

1 **Different underlying mechanisms for high and low arousal in probabilistic**
2 **learning in humans**

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20 **ABSTRACT**

21 Humans are uniquely capable of adapting to highly changing environments by updating
22 relevant information and adjusting ongoing behaviour accordingly. Here we show how this
23 ability —termed cognitive flexibility— is differentially modulated by high and low arousal
24 fluctuations. We implemented a probabilistic reversal learning paradigm in healthy participants
25 as they transitioned towards sleep or physical extenuation. The results revealed, in line with
26 our pre-registered hypotheses, that low arousal leads to diminished behavioural performance
27 through increased decision volatility, while performance decline under high arousal was
28 attributed to increased perseverative behaviour. These findings provide evidence for distinct
29 patterns of maladaptive decision-making on each side of the arousal inverted u-shaped curve,
30 differentially affecting participants' ability to generate stable evidence-based strategies, and
31 introduces wake-sleep and physical exercise transitions as complementary experimental
32 models for investigating neural and cognitive dynamics.

33 INTRODUCTION

34 Making mistakes is inherent to learning and the accomplishment of any task. We make
35 mistakes every day, even when faced with the same task repeatedly. Our ability to learn from
36 these errors and flexibly adapt ongoing behaviour according to changes in the environment is
37 critical for our survival. This ability —termed cognitive flexibility— depends on our innate
38 capacity to establish associations between stimuli (S), responses (R), and outcomes (O), as well
39 as to integrate previously acquired knowledge and skills into effective strategies for coping
40 with similar future demands.¹ Here, we implement a Probabilistic Reversal Learning (PRL)
41 task to study the modulatory effect of low and high arousal on cognitive flexibility —
42 participants continue to perform as they fall asleep or with increasing physical exercise— to
43 map either side of the Yerkes-Dodson Curve (1908).²

44 Cognitive flexibility is often studied using PRL tasks, typically assigning probabilistic
45 reinforcement contingencies to abstract S-R associations, that are later abruptly reversed,
46 requiring participants to learn new S-R reinforcement contingencies by trial and error to
47 overcome prepotent ones³. Efficient performance relies on learning from the reinforcement
48 received⁴, the estimation of the likelihood that a reversal may occur,^{5,6} and the continuous
49 integration of a history of choices and reinforcements.⁷ Indeed, evidence from both human and
50 animal studies suggests that different high- and low-order strategies or series of rules are
51 adopted during reversal learning, leading to maladaptive response patterns when the external
52 pressures change or when the internal milieu varies.^{7,8} Parsing the microstructure of learning
53 derived from trial-by-trial responses enables the dissociation of the cognitive processes and
54 behavioural strategies that drive subjects' choices during reversal learning. Here we propose
55 that arousal fluctuations may differentially modulate cognitive flexibility leading to distinct
56 maladaptive behavioural patterns of performance.⁹

57 Fluctuations in arousal and alertness (hereafter described jointly as “arousal”) occur
58 constantly across the day but are exacerbated during transitions toward strained states such as
59 sleep¹⁰ or physical extenuation,¹¹ where arousal levels change drastically in a progressive and
60 nonlinear manner.^{12,13} These arousal fluctuations play a crucial role in modulating cognition,
61 facilitating or hindering certain cognitive processes and performance to internal and external
62 stimuli.^{14,15,16,17,18}

63 The interaction between arousal and cognition has been traditionally approached from
64 the perspective proposed by Yerkes and Dodson in 1908.² According to their famous inverted
65 U-shaped law, the optimal level of cognitive performance in complex tasks is reached at
66 moderate levels of arousal, whereas deviations from this optimal arousal point, below or
67 beyond, result in cognitive performance impairments. Though reductionist, the inverted U-
68 shaped law represents a useful minimal framework to characterize the neural and cognitive
69 dynamics of many physiological states across the arousal spectrum. Among these physiological
70 states, researchers have paid special attention to reduced arousal states, including sleep stages,¹⁹
71 sedation,²⁰ sleep deprivation,²¹ motivation²² and fatigue.²³

72 Sleep can be used as the gold standard model of transition toward low arousal.¹⁰ This
73 area looking at the interaction between homeostasis and cognitive function is understudied due
74 to the complexity of capturing dynamically metastable states like mild sedation^{24,25} and
75 drowsiness.¹⁷ When falling asleep, individuals manifest a wide range of changes, from
76 physiological to phenomenological, that are categorized into several well-described sleep

77 stages.²⁶ One of these stages is drowsiness, a transitional stage of consciousness between
78 attentive wakefulness and light sleep, characterized by a progressive and sometimes nonlinear
79 loss of responsiveness to external stimuli which does not immediately imply
80 unconsciousness.^{10,27,28,29} Drowsiness, as well as similar reduced arousal states, has been
81 repeatedly associated with an impairment of cognitive processing, and particularly the capacity
82 to deal with conflicting information,¹⁸ attentional performance,³⁰ and perceptual decision-
83 making.³¹ However, in drowsiness, and even during highly reduced arousal states, pre-attentive
84 and early bottom-up attentive processing can still be accomplished with and without conscious
85 awareness.^{17,32,33}

86 The transition towards the other side of the arousal spectrum (i.e., heightened arousal
87 states) has received even less attention.³⁴ The absence of a theoretical model for progressive
88 physiological transitions towards high arousal states, has also contributed to a lack of advance
89 in the field. Here, we consider endurance physical exercise as a useful experimental model of
90 arousal transition upwards, with many commonalities with sleep transition. A single bout of
91 endurance physical exercise (e.g., running or cycling) up to physical extenuation involves a
92 complex transition encompassing a wide range of changes (e.g., neural, motor, endocrinal,
93 phenomenological, etc.), that are also categorized into several well-described stages, from
94 resting, through the aerobic and the anaerobic thresholds, up to the limit where the individual
95 has to stop.³⁵ This highly fluctuating transition has been also associated with changes in
96 cognitive processing to internal and external stimuli.^{36,37,38} In particular, high-order top-down
97 processes that govern goal-directed behaviour in changing environments (i.e., cognitive
98 control) appear to benefit from increases in the level of arousal³⁹ up to a certain exercise
99 intensity. Further intensity increments approaching and exceeding the anaerobic threshold
100 seem to hinder cognitive performance,^{36,37,38,40} in line with the Yerkes-Dodson law prediction.

101 Sleep and physical exercise provide complementary perspectives on the cognitive
102 dynamics, and experimental models, when the arousal level is altered. However, and despite
103 the fact that both sides of the arousal spectrum exhibit similar cognitive performance
104 impairments, they cannot be treated as mirroring states in terms of cognitive performance
105 without a fine-grained differentiation of the behavioural dynamics that lead to these global
106 impairments. Furthermore, the theoretical differences in the transitions towards sleep or
107 complete (physical) exhaustion have to be considered in the assumptions and interpretations of
108 this and future studies. Thus, it is crucial to ask when arousal is altered (increased or decreased),
109 which specific processes of cognitive flexibility and information processing are affected, and
110 whether low and high arousal states are characterized by different strategic behaviours
111 underlying decision-making. Here, we use a PRL task to disentangle the behavioural dynamics
112 of cognitive flexibility as they get modulated by ongoing fluctuations in arousal levels and to
113 further delineate the microstructure of learning derived from trial-by-trial responses to
114 conflicting evidence. In particular, we manipulated arousal level to facilitate natural transitions
115 to low alertness, from awake to asleep; or to elicit high arousal, instructing participants to
116 exercise during 60 minutes at the highest intensity and effort possible without reaching
117 premature exhaustion. During both arousal modulations, participants performed a PRL task,
118 requiring the adaptation of behaviour following changes in reinforcement and punishment, as
119 well as the maintenance of strategic response patterns in the face of misleading (probabilistic)
120 feedback.

