TITLE

Oscillatory dynamics of sustained attention states

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ABSTRACT

Sustained attention enables individuals to concentrate on a task over an extended period of time. This ability is known to fluctuate, resulting in periods of effective task focus ('in the zone') and periods of increased performance variability and susceptibility to errors ('out of the zone'). Little is known about the oscillatory neural dynamics that underlie each of these states and their transitions during sustained attention tasks. To address this, we had thirty young adults perform the gradual onset continuous performance task (gradCPT), during which their EEG and behavioural responses were recorded. States of sustained attention (in vs. out of the zone) throughout the task were identified based on the variance time course of participants' reaction times. Out of the zone states were associated with increased errors of commission and reduced perceptual sensitivity compared to in the zone states, as expected. Importantly, a significant decline in theta oscillations at mid-prefrontal regions was found in out of the zone (vs. in the zone) states over a ~400 ms period around the transition point between stimuli, and the extent of this decline predicted commission errors, RT variability, and response bias. In addition, individual differences in the variability of frontal theta rhythm were associated with RT variability. Finally, participants exhibiting greater theta variability showed a more pronounced decline in perceptual sensitivity when out of the zone and less stable RTs compared to those with lower variability. Our results suggest that states of diminished sustained attention, even during short lapses, are characterized by a reduction in frontal theta activity, and that fluctuations in this rhythm covary with fluctuations in attentional control.

KEYWORDS

Beta, EEG oscillations, gradCPT, 'in the zone', 'out of the zone', sustained attention, theta.

INTRODUCTION

Sustained attention, namely the ability to maintain attention focus throughout any mental task, is critical for effective information processing and performance (Esterman & Rothlein, 2019). Sustained attention is known to decline with a longer time-on-task, resulting in increased RT and error rates, typically explained by increased "mental fatigue" and decreased vigilance (Warm, Parasuraman, & Matthews, 2008; Wascher, et al., 2014). Cognitive control also deteriorates with longer time-on-task, as evidenced in increased failures to inhibit responses to designated 'NoGo' target stimuli (e.g. (Manly, Robertson, Galloway, & Hawkins, 1999; Terentjeviene, et al., 2018)).

EEG research has identified increased alpha oscillations (8-14 Hz) at frontal and posterior brain regions thought to reflect reduced cortical excitability associated with reduced vigilance with a longer time-on-task. An increase in theta band (4-7 Hz) oscillations over frontal midline channels (known as FM theta) is typically found as well, and is thought to reflect increased demand on cognitive control to bring attention back to the task, due to the increased lapses of attention as the task goes on (see Clayton et al. (2015) for a review and Tran et al. (2020) for a meta-analysis).

In addition to the decline with time-on-task, sustained attention is also found to fluctuate along the task period. A greater level of attention fluctuations has been reflected in increased response variability, along with a reduction in performance accuracy (Esterman, Noonan, Rosenberg, & Degutis, 2013; Flehmig, Steinborn, Langner, Scholz, & Westhoff, 2007; Rosenberg, Noonan, DeGutis, & Esterman, 2013) especially in populations characterized by either immature attention in earlier stages of development (Hobbiss & Lavie, 2024) or clinical attention deficits (Epstein, et al., 2011; Tamm, et al., 2012). While response variability tends to increase with time-on-task (Gilsoul, Libertiaux, Depierreux, & Collette, 2024), a growing body of studies has demonstrated that fluctuations of sustained attention can be found throughout the task, with periodic states of reduced attention focus (a state of being 'out of the zone'), associated with increased response variability and reduced detection performance, interspersed between periods of effective focus (or 'in the zone' states) with a consistent level of responses and higher detection performance (Fortenbaugh, DeGutis, & Esterman, 2017; Jun & Lee, 2021; Rosenberg, Noonan, DeGutis, & Esterman, 2013). These attention states have been identified in a modified continuous performance task (CPT), which has replaced the abrupt onset of each trial in the CPT with a gradual change from one image to the next, hence termed gradual-onset continuous performance task (gradCPT, Rosenberg et al., (2013)). Since abrupt onsets are known to capture attention and can thus facilitate task focus in a bottom-up manner (reducing the demand on cognitive control), their removal in the gradCPT makes this task particularly sensitive to detect periodic states of reduced attention focus (Esterman, Noonan, Rosenberg, & Degutis, 2013; Fortenbaugh, Rothlein, McGlinchey, DeGutis, & Esterman, 2018). Work employing this task has shown that, although the frequency of out of the zone states increases with time-on-task, as would be expected from increased demand on sustained attention, these states occur even in early task periods (Esterman, Noonan, Rosenberg, & Degutis, 2013).

fMRI studies of the sustained attention states identified through the gradCPT have demonstrated changes in the levels of activity of the Default Mode Network (DMN) and the dorsal attention network (DAN) in relation to attentional states of in the zone (a moderate increase of DMN activity associated with reduced variability and errors) and out of the zone (increased DAN activity, thought to reflect the increased demand on cognitive control to maintain task responses despite reduced attention) (Esterman, Noonan, Rosenberg, & Degutis, 2013; Fortenbaugh, Rothlein, McGlinchey, DeGutis, & Esterman, 2018; Kucyi, Hove, Esterman, Hutchison, & Valera, 2017). Spontaneous changes in the level of DMN signal were also found predictive of performance (Kucyi, Esterman, Riley, & Valera, 2016). However, fMRI studies such as these are unable to tell us about the oscillatory dynamics the brain uses to coordinate its activity, and how these differ across sustained attentional states that are indicated by changes in RT variability.

One recent study in healthy adults (Wang et al., 2020) examined the relationship of RT variability and EEG oscillations in a forced choice RT task (requiring to press one of two keys to indicate the direction of an arrow) previously used to measure sustained attention deficits in children with ADHD and reported no correlation between RT variability (measured with SD) and EEG (i.e. theta) variability. However, the task used was short (eight minutes long) and involved abrupt stimulus display onsets on each trial, so it is plausible that it was not sensitive to reveal fluctuations of sustained attention states. We note that the RT variability showed a significant correlation with theta activity in terms of fluctuations of amplitude of low-frequencies (0.01–0.027 Hz) in one left frontal channel. However, as these findings did not relate to decrement in task performance, their functional significance is unclear.

