Staying in control: characterising the mechanisms underlying cognitive control in high and low arousal states

Clara Alameda[1*], Chiara Avancini[1,2], Daniel Sanabria[1], Tristan A. Bekinschtein[2], Andrés Canales-Johnson[2], Luis F. Ciria[1,2]

[1] Mind, Brain & Behavior Research Center and Department of Experimental Psychology, University of Granada, Spain.
[2] Consciousness and Cognition Lab, Department of Psychology, University of Cambridge, Cambridge, United Kingdom.

*Corresponding author: clara.alameda@ugr.es

Abstract

Throughout the day, humans show natural fluctuations in arousal that impact cognitive function. To study the behavioural dynamics of cognitive control during high and low arousal states, healthy participants performed an auditory conflict task during high-intensity physical exercise (N = 39) or drowsiness (N = 33). In line with the pre-registered hypothesis, conflict and conflict adaptation effects were preserved during both altered arousal states. Overall task performance was markedly poorer during low arousal, but not for high arousal. Modelling behavioural dynamics with drift-diffusion analyses revealed evidence accumulation and non-decision time decelerated, and decisional boundaries became wider during low arousal, whereas high arousal was unexpectedly associated with a decrease in the interference of task-irrelevant information processing. These findings show how arousal differentially modulates cognitive control at both sides of normal alertness, and further validates drowsiness and physical exercise as key experimental models to disentangle the interaction between physiological fluctuations on cognitive dynamics.

Key words: Cognitive conflict, decision-making, sleep, physical activity

1. Introduction

Rushing to get to work on time or falling asleep while watching TV are familiar scenarios that illustrate how people's arousal is endogenously altered. Ranging from deep sleep to physical extenuation, these arousal fluctuations modulate cognition (Goupil & Bekinschtein, 2012; Lambourne & Tomporowski, 2010). Here, we investigate how cognitive control is exerted across the arousal spectrum by instructing participants to perform an auditory Simon task (Simon & Rudell, 1967) while transitioning to sleep or physical exhaustion.

During reduced arousal states such as drowsiness, individuals show longer reaction times (RTs) and lower accuracy (Bareham et al., 2015). Similarly, increasing arousal with exercise close to or exceeding the anaerobic threshold seems to raise RTs (González Fernández et al., 2017). The interaction between arousal and cognition has been approached from the inverted U-shaped framework (Yerkes & Dodson, 1908), whereby levels above and below an intermediate level of arousal lead to a decrease in performance, both in drowsy and exercising participants (Ciria et al., 2021).

Of particular interest are the studies manipulating arousal to investigate cognitive control, the ability to maintain task-relevant information and inhibit non-relevant or conflicting information (Botvinick & Braver, 2015). This ability is commonly assessed by means of conflict tasks such as the Simon task (Simon & Rudell, 1967), by which two effects can be measured: 1) cognitive conflict (i.e., longer RT in incongruent vs. congruent trials); and 2) conflict adaptation (i.e., reduced conflict effect when the previous trial is incongruent vs. congruent). The existing literature suggests that stimulus-response conflict effect remains unaltered during moderate exercise (Davranche et al., 2015; Davranche & McMorris, 2009). However, the effect of exercise on overall RTs in conflict tasks is rather ambiguous: while some studies report shorter RTs (e.g., Alves et al., 2012), others show no effect or even the reverse pattern (e.g., Labelle et al., 2013; Weng et al., 2015). At the opposite side of the arousal spectrum, conflict effects seem to be preserved in sleep-deprived and drowsy participants (e.g., Gevers et al., 2015). For instance, Canales-Johnson and collaborators (2020) showed preserved stimulus-response conflict and adaptation effects during drowsiness, even if overall RTs increased.

In this study, we designed a complementary experiment to that of Canales-Johnson et al. (2020) to characterise cognitive performance at both sides of the arousal spectrum by implementing the same auditory Simon task to healthy participants during high-intensity physical exercise. Following the approach by Ciria and colleagues (2021), databases from both experiments were combined aiming to reveal not only whether drowsy and highly aroused participants perform different, but why they do so. Thus, we applied a specific drift-diffusion model (DDM) for conflict tasks (Ulrich et al., 2015) to disentangle processes involved in decision-making and cognitive control, such as rate of task-relevant evidence accumulation or the amount of the interference generated by task-irrelevant (conflicting) information. Previous studies involving conventional DDMs show that drowsy and sleep-deprived states lead to a lower drift rate, wider boundary separation and longer non-decisional time (Jagannathan et al., 2022; Ratcliff & Van Dongen, 2011), while moderate intensity exercise seem to fail to modulate decision-making parameters (Lefferts et al., 2016, 2019).

Based on the premises that (1) drowsiness and high intensity physical exercise both seem to lead to slower RTs and lower accuracy (Goupil & Bekinschtein, 2012; Lambourne & Tomporowski, 2010), and (2) changes in arousal have no apparent impact on conflict and adaptation effects (Canales-Johnson et al., 2020; Davranche et al., 2015): we expected the magnitude of cognitive conflict effects to be preserved in high and low arousal states, although both states would result in higher overall RTs

and lower accuracy than their respective baseline conditions. Consistent with recent accounts for perceptual decision-making (Jagannathan et al., 2022), we expected DDM analyses to reveal a slower rate of evidence accumulation and a greater separation of the decisional boundaries in the low arousal condition. Further, comparisons between high arousal and its baseline were of a broader exploratory nature. All hypotheses here tested, together with the analysis plan, were pre-registered after data collection (Alameda et al., 2022), except for the DDM analyses.

