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Nicolas Clairis, Mathias Pessiglione

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1 **Value estimation versus effort mobilization: a general dissociation between**
2 **ventromedial and dorsomedial prefrontal cortex**

3

4 **Abbreviated title:** Value vs. effort: vmPFC vs. dmPFC

5 **Authors:** Nicolas Clairis^{1,2,3} and Mathias Pessiglione^{1,2}

6

7 ¹Motivation, Brain and Behavior team, Paris Brain Institute (ICM), Paris, France

8 ²Sorbonne Université, Inserm U1127, CNRS U7225, Paris, France

9 ³Laboratory of Behavioral Genetics (LGC), Brain Mind Institute (BMI), École
10 Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland

11

12 **Corresponding author email address:**

13 nicolas.clairis@protonmail.com; mathias.pessiglione@gmail.com

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22 modeling and data analysis.

23 **Key words:** *Decision-making, learning, reward, effort, confidence, grip, Stroop,*
24 *prefrontal cortex, fMRI, computational model*

25 **Abstract**

26 Deciding for a course of action requires both an accurate estimation of option values
27 and a right amount of effort invested in deliberation to reach sufficient confidence in
28 the final choice. In a previous study, we have provided evidence, across a series of
29 judgement and choice tasks, for a dissociation between the ventromedial prefrontal
30 cortex (vmPFC), which would represent option values, and the dorsomedial prefrontal
31 cortex (dmPFC), which would represent the duration of deliberation. Here, we first
32 replicate this dissociation and extend it to the case of an instrumental learning task, in
33 which 24 human volunteers (13 women) choose between options associated with
34 probabilistic gains and losses. According to fMRI data recorded during decision-
35 making, vmPFC activity reflects the sum of option values generated by a reinforcement
36 learning model, and dmPFC activity the deliberation time. To further generalize the
37 role of the dmPFC in mobilizing effort, we then analyze fMRI data recorded in the same
38 participants while they prepare to perform motor and cognitive tasks (squeezing a
39 handgrip or making numerical comparisons) to maximize gains or minimize losses. In
40 both cases, dmPFC activity is associated with the output of an effort regulation model,
41 and not with response time. Taken together, these results strengthen a general theory
42 of behavioral control that implicates the vmPFC in the estimation of option values and
43 the dmPFC in the energization of relevant motor and cognitive processes.

44

45 ***Significance statement***

46 The medial prefrontal cortex (mPFC) is known to represent key variables needed for
47 choosing a course of action. We previously suggested a functional partition of this
48 brain region: the expected values of choice options are signaled by the ventral part
49 (vmPFC) and the effort invested in decision-making by the dorsal part (dmPFC). Here,
50 we generalize this functional partition to various motor and cognitive tasks, using fMRI
51 in healthy volunteers. Results show that vmPFC activity reflects the expected value of
52 options generated by a reinforcement learning model (whether the goal is to maximize
53 reward or avoid punishment), while dmPFC activity reflects the output of an effort
54 regulation model (whether the task is to produce force or to compare digits).

55 **Introduction**

56

57 Standard economic decision theory assumes that choice options can be ordered on a
58 common value scale. Functional neuroimaging studies have identified value signals in
59 specific regions of the human brain, with the ventromedial prefrontal cortex (vmPFC)
60 as a key node (Peters and Büchel, 2010; Bartra et al., 2013; Clithero and Rangel,
61 2014). Neural activity in the vmPFC reflects the values of stimuli belonging to different
62 categories such as money, food, faces or paintings (Chib et al., 2009; Lebreton et al.,
63 2009; Lopez-Persem et al., 2020; Tom et al., 2007), whatever the modality of
64 presentation such as with text, image, taste or sound (Plassmann et al., 2007;
65 Lebreton et al., 2015; Abitbol et al., 2015; Chang et al., 2021) and for different types
66 of tasks such as rating or choice (Kable and Glimcher, 2009; Suzuki et al., 2017;
67 Shenhav and Karmarkar, 2019; Clairis and Pessiglione, 2022). The vmPFC
68 aggregates not only the positive features of expected rewards but also negative
69 discounters such as risk (Levy et al., 2010; Schonberg et al., 2012; Seaman et al.,
70 2018; Silston et al., 2021), delay (Economides et al., 2015; Jimura et al., 2013; Kable
71 and Glimcher, 2007; Lee et al., 2021), and even physical and mental efforts (Aridan et
72 al., 2019; Westbrook et al., 2019; Lopez-Gamundi et al., 2021; Clairis and Pessiglione,
73 2022). Thus, the vmPFC signal may provide a common neural currency, based on
74 which options could be compared for making decisions (Levy and Glimcher, 2012).

75 The dorsomedial prefrontal cortex (dmPFC) has also been implicated in decision-
76 making, but its precise role is more debated (Clairis and Lopez-Persem, 2023). Neural
77 activity in this region (sometimes labeled dorsal anterior cingulate cortex, dACC) has
78 been related to diverse variables, including negative net action value (Bartra et al.,
79 2013; Pessiglione et al., 2018), choice uncertainty (Volz et al., 2005; Hogan et al.,
80 2019), environment volatility (Behrens et al., 2007), exploration value (Kolling et al.,
81 2012), model updating (Kolling et al., 2016; Fouragnan et al., 2018), etc. Thus, figuring
82 out a single overarching function for this region remains a challenge. Some authors
83 have noticed that the task features inducing an increase in dmPFC activity are often
84 related to a higher demand in mental effort or cognitive control (Shenhav et al., 2013).
85 Accordingly, dmPFC activity was shown to increase with the effort invested in the task,
86 whether it is physical effort as when squeezing a handgrip (Kurniawan et al., 2021;
87 Skvortsova et al., 2014), cognitive effort as when facing conflict (Pochon et al., 2008;

88 Shenhav et al., 2014) or simply deliberation time when making decisions (Clairis and
89 Pessiglione, 2022; Grinband et al., 2011). The dmPFC may therefore be responsible
90 for the mobilization of effort, defined as the investment of the physical or mental
91 resources needed to attain a certain goal (Richter et al., 2016).

92 In a previous study (Clairis and Pessiglione, 2022), we dissociated the roles of the
93 vmPFC and dmPFC in tasks involving an expression of subjective preference (rating
94 and choice): while vmPFC activity reflected the value of options, dmPFC activity
95 reflected the duration of deliberation. This suggests that the vmPFC signals an option
96 value that integrates expected reward and effort, while the dmPFC signals the effort
97 to invest in the deliberation process. Here, we first test whether this dissociation can
98 be extended to the context of an instrumental learning task (adapted from (Pessiglione
99 et al., 2006), in which cues are probabilistically associated with gain versus loss
100 outcomes. The prediction was that dmPFC activity would reflect response time (RT),
101 while vmPFC activity would represent option values estimated using a reinforcement
102 learning model. We then test the functional interpretation that dmPFC activity reflects
103 effort mobilization, using an incentive motivation task (adapted from (Schmidt et al.,
104 2012), in which participants make either a physical effort (squeezing a handgrip as
105 hard as possible) or a mental effort (doing numerical Stroop comparisons as fast as
106 possible), to maximize gains and minimize losses. The prediction was that dmPFC
107 activity would reflect the amount of exerted effort, estimated using an effort regulation
108 model, irrespective of RT.

109 **Methods**

110 *Subjects*

111 In total, 24 volunteers (13 women), aged 25.9 ± 3.7 years (mean \pm standard deviation)
112 participated in this study, which was approved by the Pitié-Salpêtrière Hospital local
113 ethics committee. Participants were recruited through the online RISC (Relais
114 d'Information en Sciences de la Cognition) platform (<https://www.risc.cnrs.fr/>). All
115 participants were screened for the use of psychotropic medications and for any history
116 of psychiatric or neurologic disorders. The inclusion criteria imposed being right-
117 handed, fluent in French, between 20 and 39 years old, having normal or corrected-
118 to-normal vision, not being pregnant and not wearing tattoos or metallic implants.

119 Participants were told that they would receive a fixed amount of 50€ for their
120 participation, plus an additional bonus between 0 and 25€, depending on cumulative
121 outcomes across tasks and sessions. In practice, all participants were paid the same
122 amount in the end (75€). One participant was excluded from all analyses due to poor
123 performance in all tasks. Another participant was excluded because of excessive
124 movement inside the scanner (>5 mm) in all sessions. The dataset therefore includes
125 a total of 22 participants (12 women), aged 25.6 ± 3.6 years (mean \pm standard
126 deviation). For the pupil data analysis, we had to remove 2 additional subjects because
127 of poor-quality recordings (leaving $n=20$ participants).

128 *Behavioral tasks*

129 Subjects were given both written and oral instructions about the tasks, which were
130 programmed using Psychtoolbox (<http://psychtoolbox.org/>) in Matlab 2012, see scripts
131 at https://github.com/NicolasClairis/value_estimation_vs_effort_mobilization.

132 The learning task employed here (see Figure 1) was similar to that used in previous
133 studies (Pessiglione et al., 2006; Palminteri et al., 2012). Participants were told that,
134 in a given session, they would be confronted to 6 different visual cues (actually letters
135 taken from the Agathodaimon alphabet). They had to find out, by trial and error, which
136 ones they should select in order to maximize their payoff. There were 3 possible
137 outcomes: a gain (+10€), nothing (0€), or a loss (-10€). The 6 cues of a session were
138 grouped in 3 fixed pairs: one associated with gain (winning 10€ or 0€), one with neutral
139 outcomes (0€ always) and one with loss (losing 10€ or 0€). Neutral pairs were useless
140 for learning assessment but were nevertheless maintained to keep the number of cues

141 (hence the level of difficulty) included in the original task. Within each pair, the two
142 cues were associated to the two possible outcomes with reciprocal probabilities
143 (0.75/0.25 and 0.25/0.75). On each trial, one pair was randomly presented on screen.
144 For each pair, the position of the cues on the left versus right side of the screen was
145 counterbalanced across trials within a session. Gain and loss pairs were presented in
146 24 trials each, while neutral pairs only appeared in 12 trials. The 60 trials of a session
147 were divided into 12 mini-blocks comprising two gain, one neutral and two loss trials.
148 The order of conditions (gain, loss, neutral) within each mini-block was randomized.
149 Participants were not informed about the conditions nor about the mini-block structure.

150 Participants completed four sessions of this learning task. The first session served as
151 a training session and was performed on a laptop computer outside the scanner. It
152 was repeated if performance was below 75% of correct choices, or if it appeared that
153 the participant misunderstood the instructions. Each session comprised 3 novel pairs
154 of cues. The associations between cues and outcomes were counterbalanced across
155 participants (except for the training session). Participants were given a 4-button box
156 (fORP 932, Current Designs Inc, Philadelphia, USA) placed under their right hand to
157 make their choices. Once the cues appeared on screen, participants had 3 seconds
158 to press a left button with their index finger for selecting the left option, or a right button
159 with their major finger for selecting the right option. They were asked to keep pressing
160 the button until the selected option appeared in red on the screen. The choice was
161 considered valid only if the button was still being pressed at the end of the 3s delay,
162 otherwise it was considered as a 'miss'. Participants were explained that a missed trial
163 always resulted in the worse possible outcome of a given pair (0€ in the gain and
164 neutral conditions, and -10€ in the loss condition). After the 3s delay, the chosen cue
165 was framed in red and then the outcome (-10€/0€/10€) was displayed on screen. At
166 the end of a session, participants were provided with feedback about their cumulative
167 payoff. In order to maximize payoff, participants learned to choose the most rewarding
168 cue in the gain condition and the less punishing cue in the loss condition.

169 The motor and cognitive performance tasks (i.e., grip and Stroop tasks, Figure 2) were
170 similar to those used in previous studies (Pessiglione et al., 2007; Schmidt et al., 2008,
171 2009, 2012; Meyniel et al., 2013; Vinckier et al., 2022). Participants were told that their
172 goal was to accumulate as much money as possible across trials. Every trial started
173 with a fixation cross displayed at the center of the screen for 500ms. Then, the money

174 at stake for the current trial was displayed as a coin or banknote image for a jittered
175 duration (1 to 4 s), which was either crossed for loss trials or not crossed for gain trials.
176 There were 12 possible incentive levels: -20€, -5€, -1€, -0.5€, -0.2€, -0.01€ in the loss
177 condition and 0.01€, 0.2€, 0.5€, 1€, 5€ or 20€ in the gain condition. Next, a graduate
178 scale appeared on screen, which was the trigger for participants to perform the task
179 (squeezing a handgrip or making numerical comparisons). Each graduation of the
180 scale corresponded to 10% of the monetary incentive. The time window allocated to
181 task performance was 5s for the grip task and 70% of calibration time for the Stroop
182 task (see below). The trial ended by a screen providing feedback on the money gained
183 or lost with the last performance and a cumulative total over all preceding trials of the
184 current task. Feedback display lasted for a randomly jittered duration between 1 and
185 4 seconds.