Overall then, the oscillatory dynamics associated with fluctuations of sustained attention states from being in versus out of the zone and their potential role in predicting individual differences in sustained attention have not yet been identified. We thus set out to investigate these questions in the present study using the gradCPT and investigating the relationship of EEG power, both at channel and source levels, as well as power variability of relevant brain rhythms, with states of sustained attention. In addition, since the phase steadiness of neuronal oscillations has been shown to play an important role in the fine temporal attunement of attentional and cognitive control (Bonnefond & Jensen, 2012; Solis-Vivanco, Jensen, & Bonnefond, 2018), phase alignment across trials (phase-locking factor, PLF) was also explored. Finally, we sought to identify whether the variability (i.e. power levels) along the task can directly predict variability in performance.

METHODS

Participants

Thirty-one adults were recruited via the University College London SONA system. This sample size allowed a power of 0.85 to detect effect sizes of 0.5 and above in paired samples t- tests (comparisons of in the zone versus out of the zone states). One participant was excluded from the

analysis due to difficulties to record their EEG data. The final sample was of 30 participants (mean age=25±5.1, 15 women, 26 right-handed). All participants reported normal vision and no clinical (neurological or mental health) diagnosis. The study was approved by the UCL Research Ethics Committee, and all participants gave a written informed consent before any experimental procedure took place. Participants were compensated £20 for taking part in the study.

Experimental paradigm

The gradCPT was administered. Similar to Esterman et al. (2013), the task included 10 round, grayscale photographs of mountain scenes and 10 of city scenes of 8.9 cm circumference, which at a fixed viewing distance of 64 cm (held with a head rest) subtended 8 degrees of visual angle. All the images were displayed against a gray background on a gamma-corrected Dell monitor with 2560 x 1440 resolution and refresh rate set to 60 Hz. The images were calibrated to have a mean luminance matching the gray background and 20% Michelson contrast. On 90% of the trials a city scene was presented, and on 10% a mountain scene was presented. The images were presented randomly with a smooth transition between them on a frame-by-frame basis, reaching full transition every 800 ms, using a linear pixel-by-pixel interpolation (in steps of 2.08% coherence per frame). Any one scene was not allowed to be repeated on consecutive trials. Participants were instructed keep their gaze on a white fixation point in the middle of the images throughout the experiment and to press the spacebar on a standard computer keyboard using their dominant hand each time they detected a city scene (Go trials) and withhold their response for mountain scenes (NoGo trials).

Procedure

After the signing of the informed consent, participants underwent 2 practice blocks. The first one was presented at ~ 50% of the normal speed for 30 seconds. The second one was presented at normal speed for 60 seconds. After practice, each participant completed a total of 2250 trials made up of 5 blocks with 6 minutes duration each. Participants were forced to take at least 30 seconds break between each block. The total duration of this experiment was approximately 40 minutes. Participants were encouraged to respond as quickly and accurately as possible.

EEG recording and pre-processing

We recorded a digital EEG while participants performed the gradCPT in a dimly lit room. We used a BioSemi Active Two system with a sampling rate of 1024 Hz and offsets between +/-20 along the recording. The EEG recording was obtained from 57 silver-chloride electrodes placed according to the international 10/10 system. In parallel, we recorded the pupillary dilation of both eyes during task execution with an Eyelink 1000 eye tracker (reported in Liu (2019)). Seven electrodes (F7, AF7, FP1, FPZ, FP2, AF8, F8) were excluded from the standard 64 channels due to the use of a forehead rest to stabilize the participants' heads, as required by the eye tracking system. The Common Mode Sense (CMS) and Driven Right Leg (DRL) electrodes were employed as grounds. All scalp electrodes were referenced to the CMS during recording.

All offline EEG analyses were conducted using custom MATLAB 2017b scripts and the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The EEG was down sampled to 500 Hz and segmented in 1600 ms windows, with -800 ms and +800 ms relative to the transition point between stimuli (100% Nth-1/ 0% Nth coherence). The EEG segments were re-referenced to the average of all EEG channels and baseline-corrected for the entire segment. Subsequently, we removed noisy or atypical segments in terms of voltage variance using the ft_rejectvisual function. The remaining segments were visually inspected using the ft_databrowser function to eliminate those with noise or artifacts, including blinks and muscle-related artifacts. For all segments, we identified RT, response type, and falling out or in the zone (as described below). The mean number of selected trials for being out and in the zone was 501±95 and 1249±175, respectively. Before the task, we recorded 3 minutes of resting-state EEG while participants kept their eyes closed, whose results will be reported elsewhere.

Behavioural analysis

We recorded responses and calculated accuracy and error rates, as well as RTs from the transition point of Go trials (100% coherence of the previous scene and 0% of the current one). Following the protocol in Esterman et al. (2013), trials with deviant RTs (before 70% coherence of the previous image and after 40% coherence of the current scene) or with more than one button presses (ambiguous presses) were treated as follows. Presses were assigned to an adjacent trial if 1 of the 2 had no response. If both adjacent trials had no response, the press was assigned to the closest trial, unless one was a NoGo scene, in which case it was assumed that participants correctly responded to the Go scene. Finally, if there were multiple presses that could be assigned to any 1 trial, the fastest response was selected.

Performance was evaluated in terms of mean RT, variability of responses measured by the coefficient of variation (CoV = SD/M), commission response rates for both Go (i.e. correct commissions) and NoGo (i.e. errors of commission) trials, as well as the non-parametric estimate (A') of discrimination sensitivity index (Zhang & Mueller, 2005) and response criterion (β).

Attention zones (in and out) were defined using a variance time course (VTC) analysis (Esterman, Noonan, Rosenberg, & Degutis, 2013), which consists of calculating the absolute z-scores of RTs in Go trials. The sliding window approach of averaging VTC values over nine consecutive trials (7.2 s) was applied to extract accuracy measures during the attention zones. Trials in the zone were those whose RTs were within 1 SD with respect to the mean, while out of the zone were those either over 1SD or below -1 SD.

EEG analysis

The EEG data were explored through time-frequency (TF) representations of power and phase alignment across trials. All TF analyses were centered around the transition point between stimuli (100% Nth-1/ 0% Nth coherence) and included 3 to 40 Hz oscillations, therefore encompassing

theta (3-7 Hz), alpha (8-14 Hz), and beta (15-40 Hz) bands. Only segments centered around correct commissions (Go trials) were further analyzed.

