High arousal disrupts the neural signatures of conflict processing but not behavioural performance

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ABSTRACT

Fluctuations in physical arousal occur constantly along the day and become particularly pronounced at extreme states such as deep sleep or intense physical exertion. While changes in arousal are thought to affect cognitive control, it has been suggested that cognitive control is resilient during the drowsy state as a result of neural compensatory mechanisms. Here, we investigate the higher end of the arousal spectrum by looking at the modulatory effect of high arousal on behavioural and neural markers of cognitive control. We predicted that preserved behavioural measures of cognitive control under high arousal would be accompanied by changes in its typical neural correlates. We conducted an electroencephalography study in which 39 expert cyclists (37 males, 2 females) were presented with an auditory stimulus-response conflict task while cycling on a stationary bike. Participants performed two experimental sessions on different days: one at low intensity and one at high intensity pedalling. Consistent with our predictions, we found no behavioural difference in cognitive conflict measures between the two exercise conditions. However, the typical midfrontal-theta power signature of cognitive control was no longer reliable at high-intensity exercise. Similarly, time-frequency multivariate decoding failed to decode stimulus conflict. On the other hand, we found no difference between intensity levels in whole-brain connectivity measures. Therefore, we suggest that the human cognitive control system is resilient even at high arousal states and propose that the dissociation between behavioural and neural measures could indicate the activation of neural compensatory mechanisms as a response to physiological pressure.

SIGNIFICANCE STATEMENT

Effects of spontaneous physiological changes on brain and cognition have traditionally been studied in states of decreased arousal. However, virtually no research has been conducted on the higher end of the arousal spectrum. In this study, participants performed an auditory conflict task while cycling at low and high intensity. Behavioural performance was robust in both conditions. However, changes in the typical univariate and multivariate signatures of cognitive control induced by arousal suggest a reconfiguration of the neural processes supervising cognitive control during heightened states of strain.

INTRODUCTION

Fluctuations in physical arousal occur naturally throughout the day. These spontaneous fluctuations unfold in a nonlinear manner (Bernaola-Galván et al., 2017, Ogilvie and Wilkinson, 1984) and become severe at extreme states such as deep sleep (Goupil and Bekinschtein, 2012) or intense physical exertion (Schmit and Brisswalter, 2020), modulating cognitive processing (Ciria et al., 2021, McMorris et al., 2011, Noreika et al., 2020, Wickens et al., 2015). In particular, it has been shown that cognitive control (i.e., the ability to adaptively adjust cognitive processes to inhibit distracting information while maintaining task relevant information) is markedly impacted as the level of arousal decreases (Cain et al., 2011, Canales-Johnson et al., 2020, Goupil and Bekinschtein, 2012, Tucker et al., 2010). However, the majority of research on cognitive control has focused on low arousal fluctuations, with limited investigation into its effects under high arousal conditions. In the current study, we aim at investigating the modulatory effect of high arousal on behavioural and neural markers of cognitive control. To do so, we implemented an auditory conflict task combined with electroencephalography (EEG) recording in healthy human participants under a natural state of high arousal (i.e. physical stress via exertion).

The interaction between heightened arousal states (physical exercise) and cognitive performance in complex tasks does not appear to follow a linear relationship (Ciria et al., 2021) and varies according to several variables such as the intensity of the exercise and the characteristics of the task. Some studies have reported better performance at medium intensity and worst at high intensity exercise (Chang et al., 2012, González-Fernández et al., 2017, Lambourne and Tomporowski, 2010, Verburgh et al., 2014). However, in the specifics of cognitive control tasks, physical arousal induced by exercise does not appear to hinder performance during acute exercise even if at high intensity (Chang et al., 2012, Ciria et al., 2018, Davranche et al., 2015, Moreau and Chou, 2019). This is consistent with observations in the low end of the spectrum (drowsiness and sleep), which has received much more attention in the study of the interaction between arousal and cognitive control. In fact, the ability to resolve cognitive conflict is not hampered by sleep deprivation and circadian rhythm (Bratzke et al., 2012, Cain et al., 2011, Canales-Johnson et al., 2020, Sagaspe et al., 2006), similarly to what observed during acute exercise. Interestingly, in the case of reduced arousal, even if behavioural performance in conflict tasks appears to remain intact, univariate midfrontal (MF) theta and multivariate (congruency decoding) measures of cognitive conflict are no longer noticeable (Canales-Johnson et al., 2020). Such discrepancy between behavioural and neural measures suggests that networks associated with the resolution of cognitive conflict may undergo reconfiguration when transitioning towards strained states.

Does the neural reconfiguration observed during the resolution of cognitive conflict under decrease alertness occur at the opposite end of the arousal spectrum (i.e., high arousal)? In this pre-registered study (Avancini et al., 2022), participants performed an auditory Simon task (Simon and Rudell, 1967) during two bouts of aerobic exercise (cycling) at low and high intensity. We hypothesized that high-arousal would not affect cognitive control at the behavioural level but it would disrupt univariate MF theta and multivariate spectral measures of cognitive conflict, similar to the case of drowsiness. In other words, we expected to gather evidence that under high intensity strained states the networks associated with conflict processing undergo reconfiguration.

MATERIALS AND METHODS

Participants

Thirty-nine healthy subjects (2 females; age-range= 18-50 years; mean age = 30.55 years; SD age = 10.65) were included for analyses . Initially, fourty participants were recruited, however one participant was excluded because of an excessively low heart rate at high-arousal. Participants were recruited by word of mouth and written advertisement amongst cycling and triathlon sport clubs, and received monetary compensation for their participation. Only expert cyclists were included in the study. They were required to have a minimum of three years experience and to train at least three times a week. All participants had normal or corrected-to-normal vision, normal hearing, no history of head injury or physical and mental illness. This study was approved by the ethical committee of the University of Granada (978/CEIH/2019). Written informed consent was obtained from all participants during the first experimental session, after explanation of the experimental protocol.

Study design

To test the effect of arousal on the resolution of cognitive conflict, we adopted a 2×2 factorial design with arousal level (low/high) and the congruency of the current trial (congruent/incongruent) as factors. We also investigated the moderating effect of previous trial congruency (conflict adaptation). We adopted a $2 \times 2 \times 2$ design with arousal, current trial congruency, and previous trial congruency (pre-congruent/pre-incongruent) as factors. Note that for aiding interpretation, the factor congruency was in fact reduced to a measure of conguency effect by subtracting the signal elicited by congruent trials from the signal elicited by incongruent trials. All factors of both study designs were within-subjects. Analyses on conflict adaptation were run on behavioural data only as an additional sanity check.

Experimental task

Participants performed an auditory version of the Simon task (Simon and Rudell, 1967). Recordings of the spoken words ”left” and ”right” (”izquierda” and ”derecha” in Spanish) were played monoaurally through in-ear earphones. In congruent trials (50% of the trials), the stimulus was presented at the physical location corresponding to the content of the word (i.e. ”left” played to the left eat, ”right” played to the right ear). In incongruent trials, physical location and content did not correspond (i.e. ”left” played to the right ear, ”right” played to the left ear). Participants were instructed to respond according to the content of the word, while ignoring its physical location. Response was given with the left and right thumbs by pressing one of two buttons that were attached to the bike handle (Figure 1A). Speed and accuracy were stressed. Interstimulus interval (ITI) between participant’s response and the next stimulus onset was a random number between 1500 and 2000 ms. If the participant did not respond, the ITI began 1900 ms after stimulus onset. Practice and testing blocks were fixed in time duration, therefore the total number of trials depended on the participant’s speed. The practice block lasted 30 s and on average participants responded to 12 trials (SD = 1). The testing block lasted 30 min without breaks and on average participants responded to 766 trials (SD = 41). A beep sound was played every 10 min to inform the participant of the elapsed time.

