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Tecilla, Margherita; Michael, Grossbach; Gentile, Giovanni; Holland, Peter; Antonini, Angelo and Herrojo Ruiz, Maria. 2023. Modulation of Motor Vigor by Expectation of Reward Probability Trialby-Trial Is Preserved in Healthy Ageing and Parkinson's Disease Patients. The Journal of Neuroscience, 43(10), pp. 1757-1777. ISSN 1529-2401 [Article]

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Title: Modulation of motor vigour by expectation of reward probability trial-by-trial is preserved in healthy ageing and Parkinson's disease patients

Abbreviated title: Motor invigoration by reward probabilities

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Number of pages: 66

Number of figures, tables: 9 figures, 5 tables

Number of words for abstract, introduction, and discussion: abstract (250 words), introduction (650 words), discussion (1499)

Conflict of interest statement: The authors declare no competing financial interests

Acknowledgments: We would like to thank Osama Shah for programming the task in JavaScript. The authors also thank Caterina Tagliavini and McKenna Hedman for helping in data collection of Study 3.

Data and code availability

The data that support the main findings of these studies are available from the Open Science Framework Data Repository under the accession code 7kfbj:https://osf.io/7kfbj/ Code for the main brms and HGF analyses has also been deposited in <u>https://osf.io/7kfbj/</u>

1 ABSTRACT

Motor improvements, such as faster movement times or increased velocity, have been
associated with reward magnitude in deterministic contexts. Yet whether individual
inferences on reward probability influence motor vigour dynamically remains undetermined.

5 We investigated how dynamically inferring volatile action-reward contingencies modulated 6 motor performance trial-by-trial. We conducted three studies that coupled a one-armed 7 bandit decision-making paradigm with a motor sequence task and used a validated 8 hierarchical Bayesian model to fit trial-by-trial data. In Study 1, we tested healthy younger 9 (HYA, 37 [13 males]) and older adults (HOA, 37 [20 males]), and medicated Parkinson's 10 Disease patients (PD, 20 [13 males]). We showed that stronger predictions about the 11 tendency of the action-reward contingency led to faster performance tempo-commensurate 12 with movement time—on a trial-by-trial basis without robustly modulating reaction time (RT). 13 Using Bayesian linear mixed models, we demonstrated a similar invigoration effect on 14 performance tempo in HYA, HOA and PD, despite HOA and PD being slower than HYA. In 15 Study 2 (HYA, 39 [10 males]), we additionally showed that retrospective subjective inference 16 about credit assignment did not contribute to differences in motor vigour effects. Last, Study 17 3 (HYA, 33 [6 males]) revealed that explicit beliefs about the reward tendency (confidence 18 ratings) modulated performance tempo trial-by-trial.

Our study is the first to reveal that the dynamic updating of beliefs about volatile actionreward contingencies positively biases motor performance through faster tempo. We also provide robust evidence for a preserved sensitivity of motor vigour to inferences about the action-reward mapping in ageing and medicated PD.

23 SIGNIFICANCE STATEMENT

24 Navigating a world rich in uncertainty relies on updating beliefs about the probability that our 25 actions lead to reward. Here we investigated how inferring the action-reward contingencies 26 in a volatile environment modulated motor vigour trial-by-trial in healthy younger and older 27 adults, and in Parkinson's Disease patients on medication. We found an association 28 between trial-by-trial predictions about the tendency of the action-reward contingency and 29 performance tempo, with stronger expectations speeding the movement. We additionally 30 provided evidence for a similar sensitivity of performance tempo to the strength of these 31 predictions in all groups. Thus, dynamic beliefs about the changing relationship between 32 actions and their outcome enhanced motor vigour. This positive bias was not compromised 33 by age or Parkinson's disease.

34 INTRODUCTION

35 The prospect of obtaining rewards invigorates motor performance, with incentives leading to 36 faster and more accurate movements (Summerside et al., 2018; Sedaghat-Nejad et al., 37 2019; Codol et al., 2020). Several non-mutually exclusive mechanisms have been proposed 38 to account for the beneficial effects of reward on movement. These include the reward-39 driven strengthening of motor representations at the cortical level (Galaro et al., 2019; 40 Adkins & Lee, 2021), enhanced feedback-control processes (Padmala & Pessoa, 2011; 41 Carroll et al., 2019; Manohar et al., 2019), increased limb stiffness (Codol et al., 2020) and 42 coarticulation (Sporn et al., 2022; Aves et al., 2021). Despite the growing number of studies 43 demonstrating how rewards positively bias motor behaviour, the evidence so far is limited to 44 simple manipulations of reward magnitude (presence/absence; large/small). Yet, in our 45 everyday life we are exposed to environments rich in uncertainty, where adaptive behaviour 46 relies on estimating the changing relationship between actions and their outcomes. How 47 beliefs about the probabilistic structure of reward contingencies modulate motor performance 48 remains largely unexplored. In addition, whether this modulation is compromised with age 49 and in neurological conditions is unclear.

50 Hierarchical Bayesian inference models explain how individuals learn and make decisions 51 under uncertainty (den Ouden et al., 2010; Feldman & Friston, 2010). On a neural level, 52 processing uncertainty and updating beliefs about action-reward contingencies likely 53 involves the anterior cingulate cortex (ACC, Behrens et al., 2007; Hayden et al., 2011), 54 medial prefrontal cortex (mPFC; Rouault et al., 2019) and orbitofrontal cortex (OFC; Rolls et 55 al., 2019). In multi/one-armed bandit tasks, these models describe learning as governed by 56 inferences on the probabilistic stimulus-outcome mappings, as well as higher-level beliefs 57 about the rate of change of these contingencies over time, labelled volatility (de Berker et al., 58 2016; Sheffield et al., 2022). In Bayesian predictive coding, beliefs about the probable 59 causes of sensory data are updated via prediction errors weighted by uncertainty or 60 precision (Friston et al., 2014; Mathys et al., 2014). Thus, dynamic estimates of uncertainty 61 allow for the expression of individual differences in belief updating. If motor vigour is

62 modulated by beliefs about the action-reward contingencies, then individual differences in 63 uncertainty estimates could explain differences in motor vigour. Alternatively, under 64 equivalent signatures of decision-making behaviour, individuals could exhibit differential 65 sensitivity of motor performance to the expectation of reward probability.

We tested these hypotheses in three behavioural studies that used a reward-based motor
decision-making task based on a one-armed bandit paradigm with changing stimulusoutcome contingencies over time.

69 In the first study we investigated whether dynamic predictions about volatile action-reward 70 contingencies influence motor sequence performance trial-by-trial. We additionally assessed 71 whether the sensitivity of motor performance to the strength of these expectations 72 undergoes changes in later stages of life and in patients with Parkinson's Disease (PD) on 73 their dopamine-replacement medication. This is motivated by the lack of evidence regarding 74 how reward sensitivity and reversal learning interact to modulate motor vigour in PD and 75 older adults. On the one hand, evidence supports preserved sensitivity to rewards and 76 probabilistic learning in ageing and medicated PD (Fera et al., 2005; Euteneuer et al., 2009; 77 Aves et al., 2021). Yet other work suggests impoverished decision making and reward-78 based learning in both groups. Specifically, ageing and medicated PD can underperform in 79 tasks using volatile probabilistic stimulus-outcome mappings (Cools et al., 2001; Eppinger et 80 al., 2011; Nassar et al., 2016). However, the medication effects on decision making in PD 81 (on/off states) is still under debate (Ryterska et al., 2013; Kjær et al., 2019). Accordingly, 82 whether ageing and medicated PD can use their dynamic belief estimates to invigorate 83 motor performance trial-by-trial remains unspecified.

In the second study we evaluated the potential contribution of retrospective subjective inferences about credit assignment to explain the motor vigour results. Last, we assessed how explicit beliefs about the reward tendency (confidence ratings) modulated motor performance trial-by-trial. This aimed at providing a more comprehensive understanding of the motor invigoration effect by beliefs about volatile reward probabilities.

89

90 MATERIALS AND METHODS

91 Participants

92 All studies received ethical approval by the review board of Goldsmiths (healthy sample), 93 University of London, and the Neurology Clinic, Padua University Hospital (Parkinson's 94 Disease [PD] sample). Informed consent was acquired for each participant. Healthy younger 95 (HYA) and older adults (HOA) were recruited through online advertisement and via the 96 Research Participation Scheme (RPS) at Goldsmiths University, while PD were enrolled at 97 the Neurology Clinic, Padua University Hospital.

98

99 Study 1

100 37 HYA (13 males, age 18-40, mean age 27.8, standard error of the mean [SEM] 0.67; 101 hereafter we follow the intrinsic measures of precision for rounding descriptive and inferential 102 statistics as reported in Cousineau, 2020), 20 PD patients (13 males, age 40-75, mean age 103 58.9, SEM 1.32) and an age-matched group of 37 HOA (20 males, age 40-75, mean age 104 61.5, SEM 1.25) participated in this research. The sample size for healthy samples was 105 informed by previous work assessing differences between HYA and HOA in decision-making 106 under uncertainty (de Boer et al., 2017: N = 30, 30) and our own work assessing group effects in parameters of hierarchical Bayesian models (Hein et al., 2021; 2022; N = 20, 20). 107 108 We increased the sample size to allow for variability being introduced due to the nature of 109 the online study.

110 All participants were right-handed, had normal or corrected vision and were able to perform 111 controlled finger movements. Amateur/professional pianists and participants diagnosed with 112 a mental health disorder were excluded from the study. Additionally, exclusion criteria for PD 113 patients were: implanted with Deep Brain Stimulation (DBS), taking antidepressant 114 medications, diagnosed with dementia and displaying tremor as an onset symptom. One PD 115 patient declared to take Laroxyl, yet confirmed not to be diagnosed with depression. PD 116 were evaluated through ITEL-Mini Mental state examination (ITEL-MMSE; Metitieri et al., 117 2001), Unified Parkinson's Disease Rating Scale part III (UPDRS-III; Fahn & Elton, 1987),

Hospital Anxiety and Depression Scale (HADS; Zigmond & Snaith, 1983) and State-Trait Anxiety Inventory (STAI Y2; Spielberger, 1983). Supplementary disease-related information was also gathered (**Table 1**). Patients completed the experiment in the ON medication state according to their usual dopamine-replacement treatment. The individual dopaminergic medication details were collected and converted to a levodopa-equivalent daily dose (LEDD) value (**Table 1**).

124 All participants took part in the study remotely (online), except for five PD patients, who 125 completed the study in the laboratory facilities of the Neurology Clinic of Padua. An Italian 126 translation of the original experimental instructions in English was created to test some of the 127 HOA participants (N = 24) and all PD patients (see the Results section for details on our 128 control analyses to assess the effect of the language of the instructions). The previously 129 validated Italian translations of the HADS, ITEL-MMSE, UDPRS-III and STAI Y2 scales were used. HYA and HOA participants received a monetary compensation of £5 (5€ for those 130 131 completing the task in Italian), which could be increased up to £10 (10€) as a function of 132 their task performance. PD patients did not receive a monetary prize, in line with the clinical 133 research policies at the Neurology Clinic of Padua.

134

135 Study 2

136 A separate sample of 39 HYA took part in Study 2, which was aimed at evaluating the potential contribution of subjective inferences about task-related reward (credit) assignment 137 to explain our results (McDougle et al., 2016). HYA participants in this control experiment 138 139 were divided into two subsamples as a function of their reply (True/False) to a post-140 performance question (Q8; **Table 2**). Group $Q8_T$ consisted of 26 participants (8 males, age 141 18-40, mean age 24.1, SEM 1.13) and Q8_F of 13 participants (2 males, age 18-40, mean age 142 25, SEM 1.7). The same inclusion/exclusion criteria and compensation as for HYA in Study 1 143 applied.

144

145 Study 3

For Study 3, we recruited 33 HYA (6 males, age 18-40, mean age 22.4, SEM 1.14) with the aim of understanding how trial-by-trial explicit confidence ratings about action-reward contingencies modulate motor performance. The same inclusion/exclusion criteria and compensation as for HYA in Study 1 applied.

150

Table 1

151

152 Experimental design

153 In Study 1 and 2, the experiment ran completely online on the Qualtrics platform 154 (https://www.qualtrics.com) and was accessible through a study link. The task was 155 programmed in JavaScript and embedded into the Qualtrics form. We provide more details 156 of the data acquisition below (see Acquisition of online data using JavaScript section).

Participants performed a novel computerised reward-based motor decision-making task based on a one-armed bandit paradigm with changing stimulus-outcome contingencies over time (e.g., de Berker et al., 2016). Participants were instructed to play one of two sequences of finger movements on a virtual piano to express their decision, which is an extension of standard one-armed bandit tasks that instruct participants to manifest their choice by pressing a right or left button (Hein et al., 2021).

163 The task consisted of a familiarisation and a reward-based learning phase. In the 164 familiarisation phase participants learned how to play two short sequences (seq1 and seq2) of four finger presses each. Each sequence was uniquely represented by one of two 165 166 different fractal images (Figure 1A). They were asked to position their right hand on the 167 keyboard as follows: index finger on "g" key, middle finger on "h" key, ring finger on "j" key and little finger on "k" key. Each key press reproduced a distinct auditory tone, simulating a 168 virtual piano. Participants were trained to press "g-j-h-k" for seq1 (red fractal) and "k-g-j-h" for 169 seq2 (blue fractal). Online videos showing the correct hand position on the keyboard and 170 171 how to perform the two sequences were provided to increase inter-individual consistency. 172 The familiarisation phase terminated when an error-free performance was achieved for five 173 times in succession for both sequences. The number of sequence renditions during174 familiarisation was recorded and used for subsequent analyses.

175 The reward-based learning phase consisted of 180 trials. On each trial, participants were 176 instructed to choose between two coloured fractals (blue and red) and correctly play the 177 associated sequence (seq1 and seq2) in order to receive a reward (five points; Figure 1B). 178 Trial-by-trial reward feedback about participants' choices was provided on the screen 179 (binary: "You earned 5 points!" or "You earned 0 points"). The reward probability associated 180 with each sequence (or icon) changed every 30-42 trials (as in de Berker et al., 2016). The 181 mapping governing the likelihood of sequences being rewarded was reciprocal (p(win|seq1) 182 = 1-p(win|seq2)) and consisted of five stimulus-outcome contingency blocks (90/10, 70/30, 183 50/50, 30/70, 10/90) (Figure 1C). The order of the contingency blocks was randomly 184 generated for each participant.

After the first key press, subjects had 5000 ms to perform the sequence, terminating in a Stop signal. Visual hints suggesting the first key to press for both sequences were displayed: "It starts with a "g"" – for seq1 (red fractal); "It starts with a "k"" – for seq2 (blue fractal). Participants were instructed to press key "q" if they needed a reminder of the order of finger presses for each sequence. No participant required this reminder.