186 Both motor and cognitive performance tasks comprised 60 trials per session, divided
187 into 5 mini-blocks of 12 trials presenting each incentive level once, in a randomized
188 order. Before scanning sessions, participants were trained on both tasks with a short
189 12-trial version. All tasks were performed with the right hand.

190 In the motor performance task, force was produced on a fMRI-compatible homemade
191 power handgrip that has already been used in previous studies (Meyniel et al., 2013;
192 Schmidt et al., 2009). The handgrip was composed of two plastic cylinders
193 compressing an air tube when squeezed. The tube led to the control room, where it
194 was connected to a transducer converting air pressure into voltage. Thus, grip
195 compression resulted in the generation of a differential voltage signal, linearly
196 proportional to the force exerted. The signal was fed to the stimuli presentation PC via
197 a signal conditioner (CED 1401; Cambridge Electronic Design) and then read inside
198 Matlab. Performance in the scanning sessions was normalized to the maximal force
199 assessed during calibration, when participants were asked to squeeze the handgrip
200 as hard as they could with their right hand. Maximal force was taken as the greatest
201 peak reached over three calibration trials. Unbeknownst to participants, the top of the
202 performance scale (100% of the incentive) in grip task trials was adjusted such that
203 producing the maximal force observed during calibration would correspond to 75% of
204 the incentive (gained or not lost). In case a higher peak was reached during task
205 performance, the new maximal force was used to normalize the scale in the next
206 session. Note that participants could not win more than the full incentive offered in a

207 given trial. During the 5-s performance window, participants could see a bar indicating
208 the instantaneous force being produced on the handgrip. Participants were informed
209 that payoff was based on peak force and not on the duration of squeezing, so they
210 tended to produce short pulses. Because force was measured through air pressure,
211 which can vary within a task session (with temperature for instance), performance was
212 actually calculated as the difference between the peak reached (within the 5-s window)
213 and a baseline signal (mean over the 500-ms fixation cross window), normalized by
214 the maximal force.

215 In the cognitive performance task, participants were shown 10 pairs of digits aligned
216 to the graduations of the scale dividing the incentive into 10% steps. To move up one
217 step, participants had to indicate which digit was numerically higher, by pressing the
218 button on the correct side with their right hand. The digits varied in both their numerical
219 size (between 0 and 9) and their physical size (two possible fonts). In each pair, the
220 two digits had both a different numerical size and a different physical size. Incongruent
221 pairs, where the numerically bigger digit is not the same as the physically bigger digit,
222 are known to generate a Stroop effect (Dadon and Henik, 2017). They therefore
223 require allocation of attention to prevent interference and maintain accurate
224 performance. There were 5 incongruent and 5 congruent pairs in each trial, displayed
225 from bottom to top in a randomized order, the numerical distance between the two
226 digits of a pair being varied from 1 to 5. The time given to participants was based on
227 their performance during calibration. Before scanning sessions, participants
228 performed three calibration trials in which they were to make 10 numerical
229 comparisons as fast as possible. The shortest of the three calibration trials provided a
230 duration that was used similarly to maximal force in the grip task. Unbeknownst to
231 participants, the time window for Stroop task trials was set to 70% of the shortest
232 duration measured during calibration. When participants made an error (pressing the
233 button on the wrong side), digits turned red and the bar was frozen for 10% of the total
234 time window. This time penalty for errors was meant to prevent participants from
235 pressing both buttons at random.

236 Participants were trained on each task before going to the MRI scanner. During fMRI
237 recording, they did 7 task sessions, with learning task in sessions 1, 4 and 7, and
238 performance tasks in sessions 2-3 and 5-6, the order between grip and Stroop tasks
239 being counterbalanced across participants.

240 *Behavioral data analysis*

241 All data were analyzed using MATLAB 2017a (The MathWorks), using scripts that can
242 be found at https://github.com/NicolasClairis/value_estimation_vs_effort_mobilization.
243 Dependent variables were choice (selected cue) and choice RT (from cue onset to
244 button press) in the learning task. In the other tasks, the main dependent variable was
245 performance, defined as the proportion of the incentive gained or not lost in both the
246 grip task (where it corresponds to the proportion of maximal force) and the Stroop task
247 (where it corresponds to the number of numerical comparisons correctly done). RT
248 was defined as the latency at which produced force exceeded 1% of maximal force in
249 the grip task and at which the first button press was made in the Stroop task.
250 Dependent variables were analyzed using general linear models at the individual level
251 followed by t-tests on regression estimates at the group level (as explained in the
252 Results). More specific effects of experimental factors were tested using
253 computational models.

254 *Computational modeling*

255 All computational models were inverted using Matlab VBA toolbox (available at
256 <http://mbb-team.github.io/VBA-toolbox/>), which implements a variational Bayesian
257 algorithm under the Laplace approximation (Daunizeau et al., 2014). The algorithm
258 provides efficient and robust estimates of posterior distributions for the model free
259 parameters, initially defined using Gaussian prior distributions.

260 *Learning task.* Choice behavior was fitted at the individual level using a standard "Q-
261 learning" model (Watkins and Dayan, 1992), as was previously done with this task
262 (Palminteri et al., 2012; Pessiglione et al., 2006). Each cue is associated to a Q-value
263 that represents the expected reward (or punishment) if selected. As participants have
264 no prior information when starting a learning session, all Q-values are initialized at
265 zero. Q-values are then updated after every choice according to a delta rule adapted
266 from the Rescorla and Wagner model:

267
$$Q_{CH}(t + 1) = Q_{CH}(t) + \alpha \cdot (\text{outcome}(t) - Q_{CH}(t)) \quad (1)$$

268 where $Q_{CH}(t)$ is the expected value of the option chosen at trial t , $Q_{CH}(t + 1)$ the
269 expected value of the same option after updating, α a learning rate that adjusts the
270 weight of the last observation relative to older ones, and $\text{outcome}(t)$ coded as 1 in

271 case of gain (+10 €), 0 in case of neutral feedback (0 €), and -1 in case of loss (-10 €).

272 Note that the expression $outcome(t) - Q_{CH}(t)$ corresponds to prediction error, PE_{CH} .

273 To improve the fit, we integrated counterfactual reasoning (Ben-Artzi et al., 2023),

274 using the same equations (with the same parameters) for updating the expected value

275 of the cue that was not chosen. This implies that participants understood, during the

276 training session, that the two cues of a given pair at a given trial yielded opposite

277 outcomes (counterfactual outcome is 0 / 1 if actual outcome is 1 / 0 in the gain

278 condition, and -1 / 0 if actual outcome is 0 / -1 in the loss condition).

279 Q-values were then used to derive the probabilities of selecting each option, according

280 to the softmax formula:

$$281 \quad p(\text{cue}) = \frac{1}{1 + e^{-\frac{DV}{\beta}}} \quad (2)$$

282 where β is a temperature parameter that controls the stochasticity of choices and DV

283 the difference between the value of the considered cue and that of the other cue in the

284 pair.

285 The same parameters α and β were used to fit choices made in all conditions and

286 session. Prior distributions were centered on 0 for α and 1 for β (which was

287 constrained to be strictly positive).

288 *Performance tasks.* In both grip and Stroop tasks, performance was fitted at the

289 individual level using an effort regulation model, as was done previously with similar

290 tasks (Le Bouc et al., 2016; Vinckier et al., 2022). This model is based on the principle

291 that participants exert the amount of effort that maximizes a cost/benefit tradeoff. For

292 each possible effort level, the benefit is the money gained or not lost. The cost is

293 directly proportional to the effort invested, but may increase with fatigue across trials

294 for a same fatigue level. The expected value function EV at a given trial t can be written

295 as:

$$296 \quad EV(E, t) = B(E, t) - C(E, t) \quad (3)$$

297 where $B(E, t)$ and $C(E, t)$ are benefit and cost expected at trial t if investing the amount

298 of effort E .

299 The subcomponents can be decomposed as follows:

300
$$B(E, t) = P(E) + k_I \cdot (P(E) \cdot G(t) + (1 - P(E)) \cdot L(t)) \quad (4)$$

301 where $P(E)$ is the performance expected if investing an amount of effort E , $G(t)$ and
 302 $L(t)$ the signed monetary incentive proposed at trial t ($G=0$ in a loss trial and $L=0$ in a
 303 gain trial). The first term accounts for performance increasing the benefit
 304 independently of financial outcomes (i.e., good performance is intrinsically valuable).
 305 The two other terms allow maximal performance to win the full incentive in gain trials,
 306 and to lose nothing in loss trials. Note that gain and loss terms were normalized to
 307 their maximum (i.e., divided by 20€).

308
$$C(E, t) = k_C \cdot (1 + k_T \cdot t) \cdot E \quad (5)$$

309 where t is the normalized trial number (divided by 60, the total number of trials).

310 The k_X constants are weight parameters that control the sensitivity to the different
 311 factors (incentives and effort cost).

312 Finally, the impact of effort mobilization on performance was defined by a saturation
 313 function such that maximal performance is reached with infinite effort exertion:

314
$$P(E) = \frac{E}{\gamma + E} \quad (6)$$

315 where γ is a (positive) parameter that controls the curvature of the E to P mapping.

316 The optimal effort E^* to be invested in a given trial t is obtained when the derivative
 317 $\frac{dEV}{dE}$ is null, which gives:

318
$$E(t) = \sqrt{\gamma \cdot \frac{1 + k_I \cdot (G(t) - L(t))}{k_C \cdot (1 + k_T \cdot t)}} - \gamma \quad (7)$$

319 From this equation can be derived the optimal performance that represents the model
 320 prediction for trial t

321
$$P(t) = 1 - \sqrt{\gamma \cdot \frac{k_C \cdot (1 + k_T \cdot t)}{1 + k_I \cdot (G(t) - L(t))}} \quad (8)$$

322 All prior distributions were centered on one and all parameters were forced to be
 323 positive. The VBA_toolbox allowed us to obtain, for a given participant, the set of
 324 posterior means k_I , k_C , k_T and γ with which the model best matches the observed
 325 pattern of performance across trials. The two sessions of the same task were modeled

326 with the same parameters, but motor and cognitive performance tasks were modeled
327 with different sets of parameters.

328 *MRI data acquisition*

329 Magnetic Resonance Imaging (MRI) was performed at the research neuroimaging
330 center (CENIR) with a Siemens Magnetom Prisma 3-T scanner using a 64-channel
331 head/neck coil. Structural T1-weighted images were co-registered to the mean echo
332 planar image (EPI), segmented and normalized to the standard T1 template and then
333 averaged across subjects for anatomical localization of group-level functional
334 activation. Functional T2*-weighted EPIs were acquired with blood-oxygen-level
335 dependent (BOLD) contrast using the following parameters: repetition time TR = 1.10
336 seconds, echo time TE = 25ms, flip angle = 60°, number of slices = 54, slice thickness
337 = 2.0mm, field of view = 208mm, multiband accelerating factor: 3, voxel size: 2x2x2
338 mm. Note that the number of volumes per session was not predefined, because the
339 time available for performance in the Stroop task varied across individuals. Volume
340 acquisition was just stopped when the task session was completed. The number of
341 volumes per session (mean±SD) was 369±5 in the learning task, 565±58 in the Stroop
342 task, 592±6 in the grip task. Across participants, the total duration was between 17
343 and 27 minutes for the 3 sessions of the learning task, the 2 sessions of the grip task
344 and the 2 sessions of the Stroop task.

345 *fMRI data analysis*

346 Functional images were preprocessed and analyzed using the SPM12 toolbox
347 (Wellcome Trust Center for NeuroImaging) running in MATLAB 2017a. Preprocessing
348 consisted of spatial realignment, normalization using the same transformation as
349 structural images, and spatial smoothing using a Gaussian kernel with a full width at
350 half maximum (FWHM) of 8 mm.

351 Preprocessed data were analyzed using generalized linear models (GLM) in SPM12
352 at the first (individual) level and then tested for significance at the second (group) level.
353 All GLM included the 6 movement regressors generated during realignment of
354 successive scans. Each task session was modeled separately.

355 For the learning task, the main GLM (GLM1) included a boxcar function encompassing
356 the choice period (from cue onset to the end of the 3-s window), modulated by the
357 following parametric regressors: (1) value (Val), (2) confidence (Conf), (3) deliberation

358 time (DT). Val was defined as the sum of cue values weighted by their choice
359 probabilities ($p_{CH} \cdot Q_{CH} + p_{UC} \cdot Q_{UC}$), which has been referred to as state value in the
360 reinforcement learning framework (e.g., (Palminteri et al., 2009). Following on our
361 previous publication (Clairis and Pessiglione, 2022), Conf was defined as the squared
362 distance from choice probability to chance level, normalized to a 0-1 range
363 (*i. e.*, $[2(p(left) - 0.5)]^2$). This is equivalent to taking the squared difference in choice
364 probability between the left and right options (*i. e.*, $[(p(left) - p(right))]^2$). DT was
365 defined as the duration from cue onset to the start of button pressing. Gain and loss
366 pairs of cues were modeled in a same regressor, but neutral pairs were modeled
367 separately, with DT as a single parametric modulation, and were not included in the
368 following analyses. The GLM also included a boxcar function encompassing the period
369 from chosen option to outcome onset, and a stick function for the outcome itself,
370 modulated by the prediction error generated by the model (PE_{CH}).