2. Materials and methods

2.1. Participants

Seventy-two healthy participants (18-50 years old) were involved in this study. All participants reported normal binaural hearing and no history of physical and mental illness. Before the experimental sessions, participants were informed of the protocol and signed a consent form. They were given monetary compensation for their participation. The studies were approved by the local committee of ethics of the University of Cambridge (CPREC.2015; Experiment 1) and the University of Granada (978/CEIH/2019; Experiment 2).

Experiment 1 consisted of 33 participants (18 females; age range, 18–30) of a cohort of 41, pruned after rejecting those who did not attain enough drowsiness for single participant comparisons. Participants were recruited from Cambridge (UK). Only non-pathological easy sleepers, with a sleepiness score 7-14 assessed with the Epworth Sleepiness Scale (Johns, 1991), were selected. They were instructed to get a regular night's rest on the night previous to testing, and to avoid stimulants on the day of the experiment.

Experiment 2 consisted of 39 participants (2 females; age range, 18-50) recruited from Granada (Spain). Although a total of 40 participants were initially recruited, data from one participant was discarded, as heart rate (HR) in the high intensity condition was considered too low (see Supplementary material). Cyclists with a training regime of at least 4 times or more per week and at least 5 years cycling experience were selected, in order to minimise dual-task effects and improve EEG signal-to-noise ratio (cf. Ciria et al., 2018). Participants were asked not to engage in strenuous physical activity in the 48 hours prior to the sessions.

2.2. Experimental task

Participants performed a modified auditory version of the Simon task (Simon & Rudell, 1967) in English —in Experiment 1— or Spanish —in Experiment 2—. Recorded spoken words ("left"/"izquierda" or "right"/"derecha") were presented to either the right or the left ear through earphones. Trials were considered congruent when the word meaning corresponded to the side from which they were heard, and incongruent when they did not. Participants were asked to press with their thumbs the button located on the side which was congruent with the meaning of the word (Figure 1A). All types of trials were presented equally often in a random order. The interval between the participant's response and the presentation of the following stimulus ranged between 2 and 2.5 seconds in Experiment 1, and between 1.5 and 2 seconds in Experiment 2. The shorter inter-trial interval in Experiment 2 was aimed at increasing the number of trials in a shorter total task time. Participants were allowed to respond within 1.99 seconds after the word.

2.3. Procedure

2.3.1. Experiment 1

In Experiment 1, participants were fitted with an 129-channel EEG cap (Electrical Geodesics, USA) while sitting in a reclining chair. A single experimental session was divided into two parts: 1) wakefulness, in which the chair was set upright and the lights were on, while participants remained awake with their eyes closed and responded to the task for approximately 25 minutes (~500 trials); 2) drowsiness, in which the chair was reclined, lights were off, and participants were allowed to fall asleep while they kept responding to the task for approximately 1 hour and 30 minutes (~2000 trials; Figure 1B). If participants stopped responding for 5 consecutive trials, the experimenter knocked on the door to wake them up. The whole session lasted for approximately 3 hours.

Subsequently, for each participant, the trials of both parts of the session were classified as "low baseline" (wakefulness) or "low arousal" (drowsiness) using the algorithmic method developed by Jagannathan and collaborators (2018).

2.3.2. Experiment 2

Experiment 2 consisted of three sessions.

Incremental effort test. After a 5 min warming up at 120 watts, participants were asked to pedal on a cycle-ergometer while HR, volume of oxygen (VO_2) capacity and respiratory exchange ratio were measured. The test consisted of increments of 20 watts in power output every 3 minutes, until participants reached full exhaustion. The watts output when the participant reached 80% of their maximum VO_2 consumption ($VO_{2\ max}$) was used as target watts during the "high arousal" condition. Whereas, in the "high baseline" condition, the target was 10% of the watts reached at $VO_{2\ max}$. Next sessions were held about 1 week after.

Experimental sessions. The two sessions (i.e., high arousal and high baseline) were conducted on different days, separated by an interval of 24-72 hours (Figure 1B), counterbalanced across participants. Each individual attended both sessions at the same time of the day.

Upon arrival at the laboratory, participants were fitted with 3-ECG electrodes (Ambu, Ballerup, Denmark) and a 64-channel actiCHamp EEG system (Brain Products, Munich, Germany). Then, they got on a cycle-ergometer (SRM, Germany), and were fitted with a HR monitor (SRM, Germany) and earphones (Kingston, USA). After a 5-minutes warm-up, the task was administered while participants were cycling either at low (10% of $VO_{2\ max}$) or high (80% of $VO_{2\ max}$) intensity for 30 minutes (~750 trials per session). Individual HR and watts mean values per condition are provided in Supplementary material. The resistance of the bike was controlled by the software MagDays, stimuli were presented using a PsychToolbox software in Matlab, and data were acquired with Brain Vision and AcqKnowledge softwares, and a BIOPAC amplifier, on Dell (USA) computers. Note that EEG data are reported in Avancini et al. (2022).

2.4. Data analyses

2.4.1. Reaction times and accuracy

Incorrect or missed trials and trials with RT below 200 ms were excluded from behavioural analyses[1]. We collapsed data from the two experiments into a single dataset with RT and accuracy as the main indexes of performance, and fitted the variables using multilevel linear mixed-effects modelling, using the *lme4* R package (Bates et al., 2014). Hierarchical modelling allows to account for potential differences between the databases that may have not been exclusively caused by the experimental manipulation. Participant nested into experiment were set as random factors, and arousal as fixed factor. This structure was common to all models. We performed further models including current congruency and previous congruency, and their interactions, to test our hypotheses (details on testing model assumptions can be found in the Supplementary material). Additionally, we conducted Bayesian repeated measures t-tests with JASP (version 0.15.0) to examine the favourability towards the null or the alternative hypothesis when comparing high and low arousal conditions with their respective baselines[2]. Priors were fixed at a Cauchy scale value of 0.4 (i.e., small-to-moderate effect size predicted).