190 Correctly playing the rewarded sequence added five points to the participants' total score 191 (win trial). Thus, receiving five points indicated that participants chose the rewarded 192 sequence on the trial and did not make performance execution errors when playing it. Zero 193 points, however, could reflect participants choosing an unrewarded sequence on that trial or, 194 alternatively, choosing a rewarded sequence but performing it incorrectly (performance 195 execution error) (McDougle et al., 2016). No reward was provided when sequence 196 performance exceeded the 5000 ms limit (no response trial) and participants were informed 197 they played too slowly.

Thus, to maximise the total cumulative points over the experiment, participants had to infer the probability of reward associated with each sequence and adapt their choices when contingencies changed. They also had to perform the sequences correctly. Participants were

201 informed at the beginning of the experiment that the stimulus-outcome mapping would 202 change from time to time. However, they received no detailed information regarding the 203 frequency or magnitude of those changes. We validated that each participant group 204 completed the task correctly using two measures: (a) the percentage of trials that they 205 performed either seq1 or seq2 (percPlayed, referring to playing seq1); and (b) percPlayed by 206 contingency phase. In the first case, percPlayed was used to demonstrate that participants 207 did not have a preference towards one of the sequences, which could emerge if they 208 perceived one sequence to be easier with regard to motor skills. On average, we expected 209 percPlayed to be 50%. Next, (b) was used to assess whether their chosen sequences 210 tracked the contingency changes over time. To compute percPlayed by contingency phase, 211 we estimated the rate of choosing seq1 in each contingency phase, separately in each 212 participant. We then pooled these data across participants in each group, sorted by phases 213 of increasing contingency values [0.1, 0.3, 0.5, 0.7, 0.9], as defined for seq1. See further 214 details below (Behavioural and computational data analysis and Results sections).

215 In Study 2 we additionally asked participants at the end of the reward-based learning phase 216 to reply to some questions about their performance. We were particularly interested in 217 assessing whether participants could correctly infer what zero points meant, that is, whether 218 they could distinguish between a performance execution error or a decision to play a 219 sequence that was unrewarded on the trial. Both scenarios would result in zero points. We 220 reasoned that participants who could not always infer the meaning of zero might show a 221 reduced invigoration effect. Table 2 lists the questions of the post-performance 222 questionnaire, which required binary responses (True/False) and was designed based on 223 previous work (McDougle et al., 2016; Herrojo Ruiz et al., 2017). The binary answer to 224 Question 8 "I could always distinguish whether 0 points reflected a performance error or a 225 bad decision" was used as criterion to split the control sample into $Q8_T$ (i.e., participants 226 were *always* sure about the hidden causes for the lack of reward) and $Q8_{F}$ (i.e., participants 227 were not always sure about the hidden causes for receiving zero points). Among other 228 questions, participants were asked whether the subjective number estimate of performance

229 errors was less than 10, between 10 and 30 or more than 30. This information was used to 230 investigate whether $Q8_T$ and $Q8_F$ differed in the rate of subjective execution errors. The 231 rationale here was that $Q8_F$ participants relative to $Q8_T$ could attribute more zeros to 232 performance errors rather than inferring that their choice was not rewarded on that trial. 233 Alternatively, they could misattribute zeros to bad decision outcomes. In both cases, their 234 biased credit assignment would be reflected in a more pronounced difference between 235 estimated and empirical error rates in $Q8_{F}$. However, their belief updating would differ; in the 236 first case, $Q8_F$ participants relative to $Q8_T$ would not update their beliefs following a zero 237 outcome, as this would be rendered as not informative feedback regarding the underlying 238 probabilistic structure. Thus, differences in credit assignment could explain differences in 239 decision making and, potentially, associated motor vigour effects. Finally, we also assessed 240 the strategy that participants used to memorise the sequences (79.5% of participants 241 declared to have memorised the sequences focusing both on the finger movements and the 242 tones; Q7).

In Study 3, we conducted an offline version of the task described above. The paradigm was coded in psychtoolbox (<u>http://psychtoolbox.org</u>) and run in MATLAB (version 2021b). In order to better capture measures of trial-wise reaction times (RT), excluding deliberation time, the 5000 ms time window for performing the sequence started at the fractals presentation (and not when the first key was pressed, as in Study 1 and 2). Hence, reward delivery was contingent on RT and movement time.

249 Importantly, after each sequence performance we asked participants how certain they were 250 to be rewarded on that round (following Frömer et al, 2021). This aimed at unveiling a 251 potential association between trial-by-trial explicit beliefs about the reward tendency 252 (confidence ratings) and motor performance. Participants were instructed to type a number 253 in the 0–99 range on the computer keyboard with their left hand. Value 0 denoted having no 254 clue about receiving the points, while 99 reflected being absolutely certain of being 255 rewarded. Participants were encouraged to explore the full 0-99 range. They were 256 additionally asked to press the key "z" if they thought to have committed a performance

execution error. This allowed us to estimate the percentage of correctly identified errors, which expands on Study 2 findings by informing about trial-by-trial (real-time) subjective inference on credit assignment.

260

Figure 1

Table 2

- 261
 - 262

263 Acquisition of online data using JavaScript

264 In Study 1 and 2, due to the nature of the online experiment, cross-browser issues could 265 emerge. A potential issue was that participants could use a variety of computer hardware, 266 running on different web browsers, operating systems and keyboard types (e.g., tablets vs 267 laptops). To mitigate the effect of hardware variability on the acquisition of motor 268 performance data, we instructed participants to complete the task on a desktop or laptop 269 computer. An inspection of browser user agent data suggests that the experiment was 270 performed on a mixture of desktops or laptops running the Chrome & Safari browsers on 271 Windows and Macintosh operating systems.

Timing data was collected using the web browser's high-resolution timer. This browser resolution timer has an upper resolution limit of 2 ms on some web browsers. Therefore, all analysis scripts *truncated* timing data to 2 ms precision. When estimating the mean and standard error of the mean in time variables, we therefore considered a systematic error of 1 ms (2 ms precision means that our time measures were on average 1 ms too short).

For each participant, keypresses, timing data, points, contingency mapping, outcome, and other data were extracted on each trial, then stored and uploaded via JSON to the data folder in Pavlovia (see <u>https://gitlab.pavlovia.org/oshah001/reward-learning-experiment</u>).

280

281 The hierarchical gaussian filter

To model intra-subject trial-by-trial performance in our task, we used a validated hierarchical Bayesian inference model, the Hierarchical Gaussian Filter (HGF; Mathys et al. 2011, 2014; Frässle et al., 2021). The HGF toolbox is an open source software and is freely available as

285 part of TAPAS (http://www.translationalneuromodeling.org/tapas; Frässle et al., 2021). Here 286 we used the HGF version 6.1 implemented in MATLAB® 2020b. The HGF is a generative 287 model that describes how individual agents learn about a hierarchy of hidden states in the 288 environment, such as the latent causes of sensory inputs, probabilistic contingencies, and 289 their changes over time (labelled volatility). Beliefs on each hierarchical level are updated 290 through prediction errors (PEs) and scaled (weighted) by a precision ratio (precision as 291 inverse variance or uncertainty). The precision ratio effectively operates as a learning rate, 292 determining how much influence the uncertainty about the belief distributions has on the 293 updating process (Mathys et al., 2011, 2014).

294 In our studies, the HGF was used to characterise subject-specific trial-by-trial trajectories of 295 beliefs about stimulus-outcome contingencies (level 2) and their changes over time 296 (environmental volatility, level 3). These belief distributions are Gaussian, summarised by the posterior mean (μ_2 , μ_3) and the posterior variance (σ_2 , σ_3). The latter represents 297 298 uncertainty about the hidden states on those levels, that is, our imperfect knowledge about 299 the true hidden states. On level 2, σ_2 is termed estimation or informational uncertainty. More generally, the inverse $1/\sigma$ is termed precision, labelled π . The HGF provides trajectories of 300 301 updated beliefs on the current trial, k, after observing the outcome (posterior mean $\mu_i^{(k)}$ for level i = 2, 3). Before observing the outcome, participants' predictions are denoted by the hat 302 operator $\hat{\mu}_{i}^{(k)}$ and correspond to the values in the previous trial ($\mu_{i}^{(k-1)}$). As in previous work 303 304 using one-armed bandit paradigms (Iglesias et al., 2013; Mathys et al., 2014; Hein et al., 305 2021), we modelled learning using the 3-level HGF (HGF₃) for binary outcomes (Figure 2A). In this hierarchical perceptual model, the hidden state on the lowest level, x₁, represents the 306 binary categorical variable of the experimental stimuli (for each trial k, $x_1^{(k)} = 0$ if the red 307 icon/seg1 is rewarded [or blue/seg2 loses]; $x_1^{(k)} = 1$ when red fractal/seg1 is not rewarded [or 308 309 blue/seq2 wins]). Higher in the hierarchy, x₂ reflects the true value of the tendency of the 310 stimulus-outcome contingency, and x_3 the true volatility of the environment (i.e., of x_2). Belief 311 updating in the HGF depends on various parameters, which can be estimated in each

312 individual or fixed depending on the hypotheses. This allows for the assessment of individual 313 learning characteristics. Here we chose to individually estimate parameter ω_2 , representing 314 the tonic (time-invariant) volatility on the second level, and ω_3 , denoting the tonic volatility 315 on the third level. Generally, ω_2 and ω_3 parameters describe an individual's learning motif. 316 Larger ω_2 values are associated with faster learning about stimulus outcomes, and thus 317 greater update steps in μ_2 (see simulations in Hein et al., 2021). Similarly, greater levels of 318 tonic volatility on level 3, ω_3 , increase the update steps on μ_3 . See details on our priors in 319 **Table 3.** Using simulations to assess the accuracy of parameter estimation in the HGF₃, we 320 and others have previously demonstrated that ω_2 can be estimated accurately, while ω_3 is 321 not estimated well (Reed et al., 2020; Hein et al., 2021).

322 We then coupled the perceptual HGF model to a response model for binary outcomes, which 323 defined how beliefs about the tendency of the stimulus-outcome contingencies were mapped 324 onto decisions (e.g., which sequence should be chosen and played according to the beliefs 325 on the current trial; Mathys et al., 2014). Our response model was the unit-square sigmoid 326 observation model for binary responses (Iglesias et al., 2013; Mathys et al., 2014). This 327 model estimates on each trial k the probability that the agent's response y is either 0 or 1 (**Figure 2B**; $p[y^{(k)} = 1]$ and $p[y^{(k)} = 0]$), as a function of the predicted probability that the 328 329 icon/sequence is rewarding. This mapping from beliefs to decisions depends on the 330 response parameter ζ (interpreted as inverse decision noise). Higher ζ values indicate a 331 greater probability for the agents to select the option that is more likely to be rewarding 332 according to their beliefs. Simulations demonstrate that ζ is recovered well (Hein et al., 333 2021).

In the following, as stimuli (red and blue icons) are one-to-one associated with motor sequences (seq1 and seq2, respectively), we will use the term action-reward contingency when referring to stimulus-reward or stimulus-outcome mappings.

337

Figure 2

339 Models and priors

340 In line with previous work (Iglesias et al., 2013; Hein et al., 2021) we fitted the empirical data 341 with different models. We started by modelling our data with the HGF3 perceptual model + 342 sigmoid response model, as described above. In this model, the third hierarchical level 343 represents environmental volatility, that is the rate of change in the action-reward 344 contingencies. In our paradigm the true volatility was constant across participants, as the 345 reward contingencies changed approximately every 30-42 trials. In Study 1, using relatively 346 uninformative priors for ω_2 , ω_3 as in previous work (prior mean -4, -7, respectively; prior 347 variance 16 in both cases; Iglesias et al., 2017; de Berker et al., 2016; Hein et al., 2021) led 348 to numerical instabilities in the HGF_3 in 20% of our participants across all groups, in 349 particular in those exhibiting high win rates and thus learning well. The numerical instabilities 350 also manifested when using tight priors (small variance of 4 or 1 in the prior distribution of ω_2 , 351 ω_3), and when using prior values estimated in our data using an ideal observer model. An 352 ideal observer is typically defined as the set of parameter values that minimise the overall 353 surprise that an agent encounters when processing the series of inputs (see an application 354 of an ideal observer model in e.g., Weber et al., 2020). It is likely that the divergence of the 355 HGF₃ in 20% of our datasets is due to the trial number being smaller than in previous studies 356 using the HGF₃ (180 instead of 320 or 400). We therefore proceeded to use the 2-level HGF 357 (HGF_2) in all our three studies, in which beliefs on volatility on the third level are fixed. Priors for the perceptual HGF₂ model were chosen by simulating an ideal observer receiving the 358 359 series of inputs that the participants observed (Table 3). We then used the estimated posterior values on those model parameters as priors for the HGF₂ perceptual model 360 361 coupled with our response model. Complementing the HGF, we used two standard 362 reinforcement learning models, the Rescorla-Wagner model (RW; fixed learning rate 363 determined by PEs; Rescorla & Wagner, 1971) and Sutton K1 model (SK1; flexible learning 364 rate driven by recent PEs; Sutton, 1992). Priors for reinforcement learning models were set 365 according to previous literature (Diaconescu, 2014; Hein et al., 2021).

366 The different models (HGF₂, RW, SK1) were fitted to the trial-by-trial inputs and responses in 367 each participant using the HGF toolbox, which generates maximum-a-posteriori (MAP) 368 parameter estimates in each individual. To identify the model that explained the behavioural 369 data across all participants best, we used random effects Bayesian model selection (BMS, 370 through the freely available MACS toolbox https://github.com/JoramSoch/MACS; Soch & 371 Allefeld, 2018). Importantly, in Study 1 we used the same priors in all participant groups 372 (HYA, HOA, PD) as in previous studies (Powers et al., 2017; Hein et al., 2021). Note, 373 however, that recent computational modelling work suggests that using different prior values 374 in each participant group may be more suitable to capture dissociable group effects (e.g., for 375 mental health: Valton et al., 2020). This approach, albeit interesting, would not favour a 376 standard statistical comparison between groups: any between-group differences could be 377 explained by the underlying models having been constructed differently.

378

Table 3

379

380 Behavioural and computational data analysis

First, we validated the task by assessing (a) the percentage of trials that each sequence type was played (percPlayed) and (b) whether percPlayed followed the contingency changes. See details in Experimental design. We additionally examined the percentage of trials in which each sequence type was played without performance execution errors (percCorrectlyPlayed).

386 General task performance in each participant was assessed by analysing the percentage of 387 errors (percError: rate of sequences with performance execution errors due to one or several 388 wrong key presses), win rate (percWin: rate of trials in which the rewarded sequence is 389 played without execution errors), the average of the trial-wise performance tempo (mIKI in 390 ms: trial-wise mean of the three inter-keystroke-intervals [IKI] across four key presses within 391 the same trial; see Figure 1D for trial-wise mIKI in Study 1) and the mean of the trial-wise 392 RT (in ms: time interval between the fractal presentation and first key press). Importantly, 393 mIKI is commensurate with movement time (MT), the time between the first and last key

394 press (MT = mIKI * 3). Finally, we also assessed the number of sequence renditions that 395 participants completed during the familiarisation phase (rendFam: average of renditions 396 across both sequence types). Time out trials and trials with performance execution errors 397 were excluded from analyses on performance tempo and RT to avoid potential confounds, 398 such as slowing following errors (Herrojo Ruiz et al., 2009).

