JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Behavioral/Cognitive

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

https://doi.org/10.1523/JNEUROSCI.1583-22.2022

Cite as: J. Neurosci 2023; 10.1523/JNEUROSCI.1583-22.2022

Received: 18 August 2022
Revised: 13 December 2022
Accepted: 31 December 2022

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

Author names and affiliations, including postal codes:

1. Margherita Tecilla, Department of Psychology, Goldsmiths, University of London, London SE146NW, UK
2. Michael Großbach, Institute of Music Physiology and Musicians' Medicine, Hannover University of Music Drama and Media, Hannover 30175, Germany
3. Giovanni Gentile, Parkinson and Movement Disorders Unit, Study Center for Neurodegeneration (CESNE), Department of Neuroscience, University of Padua, 35131 Padua, Italy
4. Peter Holland, Department of Psychology, Goldsmiths, University of London, London SE146NW, UK
5. Sebastian Sporn, Department of Clinical and Movement Neuroscience, Queens Square Institute of Neurology, UCL, London WC1N3BG, UK
6. Angelo Antonini, Parkinson and Movement Disorders Unit, Study Center for Neurodegeneration (CESNE), Department of Neuroscience, University of Padua, 35131 Padua, Italy
7. Maria Herrojo Ruiz, Department of Psychology, Goldsmiths, University of London, London SE146NW, UK

Corresponding author email address: Margherita Tecilla, mteci003@gold.ac.uk

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 https://osf.io/7kfbj/

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.

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

Our study is the first to reveal that the dynamic updating of beliefs about volatile action-reward 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.

SIGNIFICANCE STATEMENT

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

INTRODUCTION

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

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

modulated by beliefs about the action-reward contingencies, then individual differences in uncertainty estimates could explain differences in motor vigour. Alternatively, under equivalent signatures of decision-making behaviour, individuals could exhibit differential 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 stimulus-outcome contingencies over time.

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

MATERIALS AND METHODS

Participants

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

Study 1

37 HYA (13 males, age 18-40, mean age 27.8, standard error of the mean [SEM] 0.67; hereafter we follow the intrinsic measures of precision for rounding descriptive and inferential statistics as reported in Cousineau, 2020), 20 PD patients (13 males, age 40-75, mean age 58.9, SEM 1.32) and an age-matched group of 37 HOA (20 males, age 40-75, mean age 61.5, SEM 1.25) participated in this research. The sample size for healthy samples was informed by previous work assessing differences between HYA and HOA in decision-making 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). We increased the sample size to allow for variability being introduced due to the nature of the online study.

All participants were right-handed, had normal or corrected vision and were able to perform controlled finger movements. Amateur/professional pianists and participants diagnosed with a mental health disorder were excluded from the study. Additionally, exclusion criteria for PD patients were: implanted with Deep Brain Stimulation (DBS), taking antidepressant medications, diagnosed with dementia and displaying tremor as an onset symptom. One PD patient declared to take Laroxyl, yet confirmed not to be diagnosed with depression. PD were evaluated through ITEL-Mini Mental state examination (ITEL-MMSE; Metitieri et al., 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**).

All participants took part in the study remotely (online), except for five PD patients, who completed the study in the laboratory facilities of the Neurology Clinic of Padua. An Italian translation of the original experimental instructions in English was created to test some of the HOA participants (N = 24) and all PD patients (see the Results section for details on our control analyses to assess the effect of the language of the instructions). The previously 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 completing the task in Italian), which could be increased up to £10 (10€) as a function of their task performance. PD patients did not receive a monetary prize, in line with the clinical research policies at the Neurology Clinic of Padua.

Study 2

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 to explain our results (McDougle et al., 2016). HYA participants in this control experiment were divided into two subsamples as a function of their reply (True/False) to a post-performance question (Q8; **Table 2**). Group $Q8_T$ consisted of 26 participants (8 males, age 18-40, mean age 24.1, SEM 1.13) and $Q8_F$ of 13 participants (2 males, age 18-40, mean age 25, SEM 1.7). The same inclusion/exclusion criteria and compensation as for HYA in Study 1 applied.

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.

Table 1

Experimental design

In Study 1 and 2, the experiment ran completely online on the Qualtrics platform (https://www.qualtrics.com) and was accessible through a study link. The task was programmed in JavaScript and embedded into the Qualtrics form. We provide more details 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).

The task consisted of a familiarisation and a reward-based learning phase. In the 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 different fractal images (**Figure 1A**). They were asked to position their right hand on the 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 virtual piano. Participants were trained to press “g-j-h-k” for seq1 (red fractal) and “k-g-j-h” for seq2 (blue fractal). Online videos showing the correct hand position on the keyboard and how to perform the two sequences were provided to increase inter-individual consistency. The familiarisation phase terminated when an error-free performance was achieved for five

times in succession for both sequences. The number of sequence renditions during familiarisation was recorded and used for subsequent analyses.