2.4.2. Drift-diffusion modelling

By implementing the *DMCfun* package in R (Mackenzie & Dudschig, 2021), we estimated for each participant under each condition the following parameters: (1) drift rate of controlled processes, (2) non-decision time, (3) distance between decision boundaries, and (4-5) amplitude and time to peak of automatic processing pulse function. Parameters were estimated from fitting the DMC to our data with the differential evolution optimization algorithm (Storn and Price, 1997), relying on the *DEoptim* R package (Mullen et al., 2011; see Supplementary material, for further information about fitting procedure and parameter recovery test). We analysed the DDM parameters by fitting multilevel linear mixed-effects modelling and Bayesian tests.

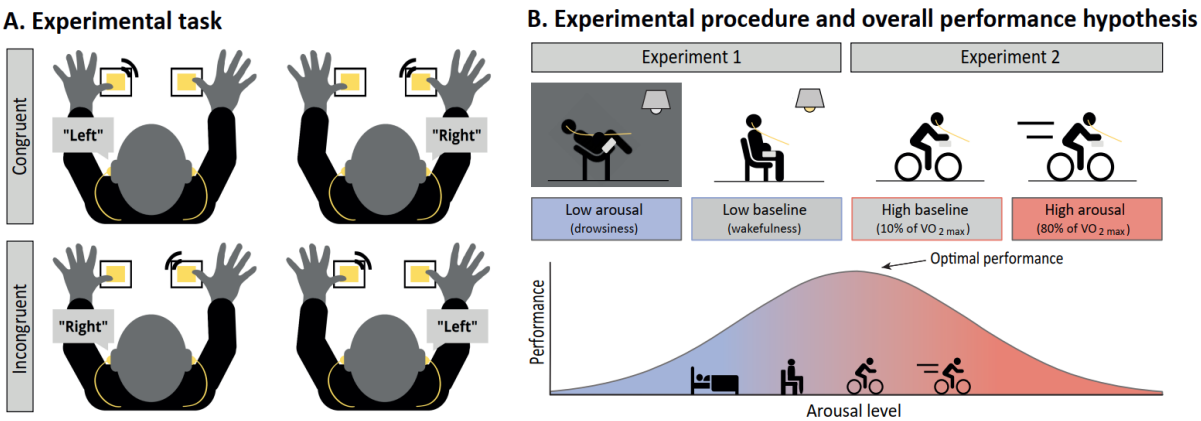

Figure 1: Experimental design. A) Schematic representation of the auditory Simon task implemented. Trials were considered congruent when the meaning of the word matched the ear through which it was presented, and incongruent when it did not. Participants were asked to press the button corresponding to the meaning of the word, ignoring the location in which it was heard. B) Schematic representation of experimental procedure and main hypothesis on overall performance. In Experiment 1, the experimental session was divided into two parts: wakefulness and drowsiness. Experiment 2 consisted of two experimental sessions in which participants performed the task while pedalling at high or low intensity. Optimal performance (i.e., overall RT and accuracy irrespective of trial type) was expected at a moderate arousal state (e.g. exercising at low intensity), while lower (drowsiness) and higher (exercising at high-intensity) arousal states were expected to result in poorer task performance (longer RT and lower accuracy).

[1] Data exclusion procedure not included in the pre-registration. Following Canales-Johnson and collaborators' (2020) behavioural data processing, we excluded anticipatory responses, errors and omissions.
[2] Bayesian analyses were not included in the pre-registration. The analyses were conducted after multilevel models aiming to test those hypotheses concerning the absence of differences.

3. Results

3.1. The impact of arousal on overall task performance

To test whether overall performance deteriorates at extreme levels of arousal, we first examined whether the relationship between arousal level and the average RT and accuracy fitted a quadratic model. Both overall RT and accuracy were better fitted to a quadratic model (RT: *AIC* = -671.33; accuracy: *AIC* = -1077.3) than to a linear one (RT: *AIC* = -611.97; accuracy: *AIC* = -1066.1), pointing to a curvilinear relationship between arousal level and general performance (Figure 2A-B).

Next, we tested whether arousal influenced overall RT and accuracy. The hierarchical linear mixed-effects model revealed a strong effect of arousal in RT, F (214) = 55.24, $p < 0.001$, $\eta p^2 = 0.34$, and accuracy, F (235) = 10.24, $p < 0.001$, $\eta p^2 = 0.08$. When splitting the comparisons to each experiment, reliably slower RT, t (214) = -10.46, $p < 0.001$, $d = 1.10$, $BF_{10} = 31166$, and lower accuracy, t (239) = 4.50, $p < 0.001$, $d = 0.79$, $BF_{10} = 271.61$, were only found in low arousal compared to its baseline condition. Neither RT, t (214) = -1.01, $p = 0.32$, $d = 0.12$, $BF_{10} = 0.35$, nor accuracy, $t < 1$, $BF_{10} = 0.298$, showed reliable differences between high arousal and its baseline (Figure 2C-D). Hence, overall performance was negatively impacted only at the lower side of the arousal spectrum.