Power was calculated through a fast Fourier transformation (FFT) along an adaptive sliding time window including 2 cycles of each oscillation (ΔT = 2/f; e.g. 200 ms for 10 Hz). A Hanning taper (also ΔT long) was multiplied by the data before the FFT. All power values were log-transformed and averaged across trials regarding their evaluated condition (i.e., attention zones).

The phase stability across trials was explored using the phase data from the FFT and calculating the the Phase Locking Factor (PLF), also known as Inter-trial Phase Clustering (ITPC) (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). The PLF over N trials is defined as:

$$PLF(f_o, t) = \frac{1}{N}\left|\sum_{k=1}^{N} e^{i\varphi^k(f_0,t)}\right|$$

where $\varphi^k(f_0, t)$ corresponds to the estimated phase at frequency f_0 and time t resulting from the time-frequency analysis. The PLF quantifies the degree to which the distribution of phase angles across trials at each time-frequency-sensor point is not uniformly distributed. A PLF value approaching 0 suggests high phase variability, while a PLF value of 1 indicates that all trials exhibit the same phase at a particular frequency and time point. Similar to the TF representation analysis of power, the PLF was computed using a sliding time window that was 2 cycles in length, and a Hanning taper was applied to it. For the PLF calculation, we randomly selected the same number of trials for being in the zone with respect to being out of the zone. This was done because the PLF is sensitive to the number of observations (Cohen, 2014) and comparisons between zones were planned.

Source analysis

The significant power effects (see results) were described from a source perspective as well. We used the Dynamic Imaging of Coherent Sources (DICS) technique, a frequency-domain beamforming approach, to estimate the absolute power at the source level in the entire brain. The cross-spectral density matrices were obtained by applying a multitaper frequency transformation approach on data measured from the channels. For each participant, a realistically shaped single-shell description of the brain was constructed based on an adult template MRI provided by the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), whose volume was divided into a grid with a 1 cm resolution and normalized with respect to a template MNI brain. The lead field and the cross-spectral density were used to calculate a spatial filter for each grid point and the spatial distribution of power was estimated for each zone state (in and out) in each participant. A common filter was used when comparing the zone states (based on the cross-spectral density matrices of the combined states). The estimated power was averaged over trials and log transformed. The power difference between zone states was calculated and averaged across participants. The source estimates were plotted on a standard MNI brain found in SPM8.

Statistical analyses

For behavioural data, paired t-tests were performed to evaluate the effect of time-on-task within a continuous task-block (0-3 minutes vs. 3-6 minutes) on performance measures and on the out of the zone occurrence rate. We also ran comparisons between attention zones (out vs. in the zone) on accuracy and sensitivity rates using paired t-tests.

For EEG data, we first compared the time-frequency representations of power and PLF between out vs. in the zone periods using a cluster-based nonparametric randomization test (Maris & Oostenveld, 2007). This test manages the control of the Type I error rate in scenarios where there are multiple comparisons involving sensors, frequencies, and time periods. It does so by grouping together neighboring sensors, time points, and frequency points that exhibit a similar effect. We examined frequencies ranging from 3 to 40 Hz, incrementing by 1 Hz. This analysis was performed from -800 ms to +800 ms with respect to the transition point between stimuli (100% Nth-1/0% Nth coherence). Electrodes that exhibited a t value difference between conditions exceeding a pre-established threshold ($p < .05$) were chosen and subsequently clustered based on their spatial proximity. The sum of the t values within a cluster served as the cluster-level statistic. The cluster with the highest cumulative t values was used as the test statistic. To determine the statistical significance of a particular effect, we generated a reference distribution by randomly permuting the data between the two conditions and recalculating the test statistic 1000 times (Monte Carlo estimation). Effect sizes for these tests were calculated from the average over the cluster as detailed in the Fieldtrip website (https://www.fieldtriptoolbox.org/example/effectsize/).

To determine whether EEG changes between out vs. in the zone were associated with task performance differences between participants, we calculated the magnitude of power change between zones (out-in) in time-frequency-channels of interest (as revealed by the nonparametric test, see Power section of Results) and ran Pearson correlation analyses with RT CoV, responses rate, sensitivity (A'), and response criterion (β).

In addition, we explored whether the variability of EEG power along the task was able to predict differences in task performance between participants. Specifically, for time-frequency-channel regions with significant differences of power between zones (as revealed by the nonparametric test), we calculated the power CoV among trials. We then compared the power CoV between out vs. in the zone with a paired t-test. Also, as with power, we explored the association between power CoV and behavioural variability measures through Pearson correlations. Finally, we explored whether individual differences in power CoV were associated with behavioural instability along the task: participants were divided by a median split based on power CoV (low/high) and compared them in terms of behaviour (mean RT, RT CoV, and responses rate) using repeated measures ANOVA considering group as the between-subject factor and time-on-task (0-3 min/3-6 min) as the within-subject factors. These groups were also compared for discrimination sensitivity (A') and response criterion (β) along the task with independent samples t-tests. All ANOVA comparisons were adjusted by sphericity according to the Greenhouse-Geisser correction, and all post hoc analyses were done with a Bonferroni correction. Finally, we ran multiple regression models to

assess the different predictive power of the EEG measures of power and power CoV in relation to the different performance measures.

Statistical significance for all analyses was established at $p<.05$. JASP (https://jasp-stats.org) and Matlab (MathWorks Inc.) software were used for all statistical analyses.

RESULTS

Behaviour

Across the 6-min runs, time-on-task led to slower ($t(29)=-4.4$, $p<.001$, Cohen's $d=-0.803$, Figure 1A) and more variable ($t(29)=-3.86$, $p=.001$, Cohen's $d=-0.706$, Figure 1B) RTs. Discrimination sensitivity (A') decreased over time ($t(29)=2.66$, $p=.013$, Cohen's $d = 0.486$, Figure 1C) as did the rate of correct commissions in Go trials ($t(29)=4.09$, $p<.001$, Cohen's $d=0.746$, Figure 1D). These effects demonstrate the expected effect of time-on-task on sustained attention. The rate of errors of commission in NoGo trials however was unaffected ($t(29)=0.02$, $p=.984$, Cohen's $d=0.004$, Figure 1E).