399 Next, to investigate decision-making processes we analysed group effects on three 400 computational variables that characterised learning in each individual. The model that best 401 explained the behavioural data across all participants according to BMS was the HGF₂ (see 402 Results section). We therefore assessed the perceptual model parameter ω_2 (subject-403 specific tonic volatility, which influences the speed of belief updating on level 2), ζ (the 404 decision noise of the response model), and the average across trials of σ_2 (posterior variance of the belief distribution). The quantity σ_2 is particularly interesting, as it represents 405 406 informational uncertainty about the tendency of the action-reward contingency. Moreover, 407 beliefs on level 2 are updated as a function of PEs about the stimulus-outcome mapping (the 408 mismatch between the observed outcomes u = 1 or 0 and the agent's beliefs about the 409 probability of such an outcome) and weighted by σ_2 (the precision ratio on level 2). 410 Accordingly, if agents are more uncertain about the contingencies governing their 411 environment, they will rely more on PEs to update their beliefs on that level.

To test our main research hypothesis that the strength of expectations about the actionreward contingency modulates the trial-by-trial motor performance, as a function of the group, we focused on the trajectory $\hat{\mu}_2$ (dropping trial index *k* for simplicity; prediction about the tendency of the action-reward contingency).

In Study 3, we also measured the explicit trial-wise confidence ratings (conf: number
between 0 and 99) about the reward outcome to assess whether motor performance was
sensitive to explicit beliefs about the reward tendency.

419

420 Statistical analyses

421 Bayesian analyses on Study 1

422 General task performance and computational variables

423 First, we calculated the mean and SEM as summary statistics for each of our general task 424 performance (mIKI, RT, percError, percWin, rendFam) and computation variables (ω_2 , ζ , σ_2). 425 Next, we evaluated between-group differences by computing Bayes Factors (BF) using the 426 bayesFactor toolbox (https://github.com/klabhub/bayesFactor) in MATLAB. This toolbox 427 implements tests that are based on multivariate generalisations of Cauchy priors on 428 standardised effects (Rouder et al., 2012). For each dependent variable (DV), we calculated 429 the BF on the model DV \sim 1 + group, where DV is explained by a fixed effect of group (HYA, 430 HOA, PD). The model was fitted using the fitlme function of the MATLAB Statistics toolbox. 431 Computing BF allowed us to quantify the evidence in support of the alternative hypothesis 432 (full model, in our case assessing the main effect of the group) relative to the null model (intercept-only model, i.e., $DV \sim 1$). BF values were interpreted as in Andraszewicz et al. 433 434 (2015). As BF is the ratio between the probability of the data being observed under the 435 alternative hypothesis and the probability of the same data under the null hypothesis, a BF of 436 20 would indicate strong evidence for the alternative hypothesis. On the other hand, BF of 437 0.05 would provide strong evidence for the null hypothesis (see Table 1 by Andraszewicz et 438 al., 2015 for further details). Accompanying the BF results, we provided the outcomes of 439 standard one-way analysis of variance (ANOVA) for completion. In the case of main effects being observed in the group-level BF analysis, we conducted follow-up BF analyses on 440 441 independent two-sample t-tests.

When analysing RT, we excluded outliers (RT values larger than three standard deviations above the mean) at the subject level. For BF analyses, we used the individual average across 180 trials for the mIKI, RT, and σ_2 variables. As mIKI and RT were not normally distributed, values were log-transformed (natural logarithm, log_mIKI and log_RT). The same preprocessing steps were applied to RT and mIKI values in Studies 2 and 3. The 447 number of renditions during the familiarisation phase was averaged between both types of448 sequence.

449 Sanity checks were performed to assess that participants chose to play each sequence as a 450 function of the inferred action-reward contingencies and not based on individual sequence 451 preferences. These were carried out by computing mean and SEM along with BF analyses 452 for paired t-tests on the percentage of trials each sequence type was (correctly) played 453 (percPlayed; percCorrectlyPlayed; outcomes of standard paired t-test reported for 454 completion). We also report the group mean and SEM of percPlayed by contingency phases, 455 which allowed us to observe whether participants' choices followed the changes in 456 contingencies over time.

457

458 Assessing the association between predictions about the action-reward contingency and 459 motor performance using Bayesian Linear Mixed Models

460 Our main goal was to investigate whether trial-by-trial sequence performance tempo (mIKI) 461 is modulated by the expectation about the tendency of the action-reward contingency ($\hat{\mu}_2$) in 462 our participant groups. In addition, we aimed to determine whether the group factor 463 modulated the sensitivity of performance tempo to $\hat{\mu}_2$, resulting in different slopes of the 464 association.

465 We addressed these questions by implementing a series of Bayesian Linear Mixed Models 466 (BLMM) in R (version 4.0.3). We used the Bayesian Regression Models using Stan (brms; 467 Bürkner. 2017: 2018: 2021) package, freelv available on 468 https://cran.r-project.org/web/packages/brms/index.html. Brms relies on the probabilistic 469 programming language Stan, which implements Bayesian inference using Markov Chain 470 Monte Carlo (MCMC) sampling methods to estimate approximate posterior probability distributions for model parameters. 471

472 In the HGF for binary categorical inputs, the sign of $\hat{\mu}_2$ (and similarly μ_2) is not informative, 473 as it represents the tendency of an action-reward mapping for an *arbitrary* action (e.g., for

474 seq1). Yet, we could similarly define the model in reference to the other action (e.g., seq2). 475 In line with previous work (Stefanics et al., 2018; Hein et al., 2022), we therefore took the 476 absolute value of $\hat{\mu}_2$ ($|\hat{\mu}_2|$) for our analysis to represent the strength of predictions about the tendency of the action-reward mapping. Trials with greater $|\hat{\mu}_2|$ values are trials in which the 477 478 participants will have a stronger expectation of receiving a reward, given they select the 479 correct action. Thus, $|\hat{\mu}_2|$ represents the *strength* of the predictions. In one participant (HYA), 480 we excluded $|\hat{\mu}_2|$ values of the last 27 trials, as the HGF trajectories diverged, despite the participant exhibiting normative learning patterns. Next, we centred the $|\hat{\mu}_2|$ values ($|\hat{\mu}_2 \lor \dot{\iota}|$ 481 482 c) to allow the intercept estimate for mIKI to reflect the average $|\hat{\mu}_2|$ value. As for Bayesian 483 ANOVAs (see General task performance and computational variables), mIKI was log-484 transformed to approach normality (log mIKI). In one HOA participant, two log mIKI values 485 were discarded from the analyses as they were not registered correctly in the JSON file (i.e., 486 represented an impossible value of mIKI ~ 50 ms).

In BLMM with brms, it is standard to select one group as reference for the parameter estimates. Brms then estimates the posterior distribution of parameter differences between each group and the reference group, as well as the posterior distributions of parameters in the reference group itself. We set HOA as the reference group, and therefore posterior distributions of between-group differences on response variables were assessed for HOA vs HYA and HOA vs PD.

493 We implemented six models of increasing complexity, with every model including a larger 494 number of explanatory variables (Table 4). For simplicity, in the following we used variable 495 label y to represent our dependent variable log mIKI, and x to represent the explanatory 496 variable $|\hat{\mu}_2 \vee_i i_c$. To answer our research questions, we primarily focused on: (i) the fixed 497 effect of x (sensitivity [slope] of the performance tempo to the strength of predictions about 498 the action-reward contingency in the reference group, HOA); and (ii) the interaction effect x * 499 group (differences between groups in the sensitivity [slope] of the performance tempo to the 500 strength of expectations about the action-reward mapping).

501 For each model we ran four independent chains with 5000 iterations each, of which the first 502 1000 were discarded as warmup. This resulted in a total of 16000 posterior samples. In all 503 models we used default prior distribution for the intercept, and a normal distribution for each 504 fixed and random effect (fixed effects for group and x, normal [0,2)]; interaction term group * 505 x, normal [0,1]; random effects for intercept by subject and intercept by trial, normal [0,2]; 506 random effect x by subject, normal [0,1]). The prior on the LKJ-Correlation, the correlation 507 matrices in brms (Lewandowski, Kurowicka, & Joe, 2009), was set to 2 as recommended in 508 Bürkner and colleagues (2017). Chain convergence was assessed using the Gelman-Rubin 509 statistics (R-hat < 1.1; Gelman and Rubin, 1992).

510 Models were compared using leave-one-out cross-validation of the posterior log-likelihood 511 (LOO-CV) with Pareto-smoothed importance sampling (Vehtari et al., 2017). The 512 identification of the best fitting model was based on the highest expected log point-wise 513 predictive density (ELPD). We also checked that the absolute mean difference in ELPD 514 between two models (elpd diff in brms) exceeded twice the standard error of the differences 515 (2*se diff). LOO-CV identified the most complex model (model number 6 in Table 4) as the 516 best fitting model (see Results section for further details). This model explained the 517 performance tempo as the interaction between groups and the strength of the expectation about the action-reward contingency (in addition to main effects). Further, it modelled the 518 519 effect of subjects on the intercept and $|\hat{\mu}_2 \vee_i \hat{c} c$ as a random effect, and the effect of trials on 520 the intercept as a random effect. We reported for each parameter the posterior point 521 estimate and the associated 95% credible interval (CI). See Results section for further 522 details.

Because reward expectations could also modulate RT as shown previously (Codol et al., 2020), we conducted additional analyses to assess the effect of $|\hat{\mu}_2 \lor i$ on RT trial-by-trial. Further, we evaluated whether the group factor influences the sensitivity of RT to $i\hat{\mu}_2 \lor i$. In these analyses, we followed the same procedure as for the sequence performance tempo analysis. In particular, the associations between RT (log-transformed) and $|\hat{\mu}_2 \lor_i i$ were

assessed by implementing and comparing six models of increasing complexity in brms (**Table 4**; see Results for further details). RT values three standard deviations above the mean were excluded from statistical analyses. This approach was also followed in Studies 2 and 3. As for performance tempo, in the results section we use the variable label y for the dependent variable (log RT) and x for $|\hat{\mu}_2 \vee_i \hat{c}c|$.

533

Table 4

534

535 Bayesian analyses on Study 2

536 As described above, in Study 2 participants were allocated to two different analysis groups 537 $(Q8_T \text{ and } Q8_F)$ depending on their answer to a post-performance question ("I could always 538 distinguish whether 0 points reflected a performance error or a bad decision", binary answer: 539 True/False). This allowed us to test the potential influence of subjective inferences about 540 task-related reward assignment on the motor invigoration effect observed in Study 1. 541 Specifically, we reasoned that participants who could not always infer the meaning of zero 542 might show a reduced sensitivity of motor performance by beliefs about the reward 543 tendency.

544 As for Study 1, we computed the mean and SEM as summary statistics for each dependent 545 variable. Next, we used the bayesFactor toolbox to calculate the evidence in support of (or 546 against) group differences in general task performance (mIKI, RT, percError, percWin) and 547 computational variables (ω_2 , ζ , σ_2). We intentionally did not analyse the rate of sequence 548 renditions during the familiarisation phase as here we were only interested in assessing the 549 role of subjective inferences about credit assignment on motor sequence performance 550 decision-making behaviour. We performed BF analysis on independent two-sample t-tests to 551 assess between group-differences on the variables of interest (results on standard 552 independent t-tests also reported for completion). RT and mIKI were log transformed and 553 followed the same preprocessing steps as described for Study 1.

Next, to test potential between-group differences in the mIKI- $\hat{i}\mu_2 \lor \hat{i}$ association, we implemented six BLMM of increasing complexity (same models as in Study 1, **Table 4**). As for Study 1, the most complex model (model number 6 in **Table 4**) was identified as the best fit by LOO-CV (see Results section for further details). The same procedure was used to investigate the associations between RT with $\hat{i}\mu_2\lor\hat{i}$.

559 Finally, we evaluated whether $Q8_T$ and $Q8_F$ differed in the rate of retrospective subjective 560 number estimate of performance errors. In particular, we were interested in assessing 561 between-group differences in the tendency of under/overestimating the number of performance errors. For each participant, the rate of subjective performance execution errors 562 563 (subjective percError) was calculated through the post-performance questionnaire (see 564 Questions 1,2,3 **Table 2**). We arbitrarily assigned a value of 0.028 (= 5/180) if subjects 565 thought to have committed less than 10 performance errors; 0.111 (= 20/180) for between 566 20 and 40 estimated performance errors; 0.222 (= 40/180) for more than 40 subjective performance errors. To assess whether this rough estimate of the percentage of 567 568 performance errors reflected a general over or underestimation of the true performance error 569 rate in the total sample (N = 39), we first conducted a BF analysis on the correlation between 570 the subjective and empirical error rates (Pearson's r coefficient and p-value reported for 571 completion). Next, we identified potential group-related systematic biases in the subjective 572 estimate. This was done with a BF analysis using independent two-sample t-tests on the 573 normalised rate of subjective errors ([subjective percError-percError]/percError; results on 574 standard independent t-tests reported for completion).

575

576 Bayesian analyses on Study 3

577 In Study 3, we aimed at assessing the association between trial-by-trial explicit beliefs about 578 the reward tendency (confidence ratings) and motor performance. We were particularly 579 interested in understanding whether being more certain (following Frömer et al, 2021) about 580 obtaining the reward—given the right choice—would speed up motor responses. 581 First, following the same steps as for Study 1 and 2, we calculated the mean and SEM as 582 summary statistics for the general task performance variables (mIKI, RT, percWin, conf). 583 Trial-by-trial confidence ratings were converted to a 0-0.99 scale.

584 We aimed to use the confidence rating as a predictor in our BLMM analyses to assess the 585 sensitivity of motor performance (mIKI and RT) to explicit beliefs about the reward tendency. 586 This was tested by implementing four BLMM of increasing complexity (**Table 4**).

As for Study 1 and 2, we used the label y to represent our dependent variable (mIKI or RT), and x for the explanatory variable (conf). To test our hypothesis, we specifically focused on the fixed effect of x (sensitivity [slope] of the motor performance to the confidence ratings about the predicted outcome). We used the same priors as in Study 1 for the corresponding factors. The most complex model number 4 and the model number 3 (**Table 4**) were identified as the best fit by LOO-CV for performance tempo and RT, respectively (see Results section for further details).

594 In addition, as a sanity check, we evaluated the association of confidence ratings with the 595 strength of predictions about the action-reward contingency trial-by-trial. The investigation of 596 motor vigour effects in Study 1 and 2 assumed that the unsigned $|\hat{\mu}_2|$ values estimated in 597 the HGF reflect the strength of participants' expectation on the reward tendency. However, 598 whether this HGF quantity reflects true explicit beliefs, assessed as confidence ratings, is not 599 clear. We evaluated the association between confidence ratings and the unsigned $|\hat{\mu}_2|$ 600 values using the formula conf ~ 1 + $|\hat{\mu}_2|_c$ + (1 + $|\hat{\mu}_2|_c$ |subj) + (1|trial) in brms. We chose a 601 default prior distribution for the intercept, and a normal distribution for the fixed and random 602 effects (fixed effect for $|\hat{\mu}_2|$ c, normal [0,2)]; random effects for intercept by subject and intercept by trial, normal [0,2]; random effect $|\hat{\mu}_2|$ c by subject, normal [0,1]). The prior on 603 604 the LKJ-Correlation was set to 2 as recommended in Bürkner and colleagues (2017).