371 All regressors of interest were z-scored and convolved with the canonical
372 hemodynamic response function (HRF). Parametric modulators were not
373 orthogonalized in the main GLM so that they could compete for explaining the variance
374 of fMRI time series. Several alternative GLM were built to test variants of GLM1. Two
375 GLM were identical to GLM1, except that all regressors were serially orthogonalized,
376 in either the Val/Conf/DT (GLM2) or the DT/Conf/Val (GLM3) order. Two other GLM
377 were identical to GLM1, except that Val was defined as the sum of option values
378 ($Q_{CH} + Q_{UC}$) in GLM4 and the difference between the chosen and unchosen option
379 values ($Q_{CH} - Q_{UC}$) in GLM5.

380 For the performance tasks, the main GLM (GLM1) included a stick function for
381 incentive onset, modulated by the following regressors (not orthogonalized): (1) the
382 optimal effort E^* generated by our computational model and (2) reaction time (RT).
383 The performance time window (from scale onset to feedback display) was also
384 modeled as a boxcar function, and the feedback onset as a stick function. As done for
385 the learning task, we tested alternative GLM identical to GLM1, except that the two
386 parametric regressors were orthogonalized, either in the E^*/RT order (GLM2) or the
387 RT/E^* order (GLM3). A last alternative to GLM1 was built (GLM4) where, instead of
388 modulating the time of incentive onset, E^* and RT (not orthogonalized) were
389 modulating the performance time window.

390 Note that images at the individual-level analysis were masked following the default
391 SPM procedure, which removes any voxel with a signal intensity below 20% of the
392 global mean, to exclude voxels outside the brain for group-level analyses. We verified
393 that our main conclusions were still valid when using a white+grey matter mask
394 (including all voxels with a probability to be in either grey or white matter above 5%,
395 based on the average anatomical segmentation performed by SPM). Uncorrected
396 maps obtained with this more inclusive mask can be found in Neurovault at the
397 following repository address: <https://neurovault.org/collections/15543/>.

398 For the maps shown in the figures, we used an additional medial PFC (mPFC)
399 inclusive mask (see Extended Data Figure 4-1) based on the aggregation of
400 supplementary motor area, anterior and mid-cingulate area, gyrus rectus, middle
401 frontal gyrus and superior frontal medial gyrus from the AAL atlas (Tzourio-Mazoyer
402 et al., 2002). This masking procedure just filtered the voxels within the mPFC and was
403 only used for display purposes; it did not impact statistical results, which were always
404 calculated across the whole brain. In all figures and tables, the statistical threshold
405 was set at $p < 0.001$ uncorrected at the voxel level and $p < 0.05$ family-wise error
406 corrected for multiple comparisons at the cluster level. We defined our regions of
407 interest as 8mm-radius spheres centered on the MNI coordinates of group-level
408 clusters associated with Val (-10; 48; -12), Conf (-8; 52; 18) and DT (10; 12; 48) in our
409 previous study (see Figure 3A). Violin plots were generated using the *violinplot* Matlab
410 function developed by Bastian Bechtold (<https://github.com/bastibe/Violinplot-Matlab>,
411 doi: 10.5281/zenodo.4559847).

412 *Pupil size*

413 Pupil diameter was recorded at a sampling rate of 1 kHz, using an EyeLink 1000 plus
414 (SR Research) eye-tracker. The eye-tracker was calibrated before the start of fMRI
415 sessions, once the subject was positioned inside the scanner. Interpolation was
416 performed with Matlab *interp1* function, which implements the *pchip* cubic interpolation
417 method to compensate for any period of time when the pupil signal was lost because
418 of blinks. The pupil size time series were subsequently band-pass filtered (1/128-1 Hz)
419 and z-scored per individual and per session.

420 Within-trial variations in pupil size were baseline-corrected by removing the mean
421 signal over the 200ms preceding stimulus onset and time-locked to stimulus onset.

422 Then trial-wise variations in pupil size were fitted separately for the grip and for the
423 Stroop task with a linear regression model that included factors of no interest (an
424 intercept per block and stimulus luminance) and variables of interest (the effort E and
425 the reaction time RT). Within-trial individual time series of regression estimates were
426 then smoothed using a 200ms kernel. Group-level significant time clusters were
427 identified after correction for multiple comparisons estimated according to random field
428 theory, as implemented in the VBA toolbox (available at [http://mbb-
429 team.github.io/VBA-toolbox/](http://mbb-team.github.io/VBA-toolbox/)). To complement this analysis, we also averaged the
430 betas over a 5-second period following stimulus onset for each individual, and then
431 performed a one-sample t-test against zero at the group-level.

432 **Results**

433 *Behavior in the learning task*

434 Participants (n=22) performed three sessions of a probabilistic instrumental learning
435 task (Figure 1). They learned to select cues with high gain probability (75%) and low
436 loss probability (25%), reaching an average correct choice of $88.51 \pm 2.98\%$ in the gain
437 condition and $80.13 \pm 2.15\%$ in the loss condition (Figure 3A), which was significantly
438 above chance level in both cases ($p = 2 \cdot 10^{-11}$ and $p = 4 \cdot 10^{-12}$, respectively). Learning
439 curves were fitted using a standard Q-learning algorithm (with a balanced accuracy of
440 0.706 ± 0.018), the two free parameters being adjusted individually (0.130 ± 0.015 for
441 the learning rate α and 0.164 ± 0.017 for the choice temperature β). We used the cue
442 values and choice probabilities provided by the fitted model to generate the constructs
443 that we regressed against fMRI data. At each trial, value (Val) was defined as the sum
444 of cue values weighted by choice probabilities, and confidence (Conf) as the squared
445 difference between choice probability and chance level (0.5). Note that, by design
446 (Figure 3B), Val and Conf were partially decorrelated in this task ($r = 0.204 \pm 0.009$),
447 because while Conf always increased across trials (with learning), Val increased in the
448 gain condition but decreased in the loss condition. There was also a modest but
449 significant correlation between deliberation time (DT) and Val ($r = -0.464 \pm 0.022$), due
450 to faster responses in the gain relative to loss condition, and between DT and Conf (r
451 $= -0.257 \pm 0.032$), due to speed and accuracy improvement across trials in both
452 conditions. Indeed, linear regression (Figure 3C) showed that DT was shorter both
453 when Val was higher ($\beta_{\text{Val}} = -0.452 \pm 0.039$, $p = 1 \cdot 10^{-10}$) and when Conf was higher
454 ($\beta_{\text{Conf}} = -0.858 \pm 0.241$, $p = 0.0018$). Together, Val and Conf explained $32.01 \pm 2.14\%$ of
455 the variance in DT, which may call for orthogonalization of these regressors (see
456 below).

457 *Neural activity in the learning task*

458 As in our previous study (Clairis and Pessiglione, 2022), whole-brain maps (corrected
459 for multiple comparisons) revealed a functional partition between the ventromedial,
460 midmedial and dorsomedial regions of the prefrontal cortex (vmPFC, mmPFC and
461 dmPFC), which respectively reflected the Val, Conf and DT constructs (Figure 4A).
462 There was no negative association with any of these constructs that would survive
463 correction at the whole-brain level. We systematically tested the links between all three

464 variables and all three regions of interest defined using the previous dataset to avoid
465 non-independence issues (Figure 4B). The same 3 correlations were observed
466 between Val and vmPFC activity ($\beta = 0.297 \pm 0.101$; $p = 0.008$), between Conf and
467 mmPFC activity ($\beta = 0.252 \pm 0.073$; $p = 0.002$) and between DT and dmPFC activity (β
468 $= 0.321 \pm 0.065$; $p = 7 \cdot 10^{-5}$). All 3 correlations remained significant (Extended Data
469 Figure 4-2) when orthogonalizing regressors, whatever the order (Val/Conf/DT in
470 GLM2 or DT/Conf/Val in GLM3). We note however that the orthogonalization might
471 have generated spurious correlations. Indeed, when Val was orthogonalized to DT,
472 the correlation between DT and vmPFC activity became significant, and reciprocally,
473 when DT was orthogonalized to Val, the correlation between Val and dmPFC activity
474 became significant. This is likely due to Val and DT sharing some common variance,
475 which was attributed to one regressor or the other, depending on the order of serial
476 orthogonalization. Apart from the 3 main ROI-variable associations, we also observed
477 a correlation between Conf and vmPFC activity ($p < 0.001$ in all GLM). Beyond the
478 medial prefrontal cortex, significant correlation with DT (after cluster-wise correction
479 for multiple comparisons) was observed in several other brain regions (see Extended
480 Data Table 4-6), including the anterior insula and dorsolateral PFC, two brain regions
481 classically involved in exerting effort and/or cognitive control.

482 While the link between vmPFC activity and subjective value is well established, there
483 is still some debate about what values exactly are represented during a binary choice.
484 We have therefore regressed vmPFC activity against alternative GLM in which the
485 weighted sum of option values (GLM1) was replaced either by the straight sum (GLM4)
486 or the difference between chosen and unchosen option values (GLM5). Significant
487 regression estimates (see Extended Data Figure 4-3) were observed with the sum
488 (GLM4: $\beta = 0.284 \pm 0.098$; $p = 0.009$), but not with the difference (GLM5: $\beta =$
489 0.132 ± 0.115 ; $p = 0.263$). We kept the weighted sum regressor because it explained
490 more variance in vmPFC activity (GLM1: $\beta = 0.297 \pm 0.101$; $p = 0.008$), but we conclude
491 that any regressor modeling a positive correlation with option values would also
492 provide a significant fit.

493 *Behavior in the performance tasks*

494 Between learning sessions, participants performed two sessions of the motor and
495 cognitive performance tasks (Figure 2). These tasks required the allocation of either
496 force (grip task) or attention (Stroop task) in order to maximize the monetary payoff,

497 which depended on both the incentive level and the performance achieved in a
498 particular trial. We verified that, as intended, performance improved with incentive
499 level (Figure 5) in both grip and Stroop tasks, and both gain and loss conditions.
500 Indeed, higher performance was achieved when unsigned incentives (*i.e.* stakes),
501 were greater in both the grip task ($\beta_{||} = 1.164 \pm 0.128$; $p = 9 \cdot 10^{-9}$) and the Stroop task
502 ($\beta_{||} = 0.190 \pm 0.053$; $p = 0.0016$). This effect of incentive motivation on performance
503 was similar in gain and loss trials. Also, performance decreased with trial number in
504 both the grip task ($\beta_{\tau} = -0.125 \pm 0.033$; $p = 0.0011$) and the Stroop task ($\beta_{\tau} = -$
505 0.077 ± 0.021 ; $p = 0.0015$), probably reflecting the emergence of fatigue. This pattern
506 was not observed with response time (RT), defined as the start of force production in
507 the grip task and first button press in the Stroop task (Figure 5). Although not significant
508 in all cases, the trend was the opposite: RT tended to be shorter with higher incentive
509 levels (grip: $\beta_{||} = -0.0030 \pm 0.003$; $p = 0.331$; Stroop: $\beta_{||} = -0.0035 \pm 0.0009$; $p = 8 \cdot 10^{-4}$),
510 and longer with higher trial number (grip: $\beta_{\tau} = 0.0016 \pm 0.0007$; $p = 0.041$; Stroop: $\beta_{\tau} =$
511 0.0007 ± 0.0004 ; $p = 0.075$).

512 To fit performance, we developed a computational model (see Methods) adapted from
513 previous studies using similar tasks (Le Bouc et al., 2016; Vinckier et al., 2022). The
514 model with fitted parameters was then used to generate the best possible proxy for
515 the effort invested in motor and cognitive performance, so we could use it to identify
516 the underlying neural activity.

517 *Neural activity in the performance tasks*

518 Whole-brain maps (corrected for multiple comparisons) highlighted dmPFC as
519 showing a positive association between activity triggered by incentive display and the
520 optimal effort E^* that was estimated by the computational model fitted to the behavioral
521 data. This was true across motor and cognitive performance tasks, as it was significant
522 in a conjunction analysis (Figure 6). Several other significant clusters (see Extended
523 Data Table 6-2) were observed outside the medial prefrontal cortex in this conjunction
524 analysis (even after voxel-wise correction for multiple comparisons), notably in the
525 striatum, a brain region that has been involved in incentive motivation. There was no
526 negative association with effort E^* that would survive correction at the whole-brain
527 level. When testing the dmPFC ROI identified in our previous study (Clairis and
528 Pessiglione, 2022), activity at incentive display was correlated with E^* in both grip and
529 Stroop tasks (Figure 6, both $p < 0.005$). Note that RT did not yield any significant

530 positive correlation in whole-brain analysis ($p < 0.001$, uncorrected for multiple
531 comparisons) when pooling grip and Stroop tasks together. Moreover, the correlation
532 with E^* (but not RT) also held when variables were orthogonalized in serial order
533 (Extended Data Figure 6-1), either following the E^*/RT order (GLM2) or the RT/E^*
534 order (GLM3). Also, when replacing E^* by unsigned incentive level, regression
535 coefficients were significantly lower ($\beta = 1.850 \pm 0.273$ vs. 1.952 ± 0.266 ; $p = 0.0235$),
536 indicating that dmPFC activity better reflected effort than stakes. In GLM4, which
537 focuses on the performance time window (squeezing the handgrip or making
538 numerical comparisons), the association between dmPFC activity and optimal effort
539 E^* was no longer significant (grip task: $b = 0.009 \pm 0.055$; $p = 0.868$; Stroop task: $b = -$
540 0.083 ± 0.078 ; $p = 0.299$), suggesting that dmPFC activity was reflecting an antecedent
541 more than a consequence of effort exertion.