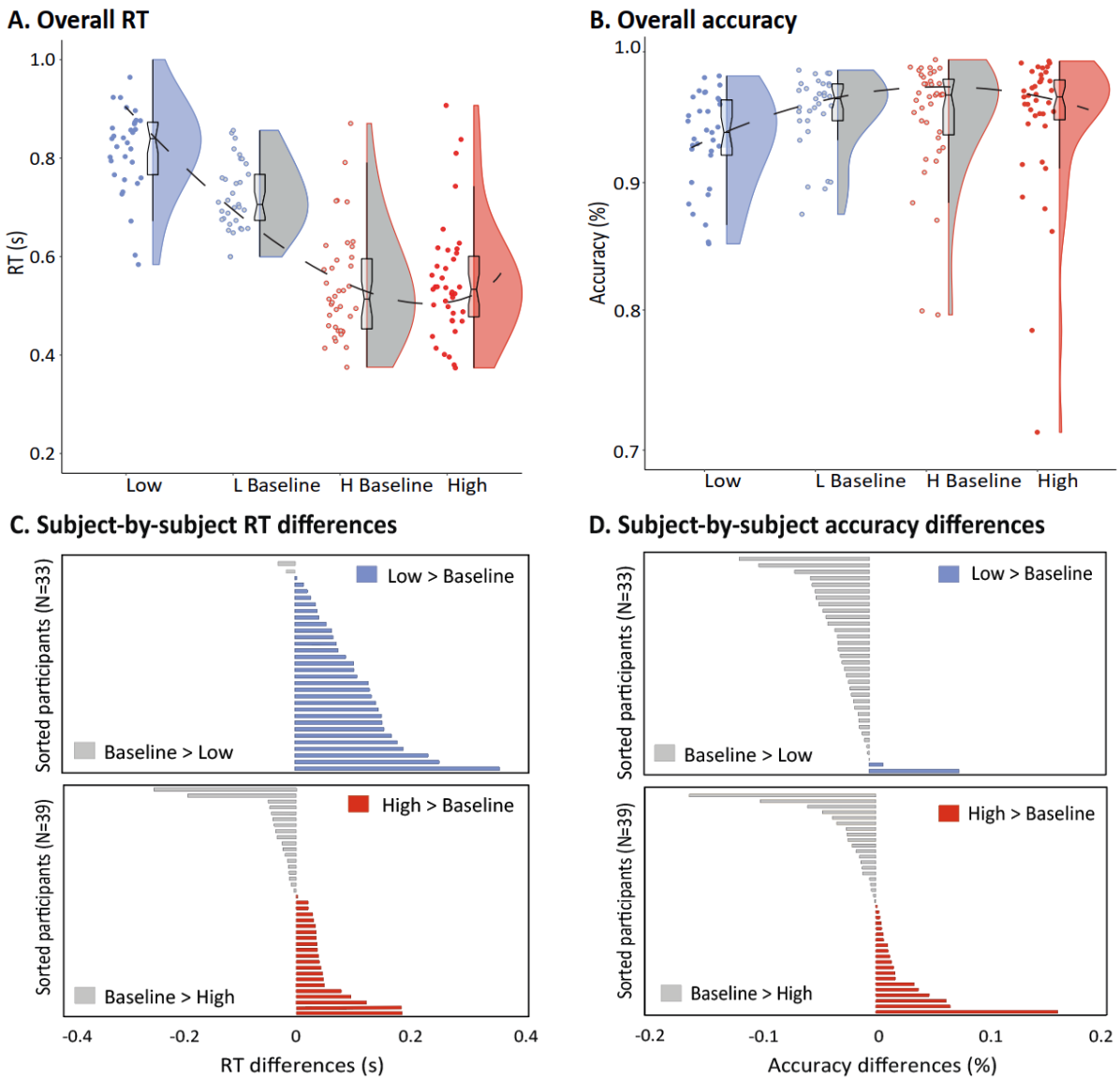

Figure 2: Overall RT and accuracy main results. A-B) Violins and overlaid box plots of mean overall RT (A) and accuracy (B) across the arousal conditions. Accuracy is represented as a ratio between 0 and 1, where 1 indicates 100% correctness (i.e., no errors). In box plots, middle black mark indicates the median, and bottom and top edges indicate 25th and 75th percentiles, respectively. The upper and lower whiskers indicate the distance of 1.5 times the interquartile range above the 75th percentile and below the 25th percentile. Adjacent to the box, on the right, there is a rotated kernel density plot; on the left, jittered dots depict the average RT (A) or accuracy (B) of each individual in each arousal state. Linear mixed-effects model analysis revealed a better quadratic fitting between arousal and RT, and between arousal and accuracy, compared to linear fitting, outlined by the dashed black line. C-D) Global RT (C) and accuracy (D) differences of each participant in both altered arousal states (i.e., high and low arousal), compared to their respective baselines. Participants are sorted by performance difference between baseline and the arousal state (i.e., the outcome of subtracting the value of RT/ accuracy in the respective baseline condition from its value in the high or low arousal condition). Grey bars indicate that these participants showed higher RT/accuracy in the baseline condition, compared with the altered arousal states; while blue and red bars depict that these participants showed slower RT or higher accuracy in the low or high arousal states, compared with their respective baselines.