Finally, we provided summary statistics for the number of empirical performance errors and the number of subjective performance errors (how many times the "z" key was pressed throughout the experiment). This aimed at expanding on the findings of Study 2, informing

- 608 about participants' ability to correctly identify performance errors and thus infer the task-
- 609 related credit assignment.

611 **RESULTS**

612 Study 1

613 Task validation

614 Participants played on average seq1 and seq2 50% of the trials (seq1: mean 0.490, SEM 615 0.008; seq2: mean 0.508, SEM 0.008). This suggests that they did not express a preference 616 towards a sequence type (percPlayed, BF = 0.2295, moderate evidence in support of the 617 null hypothesis for no differences in the percentage of performances by sequence type, $t_{(93)} =$ 618 -1.204, p = 0.232). Participants committed fewer performance execution errors in seq1 619 (mean 0.958, SEM 0.005) than seq2 (mean 0.922, SEM 0.008; percCorrectlyPlayed, BF = 620 1126.7, suggesting extreme evidence for alternative hypothesis that the rate of correct 621 performance differed in seq1 and seq2, $t_{(93)} = 4.576$, p < 0.001). Next, we observed that 622 percPlayed in each group successfully tracked the contingency changes over time. For true 623 contingencies sorted according to increasing values, [0.1, 0.3, 0.5, 0.7, 0.9], HYA 624 participants played the corresponding sequence at these rates: [0.18 (0.02), 0.33 (0.02), 625 0.48 (0.02), 0.67 (0.02), 0.81 (0.02)]. Similar values were obtained for HOA participants: 626 [0.18 (0.02), 0.34 (0.02), 0.48 (0.02), 0.62 (0.02), 0.79 (0.02)]; and for PD patients: [0.16 627 (0.02), 0.32 (0.03), 0.47 (0.03), 0.63 (0.03), 0.79 (0.03)]. Accordingly, task performance 628 demonstrated that each group of participants learned to flexibly adapt to the changing 629 contingencies over time.

630

631 General task performance

Overall, as expected, our analyses revealed between-group differences in performance tempo (mIKI in ms, HYA: 300, SEM:15.8; HOA: mean 424, SEM 19.6; PD: mean 537, SEM 26.9; **Figure 3A**), and reaction time (RT in ms, HYA: 634, SEM: 34.9; HOA: mean 838, SEM 49.4; PD: mean 918, SEM 77.5; **Figure 3B**), with movements progressively slowing down in ageing and PD patients. BF analyses on performance tempo yielded extreme evidence for a group effect (log_mIKI: BF = 1.1253e+09, demonstrating extreme evidence for the alternative hypothesis; $F_{(2,91)}$ = 35.332, p < 0.001). Post hoc pair-wise t-tests using BF

639 showed extreme evidence for between-group differences in HYA vs HOA (BF = 1.2044e+04) 640 and in HYA vs PD (BF = 3.3592e+07). We also found very strong evidence for the 641 alternative hypothesis in HOA vs PD (BF = 32.591). Thus, performance tempo (and 642 therefore movement time) was differently modulated between groups, with HYA being faster 643 than HOA and PD, and HOA faster than PD. Regarding RT, there was extreme evidence 644 supporting between-group differences (log RT: BF = 404.521; $F_{(2.91)}$ = 11.383, p < 0.001). BF 645 analysis on post hoc independent two-sample t-tests revealed extreme evidence for 646 between-group differences in HYA vs HOA (BF = 109.444) and HYA vs PD (BF = 239.335). 647 Yet, we only found anecdotal evidence in support of the null hypothesis in HOA vs PD (BF = 648 0.403). Hence, despite HYA displaying shorter RTs than HOA and PD, our analyses suggest 649 similar RTs in HOA and PD.

650 In addition, we found anecdotal evidence supporting that groups differed in the number of 651 sequence renditions during the familiarisation phase (rendFam, HYA: mean 5.6, SEM 0.1; HOA: mean 6.0, SEM 0.2; PD: mean 7.1, SEM 0.8; BF = 1.733; $F_{(2,91)}$ = 4.448, p = 0.014). 652 653 Post-hoc BF analyses to assess differences between pairs of groups revealed anecdotal and moderate evidence for between-group differences in HYA and HOA (BF = 1.900) and HYA 654 655 and PD (BF = 3.030), respectively. Still, HOA and PD practised the two sequences to a 656 similar extent (BF = 0.853, revealing anecdotal evidence for the null hypothesis). Of note, practising more during familiarisation was not associated with better win rates or average 657 performance tempo during task completion. A correlation analysis across all participants 658 between the number of repetitions during familiarisation and these variables demonstrated 659 some evidence for null correlation effects (percWin: BF = 0.290, Pearson r = -0.134, p = 660 661 0.200; log mIKI: BF = 0.397; Pearson r = 0.158, p = 0.131; note that we excluded one PD 662 patient who practised 21 times during familiarisation as outlier in this correlation analysis).

The group effects observed above were not accompanied by a dissociation between groups in the win rate or the rate of performance execution errors (**Figure 3C-D**). BF analysis on win rates provided moderate evidence for the lack of a group effect (percWin, HYA: mean 0.590, SEM 0.012; HOA: mean 0.561, SEM 0.014; PD: mean 0.553, SEM 0.021; BF = 0.210, supporting moderate evidence for the null hypothesis; $F_{(2,91)}$ = 1.848, p = 0.163). A similar outcome was observed in the analysis of performance execution error rates (percError, HYA: mean 0.061, SEM 0.009; HOA: mean 0.057, SEM 0.008; PD: mean 0.084, SEM 0.020; BF = 0.146, moderate evidence for the null hypothesis; $F_{(2,91)}$ = 1.456, p = 0.239). In sum, we found moderate evidence that HYA, HOA and PD did not differ in either the rate of win or error trials.

673

674 Computational parameters

675 Decision making was assessed by looking at between-group differences in the 676 computational variables ω_2 , ζ and σ_2 . After excluding the HGF₃ from model comparison due 677 to numerical instabilities, BMS was conducted on the HGF₂ and two reinforcement learning 678 models (RW, SK1) using the individual log-model evidence (LME) values provided by the HGF toolbox. The winning model was the HGF₂, with an exceedance probability of 0.95 and 679 680 an expected frequency of 0.90. Of note, although the HGF₃ model was not included in BMS, a qualitative comparison of LME values for the HGF₃ and HGF₂ models in the 80% 681 participants in which HGF₃ did not lead to numerical instabilities revealed extremely similar 682 683 values (LME differences < 1). This observation suggested that both models described behaviour in our task with constant true volatility to a similar degree. 684

685 Overall, we found no group effect on the signatures of reward-based learning and decision 686 making in our volatile task (Figure 3E-G). BF analysis on ω_2 demonstrated strong evidence 687 for the absence of a main effect of group (HYA: mean -1.332, SEM 0.282; HOA: mean -1.686, SEM 0.438; PD: mean -1.843, SEM 0.609; BF = 0.059; $F_{(2,91)} = 0.380 \text{ p} = 0.685$). 688 689 Similarly, we found strong evidence in favour of a lack of group effect on the informational uncertainty about beliefs on the tendency of the action-reward contingency, σ_2 (HYA: mean 690 691 1.610, SEM 0.177; HOA: mean 1.663, SEM 0.158; PD: mean 1.559, SEM 0.218; BF = 0.045; $F_{(2,91)} = 0.074$, p = 0.928). Last, groups exhibited a similar mapping from beliefs to 692 693 responses, driven by the response model parameter ζ (HYA: mean 1.735, SEM 0.191; HOA: 694 mean 1.523, SEM 0.176; PD: mean 2.095, SEM 0.469; BF = 0.114, demonstrating moderate 695 evidence for the null hypothesis; $F_{(2,91)}$ = 1.1495, p = 0.321).

696 A direct comparison between the Italian HOA subsample and (Italian) PD sample revealed 697 anecdotal or moderate evidence in support of the null hypothesis when assessing general 698 performance and decision-making variables (exception for log mIKI). These findings thus 699 converge with the outcomes of the full HOA sample analysis. On the other hand, the very 700 strong evidence in support of group effects on the performance tempo in the full sample was 701 only anecdotal when directly comparing Italian HOA and PD samples on this variable 702 (log mIKI: BF = 2.556; $t_{(42)}$ = -2.348, p = 0.024). These results suggested that Italian healthy 703 ageing was associated with slower performance tempo relative to UK healthy ageing 704 participants (log mIKI: BF = 6.637; $t_{(35)}$ = 2.871, p = 0.007; moderate evidence supporting 705 differences in performance tempo). Hence, between-group effects on general task performance and decision making cannot be accounted for by language differences. 706

707

Figure 3

708

709 Sensitivity of motor performance to the strength of expectations about the action-reward 710 contingency

711 For performance tempo, LOO-CV identified the most complex model (model number 6) as 712 the best fit. The absolute mean difference in ELPD between the winning model and the 713 second best fitting model (elpd diff) was -665.8557 and the standard error of the differences 714 (se_diff) equals 39.0404 (elpd_diff > 2*se_diff). When ELPD differences between two 715 models are larger than four, and also if the number of observations is > 100, and the model 716 is moderately well specified, then the standard error is a good estimate of the uncertainty in 717 the difference between models (Vehtari et al., 2017; Sivula et al., 2022). Posterior predictive 718 checks revealed that the best model had strong predictive power for the range of the DV 719 (Figure 4A). In the following we use variable label y to represent our dependent variable 720 log mIKI (in log-ms), and x to represent the explanatory variable $|\hat{\mu}_2 \vee_i \hat{c}$ c. **Table 5** presents 721 a summary of the posterior distributions for the winning model.

722

Table 5

723

724 First, we found that groups differed in performance tempo, as expected. This is in line with 725 our previous between-group analyses showing a progressive slowness in execution tempo in 726 HOA and PD. The posterior estimate for the intercept in the reference group, HOA, was 727 6.00, CI = [5.91, 6.09] (in ms, 404, CI = [368, 443]). The distribution of the differences 728 between intercepts in HOA and HYA had a posterior estimated value of -0.34, CI = [-0.47, -729 0.21 (in ms, -116, CI = [-163, -70]), while the distribution of the differences between 730 intercepts in HOA and PD yielded a posterior point estimate of 0.25, CI = [0.09, 0.41] (in ms, 731 114, CI = [41, 192]). As neither of the two distributions overlapped with zero, we concluded 732 that HYA performed the sequences faster than HOA, while PD was slower than HOA 733 (Figure 4B).

734 Next, we evaluated how the strength of predictions about the action-reward contingency 735 modulated performance tempo on a trial-by-trial basis. The analyses supported our hypothesis, showing that stronger expectations about the reward contingency invigorated 736 737 motor performance through faster execution tempo. Here, we focused on the distribution of 738 the fixed effect of x (slope of the association between y and x) in the reference group, HOA. 739 This distribution informs about the sensitivity of the performance tempo to the strength of 740 predictions about the action-reward contingency in HOA. The posterior estimate of x was 741 equal to -0.04, CI = [-0.07, -0.01]. As the distribution did not include zero, this highlights a 742 negative relationship between performance tempo and the strength of expectations about the action-reward contingency in the reference group (Figure 4C). 743

We were also interested in evaluating between-group differences in the sensitivity of performance tempo to the strength of expectations about the action-reward contingency. This was carried out by assessing the distribution of the interaction effect group * x on the slope. Both the posterior distributions of slope differences between HOA and HYA and between HOA and PD overlapped with zero, suggesting that the sensitivity was similar between groups (HOA vs HYA: posterior estimate = -0.00, CI = [-0.04, 0.04]; HOA vs PD:
posterior estimate = -0.00, CI = [-0.05, 0.04]; Figure 4D).

Overall, our BLMM analysis demonstrated that motor performance tempo was influenced trial-by-trial by the strength of predictions about the tendency of the action-reward contingency, with stronger expectations leading to faster execution tempo. However, the sensitivity of performance tempo to the strength of these predictions was not differently modulated between groups, suggesting that all groups could successfully use the inferred predictions to invigorate their motor performance to a similar degree.

757

Figure 4

758

759 In a separate analysis, we determined whether the motor invigoration effect extended to the 760 RT, reflecting the time to initiate the sequence performance (first key press). As for 761 performance tempo, LOO-CV identified model 6 as the best fit (elpd diff = -378.2718, se diff 762 = 30.69148; elpd diff > 2*se diff) and posterior predictive checks demonstrated good 763 predictive power for the range of the DV albeit less so than for performance tempo (Figure 764 5A). On the other hand, Gelman-Rubin statistics (R-hat values) demonstrated an excellent 765 chain convergence. Table 5 presents a summary of the posterior distributions for the 766 winning model.

767 Our brms analysis on the best fitting model revealed shorter RT in HYA compared to HOA, with no differences emerging between HOA and PD. The posterior point estimate for the 768 769 intercept in the reference group, HOA, was 6.65, CI = [6.54, 6.75] (in ms, 771, CI = [693, 6.75]) 770 856]). The distribution of the differences between intercepts in HOA and HYA was centred at 771 -0.28, CI = [-0.42, -0.13] (in ms, -188, CI = [-289, -88]), which did not overlap with zero. On 772 the other hand, the distribution of the differences between intercepts in HOA and PD yielded 773 a posterior point estimate of 0.09, CI = [-0.08, 0.27] (in ms, 77, CI = [-65, 231]) and included 774 zero (Figure 5B). These results demonstrated that HYA initiated the sequence faster than 775 HOA, consistent with our mIKI group results, whereas PD and HOA had a similar RT 776 intercept.

777 Regarding the association between the strength of predictions about the action-reward 778 contingency and RT, we observed no trial-by-trial modulation and no group effects. The 779 distribution of the fixed effect of x (slope of the association between y and x in the reference 780 group, HOA) had a posterior point estimate of -0.02, CI [-0.04, 0.01]. As the distribution's 781 centre overlapped with zero, this demonstrates that the strength of predictions about the 782 action-reward contingency did not modulate RT in this group (Figure 5C). Potential 783 between-group differences in the slope were assessed by investigating the distribution of the 784 interaction effect group * x. Both the posterior distributions of slope differences between 785 HOA and HYA and between HOA and PD included zero (HOA vs HYA: posterior estimate = 786 -0.01, CI = [-0.05, 0.03]; HOA vs PD: posterior estimate = -0.03, CI = [-0.07, 0.02]; Figure 787 **5D**). This outcome supported that the sensitivity of RT to the strength of expectations about 788 the reward mapping did not differ between groups. Thus, the strength of predictions about 789 the action-reward contingency invigorated performance tempo on a trial-by-trial basis without 790 affecting the RT.