Considering the sustained attention states as indexed with our VTC analyses, we found that out of the zone states became more prevalent as a function of time ($t(29) = -4.58$, $p < .001$, Cohen's $d = -0.836$, Figure 1F). Out of the zone states involved reduced discrimination sensitivity ($t(29) = 14.06$, $p < .001$, Cohen's $d = 2.567$, Figure 1G), reduced rate of correct commissions (Go trials) ($t(29) = 14.39$, $p < .001$, Cohen's $d = 2.627$, Figure 1H), and increased rate of errors of commission (NoGo trials) ($t(29) = 7.99$, $p < .001$, Cohen's $d =1.458$, Figure 1I) compared to in the zone states.

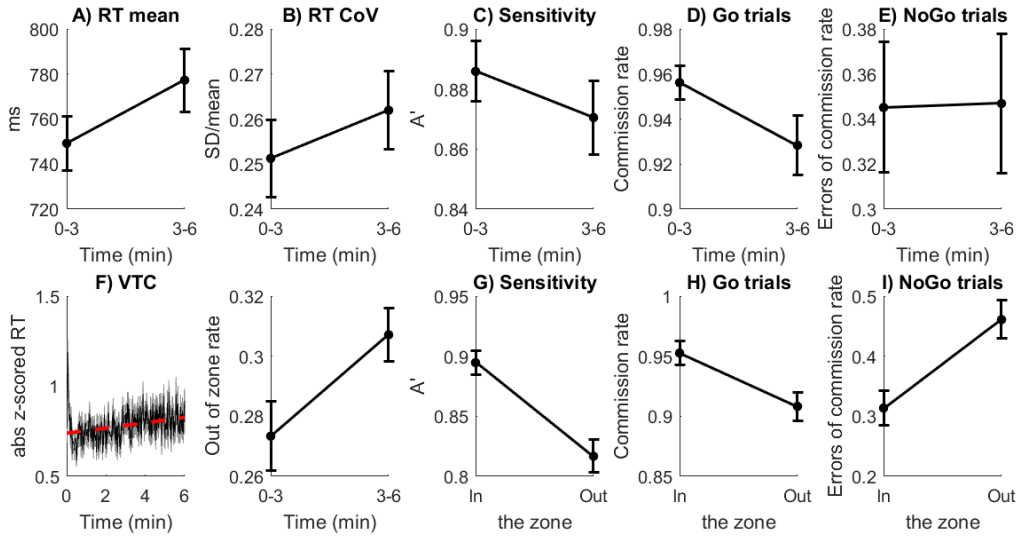

Figure 1. Participants´ performance (mean±SEM). With time-on-task, participants showed (A) increased mean RT to Go trials, (B) higher coefficient of variation (CoV) of Go RTs, (C) decreased discrimination sensitivity (A'), (D) lower rate of correct commissions (Go trials), and (E) no changes in the rate of errors of commission (NoGo trials). (F) Variation time course (VTC) analysis. Left panel: absolute z-scored RTs as a function of the time, and its linear trend represented by the dashed line. Right panel: proportion of the out of the zone state (VTC > 1) as a function of time-on-task. Being out of the zone was associated with (G) lower discrimination sensitivity (A'), (H) lower rate of correct commissions (Go trials), and (I) higher rate of errors of commission (NoGo trials).

EEG

Power

Figure 2A shows the results of the TF analysis of power which revealed a decrease within the theta range (4-7 Hz) for out vs. in the zone states. The non-parametrical permutation test showed a significant decrease (cluster statistic=-29, p=0.002, Cohen's d=.77) over a 400 ms period around the transition point (0 ms) of Go trials (Figure 2A, dashed rectangle). The significant effect covered a frontal-midline region, with the highest differences in F1, FC1, Fz, FC2, and FCz (Figure 2B). The beamformer source analysis revealed changes at frontal and cingular regions, with the maximum difference at medial frontal cortex (Figure 2C), corresponding to cognitive control regions (Widge, Heilbronner, & Hayden, 2019). Frontal theta power did not change significantly with time-on-task: it did not increase along the experiment blocks (block effect: $F(1,28)=1.97$, $p=.11$, $n^2_p=.07$) nor changed between the 1st and 2nd halves of the blocks (time effect: $F(1,28)=1.66$, $p=.21$, $n^2_p=.06$). Thus, the decrease in frontal theta power in out vs. in the zone trials was specific to the attention zone state.

Figure 2A (dotted rectangles) also shows the effects of sustained attention states on beta (15-30 Hz) power. The non-parametric permutation test revealed that out vs. in the zone states were associated with a significant increase in beta power at frontal regions around the stimulus transition point (0 ms), during Go trials (cluster statistic=45, p<.001, Cohen's d=.97; Figure 2D) together with a significant reduction about 400 ms after stimulus transition (cluster statistic=-42, p<.001; Cohen's d=.94; Figure 2D), both at left central regions, around the primary motor cortex (Figure 2E).