Procedure

Testing took place over three sessions: the first was always a maximum effort test, the second and third were EEG experimental sessions. Upon arrival for the effort test, participants were informed on the overall experiment including that one of the subsequent EEG sessions would have been at high-intensity and one at low-intensity. Then, they gave written consent. The order of the EEG sessions was counterbalanced across participants and it was not communicated until the first EEG session. Participants were instructed not to perform intense exercise during the 48 hours preceding any of the three sessions. The maximum effort test took place about one week before the first EEG session, while the EEG sessions were 48 to 72 hours apart to avoid fatigue effects. To accommodate for participants life commitments, four participants had more than 72 hours in between EEG sessions, and three only had 24 hours. In the case of the three latter, the low-intensity session was done first. Finally, to control for circadian rhythms, participants performed the two EEG sessions during the same time of day.

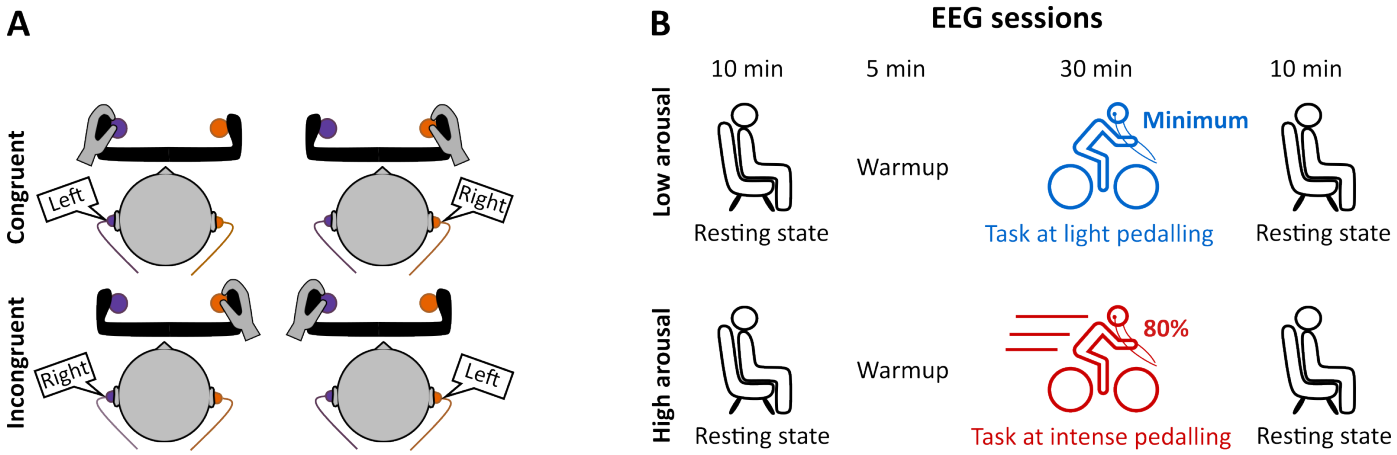

Figure 1: Task and procedure.
(A) Participants were presented with the words "left" and "right" in their left and right ear. The task required to respond to the content of the word by pressing a button with their right or left thumb while ignoring the stimulus spatial location. Stimulus content and spatial location could be either congruent or incongruent. **(B)** The session started with a seated 10 min resting state. After that, participants mounted on the bike and warmed up for 5 min, during which a 30 s practice block was presented. Then, the experimental task was presented for 30 min during which participants had to pedal without stopping. In the low arousal condition, the resistance of the bike was set at 10% of the maximum W that the participant had moved in the effort test. In the high arousal condition, the resistance was set at 80%. The session ended with a seated 10 min resting state. Note that in this paper resting state data are not analysed.

Maximum effort test

The maximum effort test consisted of an incremental cycle-ergometer test (ergoline GmbH, Germany) to confirm participants' fitness and individually adjust the exercise intensity in the following EEG sessions. Participants were fitted with a wireless 12-lead PC ECG (AMEDTEC Medizintechnik Aue GmbH, Germany) to record heart rate (HR) and with a gas analyser mask (Geratherm Respiratory GmbH, Germany) to measure oxygen consumption (VO2). Participants were informed about the protocol and instructed to keep pedalling at above 60 rpm until they reached full exhaustion and could no longer keep going. The protocol started with 5 min warmup at 120 watts (W) immediately followed by the

incremental test of 20 W every 3 min.

For each individual participant, the power output in W corresponding to when they reached their maximum oxygen consumption was used as marker to calculate the intensity of the following EEG sessions.

EEG sessions

Upon arrival, participants were seated in a comfortable chair in an electrically shielded room, and were fitted with a 64-channels EEG cap (EASYCAP GmbH, Germany) and three ECG electrodes (Ambu A/S, Denmark). During electrodes placement, participants received task instructions in written form. The session started with 10 min resting state. Note that resting state data were collected for a different study and therefore are not included in the manuscript. Then, participants mounted on a stationary bike (SRM International SRM GmbH, Germany) and fitted with a heart rate monitor SRM HR (SRM International SRM GmbH, Germany) and in-ear earphones (Hyperx, HP Inc., USA). Participants were reminded to respond as accurately and fast as possible and to keep a cadence of 60 rpm or above during testing. Participants were first given 5 min to warm up on the bike. In the warmup before the low-arousal session, the resistance of the bike was set at the minimum load possible while preventing the wheel to spin freely. For the high-arousal session, the warmup was incremental, with resistance increases of 20 W every minute with the last step being the 80% of the W at $VO2_{max}$. During the warmup of the first session, the practice block was presented. Then, the experimental test began during which participants performed the auditory Simon task while pedalling (Figure 1B). In the low-arousal session, the resistance of the bike was set at the minimum load and in the high-arousal session at 80%. Given the importance of finishing the session and the heavy physiological demand of the high-arousal session, W were adjusted manually if the participants' cadence dropped below 60rpm or if their HR exceeded the 90% of their HR max as measured during the effort test. The resistance of the stationary bike was controlled with Gobat-Software (Magnetic Days O.R.F. s.r.l., Italy). W output and HR were recorded with SRM powercontrol 8 (SRM International SRM GmbH, Germany). The session ended with 10 min resting state not included in the current manuscript. Stimuli were presented using PsychToolbox (Kleiner et al., 2007) software on a Windows computer.

Behavioural data analysis

The first trial of each session, incorrect responses, omissions and responses faster than 200 ms were removed. Analyses were conducted on both reaction times (RT) and accuracy (ACC). To test the conflict effect, we run 2 (arousal level) $\times$ 2 (congruency) repeated measure ANOVAs. Post-hoc planned comparisons corrected for multiple comparisons were conducted comparing congruent vs incongruent in low-arousal and high-arousal. To test the conflict adaptation effect, we run 2 (arousal level) $\times$ 2 (pre-congruency) repeated measure ANOVAs with the conflict effect (incongruent minus congruent) as dependent variable. Post-hoc planned comparisons corrected for multiple comparisons compared pre-congruent vs pre-incongruent in low-arousal and high-arousal. In addition to the frequentist approach, we also performed the correspective bayesian ANOVAs and planned comparisons.