791

Figure 5

792

793 Study 2

794 Subjective inference about task-related reward assignment

We conducted Bayesian analyses on the HYA sample of Study 2 to evaluate whether subjective inferences about the hidden causes for the absence of reward could modulate the motor invigoration effect observed in Study 1.

Overall, our analyses provided anecdotal and moderate evidence for the lack of differences between $Q8_T$ and $Q8_F$ in the main markers of general task performance (log_mIKI: BF = 0.417; $t_{(37)} = -0.795$, p = 0.432; log_RT: BF = 0.329; $t_{(37)} = 0.156$, p = 0.877; percWin: BF = 0.408; $t_{(37)} = 0.758$, p = 0.453; percError: BF = 0.596; $t_{(37)} = -1.252$, p =0.219; see **Figure 6A**-**D** for summary statistics).

Random effects Bayesian model selection yielded substantially greater evidence in favour of
 model HGF₂ (exceedance probability 0.94, and expected frequency 0.68). Using this model

to characterise decision-making processes in Q8_T and Q8_F samples, we observed that a BF analysis on ω_2 , ζ and σ_2 provided anecdotal evidence for the absence of a group effect (ω_2 : BF = 0.560; t₍₃₇₎ = -1.183, p = 0.244; ζ : BF = 0.445; t₍₃₇₎ = 0.895, p = 0.377; σ_2 : BF = 0.463; t_(.37) = -0.951, p = 0.348; see **Figure 6E-G** for summary statistics).

Hence, whether participants were *always* certain $(Q8_T)$ or not $(Q8_F)$ of the implications of receiving zero points, their general motor sequence performance and decision-making behaviour seemed similar, albeit this interpretation is based on anecdotal evidence.

812

Figure 6

813

We further investigated whether not being *always* sure about the causes for the lack of reward could impact the sensitivity of motor performance (mIKI and RT) to the strength of predictions about the action-reward contingency. As for the main experiment, LOO-CV identified the most complex model (model number 6) as the best fit (mIKI, elpd_diff = -144.9434, se_diff = 20.33661; elpd_diff > 2*se_diff; RT, elpd_diff = -106.3677, se_diff = 17.4019; elpd_diff > 2*se_diff). **Table 5** presents a summary of the posterior distributions for the winning models.

821 For performance tempo, the posterior predictive checks demonstrated a very strong 822 predictive power for the range of DV values in the best model (Figure 7A). Consistent with 823 our previous BF analyses on mIKI, the distribution of the differences between intercepts in 824 $Q8_T$ and $Q8_F$ overlapped with zero, suggesting that subjective inferences about credit 825 assignment did not impact performance tempo (Figure 7B). BLMM analyses also revealed a 826 negative association (slope) between the strength of predictions about the action-reward 827 contingency and performance tempo. This replicates our findings in Study 1, showing that 828 stronger predictions about the reward contingencies are followed by faster execution tempo 829 (Figure 7C). Yet, no between-group slope differences were observed. Thus, subjective 830 inferences about the causes for the absence of reward did not modulate the sensitivity of 831 performance tempo to the strength of expectations about the action-reward contingency832 (Figure 7D).

Figure 7

833

834

835 Regarding RT, the predictive power for the range of RT values was weaker compared to 836 performance tempo (Figure 8A), yet Gelman-Rubin statistics demonstrated an excellent 837 chain convergence (R-hat values equal to 1.00). BLMM analyses showed no differences 838 between $Q8_T$ and $Q8_F$ (intercepts) on RT, which is in line with our BF results (Figure 8B). 839 We found no robust evidence for an association (slope) between the strength of predictions 840 about the action-reward contingency and RT (Figure 8C). The 95% CI of the slope 841 distribution ranged from -0.04 to 0.00. A closer look at the upper bound of the distribution 842 including three decimal digits revealed a value of 0.002, demonstrating that 0 was marginally 843 part of the 95% CI. This outcome suggests that RT is not robustly modulated by the strength 844 of predictions about the action-reward contingency, unlike performance tempo.

No between-group slope differences were observed. Thus, as for performance tempo, subjective inferences about credit assignment did not modulate the association between RT and the strength of expectations about the action-reward contingency (**Figure 8D**).

848

Figure 8

849

850 Finally, we investigated the effect of differences in inferences about reward assignment on 851 the post-performance subjective error rate. First, the subjective error rate estimation was 852 validated by computing BF analysis on the correlation between subjective and empirical 853 error rates. Results provided strong evidence for a positive association in the full sample (N = 39; BF = 10.204; r = 0.448, p = 0.004). Next, we found no support for between-group 854 855 differences in the subjective error rate (BF = 0.432, demonstrating anecdotal evidence for 856 the null hypothesis; $t_{(36)} = -0.850$, p = 0.401). Thus, being not *always* sure about the causes 857 for the lack of reward did not influence the rate of subjective number estimate of 858 performance errors.

859 To conclude, our analyses provided evidence for the lack of differences between Q8_T and 860 $Q8_{F}$ in the evaluated parameters, suggesting that subjective inferences about task-related 861 credit assignment do not modulate decision-making, general motor performance or the 862 association between expectation on reward probability and motor vigour. Thus, even if the 863 groups in Study 1 would have had differences in credit assignment, it is unlikely that this 864 would have led to a modulation of group effects. In addition, here we found further support 865 for our main research hypothesis, whereby stronger predictions about the action-reward 866 contingency enhanced motor vigour through faster movement.

867

868 Study 3

869 Sensitivity of motor performance to confidence ratings about reward

In this study we focused our BLMM analysis on the association between motor performance
(mIKI and RT) and confidence ratings to investigate how explicit beliefs about the reward
outcome modulated motor vigour. **Table 5** presents a summary of the posterior distributions
for the winning models.

874 For performance tempo, LOO-CV identified the most complex model (model number 4) as 875 the best fit (mIKI, elpd_diff = -112.4178, se_diff = 15.74263; elpd_diff > 2*se_diff). The 876 posterior predictive checks demonstrated that the observed outcome variable y overlapped 877 well with the simulated datasets y^{rep} from the posterior predictive distribution (Figure 9A). The y distribution exhibited two peaks, however, denoting two modes of mean performance 878 tempo in our sample. The BLMM analyses showed a negative association (slope) between 879 880 the confidence ratings and the performance tempo, with stronger explicit beliefs about the 881 reward tendency speeding up performance (Figure 9B). The slope estimate was -0.04 (95% 882 Cl from -0.08 to -0.001, including three decimal digits in the upper bound; Figure 9C).

In the case of RT, LOO-CV identified the model number 3 as the best fit (elpd_diff = -45.046830, se_diff = 18.255767; elpd_diff > 2*se_diff). This model did not include trials as random effect. The posterior predictive checks showed in this case that the y and y^{rep} distributions overlapped perfectly (**Figure 9D**). As opposed to performance tempo, we found no robust modulation of RT by confidence ratings (Figure 9E). The 95% CI of the slope
distribution ranged from -0.20 to 0.01. Thus, a zero effect was a credible value of the slope
distribution (Figures 9F).

890 Overall, these results support the conclusion that being more certain about obtaining the 891 reward speeds up performance tempo—and thus movement time—without having a clear 892 effect on RT. This expands our previous findings on the computational parameter $|\hat{\mu}_2 \vee_i ic$, 893 supporting a motor invigoration effect by explicit beliefs about the reward tendency under 894 volatility.

895 In a separate sanity check, we assessed whether our measure of confidence was correlated 896 with $|\hat{\mu}_2 \vee \hat{\iota}|$ in the HGF₂. This would suggest that implicit beliefs about the tendency of the 897 action-reward contingency-captured with computational modelling-can be a proxy for 898 explicit ratings about the confidence of reward delivery. Indeed, a BLMM analysis demonstrated a strong association between $|\hat{\mu}_2 \vee \hat{\iota}|$ and confidence ratings. The posterior 899 900 point estimate for the intercept was 0.53, CI = [0.47, 0.59]. The distribution of the fixed effect 901 of the association between $|\hat{\mu}_2 \vee \hat{i}|$ and the confidence ratings had a posterior point estimate 902 of 0.09, CI [0.04, 0.14]. R-hat values were below 1.1, indicating chain convergence (Gelman 903 and Rubin, 1992).

Last, descriptive statistics of performance variables in this task revealed values consistent with HYA samples in Studies 1 and 2 (mIKI, in ms, mean 335, SEM 14.4; RT, in ms, mean 662, SEM 26.7; percWin, mean 0.542, SEM 0.011; conf, mean 0.527, SEM 0.028). Also, out of the 180 trials, participants made 9.1 (SEM 1.6) performance errors on average, while they subjectively reported making 4.8 (SEM 0.7) errors. Thus, they subjectively reported only 53% of the performance errors they committed.

910 **DISCUSSION**

911 We investigated how predictions about the tendency of the action-reward contingency 912 invigorated motor performance trial-by-trial in healthy younger adults (HYA), in medicated 913 Parkinson's Disease patients (PD), and in an age-matched sample of healthy older adults 914 (HOA). The task was a combination of a standard one-armed bandit decision-making 915 paradigm with a motor sequence task. We fitted the trial-by-trial behavioural data using the 916 Hierarchical Gaussian Filter (HGF; Mathys et al. 2011, 2014; Frässle et al., 2021) and 917 performed Bayesian analyses (Bayes Factor and Bayesian Linear Mixed Models [BLMM]).

918 Study 1 showed a trial-by-trial modulation of performance tempo-commensurate with 919 movement time—by the strength of expectations about the action-reward contingencies. The 920 invigoration effect was limited to performance tempo and was not observed for reaction time (RT). Moreover, BLMM revealed a similar sensitivity of performance tempo to these 921 922 predictions in our three groups. This provides compelling evidence for a preservation of 923 motor invigoration by expectations of reward probability in HOA and PD, expanding the 924 understanding on how reward sensitivity and reversal learning interact to modulate motor 925 vigour in ageing and medicated PD.

926 Previous investigations of the beneficial effects of reward on motor behaviour (e.g., faster 927 and more accurate motor performance; Sedaghat-Nekad et al., 2019) have been limited to 928 manipulations of reward magnitude (presence/absence: large/small) in deterministic contexts 929 (Codol et al., 2020; Sporn et al., 2022; Aves et al., 2021). Our findings expand on 930 computational work that demonstrated the updating of beliefs in a perceptual task to speed 931 RT (Marshall et al., 2016). The authors found that, as participants learned to track the 932 transition probabilities between stimuli, different decision-making variables affected RT. Our 933 results show that the trial-by-trial influence of motor vigour by belief updating can be 934 extended beyond the perceptual domain to learning about action-reward contingencies.

Despite the preserved motor invigoration effect in HOA and PD, we found extreme evidence 935 936 for between-group differences in the mean performance tempo. HYA were faster than HOA 937 and PD, and HOA quicker than PD. The slower sequence execution in HOA is consistent 938 with a general slowness of hand movements in later stages of life (Ketcham et al., 2002; 939 Aves et al., 2021). Regarding PD, the slower performance is likely explained by a sequence 940 effect (SE). SE is a common bradykinetic symptom in PD, which manifests through slower 941 and attenuated sequential movements (Kang et al., 2010). Dopamine (DA) intake does not 942 ameliorate symptoms associated with SE, suggesting a non-DA involvement in the 943 pathophysiology of this effect (Bologna et al., 2016). Similar results were found for RT, with 944 HYA displaying shorter RT than HOA and PD. Yet, RT did not dissociate between HOA and 945 PD.

946 We additionally found evidence for similar win and error rates in our three groups. Empirical 947 findings on reward learning in ageing and medicated PD have been mixed. Some studies 948 have shown reduced probabilistic and reversal learning in older adults and PD ON 949 medication, suggesting difficulties in establishing new stimulus-outcome associations and 950 updating reward beliefs (Cools et al., 2001; Eppinger et al., 2011; Nassar et al., 2016). 951 Consistent with this, de Boer et al. (2017) demonstrated poorer probabilistic reversal 952 learning in ageing compared to young participants, with the attenuation of the anticipatory 953 values signals in the prefrontal brain accounting for the impoverished performance. 954 However, other work argued for preserved reward sensitivity and learning in older adults and 955 medicated PD (Fera et al., 2005; Euteneuer et al., 2009; Aves et al., 2021). Specifically, PD 956 ON medication have been found to successfully learn from rewards, and exhibit deficits in 957 reversal learning exclusively for negative feedback (Frank et al., 2004; Levy-Gigi, 2019). 958 Also, Hird et al. (2022) reported that age does not modulate the invigorating effect of reward

959 on motor responses. This is consistent with our findings, highlighting a preserved motor 960 invigoration effect by reward in ageing and medicated PD.

961 Our groups did not differ in the main markers of decision making. We provided some 962 evidence for the absence of a group effect on tonic volatility (ω_2 ; index of individual learning 963 about the action-reward mapping under volatility [Hein et al., 2021]), estimated uncertainty 964 about the action-reward tendency (σ_2) and on the mapping from beliefs to responses (ζ). 965 Accordingly, belief updating in our task with changing action-reward contingencies was 966 comparable across HYA, HOA and PD groups.

967 One aspect that was not identified in Study 1 was whether participants correctly inferred the 968 hidden causes for the lack of reward (McDougle et al., 2016). Study 2 demonstrated that 969 retrospective subjective inference about credit assignment did not contribute to differences in 970 general motor performance, decision making, motor vigour or the subjective estimate of 971 performance errors. Because the feedback that participants received was veridical (unlike in 972 McDougle et al., 2016), the effects of misattribution of the causes of zero reward in our study 973 are likely very small, as the anecdotal evidence suggests. A limitation of this study, however, 974 was that it relied on retrospective self-report. Accordingly, we conducted a third study to 975 determine whether trial-by-trial explicit beliefs about the reward tendency (confidence 976 ratings) are associated with faster motor performance.

977 Study 3 demonstrated that performance tempo is associated with confidence ratings trial-by-978 trial: being more certain about obtaining the reward speeded up the movement. Moreover, 979 the confidence ratings were robustly correlated with the strength of the predictions. This 980 outcome supports that implicit beliefs about the tendency of the action-reward contingency— 981 captured with computational modelling—can be a proxy for explicit ratings about the 982 confidence of reward delivery.

The invigoration effect of beliefs (both implicit and explicit) did not extend to RT. Accordingly, across our three studies, RT was not robustly modulated in the same dynamic trial-wise manner as performance tempo was. In Study 1 and 2, RT included deliberation time (no constraints on initiating the sequence), which could have introduced noise to the RT distribution and weakened the motor vigour effects. By contrast, RT in Study 3 excluded deliberation time.