121 Based on the premises that (1) drowsiness hinders the extraction of task-relevant
122 information from external stimuli and its integration, fragmenting specific aspects of cognition
123 while preserving crucial executive control processes;^{18,31,33,41} (2) drowsiness has been
124 associated with more liberal decision-making;^{17,30,31} (3) moderate-to-high intensity endurance
125 exercise leads to a selective enhancement of executive control processes while lower and higher
126 intensities result in an impairment or minimal effect;^{40,42,43} and (4) high arousal promotes
127 habitual responding and reduced engagement of complex cognitive strategies;^{44,45,46} we
128 predicted that behavioural performance would be enhanced in moderate-intensity physical
129 exercise, while drowsiness and high-intensity exercise would lead to diminished performance
130 in light of the inverted U-shaped Yerkes-Dodson Law. Specifically, we hypothesized that
131 reduced arousal states would be associated with an impairment of performance (compared to
132 baseline), which would be attributed to a tendency to apply a simple strategy (win-stay/lose-
133 shift) instead of using an integrated history of choices and outcomes to drive performance
134 (probabilistic switching behaviour). In contrast, while we also expected an impairment of
135 performance during heightened arousal states, we hypothesized it would be attributed to a
136 failure to disengage from ongoing behaviour (perseveration). In addition, we hypothesized that
137 altered arousal states might reduce the ability of participants to apply a proper higher order
138 strategy, resulting in wide periods of time-on-task in which participants would perform the task
139 simply responding to the tones (i.e., automatic rule) but without applying any strategy (i.e.,
140 higher order rule).⁹

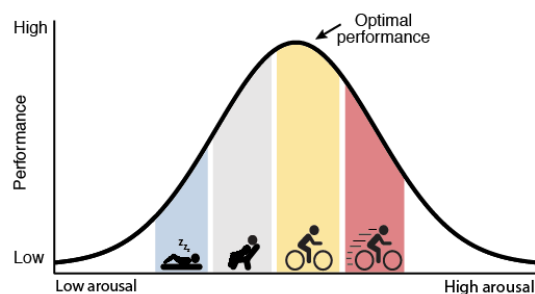
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142 **RESULTS**

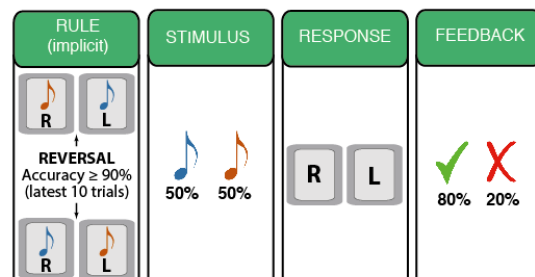
143 To investigate the modulatory effect of arousal fluctuations on cognitive flexibility, a PRL task
144 was carried out with human participants (n=100) while they were transitioning toward deep
145 sleep or physical extenuation. Participants were instructed to associate an auditory stimulus (S)
146 —high pitch sound or low pitch sound— with a response (R) button —left or right. In this
147 auditory version of the PRL task, each S-R association leads to an auditory outcome (O) —
148 correct (ding sound) or incorrect (white noise)— which participants use to assess their choice,
149 and apply this knowledge to guide the next choices. Therefore, the task entails the use of, at
150 least, two rules to success, as participants have to press a button after each auditory stimulus
151 (i.e., automatic rule) and to use an integrated history of S-R-O associations to determine the
152 correct S-R association (i.e., high order rule). Once participants reach 90% accuracy or greater
153 on the latest 10 trials, the implicit abstract S-R association is reversed, and participants have to
154 infer the new association from the feedback received. The number of responses needed to attain
155 a reversal (RAR) of the abstract association is used as the main index of performance. We
156 hypothesized⁹ that reduced arousal states would lead to reductions in behavioural performance
157 compared to baseline arousal state; while heightened arousal states would lead to improved
158 performance relative to baseline, but only to an optimal point (i.e., moderate arousal) after
159 which the performance will be deteriorated with further increases in arousal level (see figure
160 1A). These hypotheses were formulated in line with the famous psychology inverted u-shaped
161 law originally attributed to Yerkes and Dodson (1908)² relating arousal modulation
162 performance in complex tasks, but later more formally defined by Broadhurst (1958)⁴⁷ and
163 Brown (1961).⁴⁸

164 Note that, as a probabilistic task, the feedback provided is not always truthful nor
 165 reliable and misleads the participant 20% of the time (see figure 1B). Thus, the participant
 166 could correctly apply the S-R association and press the correct button in response to the
 167 auditory stimulus, and still receive negative feedback, thus indicating an incorrect choice. This
 168 scenario of conflicting evidence can lead participants to two different maladaptive response
 169 patterns (see figure 1C) while performing the task: 1) switching the pattern choice across trials
 170 with little (i.e., one negative feedback against the choice) or no evidence (i.e., no feedback
 171 against the choice) of an actual rule change (probabilistic switching); or 2) sticking with the
 172 previous choice despite having strong evidence (i.e., two or more negative feedbacks against
 173 the choice) of an actual rule change (perseveration). Relying on these response patterns lead to
 174 poor performance,⁷ as the optimal strategy in this task is to stick with the previous choice with
 175 zero or one negative feedback against the choice, and to switch the pattern choice if two or
 176 more consecutive negative feedbacks against the choice happen.

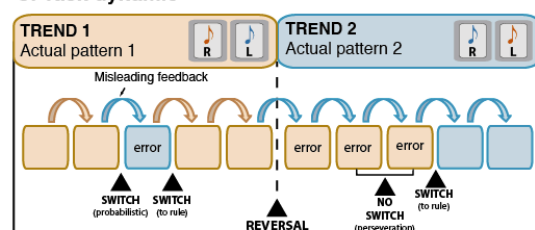
A. Experimental design and main hypothesis