3.2. Cognitive control preservation under altered arousal states

To test whether arousal had an impact on the conflict effect, the average RT and accuracy per participant for congruent and incongruent trials were fitted using a hierarchical linear mixed-effects model, with arousal, congruency and 'arousal x congruency' as fixed effects. RT yielded a robust effect of congruency, F (211) = 46.06, $p < 0.001$, $\eta p^2 = 0.18$, but no reliable interaction between arousal level

and congruency, $F < 1$ (Figure 3A). To further examine the favourability towards the absence of differences in conflict effect between arousal conditions, we splitted the data per arousal conditions and performed additional frequentists and Bayesian tests. No reliable differences were found in the magnitude of congruency effect on RT between high arousal and its baseline, $t < 1$, $BF_{10} = 0.69$, as well as between low arousal and its baseline, $t < 1$, $BF_{10} = 0.53$. Thus, although Bayesian contrasts yielded inconclusive evidence, global results point towards a relative preservation of the RT conflict effect in both high and low arousal states (Figure 3C). Accuracy analysis revealed a reliable main effect of congruency, F (211) = 51.21, $p < 0.001$, $\eta p^2 = 0.15$, but no reliable interaction between arousal and congruency , F (211) = 3.07, $p = 0.49$, $\eta p^2 = 0.03$. When comparing high and low arousal conditions with their respectives baselines, no differences were found in conflict effect between low arousal and its baseline, t (211) = 1.59, $p = 0.11$, $d = 0.16$, $BF_{10} = 0.43$, or between high arousal and its baseline, t (211) = -1.27, $p = 0.21$, $d = 0.06$, $BF_{10} = 0.30$.

The impact of arousal on conflict adaptation was assessed with a hierarchical mixed-model fitting RT, with arousal, congruency, previous congruency and all their interactions as fixed factors. The model showed a robust interaction between current trial congruency and previous trial congruency, F (493) = 45.10, $p < 0.001$, $\eta p^2 = 0.08$, reflecting a decreased conflict effect when the previous trial was incongruent. Hierarchical linear mixed-effects model revealed no effect for the 'arousal x congruency x previous congruency' interaction, F (493) = 1.38, $p = 0.25$, $\eta p^2 = 0.005$ (Figure 3B). The comparison between altered arousal states and their baselines also yielded no reliable differences in conflict adaptation effect, $t < 1$, $BF_{10} = 0.39$ (low arousal vs. baseline), t (493) = -1.31, $p = 0.19$, $d = 0.26$, $BF_{10} = 0.79$ (high arousal vs. baseline; Figure 3D).