989 According to current hypotheses, motor vigour is based on trading-off future efforts and 990 gains, reflecting a subject's willingness to invest energy to harvest future rewards (Shadmehr 991 et al., 2010; Yoon et al., 2020). Specifically, it increases when the option is inferred to be 992 valuable and decreases for perceived effort. This has been demonstrated both for movement 993 times and RT (Summerside et al., 2018, Codol et al., 2020). It follows that changes in vigour 994 should be modulated by inferences on the tendency of reward probability. We demonstrated 995 that exclusively performance tempo-commensurate with movement time-is affected by 996 beliefs about the action-reward contingency on a trial-by-trial basis. The lack of robust 997 invigoration effects on RT is consistent with sequential planning effects introducing noise to 998 the RT distribution. Recent work has demonstrated that the preparatory state of discrete 999 sequential finger movements reflects sequence planning skills (Mantziara et al., 2021). 1000 Accordingly, RT in our task would include trial-by-trial variability in sequence preparation, 1001 which may mask the underlying motor vigour effects. A prediction for future work would be a 1002 trial-by-trial invigoration of RT, beyond movement time, in motor tasks that do not require 1003 preparation of discrete movements.

A limitation of the present work is that, due to the nature of our online experiment, we only tested PD ON medication. Future work should investigate the effect of DA on the trial-by-trial association between the expectations of reward probability and motor vigour. Interestingly, a recent study by Hird et al. (2022) found only a weak association between dopamine D1

receptor availability and the invigorating effect of reward. This outcome, together with our finding of preserved dynamic motor vigour effects in medicated PD, raises an interesting question: if motor vigour and learning are driven by the dopaminergic system as previously postulated (Balleine et al., 2007; Eppinger et al., 2011), how robust is this association in more complex scenarios rich in uncertainty and with changing reward probabilities over time? Our results suggest that DA-replacement therapy could restore putative decisionmaking deficits during learning in volatile environments in PD.

1015 In addition, the interplay between dynamic decision making and motor performance might be 1016 driven by several neurotransmitter systems linked to precision weighting of prediction errors 1017 during belief updating: acetylcholine (Moran et al., 2013); noradrenaline (Dayan and Yu, 1018 2006); in addition to dopamine (Iglesias et al., 2013; Haarsma et al., 2021). On a neural 1019 level, learning uncertain stimulus-reward contingencies relies on the ACC, OFC, and 1020 portions of the mPFC (Hayden et al., 2011; Rolls et al., 2019; Rouault et al., 2019). The 1021 mPFC is also involved in mapping beliefs to actions during exploration-exploitation 1022 (Domenech et al., 2021). Follow-up neuroimaging studies could assess the role of these 1023 regions in the motor vigour effects reported here, including the preserved effects in ageing 1024 and PD.

To conclude, this study is the first to demonstrate that inferring the probabilistic reward mappings positively biases motor performance through faster performance tempo. Additionally, we provided novel evidence for a preserved sensitivity of the motor invigoration effects in HOA and PD. Thus, healthy young, old and medicated PD can similarly obtain benefits in their motor performance when updating beliefs about the volatile action-reward contingencies.

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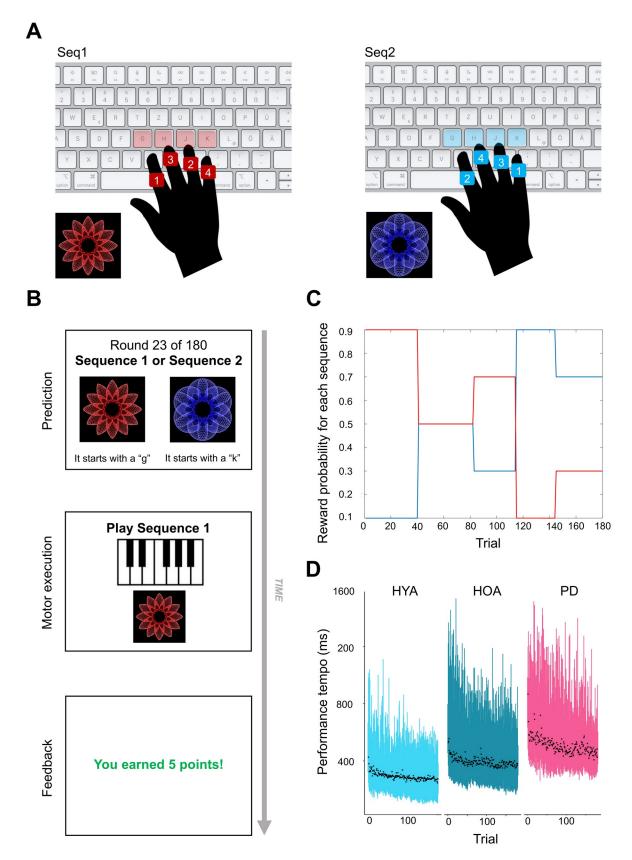
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1241 Figure 1. Task structure. A, In the task familiarisation phase participants learnt to play two 1242 sequences associated with two images (red fractal - seq1 "g-j-h-k"; blue fractal - seq2 "k-g-1243 j-h"). B. On each trial of the reward-based learning phase, subjects decided which sequence 1244 to play in order to get the reward. The two icons were always either red or blue and presented to the left or right part of the screen, respectively. First, participants made a 1245 1246 prediction about which sequence (associated to the corresponding icon) was more likely to 1247 give them a reward. When a decision was reached, they played the corresponding sequence 1248 using the keyboard. Finally, the outcome (win +5p or 0p) was revealed. In the example, the 1249 participant played seq1 and obtained five points, suggesting correct prediction and 1250 execution. In Study 3, participants were instructed to rate how certain they were of being 1251 rewarded on each trial after they performed their chosen sequence. Confidence ratings were 1252 provided by typing any number between 0 and 99 (not shown in the figure). C, Displays the 1253 typical subject-specific mapping of probabilistic stimulus-outcome contingency over the 1254 course of 180 trials. In the example, the order of reward mappings for the blue icon (and 1255 corresponding seq2) is 10-50-30-90-70% (reciprocal for red icon and corresponding seq1). 1256 In order to obtain the maximal reward, participants needed to track these changes and adapt 1257 their choices throughout the experiment. **D**, The trial by trial changes in performance tempo 1258 in ms (mIKI; mean inter-keystroke-intervals; see Behavioural and computational data 1259 analysis section for further details) for healthy younger adults (HYA; light blue), healthy older 1260 adults (HOA; dark blue) and patients with Parkinson's Disease (PD; in purple) across 180 1261 trials in Study 1. Black dots represent the trial-by-trial within-group averages of performance 1262 tempo. Bars indicate 95% interval probabilities. Participants tended to play the sequences 1263 faster towards the end of the experiment, possibly reflecting a practice effect.

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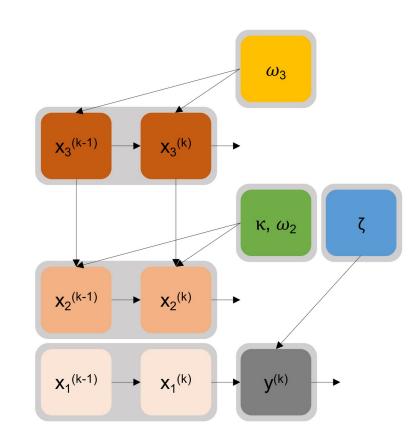
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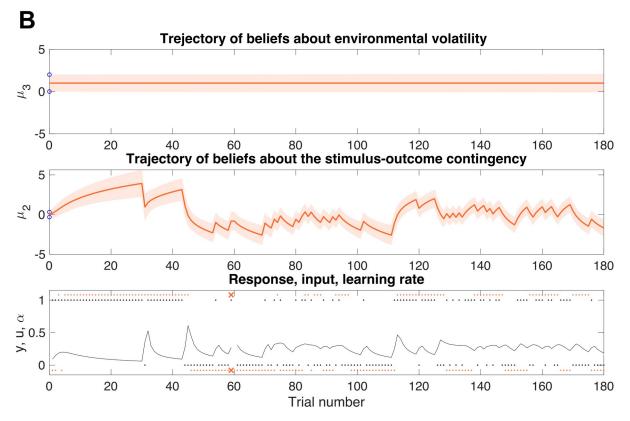
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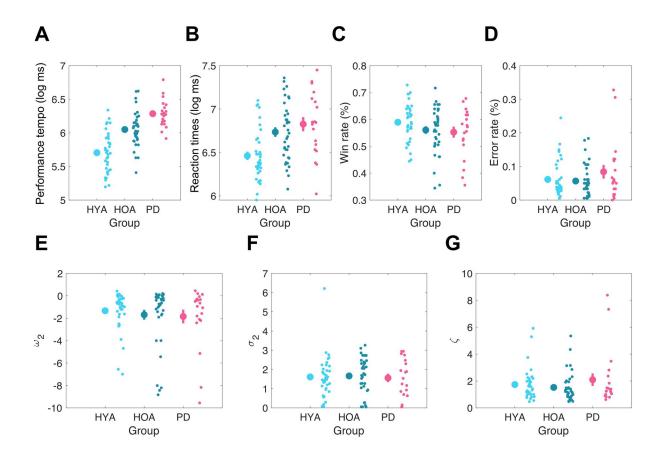






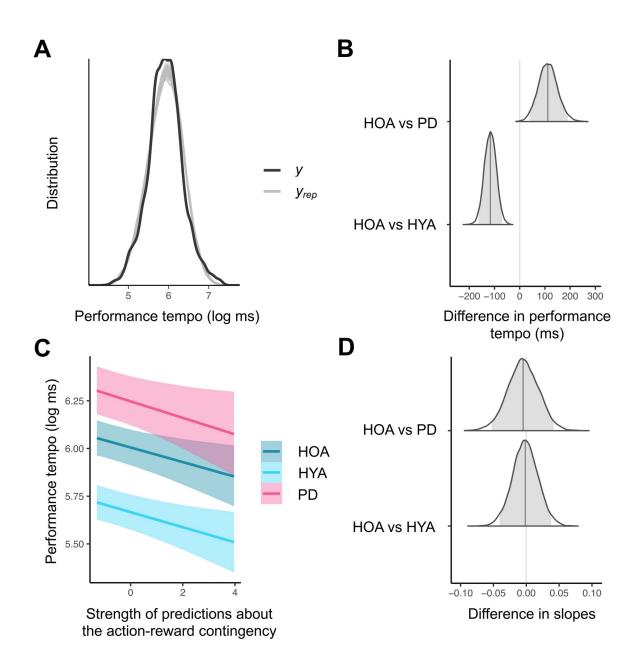


1271 Figure 2. The Hierarchical Gaussian Filter (HGF) for binary outcomes. A, Illustration of 1272 the 3-level HGF model (HGF₃) with relevant parameters modulating each level (adapted 1273 from Hein et al., 2021). Level x_1 represents the binary categorical variable of the 1274 experimental stimuli on each trial k; x_2 reflects the true value of the tendency of the stimulus-1275 outcome contingency, and x_3 the true volatility of the environment. In our experiment, ω_2, ω_3 1276 and ζ were free parameters and were estimated by fitting individual responses and observed 1277 inputs with the HGF. κ represents the strength of coupling between level 2 and 3 (fixed to 1 1278 in our study; not shown in the text; see Mathys et al., 2014 for the model equations). B, 1279 Belief trajectories for the HGF₃ across the total 180 trials in a representative participant in 1280 Study 1. At the lowest level, black dots (u) represent the outcomes, denoting whether seq1 1281 was rewarded or not (1 = seq1 wins [seq2 loses]; 0 = seq2 wins [seq1 loses]); orange dots1282 (y) represent the participant's choices (1 = seq1 is played; 0 = seq2 is played); orange 1283 crosses depict performance execution errors; the black line is a subject-specific learning rate 1284 about stimulus outcomes (α ; see Mathys et al. 2014 for the full HGF equations). At the 1285 second level, $\mu_2(\sigma_2)$ is the trial-by-trial trajectory of beliefs (mean and variance) about the 1286 tendency of the stimulus-outcome contingencies (x₂). A mean estimate μ_2 shifted towards 1287 positive values on the y-axis indicates that the participant had a greater expectation that 1288 seq1 was rewarded relative to seq2. In addition, larger (absolute) μ_2 values on that axis 1289 denote a stronger expectation that given the correct sequence choice a reward will be 1290 received. The trajectory of beliefs about phasic (log)volatility (μ_3 [σ_3]) is displayed at the top 1291 level. The true volatility in our task, x_3 , was constant, as the stimulus-outcome contingencies 1292 changed every 25-35 trials. Participants could, however, express individual differences in 1293 their log-volatility estimates, which could be captured by the HGF₃ (e.g., Powers et al., 1294 2017). In our three studies, the winning model was the 2-level HGF (HGF₂), in which volatility 1295 was fixed across participants. Blue circles on the y-axis denote the upper and lower priors of 1296 the posterior distribution of beliefs, $\mu_i^{(0)} \pm \sigma_i^{(0)}$, *i* = 2,3.



1299 Figure 3. Markers of general task performance and decision making across groups. 1300 Data presented for healthy younger adults (HYA; in light blue), healthy older adults (HOA; in 1301 dark blue) and patients with Parkinson's Disease (PD; in purple) in Study 1. A, Performance 1302 tempo (mIKI, mean inter-keystroke-interval, in ms); **B**, Reaction time (RT, in ms); **C**, Rate of 1303 win trials (percWin); **D**, Rate of performance execution errors (percError); **E**, Tonic volatility 1304 (ω_2) ; **F**, Informational uncertainty on level 2 (σ_2) ; **G**, Response model parameter (ζ). Values 1305 mIKI, RT and σ_2 are averaged across 180 trials within each participant. mIKI and RT values 1306 are log-transformed. In every plot, to the right of each mean (large dot) and standard error of 1307 the mean (denoted by the vertical bar) the individual data points in each group are shown to 1308 visualise group population variability.

- 1309
- 1310
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1313 Figure 4. Invigoration of performance tempo by beliefs is preserved in healthy ageing 1314 and in Parkinson's disease. Bayesian Linear Mixed Model (BLMM; model number 6, y ~ 1 + group * x + [1 + x|subject] + [1|trial]) with healthy older adults (HOA) as the reference 1315 1316 group in Study 1. A, Illustration of the posterior predictive checks where the distribution of 1317 the observed outcome variable (y, in our case performance tempo) is compared to simulated 1318 datasets (y_{rep}) from the posterior predictive distribution (100 draws). **B**, Distributions of the 1319 difference in ms between performance tempo (intercept) in HOA and healthy younger adults 1320 (HYA), and in HOA and patients with Parkinson's Disease (PD). For each distribution, the

grey vertical bar indicates the posterior point estimate, while the grey area under the curve represents the 95% credible interval (CI). In the current plot, CIs do not overlap with zero (the null hypothesis). This indicates that there is a 95% probability of between-group differences in performance tempo. C, Results of the BLMM analysis. We analysed how the strength of predictions about the action-reward contingency modulates performance tempo separately for HYA (in light blue), HOA (in dark blue) and PD (in purple). Here, mIKI (performance tempo: mean inter-keystroke-interval) values are represented in the log-scale. The negative slopes suggest that stronger predictions about the action-reward contingency are associated with faster performance tempo. D, Distributions of the difference between slopes in HOA vs HYA, and HOA vs PD. Here, as CIs include zero we can conclude with 95% probability that groups do not differ in how the strength of predictions about the reward contingency influences motor performance tempo. Thus, the sensitivity of performance tempo to the strength of predictions about the reward mapping is not differently modulated between groups.