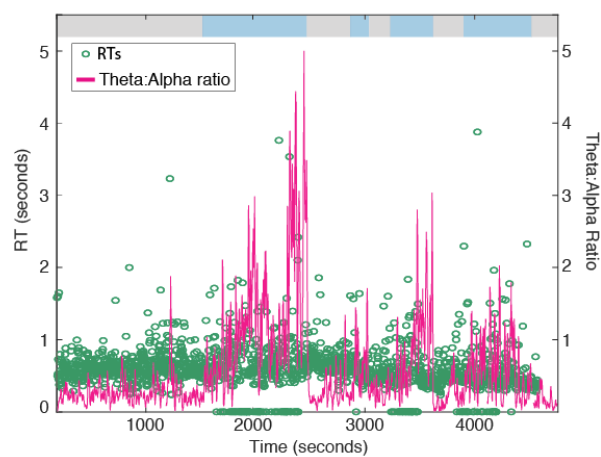
B. Trial structure



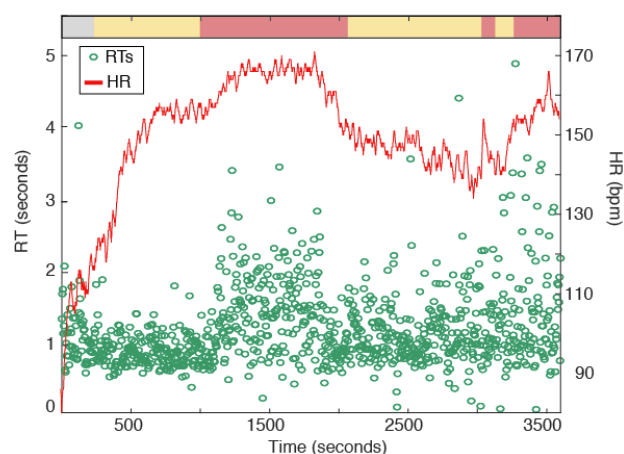
C. Task dynamic



D. Classification of arousal level in drowsy session



E. Classification of arousal level in exercise session



177 **Figure 1. Experimental design and arousal level classification:** A) Schematic representation of the
 178 experimental design and main hypotheses. Arousal level was endogenously manipulated by facilitating the natural
 179 transition of participants from awake to sleep, or instructing them to exercise during 60' at the highest intensity
 180 and effort they could maintain without reaching premature extenuation. A probabilistic reversal learning task was
 181 assessed continuously during the arousal modulation. Optimal performance of the task was expected at moderate
 182 arousal state (exercising at moderate intensity), while lower (drowsiness) and higher (exercising at high-intensity)
 183 arousal state were expected to result in task performance deterioration. B) In this auditory version of the
 184 probabilistic reversal learning paradigm, an auditory stimulus was presented on each trial, and participants had to
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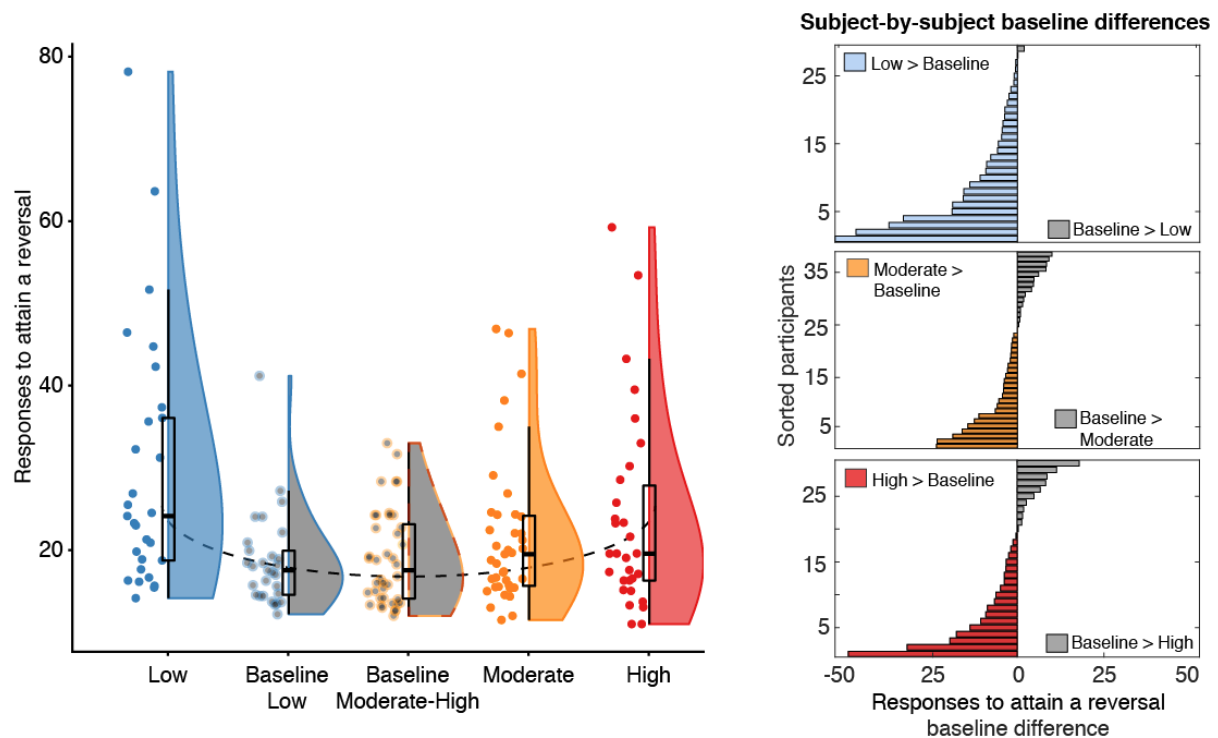
186 associate the sound with a response button, left or right. After that, auditory feedback was provided according to
187 the ongoing implicit rule. Notice that the feedback provided was not always truthful nor reliable, and attempted
188 to mislead the participant 20% of the time. C) Task trials were grouped into sequences of trials following a
189 particular rule (trend) where a particular sound was implicitly associated with a response button (e.g., high pitch
190 sound with the left button, and low pitch sound with the right button). Participants were instructed to infer the rule
191 from the provided feedback to assess their previous choice and apply the knowledge of their accuracy to guide the
192 next choices, knowing that the rule might change after a certain time. Based on the feedback received, participants
193 could make probabilistic or perseverative errors in the following trials. D) Automatic classification of arousal
194 during a drowsy session (representative participant). The pink line depicts changes in the theta:alpha ratio
195 (occipital electrodes cluster) during the pre-trial period (2 seconds before the auditory stimulus onset). The
196 horizontal bars on top represent trials classified as baseline (grey) or low arousal (blue). The variability in the
197 reaction times (green circles) closely follows the changes in theta:alpha ratio. Notice that circles on the horizontal
198 axis (reaction time equal to zero) were non-responsive trials, usually during low arousal (drowsy) periods but also
199 observed during exercise periods. E) Automatic classification of arousal during a physical exercise session
200 (representative participant). The red line depicts changes in the heart rate during the pre-trial period (2 seconds
201 before sound onset), and the horizontal bars on top represent trials classified as baseline (grey), moderate (yellow)
202 or high arousal (red). Similar to the low arousal session, the reaction times (green circles) fluctuates with the
203 changes in heart rate.

204

205 **Arousal modulates probabilistic information during a stream of conflicting evidence.**

206 First, we calculate the average RAR per participant in each arousal state (low, baseline sitting,
207 baseline cycling, moderate, high). To account for the dependencies potentially generated by
208 any procedural differences between Experiments, we fitted RAR using hierarchical linear
209 mixed-effects modelling, with arousal as fixed effect, and participant nested into Experiment
210 as random effects. The model showed a strong effect of arousal on RAR, $F(3, 113.02) = 11.59$,
211 $p < 0.001$, $\beta = 0.61$. indicating that the processing of probabilistic information that allows the
212 detection of changing patterns in a stream of conflicting evidence was modulated by the arousal
213 level. Next, we checked for non-linearity in the relationship between arousal and RAR, to test
214 the famous u-shaped curve. As expected, we found that the quadratic ($AIC = 1243.6$; $BIC =$
215 1262.3) outperformed linear fitting ($AIC = 1264.8$; $BIC = 1280.4$), confirming a possible
216 curvilinear pattern (U shaped) of the effect of arousal on RAR (see figure 2), with a reliable
217 increase in the number of responses required by the participants to complete a trend reversal
218 (i.e., decrease of performance) as the level of arousal progress towards the extremes of the
219 defined arousal range, confirming, for reversal learning, convergence with the Yerkes-Dodson
220 law, later reformulated by Broadhurst in 1958.⁴⁷

221 Splitting the comparisons to its specific baselines per arousal condition (i.e., sitting
222 baseline compared to low arousal in the drowsiness condition; cycling baseline compared to
223 moderate and high arousal in the exercise condition) yielded a reliable increase of RAR in low
224 arousal, $t(124.62) = 5.67$, $p < 0.001$, $\beta = 1.02$, and high arousal state, $t(117.93) = 2.57$, $p =$
225 0.011 , $\beta = 0.45$, compared with their corresponding baselines. Notably, baseline performance
226 did not differ across arousal conditions (see supplementary figure 1). Contrary to what we
227 expected, moderate arousal state was not associated with a decrease of RAR (the expected peak
228 in performance), relative to baseline ($t(114.85) = 1.61$, $p = 0.11$, $\beta = 0.25$). Moreover, that we
229 did not find evidence for a potential dual-task confounding effect in the heightened arousal
230 conditions (see supplementary material). In sum, these findings provide evidence for an
231 impairment in the processing of probabilistic information when the arousal level is altered,
232 regardless of the side of the arousal spectrum.



233
 234 **Figure 2. Number of responses needed to attain a trend reversal as a function of the arousal state.** A) Violins
 235 and overlaid box plots of mean responses to reverse across arousal states. In box plots, middle black mark indicates
 236 the median, and bottom and top edges indicate 25th and 75th percentiles, respectively. The upper and lower
 237 whiskers indicate the maximum value of the variable located within a distance of 1.5 times the interquartile range
 238 above the 75th percentile and below the corresponding distance to the 25th percentile value. Surrounding the
 239 boxes (shaded area) is a rotated kernel density plot, which is comparable to a histogram with infinitely small bin
 240 sizes. Jittered dots represent the averaged response to reverse score for each participant in each arousal state.
 241 Linear mixed-effects model analysis revealed a reliable quadratic fitting between arousal and task performance,
 242 outlined by the dashed line. Low and high arousal states were associated with a worse task performance relative
 243 to their own baseline arousal states. Moderate arousal state was not associated with the expected optimal
 244 performance as no differences were found with the baseline arousal state. B) Baseline differences of each
 245 participant across altered arousal states are represented by the bars (grey bars indicate that these participants
 246 needed more trials to attain a trend reversal in the baseline compared with the altered arousal states; blue, yellow
 247 and red bars depict that these participants needed more trials to attain a trend reversal when arousal level was
 248 altered -increased or decreased- compared with baseline arousal state). Participants are sorted by performance
 249 difference between baseline and the arousal state. Upper and bottom panels show a consistent impairment of task
 250 performance across participants in low and high arousal states. Non-reliable differences were found between
 251 moderate and baseline arousal.

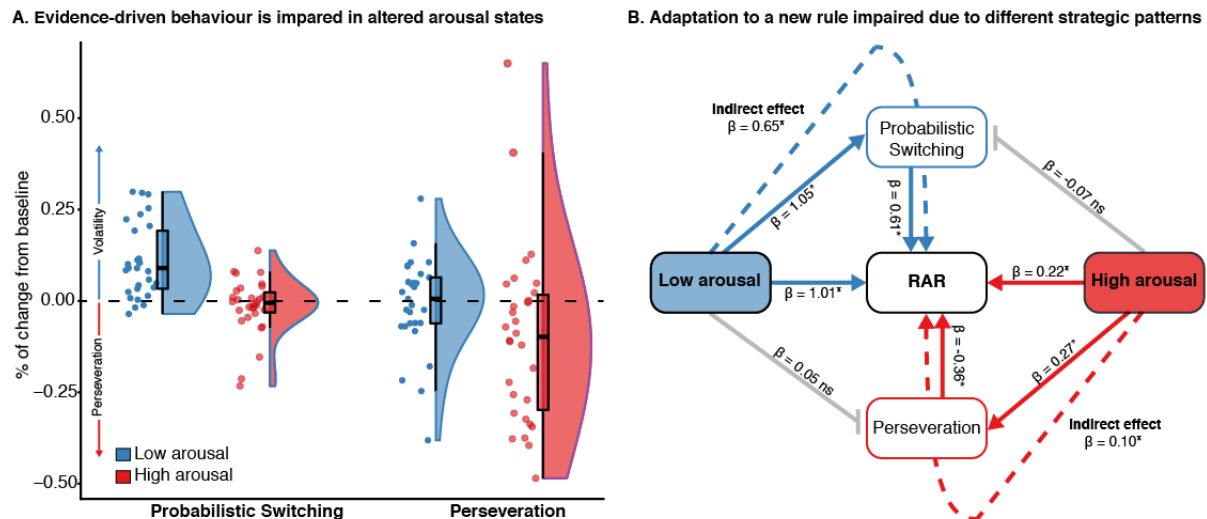
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 253 **Different underlying mechanisms explain decreased performance in low and high arousal**
 254 **states**