542 *Pupil dilation in the performance tasks*

543 As another marker of effort exertion, we investigated pupil dilation in the grip and
544 Stroop task (Figure 7). Over the 0-5s time window, the correlation with pupil diameter
545 was globally positive for optimal effort E^* (grip: $\beta_{E^*} = 0.094 \pm 0.038$, $p = 0.022$; Stroop:
546 $\beta_{E^*} = 0.042 \pm 0.031$, $p = 0.184$) and negative for RT (grip: $\beta_{RT} = -0.069 \pm 0.017$, $p =$
547 $6 \cdot 10^{-4}$; Stroop: $\beta_{RT} = -0.072 \pm 0.013$, $p = 3 \cdot 10^{-5}$). In the grip task, pupil size was
548 significantly correlated (after correction for multiple comparisons) with effort E^* from
549 3.11s to 6.26s following scale onset. The trend was similar in the Stroop task but there
550 was no time point at which correlation between E^* and pupil size would survive
551 correction for multiple comparisons. Nevertheless, these results support the notion
552 that more effort is associated to shorter RT in these performance tasks, in contrast
553 with what was observed in the deliberation tasks (i.e., during rating, choice and
554 learning).

555 *Conjunction across learning and performance tasks*

556 Finally, we tested the conjunction between activity associated with DT in the learning
557 task and E^* in the grip and Stroop tasks. The conjunction was significant in a dmPFC
558 cluster (Figure 8A), together with clusters in the anterior insula and dorsolateral PFC
559 (Extended Data Table 8-1). Thus, the same dmPFC region reflected the time invested
560 in deliberation and the effort invested in motor and cognitive performance. We also
561 overlapped this dmPFC cluster with the dmPFC cluster associated with DT in our

562 previous study (Clairis and Pessiglione, 2022). The overlap (Figure 8B) confirmed that
563 a common dmPFC region was also reflecting the time invested in expressing
564 preference (during rating and choice tasks). Together, these results support the
565 implication of the dmPFC in effort mobilization across preference, learning and
566 performance tasks.

567 **Discussion**

568 In this study, we first replicate, in the context of instrumental learning, the functional
569 partition of the mPFC that was initially demonstrated across choice and rating tasks
570 (Clairis and Pessiglione, 2022). When values are generated by a reinforcement
571 learning model, instead of expressed as subjective preferences, we still observe that
572 option values (Val), choice confidence (Conf) and deliberation time (DT) are
573 respectively reflected in the activity of vmPFC, mmPFC and dmPFC during decision-
574 making. We then strengthen our functional interpretation of the correlation with DT as
575 signaling effort mobilization, in performance tasks where participants maximize a
576 tradeoff between reward prospect and effort cost. During preparation of both motor
577 and cognitive performance, we find that dmPFC activity reflects the optimal effort to
578 be exerted according to an effort regulation model.

579 The functional partition was based on a theoretical analysis of judgment and decision
580 processes. In brief, we argue that what is maximized in rating and choice tasks is the
581 confidence in the eventual response (Lebreton et al., 2015; Lee and Daunizeau, 2021).
582 Thus, on top of the first-level decision process that estimates option values, a second-
583 level metacognitive process arbitrates the tradeoff between an expected gain in
584 confidence and the time invested in deliberation. There is therefore a need for
585 representing these three types of variables in brain activity. A difficulty for the
586 dissociation of these variables in the analysis of fMRI data is that they are more or less
587 correlated, depending on the task. Here, we take advantage of gain and loss
588 conditions to decorrelate value and confidence: while confidence increases across
589 trials with learning, values increase in the gain condition but decrease in the loss
590 condition. To infer both value and confidence from choice behavior, we use a classical
591 reinforcement learning model that was already validated as providing a good account
592 of choice behavior in this task (Palminteri et al., 2012; Pessiglione et al., 2006). We
593 find option value representations in more ventromedial regions, and choice confidence
594 representations in more dorsomedial regions. This is reminiscent of the dissociation
595 previously reported (Clairis and Pessiglione, 2022), where confidence was
596 decorrelated from the option value (in rating tasks) or the sum of option values (in
597 choice tasks). It is also consistent with previous demonstration that value-to-
598 confidence representation follows a ventral-to-dorsal gradient in the PFC (De Martino
599 et al., 2017).

600 The dissociation observed here is only partial, as activity in our ventromedial ROI is
601 significantly associated with both option values and choice confidence. Although the
602 vmPFC has been identified in meta-analyses of fMRI studies as a valuation hub
603 (Bartra et al., 2013; Clithero and Rangel, 2014), it has also been shown to signal
604 confidence in non-valuation tasks (e.g., (Gherman and Piliastides, 2018; Rouault et
605 al., 2023)). A similar overlap of value and confidence representations in the vmPFC
606 has been reported in previous fMRI studies using both rating and choice tasks (De
607 Martino et al., 2012; Lebreton et al., 2015; Shapiro and Grafton, 2020). This is also
608 consistent with a MEG study that observed both the sum and difference of option
609 values being reflected in the vmPFC low-frequency activity (Hunt et al., 2012),
610 because our confidence construct is close to the difference between chosen and
611 unchosen option values. Unsurprisingly, many studies have reported correlations
612 between vmPFC activity and chosen option value, which is correlated with both the
613 sum and the difference (e.g., (Baram et al., 2021; Gershman et al., 2009; Gläscher et
614 al., 2009; Seaman et al., 2018; Wunderlich et al., 2009)). The correlation with value
615 difference is inconsistent studies, being significant in some (Boorman et al., 2009;
616 Chau et al., 2014) but not in others (Jocham et al., 2014; Lim et al., 2011; Lopez-
617 Persem et al., 2016; Qin et al., 2011; Ting et al., 2023; Van der Laan et al., 2012). We
618 suspect that the issue might relate, at least in some cases, to the potential confound
619 between value difference and choice confidence. Indeed, when comparing different
620 combinations of option values, we observe that vmPFC activity correlates with either
621 the straight sum or the sum weighted by choice probability, but not with the difference
622 (when included together with confidence in a same GLM).

623 Yet the correlation with the sum does not tell whether the vmPFC signals the overall
624 value of the option set, as previously suggested (Shenhav and Karmarkar, 2019), or
625 the value of each option, independently. The sum of option values weighted by their
626 choice probability could represent a state value, as defined in reinforcement learning
627 theory (Sutton and Barto, 1998), but also a succession of option value estimates
628 modulated by attention, as proposed in some versions of sequential sampling models
629 (Krajbich et al., 2010). A time-resolved recording technique, such as intracerebral
630 EEG, coupled with an eye-tracking device, might help address this issue. Finally, we
631 acknowledge that the identification of confidence representation is limited by the
632 absence of trial-by-trial confidence rating, which would have provided a finer

633 estimation than the approximation generated by our model. The function that we use
634 here is clearly not the only one possible, but it was previously validated as an accurate
635 proxy for how confidence ratings vary with option values, on average (Clairis and
636 Pessiglione, 2022).

637 Contrary to value and confidence, we find correlates of DT in the dorsomedial part of
638 the prefrontal cortex. This is a direct replication of the correlation previously observed
639 in rating and choice tasks (Clairis and Pessiglione, 2022) and also reported in several
640 fMRI studies (e.g., (Grinband et al., 2011; McGuire and Botvinick, 2010; Wu et al.,
641 2018). Because DT is correlated with both value and confidence in our task, we have
642 tested whether GLMs with and without orthogonalization would account for dmPFC
643 activity. The Val-vmPFC and DT-dmPFC associations are significant whether or not
644 regressors are orthogonalized, and whatever the order of orthogonalization. Yet the
645 correlation cannot tell whether dmPFC activity reflects some relevant cognitive
646 variable that would determine DT, such as the presence of conflict (Yeung et al., 2011)
647 or the need for cognitive control (Shenhav et al., 2013). Indeed, variations in RT are
648 susceptible to many factors (such as distraction, fatigue or mind wandering) that may
649 induce changes in dmPFC activity. Alternatively, the increase in dmPFC activity with
650 DT might not reflect a cognitive antecedent but a by-product of any process lasting
651 longer (Alexander and Brown, 2011; Grinband et al., 2011; Weissman and Carp,
652 2013).

653 We therefore test our initial interpretation that the correlation with DT denotes a
654 representation of the effort invested in deliberation, across two other tasks assessing
655 motor and cognitive performance (grip force production and Stroop numerical
656 comparison). Although incentives are varied to manipulate motivation, these tasks do
657 not involve proper valuation processes, because coins and banknotes have an
658 obvious monetary value. There is no clear need for an estimation of confidence either,
659 because there is no uncertainty in how much reward each performance level would
660 bring (this is explicitly indicated on the screen). We therefore dropped the value and
661 confidence constructs and focused on effort mobilization. The amount of effort exerted
662 can be inferred from behavioral performance by fitting a computational model that was
663 previously validated using the same tasks (Le Bouc et al., 2023; Vinckier et al., 2022).
664 Here, we further validate the theoretical effort output by the model as being positively
665 associated with pupil dilation, which can arguably be considered a measure of physical

666 and mental effort exertion (Hess and Polt, 1964; Kahneman and Beatty, 1966; van der
667 Wel and van Steenbergen, 2018; Zénon et al., 2014).

668 Critically, dmPFC activity reflects this effort proxy but not RT, during the preparation
669 period but not during effort exertion. This result provides a strong argument for the
670 idea that dmPFC activation is not a mechanical by-product of RT prolongation but a
671 reflection of effort mobilization for the upcoming task. This idea might be more general
672 than triggering cognitive control, since the association between the effort proxy and
673 dmPFC activity was observed for both motor and cognitive performance. It is
674 consistent with previous observations that reward and effort are both represented in
675 dmPFC activity (often called dACC), whatever the types of reward and effort (Le Bouc
676 et al., 2022; Pessiglione et al., 2018; Shenhav et al., 2013). Finally, the conjunction
677 between preference, learning and performance tasks shows that the same dmPFC
678 cluster reflects DT during decision and theoretical effort during motor and cognitive
679 preparation. We cannot rule out that the correlation with DT and E^* might arise while
680 the dmPFC cluster would still serve different functions in the different tasks, but a more
681 parsimonious interpretation would involve the dmPFC in mobilizing effort in all tasks,
682 as suggested by a recent meta-analysis of fMRI studies (Lopez-Gamundi et al., 2021).

683 In conclusion, we provide here evidence that implicate ventromedial regions of the
684 PFC in the estimation of option value and response confidence, and dorsomedial
685 regions in the adjustment of effort mobilization for an appropriate performance. These
686 results extend previous findings and thereby contribute to establishing functional
687 specifications of brain regions that are robust across a variety of behavioral tasks.
688 However, many questions remain unaddressed. Notably, we have dissociated the
689 neural representations of value, effort, and confidence, but have not brought any
690 insight into the mechanisms that must link these representations, such that investing
691 effort would enable refining value estimates to gain confidence in the response. Also,
692 we have used a computational definition of effort mobilization, but have not contributed
693 to elucidating what effort might represent at the biological level. It could be related to
694 autonomic arousal, given the link observed with pupil dilation, and the known
695 connections between dmPFC regions and the autonomic nervous system (Amiez and
696 Procyk, 2019; Beissner et al., 2013; Critchley et al., 2003). It could also be related to
697 metabolic support within the brain, as suggested by studies that examined the cost of
698 cognitive effort (Holroyd, 2016; Wiehler et al., 2022; Zénon et al., 2019). Further

699 research is needed to bridge the informational and biophysical notions of effort
700 mobilization.