EEG recording and preprocessing

64-channel EEG data sampled at 1000 Hz and referenced to FCz according to the extended 10-20 system were collected using the actiCHamp amplifier and Brain Vision software (Brain Products GmbH, Munich, Germany). Electrode impedances were kept below 10 kΩ. EEG preprocessing was conducted using custom MATLAB scripts, the EEGLAB (Delorme and Makeig, 2004), and FieldTrip (Oostenveld et al., 2011) toolboxes. Continuous data were dowsampled to 500Hz, notch-filtered and band-pass filtered 0.5 Hz-90 Hz. Bad channels were detected using joint probability with a threshold set at $\pm$ 3.5 SD. Independent component analysis was then run on good channels. We used the ICLabel EEGLAB plugin to identify IC components that were classified as having above 80% probability to be generated by eye-movements, muscle, or heart activity. To avoid the effects that filtering can have on multivriate pattern analysis classification (MVPA; van Driel et al., 2021), those IC were then rejected from unfiltered data downsampled at 500Hz. The signal was then rereferenced to the average and bad channels were interpolated. The continuous recording was epoched between -1500 and +2000 ms relative to stimulus onset. The epochs corresponding to those trials that had been removed from behavioural data were rejected. To further clean from eye movements and muscle activity, we rejected abnormal spectra epochs whose spectral power deviated from the mean by $\pm$50 dB in the 0–2 Hz frequency band and by +25 or −100 dB in the 20–40 Hz frequency band. After trial rejection, an average of 710.2 (SD = 89.199) trials per participant were retained in the high-arousal condition and an average of 713.05 (SD = 82.817) per participant were retained in the low-arousal condition.

EEG time-frequency analysis

Epochs were grouped based on current trial congruency. Time-frequency decomposition was run using FieldTrip (Oostenveld et al., 2011). Morlet wavelets of 3 cycles were adopted to conduct trial by trial time-frequency decomposition. The signal was decomposed between 2 and 30 Hz in linear steps of 2 Hz. The wavelet slid from -400 to 1250 ms (relative to stimulus onset) in steps of 10 ms. Then, the epochs were transformed into decibels (dB) and normalized to a baseline of -400 to -100 ms relative to stimulus onset. For each participant, epochs were averaged according to the two trial types. Then, the signal corresponding to the MF region of interest (ROI) was selected and averaged across electrodes (C1, Cz, C2, FC1, FCz, FC2, F1, Fz, F2. See Figure 3A). We obtained the time-frequency conflict effect at the participant level by subtracting the signal to congruent trials from the signal to incongruent trials. This allowed us to use cluster-based permutation testing (Oostenveld et al., 2011) to directly test the interaction between congruency and arousal level by comparing the conflict effect between high- and low- arousal. For the cluster-based permutation tests, the Monte Carlo method was implemented with 1000 iterations and the alpha threshold at the cluster level was set at 0.05. The test were run on all frequencies and timepoints between -200 ms and 1200 ms. To evaluate the effect, we used dependent samples t-statistic with alpha at 0.05.

EEG multivatiate spectral decoding

Multivariate spectral decoding was applied on the time–frequency data. Multivariate analysis increase sensitivity and allows to query how stimulus features are processed at different levels of arousal. To do so, we used the ADAM toolbox

(Fahrenfort et al., 2018) which has been developed to specifically implement Multivariate Pattern Analysis (MVPA) on EEG data. We input the raw data which were first downsampled to 64 Hz and then converted to time-frequency directly by the ADAM toolbox using default options. Continuous data were epoched between -1500 ms to 2000 ms and in the frequency domain were decomposed between 2 Hz and 30 Hz in steps of 2 Hz. To avoid biased decoding, we balanced the number of trials between conditions per state of arousal.

We performed three separate decoding analyses taking current trial congruency (congruent/incongruent), content ("right"/"left"), and physical location (right/left) as classes [1]. 10-fold cross-validation was performed applying a backward decoding algorithm. Linear discriminant analysis (LDA) was used to discriminate between stimulus classes, then classification accuracy was computed as the area under the curve (AUC). Finally, AUC scores were tested per time point and frequency bin with double-sided t-tests against a 50% chance level across participants. To control for multiple comparisons, t-tests were conducted with cluster-based permutations with alpha 0.05 and 1000 permutations.

weighted Symbolic Mutual Information

We quantified long-range information sharing between electrodes by means of weighted symbolic mutual information (wSMI; Imperatori et al., 2019, King et al., 2013, Sitt et al., 2014). The wSMI has the advantage of making a rapid and robust estimation of the entropy of the signals, detecting nonlinear coupling while discarding the spurious correlations between signals arising from common sources. For each trial, the EEG signal was transformed into a sequence of discrete symbols. Such transformation depends on the length of the symbols k and their temporal separation τ. We chose a kernel size (k) of 3, τ values of 32 ms to obtain sensitivity to frequencies spanning the theta band (4–9 Hz). For each pair of transformed signal, the wSMI was estimated by calculating the joint probability of each pair of symbols. The joint probability matrix was multiplied by binary weights to reduce spurious correlations between signals. For pairs of identical symbols that could be elicited by a common source, and for pairs of opposite symbols that could reflect the two sides of a single electric dipole, the weights were set to zero. wSMI was calculated between each MF ROI electrode and every other electrode outside the ROI. We discarded from the analysis the wSMI values within the ROI so that to evaluate only information integration between distant electrode pairs. The timewindow where we applied the wSMI was chosen based on the significant cluster representing the MF theta frequency interaction.

Statistics

Statistical analyses were run with MATLAB 2019b and R version 4.2.1. Bayes factors were calculated with the R package BayesFactor 0.9.12.4.4 and are reported as the degree of evidence for the alternative over the null hypothesis (BF_{10}), with the null hypothesis being the denominator and the prior scale set to r = 0.5. Hypotheses and analyses plan had been preregistered prior to data collection (Avancini et al., 2022) [2].

All data and analysis scripts are available at the OSF preregistration page https://osf.io/rdnmf.

[1] Content and physical location decoding had not been preregistered. However, they follow the methodology of (Canales-Johnson et al., 2020)

[2] Please note that we expected the behavioural conflict adaptation effect results to follow the same pattern of those of the conflict effect, consistently with previous literature (Canales-Johnson et al., 2020). The fact that the preregistered hypothesis on the behavioural conflict adaptation effect says otherwise, is a genuine mistake made at the time of the drafting of the preregistered report.

RESULTS

Bike and Physiological measures

During the effort test, participants reached a mean maximum $VO2_{max}$ of 3.374 l/min (SD = 0.478), a mean maximum HR of 180.589 bpm (SD = 13.224), and a mean maximum power output at $VO2_{max}$ of 291.282W (SD = 34.273). During the low-arousal session, on average participants maintained 54.322% (SD = 6.422) of their maximum HR and moved 24.043% (SD = 6.109) of their maximum power output. During the high-arousal session, on average participants maintained 85.710% (SD = 4.225) of their maximum HR and moved 73.82% (SD = 6.18) of their maximum power output.

Behavioural conflict and conflict adaptation effects

All participants showed positive conflict effects at both low- and high- arousal (Figure 2A). To test the effect of arousal on the conflict effect we run a repeated measure ANOVA with arousal and congruency as factors. RT analyses revealed a main effect of congruency ($F_{(1,38)}$ = 191.334, $p < 0.001$, η_p^2 = 0.834, BF_{10} = 2730.817) with slower RT for incongruent than congruent trials (Figure 2B). Neither the main effect of of arousal (F(1,38) = 0.554, p = 0.461, η_p^2 = 0.014, BF_{10} = 0.314) nor the interaction (F(1,38) = 2.304, p = 0.137, η_p^2 = 0.057, BF_{10} = 0.239) showed reliable differences. In ACC, the ANOVA revealed a main effect of congruency ($F_{(1,38)}$ = 12.112, p = 0.001, η_p^2 = 0.242) with higher accuracy to congruent than incongruent trials (Figure 2C). However, bayesian statistics suggested anecdotal evidence for the null hypothesis (BF_{10} = 0.375). Neither the main effect of arousal (F(1,38) = 0.115, p = 0.736, η_p^2 = 0.003, BF_{10} = 0.198) or the interaction (F(1,38) = 0.283, p = 0.598, η_p^2 = 0.007, BF_{10} = 0.236) were significant.

