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Passive visual stimulation induces fatigue or improvement depending on cognitive load

Stefano Ioannucci¹, Guillermo Borragán², Alexandre Zénon¹

¹ Motor Control & Cognition (MOCOCO), Institut de Neurosciences Cognitives et Intégratives d'Aquitaine (INCIA) - UMR 5287, CNRS, University of Bordeaux, Bordeaux, France

² Neuropsychology and Functional Neuroimaging Research Unit (UR2NF), Neuroscience Institute (UNI), Université Libre de Bruxelles, Bruxelles, Belgium

Abstract:

Theories of mental fatigue disagree on whether performance decrement is caused by motivational or functional alterations. We tested the assumption that keeping neural networks active for an extensive period of time entrains consequences at the subjective and objective level – the defining characteristics of fatigue – when confounds such as motivation, boredom and level of skill are controlled. We reveal that passive visual stimulation affects the performance of a subsequent task that is carried out in the same portion of visual space. This outcome, consisting either in an enhancement or deterioration of performance, was determined by the participants' level of cognitive load and arousal, which were manipulated through variations in the difficulty of concurrent auditory tasks. Thus, repeated stimulation of neural networks leads to their altered functional performance, a mechanism which may play a role in the development of global mental fatigue.

44 **Introduction**

45 Prolonged mental activity leads to a sensation of discomfort with well-known adverse consequences
46 on overall quality of life (Åkerstedt et al., 2007; Raslear et al., 2011), productivity (Ricci et al.,
47 2007), impulsivity (Blain et al., 2016), emotional regulation (Grillon et al., 2015) and workplace
48 accidents (Goode, 2003; Swaen et al., 2003), all regrouped under the umbrella term of Mental
49 Fatigue (MF). MF manifests itself in two empirically measurable components: the *subjective* feeling
50 of tiredness and the *objective* decrease in performance (DeLuca, 2007). To this day, the neural
51 origin of MF remains elusive, and this lack of understanding stems in part from MF's dependence
52 on the duration and difficulty of the task (Hockey, 2013), as well as on the motivation (Boksem et
53 al., 2006), fatiguability and skills of the agent performing it (Borragán et al., 2017).

54
55 Theories of mental fatigue generally concur on its role in disengaging individuals from cognitive
56 tasks to seek rest. Yet, the underlying cause of this need to withdraw from effortful tasks continues
57 to be debated by two schools of thought. Functional theories assume that fatigue arises as a
58 consequence of alterations in the neural circuitry (e.g. depletion of finite resources or accumulation
59 of metabolites), or as an outcome of mechanisms that prevent such alterations (Blain et al., 2016;
60 Dongen et al., 2011; Schellekens et al., 2000; Zénon et al., 2019). Despite their intuitive appeal,
61 these accounts have suffered from a lack of evidence (Hockey, 2013; Kurzban et al., 2013). In
62 response, motivational theories view fatigue as a cognitive strategy, responsible for the reallocation
63 of effort when the cost-benefit ratio of ongoing behaviour is disadvantageous (Boksem & Tops,
64 2008; Hopstaken, Linden, et al., 2015; Kurzban et al., 2013). However, this motivational view of
65 fatigue has also been challenged (Benoit et al., 2019; Gergelyfi et al., 2015).

66 From a neuroscientific perspective, the fact that fatigue may arise from any type of task complicates
67 the process of pinpointing it to specific brain areas (Harrington, 2012), due to the risk of conflating
68 fatigue-specific effects with unrelated activity across brain regions. Rigorous exploration of fatigue
69 should first contemplate its functioning at the lowest degrees of complexity, to rule out as many
70 confounds as possible. A prediction of the functional paradigm is that repeated stimulation of
71 specific neural networks should lead to their altered performance over time.

72
73 We coin as *neural fatigue* this putative specific functional deterioration, which we tested by drawing
74 inspiration from a line of research on sleep that found a decrease in visual perception performance
75 due to repetitions of a visual task, the texture discrimination task (TDT), where participants are
76 required to identify the orientation of briefly presented peripheral targets (Mednick et al., 2002).
77 Remarkably, in this study, participants' performance was restored when perceptual characteristics of
78 the targets (orientation and location) were changed, but not when they were offered money to
79 manipulate motivation. Additionally, a follow-up neuroimaging study found this perceptual
80 deterioration to correlate with decreased BOLD signal in V1 (Mednick et al., 2008). Here, we
81 sought to determine if this perceptual deterioration in the TDT task could be passively induced by
82 prolonged stimulation of specific portions of the visual field.

83
84 Given gain theories of arousal (Aston-Jones & Cohen, 2005; Mather et al., 2016), we predicted that
85 being engaged in concomitant auditory tasks of varying cognitive load during saturation would
86 modulate its impact on behaviour. Our hypothesis was to expect a stronger effect in agents
87 performing tasks with harder demands, given the stimulating effects of arousal on cortical response
88 to stimulation (Jones, 2003; Mather et al., 2016; McGinley et al., 2015).

89 Furthermore, cerebral activity was recorded by electroencephalography (EEG) to assess alterations
90 in the steady-state response at stimulation frequency (~7.5 hertz), as we were expecting to disrupt
91 low-level bottom-up visual processing. Lastly, the relationship between behavioural consequences
92 of saturation and subjective feeling of fatigue was investigated.

93
94
95

96 **Methods**

97 Forty-eight participants took part voluntarily in the experiment (24m and f, age = 22.1 ± 2.24). All
98 of them were naive to the experimental procedure, with no history of mental or visual conditions.
99 Participants had normal or corrected-to-normal vision and provided written informed consent to
100 participate. They received 10€ per hour in compensation for their participation. The study was
101 approved by the Ethical Review Board. Due to the lack of literature on the effect we sought to test,
102 the sample size was arbitrarily preplanned to have a balanced and sufficient number of participants
103 for the various experimental conditions and randomisations.

104 In total, 56 participants were recruited, given that 7 participants were excluded; 4 due to failure to
105 respond to an adequate number of trials in the behavioural task (less than half the trials in two or
106 more blocks of the first session), 2 spontaneously dropped out during the experiment and 1 for
107 being an outlier (performance > 4 std).