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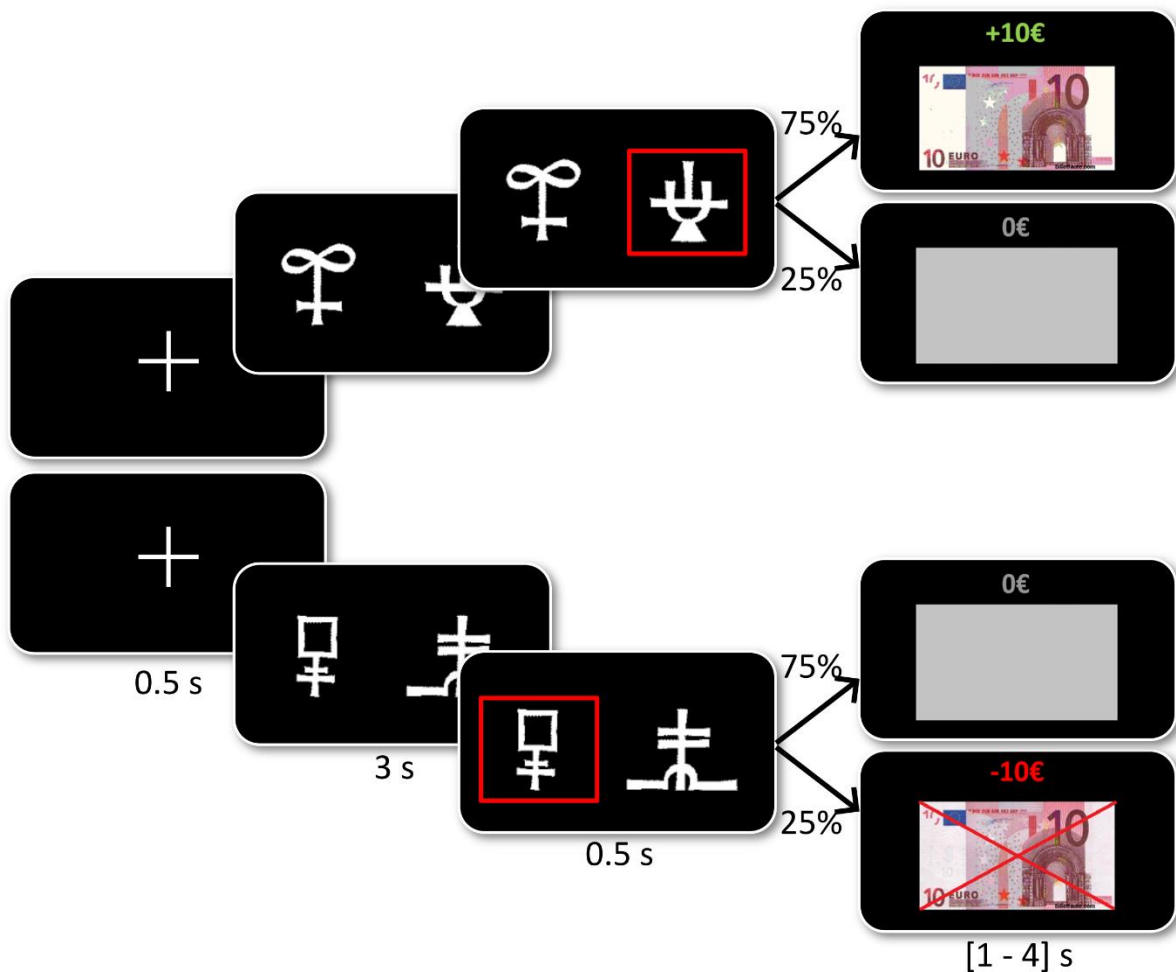
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1031 **Figures**

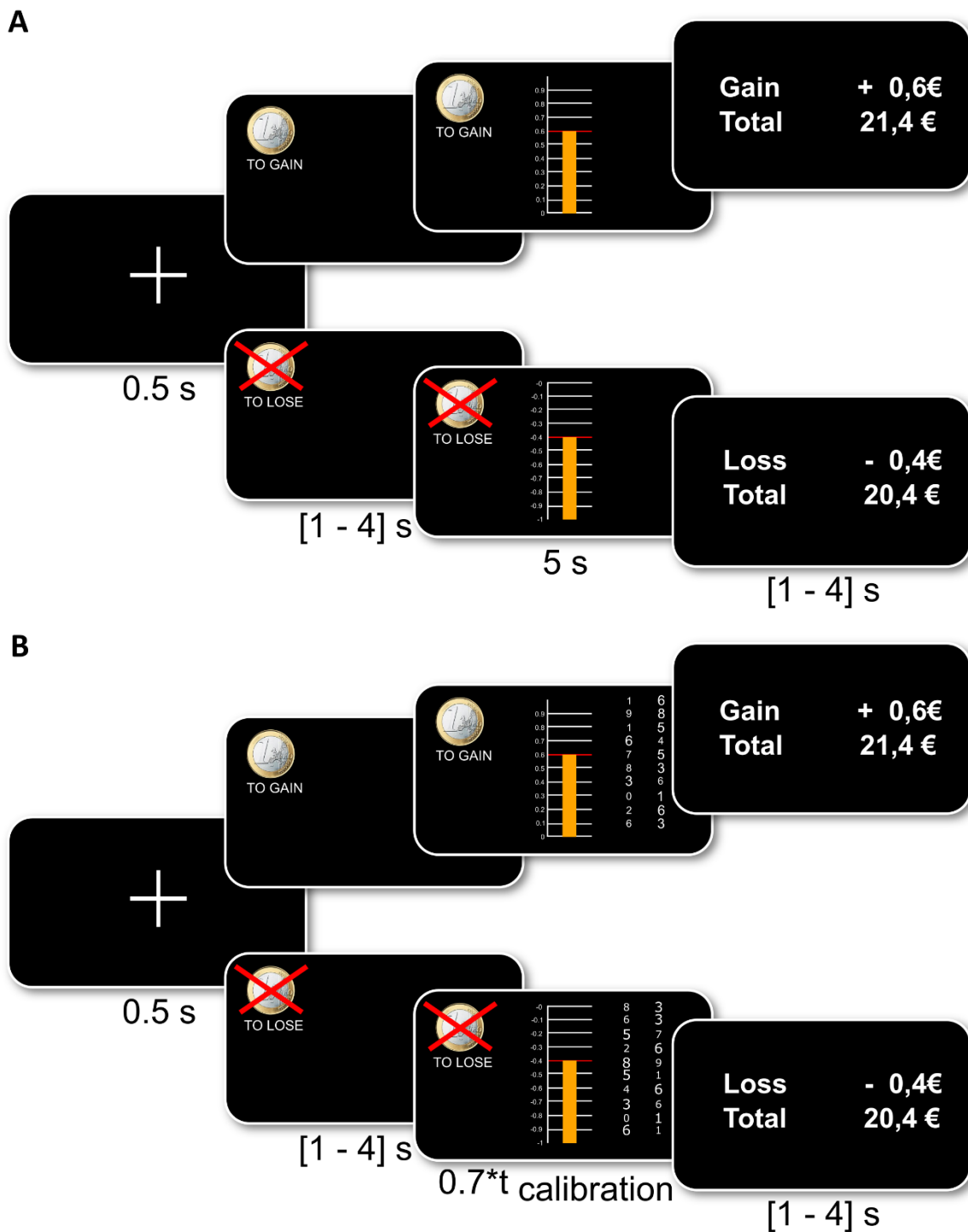
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1034 **Figure 1. The learning task.**

1035 Screenshots presented in example trials are presented from left to right, with their duration in
1036 seconds indicated below. Every trial started with the display of a fixation cross. Participants
1037 chose between two visual cues and then observed the outcome of their choice. In a given
1038 learning session, there were only 6 cues always displayed in pairs. The gain pair provided
1039 either a reward or a neutral outcome, with different probabilities (25/75 or 75/25%) depending
1040 on which cue was chosen (top row). The loss pair provided either a neutral outcome or a loss
1041 outcome, with different probabilities (25/75 or 75/25%) depending on which button (left versus right) was being
1042 pressed. In the examples, choices are correct (selected cues are associated with 75%
1043 probability of winning / not losing). The choice was recorded and shown on screen (with red
1044 frame) at the end of a fixed 3-s delay, depending on which button (left versus right) was being
1045 pressed. Outcomes (10€ banknote for gain, grey rectangle for zero, crossed 10€ banknote for
1046 loss) were last presented on screen with a jittered duration.



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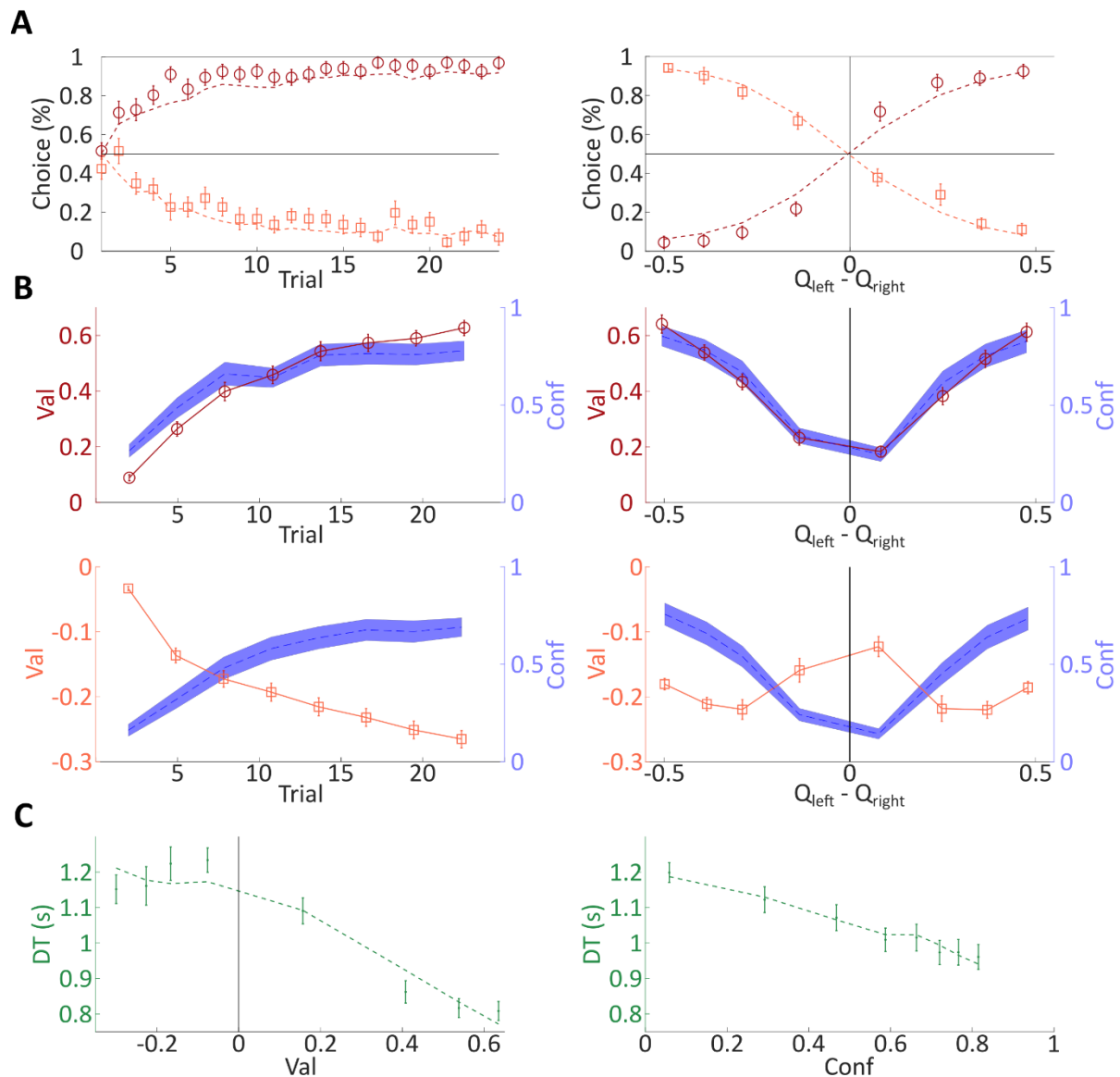
1048 **Figure 2. The performance tasks (grip and Stroop).**

1049 Screenshots presented in example trials are presented from left to right, with their duration in
 1050 seconds indicated below. Every trial started with the display of a fixation cross. Then the
 1051 incentive (among 6 possible amounts: 0.01, 0.20, 0.50, 1.00, 5.00, or 20.00€) was displayed
 1052 with a cue for the condition (gain vs. loss trial). Real-time visual feedback on performance was
 1053 provided as a bar that moved up within a scale graduated from 0 to maximum. In gain trials,
 1054 participants received a fraction of the incentive proportional to their performance (e.g., 60
 1055 cents if they reached 60% of the scale for a 1€ incentive). In loss trials, participants avoided
 1056 losing the fraction of the incentive proportional to their performance (i.e., they would only lose

1057 40 cents in the example as they reached 60% of the scale). The money gained or lost in the
1058 current trial, and the cumulative total over all preceding trials, were shown in a last screen.

1059 A] The grip task. Participants had to squeeze the handgrip as hard as they could. Performance
1060 was defined as the peak of the force pulse, expressed as a percentage of maximal force
1061 produced during calibration. The scale was adjusted such that the participant's maximal force
1062 corresponded to 75% of the incentive.