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

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

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

In Study 2 we additionally asked participants at the end of the reward-based learning phase to reply to some questions about their performance. We were particularly interested in assessing whether participants could correctly infer what zero points meant, that is, whether they could distinguish between a performance execution error or a decision to play a sequence that was unrewarded on the trial. Both scenarios would result in zero points. We reasoned that participants who could not always infer the meaning of zero might show a reduced invigoration effect. **Table 2** lists the questions of the post-performance questionnaire, which required binary responses (True/False) and was designed based on previous work (McDougle et al., 2016; Herrojo Ruiz et al., 2017). The binary answer to Question 8 “I could *always* distinguish whether 0 points reflected a performance error or a bad decision” was used as criterion to split the control sample into $Q8_T$ (i.e., participants were *always* sure about the hidden causes for the lack of reward) and $Q8_F$ (i.e., participants were *not always* sure about the hidden causes for receiving zero points). Among other questions, participants were asked whether the subjective number estimate of performance

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

In Study 3, we conducted an offline version of the task described above. The paradigm was coded in psychtoolbox (http://psychtoolbox.org) 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.

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

Figure 1

Table 2

Acquisition of online data using JavaScript

In Study 1 and 2, due to the nature of the online experiment, cross-browser issues could emerge. A potential issue was that participants could use a variety of computer hardware, running on different web browsers, operating systems and keyboard types (e.g., tablets vs laptops). To mitigate the effect of hardware variability on the acquisition of motor performance data, we instructed participants to complete the task on a desktop or laptop computer. An inspection of browser user agent data suggests that the experiment was performed on a mixture of desktops or laptops running the Chrome & Safari browsers on 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 https://gitlab.pavlovia.org/oshah001/reward-learning-experiment).

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

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

In our studies, the HGF was used to characterise subject-specific trial-by-trial trajectories of beliefs about stimulus-outcome contingencies (level 2) and their changes over time (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 uncertainty about the hidden states on those levels, that is, our imperfect knowledge about 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 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 operator $\hat{\mu}_i^{(k)}$ and correspond to the values in the previous trial ($\mu_i^{(k-1)}$). As in previous work using one-armed bandit paradigms (Iglesias et al., 2013; Mathys et al., 2014; Hein et al., 2021), we modelled learning using the 3-level HGF (HGF_3) for binary outcomes (**Figure 2A**). In this hierarchical perceptual model, the hidden state on the lowest level, x_1, represents the binary categorical variable of the experimental stimuli (for each trial *k*, $x_1^{(k)}$ = 0 if the red icon/seq1 is rewarded [or blue/seq2 loses]; $x_1^{(k)}$ = 1 when red fractal/seq1 is not rewarded [or blue/seq2 wins]). Higher in the hierarchy, x_2 reflects the true value of the tendency of the stimulus-outcome contingency, and x_3 the true volatility of the environment (i.e., of x_2). Belief updating in the HGF depends on various parameters, which can be estimated in each

individual or fixed depending on the hypotheses. This allows for the assessment of individual learning characteristics. Here we chose to individually estimate parameter ω_2, representing the tonic (time-invariant) volatility on the second level, and ω_3, denoting the tonic volatility on the third level. Generally, ω_2 and ω_3 parameters describe an individual's learning motif. Larger ω_2 values are associated with faster learning about stimulus outcomes, and thus greater update steps in μ_2 (see simulations in Hein et al., 2021). Similarly, greater levels of tonic volatility on level 3, ω_3, increase the update steps on μ_3. See details on our priors in **Table 3.** Using simulations to assess the accuracy of parameter estimation in the HGF_3, we and others have previously demonstrated that ω_2 can be estimated accurately, while ω_3 is not estimated well (Reed et al., 2020; Hein et al., 2021).

We then coupled the perceptual HGF model to a response model for binary outcomes, which defined how beliefs about the tendency of the stimulus-outcome contingencies were mapped onto decisions (e.g., which sequence should be chosen and played according to the beliefs on the current trial; Mathys et al., 2014). Our response model was the unit-square sigmoid observation model for binary responses (Iglesias et al., 2013; Mathys et al., 2014). This 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 icon/sequence is rewarding. This mapping from beliefs to decisions depends on the response parameter ζ (interpreted as inverse decision noise). Higher ζ values indicate a greater probability for the agents to select the option that is more likely to be rewarding according to their beliefs. Simulations demonstrate that ζ is recovered well (Hein et al., 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.