108 *Experimental design*

110 All aspects of the experiment, except the questionnaires, were implemented through Matlab 2019a
111 (The MathWorks, Inc., Natick, Massachusetts, United States), using Psychtoolbox (Brainard, 1997;
112 Pelli, 1997) and displayed on a computer screen with 1280 by 1024 resolution. Participants sat in
113 front of the screen at a distance of 60 cm and accommodated their heads on a chin-rest. A keyboard
114 was used to respond across the various tasks. Below the screen there was an Eyetracker 1000 (SR
115 Research Ltd., Mississauga, Canada), which was employed to ensure central fixation of the
116 participants' gaze while tracking variations in the size of their pupils. A 32-channel Active Two
117 Biosemi system (Biosemi, Amsterdam, Netherlands) EEG headset was mounted on their heads.
118 Lastly, a pair of in-ear headphones was provided (Cellularline spa., Reggio Emilia, Italy).

119
120 The experimental design was divided into different phases, which will be detailed in the following
121 sections. First of all, a brief training with reduced number of trials of the various tasks was carried
122 out in order to have the participants familiarise with their procedures (see Figure 1 panel 1a).
123 Behavioural and physiological measures were taken at different timepoints of the experiment,
124 namely: BASELINE, MIDDLE and CONCLUSION (see Figure 1 panel 1b,d,f). In-between these
125 measurements, subjects underwent continuous stimulation ('saturation') of a specific portion of
126 their visual field ('quadrant') (see Figure 1 panel 1c,e). During saturation, volunteers were engaged
127 in auditory tasks, the difficulty of which differed based on the experimental group to which they
128 were randomly assigned, being either in an "EASY" (n=24, 12m and f, age: 22.37 ± 2.7) or "HARD"
129 (n=24, 12 m and f, age: 21.92 ± 1.69) condition. The assignment of SATURATED quadrant and group
130 was counter-balanced across participants. Overall, an experimental run lasted approximately 2h and
131 30 minutes, depending on the time spent to install the EEG headset.

132 *Auditory tasks*

134 As outlined, during each saturation session participants were engaged in auditory tasks, the
135 demands of which varied according to the experimental group to which they were assigned for the
136 duration of the whole experiment, being either EASY or HARD. This experimental condition was
137 introduced to evaluate potential effects of differing cognitive loads, and resulting arousal levels, on
138 the time course of fatigue. Therefore 3 different tasks were adopted, based on the fact that their
139 complexity could be manipulated and that they provided variety in demands (working memory,
140 executive functions, attention). These tasks were randomly cycled across a saturation session, until
141 its pre-scripted duration of 41 minutes had passed. Specifically, the following tasks were used: the
142 n-back task, a pitch-sequence reproduction task, and a switch task which we named the side task
143 (Table 1). All tasks of the experiment employed the same response keys (F and J), except for the
144 pitch-sequence task where 2 additional keys were added (D and K).

145 N-back: a trial would consist of a list of 12 letters where
 146 participants had to report the occurrence of the target letter.
 147 In the EASY group, the target letter was 'X' (0-back), while
 148 in the HARD group the target letter was any letter repeated 2
 149 steps before (2-back). A block of N-back was composed of
 150 35 trials for both conditions, each trial lasted 15 seconds for
 151 both groups.

152
 153 Pitch-sequence: In this task, participants were required to
 154 replicate a sequence of beeps that was presented to them.
 155 Four different beeps (from low-pitch (336hz) to high-pitch
 156 (475hz) and in between (377hz, 424hz) were put together in
 157 randomly generated sequences. To each beep corresponded
 158 a key on the keyboard. For the EASY group these sequences
 159 comprised 2 beeps, while for the HARD group they
 160 comprised 5 to 8 beeps. A block of pitch-sequence task
 161 consisted in 80 trials for both conditions, with longer
 162 intervals between beeps for the EASY group and shorter
 163 intervals for the HARD group. On average, the duration of
 164 stimuli presentation for the EASY group lasted 2.7 seconds,
 165 while the mean duration for the HARD group was of 8.9
 166 seconds.

167
 168 Side: In this task sounds were presented randomly either to
 169 the left or to the right earphone of the participant. These sounds came from different categories,
 170 namely: animal sounds or vehicle sounds. For the EASY group, participants only had to indicate if
 171 the current sound was played on the left or the right. The HARD group had instead a cue voice
 172 indicating, at random points during the block, which category they had to answer coherently to (i.e.
 173 if a sound of that category was presented to the left, they had to press the left key and *vice-versa*),
 174 this implicitly signalled they had to answer incoherently to the unmentioned category (i.e. if the
 175 sound was on the left, they had to press right and *vice-versa*). Furthermore, for this group a third
 176 category of sounds was added, the computer/electronics category, to which they were instructed not
 177 to respond. A block would be made up of 135 sounds with shorter silences in-between for the HARD
 178 group, and 80 sounds with longer distances in-between for the EASY group, subdivided into trials of
 179 5 sounds for both groups. A trial would last on average 30 seconds in the EASY condition, and 18 for
 180 the HARD group.

181
 182 *Behavioural index of fatigue*

183 As a behavioural measure of fatigue, we adopted the participants' performance in the Texture
 184 Discrimination Task (TDT), based on the task developed by Karni and Sagi (Karni & Sagi, 1991).
 185 The task's goal is to discriminate the orientation of a peripheral target, which consists of three
 186 diagonal lines aligned either vertically or horizontally, against a background of horizontally oriented
 187 bars (see Figure 1 panel 2b). Participants were instructed to maintain their gaze on a central fixation
 188 cross and report the perceived orientation of a peripheral target at the end of each trial.
 189 These targets would relocate from trial to trial, within a defined quadrant of the screen. Quadrants
 190 would vary depending on the block, either on the upper right or upper left portion of the screen.
 191 Each experimental trial comprised a pre-stimulus window of 700 ms (see Figure 1 panel 2a),
 192 followed by the target screen for 32 ms (see Figure 1 panel 2b), a blank screen, known as ISI (inter
 193 stimulus interval), with variable length between 6 and 600 ms, determined by a Bayesian staircase
 194 procedure (see below) (see Figure 1 panel 2c), followed by a mask of 100 ms (see Figure 1 panel
 195 2d). The mask is designed to disrupt the subjects' processing of the peripheral target lines, therefore
 196 shorter ISIs translated into harder trials.