1063 B] The Stroop task. Participants had to make as many numerical comparisons as they could,
1064 starting with the first pair of digits at the bottom. Performance was the number of correct
1065 numerical comparisons made within a predefined time window (70% of the time taken to
1066 complete all 10 comparisons during calibration). Note that in half the pair of digits, font size
1067 and numerical size were incongruent, creating a Stroop effect.



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1070 Figure 3. Behavior in the learning task.

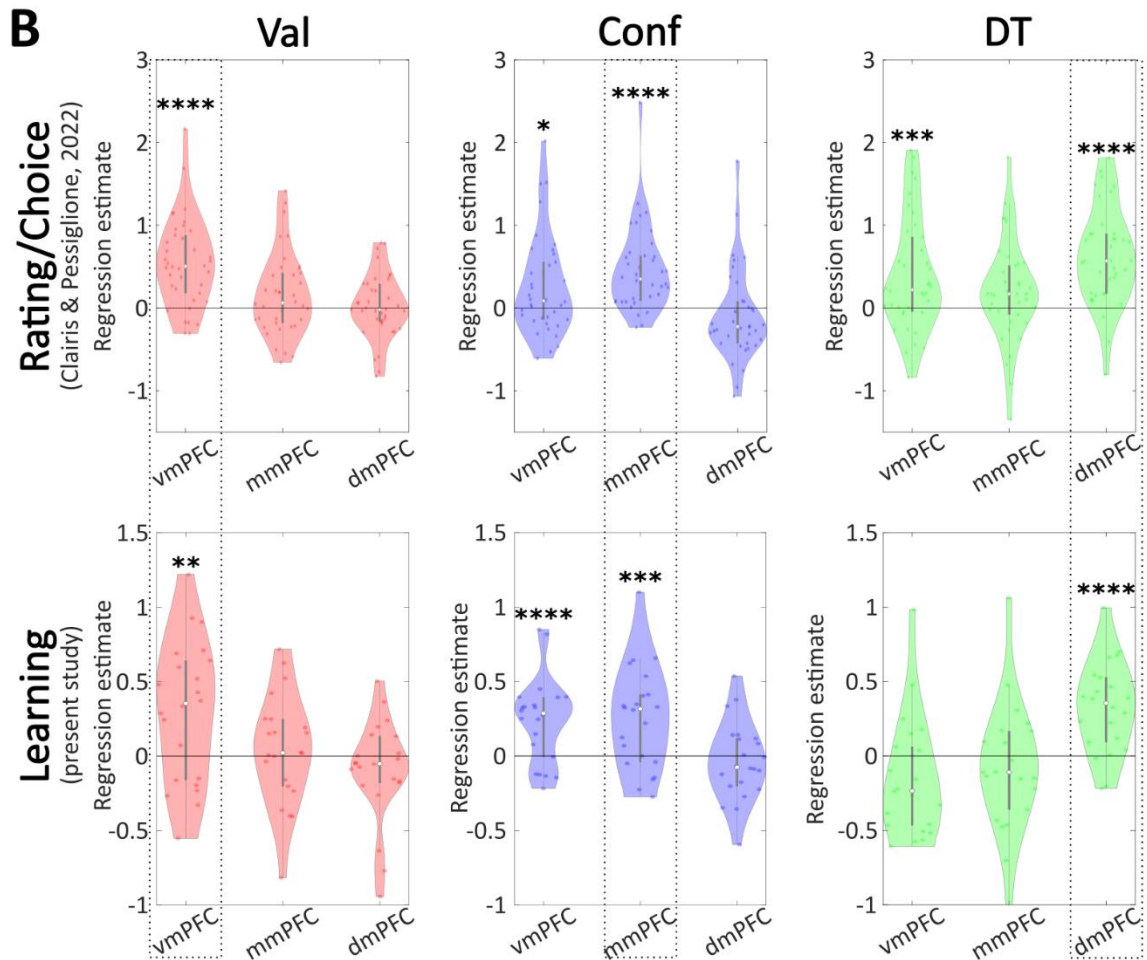
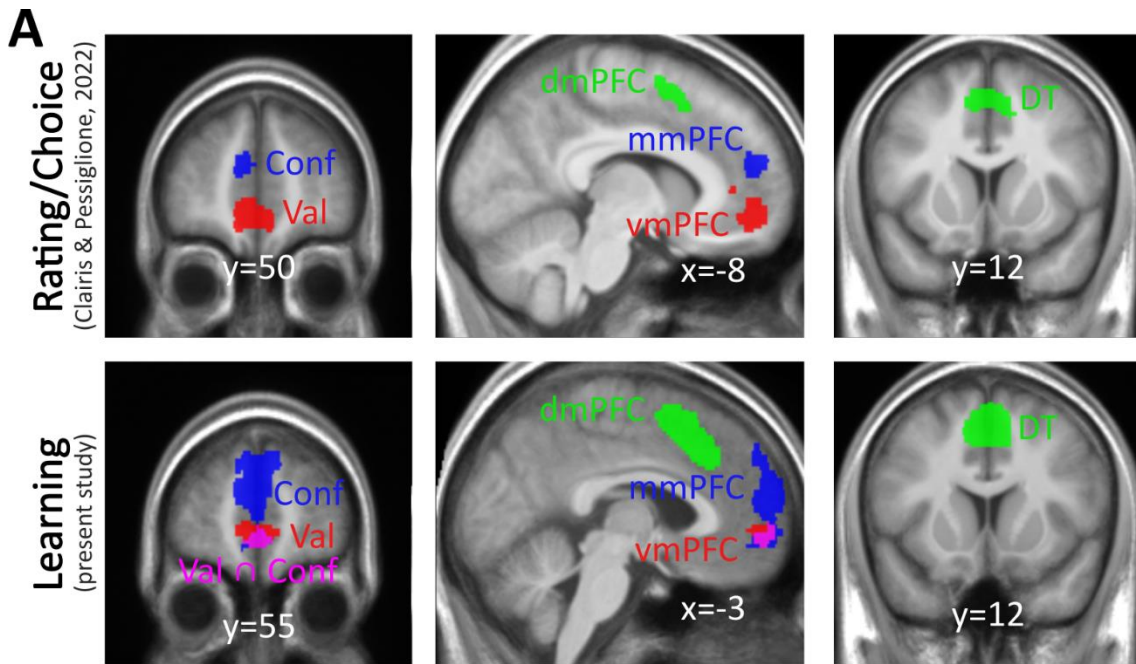
1071 A] Choice behavior. Left panel: percentage of correct choice (for gains) and incorrect choice
 1072 (for losses) is shown as a function of the trial number within a session. Depending on the
 1073 condition (i.e., the pair of cues), correct choice means selecting the cue with 75% chance of
 1074 winning or 25% chance of losing 10€. Right panel: percentage of left choices (for gains) and
 1075 right choices (for losses) is shown as a function of decision value (difference between left and
 1076 right option values). The two conditions (gain and loss pairs) are plotted separately (dark red
 1077 circles and light red squares, respectively). Choice data were fitted with a Q-learning model.
 1078 Both observed and modeled choice data have been averaged across sessions and
 1079 participants.

1080 B] Val and Conf variables. Graphs show how our constructs for value (sum of option values
 1081 weighted by their selection probabilities) and confidence (squared difference between
 1082 selection probability and chance level) vary with trial number (left panels) and decision value
 1083 (right panels), separately for the gain (top panels) and the loss (bottom panels) conditions.

1084 C] Deliberation time (DT). The plots show how DT (time from option display to button press)
1085 varies with the Val (left panel) and Conf (right panel) constructs, pooling over gain and loss
1086 conditions. DT was fitted with a linear combination of Val and Conf variables.

1087 In all figures, data points and error bars indicate the mean and standard error of the mean
1088 (SEM) across participants. Dotted lines indicate mean model fits.

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Figure 4. Neural activity during learning (versus rating and choice).

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A) Activation maps. Colored voxels show group-level clusters within the medial prefrontal cortex mask (see Extended Data Figure 4-1) that were significantly associated with Val (red), Conf (blue) and DT (green) during rating and choice tasks (top panels) in our previous study

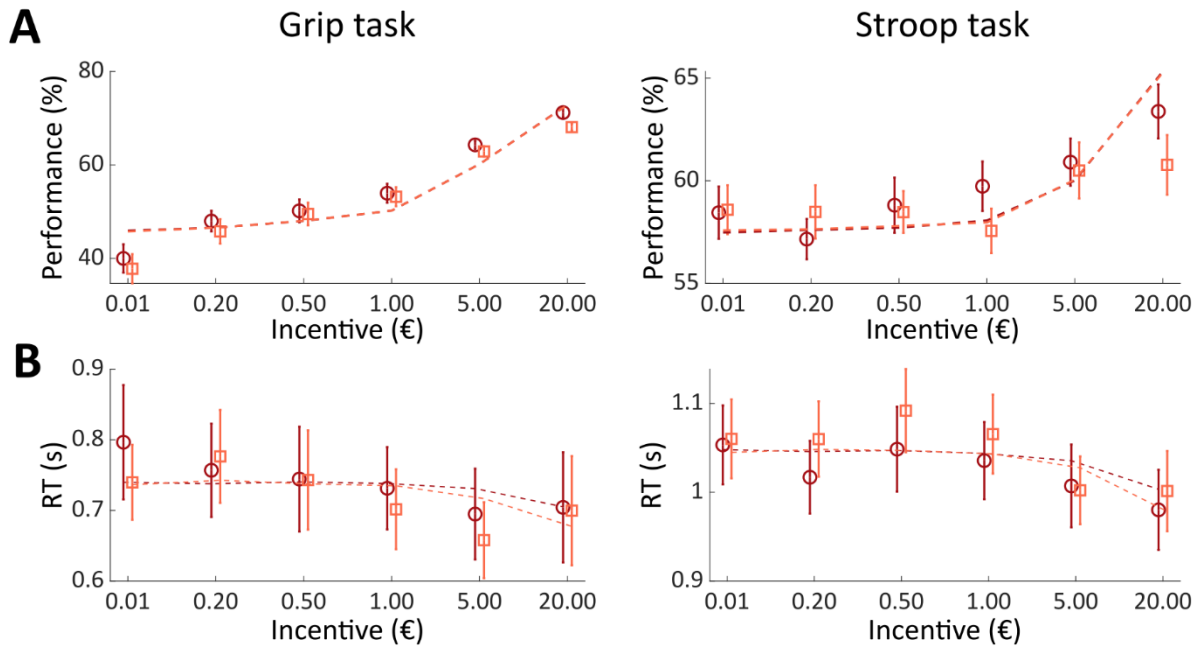
1095 (Clairis and Pessiglione, 2022) and during the choice period of the learning task (bottom
1096 panels) in the present study. The overlap between Val and Conf clusters is shown in purple.
1097 The statistical thresholds were whole-brain FWE-corrected for multiple comparisons at the
1098 voxel level for rating / choice and at the cluster level for learning, due to a difference in
1099 statistical power between the two studies (n=38 vs. n=22). Clusters are overlaid on the
1100 average anatomical scan across participants of each study, normalized to the canonical
1101 Montreal Neurological Institute (MNI) template. They are labeled vmPFC, mmPFC and
1102 dmPFC for ventromedial, midmedial and dorsomedial prefrontal cortex. The 3 corresponding
1103 whole-brain activation tables for Val, Conf and DT can be found in Extended Data Tables 4-4,
1104 4-5 and 4-6, respectively.

1105 B] Region-of-interest analysis. In the previous study (top panels), regression estimates of Val,
1106 Conf and DT were extracted with a leave-one-out procedure to avoid double-dipping. In the
1107 current study (bottom panels), regression estimates of Val, Conf and DT were extracted from
1108 spheres positioned on the peaks of group-level significant clusters obtained in the previous
1109 study (Clairis and Pessiglione, 2022). The three regressors were not orthogonalized in the
1110 main GLM used to fit neural activity during the choice period of the learning task. However,
1111 the same associations between the 3 ROI and the 3 variables are observed when the
1112 regressors are orthogonalized (see Extended Data Figure 4-2). Other combinations of option
1113 values (notably, chosen minus unchosen) have also been tested as possible definitions for
1114 Val (see Extended Data Figure 4-3). Dots are individual regression estimates. Error bars
1115 indicate the mean and standard error of the mean (SEM) across individuals. Stars denote
1116 significance of t-test against zero: ****p<0.001; ***p<0.005; **p<0.01; *p<0.05. Abbreviations:
1117 vmPFC, mmPFC and dmPFC designate ventromedial, midmedial and dorsomedial prefrontal
1118 cortex.