Figure 2

Models and priors

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

The different models (HGF_2, RW, SK1) were fitted to the trial-by-trial inputs and responses in each participant using the HGF toolbox, which generates maximum-a-posteriori (MAP) parameter estimates in each individual. To identify the model that explained the behavioural data across all participants best, we used random effects Bayesian model selection (BMS, through the freely available MACS toolbox https://github.com/JoramSoch/MACS; Soch & Allefeld, 2018). Importantly, in Study 1 we used the same priors in all participant groups (HYA, HOA, PD) as in previous studies (Powers et al., 2017; Hein et al., 2021). Note, however, that recent computational modelling work suggests that using different prior values in each participant group may be more suitable to capture dissociable group effects (e.g., for mental health: Valton et al., 2020). This approach, albeit interesting, would not favour a standard statistical comparison between groups: any between-group differences could be explained by the underlying models having been constructed differently.

Table 3

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).

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

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

Next, to investigate decision-making processes we analysed group effects on three computational variables that characterised learning in each individual. The model that best explained the behavioural data across all participants according to BMS was the HGF_2 (see Results section). We therefore assessed the perceptual model parameter ω_2 (subject-specific tonic volatility, which influences the speed of belief updating on level 2), ζ (the 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 informational uncertainty about the tendency of the action-reward contingency. Moreover, beliefs on level 2 are updated as a function of PEs about the stimulus-outcome mapping (the mismatch between the observed outcomes u = 1 or 0 and the agent's beliefs about the probability of such an outcome) and weighted by σ_2 (the precision ratio on level 2). Accordingly, if agents are more uncertain about the contingencies governing their 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 action-reward 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.

Statistical analyses

Bayesian analyses on Study 1

General task performance and computational variables

First, we calculated the mean and SEM as summary statistics for each of our general task performance (mIKI, RT, percError, percWin, rendFam) and computation variables (ω_2, ζ, σ_2). Next, we evaluated between-group differences by computing Bayes Factors (BF) using the bayesFactor toolbox (https://github.com/klabhub/bayesFactor) in MATLAB. This toolbox implements tests that are based on multivariate generalisations of Cauchy priors on standardised effects (Rouder et al., 2012). For each dependent variable (DV), we calculated the BF on the model DV ~ 1 + group, where DV is explained by a fixed effect of group (HYA, HOA, PD). The model was fitted using the fitlme function of the MATLAB Statistics toolbox. Computing BF allowed us to quantify the evidence in support of the alternative hypothesis (full model, in our case assessing the main effect of the group) relative to the null model (intercept-only model, i.e., DV ~ 1). BF values were interpreted as in Andraszewicz et al. (2015). As BF is the ratio between the probability of the data being observed under the alternative hypothesis and the probability of the same data under the null hypothesis, a BF of 20 would indicate strong evidence for the alternative hypothesis. On the other hand, BF of 0.05 would provide strong evidence for the null hypothesis (see Table 1 by Andraszewicz et al., 2015 for further details). Accompanying the BF results, we provided the outcomes of 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 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 number of renditions during the familiarisation phase was averaged between both types of sequence.

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

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

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

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

In the HGF for binary categorical inputs, the sign of $\hat{\mu}_2$ (and similarly μ_2) is not informative, as it represents the tendency of an action-reward mapping for an *arbitrary* action (e.g., for seq1). Yet, we could similarly define the model in reference to the other action (e.g., seq2). In line with previous work (Stefanics et al., 2018; Hein et al., 2022), we therefore took the 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 participants will have a stronger expectation of receiving a reward, given they select the correct action. Thus, $|\hat{\mu}_2|$ represents the *strength* of the predictions. In one participant (HYA), 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 ($|\hat{\mu}_2|$_c) to allow the intercept estimate for mIKI to reflect the average $|\hat{\mu}_2|$ value. As for Bayesian ANOVAs (see General task performance and computational variables), mIKI was log-transformed to approach normality (log_mIKI). In one HOA participant, two log_mIKI values were discarded from the analyses as they were not registered correctly in the JSON file (i.e., 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.

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

For each model we ran four independent chains with 5000 iterations each, of which the first 1000 were discarded as warmup. This resulted in a total of 16000 posterior samples. In all models we used default prior distribution for the intercept, and a normal distribution for each

fixed and random effect (fixed effects for group and x, normal [0,2)]; interaction term group * x, normal [0,1]; random effects for intercept by subject and intercept by trial, normal [0,2]; random effect x by subject, normal [0,1]). The prior on the LKJ-Correlation, the correlation matrices in brms (Lewandowski, Kurowicka, & Joe, 2009), was set to 2 as recommended in Bürkner and colleagues (2017). Chain convergence was assessed using the Gelman-Rubin statistics (R-hat < 1.1; Gelman and Rubin, 1992).