The conflict adaptation effect was positive for 37 out of 39 participants at both low- and high- arousal (Figure 2D). To test the effect of arousal on the adaptation effect we run a repeated measure ANOVA with arousal and pre-congruency as factors and the behavioural conflict effect as dependent variable. In RT, there was a significant main effect of pre-congruency (F(1,38) = 134.735, $p < 0.001$, η_p^2 = 0.780, $BF_{10} > 10000$) with a smaller conflict effect when preceded by incongruent trials (Figure 2E). Neither the main effect of arousal (F(1,38) = 2.11, p = 0.154, η_p^2 = 0.53, BF_{10} = 0.214) or the interaction (F(1,38) = 1.707, p = 0.199, η_p^2 = 0.043, BF_{10} = 0.287) were significant. In ACC, there was a main effect of pre-congruency (F(1,38) = 55.975, $p < 0.001$, η_p^2 = 0.596, $BF_{10} > 10000$) with a smaller conflict effect when preceded by incongruent trials (Figure 2F). Neither the main effect of arousal (F(1,38) = 0.014, p = 0.908, η_p^2 = 0.00036, BF_{10} = 0.170) or the interaction (F(1,38) = 0.168, p = 0.684, η_p^2 = 0.0040, BF_{10} = 0.234) were significant.

Univariate MF theta

The analysis on MF theta revealed significant difference between arousal condition. This was shown by a positive cluster between 270-720 ms at 4-12Hz (Figure 3A). To explore what drove the effect we performed t-test against zero in low and high arousal on the power within the cluster area (Figure 3B) [3]. The one-sample t-test against 0 was significant in low arousal (t(38) = 7.233, $p < 0.001$, Cohen's d = 1.16, $BF_{10} > 10000$). On the other hand, a conflict effect was not reliably detected in high-arousal as shown by both frequentist and bayesian statistics (t(38) = 1.985, p = 0.054, Cohen's d = 0.318, BF_{10} = 1.009). The power within the ROI showed positive conflict effect in 34 out of 39 participants at low-

[3] This additional analysis had not been preregistered

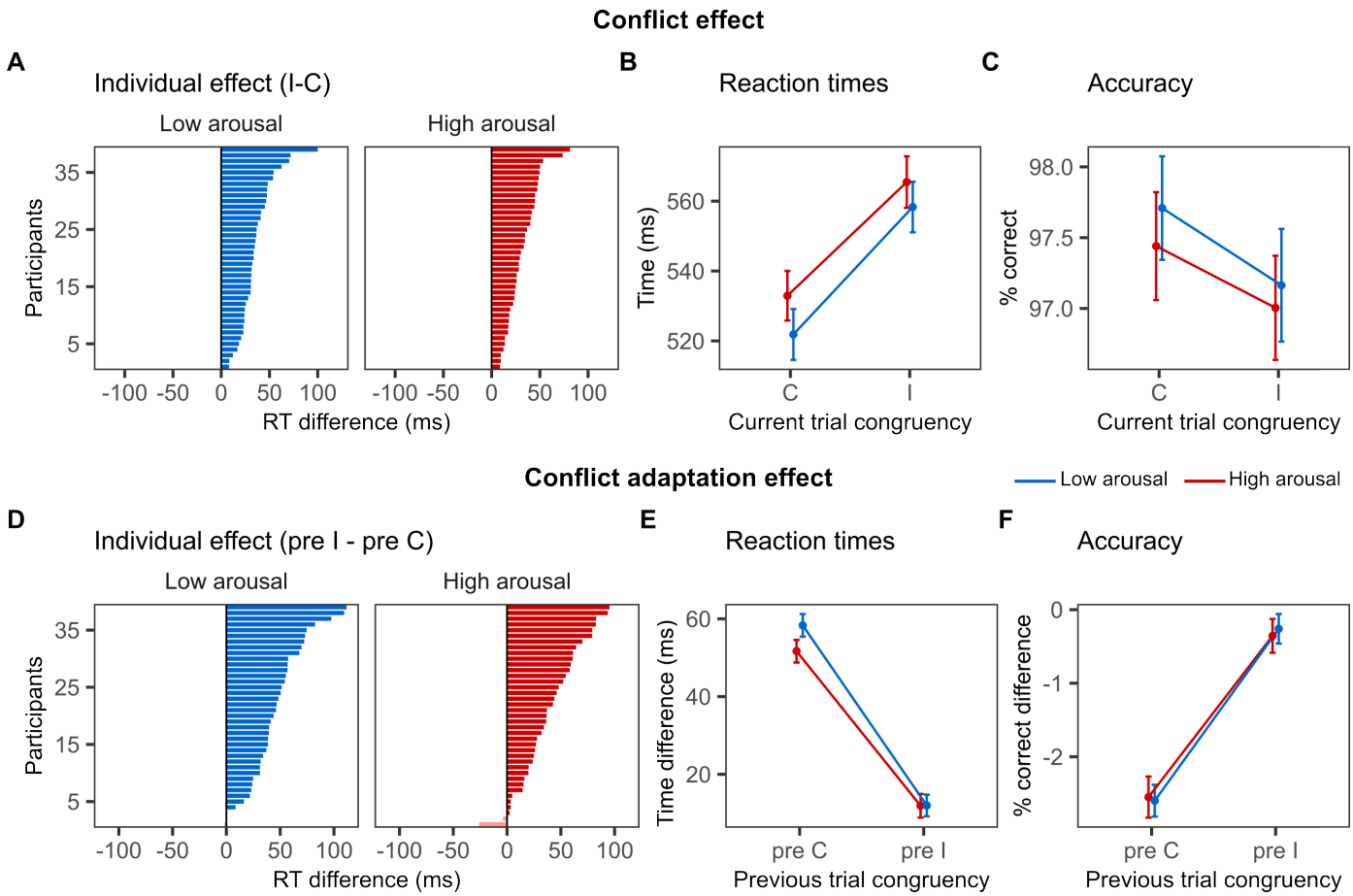

Figure 2: Behavioural results.

(A) Individual conflict effect ordered according to increasing magnitude of the effect. **(B)** Effect of arousal level on the RT of the responses to congruent (C) and incongruent (I) trials. Vertical bars represent the standard error. **(C)** Effect of arousal level on the ACC of the responses to congruent and incongruent trials. Vertical bars represent the standard error. **(D)** Individual conflict adaptation effect ordered according to increasing magnitude of the effect. **(E)** Effect of arousal level on the RT of the responses to trials preceded by congruent (pre C) and preceded by incongruent (pre I) trials. Vertical bars represent the standard error. **(F)** Effect of arousal level on the ACC of the responses to trials preceded by congruent and preceded by incongruent trials. Vertical bars represent the standard error.

arousal and 26 out of 39 at high-arousal (Figure 3C). Therefore, as predicted, the difference is conflict effect between arousal states was significant for the neural signature of MF theta, suggesting that arousal modulates the processing of cognitive conflict. Moreover, the effect was driven by a reliable conflict effect during the control condition of low-arousal but not during high-arousal, similarly to what found in the drowsy state (Canales-Johnson et al., 2020).