255 In the analysis above, performance under high and low arousal states was compared
 256 irrespective of the strategy participants may have used to solve the task. To test for the
 257 hypotheses of the differential mechanism driving changes in performance for each arousal side
 258 of the u-shaped curve, we calculated: a) probabilistic switching, as the proportion of trials when
 259 the participants change the pattern choice with little or no evidence (i.e., zero or one negative
 260 feedback against the choice); and b) perseveration, the likelihood of sticking with the previous
 261 choice despite strong evidence (i.e., receiving two or more negative feedbacks in a row) that
 262 the pattern has changed. We hypothesized that the impairment of performance in low arousal

263 would be primarily attributed to an increase in probabilistic switching, relative to the baseline
264 arousal state; and in contrast, the observed impairment of performance in high arousal state
265 will be primarily due to an increase in perseverative behaviour. To test these hypotheses, we
266 fitted probabilistic switching and perseveration (separately for low and high arousal states)
267 using the hierarchical linear mixed-effects model structure defined previously. The analyses
268 revealed that, while the probabilistic switching increased consistently across subjects during
269 low arousal state compared with baseline arousal, $F(1,56) = 12.65$, $p < 0.001$, $\beta = 1.02$, no
270 reliable differences were observed in perseveration between these arousal states ($F < 1$). On the
271 other hand, high arousal states led to a reliable increase in perseverative behaviour compared
272 to the baseline state, $F(1,68) = 4.80$, $p = 0.031$, $\beta = 0.22$, with no reliable differences observed
273 in probabilistic switching ($F < 1$). These results suggest that altered arousal states lead to
274 distinct maladaptive decision-making patterns that affect participants' ability to generate stable
275 evidence-based strategies, although evidence-driven responses were present (see figure 3A).

276 To further prove that the impairment in performance in low and high arousal states
277 could be attributed to the different maladaptive behavioural patterns, we carried on a mediation
278 analysis separately for each arousal state (low, high). We first confirmed that probabilistic
279 switching and perseveration have an effect on the RAR, while controlling for the arousal state
280 (see figure 3B). These results, together with the previous analyses where we found an effect of
281 arousal state on probabilistic switching and perseveration, revealed a full mediation between
282 these variables. As figure 3B illustrates, the regression coefficient between arousal and RAR,
283 and the regression coefficient between probabilistic switching and RAR were statistically
284 reliable, showing a full mediation of probabilistic switching on the effect of low arousal on
285 RAR. The bootstrapped standardized indirect effect of low arousal on RAR, mediated by
286 probabilistic switching, was 0.65 ($p < 0.001$), and the 95% confidence interval ranged from
287 0.29 to 1.07. A similar fully mediation effect was observed in high arousal state, showing that
288 the effect of high arousal on behavioural performance was fully mediated via the perseverative
289 behaviour. The bootstrapped standardized indirect effect was 0.10 ($p = 0.014$), and the 95%
290 confidence interval ranged from 0.14 to 0.24. As predicted, participants showed an impairment
291 of performance during low arousal state, relative to baseline arousal, which was primarily
292 attributed to an increase of probabilistic switching (i.e., changing pattern choice with little or
293 no evidence of an actual rule change). In contrast, while participants also showed an
294 impairment of performance during high arousal state, relative to the baseline arousal, it was not
295 attributed to an increase in probabilistic switching, but to an increase in perseverative behaviour
296 (i.e., sticking with the previous choice despite consecutive negative feedbacks).

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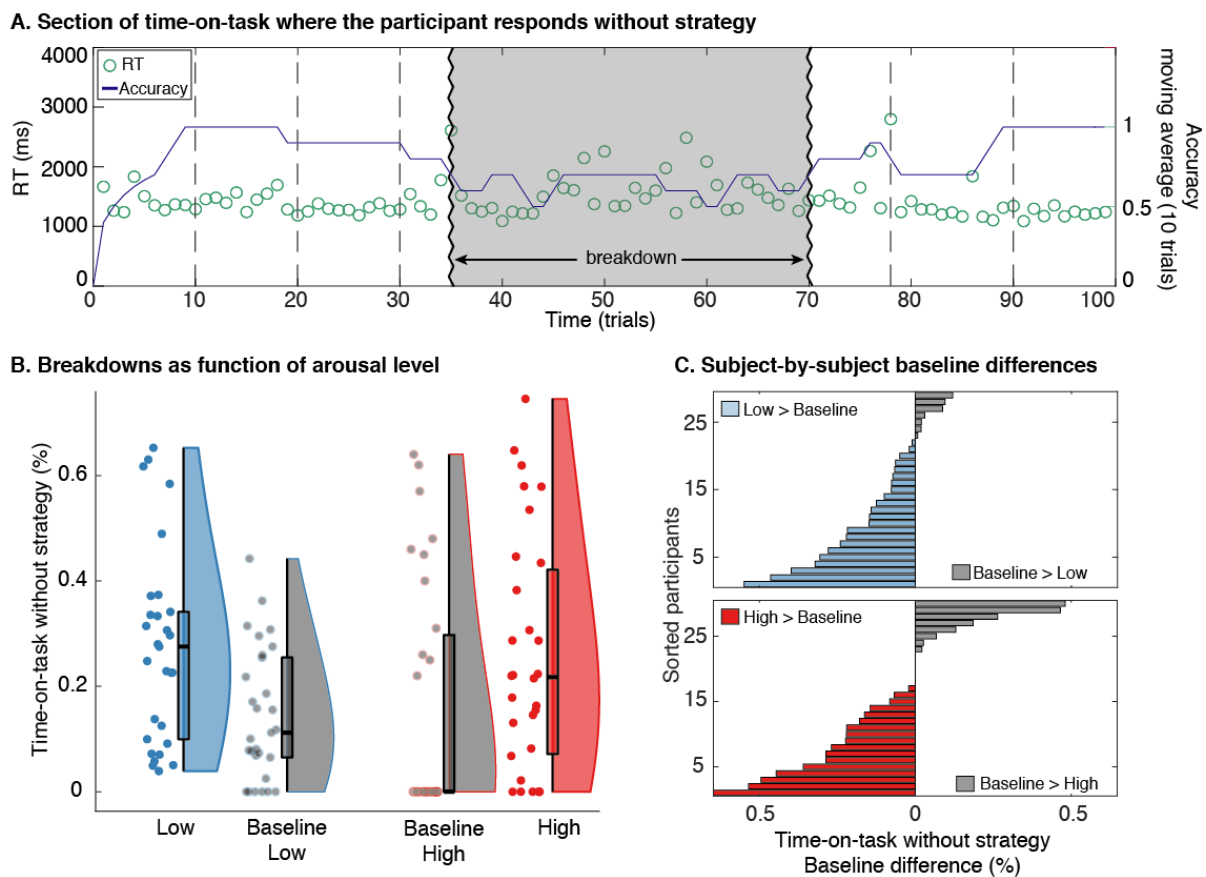
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 299 **Figure 3. Maladaptive behavioural patterns across participants in low and high arousal states.** A) Violins
 300 and overlaid box plots of the percentage of change from baseline to low (blue) and high (red) arousal states in
 301 probabilistic switching and perseveration. In box plots, middle black mark indicates the median, and bottom and
 302 top edges indicate 25th and 75th percentiles, respectively. The upper and lower whiskers indicate the maximum
 303 value of the variable located within a distance of 1.5 times the interquartile range above the 75th percentile and
 304 below the corresponding distance to the 25th percentile value. Surrounding the boxes (shaded area) is a rotated
 305 kernel density plot, which is comparable to a histogram with infinitely small bin sizes. Jittered dots represent the
 306 averaged response to reverse score for each participant in each arousal state. B) Mediation model diagram to
 307 illustrate that the general impairment in task performance found in low and high arousal states was mediated by
 308 different maladaptive behavioural patterns. Dashed lines (indirect effects) represent the effect of low (blue) and
 309 high (red) arousal on task performance (indexed by the averaged responses to attain a trend reversal) through
 310 probabilistic switching and perseveration, respectively. Solid lines depict direct effects between variables. Grey
 311 lines represent the absence of a direct effect of low arousal on perseveration and high arousal on probabilistic
 312 switching. Notice that a direct effect of an independent variable (arousal) onto the mediator (probabilistic
 313 switching, perseveration) is a prerequisite for mediation being possible. Standardized β regression coefficients are
 314 indicated in each effect (* depicts $p < 0.05$). Accordingly, the values of all effects are expressed as the number of
 315 standard deviations from the mean. For example, the direct effect of high arousal on RAR ($\beta = 0.22$) implies that
 316 a standard deviation change of 1 in the arousal variable would result in a standard deviation increase of 0.22 in
 317 RAR.