TASK	EASY GROUP	HARD GROUP
N-back	Press key when hearing the letter X	Press key when current letter corresponds to a letter presented 2 steps before in the sequence
Pitch-sequence	Reproduce a sequence of two beeps	Reproduce a sequence of 5 to 8 faster beeps
Side	Indicate if a sound was played through the left or the right headphone	Same as easy, but the response keys could be inverted throughout the block depending on sound category. Inhibit response to an additional category

Table 1: Summary of the demands in the auditory tasks (rows) by difficulty condition (columns)

197 Finally, there was a 1000 ms time window where the participant indicated, by pressing on the
 198 keyboard, if the target was perceived as horizontal or vertical (see Figure 1 panel 2e).
 199 A single TDT trial lasted on average 2.26 seconds (± 0.28 sec) and 80 trials composed a block.
 200 A complete TDT session consisted of 4 blocks, 2 per quadrant, and lasted 12.4 minutes on average
 201 (± 37 sec). The order of blocks was random for every session and participant. A block would begin
 202 when the participant pressed spacebar, after which he or she was informed on the quadrant within
 203 which the target would appear, by means of a message at the centre of the screen.

204

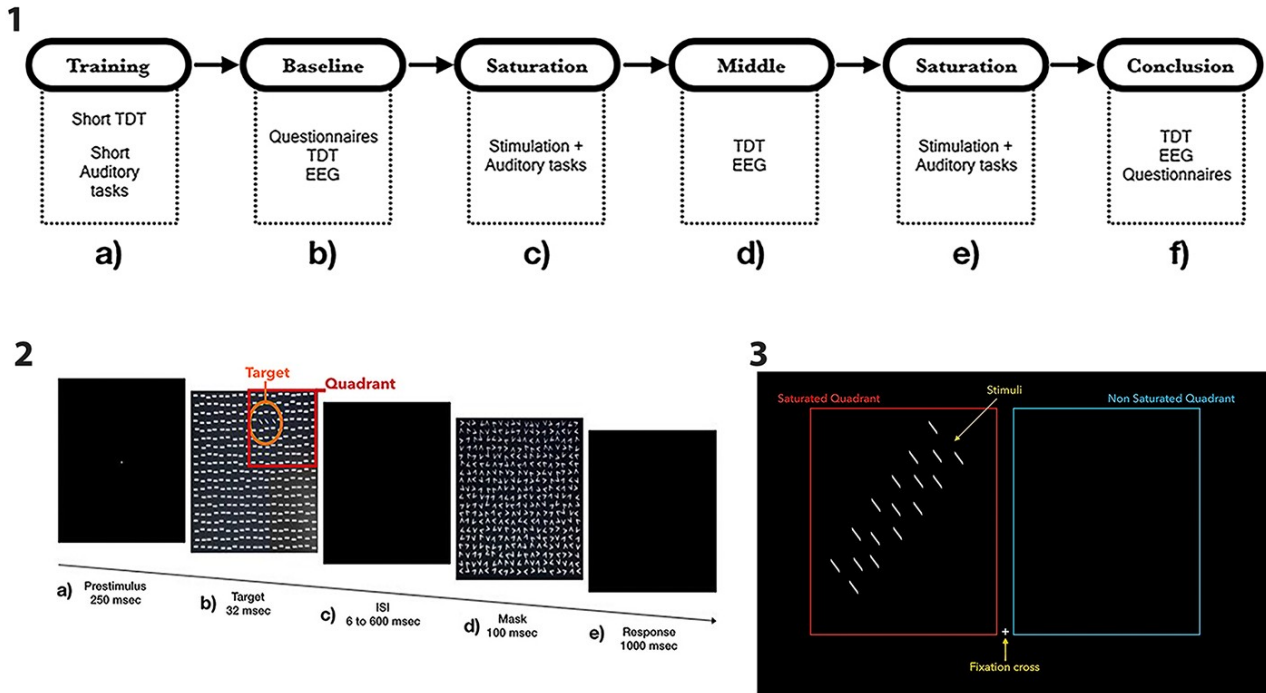


Figure 1: : Panel 1: Flowchart of the experimental design. Panel 2: Visual representation of the Texture Discrimination Task (TDT). Please note that across the whole trial a fixation cross stayed in the centre in order to help participants maintain their gaze fixated. Panel 3: Visual representation of saturation and EEG sessions. While fixating the centre a participant would be presented with stimuli identical to the targets of the TDT (here they appear larger due to representation), appearing in all possible target locations within a quadrant at 7.5 Hz. During EEG sessions the quadrants alternated (see EEG methods for details), while during saturation sessions the stimuli flashed in a single quadrant (the saturated quadrant), and participants were engaged in concurrent auditory tasks, the difficulty of which depended upon their experimental group

205

206

207

208 Adaptive ISI selection procedure

209 In order to optimize inference of participants' psychometric curve from limited data, we opted for
 210 an adaptive procedure to select ISI values (inspired from (Kontsevich & Tyler, 1999)). This
 211 procedure was applied following the five first trials (in which ISI was selected randomly). In each
 212 trial, a variational Bayesian logistic regression was performed on currently acquired data
 213 (Drugowitsch, 2019), resulting in parameter estimates and variance. Then, the expected update in
 214 these parameters was computed under the hypotheses of correct or incorrect response in the next
 215 trial, and for all possible ISI values:

$$216 \theta_{n+1}(x_{n+1}, y_{n+1}) = f([x_{1:n}, x_{n+1}], [y_{1:n}, y_{n+1}]),$$

217 for θ the mean (θ^μ) and variance (θ^Σ) estimates of the parameters, f the variational logistic
 218 regression, $y_{1:n}$ the acquired response data and y_{n+1} the expected response, $x_{1:n}$ the past ISI values
 219 and x_{n+1} the ISI value for the next trial.

220 The Kullback-Leibler (KL) divergence between current and future estimates, representing how
 221 much information one would expect to gain about the parameter estimates, was computed for each
 222 ISI and possible response according to the following formula:

223
$$KL(\theta_i, \theta_j) = \frac{1}{2} \log\left(\frac{|\theta_j^x|}{|\theta_i^x|}\right) - 2 + \text{tr}\left((\theta_j^x)^{-1} \theta_i^x\right) + (\theta_j^\mu - \theta_i^\mu)^T (\theta_j^x)^{-1} (\theta_j^\mu - \theta_i^\mu).$$

224 These KL values for correct and incorrect expected response were then averaged and weighted as a
225 function of the probability of obtaining either correct or incorrect response given current parameter
226 values:

227
$$V(x_{n+1}) = p(y_{n+1}=1|\theta_n) KL(\theta_n, \theta_{n+1}(x_{n+1}, 1)) + p(y_{n+1}=0|\theta_n) KL(\theta_n, \theta_{n+1}(x_{n+1}, 0)).$$

228 These KL values were then softmax-transformed to lead to a probability distribution over all ISI
229 values, which was then sampled randomly to select the value of the ISI for the next trial.