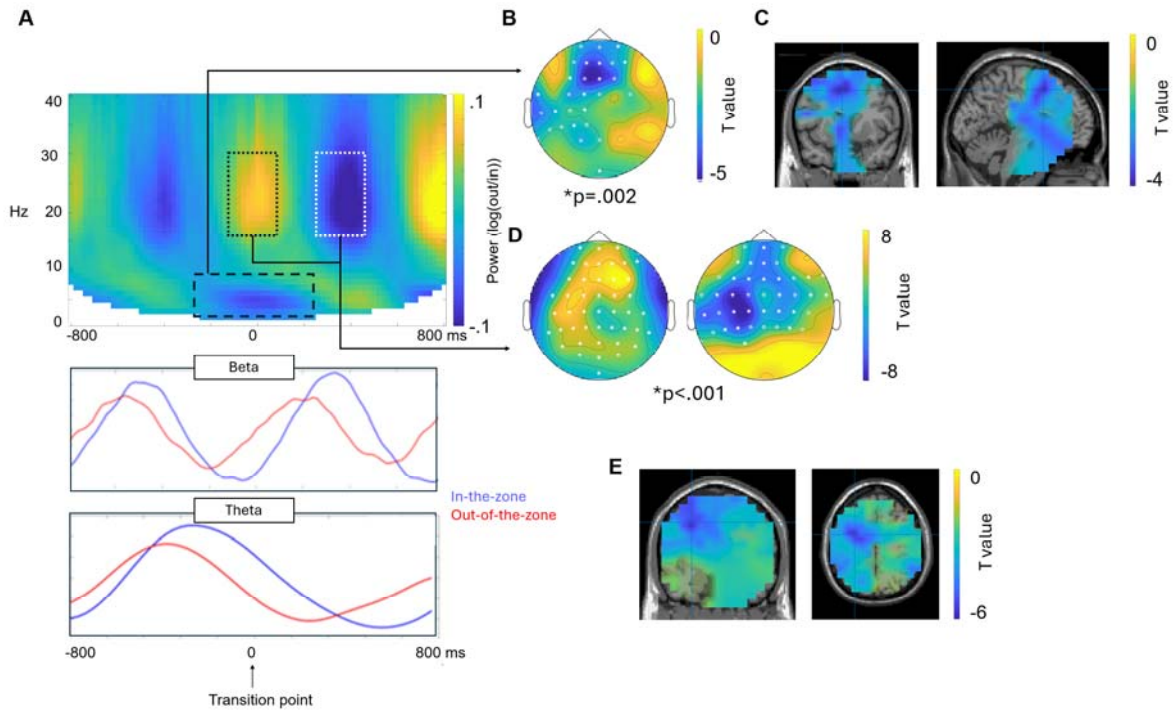

Figure 2. EEG power differences between out- vs. in the zone during sustained attention. A) Time-frequency representations of power revealed significant decreases of theta (dashed rectangle) and a fluctuating change in beta power (dotted rectangles) around the stimuli transition point (100% Nth-1/0% Nth coherence) of Go trials. The lower panels show the temporal dynamics of each band along the trial. The figures correspond to the mean across channels with significant differences. B) Statistical topography with channels where differences were significant for theta power *p=.002. C) Source projection of significant differences for theta power. D) Statistical topographies with channels where differences were significant for beta power *p<.001. E) Source projections of significant differences for beta power.

EEG power and differences in task performance

We further tested whether power changes when out- vs. in the zone were associated with differences in task performance between participants. Pearson analyses revealed that a stronger decline in theta power when out vs. in the zones was associated with higher RT CoV (r=.49, p=.006, Fisher's z=-.53; Figure 3A) as well as higher rates of commission responses both on Go (r=.41,

p=.02, Fisher's z=-.44; Figure 3B) and on NoGo trials (i.e. errors of commission, or attention lapses) (r=.45, p=.01, Fisher's z=.48; Figure 3C). These findings suggest that a greater decline in theta power during out of the zone states results not only in increased CoV but also in a response bias, with a greater decline involving increased commission responses on all trials (r=.58, p<.001, Fisher's z=.66; Figure 3D). In addition, a stronger decline in theta power during out the zone (vs. in the zone) states was associated with a greater increase in the number of errors of commission (i.e. failures to withhold response in NoGo trials) when out of the zone as compared to in the zone states: r=.40, p=.028, Fisher's z=-.43; Figure 3E). There was no significant association between theta power decline in out (vs. in the zone) states and the effect of attention state on the number of correct commissions in Go trials (r=.31, p=.09, Fisher's z=.32; Figure 3F). No associations were found for theta power decline and sensitivity (A', r=.14, p=.47, Fisher's z=.14) nor with sensitivity difference between zones (r=-.05, p=.79, Fisher's z=.05).

Beta power was found to be associated with task performance, such that stronger beta power decline 400 ms after stimulus transition point was associated with the rate of correct commissions (Go trials) (r=.39, p=.03). No correlations were found between the beta power differences between zones around the transition point of stimuli and behaviour (all r<.35, all p>.06).