318

319 **Arousal disrupt the reversal strategy**

320 To maximise performance in the task, a good strategy is to not fall for the false feedback and
 321 stand your ground until the next feedback, as well as switch to the second consecutive feedback.
 322 The fact that participants sometimes needed an unreasonable high number of responses to attain
 323 a reversal in low and high arousal states suggests the existence of sections of time on task in
 324 which they responded to the tones but could not apply the strategy rules (see fig 4A). These
 325 sections without clear strategic behaviour, that we call breakdowns, have been often neglected
 326 in previous studies using PRL tasks as failures of compliances or “bad participant”. The
 327 transient on/off nature of these breakdowns may provide valuable insight into the behavioural
 328 dynamics of participants in different states of arousal. We hypothesized that breakdowns
 329 sections would increase in low and high arousal states, relative to a baseline arousal state. First,
 330 we traced the sections of the task (more than 20 trials) in which participants did not attain a
 331 reversal. Second, we calculated the proportion of time these sections represented to the total
 332 time-on-task, and finally, we implemented a hierarchical linear mixed-effects model with the

333 structure defined in previous analyses, separately for each arousal state (low, high), with the
 334 number of breakdowns as the index of performance. As hypothesized, low and high arousal
 335 states lead to longer breakdown sections compared with baseline arousal state ($t(127.99) =$
 336 $3.40, p < 0.001, \beta = 0.13$; $t(121.69) = -2.97, p = 0.003, \beta = 0.11$). Subject-by-subject results
 337 (fig 4C) show a consistent increase of breakdowns across participants in low arousal state.
 338 Although high arousal states also showed a reliable increase of breakdowns as a group, this
 339 effect was less systemic, with half of the participants showing the opposite effect, no difference
 340 or no breakdowns.
 341



342 **Figure 4. Behavioural strategy breaks as arousal changes.** A) Automatic classification of a section of time
 343 where a representative participant responded without a clear behavioural strategy. The green circles show RTs
 344 and the blue line shows the ongoing accuracy of the task (10-points moving average). The grey shaded area flanked
 345 by the zigzagging vertical lines depicts the section of time classified as a breakdown. B) Violins and overlaid box
 346 plots of the averaged percentage of time-on-task without strategy across participants in low and high arousal states,
 347 compared with their respective baseline states. In box plots, the middle black mark indicates the median, and
 348 bottom and top edges indicate 25th and 75th percentiles, respectively. The upper and lower whiskers indicate the
 349 maximum value of the variable located within a distance of 1.5 times the interquartile range above the 75th
 350 percentile and below the corresponding distance to the 25th percentile value. Surrounding the boxes (shaded area)
 351 is a rotated kernel density plot, which is comparable to a histogram with infinitely small bin sizes. Jittered dots
 352 represent the averaged percentage of time-on-task without a strategy of each participant in each arousal state.
 353 Linear mixed-effects model analyses revealed that low and high arousal states lead to longer periods of breakdown
 354 relative to the baseline arousal state. Interestingly, violin plots show a considerable number of participants who
 355 had no breakdowns at baseline arousal states, something that completely disappears in low arousal state (all
 356 participants had breakdowns), and that is reduced in high arousal state. C) Baseline differences of each participant
 357 in low and high arousal states represented by horizontal bars (grey bars indicate that these participants spent more
 358 time performing the task without a particular strategy in the baseline arousal state compared with the altered
 359

360 arousal states; blue and red bars depict that these participants were applying behavioural strategies less time when
361 arousal level was altered (increased or decreased) than in baseline arousal state. Participants are sorted by
362 performance difference between baseline and the arousal state. Both panels show a consistent impairment of task
363 performance across participants in low and high arousal states.

364

365 **DISCUSSION**

366 In the present study, we facilitated natural transition of healthy participants towards the borders
367 of non-pharmacological arousal states (drowsiness, physical exertion) to investigate the
368 behavioural dynamics of cognitive flexibility. In line with our pre-registered hypotheses,⁹ the
369 findings revealed a quadratic-like pattern (inverted U-shape) of the effect of arousal
370 fluctuations on cognitive performance. As the level of arousal progressed towards the extremes
371 of the defined arousal range reversal learning performance decreased, in agreement with the
372 predictions of the Yerkes-Dodson law (1908).² Although cognitive flexibility diminished in
373 both under high and low arousal states, different maladaptive behavioural patterns drove this
374 performance impairment. As predicted, the performance decline exhibited by our participants
375 under drowsy states was primarily attributed to a more decision volatility (i.e., shifting pattern
376 choice with little or no evidence of reinforcement contingencies change). In contrast,
377 participants also showed a decline in performance during high arousal state but attributed to
378 increased perseverative behaviour (i.e., sticking with a particular pattern choice despite having
379 strong evidence that the contingencies have changed). Our findings also revealed that most
380 participants undergo prolonged periods of time-on-task in which they seem unable to apply any
381 specific higher order strategy. These breakdown periods, which can last for several minutes,
382 are more frequent and sustained during high or low arousal. In short, our results provide solid
383 evidence for distinct maladaptive decision-making patterns under altered arousal states,
384 differentially affecting the participants' ability to generate stable evidence-based strategies.

385 Arousal fluctuations thus seem to elicit a distinctive behavioural distortion of cognitive
386 flexibility as further indicated by the microstructure of learning derived from trial-by-trial
387 responses to negative feedback. Healthy participants under high arousal exhibited normal
388 acquisition of S-R reinforcement contingencies but perseverative response patterns when
389 contingencies were reversed. This failure to disengage from ongoing behaviour is a
390 translational phenomenon strongly linked to impulsivity and compulsivity,⁴⁹ and prevalent in
391 numerous neuropsychiatric and medical conditions.^{7,50,51} For instance, patients with lesions that
392 include ventral prefrontal cortex and orbitofrontal cortex,⁵² as well as chronic cocaine users⁵³
393 and patients with schizophrenia,⁵⁴ show normal acquisition of S-R contingencies but are
394 severely impaired when those S-R reinforcement contingencies are abruptly reversed,
395 exhibiting perseverative responding to the previously reinforced S-R contingency. Altogether,
396 these findings suggest that high arousal undermines healthy individuals' capacity to engage in
397 complex cognitive strategies driving them to rely on habitual response patterns, which,
398 paradoxically, might also enhance behavioural control in terms of response inhibition.⁴⁶ Our
399 findings not only further the understanding of the processes underlying automatized behaviour
400 and habitual response tendencies, but high arousal may be used as a model to inform both
401 impulsive and compulsive aspects of psychopathology.

402 In contrast, healthy participants under low arousal seemed unable to maintain the
403 learned S-R reinforcement contingency and started to deviate from the evidence, revealing a

404 volatile pattern of behaviour. Since a crucial aspect of the PRL experimental design was the
405 existence of a 20% of misleading feedback, to maximise performance, individuals should not
406 fall for the false feedback and —ideally— stand their ground until the next feedback. Further
407 and as part of a successful strategy, they should switch if two or more consecutive feedbacks
408 are given against the previously reinforced choice pattern. Consequently, adaptive behaviour
409 during the task requires a balance between both types of behaviour (stability and flexibility).
410 Those participants under low arousal fell repeatedly for the misleading feedback, switching
411 prematurely after negative feedback. Furthermore, they showed increased decision volatility
412 by spontaneously switching even without any negative feedback. This volatile pattern of
413 cognitive flexibility has been linked to serotonin⁵⁵ and dopamine systems,⁵⁶ and is observed in
414 patients with major depression,^{57,58,59} often linked to either an oversensitivity to punishment or
415 an impaired control over negative feedback.^{60,61} It is reasonable to speculate that low arousal
416 levels render individuals more sensitive in updating S-R reinforcement contingencies, rather
417 than increase sensitivity to punishment as in major depression. Moreover, low arousal may
418 increase volatility by decreasing attentional resources, leading to spontaneous explorations,
419 higher RT variability and periodic omissions (see supplementary figure 2).