230

231 *Saturation*

232 A saturation session lasted for 41 minutes and consisted of a prolonged visual stimulation, during
233 which participants had to maintain their gaze on a central fixation point while stimuli were
234 continuously flashed at 7.5Hz (see Figure 1 panel 3). Stimuli were composed of all the possible
235 targets within a quadrant in the TDT. The SATURATED quadrant was kept constant for each
236 participant across all saturation sessions. This ensured the entraining of specific neuronal
237 populations across the whole experiment, providing a way to test whether the neural (EEG) and
238 behavioural (TDT) response would differ between SATURATED and NON-SATURATED quadrants.

239

240 *EEG*

241 EEG recordings of whole brain activity in response to the presentation of the saturation stimulus
242 (See Figure 1 panel 3) were performed. A complete EEG session comprised four repetitions of 1-
243 minute long stimulations (two per quadrant), with a 5-second pause in between. Visual stimulation
244 during EEG blocks was identical to the one used during saturation blocks, except that the quadrants
245 with stimuli alternated, their order being counterbalanced across participants.

246

247 FieldTrip toolbox (Oostenveld et al., 2011) was employed for the analysis of EEG data.
248 Specifically, we focused our analysis on the stimulation frequency (7.5 Hz), reasoning that
249 alterations in bottom-up visual processing should lead to modulation of the steady-state response.

250

251 The preprocessing consisted in a low-pass filter at 100 hertz, a high-pass filter at 0.4 hertz and a
252 line-noise filter at 50 and 100 hertz applied to the raw data, which was then re-referenced on the
253 average of all 32 channels. Before segmentation into trials, artefacts were rejected upon visual
254 inspection of the data and then by independent component analysis.

255 Subsequently, one Fourier transform with a single Hanning taper was applied to extract the power
256 spectrum around stimulation frequency, (7.3 to 7.7 hertz, in steps of 0.1). Signal from neighbouring
257 frequencies (7.3 to 7.4 and 7.6 to 7.7 hz) was subtracted from the 7.5 Hz signal, to highlight the
258 specific response to stimulation (Norcia et al., 2015), and this noise-subtracted 7.5hz was then used
259 in subsequent analyses.

260

261 *Pupil*

262 We also recorded the pupil size of participants as a physiological index of arousal, as it is a well-
263 established physiological marker of this construct (McGinley et al., 2015; Wang et al., 2018).

264 Variations in pupil size were tracked during saturation sessions, while participants were engaged in
265 the concurrent auditory tasks, the difficulty of which varied according to the experimental group
266 they were assigned to. Specifically, after linear interpolation of blinks, filtering (high-pass with
267 0.01Hz cutoff frequency) and baseline correction, the pupil responses between the onset of the first
268 stimulus of trial n and the onset of the first stimulus in trial n+1 were averaged. These estimates of
269 trial-wise average pupil responses were then averaged by auditory task and session, thus resulting in
270 one data point for each subject and task in both saturation sessions.

271

272

273

274 *Questionnaires*

275 In order to measure the participants' subjective feeling of fatigue and sleepiness, two pen-and-paper
276 questionnaires were administered at the beginning and end of the experiment; the Multidimensional
277 Fatigue Inventory (Gentile et al., 2003) and the Karolinska Sleepiness Scale (Shahid et al., 2011).

278

279 *Statistical Analysis*

280 First, behavioural effects were assessed by means of a Generalised Linear Mixed Model (GLMM)
281 on response accuracy in the TDT task. Correct response in the task was modelled as a logistic
282 dependent variable, with ISI as a covariate and participants as a random variable. Difficulty group
283 (EASY, HARD), experimental session (BASELINE, MIDDLE, CONCLUSION) and saturated quadrant (YES,
284 NO) were set as explanatory variables, testing their main effects and interactions. This was done on
285 Jamovi (The jamovi project, 2019) through its module GAMLj (Gallucci, 2019). Random effects
286 were included step-by-step as long as the Bayesian Information Criterion and deviance values kept
287 decreasing and no convergence issues were encountered. Specifically, intercept, ISI and Session
288 were included in the random part of the model and were therefore allowed to vary across
289 participants.

290

291 Second, effects on brain activity were evaluated by examining changes in the EEG signal.
292 To evaluate the interaction of session and condition, the difference of EEG activity between
293 SATURATED and NON-SATURATED condition was computed, for each of the three sessions and for each
294 participant.

295

$$296 (\Delta EEG_{session}) = (sat_{session} - nonsat_{session})$$

297

298 These values were then analysed in dependent sample two-tailed t-tests to assess changes across
299 sessions. Correction for multiple comparisons across electrodes was enforced by means of a non-
300 parametric Monte Carlo cluster-based permutation approach with 1000 randomisations (Maris &
301 Oostenveld, 2007).

302

303 Third, the participants' performance in each of the auditory tasks was evaluated by means of a
304 mixed model on the ratio of correct responses, by saturation session and difficulty condition, for
305 each of the tasks. This approach was preferred to a repeated measures ANOVA due to missing data
306 points at a subject-wise level (3 on average across tasks).

307

308 Fourth, we assessed the efficacy of the auditory tasks in inducing different cognitive load and
309 arousal levels based on their difficulty. Again, given the missing data points, a mixed model was
310 performed with the pupil data of each task as dependent variable. As above, group and session were
311 set as explanatory variables.

312

313 Fifth, participants' subjective evaluation of fatigue was assessed by comparing the values reported
314 before and after the experiment in the Karolinska Sleepiness Scale and Multidimensional Fatigue
315 Inventory. Separate repeated measures ANOVAs were carried out for the responses in the two
316 questionnaires, with session as within-subjects factor and difficulty as between-subjects factor.

317

318 Lastly, estimates of behavioural performance change between BASELINE and CONCLUSION session
319 obtained by the psychometric function, and the change in the both questionnaire scores were
320 correlated. This test was carried out in Matlab.