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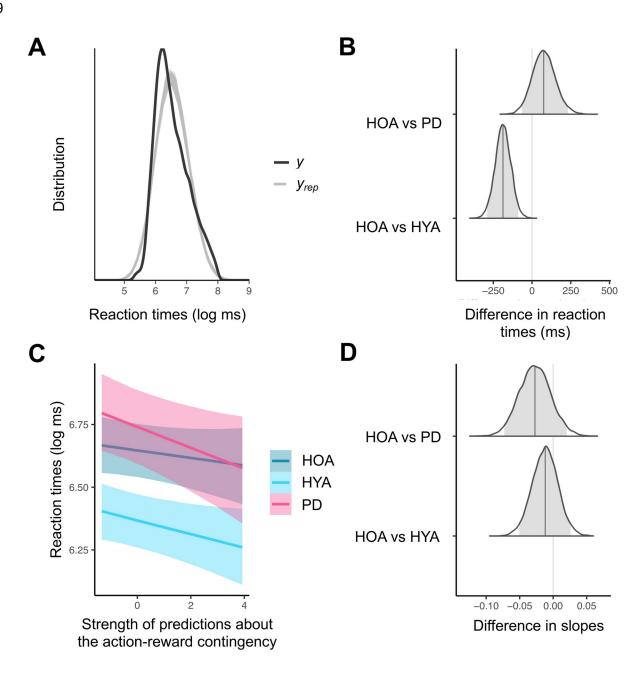
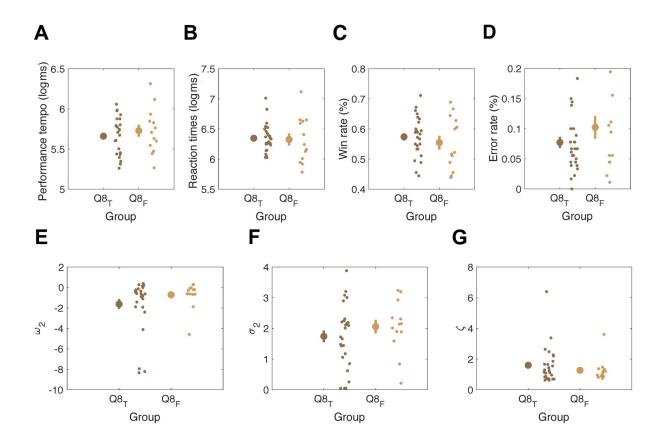
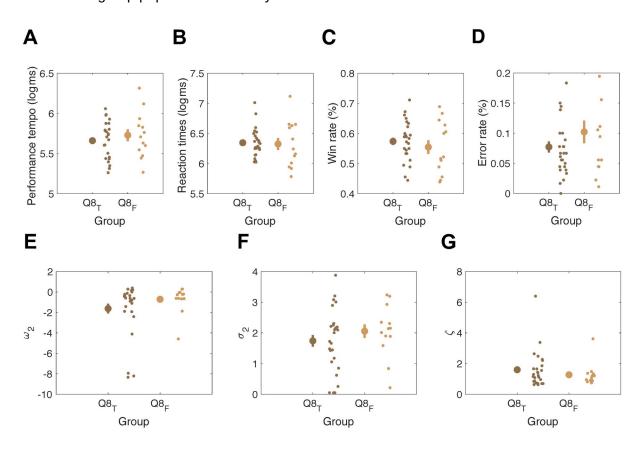


Figure 5. Motor vigour effects on reaction times across healthy young, older and Parkinson's participants. Bayesian Linear Mixed Model (BLMM; model number 6, $y \sim 1 +$ group * x + [1 + x|subject] + [1|trial]) with healthy older adults (HOA) as the reference group in Study 1. *A*, Illustration of the posterior predictive checks where the distribution of the observed outcome variable (y, in our case reaction times [RT]) is compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). *B*, Distributions of the difference in ms between RT (intercept) in HOA and healthy younger adults (HYA), and in HOA and patients with Parkinson's Disease (PD). For each distribution, the grey vertical bar indicates the posterior point estimate, while the grey area under the curve represents the 95% credible interval (CI). In the current plot, CI of the bottom distribution does not overlap with zero (the null hypothesis). This indicates that there is 95% probability of between-group differences in RT. On the other hand, the distribution at the top includes zero. This suggests that there is 95% probability of HOA and PD not differing in RT. C, Results of the BLMM analysis. We analysed how the strength of predictions about the action-reward contingency modulates RT separately for HYA (in light blue), HOA (in dark blue) and PD (in purple). Here, RT values are represented in the log-scale. We found no modulation of RT by the strength of expectations about the reward mapping. D, Distributions of the difference between slopes in HOA vs HYA, and HOA vs PD. Here, as CIs include zero we can conclude with 95% probability that groups do not differ in how the strength of predictions about the reward contingency influences RT. Thus, the sensitivity of RT to the strength of predictions about the reward mapping is not differently modulated between groups.



1386 Figure 6. Effect of retrospective credit assignment on general task performance and 1387 decision making. Markers of general task performance and decision making in participants 1388 that replied True to Question 8 (Q8_T; in dark brown) and participants that replied False to 1389 Question 8 (Q8_F; in light brown) in the post-performance questionnaire (see **Table 2**) in 1390 Study 2. **A**, Performance tempo (mIKI, mean inter-keystroke-interval; in ms, Q8_T: mean 287, 1391 SEM 13.2; O8_F: mean 307, SEM 27.2); **B**, Reaction times (RT; in ms, O8_T: mean 564, SEM 1392 30.5; Q8_F: mean 555, SEM 68.7); **C**, Rate of win trials (percWin; Q8_T: mean 0.574, SEM 1393 0.013; Q8_F: mean 0.555, SEM 0.024); **D**, Rate of performance execution errors (percError; 1394 $O8_{T}$: mean 0.077, SEM 0.010; $O8_{F}$: mean 0.102, SEM 0.020); *E*, Tonic volatility, (ω_2 ; $O8_{T}$: 1395 mean -1.624, SEM 0.510; Q8_F: mean -0.715, SEM 0.357); F, Informational uncertainty on 1396 level 2 (σ₂; Q8_T: mean 1.740, SEM 0.203; Q8_F: mean 2.057, SEM 0.237); **G**, Response 1397 model parameter, (ζ ; Q8_T: mean 1.599, SEM 0.237; Q8_F: mean 1.271, SEM 0.206). Values 1398 mIKI, RT and σ_2 are averaged across 180 trials within each participant. mIKI and RT values 1399 are log-transformed. In every plot, to the right of each mean (large dot) and standard error of the mean (denoted by the vertical bar) are displayed the individual data points in each groupto visualise group population variability.



1402 Figure 7. No effect of retrospective credit assignment on motor vigour: performance **tempo.** Bayesian Linear Mixed Models (BLMM; model number 6, $y \sim 1 + \text{group} * x + [1 + x]$ 1403 1404 subject] + [1|trial]) with participants that replied True to Question 8 (Q8_T; see **Table 2**) as 1405 reference group in Study 2. A, Illustration of the posterior predictive checks where the 1406 distribution of the observed outcome variable (y, in our case performance tempo) is 1407 compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). 1408 **B**, Distribution of the difference in ms between performance tempo (intercept) in $Q8_T$ and in 1409 participants that replied False to Question 8 ($Q8_{F}$; see **Table 2**). The grey vertical bar 1410 indicates the posterior point estimate, while the grey area under the curve represents the 1411 95% credible interval (CI). In the current plot, CI does overlap with zero (the null hypothesis). 1412 This indicates that there is 95% probability of no between-group differences in performance 1413 tempo. C, Results of the BLMM analysis. We analysed how the strength of predictions about

1414 the action-reward contingency modulates performance tempo separately for Q8_T (in dark 1415 brown) and Q8_F (in light brown). Here, mIKI (performance tempo: mean inter-keystroke-1416 interval) values are represented in the log-scale. The negative slopes suggest that stronger 1417 predictions about the action-reward contingency are associated with faster performance 1418 tempo, which replicates our findings in the main experiment (see Figure 4C). D, Distribution 1419 of the difference between slopes in $Q8_T$ and $Q8_F$. Here, as CIs include zero we can conclude 1420 with 95% probability that groups do not differ in how the strength of predictions about the 1421 reward contingency influences motor performance tempo. Thus, the sensitivity of 1422 performance tempo to the strength of predictions about the reward mapping is not differently 1423 modulated between groups.

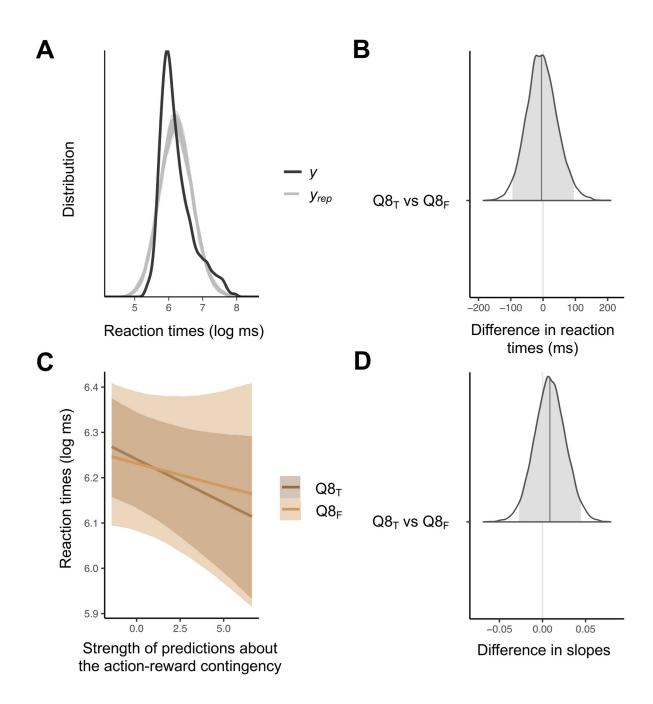
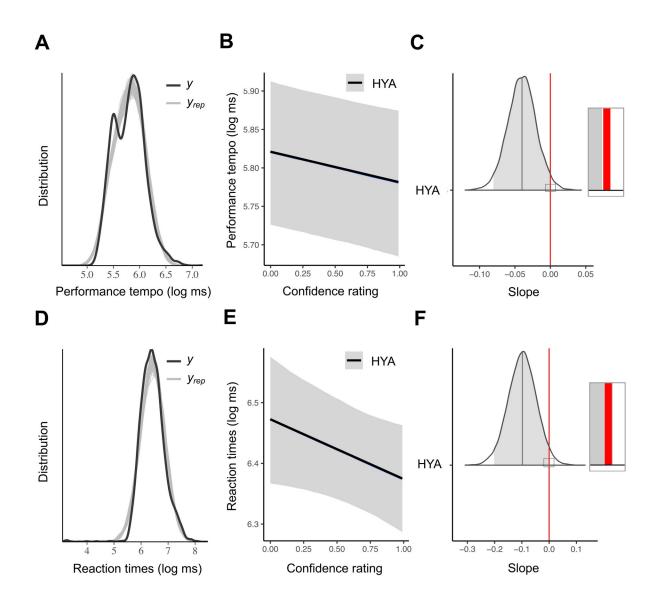


Figure 8. No effect of retrospective credit assignment on motor vigour: reaction times. Bayesian Linear Mixed Models (BLMM; model number 6, $y \sim 1 + \text{group } * x + [1 + x|\text{subject}] +$ [1|trial]) with participants that replied True to Question 8 (Q8_T; see **Table 2**) as reference group in Study 2. *A*, Illustration of the posterior predictive checks where the distribution of the observed outcome variable (y, in our case RT) is compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). *B*, Distribution of the difference in ms between RT (intercept) in Q8_T and in participants that replied False to Question 8 (Q8_F; see **Table 2**). The grey vertical bar indicates the posterior point estimate, while the grey area under the curve represents the 95% credible interval (CI). In the current plot, CI does overlap with zero (the null hypothesis). This indicates that there is 95% probability of no between-group differences in performance tempo. C, Results of the BLMM analysis. We analysed how the strength of predictions about the action-reward contingency modulates RT separately for $Q8_T$ (in dark brown) and $Q8_F$ (in light brown). Here, RT values are represented in the log-scale. We found no robust evidence for a modulation of RT by the strength of expectations about the reward mapping. The upper bound of the distribution including three decimal digits revealed a value of 0.002, demonstrating that 0 was marginally part of the 95% CI. **D**, Distribution of the difference between slopes in $Q8_T$ and $Q8_F$. Here, as CIs include zero we can conclude with 95% probability that groups do not differ in how the strength of predictions about the reward contingency influences RT. Thus, the sensitivity of RT to the strength of predictions about the reward mapping is not differently modulated between groups.

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1461 Figure 9. Explicit confidence ratings invigorate performance tempo. Bayesian Linear Mixed Models (BLMM; model number 4, $y \sim 1 + x + [1 + x|subject] + [1|trial])$ in Study 3 for 1462 1463 performance tempo (left) and reaction times (RT; right). A, Illustration of the posterior 1464 predictive checks where the distribution of the observed outcome variable (y, in our case 1465 performance tempo) is compared to simulated datasets (y_{rep}) from the posterior predictive 1466 distribution (100 draws). B, Results of the BLMM analysis. We analysed how explicit beliefs 1467 about the reward tendency (confidence ratings) modulate performance tempo. Here, mIKI 1468 (performance tempo: mean inter-keystroke-interval) values are represented in the log-scale. 1469 The negative slope had a point estimate of -0.04 (95% credible interval [CI] from -0.08 to -1470 0.001, including three decimal digits in the upper bound). The 95% CI did not include zero.

1471 This suggest that being more certain about receiving a reward outcome is associated with 1472 faster performance tempo, which replicates our findings with the computational parameter 1473 $i\hat{\mu}_2 \vee i$ (see Figure 4C and Figure 7C). C, Distribution of the slope. The grey vertical bar 1474 indicates the posterior point estimate, while the grey area under the curve represents the 1475 95% CI. The vertical red line denotes zero. D, Illustration of the posterior predictive checks 1476 where the distribution of the observed outcome variable (y, in our case RT) is compared to 1477 simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). *E*, Results of 1478 the BLMM analysis. Here, RT values are represented in the log-scale. We found no robust 1479 evidence for a modulation of RT by the strength of expectations about the reward mapping 1480 (95% CI from -0.20 to 0.01). F, Distribution of the slope. The grey vertical bar indicates the 1481 posterior point estimate, while the grey area under the curve represents the 95% CI. The 1482 vertical red line denotes zero.