We conducted exploratory analyses to investigate the relationship between behavioural measures and MF theta power changes induced by arousal modulation (Figure 6). We fitted hierarchical linear mixed models with RT as dependent variable and arousal state and MF power changes as predictors. Exploratory analyses further support that at high arousal MF theta does not bear relationship with behavioural measures of cognitive control as suggested by the lack of correlation between RT and MF theta power changes (Figure 6D). Indeed, the intercept was the best fitting model, having the lowest AIC (659.19) and BIC (666.26). Furthermore, we explored the possibility that MF power changes are predicted by latent automatic (task-irrelevant) processes underlying decision making. We used Drift Diffusion Modelling

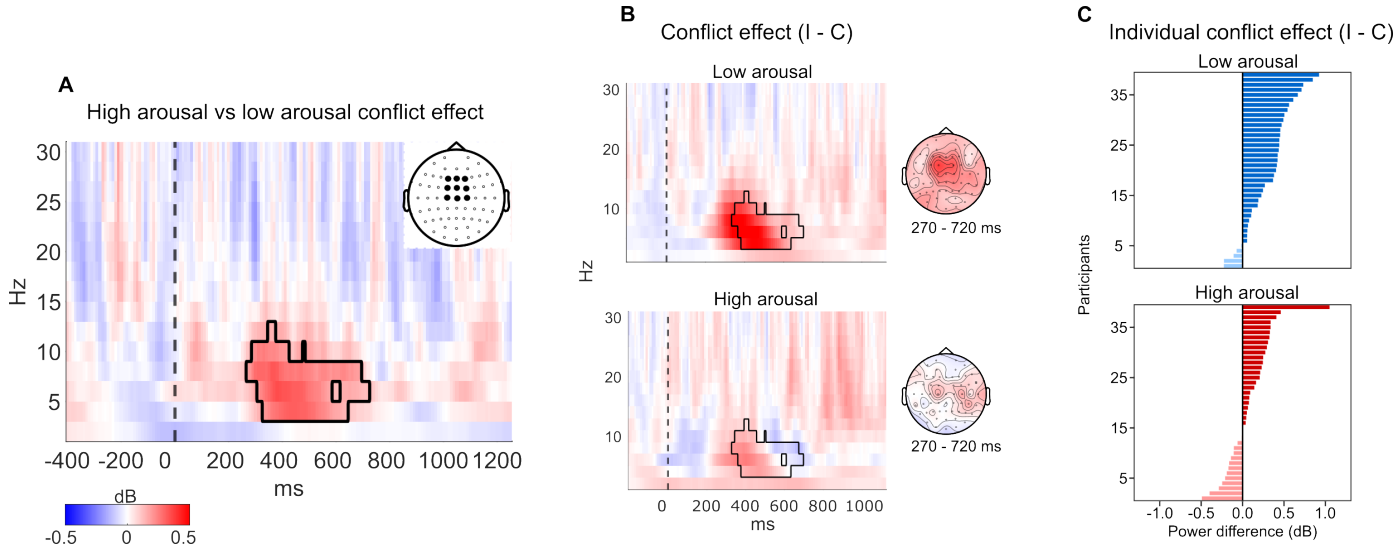

Figure 3: Univariate spectral analysis of MF theta-band oscillations

(A) Cluster permutation analysis capturing the difference between the conflict effect at high arousal and the conflict effect at low arousal. The solid black line delineates the significant positive cluster with $\alpha = 0.05$. Bold dots in the top-right headplot represent the ROI included in the analysis. **(B)** Conflict effect computed by subtracting the congruent (C) from the incongruent (I) condition separately for low and high arousal levels. The topographies represent theta-band power distribution within the timing of the significant cluster, which is delineated by a solid black line. **(C)** Individual MF theta conflict effect. For each participant, the power of the conflict effect was extracted from the area of the significant cluster as delineated in the interaction plot and then ordered according to increasing values. The lighter shade represent a negative conflict effect.

for conflict tasks on the behavioural data (DMC; Ulrich et al., 2015) to estimate the influence of automatic processes on decision time (Alameda et al., 2023) and fitted hierarchical linear mixed with MF theta power as dependent variable and state and the automatic estimate as predictors. The DMC estimate of automatic processes held a relationship with mean RT suggested that the effect of arousal level on MF theta power depends on task-irrelevant automatic processes. In fact, the model with the interaction between the predictors was the best fitting model, having the lowest AIC (23.173) and BIC (37.313). Specifically, increase in MF theta power was associated with an increase of interference effects from task-irrelevant features when fitting the data in the low arousal condition ($F(1,37) = 4.751$, $p = 0.036$), but this relationship was lost when fitting the data in the high arousal ($F(1,37) = 0.237$, $p = 0.630$) (Figure 6E). Further details about the methodology and the results of the exploratory analyses are available on the page of the preregistered report (https://osf.io/rdnmf).

Multivariate spectral decoding

To overcome the shortcomings of univariate analysis and to capture more distribute networks, we turned to multivariate spectral decoding. Multivariate analysis allow us to quantify conflict processing without ROI selection, capturing conflict-related changes harder to detect using conventional univariate analyses (Fahrenfort et al., 2018). Multivariate analysis on time-frequency data was able to decode congruency in the low-arousal state but not in the high-arousal state (Figure 4A). The significant cluster ($p < 0.05$, corrected for multiple comparison) appeared in the 219 - 609 ms timewindow between 2 - 6 Hz with peak frequency at 6 Hz. The cluster was consistent with a congruency effect in the theta range. To further examine this effect, we run cluster-based permutation tests on the two conditions restricted to