321

322 *Open code and data policy*

323 Source code is available at [<https://github.com/ste-ioan/TDT2019>], data is available upon request to
324 the corresponding author.

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Results

Behaviour

The GLMM revealed the quadruple effect of ISI, Saturation, Difficulty and Session to be strongly significant (see Figure 2; $X^2_{(2, 46080)} = 21.96$, $p < 0.0001$; together with Session: $X^2_{(2, 46080)} = 28.18$, $p < 0.0001$; ISI: $X^2_{(1, 46080)} = 95.56$, $p < 0.0001$; ISI and Session interaction: $X^2_{(2, 46080)} = 29.43$, $p < 0.0001$; Saturation, Difficulty and Session interaction: $X^2_{(2, 46080)} = 12.68$, $p = 0.002$; ISI, Difficulty and Session interaction: $X^2_{(2, 46080)} = 51.89$, $p < 0.0001$; and ISI, Saturation and Session interaction: $X^2_{(2, 46080)} = 6.88$, $p = 0.032$).

In order to investigate this four-way interaction, we performed separate GLMMs for the two difficulty groups and for the first and second half of the experiment, applying Holm-Bonferroni correction for multiple comparisons. For the EASY group, in the SATURATED quadrant, performance largely improved between BASELINE and MIDDLE sessions ($Z = 3.67$, $p_{\text{corrected}} = 0.001$, $\exp(\beta) = 18.5$) and fairly decreased between MIDDLE and CONCLUSION sessions ($Z = -2.47$, $p_{\text{corrected}} = 0.039$, $\exp(\beta) = 6.9$). However, there wasn't a significant change between BASELINE and CONCLUSION ($Z = 1.06$, $p_{\text{corrected}} = 0.287$).

On the other hand, the HARD group displayed a major loss of performance in the SATURATED quadrant, between BASELINE and MIDDLE sessions ($Z = -4.168$, $p_{\text{corrected}} = 0.0002$, $\exp(\beta) = 24.4$) and BASELINE and CONCLUSION ($Z = -3.93$, $p_{\text{corrected}} = 0.0004$, $\exp(\beta) = 15.3$), but not between MIDDLE and CONCLUSION ($Z = 1.13$, $p_{\text{corrected}} = 0.518$), as between these sessions their performance decreased also in the NON-SATURATED quadrant.

To further confirm this finding, we explored its session-wise evolution, by performing the same statistical procedure, per group, session-by-session. The absence of a significant interaction between ISI and Saturation in the BASELINE session was confirmed, for the EASY group ($X^2_{(1, 7680)} = 0.99$, $p = 0.32$), and the HARD group ($X^2_{(1, 7680)} = 3.3$, $p = 0.07$). In the MIDDLE session, this interaction became significant for both EASY ($X^2_{(1, 7680)} = 4.95$, $p = 0.026$) and HARD groups ($X^2_{(1, 7680)} = 4.63$, $p = 0.031$) and similarly so in the CONCLUSION session, for EASY ($X^2_{(1, 7680)} = 4.87$, $p = 0.027$), and HARD ($X^2_{(1, 7680)} = 6.19$, $p = 0.013$).

Thus, repeated visual stimulation led to changes in performance within the SATURATED quadrant, depending on the difficulty condition. Specifically, participants assigned to the HARD condition saw their performance drop, particularly in the first half of the experiment. In contrast, participants in the EASY group initially exhibited an improvement in their TDT performance, which disappeared following the second saturation session.