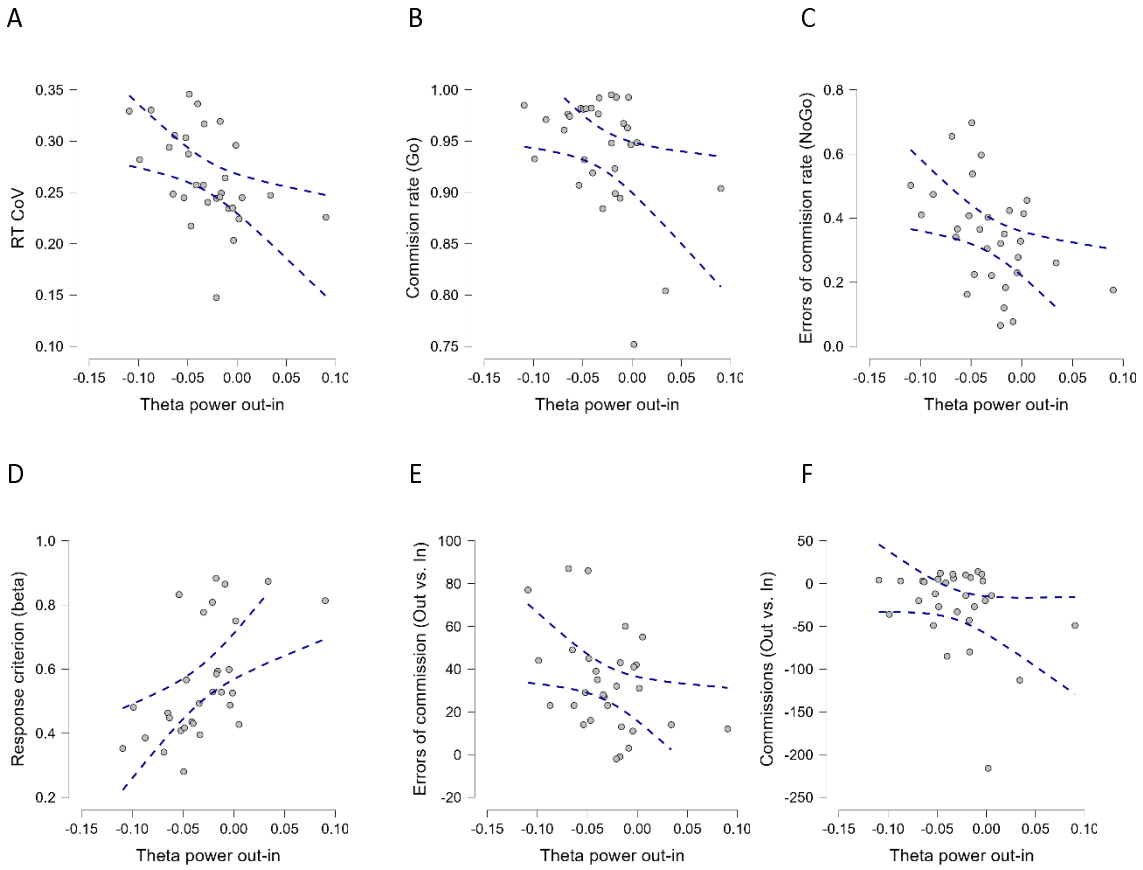

Figure 3. Theta power differences between attention zones (out vs. in) and its association with task performance. Greater theta decline in out of (vs. in) the zone is associated with (A) increased RT CoV, (B) increased (correct) commission rates in Go trials and (C) in NoGo trials (errors of commission), (D) lower response criterion, as well as (E) higher number of errors of commission in NoGo trials in out vs. in the zone states and (F) an increase in the commission responses in Go trials in out vs. in the zone states. Blue dotted lines indicate confidence intervals (95%).

EEG power variability

Just as response variability provides insight into attention levels, we hypothesized that variability in power levels could also offer significant predictive information about the underlying attention processes. When comparing theta and beta power CoV between out vs. in the zones, we did not find significant differences (t(29)=.46, p=.65, and t(29)=.06, p=.96, respectively).

To assess power variability within participants, in each trial we averaged the theta and beta power within the channels that showed zone effects (see Figure 2B for theta and 2D for beta) and then calculated their power CoV. For beta power, we calculated the CoV at each time window with significant effects (Figure 2D). We found that theta power CoV was positively correlated with RT

CoV (r=.38, p=.04, Fisher's z=.39; Figure 4A). No more significant correlations were found between theta power CoV and behavioural measures (all p>.1). No significant correlations were found between beta power CoV at any time windows and any behavioural measures either (all p>.2).

We also looked at individual differences by dividing the sample by a median-split in terms of theta or beta CoV (high vs. low power CoV) and running repeated measures ANOVAs with the within-factors of time-on-task and block, comparing the mean RT, RT CoV, and correct responses rate.

When comparing the participants with high vs. low theta power CoV, a significant interaction of group*time-on-task for mean RT (F(1,27)=6.98, p=.014, n^2_p=.21) revealed that participants with high theta CoV showed reduced RT during the second half of the blocks compared to the first half (MDiff=-15.64 ms, p=.016, Cohen's d=-.29), contrary to participants with low theta CoV, who showed no significant differences (MDiff=-6.79 ms, p>.2, Cohen's d =-.13; Figure 4B). An additional t test comparing the performance sensitivity (A') differences between out vs. in the zone between groups revealed higher differences in the participants with high theta CoV compared to those with low theta CoV (t(28)=2.15, p=.04, Cohen's d=.79; Figure 4C).

For beta power around 400 ms following the transition point between stimuli (100% Nth-1/0% Nth), a significant interaction of group*block*time-on-task was found for RT CoV (F(4,108)=4.64, p=.002, n^2_p=.15). The posthoc analysis indicated that participants with high beta CoV showed significant differences among the blocks during the first half (0-3 min, p <.05), but not in the second half of the blocks, while no significant differences were found in participants with low beta CoV (all p>.1).

In addition, a significant interaction of group*time (F(1,27)=8.54, p=.007, n^2_p=.24) revealed that participants with high beta CoV showed a significant decrease of correct commissions rate during the second half of the blocks (MDiff=-.06, p=.002, Cohen's d=.43), while participants with low beta CoV showed no significant differences (MDiff=.01, p>.2, Cohen's d=.08; Figure 4D). No significant differences were found between beta CoV groups for mean RT nor sensitivity.

We ran a similar comparison of behavioural measures between groups but this time dividing them in terms of high vs. low differences between zones in theta and beta power. No significant results were found for any repeated measures ANOVA (all p>.2).

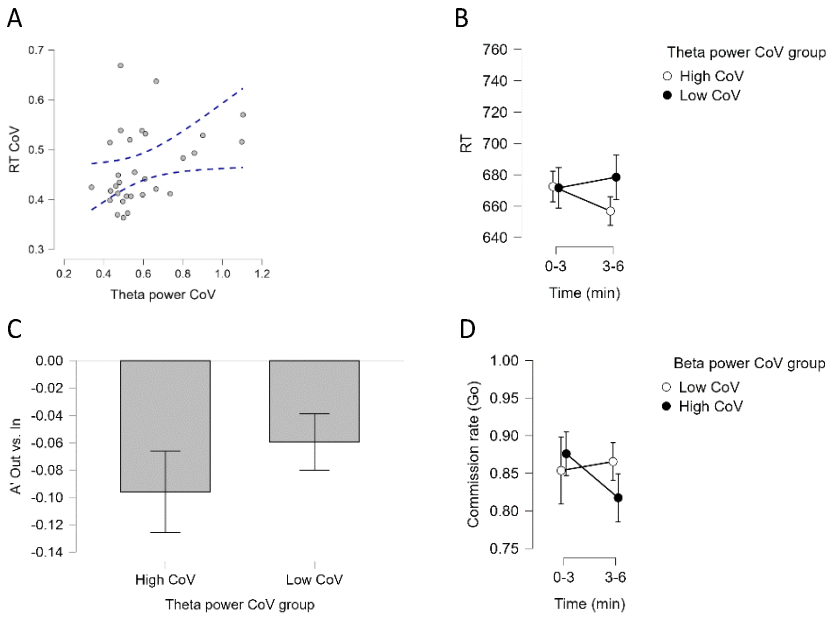

Figure 4. Theta and beta power variability and task performance. (A) Theta power CoV was associated with RT CoV. (B) Participants with high theta power CoV showed reduced RT with time-on-task and (C) a stronger decline in sensitivity (A') during out vs. in the zone states. (D) Participants with high beta power CoV showed a decline in the rate of correct commissions (Go trials) with time-on-task.

Phase alignment across trials

We did not find significant differences between in vs. out of the zone for phase alignment (PLF) for any oscillation. Therefore, no further analyses were done.