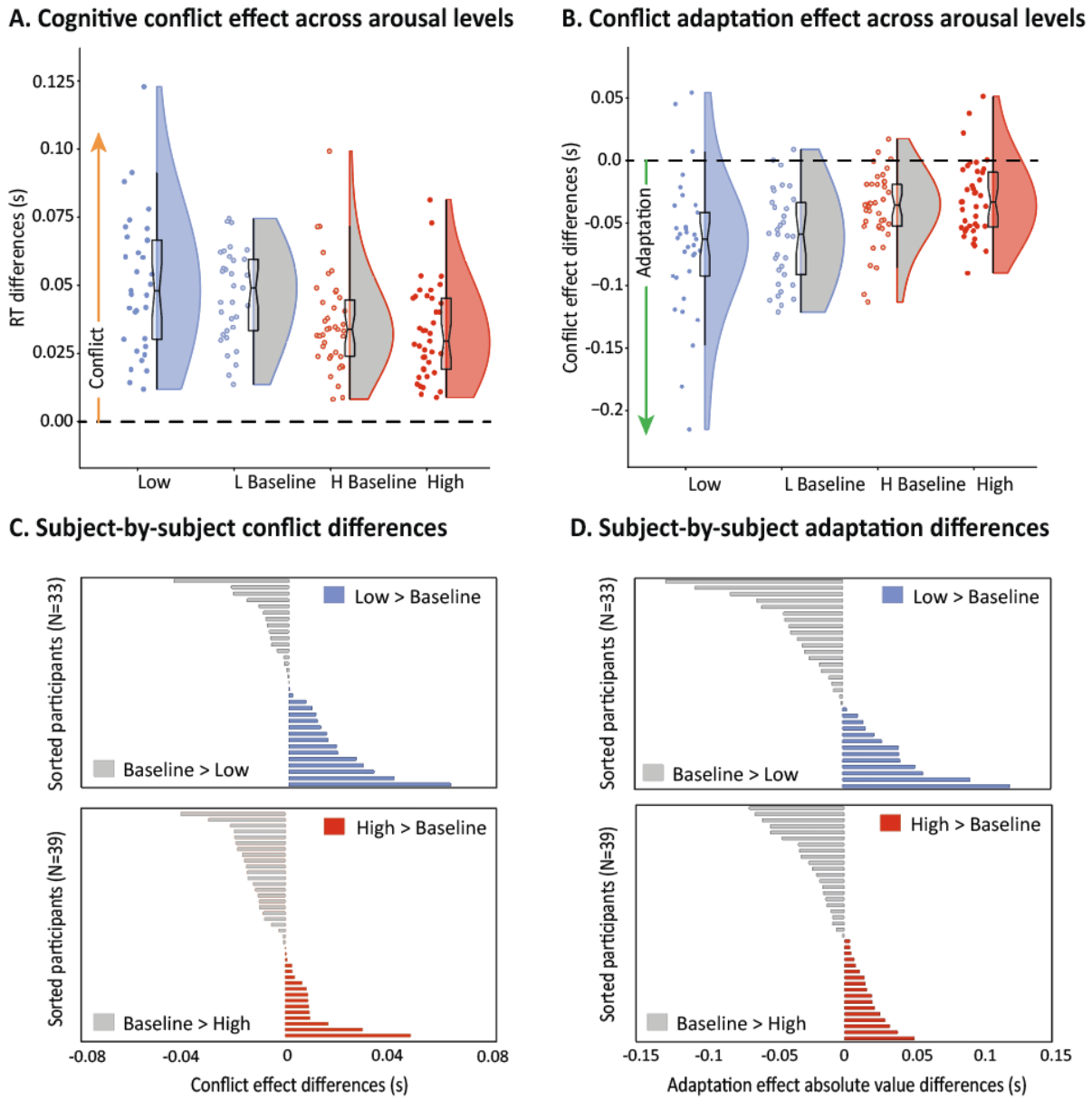

Figure 3: Current and previous trial congruency effects as a function of arousal level. A) Violins and overlaid box plots of RT conflict effect (i.e., RT for incongruent trials minus RT for congruent trials) for each arousal condition. In box plots, middle black mark indicates the median, and bottom and top edges indicate 25th and 75th percentiles, respectively. The upper and lower whiskers indicate the distance of 1.5 times the interquartile range above the 75th percentile and below the 25th percentile. Adjacent to the box, on the right, there is a rotated kernel density plot; on the left, jittered dots represent the average RT conflict effect of each individual in each arousal state. Every participant showed a global conflict effect in all experimental conditions and, as expected, no statistically reliable differences were found in the magnitude of the conflict effect between the altered arousal states and their respective baseline conditions. B) Violins and overlaid box plots of RT conflict adaptation effect (i.e., conflict effect for previous incongruent trials minus conflict effect for previous congruent trials). According to linear mixed-effects analyses, conflict adaptation is preserved in every arousal condition, and there are no statistically reliable differences in the magnitude of conflict adaptation effect between high arousal and high baseline, or low arousal and low baseline. C-D) Global conflict (C) and adaptation absolute values (D) differences of each participant in both altered arousal states (i.e., high and low arousal), compared to their respective baselines. Participants are sorted by performance difference between baseline and the arousal state (i.e., the value of the conflict/adaptation effect in the high or low arousal condition minus its value in the respective baseline condition). Grey bars indicate that these participants showed higher conflict/adaptation in the baseline condition, compared with the altered arousal states. Blue and red bars depict that these participants showed higher conflict/adaptation effect in the low or high arousal states, compared with their respective baselines.

3.3. High and low arousal modulate decision-making parameters differently

To assess the influence of arousal level on decision-making, we fitted a DDM for conflict tasks to our databases (Table 1). The hierarchical linear mixed-effects model revealed a robust effect of arousal in drift rate of controlled processes, F (70) = 70.9, $p < 0.001$, $\eta p^2 = 0.67$, separation between decision boundaries, F (62) = 5.28, $p = 0.008$, $\eta p^2 = 0.14$, and non-decisional time, F (59) = 24.22, $p < 0.001$, $\eta p^2 = 0.45$. The effect of arousal on automatic processing parameters was not statistically reliable, F (63) = 2.27, $p = 0.11$, $\eta p^2 = 0.07$ (amplitude), F (91) = 1.71, $p = 0.19$, $\eta p^2 = 0.04$ (time to peak).

Table 1. Group average of DMC estimated parameters across the arousal conditions.

	amp	tau	drc	bnds	resMean	cost
High arousal	14.05	167.66	0.63	106.12	361.14	14.07
High baseline	17.12	143.14	0.67	110.16	362.77	10.47
Low baseline	13.19	129.99	0.53	120.79	407.83	25.08
Low arousal	13.62	151.53	0.24	131.92	529.34	84.18

Amp: amplitude of automatic processes; tau: time to peak of automatic processes; drc: drift rate of the controlled processes; bands: boundary separation; resMean: residual or non-decision time mean; cost: RMSE or cost value.

Splitting per arousal conditions, both mixed-effects modelling and Bayesian analyses pointed towards reliable differences in the amplitude of automatic processes between high arousal and its baseline condition, t (69) = 2.12, $p = 0.04$, $d = 0.49$, $BF_{10} = 9.41$, whereby the amount of interference from non-relevant information would be slightly reduced during high arousal (Figure 4A). No differences were found for the rest of the DMC parameters: duration of automatic processes, t (90) = -1.76, p = 0.08, $d = 0.29$, $BF_{10} = 1.12$; drift rate of controlled processes, t (70) = 1.70, $p = 0.09$, $d = 0.32$, $BF_{10} = 1.4$; boundary separation, t (69) = 1.26, $p = 0.21$, $d = 0.16$, $BF_{10} = 0.431$; and non-decision time, t (68) < 1, $BF_{10} = 0.29$.

When compared with its baseline, low arousal was associated with a reliably lower drift rate of controlled processes, t (70) = 11.797, $p < 0.001$, $d = 1.815$, $BF_{10} = 6.9e+8$, a wider separation of decision boundaries, t (67) = -2.95, $p = 0.004$, $d = 0.50$, $BF_{10} = 6.62$, and a higher non-decisional time, t (67) = -6.94, $p < 0.001$, $d = 0.85$, $BF_{10} = 641.73$. Automatic processing parameters did not yield statistically reliable differences, t (68) < 1, $BF_{10} = 0.39$ (amplitude), t (95) < 1, $BF_{10} = 0.42$ (time to peak). These results suggest that, during drowsiness, evidence accumulation and non-decision time become slower, while more evidence needs to be accumulated to reach a response (Figure 4B-D).