420 The fragmentation of cognitive control due to changes in arousal has been primarily
421 shown in sleep deprivation^{62,63,64,65,66} and not in spontaneous fluctuations of alertness as we
422 show in this study. The increased volatility in the PRL with low arousal suggests a decrease in
423 cognitive control that is different from an increase in perseverative behaviour seen in high
424 arousal. Indeed, we have previously shown that decreased levels of arousal can fragment or
425 reconfigure specific aspects of cognition while preserving crucial executive control processes
426 such as the capacity to detect and react to incongruity,¹⁸ the efficiency in perceptual decision
427 making,³¹ and the precision of conscious access.¹⁷ Here, we add further evidence showing that
428 individuals under reduced arousal state, although struggling to maintain stable evidence-based
429 decision-making patterns, are able to learn new S-R reinforcement contingencies,
430 demonstrating flexibility of the human brain to adapt to increasing levels of endogenous
431 (arousal) noise. The evidence of cognitive and —indirectly— neural reconfiguration of
432 cognitive control networks suggests compensatory mechanisms elicited by the change in
433 arousal.

434 Upon further examining the microstructure of learning derived from trial-by-trial
435 performance of the PRL task, we uncovered the existence of prolonged periods of time-on-task
436 in which participants did not seem to apply any particular high-order behavioural strategy.
437 Although these breakdown periods emerged regardless of the arousal level, they were prevalent
438 under low and high arousal states, lasting from few to several minutes. Remarkably, the
439 transient on/off nature of these breakdowns suggests that extreme arousal levels alternate
440 between different metastable cognitive states. The first state can be defined by a relatively
441 successful application of the reinforcement information where participants can navigate the
442 uncertainty of the PRL, while in the other metastable state they seem to only apply the simple
443 auditory-motor S-R rule to respond to the auditory tones but are unable to use choice history
444 to develop a successful strategy.

445 In the context of this study, arousal as a biological construct defined by the homeostatic
446 regulatory capacity of the system and its responsiveness,⁶⁷ helps to link drowsiness and
447 increased alertness during physical exercise in a common framework where the predictions of

448 the Yerkes-Dodson inverted U-shaped law can be experimentally tested. Despite the obvious
449 difference at the biological, neural and psychological level between both sides of the curve, the
450 common decrease in performance highlights the commonalities between the extremes in human
451 performance, adding to the fact that both —sleep and physical exertion— emerge as natural
452 transitions from a similar state (resting) traversing different stages, and exhibit nonlinear
453 dynamics and hysteresis processes in their transitions.¹² Thus, drowsiness and physical exertion
454 provide complementary perspectives on cognitive dynamics when the arousal level is altered.
455 The present findings point out their differences in the cognitive fragmentation leading to a
456 general decline in task performance.

457 Though the Yerkes-Dodson law was not initially formulated to be a general rule to
458 apply to all psychology subfields (learning, motivation, emotion, etc.), through the years, and
459 with the pressure to find common mechanisms in psychology, the findings initially defined for
460 learning were further extended and reinterpreted as a law about the relationship between
461 arousal and other physiological constructs to perceptual and cognitive performance.⁶⁸ Despite
462 this overgeneralization from its genuine formulation and its reductionist nature, our findings
463 rely on such inverted U-shaped law as a basic useful theoretical framework, providing an
464 attractive theoretical model to characterize the neural, cognitive and behavioural dynamics
465 involved in the impact of arousal fluctuations in a wide range of physiological states and
466 neuropsychiatric conditions.

467 Our findings bring some generalizations about the need to extend the traditional
468 framework of understanding the interplay between cognitive dynamics and arousal through the
469 prism of the homeostatic steady-state dynamics using pharmacological interventions³⁴ or
470 transient alterations of emotional state.⁶⁹ In addition to this classical approach, we believe that
471 drowsiness and physical exertion provide fruitful -naturally occurring- alterations of the arousal
472 level with a preserved capacity to behaviourally respond, which can be utilized to study the
473 modulation of neural function and cognitive processing. In the traditional steady-state
474 approach, such natural fluctuations of the arousal level may be undetected,⁷⁰ hindering or
475 distorting cognitive and neural markers of crucial aspects of information processing.¹⁷
476 Pharmacological and lesion perturbations of the brain are regarded as causal in cognitive
477 neuroscience and regarded as stronger in their explanatory power than conditions relying on
478 stimuli or psychological modulations. Arousal is an internally modulated change that can be
479 used to study cognition and may be regarded in the strong causality range due to its partial
480 independence from psychological processes.¹⁸ The cases of drowsiness and physical exertion
481 as causal models to study the neural mechanism of cognitive flexibility may prove to be very
482 useful in the exploration of how cognition is fragmented or remain resilient under (reversible)
483 perturbations of arousal^{17,33,71} Our findings highlight that further research should focus on the
484 rapidly changing dynamics of brain function and cognitive processing that appear to capture
485 key dynamics relevant to our behavioural and perhaps even phenomenological experience, as
486 we drift into strained physiological states.

487

488 **METHODS**

489 **Participants**

490 A total sample of 100 participants of an age range between 18 and 40 years old was included
491 in the present study. All participants reported normal binaural hearing, no visual impairment

492 and no history of cardiovascular, neurological or psychiatric disease. They were asked to get a
493 normal night rest on the day previous to testing, and not to consume stimulants like coffee or
494 tea on the day of the experiment.

495 The first experiment (herein Experiment#1) consisted of 35 participants (15 female; age
496 range 18-40). In addition to the general aforementioned inclusion criteria, only easy sleepers,
497 as assessed by the Epworth Sleepiness Scale (ESS),⁷² were selected to increase the probability
498 that participants fell asleep. Recruited participants were considered healthy with relatively high
499 ESS scores but not corresponding to a condition of pathological sleep such as hypersomnia
500 (i.e., scores 7–14). They were recruited via the Cambridge Psychology SONA system.

501 The second experiment (herein Experiment#2) consisted of 15 participants (11 female;
502 age range 18-40). Inclusion criteria and recruitment processes were similar to Experiment#1.

503 The third experiment (herein Experiment#3) consisted of 50 participants (6 female; age
504 range 19-39). Additionally to the common inclusion criteria, only individuals who reported at
505 least 8 hours of cycling or triathlon per week were selected. Well-trained cyclists were selected
506 because they are used to maintaining the pedalling cadence at high intensity during long periods
507 of time. Furthermore, they are able to keep a fixed posture over time, which notably reduces
508 movement artefacts. They were recruited from the University of Granada (Spain) through
509 announcements on billboards and previous databases.

510 All participants from the three experiments gave written informed consent to participate
511 in the study and received a remuneration of 10€ per hour (i.e., approximately 30€ per
512 participant). The Cambridge Psychology Ethics Committee and the University of Granada
513 Ethics Committee approved the study (CPREC 2014.25; 287/CEIH/2017).

514

515 **Experimental task**

516 A modified version of the probabilistic reversal learning paradigm was used in all three
517 experiments, which was characterized by employing auditory stimuli and an abstract rule (see
518 figure 1B-C). In this task, participants learnt to choose one of two randomly presented tones
519 by receiving instructive auditory feedback tones after each response, indicating either a correct
520 or incorrect choice. When participants reached a 90% accuracy in the last 10 trials,
521 reinforcement/punishment contingencies were reversed so that the previously reinforced tone
522 was punished and vice versa. Within each reversal trend, a 20% probabilistic error trial was
523 included in which “wrong” feedback was given for correct choices, even though the
524 reinforcement contingencies had not changed. Participants were instructed to infer the rule
525 from the feedback received, knowing that sometimes it might be misleading and that the rule
526 might change after a certain time. The stimuli were binaurally presented at a random time
527 interval (between 1000 and 1500 ms) during 500 ms. They had to respond to both targets by
528 pressing a button with their right or left hand.

529

530 **Procedure**

531 In Experiment#1, participants were fitted with an EGI electrolyte 129-channel cap (Electrical
532 Geodesics, Inc. systems) after receiving the task instructions and subsequently signing the
533 informed consent. The whole session was completed in a comfortable adjustable chair with
534 closed eyes. Task instructions were to respond as fast and accurately as possible, reducing body
535 movements as possible and keeping the eyes closed. In the beginning, the back of the chair was

536 set up straight and the lights in the room were on. Participants were asked to remain awake
537 with their eyes closed whilst performing the first block (awake block) of the task which
538 consisted of 480 trials, lasting 30 min approximately. Then, the chair was reclined to a
539 comfortable position, the lights were turned off and participants were offered a pillow and a
540 blanket. They were explicitly told that they were allowed to fall asleep during this part of the
541 task and that the experimenter would wake them up by making a sound (i.e. knocking on the
542 wall) if they missed 5 consecutive trials. This block (drowsy block) also consisted of 480 trials.
543 Then, the sequence of two blocks (awake-drowsy) was repeated. In total, participants
544 completed 1920 trials divided into 4 blocks of 480 trials each one. The whole session lasted for
545 3 hours approximately.