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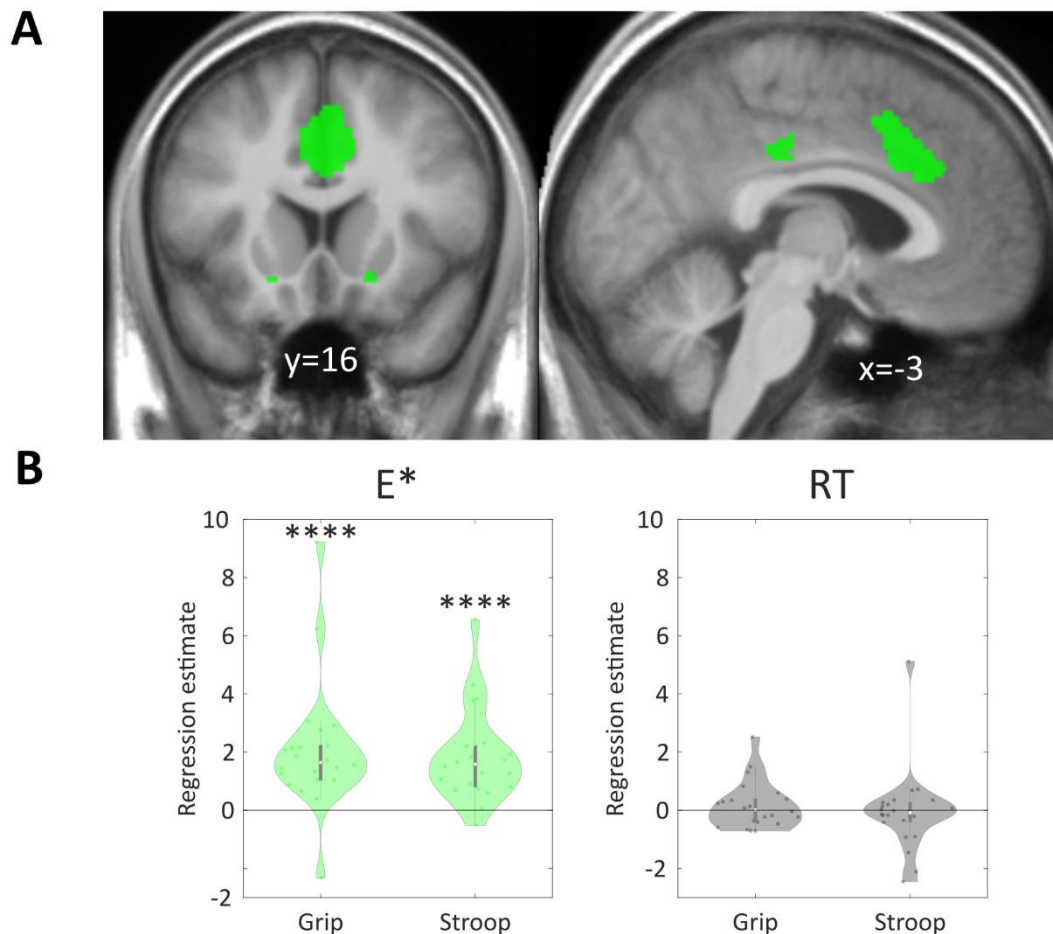
1123 **Figure 5. Behavior in motor and cognitive performance tasks.**

1124 A] Performance is the height reached within the scale, which is proportional to peak force in
1125 the grip task (left panel) and to the number of correct numerical comparisons in the Stroop task
1126 (right panel).

1127 B] Reaction time is the latency at which force exceeded 1% of maximum in the grip task (left
1128 panel) and at which the first button press was made in the Stroop task (right panel).

1129 Gain and loss conditions are shown in dark red circles and in light red squares, respectively.
1130 Error bars represent the mean and standard error of the mean (SEM) across participants for
1131 each incentive level. Dotted lines indicate the fit of the effort regulation model for performance
1132 and the fit of a multiple linear regression model for response time.

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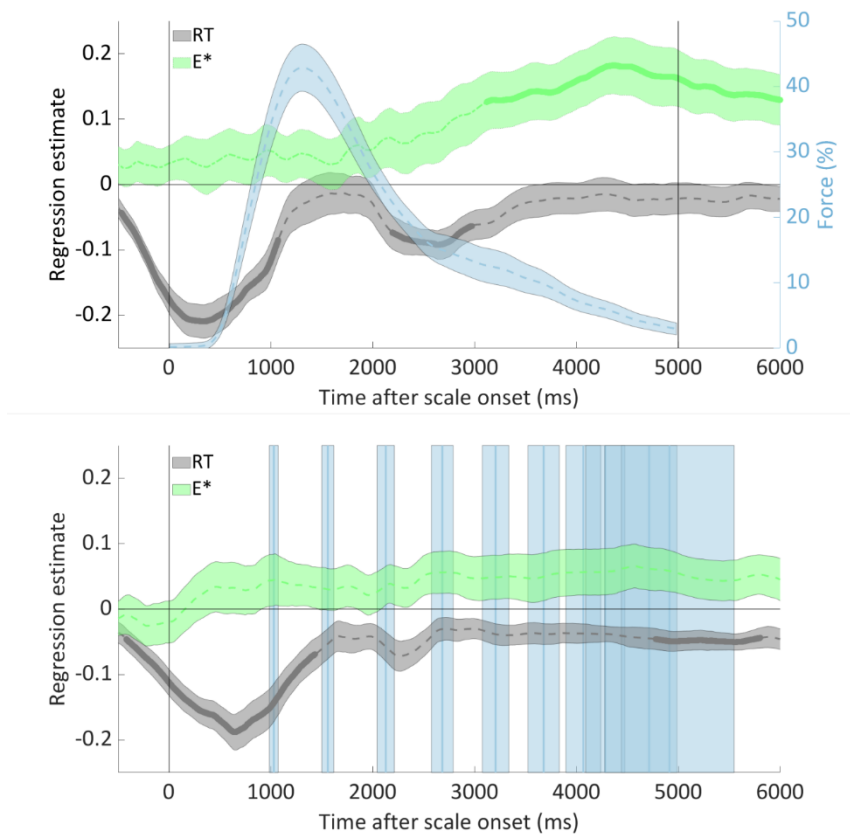
1135 **Figure 6. Neural activity during motor and cognitive performance tasks.**

1136 A] Activation maps. Colored voxels show group-level clusters within the medial prefrontal
 1137 cortex mask (see Extended Data Figure 4-1) significantly associated ($p < 0.05$ after whole-
 1138 brain family-wise error correction for multiple comparisons at the voxel level) with the
 1139 theoretical effort exerted E^* (generated with our computational model), in a conjunction
 1140 between grip and Stroop tasks, at the time of incentive display. The corresponding whole-
 1141 brain activation table is displayed in Extended Data Table 6-2. Clusters are overlaid on the
 1142 average anatomical scan across participants, normalized to the canonical Montreal
 1143 Neurological Institute (MNI) template. Sections are taken at the peak in the dmPFC, which
 1144 stands for dorsomedial prefrontal cortex.

1145 B] Regression estimates of effort exerted E^* and reaction time RT were extracted from spheres
 1146 positioned on the peaks of group-level significant clusters obtained in the previous study
 1147 (Clairis and Pessiglione, 2022). The two regressors were not orthogonalized in the main GLM
 1148 used to fit neural activity evoked by incentive display in both the grip and Stroop tasks.
 1149 However, the main results are stable, even when the regressors are orthogonalized (see
 1150 Extended Data Figure 6-1). On the opposite, the correlation between dmPFC and E^* only
 1151 holds when modeled during the incentive period but not if modeled during the performance
 1152 period (see Extended Data Figure 6-1). Dots are individual regression estimates. Error bars
 1153 indicate the mean and standard error of the mean (SEM) across individuals. Stars denote
 1154 significance of t-test against zero: **** $p < 0.001$; *** $p < 0.005$; ** $p < 0.01$; * $p < 0.05$. Abbreviations:
 1155 vmPFC and dmPFC designate ventromedial and dorsomedial prefrontal cortex.

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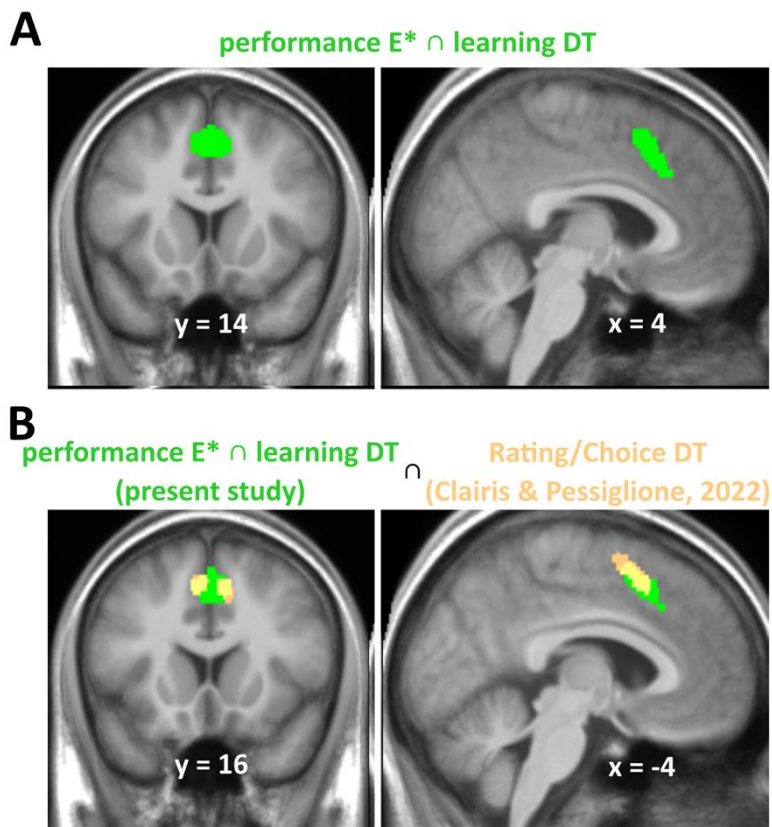
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1159 **Figure 7. Pupil dilation in the motor and cognitive performance tasks.**

1160 Plots represent the time course of regression estimates, obtained with a GLM built to explain
1161 pupil size, on the grip and Stroop tasks (top and bottom graphs). The GLM included factors of
1162 no interest (session number and stimulus luminance, not shown) and variables of interest
1163 (theoretical effort E^* and reaction time RT, shown in green and grey). Movements are indicated
1164 in blue (force produced in the grip task and button press in the Stroop task). Lines indicate
1165 means across participants and shaded areas the inter-participant standard error of the mean
1166 (SEM).



1168

1169 **Figure 8. Global conjunction of effort-related activity across all tasks.**

1170 A] Colored voxels show the significant cluster (voxel-wise threshold: $p < 0.05$ corrected for
 1171 multiple comparisons), within the medial prefrontal cortex mask (see Extended Data Figure 4-
 1172 1), resulting from the conjunction between two contrasts: DT in the learning task and E* in
 1173 performance tasks. The corresponding whole-brain activation table is displayed in Extended
 1174 Data Table 8-1.

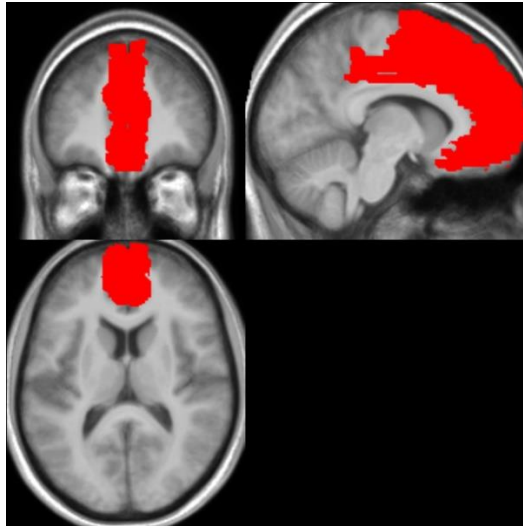
1175 B] Overlap (in yellow) between the significant cluster (in green) displayed in [A] and the
 1176 dmPFC cluster (in orange) associated with rating/choice DT in our previous study (Clairis and
 1177 Pessiglione, 2022). Clusters are overlaid on the average anatomical scan across participants,
 1178 normalized to the canonical Montreal Neurological Institute (MNI) template.