EEG predictors of performance

In order to explore which EEG feature was able to better predict performance across participants, we ran a multiple regression model including theta power decreases out vs. in the zone, theta power CoV, and beta power decrease out vs. in the zone as regressors, and correct commissions rate, correct omissions rate, and RT CoV as dependent variables. These analyses revealed a significant prediction for RT CoV (R^2=.35, F(3,26)=4.70, p=.009). Theta power decline and theta CoV were the best predictors (β=-.53, t=-3.13, p=.004 and β=.33, t=1.90, p=.069, respectively). No significant associations were found for beta power measures (β=.26, t=1.51, p=.14). For correct commissions rate, only theta power decline showed a tendency for a significant association (R2=.26, F(3,26)=3.07, p=.045; β=-.32, t=-1.76, p=.09). The same result was obtained for correct omissions rate, with an almost significant model (R2=.21, F(3,26)=2.23, p=.11; β=.43, t=2.31, p=.029).

DISCUSSION

We identified the electrophysiological changes during fluctuating states of sustained attention, using the gradCPT task, which has been shown to be sensitive to reveal states of 'in the zone' or 'out of the zone' throughout task performance. Our findings reveal changes in theta and beta power, as well as their power variability, as sensitive neural markers of states of sustained attention zones and establish also their relation to intra- and inter-individual differences in task performance. Next, we discuss each of these findings in turn.

Theta power

Our results indicated a transient power reduction of frontal theta activity in peristimulus transition periods, during out of the zone (as compared to in the zone) sustained attention state. The magnitude of the theta power decline during out vs. in the zone states was positively associated with increased RT variability, as well as increased commission rates on both Go trials and, more importantly, NoGo trials (i.e. attention lapses). Larger theta power decline during out of (vs. in) the zone states was also found to be specifically associated with a larger effect of out of the zone states on attention lapses. The reduced response criterion that was also found for those with greater decline of theta power during out of the zone (vs. in the zone) states was further suggestive of a general increase in responses, irrespective of the need to inhibit responses on the NoGo trials. Altogether, these findings provide strong support for the role of theta oscillations in cognitive control over states of sustained attention, demonstrating a direct association between theta power decline and states of being out of the zone, with the magnitude of this momentary decline specifically predictive of this reduced attention state on performance. In addition, the variability of theta power throughout the task was also found to predict response variability, and participants with high theta variability showed a larger difference in their perceptual sensitivity between out vs. in the zone states. Overall, theta power in the midfrontal regions (as shown with the source analysis) was revealed as a sensitive marker of sustained attention states and their associated effects on performance.

These results are consistent with a body of findings demonstrating the role of theta power in cognitive control over attention. Theta activity is increased in frontal regions during effective performance in continuous tasks (Wascher, et al., 2014) and during those that require inhibitory control over a conflicting response (Oehrn, et al., 2014). Theta power also increases after negative feedback during reinforcement learning (van de Vijver, Ridderinkhof, & Cohen, 2011) and prior to conflict resolution (Oehrn, et al., 2014) as well as after error commission (Cavanagh, Zambrano-Vazquez, & Allen, 2012), promoting attentional control reset. Overall, there is a general consensus that midfrontal theta serves as a neurophysiological marker of cognitive control and effort (Cavanagh & Frank, 2014), and that specific patterns of theta connectivity and amplitude can reflect specific features of cognitive control (Cooper, et al., 2015; Messel, Raud, Hoff, Stubberud, & Huster, 2021).

Our findings provide a new demonstration that theta power is specifically associated with sustained attention states and is predictive of their impact on single-trial performance, throughout a sustained attention task.

Somewhat surprisingly, other sustained attention studies have previously reported an increase in theta power associated with worse performance as a function of time-on-task or mental fatigue (Lal & Craig, 2002). For example, an increase in theta power as the task progresses has been reported, with an accumulative effect during a 2 hour repetitive time estimation (conducted on the same 1-sec duration) task (Umemoto, Inzlicht, & Holroyd, 2019). In addition, increased theta has been identified as a predictor of attentional decline, including lapses in vigilance and a higher error rate (Boksem, Meijman, & Lorist, 2005; Klimesch, 1999; Paus, et al., 1997; Peiris, Jones, Davidson, Carroll, & Bones, 2006; Wascher, et al., 2014).

While at first sight these findings appear generally inconsistent with ours and previous research suggesting that increased theta power reflects increased cognitive control over attention, this inconsistency can be reconciled by the proposal that mid-frontal theta does indicate cognitive control across all studies, including those showing an increase in theta power as a result of time-on-task, since cognitive control is important not just for achieving effective performance but also for monitoring attention and its failures. Thus, the increase in theta power as a consequence of mental fatigue and the associated increase in rates of errors with a longer time-on-task may reflect the higher demand on task monitoring (especially following errors). This interpretation is supported by findings showing increases both in tonic theta power with time-on-task and in induced theta power during successful resolution of stimulus-response mapping conflict, though we note that the findings fell short of demonstrating an interaction of time-on-task and theta power induced by conflict resolution (Wascher et al. 2014). Similarly, Chidharom et al.'s (2021) findings of a general increase of theta power following errors of commission may be taken to reflect the increased monitoring demand following these errors. Moreover, their findings that this effect was less strong in trials with high RT variability (out of the zone states in our study), especially for participants with high RT variability, is in line with our suggestion that mid-frontal theta power reflects attentional control over the task, and its decline in intra-individual states of out-of- the zone, as well as in individuals more prone to out-of- the zone states, reflect the decline in cognitive control over sustained attention.

In addition, the contrast between our findings of theta power association with sustained attention states with the fact that it was not affected by time-on-task in our paradigm, further suggests that periodic increases in theta power are associated with increased cognitive control during in the zone states. Vice versa, periodic declines in theta power are reflective of reduced cognitive control of attention during out of the zone states, as they occur throughout the task, rather than as a tonic consequence of increased mental fatigue with time-on-task.