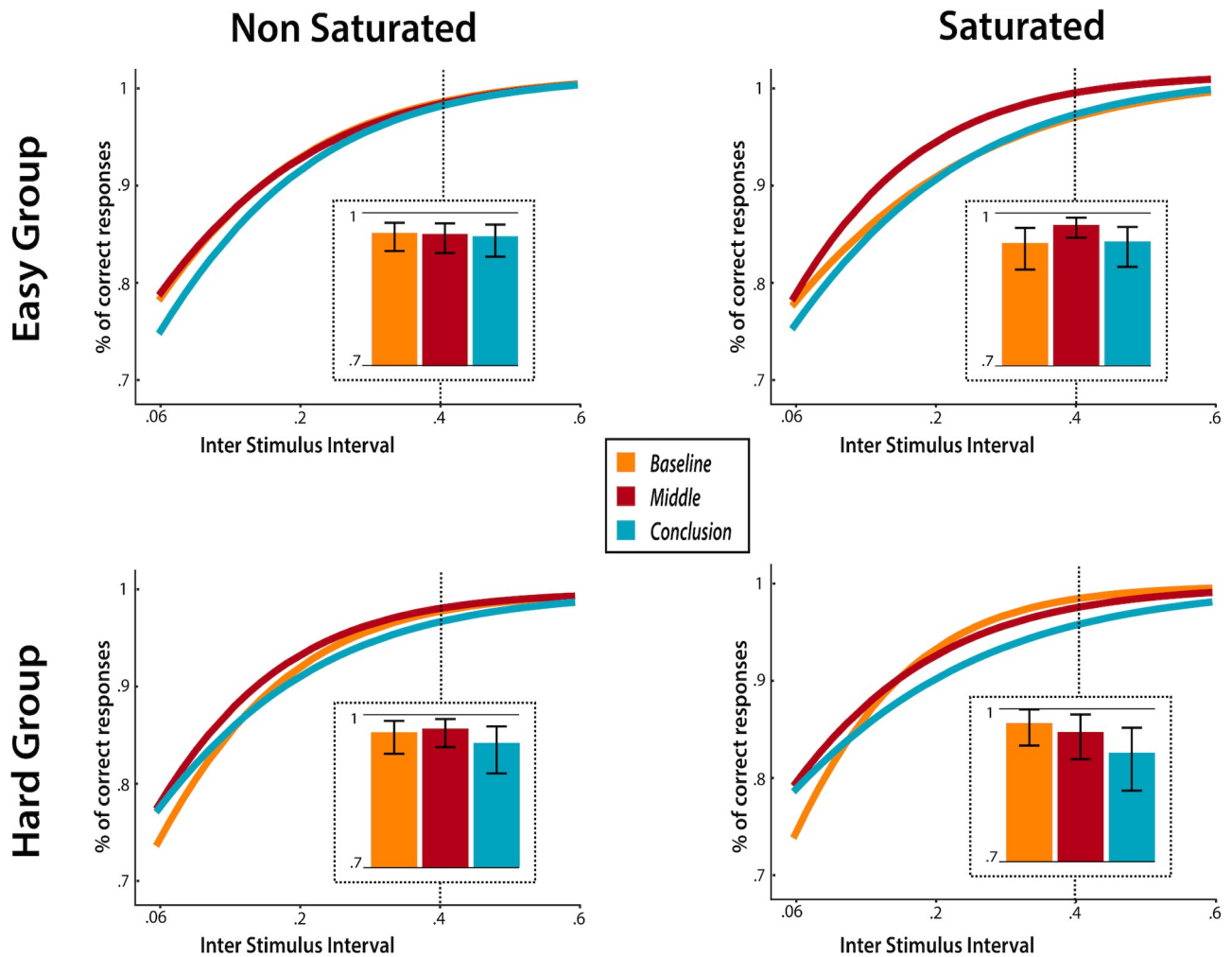


Figure 2: Percent correct responses (y axis), predicted by the GLMM for ISI values ranging from 0.06 to 0.6 (x axis) as a function of saturation condition (left and right columns) and experimental group (top and bottom rows). Error bars depict 95% confidence intervals. Insets: detailed representation of behavioural data for ISI = 400ms.

369

370 *Electrophysiology*

371 We analysed electrophysiological activity by means of cluster-based permutation methods (Maris &
372 Oostenveld, 2007). We first compared EEG steady-state responses between blocks with stimulation
373 of left and right portion of the visual field in the BASELINE session across groups (EASY, HARD). As no
374 clusters were found, we concluded that the side of stimulation did not induce significant differences
375 and grouped left and right stimulation blocks for further analyses. Comparisons of the amplitude of
376 the steady-state response to 7.5Hz stimulation were performed separately for both groups, between
377 BASELINE and MIDDLE, MIDDLE and CONCLUSION and between BASELINE and CONCLUSION. No
378 significant clusters were found.

379

380 *Audio task performance*

381 Concerning the performance of the auditory tasks carried out during saturation, the EASY group
382 outperformed the HARD group in each task. Specifically, in the n-back task the overall mean
383 accuracy of the EASY group was 93.3% versus 62.1% of the HARD group ($t_{(45)} = 10$, $p < 0.0001$). In
384 the side task, the EASY group had on average 99.2 % of correct responses, whilst the HARD group had
385 an accuracy of 89.1% ($t_{(46)} = 3.99$, $p = 0.0002$). Finally, in the pitch-sequence task, the EASY group
386 displayed 73.5% average accuracy, while the HARD group only reached 49.1% ($t_{(46)} = 6.31$, $p <$
387 0.0001).

388

389 *Pupillometry*

390 The analysis of the average pupil size recorded while participants were engaged in the auditory
391 tasks revealed a significant effect of the group condition, in each task (see Figure 3). On top of this,
392 also the effect of session was found to meaningfully impact the pupil size of participants in each
393 task. In the case of the side task, participants in the HARD condition had a larger pupil than those in
394 the EASY condition ($t_{(46)} = 3.94$, $p = 0.0003$) and the whole sample's pupil size decreased between
395 the first and second saturation sessions ($t_{(45)} = -3.58$, $p = 0.0008$). The same result was found also in
396 the n-back task, both in the group-wise effect ($t_{(46)} = 2.02$, $p = 0.049$) and in the session-wise effect
397 ($t_{(45)} = -2.16$, $p = 0.036$). On the other hand, in the case of the pitch-sequence task, the pupil
398 averages in the EASY condition were found to be larger than those in the HARD condition ($t_{(43)} = -$
399 4.18 , $p = 0.0001$), while the pupil responses decreased in the second session, similarly to the other
400 tasks ($t_{(40)} = -2.62$, $p = 0.012$).

401

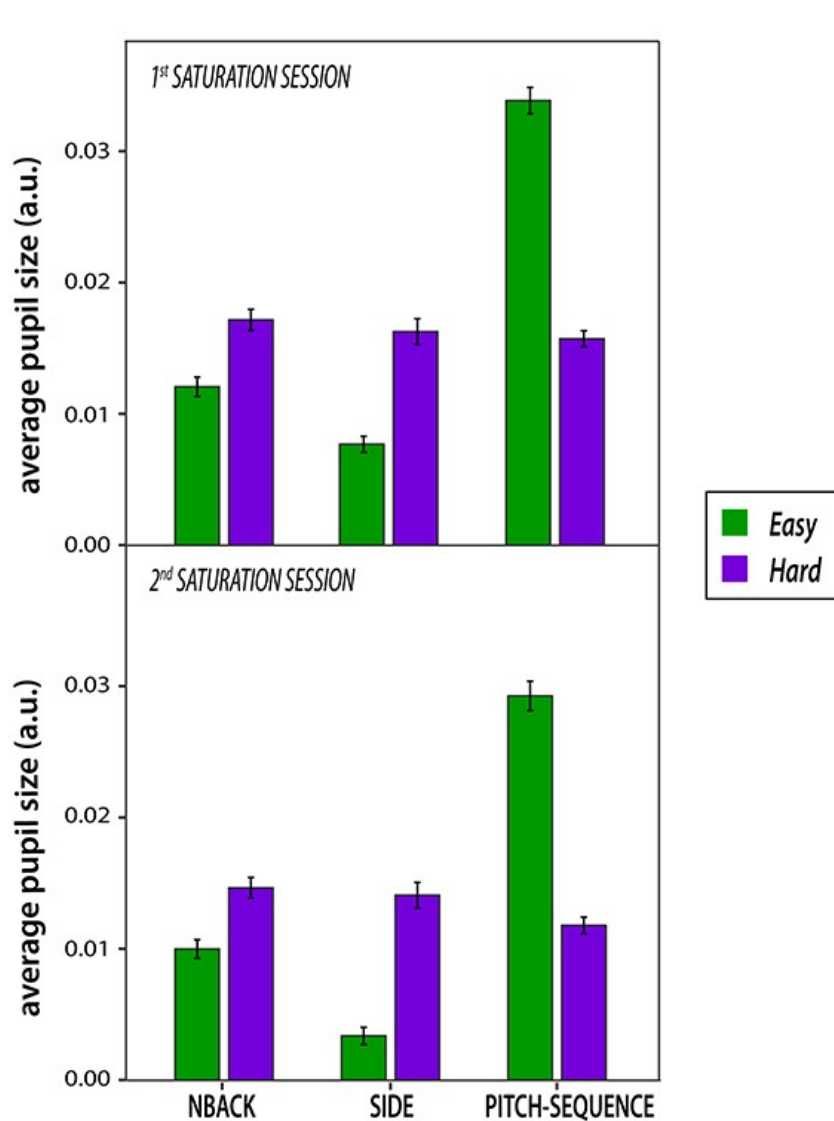


Figure 3: Average pupil size in each auditory task per saturation session, by experimental group