1489 **TABLES**

1490 Table 1. PD clinical information

| Patient # | Age | UPDRS III ON | ITEL- MMSE | STAI Y2 | HADS_A | HADS_D | Disease Duration (years) | Main Symptom | Most Impaired Side | Last Drug Intake (minutes) | LEDD | Active Substance |
|-----------|-----|-----------------|---------------|---------|--------|--------|--------------------------------|-----------------|--------------------------|----------------------------------|-------------------|--|
| 1 | 57 | 38 | 22 | 51 | 6 | 3 | 10 | R/B | SX | 30 | 920 | Benserazide, Levodopa, Rasagiline, Ropinirole |
| 2 | 46 | 17 | 22 | 40 | 10 | 16 | 7 | R | SX | 75 | 1197 | Carbidopa, Entacapone, Levodopa |
| 3 | 53 | 10 | 22 | 42 | 7 | 5 | 4 | R/B | DX | 120 | 100 | Rasagiline |
| 4 | 63 | 6 | 22 | 25 | 4 | 2 | 3 | В | DX | 720 | 50 | Selegiline |
| 5 | 57 | 6 | 22 | 33 | 7 | 7 | 2 | R | DX | 120 | 300 | Benserazide, Levodopa |
| 6 | 53 | 22 | 20 | 53 | 9 | 8 | 23 | R/LE | BOTH | 130 | 420 | Carbidopa, Levodopa, Rotigotine |
| 7 | 62 | 24 | 22 | 33 | 4 | 3 | 11 | Т | DX | 120 | 1105 | Benserazide, Levodopa, Pramipexole |
| 8 | 62 | 6 | 22 | 28 | 3 | 5 | 8 | R/B/D | DX | 75 | 450 | Carbidopa, Levodopa, Opicapone, Selegiline |
| 9 | 62 | 17 | 22 | 25 | 4 | 3 | 8 | Т | SX | 100 | 652 | Benserazide, Levodopa, Pramipexole, Selegiline |
| 10 | 69 | 7 | 21 | 45 | 5 | 6 | 3 | В | SX | 120 | 300 | Benserazide, Levodopa |
| 11 | 58 | 7 | 20 | 31 | 5 | 1 | 9 | R | DX | 30 | 970 | Amantadine, Carbidopa, Entacapone, Levodopa, Pramipexole |
| 12 | 54 | 25 | 19 | 32 | 2 | 5 | 7 | R | SX | 40 | 1780 | Benserazide, Levodopa, Rasagiline, Rotigotine |
| 13 | 66 | 16 | 19 | 34 | 4 | 10 | 12 | R/B | DX | 150 | 1580 | Amantadine, Carbidopa, Levodopa, Opicapone, Pramipexole, Safinamide |
| 14 | 53 | 21 | 22 | 44 | 5 | 5 | 8 | R | BOTH | 5 | 320 | Ropinirole |
| 15 | 55 | 4 | 22 | 37 | 4 | 1 | 2 | R/T | DX | 30 | 452 | Benserazide, Levodopa, Pramipexole, Rasagiline |
| 16 | 69 | 13 | 20 | 35 | 1 | 0 | 7 | В | SX | 437 | 470 | Benserazide, Levodopa, Ropinirole, Selegiline |
| 17 | 65 | 5 | 21 | 26 | 1 | 7 | 16 | R/B | SX | 360 | 100 + 3.9 ml/h | Levodopa, Opicapone, Pramipexole, Trihexyphenidyl |

| | | | | | | | | | | | levodopa | | |
|----|----|----|----|----|---|---|---|-----|----|-----|----------|--|--|
| | | | | | | | | | | | infusion | | |
| | | | | | | | | | | | gel | | |
| 18 | 59 | 7 | 21 | 37 | 2 | 4 | 2 | R/B | SX | 5 | 150 | Carbidopa, Levodopa | |
| 19 | 58 | 8 | 22 | 30 | 1 | 4 | 5 | R/T | DX | 100 | 452 | Benserazide, Levodopa, Pramipexole | |
| 20 | 56 | 17 | 22 | 40 | 6 | 8 | 6 | R | DX | 185 | 1110 | Amantadine, Benserazide, Levodopa, Pramipexole | |

1491 MMSE predicted score = 1.01 x ITEL-MMSE score + 5.16; HADS_A = anxiety score; HADS_D = depression score; R = rigidity, B =

1492 bradykinesia, LE = lack of energy, T = tremor, D = dyskinesia.

1493 Table 2. Post-performance questionnaire

Please, indicate whether the following statements are True or False.

Please note that performance errors mean pressing the wrong key(s) or key(s) in the wrong order, while bad choices mean playing a sequence that received no points on that attempt.

1. I made fewer than 10 performance errors [True/False]

- 2. I made between 10 and 30 performance errors [True/False]
- 3. I made more than 30 performance errors [True/False]
- 4. I recognised a performance error, because the tone sounded different than expected [True/False]

5. I recognised a performance error, because the finger movement felt different [True/False]

6. I memorised the sequences focusing on the finger movements, without paying attention to the tones [True/False]

7. I memorised the sequences focusing both on the finger movements and the tones [True/False]

8. I could always distinguish whether 0 points reflected a performance error or a bad decision [True/False]

9. I was often not sure whether 0 points reflected a performance error or a bad decision [True/False]

1494 Post-performance questionnaire included in Study 2. Question 8 (Q8) is aimed at evaluating

1495 subjective inferences about the task-related credit assignment.

1497 Table 3. Means and variances of the priors on perceptual parameters and starting

| Prior | Mean | Variance | |
|------------------------|-------|----------|--|
| | | | |
| κ (all) | 1 | 0 | |
| ω_2 (Study 1) | -2.17 | 16 | |
| ω_2 (Study 2) | -2.16 | 16 | |
| ω_2 (Study 3) | -2.22 | 16 | |
| ω_3 (all) | -7 | 0 | |
| $\mu_2^{(0)}$ (all) | 0 | 0 | |
| $\sigma_2^{(0)}$ (all) | 0.1 | 0 | |
| $\mu_{3^{(0)}}$ (all) | 1 | 0 | |
| $\sigma 3^{(0)}$ (all) | 1 | 0 | |
| ζ (all) | 48 | 1 | |

1498 values of the beliefs of the winning HGF₂ model

1499 Free parameter ω_2 was estimated in its unbounded (linear) space. The prior values on ω_2 1500 (mean [variance]) were: -2.17 (16), -2.16 (16) and -2.22 (16) for Study 1, 2 and 3, 1501 respectively. These prior values were obtained using an ideal observer model that received 1502 the input that each participant had experienced. The response model parameter, ζ , was log-1503 transformed, to allow for its estimation in an unbounded space. The remaining parameters were fixed and not estimated in each participant: $\sigma_2^{(0)}$, $\sigma_3^{(0)}$, κ , $\mu_2^{(0)}$, $\mu_3^{(0)}$. The coupling 1504 1505 strength between level 2 and 3 is κ, which was fixed to 1 (Hein et al., 2021). Among the fixed parameters, the following ones operate in their log-transformed space: $\sigma_2^{(0)}$, $\sigma_3^{(0)}$, κ , $\mu_3^{(0)}$. The 1506 1507 prior variances are given in the space in which the parameters are typically estimated.

1508

| 1510 | Table 4. Models | of increasing | complexity | used for | Bayesian | Linear | Mixed N | lodels |
|------|-----------------|---------------|------------|----------|----------|--------|---------|--------|
|------|-----------------|---------------|------------|----------|----------|--------|---------|--------|

1511 analyses

| Study # | Model # | Model |
|---------|---------|--|
| 1 - 2 | | |
| | 1 | $y \sim 1 + (1 subject)$ |
| | 2 | $y \sim 1 + \text{group} + (1 \text{subject})$ |
| | 3 | $y \sim 1 + \text{group} + x + (1 \text{subject})$ |
| | 4 | $y \sim 1 + \text{group } * x + (1 \text{subject})$ |
| | 5 | $y \sim 1 + \text{group} * x + (1 + x \text{subject})$ |
| | 6 | $y \sim 1 + \text{group } * x + (1 + x \text{subject}) + (1 \text{trial})$ |
| 3 | | |
| | 1 | $y \sim 1 + (1 subject)$ |
| | 2 | $y \sim 1 + x + (1 subject)$ |
| | 3 | $y \sim 1 + x + (1 + x subject)$ |
| | 4 | $y \sim 1 + x + (1 + x subject) + (1 trial)$ |

1512 Models of increasing complexity used in Study 1 and 2 (top) and Study 3 (bottom). In Study 1513 1 and 2, y corresponds to the motor performance (log mIKI or log RT); x is the unsigned centred value of the prediction about the tendency of the action-reward contingency (1514 $i\hat{\mu}_2 \vee_i ic$). This parameter represents the strength of the predictions. In model 1, y is 1515 1516 explained by a fixed effect of the intercept and a random effect of intercept by subject (the 1517 latter accounts for repeated measurements); model 2 adds a fixed effect of group; model 3 1518 includes the fixed effect of x, which allows to assess the sensitivity (slope) of performance tempo or RT to $i\hat{\mu}_2 \vee_i ic$ in the reference group; model 4 incorporates the interaction term 1519 1520 between group and x, which allows to investigate the between-group differences in the 1521 sensitivity (slope) of performance tempo or RT to $i\hat{\mu}_2 \vee_i ic$; model 5 includes the random 1522 effect of $i\hat{\mu}_2 \vee_i ic$ by subject; last, model 6 includes a random effect of intercept by trial. In 1523 Study 3, y corresponds to the motor performance (log_mIKI or log_RT); x is the confidence 1524 rating. In model 1, y is explained by a fixed effect of the intercept and a random effect of 1525 intercept by subject (the latter accounts for repeated measurements); model 2 adds a fixed 1526 effect of x, which allows to assess the sensitivity (slope) of performance tempo or RT to 1527 confidence ratings; model 3 includes the random effect of confidence ratings by subject; last, 1528 model 4 includes a random effect of intercept by trial.

| Study # | Dependent Variable | Fixed Effect | Estimate | I-95% CI | u-95% CI | R-hat |
|---------|--------------------|---------------------------------------|----------|----------|----------|-------|
| 1 | | | | | | |
| | Performance tempo | | | | | |
| | | y: HOA | 6.00 | 5.91 | 6.09 | 1.00 |
| | | y: HOA vs HYA | -0.34 | -0.47 | -0.21 | 1.00 |
| | | y: HOA vs PD | 0.25 | 0.09 | 0.41 | 1.00 |
| | | x: HOA | -0.04 | -0.07 | -0.01 | 1.00 |
| | | group * x: HOA vs HYA | -0.00 | -0.04 | 0.04 | 1.00 |
| | | group * x: HOA vs PD | -0.00 | -0.05 | 0.04 | 1.00 |
| | Reaction times | | | | | |
| | | y: HOA | 6.65 | 6.54 | 6.75 | 1.01 |
| | | y: HOA vs HYA | -0.28 | -0.42 | -0.13 | 1.00 |
| | | y: HOA vs PD | 0.09 | -0.08 | 0.27 | 1.00 |
| | | x: HOA | -0.02 | -0.04 | 0.01 | 1.00 |
| | | group * x: HOA vs HYA | -0.01 | -0.05 | 0.03 | 1.00 |
| | | group * x: HOA vs PD | -0.03 | -0.07 | 0.02 | 1.00 |
| 2 | | | | | | |
| | Performance tempo | | | | | |
| | | y: Q8 _T | 5.62 | 5.51 | 5.72 | 1.00 |
| | | y: Q8⊤vs Q8 _F | 0.07 | -0.11 | 0.25 | 1.00 |
| | | x: Q8 _T | -0.04 | -0.06 | -0.01 | 1.00 |
| | | group * x: $Q8_T vs Q8_F$ | -0.00 | -0.04 | 0.04 | 1.00 |
| | Reaction times | | | | | |
| | | y: Q8 _T | 6.24 | 6.13 | 6.34 | 1.00 |
| | | y: Q8 _T vs Q8 _F | -0.01 | -0.19 | 0.18 | 1.00 |
| | | x: Q8 _T | -0.02 | -0.04 | 0.002 | 1.00 |
| | | group * x: Q8⊤vs Q8⊧ | 0.01 | -0.03 | 0.04 | 1.00 |

1530 Table 5. Summary of the posterior distributions for the fixed effects of the best fitting

3

1531

Bayesian Linear Mixed Models

Performance tempo

| | У | 5.82 | 5.73 | 5.91 | 1.00 |
|----------------|---|-------|-------|--------|------|
| | x | -0.04 | -0.08 | -0.001 | 1.00 |
| Reaction times | | | | | |
| | У | 6.47 | 6.37 | 6.58 | 1.00 |
| | x | -0.10 | -0.20 | 0.01 | 1.00 |

1532 Estimates, credible intervals (CIs) and R-hat values for the fixed effects of the best fitting 1533 models in Study 1, 2 (model number 6: $y \sim 1 + \text{group } * x + [1 + x]\text{subject} + [1|\text{trial}]$) and in 1534 Study 3 (model number 4: $y \sim 1 + x + [1 + x]$ subject] + [1|trial]). In Study 1, y: HOA refers to 1535 the posterior estimate for the intercept in the reference group (healthy older adults, HOA). y: 1536 HOA vs HYA and y: HOA vs PD reflect the posterior distributions of the differences between 1537 intercepts (HOA vs healthy younger adults [HYA]; HOA vs Parkinson's patients [PD], 1538 respectively). x: HOA is the posterior distribution of the association (slope) between motor 1539 performance (either performance tempo or reaction times) and the strength of predictions 1540 about the action-reward contingency in the reference group. group * x: HOA vs HYA and 1541 group * x: HOA vs PD are the posterior distributions of slope differences between HOA and 1542 HYA and between HOA and PD, respectively. In Study 2, y: Q8_T refers to the posterior 1543 estimate for the intercept in the reference group (participants that replied True to Question 8, 1544 $Q8_T$). y: $Q8_T$ vs $Q8_F$ reflects the posterior distribution of the difference between intercepts 1545 $(Q8_T vs participants that replied False to Question 8 [Q8_F])$. x: Q8_T is the posterior distribution 1546 of the association (slope) between motor performance (either performance tempo or reaction 1547 times) and the strength of predictions about the action-reward contingency in the reference 1548 group. The upper bound of the CI for the slope effect in the BLMM analyses for RT is given 1549 with three decimal digits to demonstrate that 0 was included in the 95% CI. group * x: $Q8_T$ vs 1550 $Q8_{\rm F}$ is the posterior distribution of slope difference between $Q8_{\rm T}$ and $Q8_{\rm F}$. In Study 3, y refers 1551 to the posterior estimate for the intercept. x is the posterior distribution of the association 1552 (slope) between motor performance (either performance tempo or reaction times) and the 1553 confidence ratings. The upper bound of the 95% CI estimate of the slope effect in the BLMM

analyses for performance tempo was -0.001, when considering three decimal digits. In all studies, I-95% CI and u-95% CI refer to the lower and upper bound of the credible intervals of the posterior distributions of the fixed effects. For each parameter, we also reported the corresponding Gelman-Rubin statistics (R-hat values). Values < 1.1 indicates chain convergence (Gelman and Rubin, 1992).