546 In Experiment#2, the procedure was similar to the Experiment#1 except for the time to
547 fall asleep that was increased to get a higher amount of low-arousal (i.e., drowsy) trials.
548 Participants completed a total of 2120 trials, divided into 4 blocks. The order of the blocks was
549 the same for all participants and followed the same sequence as in Experiment#1: awake-
550 drowsy-awake-drowsy. Awake blocks had 100 trials each one, while drowsy blocks consisted
551 of 960 trials each one. The session lasted for 3 hours approximately.

552 In Experiment#3, upon arrival to the laboratory, participants were seated in front of a
553 computer in a dimly illuminated, sound-attenuated room with a Faraday cage. They received
554 verbal and written instruction about the experiment and were prepared for electrophysiological
555 measurement. They were fitted with a 64-channel high-density actiCHamp EEG system (Brain
556 Products GmbH, Munich, Germany) and a Polar RS800CX heart rate (HR) monitor (Polar
557 Electro Oy, Kempele, Finland). Notice that EEG data was acquired but was not used to test the
558 hypotheses of this study, and will be reported elsewhere. The whole session consisted of 4
559 different blocks. The first one was an adaptation (non-exercise) block in which participants
560 performed 100 trials while resting in a comfortable chair. Then, they got on a cycle-ergometer
561 and completed 100 trials while warming-up at light intensity. Subsequently, they completed a
562 self-paced 60' time-trial (i.e., high-intensity exercise) while performing the task, resulting in
563 850 trials approximately (the number of trials slightly varied as a function of the reaction time
564 of participants). In line with previous experiments from our laboratory (Holgado et al., 2018;
565 Holgado et al., 2019),^{73,74,75} in the self-paced time-trial participants were instructed to achieve
566 the highest average power (watts) during the 60' time-trial exercise, and were allowed to
567 modify the power load during the exercise. They were encouraged to self-regulate effort in
568 order to optimize physical performance without reaching premature exhaustion. That self-
569 regulation yielded fluctuations of effort during the 60' exercise period, which allowed us to
570 study the effect of arousal on the management of probabilistic information. Once the 60' time-
571 trial block was finished, participants completed the last block while cooling down at light
572 intensity, which was also composed of 100 trials. All participants completed the blocks in the
573 same order, lasting around 3 hours.

574

575 **Arousal classification**

576 In Experiment#1 and Experiment#2, the arousal level was endogenously manipulated by
577 facilitating the natural transition from awake to sleep. This transition reduces arousal and yields
578 a considerable proportion of drowsy yet responsive trials as seen in previous experiments from
579 our laboratory.^{17,30,71} This way, we were able to study the effect of arousal (i.e. baseline arousal

580 [awake] trials vs. low-arousal [drowsy] trials) on the management of probabilistic information.
581 Given that awake-sleep transition is characterized by a decreasing alpha range activity, together
582 with an increasing theta range activity (Hori et al., 1994), progression of drowsiness was
583 quantified by the spectral power of respective EEG frequency bandsⁱ. We computed the spectral
584 power of EEG frequency oscillations for each trial from -2000 ms to 0 ms in respect to the
585 onset of a target tone using continuous wavelet transform, set from 3 cycles at 3 Hz to 8 cycles
586 at 40 Hz. Theta (4-6 Hz) and alpha (10-12 Hz) power were then averaged individually for each
587 trial across central (E36, E104) and occipital (E75, E70, E83) electrodes for theta and alpha
588 rhythms respectively. Finally, theta/alpha ratio was computed and smoothed with a 4-point
589 moving average resulting in a single “sleepiness” value per trial. Visual inspection of
590 theta/alpha ratio and RT dynamics of each participant confirmed the presence of clear
591 sleepiness-related fluctuations during the experimental session, especially during drowsy
592 blocks. Those participants who did not show clear fluctuations of the theta:alpha ratio were
593 removed from final analyses (5 subjects). Then, each trial for each participant was initially
594 categorized as drowsy (top 33% of lower theta-upper alpha ratio scores) or alert (lowest 33%).
595 Further, following the sleep hysteresis physiology criteria⁷⁷ isolated awake trials within
596 prolonged periods of drowsy (≥ 10 trials) were considered as drowsy to account for the gradual
597 homeostatic change during the sleep transition. In addition, the first 100 trials of each block
598 (awake and drowsy) were considered as awake trials.

599 In Experiment#3, the arousal level was endogenously manipulated by facilitating the
600 natural transition from a resting state to high-intensity physical exercise. This transition
601 increases the arousal level progressively, with continuous fluctuations that affect cognitive
602 performance as seen in previous studies from our laboratory.^{40,75,78,79} We captured these arousal
603 fluctuations at a single trial level (moderate arousal trials, high arousal trials) by using the HR
604 response. To address the intersubject variability, HR data were transformed into differential
605 scores relative to the HRmax estimated using the equation of Tanaka et al., (2001)⁸⁰, a reliable
606 and well-established method to calculate HRmax in healthy individuals. Then, moderate and
607 high arousal trials were characterized based on percentage relative to HRmax. HR between
608 60% and 80% of HRmax were considered as moderate arousal, while HR higher than 80%
609 HRmax were considered as high arousal. Due to technical issues with HR monitoring, 4
610 subjects were removed for further analyses.

611

612 **Behavioural data analysis**

613 In probabilistic reversal learning paradigms, participants are instructed to infer an abstract rule
614 from the feedback they receive, knowing that sometimes it might be misleading and that the
615 rule might change. Since a reversal is triggered when a high-level accuracy is reached, the
616 number of responses needed to attain a reversal is considered one of the main indices of

ⁱ Deviation from pre-registration. Originally, we aimed to use the automated offline method developed by Jagannathan and collaborators based on frequency and sleep grapho elements to detect EEG micro variations in alertness and characterize awake and drowsy trials.⁷⁶ However, our PRL task design, especially the pretrial duration, which was limited to 2 seconds, did not fit the task features recommended by Jagannathan and collaborators (e.g., 4 seconds pretrial duration) for a reliable characterization of awake and drowsy trials. So we decided to classify awake/drowsy trials based on theta:alpha ratio, as seen in previous experiments from our laboratory.^{17,30,71}

617 performance. To delineate the microstructure of learning derived from trial-by-trial responses
618 we considered the likelihood of switching the pattern choice across trials as a function of the
619 amount of consecutive negative feedback received. The likelihood of switching was considered
620 the main index of strategic behaviour, and was divided into 2 different strategies: *i)*
621 Probabilistic switching: the proportion of trials when the participants change the pattern choice
622 with little (one negative feedback against the choice) or no evidence (no feedback against the
623 choice) of an actual rule change; *ii)* Perseveration: likelihood that participants stay with the
624 seemingly incorrect choice even after receiving two or more negative feedbacks in a row).

625 The number of breakdown sections was also used as an index of performance. We
626 defined a breakdown as a section of time in which participants ‘lose’ the task, and do not follow
627 any strategy, being unable to reach a change of trend during more than 20 consecutive trials.
628 RT, accuracy, and omissions were also checked as secondary indices of behavioural
629 performance.

630 Participants with overall accuracy under 60% during baseline period or a reduced
631 amount of reversals attained were excluded (i.e., 4 subjects from Experiment 1; 2 subjects from
632 Experiment 2; 6 subjects from Experiment 3).

633

634 **Statistics**

635 *Single-subject analysis*

636 In order to test the hypotheses, we took a set of strategies. We first captured the direction of
637 effects for each of the key performance variables (i.e., RAR, RT, accuracy, omissions, and
638 switching likelihood), and contrasted them for each participant, obtaining an indication of the
639 direction and strength of the effects per participant. Descriptive and distribution measures, as
640 well as single-subject statistics, were used as guidance of the variability of effect size in single
641 variables, and for guiding the previously defined exploratory hypotheses. Per participant, effect
642 sizes were calculated and depicted for each of the key performance variables to check the effect
643 size of individual differences across arousal states.ⁱⁱ

644

645 *Group analysis*

646 To investigate the management of probabilistic information as a function of arousal, we
647 conducted mixed-effects analyses including data from the three experiments collapsed into a
648 single dataset with RAR as the main index of performance. In face of the diversity of samples’
649 characteristics and experiment features, we fit RAR using hierarchical linear mixed-effects
650 modelling, as implemented in the lme4 R package.⁸¹ We treated RAR as obeying to a
651 hierarchical data structure with arousal as fixed effect, and participant (level 2) nested into
652 experiment (level 1) as random effects. This random part was common to all models. We tested
653 the specific hypothesis by using the same approach based on multilevel linear mixed-effects
654 modelling. Different variables (i.e., probabilistic switching, perseveration, breakdowns, RT
655 variability and omissions) were analysed in a multilevel data structure, with the fixed (arousal)
656 and random effects (experiment/participant) adjusted to the specific hypothesis tested.