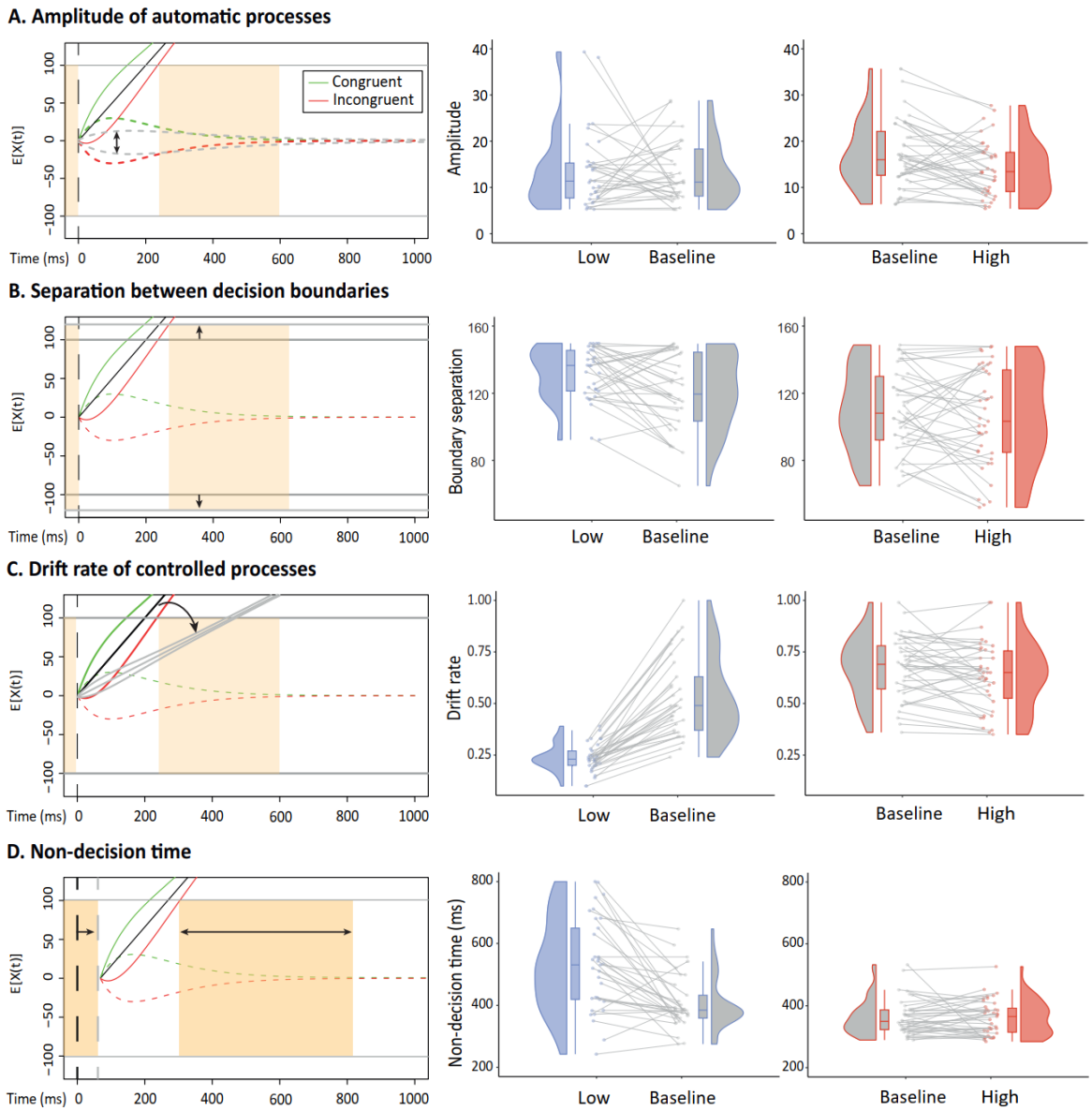

Figure 4: The impact of arousal on decision-making parameters. Panels on the left show the schematic representation of a shift in different diffusion model for conflict tasks (DMC) parameters: (A) amplitude of automatic (i.e., task-irrelevant) processing, (B) boundary separation, (C) rate of evidence accumulation of the controlled (i.e., task-relevant) processing, and (D) non-decision time (i.e., sensory encoding and motor response duration). The DMC illustrative representation on which the changes in the respective parameters have been plotted was generated from the simulation of 100,000 congruent and incongruent trials. Upper and lower grey solid lines represent the boundaries of the two potential responses (correct, above, and incorrect, below), and orange areas depict non-decision time. The black solid line constitutes the drift rate of controlled processing, while the dotted green and red lines represent the automatic processing for congruent and incongruent trials, respectively. The response will be determined by a single rate of evidence accumulation, resulting from the combination of the automatic and controlled processes, represented by the green solid line for congruent trials, and the red one for incongruent trials. Panels in the middle and on the right represent subject-by-subject baseline differences for each DMC parameter. Blue, grey and red areas are rotated kernel density plots (i.e., a histogram with infinitely small bin sizes). In box plots, middle marks indicate the median, and bottom and top edges indicate 25th and 75th percentiles, respectively. 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 the average DMC parameter value (e.g., amplitude of automatic processes in A) of each individual under each arousal state. The two values from the same subject in both experimental conditions are linked by a solid grey line. Linear mixed-effects and Bayesian analyses showed that the amplitude of automatic processes was reliably reduced during high arousal compared to its respective baseline condition, while low arousal was solidly associated with (1) slower drift rate, (2) wider separation of decision boundaries and (3) longer non-decisional time than its baseline.

4. Discussion

In the present study, participants performed a conflict task while transitioning into sleep or physical extenuation to study the behavioural dynamics of cognitive control across the arousal spectrum. As predicted, conflict and conflict adaptation effects were preserved during high and low arousal. While overall performance deteriorates at the lower side of the spectrum, this impairment is not observed at the upper side. DDM analyses revealed that the impairment of performance during low arousal might be due to: (1) a slower rate of task-related information evidence accumulation; (2) a longer non-decision time that could be caused by a deceleration in sensory encoding, motor response execution, or both; and (3) a wider separation between decision thresholds, which means that more evidence would need to be accumulated by the system to reach a response criterion. Notably, although increased levels of arousal showed minimal performance changes, they were associated with a decrease in the interference of task-irrelevant information processing. These results provide evidence that high and low arousal differentially impact the underlying decision-making processes during automated cognitive-control tasks.