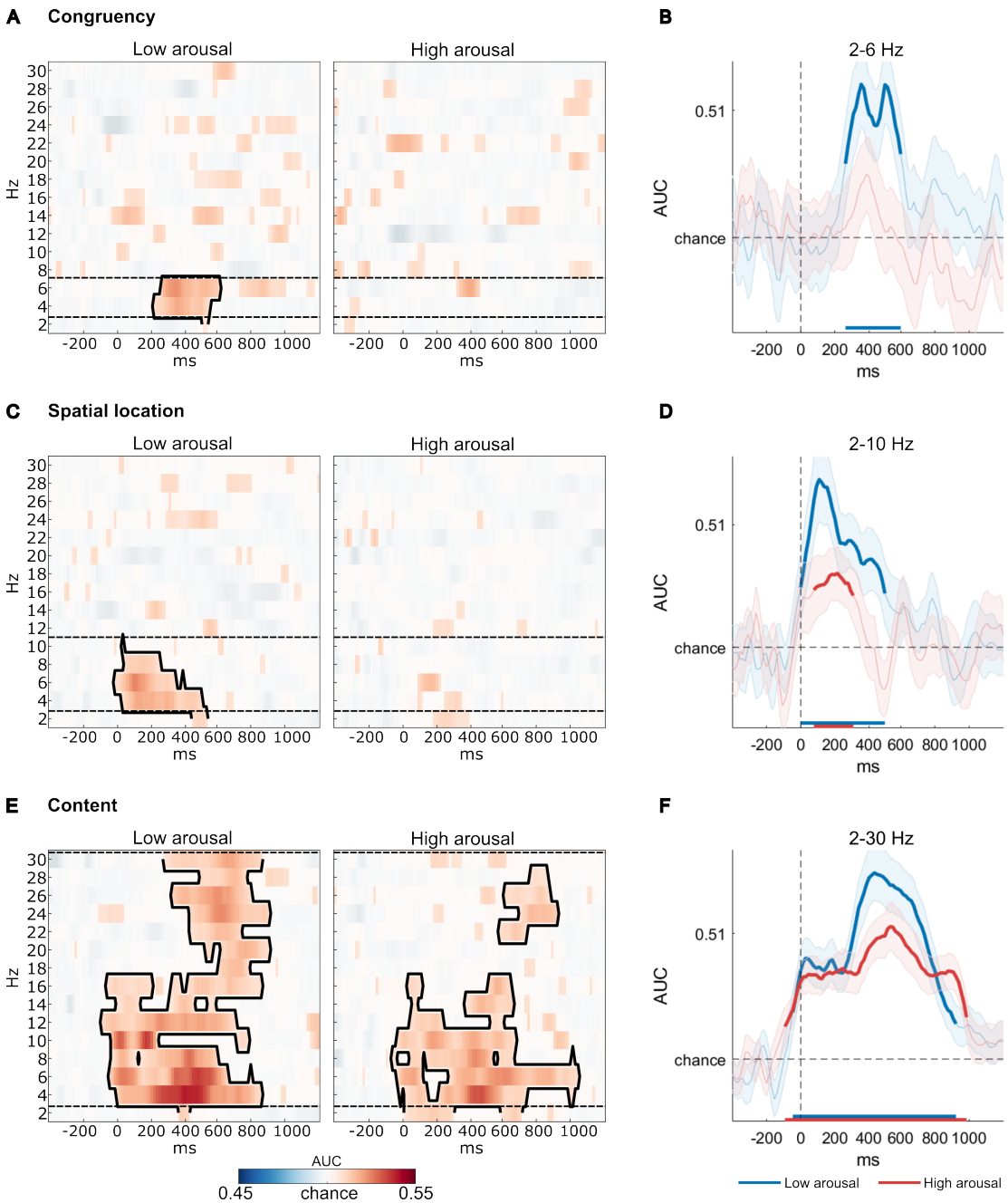

Figure 4: Multivariate spectral decoding results.

Plotting of classifier accuracy against chance across the 2-30Hz spectrum and all timepoints separately for low-arousal and high-arousal. Significant clusters ($p < 0.05$, corrected for multiple comparisons) are delimited by a solid black line. Dashed lines represent the minimum and maximum limits of significant clusters. The AUC within those limits in then averaged to depict the timecourse of classifier accuracy for low-and high-arousal (right column). Thicker lines represent statistical significance at $p < 0.05$. **(A)** Classifier accuracies for stimulus congruency. Information about congruency, and therefore the conflict effect, was only present at low-arousal in the 2-6 Hz band. **(B)** Timecourse of congruency decoding in the 2-6 Hz band in low and high arousal. **(C)** Classifier accuracies for stimulus physical location. Information about location was only present at low-arousal in the 2-10 Hz band. **(D)** Timecourse of spatial location decoding in the 2-6 Hz band in low and high arousal. Narrowing the cluster permutation analysis show that information about stimulus location is still preserved to some extent at high arousal. **(E)** Classifier accuracies for stimulus content. Information about location was present in both conditions throughout the frequency spectrum. **(F)** Timecourse of content decoding throughout the whole spectrum (2-30 Hz) in low and high arousal.

the cluster frequency range (2 - 6 Hz). In the low-arousal state only the cluster showed above chance classification between 266 - 594 ms ($p < 0.05$, corrected for multiple comparison), peaking at 359 ms (Figure 4B). Similarly, spatial location of the stimuli was decoded in time-frequency data at low-arousal ($p < 0.05$, corrected for multiple comparison). The cluster appeared in the -16 - 531 ms time-window between 2 - 10 Hz (peak frequency at 6 Hz), but not at high-arousal (Figure 4C). Cluster-based permutation testing restricted to the cluster frequency range (2 - 10 Hz) showed above chance classification In the low-arousal state between 0 - 500 ms ($p < 0.05$, corrected for multiple comparison), peaking at 109 ms. Notably, also high-arousal showed above chance classification between 78 - 313 ms peaking at 219 ms suggesting that some representation of physical features is conserved at high-arousal (Figure 4D). On the other hand, stimulus content was reliably decoded at both arousal conditions (Figure 4E). At low-arousal, content decoding was reliable between 2 - 30 Hz in the -94 - 906 ms timewindow with peak frequency at 4 Hz ($p < 0.05$, corrected for multiple comparison). At high-arousal content decoding was reliable in two time-frequency regions. One between 2 - 16 Hz in the -63 - 1047 ms timewindow with peak frequency at 4 Hz, the second between 22 - 28 Hz in the 578 - 922 ms timewindow with peak frequency at 24 Hz. Cluster-based permutation testing averaging across the 2 - 30 Hz band showed a significant cluster at low-arousal -47 - 922 ms ($p < 0.05$, corrected for multiple comparison), peaking at 438 ms. At high-arousal, a cluster was significant between -94 - 984 ms, peaking at 531 ms (Figure 4F).

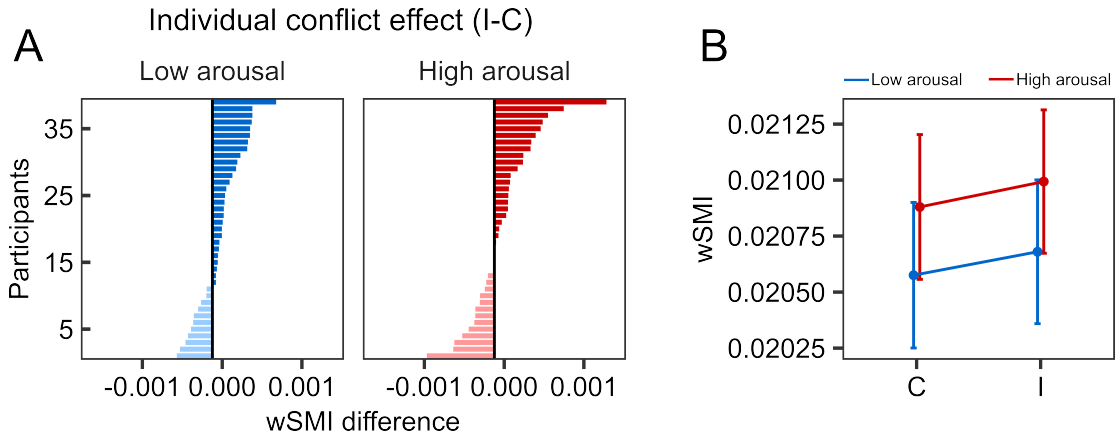

Figure 5: theta-band information sharing

(A) Individual wSMI conflict effects in the low and high arousal conditions. **(B)** Effect of arousal level on the wSMI in response to congruent (C) and incongruent (I) trials. Vertical bars represent the standard error. wSMI was calculated between each MF ROI electrode and every other electrode outside the ROI. We discarded from the analysis wSMI values within the ROI so that to evaluate only information integration between distant electrode pairs. The timewindow where we applied the wSMI was chosen based on the significant cluster representing the MF theta frequency interaction.

Theta-band information sharing

To capture more drastic network reconfiguration during high-arousal, we performed wSMI. The timewindow for wSMI analysis was 270-720 ms based on the significant interaction between arousal and congruency in MF theta (Figure 3A). We used a τ of 32ms to captures nonlinear information integration in the theta-band domain (4–9Hz). The repeated measure ANOVA showed a main effect of congruency ($F(1,38) = 7.831$, $p < 0.008$, $\eta_p^2 = 0.171$). However, the $BF_{10} = 0.180$ does not support the evidence for an effect of congruency. Neither the main effect of arousal ($F(1,38) = 0.310$, p

= 0.581, η_p^2 = 0.008, BF_{10} = 0.274) or the interaction were significant (F(1,38) = 0.011, p = 0.917, η_p^2 = 0.0002, BF_{10} = 0.232). Results are represented in Figure 5