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407 *Self-reported measures of fatigue and sleepiness*

408 The rANOVA on the Multidimensional Fatigue Inventory scores revealed an important increase
409 over the course of the experiment, as highlighted by the significance of the session factor ($F_{(1, 46)} =$
410 255.9 , $p < 0.0001$, $\eta^2_p = 0.85$), while neither the main effect of group, nor their interaction reached
411 significance. Similarly, the Karolinska Sleepiness Scale scores highlighted a strongly significant
412 increase in perceived sleepiness across sessions ($F_{(1, 46)} = 176$, $p < 0.0001$, $\eta^2_p = 0.77$), while no
413 effect was found for the group condition nor its interaction with session.

414 Additionally, the increase in subjective fatigue displayed a moderate negative correlation with the
415 change in the behavioural performance (performed across groups given lack of difference shown
416 above; $R_{(46)} = -0.29$, $p = 0.043$; see Figure 4). This indicates that larger perceived fatigue related to
417 greater loss in performance, as indexed by behavioural difference between SATURATED and NON-
418 SATURATED scores across the beginning and conclusion of the experiment. On the other hand, no
419 significant correlation was observed between changes in behaviour and perceived sleepiness ($R_{S(46)}$
420 $= -0.1$, $p = 0.5$).

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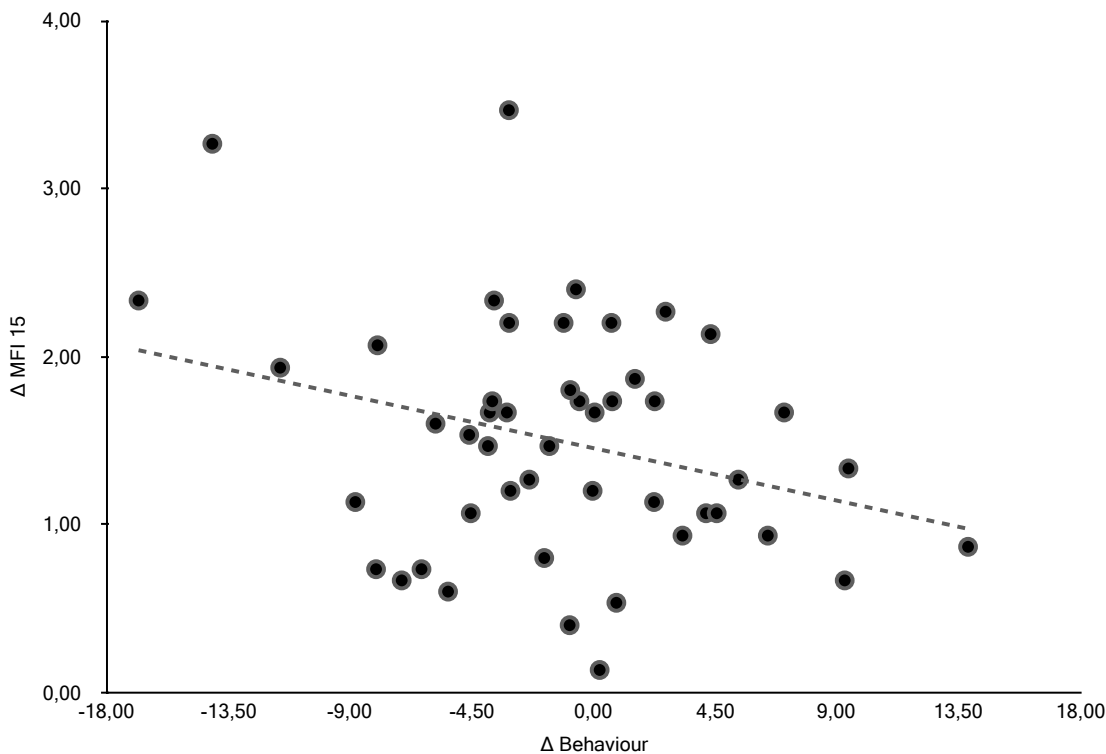


Figure 4: Scatterplot depicting the change in reported fatigue (y axis) in relation to the change in behavioural performance, consisting in the delta between conclusion and baseline in the individual slopes of the participant's psychometric curves (x axis)

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433 **Discussion**

434 In the present study, we found that prolonged stimulation of a portion of the visual field led to
435 specific deterioration of participants' performance in that portion of visual space, proving that
436 neural fatigue can be locally and passively induced. Because of its spatial specificity, this neural
437 fatigue phenomenon cannot be explained solely by motivational theories of fatigue. On the contrary,
438 such progressive functional alteration generated by repeated recruitment could constitute one of the
439 mechanisms involved in general fatigue, as suggested by the correlation we observed between the
440 feeling of fatigue and the specific behavioural consequences, which is rarely found in the pertaining
441 literature (DeLuca, 2007).

442
443 As predicted, perceptual deterioration was accelerated by concurrent performance of difficult
444 auditory tasks. We argue that increased arousal provoked by the challenging version of the tasks and
445 physiologically indexed by pupil size, led to stronger activations of the simultaneously stimulated
446 visual neurons (Mather et al., 2016; McGinley et al., 2015; Zhang et al., 2020) which in turn caused
447 faster and greater degradation of performance.

448 Alternatively, it could be argued that the difference in the impact of passive stimulation on
449 performance across groups could be due to cognitive load per se, rather than to the related changes
450 in arousal. Indeed, it cannot be excluded that the effect observed here would require taxing of the
451 cognitive control network (Asplund & Chee, 2013; Blain et al., 2016; Braver, 2012; Mandrick et al.,
452 2013; Niendam et al., 2012) on top of the saturation of the local visual processes. However, it is
453 unclear which interaction mechanism would require the concurrent disruption of spatially specific
454 visual neurons and central cognitive control networks in order to result in local performance
455 decrement. Distinguishing conclusively between our initial hypothesis of arousal modulation
456 amplifying the impact of saturation on the one hand and the possible interaction of global and local
457 saturation effects on the other hand will require more experiments.