It has been previously shown how decreased arousal fails to fully interrupt higher order cognitive processes, such as semantic discrimination (Kouider et al., 2014). However, as reported by the entire body of literature on drowsy states (e.g., Jagannathan et al., 2022; Xu et al., 2023), decreased levels of arousal lead to slower RT, lower accuracy and decreased sensitivity in decision-making. Our results replicate and enable the generalisation of previous reports, further revealing that drowsiness selectively modulates task-relevant decision-making processes but fully preserves some automated aspects of cognitive control. Notably, EEG analyses of this same database (Canales-Johnson et al., 2020) show that the robust behavioural and computational effects of efficient conflict resolution are not accompanied by their classical neural marker (i.e., increased power in mid-frontal theta), and suggest some reorganisation of the traditional (waking) neural activity to deal with conflict during a non-homeostatic state (i.e, drowsiness).

The transition towards high arousal yielded mixed results. Consistent with previous studies examining cognitive control during moderate-to-high exercise (Schmit et al., 2015), conflict detection and adaptation were both fully preserved. As in low arousal, this was not accompanied by the preservation of the classical neural correlate of conflict resolution (Avancini et al., 2023), suggesting some parallelisms between these two strained states of arousal. Yet, the absence of impaired cognitive performance when participants exercised close to the anaerobic threshold was not expected. Some accounts have shown that acute exercise might not produce a deterioration in performance when the task involves highly automated behaviours or rapid decision-making (Lambourne & Tomporowski, 2010), such as the Simon task. From a theoretical perspective, these findings would be in line with the task-difficulty assumption within the Yerkes-Dodson framework, which proposes easier tasks require higher levels of arousal for optimal performance than more difficult tasks (Sjöberg, 1977). However, whereas Yerkes-Dodson's proposal may be a useful starting point for studying the relationship between arousal and cognition, its reductionist nature, the overgeneralization from its initial formulation (Teigen, 1994) and the current state of the literature on physical activity (e.g., Cantelon & Giles, 2021; Sudo et al., 2022) raise the question of whether this theory, or even the wider notion of arousal, is sufficiently informative when interpreting performance outcomes.

As opposed to low arousal, most decision-making parameters remained relatively unaffected during high arousal, except for an unexpected small but reliable decrease in the amount of interference from task-irrelevant information. To our knowledge, only two studies have addressed decision-making

during physical exercise using a DDM approach (Lefferts et al., 2016; 2019), reporting no reliable differences on any of the estimated cognitive parameters. However, the DDM in their research did not distinguish between automatic and controlled processing, and therefore it could not detect the effect in the amplitude of automatic processes reported here, even if present. Interestingly, EEG multivariate spectral decoding analyses of the high arousal data showed that the task-irrelevant information (i.e., spatial location) was only present (decodable) in the baseline condition in the 2-10 Hz band, but not during high-intensity exercise (Avancini et al., 2023). Also consistent with a narrower focus during strained states of high arousal, reduced overt attentional capture (i.e., automatic disruption from abrupt distracting stimuli) has been previously observed right after a bout of intense physical exercise (Llorens et al., 2015). Thus, although increased arousal produces little difference in classical behavioural indices, computational and brain activity outcomes provide a hint that the system undergoes some cognitive modulations during such state, albeit in a different direction to that of low arousal.

The present study highlights the utility of inducing natural states of drowsiness and physical exercise as causal models to study cognition as our level of arousal moves towards either of its extremes. Despite their different biological nature, both transitions —towards sleep and physical exertion— involve rapid and dynamic fluctuations in arousal, accompanied by important physiological and phenomenological changes, in which the overall capacity to respond behaviourally to stimuli is preserved (Ciria et al., 2021). These features allow us to combine them in a common experimental framework to study how human cognitive and neural dynamics are modulated as our system becomes overstrained on a physiological level. Note that they are not directly compared to each other in any part of the study. On the other hand, there is a growing consensus in neuroscience that RT and accuracy, while undoubtedly useful, can sometimes be insufficiently informative about performance (Voss et al., 2013). Indeed, our findings showcase the benefits of using computational modelling as a tool to identify the specific decision-making mechanisms underlying the modulations observed through classical measures. Future steps involve further deepening the complementary nature of neural and computational analyses to disentangle the cognitive dynamics during everyday arousal fluctuations. For now, the combination of drowsiness and intense physical exercise, together with the use of behavioural computational modelling, seem to offer a fruitful approach to explore the cognitive processing during endogenously altered arousal states.

5. Funding and acknowledgements

This research was supported by a predoctoral fellowship by the Spanish Ministry of Universities to the first author (FPU21/00388), a postdoctoral fellowship by the Spanish Ministry for Science and Innovation to the second author (FJC2020-046310-I); a research project grant from the Spanish Ministry of Science and Innovation to D.S. (PID2019-105635GB-I00), a postdoctoral fellowship from the Regional Government of Andalusia to L.F.C. (DOC_00225), and a Wellcome Trust Biomedical Research Fellowship (WT093811MA) awarded to T.A.B. We thank Luc Vermeylen for his valuable help with the drift-diffusion modelling analyses.

6. Open Practices Statement

The hypotheses and analyses plan were pre-registered in AsPredicted after data collection but prior to data observation and analysis (https://aspredicted.org/x8qd6.pdf), except for DDM analyses. All

deviations from the pre-registered procedures are transparently identified in the manuscript. Raw data, sorted data and codes used for the analyses presented here are available at the OSF repository (https://osf.io/uvq3m/).

7. CRediT Author Statement

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

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