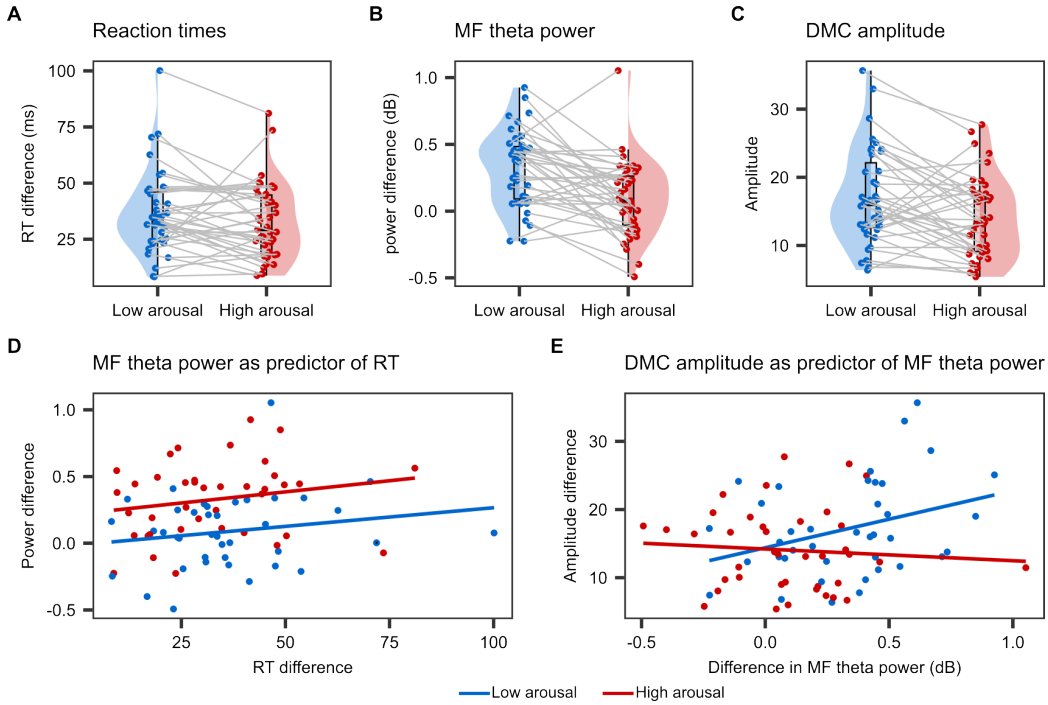

Figure 6: Visualization of individual differences across arousal levels and fitted linear model
Subject-by-subject differences elicited by arousal level manipulation. Blue and red areas are rotated kernel density plots. Box plots visualize the median (middle horizontal line), and 25th and 75th percentiles (bottom and top horizontal lines). The upper and lower whiskers indicate the distance of 1.5 times the interquartile range above the 75th percentile and below the 25th percentile. Jittered dots represent individual participants' means. Solid gray lines connect two dots from the same participant. **(A)** Conflict effect in reaction times. **(B)** Conflict effect in MF theta power. **(C)** DCM amplitude estimates as obtained in Alameda et al. (2023). **(D)** Linear model describing the effect of MF theta power on RT. Both measures are conflict effect (I-C). **(E)** Linear model describing the effect of DCM amplitude estimates on MF theta power. MF theta power represent the conflict effect (I-C).

DISCUSSION

The present study aimed at investigating behavioural and neural correlates of cognitive control during high arousal induced by physical exercise. In line with our preregistered hypotheses, behavioural performance was preserved at high arousal. At the individual level, the effects of conflict and conflict adaptation were reliably detected. At the group level, the absence of interaction between arousal and conflict effects showed that conflict processing was not hampered during high arousal. These results are consistent with previous literature showing that physical arousal does not hinder performance in stimulus-response conflict tasks during acute exercise, even if at high intensity (Chang et al., 2012, Davranche et al., 2015, Moreau and Chou, 2019). Our results mirror those obtained in drowsy participants performing an auditory Simon task, in which the behavioural conflict effect was reliably detected even under reduced alertness Canales-Johnson et al. (2020). We did not, however, detect an overall slowing of RTs as a function of increased arousal. This confirms previous findings showing that cognitive control is very robust under high arousal induced by exercise (Davranche et al., 2015). An alternative explanation is that measures of central tendency may provide only a gross representation of cognitive performance during acute exercise (Alameda et al., 2023, Chang et al., 2012). In any case,

consistently with the literature on both exercise and drowsiness, we show that even at high arousal individuals' ability to resolve cognitive conflict remains effective.

As hypothesized, the robust behavioural conflict effect was not accompanied by an equally robust neural correlate. Indeed, high arousal was associated with the degradation of neural signatures of conflict processing. The interaction between arousal and trial congruency in MF theta power suggests that conflict-induced power changes might be modulated by arousal. This effect was driven by the conflict effect being no longer reliable during high arousal. Specifically, individual data (3C) showed that the conflict effect in MF theta was not only reduced in power but some participants even exhibited a reverse effect. MF theta power is considered one of the main neural indexes of cognitive control and a measure for processing demands across various cognitive interference tasks (Adam et al., 2020, Duprez et al., 2020, Nigbur et al., 2011). The increase in theta power in response to incongruent stimuli would reflect the additional recruitment of resources needed to resolve cognitive conflict (van Driel et al., 2015). This additional recruitment was not detected at high-arousal in the present study. Or, at least, is was not detected by changes in theta power at MF locations.

Exploratory analyses appear to further support that at high arousal MF theta did not bear relationship with behavioural measures of cognitive control. In contrast, while at low arousal MF theta power changes did not show a relationship with mean RT, it did with the DMC estimate of automatic processes, i.e., increase in MF theta power was associated with an increase of interference effects from task-irrelevant features under low arousal condition, but this relationship was lost during high arousal. This might suggest that the behavioural robustness of cognitive control is linked to decreased interference effect of task-irrelevant features (Alameda et al., 2023) and that such link captured by theta power measured at MF locations is no longer reliable at high arousal. MF areas have been proposed to be the generator of conflict-modulated theta and changes in phase synchronization between MF, prefrontal and parietal regions within a frontoparietal network have been linked to cognitive control (Cohen and Van Gaal, 2013, Duprez et al., 2020, van Driel et al., 2015). MF regions would act as a central node that coordinates other regions and systems to monitor and adapt goal-directed behaviour essential for conflict processing (Cavanagh et al., 2012, Cohen and Cavanagh, 2011, Cohen and Donner, 2013, Friedman and Robbins, 2022, Menon and D'Esposito, 2022). Focusing on the MF ROI, albeit justified by previous work, carries the drawback of unvariate analysis. This approach ignores the relevance of the multiple individual electrodes in differentiating between experimental conditions and overlooks the potential benefits of utilizing the covariance between electrodes. This oversimplifies complex interactions and undermines the role of neural networks involved in cognitive processes (Anzellotti and Coutanche, 2018, Hebart and Baker, 2018). The disappearance of the conflict effect in MF theta at high-arousal in conjunction with a preserved behavioural performance might reflect the rise of a more distributed network no longer detectable by a univariate approach. In addition, the unreliability of the MF theta conflict effect in high arousal might have also been influenced by noise. This is possible given the methodological challenges of a biking paradigm. Regardless, we did in fact replicated what found in the drowsy state, where reduced arousal was accompanied by the disappearence of the MF theta conflict effect (Canales-Johnson et al., 2020). Following Canales-Johnson et al. (2020) approach, we then implemented multivariate decoding which is fairly robust to noise as classifiers model the noise in the data by assigning low weight to non-informative artefacts (Grootswagers

et al., 2017). Importantly, by performing decoding within each arousal state noise level was equal for congruent and incongruent trials and for the training and testing phases.