458
459 Interestingly, on top of perceptual deterioration, we also observed improvement of perceptual
460 performance induced by passive stimulation. This result was restricted to the participants whom
461 underwent the easy versions of the auditory tasks, and faded following the second session of passive
462 stimulation. This observation evokes the passive learning literature, where repeated, passive
463 presentation of visual stimuli leads to ameliorations in subsequent discrimination performance
464 (Watanabe et al., 2001). However, classical passive learning is usually measured on the days
465 following training while, since our experiment was not designed to investigate learning, we did not
466 measure behavioural performance on different days. Therefore, this observation relates better to the
467 older and more general concept of perceptual priming, than to perceptual learning literature (Wiggs
468 & Martin, 1998).

469 On the other hand, volunteers who were engaged in hard auditory tasks while being visually
470 stimulated failed to show this stimulation-induced enhancement in performance, suggesting that
471 increased neural fatigue induced by their arousal state counteracted perceptual priming.
472 Alternatively, this result may indicate that arousal inhibits perceptual priming processes (though in
473 contradiction of previous accounts; (Thomas & LaBar, 2005)) or that difficult auditory tasks
474 induced diversion of attention away from the visual stimulus (also not in accordance with previous
475 findings (Mulligan, 2003)).

476
477 Our results also stand out from previous publications in the field of visual fatigue, which generally
478 rely on self-reported measures of eye discomfort, or other physiological markers such as dry eyes
479 and binocular vision stress (Sheppard & Wolffsohn, 2018). Albeit we did not record these variables,
480 there is no reason to suppose there would be a difference between the experimental groups in any of
481 these measures, as they were exposed exactly to the same visual stimuli under identical conditions
482 and recruited from a homogeneous sample. Furthermore, in the few attempts where this body of
483 literature has sought to assess behavioural effects, it has failed to detect any (Chi & Lin, 1998).

484

485 Part of our findings are perhaps complementary with the literature on visual adaptation. However,
486 in that case repeated stimulation affects subsequent behaviour on the timescale of seconds
487 (Carandini, 2000), whereas our findings extend over dozens of minutes. Determining with precision
488 how these mechanisms interact would require studying the time course of the effect with better
489 resolution than the one provided in the present study.

490
491 From the neurophysiological perspective, we failed to observe significant differences in the
492 amplitude of the electrophysiological brain response to the 7.5 Hz flashing of the stimuli. This lack
493 of effect may rule out the usage of this method as a way to investigate the saturation phenomenon or
494 it may be that our study was not sufficiently powered to detect significant differences in this signal,
495 due to its effect size. It may also indicate that perceptual deterioration originates from decreased
496 signal-to-noise ratio rather than simple decrease in activation magnitude. The use of more spatially
497 sensitive instruments (e.i. fMRI) is warranted to shed light on the brain localisation of the observed
498 behavioural phenomenon, which might be explained by a different factor than electrophysiological
499 magnitude of cortical brain response. For instance, the behavioural changes may be reflected in the
500 neural encoding of the saturating stimuli, and thereby be more aptly investigated by multi-variate
501 pattern analyses (Haxby et al., 2014).

502 Despite the lack of statistical effects in the recorded brain signal, the fact that the behavioural
503 consequences were influenced by the difficulty of concurrent, cross-sensory auditory tasks still
504 argues in favour of a cortical, as opposed to retinal, origin of the effect. Such cortical origin would
505 be in line with previous perceptual deterioration results, caused by prolonged TDT performance,
506 where decreased primary visual cortex activations were observed (Mednick et al., 2008).

507
508 All participants reported an increase in fatigue and sleepiness scores at the end of the experiment,
509 providing evidence for the success of the experimental procedure in impacting the *objective* and
510 *subjective* manifestations of fatigue. In fact, the Multidimensional Fatigue Index results were
511 significantly correlated to the change in saturation-specific behavioural performance. Such
512 correlation cannot be attributable to the behavioural difference between easy and hard groups, since
513 the self-reported measures of fatigue did not significantly differ between them. However, the
514 current design does not allow us to make inferences on the causal direction of this relation.

515
516 Analysis of the arousal-related pupil response showed increased dilation in the hard version of the
517 n-back and side tasks, confirming the increased demand associated with these task conditions (van
518 der Wel & van Steenbergen, 2018; Zénon, 2019). However, surprisingly, we found the opposite
519 effect in the pitch-sequence task, the easier group displaying larger average pupil size. This may be
520 due to the excessive demands of this task for those assigned to the hard condition, potentially
521 leading to their disengagement from the task, phenomenon known to reduce pupil size (Hopstaken,
522 van der Linden, et al., 2015). Indeed, the pitch-sequence task had the lowest performance across
523 tasks and conditions (49% of correct responses overall) and several participants spontaneously
524 reported that this task was the most challenging of the three.

525
526 In conclusion, we bring new evidence that passive, repeated neuronal activation induces progressive
527 functional alteration under the modulatory influence of cross-sensory cognitive load and arousal:
528 under low cognitive load, we observed an initial perceptual priming effect followed by a decrease to
529 baseline performance, while no changes were detected in the unstimulated portion of visual field.
530 On the other hand, participants under higher cognitive load displayed an early, specific, loss of
531 performance which then generalised to the non-saturated quadrant.

532 These findings are immune to confounds such as boredom, motivation and level of skill in the
533 fatiguing task (Gergelyfi et al., 2015). Certainly, since all participants carried out the task in the
534 saturated and non-saturated portion of their visual field, any difference in performance between the
535 two, can be solely explained as the by-product of saturation – which was an artifice to keep specific
536 neuronal assemblies active all along.

537 This neural fatigue phenomenon could justify renewed interest in metabolic accounts of fatigue.
538 Indeed, while the neural mechanism underlying this recruitment-related performance deterioration
539 remains to be investigated, one may speculate the involvement of depletion or accumulation of
540 metabolites (Dalsgaard & Secher, 2007; Dienel & Hertz, 2001; Fairclough & Houston, 2004). The
541 detailed characterisation of such process is matter for subsequent studies, which may disentangle
542 how exactly the phenomena brought forward by the present results, to our best knowledge
543 previously unreported, act and interact with each other.

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