ⁱⁱ Deviation from pre-registration. Spearman rank-order correlation tests and Bayes factors were finally not performed to estimate the degree of association between switch likelihood as a function of consecutive negative feedbacks and arousal states. We will check the slope and effect.

657 Models were compared using the Akaike Information Criterion (AIC), and a likelihood
658 ratio test. Notice that AIC does not assume that the true model is among the set of candidates
659 (and is just intended to select the one that is closest to the true one). In our case, fitting decisions
660 were not about the truthiness of models, but to include or not a given factor. For model
661 comparisons performed to identify the best-fitting model, a relatively lenient 0.010 p-value
662 criterion was adopted.

663 Causal mediation analyses were conducted to estimate the proportional direct and
664 indirect effects of arousal on task performance through probabilistic switching and
665 perseveration strategies (mediators) using the “mediation” package in Rⁱⁱⁱ.⁸² This method
666 allowed us to assess a confidence interval of the mediation effect itself using rigorous sampling
667 techniques with fewer assumptions of the data. The average causal mediation effect was
668 determined using a nonparametric bootstrapping method (bias-corrected and accelerated; 1000
669 iterations) and reported as standardized β regression coefficients for direct comparison with
670 each other. Confidence intervals were obtained using a quasi-Bayesian approximation.

671

672 **Pre-registration**

673 <https://osf.io/tzw6d>

674

675 **Data and code**

676 Data and codes used for the analyses presented here are available at the OSF repository
677 (<https://osf.io/xk379/>), with unrestricted access.

678

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685

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ⁱⁱⁱ Deviation from pre-registration. The mediation analysis was not initially included in the pre-registration, however, we decided to run it in order to test whether the impairment in performance in low and high arousal states could be attributed to the different maladaptive behavioural patterns.

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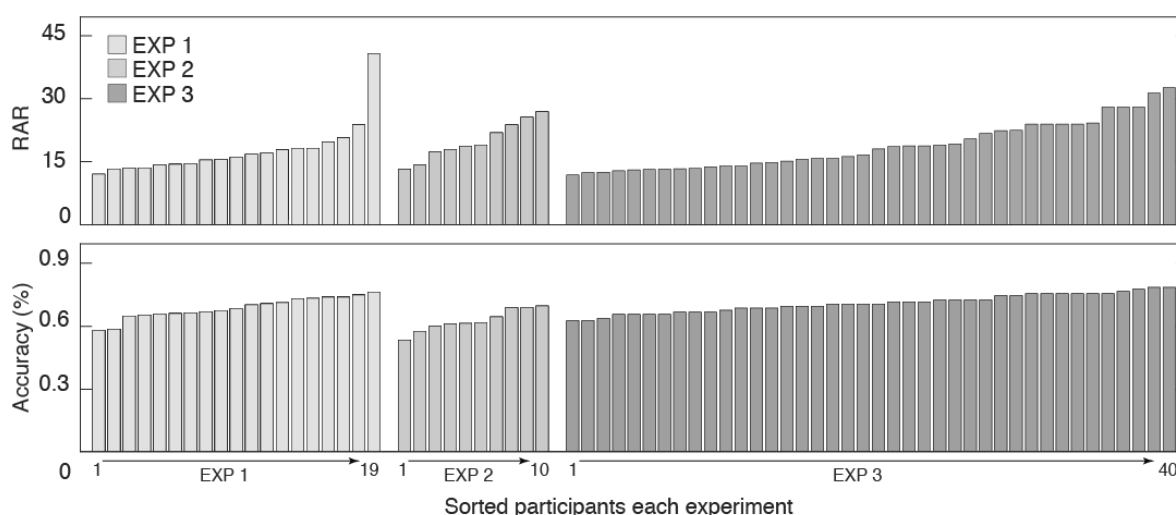
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864 SUPPLEMENTARY MATERIAL

865 Dual-tasking effect of physical exercise on baseline performance

866 Is the detrimental effect of heightened arousal on behavioural performance truly due to the
867 increased arousal level, or does it simply reflect a dual-task confounding effect of the physical
868 and the cognitive task occurring simultaneously? Although this question is partially tackled in
869 main analyses as the baseline arousal state of the heightened arousal states was also a dual-task
870 condition (i.e., warm-up), we specifically explored whether a dual-tasking arousal baseline
871 might be associated with poorer performance (i.e., higher RAR and RT variability), relative to
872 a non-exercise adaptation period that participants performed just before the warm-up. Contrary
873 to what we expected, the mixed-effects model yielded no reliable performance differences
874 between the adaptation period and the warm-up (RAR: $t(39) = 1.41, p = 0.167, \beta = 0.18$; RT
875 variability: $t(39) = 1.50, p = 0.14, \beta = 0.19$). To further confirm that baseline performance was
876 equal or similar for all experiments, we analyzed the behavioural performance during baselines
877 of Experiments 1 and 2 (i.e., wakefulness periods), as well as during baseline of Experiment 3
878 (i.e., warm-up period). Neither the number of responses needed to attain a reversal (RAR) nor
879 accuracy showed reliable differences in baseline performance between experiments ($F < 1$).
880 Subject-by-subject results show a similar distribution of performance across subjects in each
881 Experiment (see supplementary figure 1).



882
883 **Supplementary figure 1: Subject-by-subject baseline performance.** Individual behavioural measures during
884 baseline across databases. Grey bars represent individual participants within each experiment. All subjects are
885 arranged by performance, from best to worst in RAR, and from worst to best in accuracy. The analysis revealed
886 no reliable differences in behavioural performance during baseline periods across experiments.

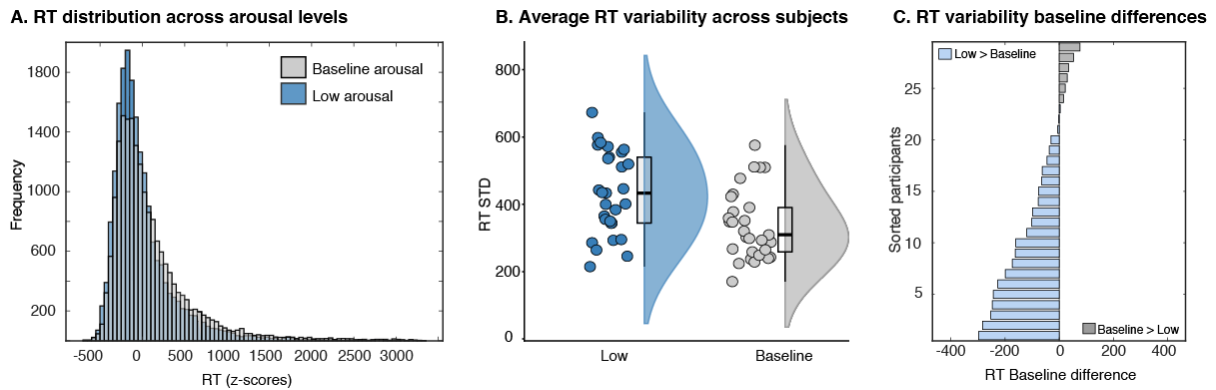
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889 Low arousal deceleration in behavioural dynamics

890 The transition from wakefulness to sleep involves a progressive, and sometimes nonlinear loss
891 of responsiveness to external stimuli and a progressive increase of RT variability.^{10,18,30} To
892 further characterise the behavioural pattern of this transition, and compared to previous falling
893 asleep tasks, we investigated the responsiveness and RT dynamics of the participants in the
894 low arousal condition. We fitted a mixed-effects model separately for RT variability and
895 omissions as dependent variables. As predicted from other cognitive tasks,^{17,18,30,33} low arousal
896 led to higher RT variability ($t(27.99) = 4.59, p < 0.001, \beta = 0.54$), which was accompanied by

897 a drastic increase in omitted response to stimuli ($t(27.99) = 5.11, p < 0.001, \beta = 0.67$),
898 compared with the baseline arousal state (see supplementary figure 2). These findings confirm
899 the convergence to other tasks of our arousal manipulation in probabilistic reversal learning in
900 its basic effects.
901



902 **Supplementary figure 2. RT dynamic in low arousal.** A) RT distribution during low (blue bars) and baseline
903 (grey bars) arousal states. B) Violins and overlaid box plots of the averaged reaction time variability across
904 participants in low and baseline arousal states. C) Subject-by-subject baseline differences in RT variability in low
905 arousal. Grey bars represent participants with a higher RT variability in the baseline compared with low arousal
906 state. Blue bars depict participants with a higher RT variability when arousal level was reduced compared with
907 baseline arousal state. Participants are sorted by the RT variability difference between baseline and the arousal
908 state.
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