage, 27*(2), 341–356. https://doi.org/10.1016/j.neuroimage.2005.04.014

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience, 2011*, 1–9. https://doi.org/10.1155/2011/156869

Papadelis, C., Chen, Z., Kourtidou-Papadeli, C., Bamidis, P. D., Chouvarda, I., Bekiaris, E., & Maglaveras, N. (2007). Monitoring sleepiness with on-board electrophysiological recordings for preventing sleep-deprived traffic accidents. *Clinical Neurophysiology, 118*(9), 1906–1922. https://doi.org/10.1016/j.clinph.2007.04.031

Perrier, J., Leufkens, T. R. M., Bulla, J., Jongen, S., Bocca, M. L., Ramaekers, J. G., & Vermeeren, A. (2015). Electroencephalography during on-the-road driving in older untreated insomnia patients and normal sleepers. *Biological Psychology, 109*, 20–28. https://doi.org/10.1016/j.biopsycho.2015.04.002

Pluetscheller, G., & Lopes Da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology, 110*(11), 1842–1857. https://doi.org/10.1016/S1388-2457(99)00141-8

Phipps-Nelson, J. O., Redman, J. R., & Rajaratnam, S. M. W. (2011). Temporal profile of prolonged, night-time driving performance: Breaks from driving temporarily reduce time-on-task fatigue but not sleepiness. *Journal of Sleep Research, 20*(3), 404–415. https://doi.org/10.1111/j.1365-2869.2010.00900.x

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component
classifier, dataset, and website. *NeuroImage*, 198, 181–197. https://doi.org/10.1016/j.neuroimage.2019.05.026

Samuel, B. H. I., Wang, C., Burke, S. E., Kluger, B., & Ding, M. (2019). Compensatory neural responses to cognitive fatigue in young and older adults. *Frontiers in Neural Circuits*, 13(February), 1–12. https://doi.org/10.3389/fncir.2019.00012

Saxby, D. J., Matthews, G., Hitchcock, E. M., Warm, J. S., Funke, G. J., & Gantzer, T. (2008). Effect of Active and Passive Fatigue on Performance Using a Driving Simulator. *Proceedings of the Human Factors and Ergonomics Society Annual Meeting*, 52(21), 1751–1755. https://doi.org/10.1177/154193120805202113

Simon, J. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology*, 81(1), 174–176. https://doi.org/10.1037/h0027448

Simon, J., Sly, P., & Vilapakkam, S. (1981). Effect of compatibility of SR mapping on reactions toward the stimulus source. *Acta Psychologica*, 47, 63–81. https://doi.org/10.1016/0001-6918(81)90039-1

Smit, A. S., Eling, P. A. T. M., Hopman, M. T., & Coenen, A. M. L. (2005). Mental and physical effort affect vigilance differently. *International Journal of Psychophysiology*, 57(3), 211–217. https://doi.org/10.1016/j.ijpsycho.2005.02.001

Tanaka, M., Shigihara, Y., Ishii, A., Funakura, M., Kanai, E., & Watanabe, Y. (2012). Effect of mental fatigue on the central nervous system: An electroencephalography study. *Behavioral and Brain Functions*, 8(1), 48. https://doi.org/10.1186/1744-9081-8-48

Thijffault, P., & Bergeron, J. (2003). Monotony of road environment and driver fatigue: A simulator study. *Accident Analysis & Prevention*, 35(3), 381–391. https://doi.org/10.1016/S0001-4575(02)00014-3

Tops, M., & Boksem, M. A. S. (2010). Absorbed in the task: Personality measures predict engagement during task performance as tracked by error negativity and asymmetrical frontal activity. *Cognitive, Affective and Behavioral Neuroscience*, 10(4), 441–453. https://doi.org/10.3758/CABN.10.4.441

Torsvall, L., & Akerstedt, T. (1987). Sleepiness on the job: Continuously measured EEG changes in train drivers. *Electroencephalography and Clinical Neurophysiology*, 66(6), 502–511. https://doi.org/10.1016/0013-4694(87)90096-4

Tran, Y., Craig, A., Craig, R., Chai, R., & Nguyen, H. (2020). The influence of mental fatigue on brain activity: Evidence from a systematic review with meta-analyses. *Psychophysiology*, 57(5), 1–17. https://doi.org/10.1111/psyp.13554

Trejo, L. J., Kubitz, K., Rosipal, R., Kochavi, R. L., & Montgomery, L. D. (2015). EEG-Based Estimation and Classification of Mental Fatigue. *Psychology*, 6(5), 572–589. https://doi.org/10.4236/psych.2015.65055

Turnbull, A., Karapanagiotidis, T., Wang, H. T., Bernhardt, B. C., Leech, R., Margulies, D., Schooler, J., Jefferies, E., & Smallwood, J. (2020). Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought. *Scientific Reports*, 10(1), 1–10. https://doi.org/10.1038/s41598-020-66698-z

Wang, C., Trongetrpunya, A., Samuel, I. B. H., Ding, M., & Kluger, B. M. (2016). Compensatory neural activity in response to cognitive fatigue. *Journal of Neuroscience*, 36(14), 3919–3924. https://doi.org/10.1523/JNEUROSCI.3652-15.2016

Wascher, E., Getzmann, S., & Karthauser, M. (2016). Driver state examination—Treading new paths. *Accident Analysis and Prevention*, 91, 157–165. https://doi.org/10.1016/j.aap.2016.02.029

Wascher, E., Heppner, H., Kobald, S. O., Arnau, S., Getzmann, S., & Möckel, T. (2016). Age-sensitive effects of enduring work with alternating cognitive and physical load. A study applying mobile EEG in a real-life working scenario. *Frontiers in Human Neuroscience*, 9, 1–14. https://doi.org/10.3389/fnhum.2015.00711

Wascher, E., Rasch, B., Sänger, J., Hoffmann, S., Schneider, D., Rinkenauer, G., Heuer, H., & Gutberlet, I. (2014). Frontal theta activity reflects distinct aspects of mental fatigue. *Biological Psychology*, 96(1), 57–65. https://doi.org/10.1016/j.biopsycho.2013.11.010

Zakrzewska, M. Z., & Brzezicka, A. (2014). Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task. *Frontiers in Human Neuroscience*, 8(June), 1–7. https://doi.org/10.3389/fnhum.2014.00399

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