Our findings that the change in theta power in relation to attentional states did not occur throughout the entire trial, but at a ~400 ms period around the transition point between stimuli further suggests that theta synchronization can adapt to critical periods where focused attention is

particularly needed in order to perceive the (gradual) transition to a new stimulus. We note that due to the gradual nature of image transitions (in steps of 2.08% change in image coherence), the gradCPT paradigm is likely to involve a gradual expectancy build up once the Nth-1 image has been discriminated and responded to in preparation for the gradual onset of the new image Nth. This process is expected to start following the midpoint of an 800 ms trial, where the image coherence of the Nth-1 image is greater than the previous trial's image (Nth-2) and terminate once the new image (Nth) has enough build-up of coherence to be detected. During in the zone states, theta synchronization would allow for enhanced attention recruitment during this critical period, which declines with a loss of attention focus (out of the zone states). This aligns with other studies demonstrating the adjustment of the amplitude of oscillations within fine temporal windows during relevant periods for attentional facilitation or blocking of distractors (Bonnefond & Jensen, 2012; Solis-Vivanco, Jensen, & Bonnefond, 2018; Solis-Vivanco, Jensen, & Bonnefond, 2021). Overall, our results support the perspective of theta as an indicator of cognitive control, attributing lower amplitude to attentional decline, especially in moments when attention focus is critical for perception.

Theta phase alignment

We did not find that phase alignment between trials (based on PLF) was different between being out- vs. in the zone for theta or other frequencies. Phase alignment can occur in anticipation of stimuli onset, allowing better encoding when they are relevant or blocking them when they are distractors (Bonnefond & Jensen, 2012; Solis-Vivanco, Jensen, & Bonnefond, 2018). In sustained attention studies that involve stimulus onset, a decrease in fronto-medial theta as well as parieto-occipital phase alignment (measured through PLF) is found both as a function of increased time-on-task and reduced motivation (Reteig, van den Brink, Prinssen, Cohen, & Slagter, 2019). This suggests that reduced sustained attention (due to either factor) results in reduced ability to focus on the points in time that are critical for stimulus processing. With the gradual change that the gradCPT paradigm involves, the critical time windows are more temporally spread, rather than based on specific time point of abrupt onset, and this may have reduced the sensitivity of our measure of PLF to reflect people's ability to specifically focus attention on the critical time windows for stimulus processing. Nevertheless, our findings that fronto-medial theta power was reduced around the (wider-spread) time window of stimulus transition in out-of-the zone states, while theta power variability increased, are generally consistent with the interpretation of reduced sustained attention involving also reduced ability to focus on (the wider spread) critical time windows for stimulus transition.

Theta power variability

The variability of frontal theta power was found as a predictor of behavioural variability throughout the task across subjects. At the group level, participants with high theta variability showed greater instability in RT, as well as poorer sensitivity when being out of the zone, compared to participants with low theta variability. This confirms that neurophysiological variability mirrors behavioural variability during attentional performance (Vanrullen, Busch,

Drewes, & Dubois, 2011). Neurophysiological variability reflects fluctuations in the local synchronization of neuronal populations, affecting the stability of their functional role. To our knowledge, this is the first study reporting a direct association between theta power variability and behavioural variability across a sustained attention task, and that is specifically associated with discrimination performance during states of being out of the zone.

Beta power and its variability

Beta power exhibited an increase in amplitude at the transition point of the scenes during Go trials, and a decrease around 400 ms afterwards. This time course and the source localization to left central regions around the primary motor cortex, suggests that these effects are attributed to motor planning of the responses (Brown, 2006; Park, Kim, & Chung, 2013), declining during the transition point and rising once motor prepartion is complete. These effects were reduced during states of out (vs. in) the zone states, suggesting reduced response preparation during out of the zone states. This is consistent also with an interpretation of the increased response bias involving also increased rates of errors of commission in NoGo trials during out of the zone states as reflective of inattentive responding. The finding of the association between a stronger effect of out of the zone on the level of beta suppression during the 400 ms following transition point and increased rates of commission responses in Go trials is in further support of such bias. Finally, the findings that participants with low beta variability at the second latency period (400 ms post transition) showed also a smaller effect of time-on-task on their rate of Go-trial commission responses hints that beta power variability may also reflect sustained attention to response (which declines with longer time-on-task more so for those with higher beta variability). However, as this was found only in between-group comparisons it is clearly not a sensitive marker of sustained attention.

Indeed, when assessing the predictive ability of theta and beta decline and variability on behaviour, we found that only the decrease in theta amplitude and theta variability predicted RT variability. This confirms frontal theta as the best indicator of sustained attention fluctuations, both within and across subjects.

Alpha power

We did not find effects of being out of the zone in the alpha band (8-12 Hz), despite its role for attentional capture and awareness (Harris, Dux, Jones, & Mattingley, 2017; Harris, Dux, & Mattingley, 2020). Alpha increase may index reduced alertness, lower engagement during boring tasks and mind wandering (Kam, Rahnuma, Park, & Hart, 2022; Wascher, Arnau, Gutberlet, Karthaus, & Getzmann, 2018; Wascher, et al., 2014), which adds to the conceptualization of alpha as a reflection of functional inhibition (Bonnefond & Jensen, 2012; Jensen & Mazaheri, 2010; Solis-Vivanco, Jensen, & Bonnefond, 2018). Alpha also increases with time-on-task (Bonnefond, Doignon-Camus, Touzalin-Chretien, & Dufour, 2010) and reduces its connectivity with mental fatigue (Sun, Lim, Kwok, & Bezerianos, 2014). Following Reteig et al. (2019), this could result from a drop in global arousal (Drapeau & Carrier, 2004; Lal & Craig, 2002). Thus, alpha modulations during

sustained attention might reflect a decrease in alertness or arousal rather than fluctuations of sustained attention states (Cajochen, Brunner, Krauchi, Graw, & Wirz-Justice, 1995; Drapeau & Carrier, 2004). Whether alpha can differentiate between mental fatigue and attentional fluctuations remains to be further explored.

In conclusion, we found reduced theta and fluctuating beta power associated with fluctuations in sustained attention. The variation over time of both bands, especially theta, predicted behavioural variability. Our results provide evidence of short-term attentional control decline due to fluctuations in frontal theta oscillations.

IMPACT STATEMENT

Our research establishes the neurophysiological correlates of sustained attention states throughout task performance, as they periodically fluctuate from focused 'in the zone' to 'out of the zone' states prone to attention lapses. The results highlight mid-frontal theta oscillations power- specifically during critical time periods for perception- as an index of attentional states and demonstrate that theta power variability can predict behavioural variability.

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