Congruency decoding was consistent with the univariate MF theta. Here, decoding showed that information about stimulus congruency was reliably represented in neural data at low arousal but not at high arousal, similarly to what found in states of reduced (i.e., drowsiness) arousal (Canales-Johnson et al., 2020). The fact that decoding of congruency was preserved during low-intensity but not during high-intensity exercise further substantiate that changes in arousal levels are associated with changes in the neural mechanisms supervising the resolution of conflict. However, consistent with our hypotheses, even time-frequency multivariate analysis did not capture the neural signatures of conflict when the level of arousal increased. We hypothesized that the reconfiguration of these networks may be so pronounced to escape the sensitivity of multivariate decoding. We therefore implemented connectivity analysis that would capture changes in a wide network of brain regions rather than changes in local power. Specifically, wSMI has been shown to reflect true nonlinear brain inter-regional interactions (Imperatori et al., 2019, King et al., 2013) and to identify variations in functional integration associated with changes in arousal (Chennu et al., 2016, Lee et al., 2017a,b). We observed a recovered conflict effect in wSMI at high arousal which hints at the possibility that at high arousal the brain undergo the engagement of wider neuronal networks to resolve cognitive conflict. However, the findings from connectivity measures did not fully meet our hypotheses, as the wSMI analysis only showed a statistically significant main effect of congruency, suggesting that the effect was present both in the high and low arousal conditions. This leaves open the question of why a reliable congruency effect did not emerge in the univariate and multivariate high arousal EEG analyses. The analysis of the processing of the most relevant stimulus features in the present study may provide insights into this neural differentiation between the high and low arousal conditions.

At high arousal, stimulus content was decoded above chance levels, showing that such information was retained. On the other hand, decoding of stimulus location was highly degraded, although when looking between 2-10Hz it appeared that some location information was retained. This finding was unexpected. A possible explanation may be that the functional organization of the auditory cortex is tonotopic rather than topographic (Humphries et al., 2010, Saenz and Langers, 2014) and that spatial information is coded by distributed and integrated cortical populations (Belin and Zatorre, 2000, Recanzone and Cohen, 2010, Zatorre et al., 2002). Hence, we consider the possibility that high arousal affected integration even in more perceptual processes such as the processing of spatial location.

With this study we propose that under heightened strained states reconfiguration of networks supervising cognitive control may occur. Whilst the interplay between arousal, cognition and its neural correlates have been traditionally studied in states of reduced arousal (Canales-Johnson et al., 2020, Noreika et al., 2020, Wickens et al., 2015), we provide a complementary view at the higher end of the arousal spectrum. Importantly, we focused on spontaneous fluctuations by inducing transitions towards high arousal in a natural way through exercise. High arousal through aerobic exercise is characterized by changes in the somatic and autonomic systems which are obtained by stressing the body with muscular, cardiovascular and respiratory demand. Similarly, somatic and autonomic changes happen when transitioning towards the lower end of the spectrum (Ogilvie and Wilkinson, 1984). Nevertheless, the changes that occur under high

physical demand are not necessarily linearly related to what occurs at states of reduced arousal. What our study suggests is that these states might share some common processes in the way that cognition and behaviour are supervised by the brain. Clarifying the nature of the commonalities at the opposite end of the arousal spectrum will be an exciting task for future research.

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AUTHOR CONTRIBUTIONS

Chiara Avancini: Conceptualization, Methodology, Software, Data curation, Formal Analysis, Visualization, Writing, Reviewing and Editing. **Luis F. Ciria** Conceptualization, Methodology, Software and Reviewing. **Clara Alameda**: Data curation, Reviewing and Editing. **Ana F. Palenciano**: Methodology. **Andres Canales-Johnson**: Conceptualization, Methodology, Reviewing and Editing. **Tristan A. Bekinschtein**: Conceptualization, Methodology, Reviewing and Editing. **Daniel Sanabria**: Conceptualization, Methodology, Reviewing, Editing, and Funding Acquisition.

AUTHOR COMPETING INTERESTS

The authors declare no competing interests.

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SUPPLEMENTARY MATERIAL: RELATIONSHIP BETWEEN MF THETA POWER AND BEHAVIOURAL MEASURES

Methods

We conducted exploratory analyses to investigate the relationship between behavioural measures and MF theta power changes induced by arousal modulation. To do so, the MF theta power conflict effect was extracted separately for the high and low arousal condition. We subtracted the time-frequency decomposition from congruent trials from that from incongruent trials. Then we averaged the power within the significant cluster region that had been observed in the previous cluster-based permutation testing.

First we investigated whether MF power changes predicted changes in RT by taking into account individual variability. We hierarchically compared three nested models which all had the RT conflict effect as dependent variable and participants as random effect: model A0 was the intercept, model A1 included arousal level as predictor. Model A2 included arousal level and MF theta power as predictors. Model 3 included an interaction term between arousal level and MF theta power. The interaction term allow for potential variation in the effect of MF theta power on RT across participants.

Furthermore, we investigated whether MF theta power changes held a relationship with the interference of task-irrelevant automatic processes. In a study conducted on the same dataset as the one presented in the current paper (Alameda et al., 2023), behavioural dynamics were modelled with Drift Diffusion Modelling for conflict tasks (DMC; Ulrich et al., 2015, for details on the methodology, see Alameda et al., 2023). DMC assume that, when an individual faces a two-alternative choice, the amount of evidence for one answer over the other accumulates gradually over time until it reaches a decision threshold, which triggers the motor response (Ratcliff et al., 2016). DMC allow to estimate the influence of both automatic (task-irrelevant) and control (task-relevant) processes on decision time. Alameda et al. (2023) observed that the estimate representing automatic processes was reduced in high-arousal compared to low-arousal, suggesting that the amount of interference from non-relevant information would be slightly reduced during the high-arousal state. We therefore explored the possibility that MF power changes are predicted by latent psychological processes underlying decision making. In particular, that it would be predicted by state-dependent variations in the processing of task-irrelevant information. To do so, we fitted linear mixed effect models to investigate the effects of arousal lever and the DMC amplitude estimate on theta power, while accounting for individual variability (random effect). Specifically, we hierarchically compared three nested models, all with participant as random intercept: model B0 was the intercept, model B1 included DMC amplitude as predictor. The model B2 included DMC amplitude and arousal level as predictors. This model assumes that the relationship between power and the DMC amplitude estimate is linear and that the effect of DMC amplitude on power is constant across all participants. Model B3 included an interaction term between DMC amplitude and arousal level. The interaction term allow for potential variation in the effect of amplitude on power across participants.

We compared the fit of the models with likelihood ratio test, Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to determine which one best explained the data. Note that these analyses had not been preregistered and were planned upon observation of the current data and the results of Alameda et al. (2023). They are therefore exploratory and will be interpreted as such.

Results

We conducted linear mixed effect models to assess the relationship between MF theta power and RT (Figure 6D). Model A0 had the lowest AIC (659.19) and BIC (666.26) and no hierarchically more complex model fitted the data better than the previous.

We then conducted linear mixed effect models to assess the influence that arousal and DCM amplitude (task-irrelevant automatic processes) had on MF theta power (Figure 6E). Model B3 had the lowest AIC (23.173) and BIC (37.313) and significantly fitted the data better than model B2 ($\chi^2(2) = 4.463$, $p = 0.035$, ΔAIC = 2.463, ΔBIC = 0.108). Model B2 fitted the data better than than Model B1 ($\chi^2(2) = 13.809$, $p = 0.0002$, ΔAIC = 11.809, ΔBIC = 9.453). Model B1 fitted the data better than than Model B0 ($\chi^2(2) = 4.396$, $p = 0.036$, ΔAIC = 2.397, ΔBIC = 0.04). Thus, model B3, which included an interaction term between arousal level and DMC amplitude on MF theta power, was the best fitting model. This suggests that the effect of arousal level on MF theta power depends on task-irrelevant automatic processes.

Note that these results were obtained after visual inspection of our data (Figure 6A - 6C) and results from Alameda et al. (2023). They are therefore to be interpreted as exploratory.