1179

1180 **Extended Data**

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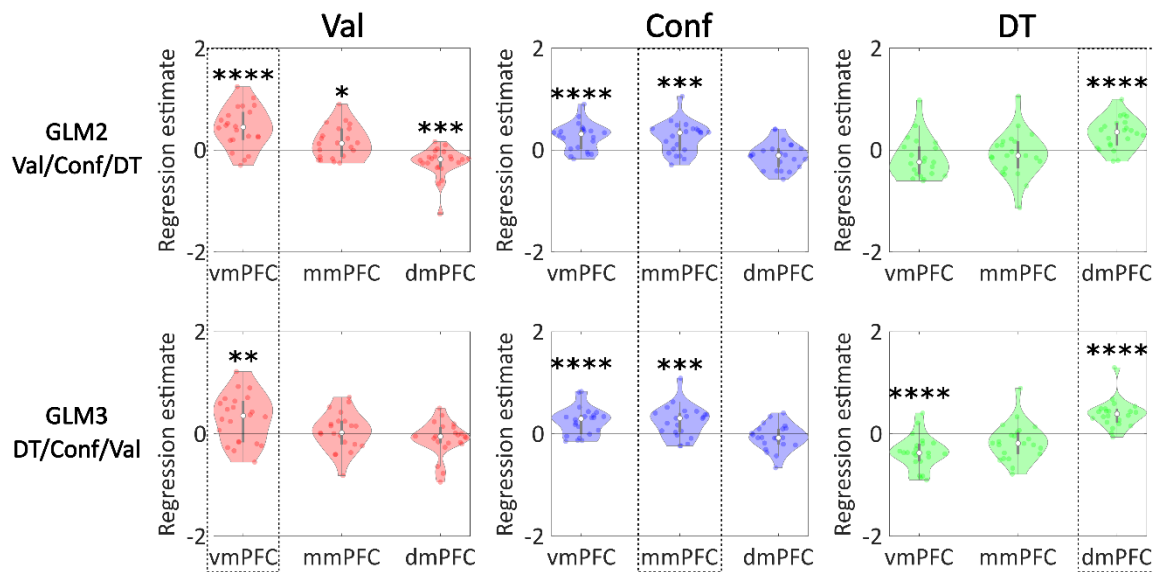
1183

1184 **Extended Data Figure 4-1. Mask of the medial prefrontal cortex.** This mask was built by
1185 merging brain regions (see Methods) of the AAL atlas parcellation (Tzourio-Mazoyer et al.,
1186 2002) and used for the display of Val, Conf and DT neural correlates in Figure 4 and 6. It is
1187 overlaid on the average anatomical scan of the 22 subjects included in the present study.

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1192 **Extended Data Figure 4-2. Neural correlates of Val, Conf and DT in the learning task**

1193 **after orthogonalization.** The regions of interest have been defined as spheres positioned on

1194 the peaks of group-level significant clusters obtained in the previous study (Clairis and

1195 Pessiglione, 2022). As in GLM1 (no orthogonalization), Val, Conf and DT are parametric

1196 modulators of choice-related activity, which have now been serially orthogonalized either in

1197 the Val/Conf/DT order (GLM2) or in the DT/Conf/Val order (GLM3). In all figures, dots are

1198 individuals, error bars show the mean and standard error of the mean (SEM) across individuals

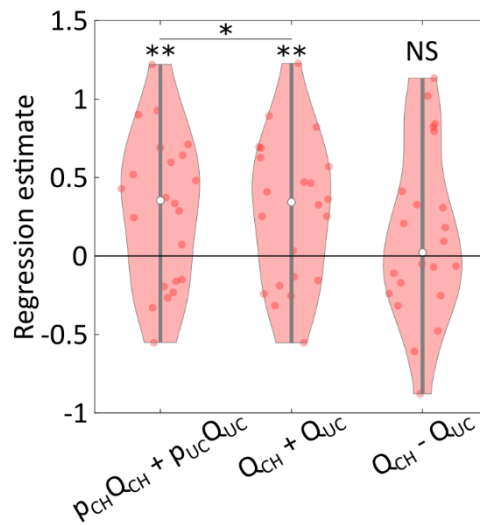
1199 and stars indicate significance level of t-test against zero: **** $p < 0.001$; *** $p < 0.005$; ** $p < 0.01$;

1200 * $p < 0.05$. Abbreviations: vmPFC, mmPFC and dmPFC designate ventromedial, midmedial and

1201 dorsomedial prefrontal cortex.

1202

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1204

1205 **Extended Data Figure 4-3. Testing different associations between option values and**
1206 **vmPFC activity.** Regression estimates were extracted from a sphere positioned on group-
1207 level activation peak observed with the Val regressor in our previous study (Clairis and
1208 Pessiglione, 2022). Graphs show regression estimates for the weighted sum of option values
1209 (GLM1), the straight sum (GLM4), and the difference between option values (GLM5). Dots are
1210 individuals, error bars show the mean and standard error of the mean (SEM) across
1211 individuals, and stars indicate significance level of t-test against zero: **** $p < 0.001$; *** $p < 0.005$;
1212 ** $p < 0.01$; * $p < 0.05$.

1213

Region	P cluster	Peak x	Peak y	Peak z	No. of Voxels
vmPFC	0.036	4	58	-4	255

1214

1215 **Extended Data Table 4-4: Whole-brain neural correlates of Val in the learning task**
1216 (voxel-wise threshold: $p < 0.001$ uncorrected; cluster-wise threshold: $p < 0.05$ FWE corrected for
1217 multiple comparisons). The table shows the positive correlations in a t-test against zero; there
1218 was no negative correlation surviving the correction.

1219

1220

Region	P cluster	Peak x	Peak y	Peak z	No. of Voxels
Right precuneus	$2 \cdot 10^{-8}$	4	-46	54	1285
mmPFC	$3 \cdot 10^{-8}$	-4	64	16	1264
Left superior temporal gyrus	0.028	-50	-38	16	202
Left superior temporal gyrus	0.011	-34	10	-24	253

1221

1222 **Extended Data Table 4-5: Whole-brain neural correlates of Conf in the learning task**
1223 (voxel-wise threshold: $p < 0.001$ uncorrected; cluster-wise threshold: $p < 0.05$ FWE corrected for
1224 multiple comparisons). The table shows the positive correlations in a t-test against zero; there
1225 was no negative correlation surviving the correction.

1226

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Region	P cluster	Peak x	Peak y	Peak z	No. of Voxels
Left inferior occipital gyrus	$6 \cdot 10^{-12}$	-44	-58	-12	3049
dmPFC	$1 \cdot 10^{-10}$	-4	8	54	2558
Left superior parietal gyrus	$9 \cdot 10^{-8}$	-22	-60	46	1605
Left middle frontal gyrus	$1 \cdot 10^{-5}$	-38	36	36	1025
Right fusiform gyrus	$2 \cdot 10^{-5}$	42	-52	-16	957
Right middle frontal gyrus	$2 \cdot 10^{-4}$	28	40	34	729
Left anterior insula	$6 \cdot 10^{-4}$	-34	14	6	585
Right anterior insula	$9 \cdot 10^{-4}$	32	22	4	557
Right angular gyrus	0.006	26	-62	46	382

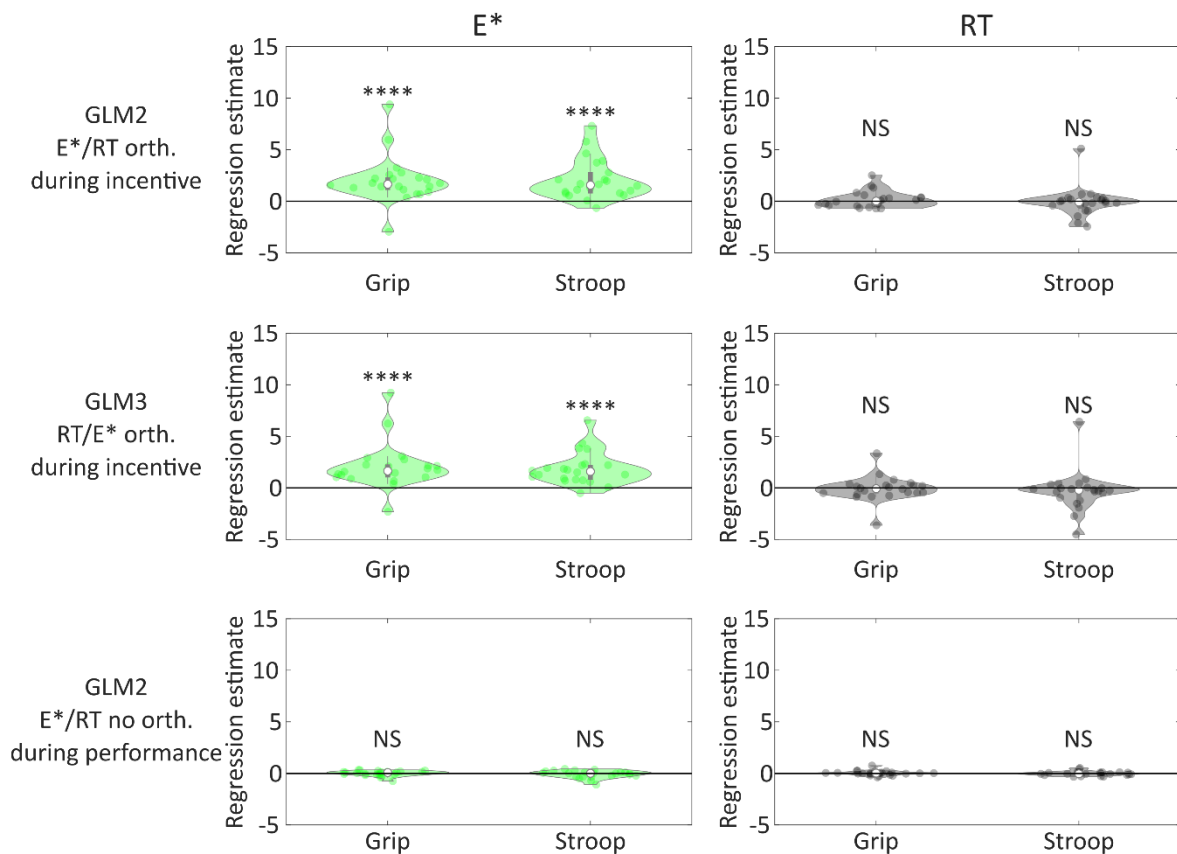
1228

1229 **Extended Data Table 4-6: Whole-brain neural correlates of DT in the learning task** (voxel-
1230 wise threshold: $p < 0.001$ uncorrected; cluster-wise threshold: $p < 0.05$ corrected for multiple
1231 comparisons). The table shows the positive correlations in a t-test against zero; there was no
1232 negative correlation surviving the correction.

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1237 **Extended Data Figure 6-1: Neural correlates of E* and RT in the performance tasks, with**
1238 **orthogonalization or at a later time.**

1239 The regions of interest have been defined as spheres positioned on the peaks of group-level
1240 significant clusters obtained in the previous study (Clairis and Pessiglione, 2022). Compared
1241 to GLM1, where E* (left graphs) and RT (right graphs) are parametric modulators of incentive
1242 display in both grip and Stroop tasks with no orthogonalization, the parametric regressors have
1243 been orthogonalized in the E*/RT (GLM2, top row) or RT/E* (GLM3, middle row) order, or
1244 moved to the performance time window without orthogonalization (GLM4, bottom row). In all
1245 figures, dots are individuals, error bars show the mean and standard error of the mean (SEM)
1246 across individuals and stars indicate significance level of t-test against zero: ****p<0.001;
1247 ***p<0.005; **p<0.01; *p<0.05. Abbreviations: vmPFC and dmPFC designate ventromedial
1248 and dorsomedial prefrontal cortex.

1249

1250

Region	P cluster	Peak x	Peak y	Peak z	No. of Voxels
Right caudate	$8 \cdot 10^{-7}$	18	16	2	1154
Right calcarine	$6 \cdot 10^{-6}$	8	-90	2	864
dmPFC	$1 \cdot 10^{-5}$	-2	16	38	738
Right cerebellum	$2 \cdot 10^{-5}$	20	-52	-24	720
Left putamen	$3 \cdot 10^{-5}$	-14	10	0	621
middle cingulate cortex	$6 \cdot 10^{-4}$	6	-22	40	287
Right supramarginal gyrus	0.002	56	-44	24	180
Left cerebellum	0.002	-32	-58	-26	175
Ventral posterolateral thalamus	0.005	-14	-18	10	117
Right middle frontal gyrus	0.006	34	42	34	100
Right inferior frontal gyrus, opercular part	0.007	40	10	30	87
Right cuneus	0.015	18	-68	30	44

1251

1252 **Extended Data Table 6-2: Whole-brain neural correlates of E* in a conjunction between**
1253 **grip and Stroop tasks** (voxel-wise threshold: $p < 0.05$ corrected for multiple comparisons,
1254 cluster-wise threshold: minimum of 33 voxels, i.e. the volume of the Gaussian kernel used for
1255 smoothing fMRI data). The table shows the positive correlations in a t-test against zero; there
1256 was no negative correlation surviving the correction.

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Region	P cluster	Peak x	Peak y	Peak z	No. of Voxels
dmPFC	$6 \cdot 10^{-8}$	4	14	50	505
Right anterior insula	$7 \cdot 10^{-5}$	32	22	4	170
Left anterior insula	$2 \cdot 10^{-4}$	-34	18	6	125
Right middle frontal gyrus	0,002	38	42	32	61
Left superior Frontal gyrus	0,005	-24	-2	62	35

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1261

1262 **Extended Data Table 8-1: Whole-brain neural correlates of the conjunction between DT**
1263 **in the learning task and E* in performance tasks** (voxel-wise threshold: $p < 0.05$ corrected
1264 for multiple comparisons, cluster-wise threshold: minimum of 33 voxels, i.e. the volume of the
1265 Gaussian kernel used for smoothing fMRI data). The table shows the positive correlations in
1266 a t-test against zero; there was no negative correlation surviving the correction.