Models were compared using leave-one-out cross-validation of the posterior log-likelihood (LOO-CV) with Pareto-smoothed importance sampling (Vehtari et al., 2017). The identification of the best fitting model was based on the highest expected log point-wise predictive density (ELPD). We also checked that the absolute mean difference in ELPD between two models (elpd_diff in brms) exceeded twice the standard error of the differences (2*se_diff). LOO-CV identified the most complex model (model number 6 in **Table 4**) as the best fitting model (see Results section for further details). This model explained the 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 effect of subjects on the intercept and $|\hat{\mu}_2|$_c as a random effect, and the effect of trials on the intercept as a random effect. We reported for each parameter the posterior point estimate and the associated 95% credible interval (CI). See Results section for further details.

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

Table 4

Bayesian analyses on Study 2

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

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

Next, to test potential between-group differences in the mIKI-$|\widehat{\mu}_2|$ 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 $|\widehat{\mu_2}|$.

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

Bayesian analyses on Study 3

In Study 3, we aimed at assessing the association between trial-by-trial explicit beliefs about the reward tendency (confidence ratings) and motor performance. We were particularly interested in understanding whether being more certain (following Frömer et al, 2021) about obtaining the reward—given the right choice—would speed up motor responses.

First, following the same steps as for Study 1 and 2, we calculated the mean and SEM as summary statistics for the general task performance variables (mIKI, RT, percWin, conf). Trial-by-trial confidence ratings were converted to a 0-0.99 scale.

We aimed to use the confidence rating as a predictor in our BLMM analyses to assess the sensitivity of motor performance (mIKI and RT) to explicit beliefs about the reward tendency. 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).

In addition, as a sanity check, we evaluated the association of confidence ratings with the strength of predictions about the action-reward contingency trial-by-trial. The investigation of motor vigour effects in Study 1 and 2 assumed that the unsigned $|\hat{\mu}_2|$ values estimated in the HGF reflect the strength of participants' expectation on the reward tendency. However, whether this HGF quantity reflects true explicit beliefs, assessed as confidence ratings, is not clear. We evaluated the association between confidence ratings and the unsigned $|\hat{\mu}_2|$ values using the formula conf ~ 1 + $|\hat{\mu}_2|$_c + (1 + $|\hat{\mu}_2|$_c|subj) + (1|trial) in brms. We chose a default prior distribution for the intercept, and a normal distribution for the fixed and random 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 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 about participants' ability to correctly identify performance errors and thus infer the task-related credit assignment.

RESULTS

Study 1

Task validation

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

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

showed extreme evidence for between-group differences in HYA vs HOA (BF = 1.2044e+04) and in HYA vs PD (BF = 3.3592e+07). We also found very strong evidence for the alternative hypothesis in HOA vs PD (BF = 32.591). Thus, performance tempo (and therefore movement time) was differently modulated between groups, with HYA being faster than HOA and PD, and HOA faster than PD. Regarding RT, there was extreme evidence supporting between-group differences (log_RT: BF = 404.521; $F_{(2,91)} = 11.383$, $p < 0.001$). BF analysis on post hoc independent two-sample t-tests revealed extreme evidence for between-group differences in HYA vs HOA (BF = 109.444) and HYA vs PD (BF = 239.335). Yet, we only found anecdotal evidence in support of the null hypothesis in HOA vs PD (BF = 0.403). Hence, despite HYA displaying shorter RTs than HOA and PD, our analyses suggest similar RTs in HOA and PD.

In addition, we found anecdotal evidence supporting that groups differed in the number of 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; $F_{(2,91)} = 4.448$, $p = 0.014$). 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 and PD (BF = 3.030), respectively. Still, HOA and PD practised the two sequences to a 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 performance tempo during task completion. A correlation analysis across all participants between the number of repetitions during familiarisation and these variables demonstrated some evidence for null correlation effects (percWin: BF = 0.290, Pearson r = -0.134, p = 0.200; log_mIKI: BF = 0.397; Pearson r = 0.158, p = 0.131; note that we excluded one PD 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,

667 supporting moderate evidence for the null hypothesis; $F_{(2,91)}$= 1.848, p = 0.163). A similar
668 outcome was observed in the analysis of performance execution error rates (percError, HYA:
669 mean 0.061, SEM 0.009; HOA: mean 0.057, SEM 0.008; PD: mean 0.084, SEM 0.020; BF =
670 0.146, moderate evidence for the null hypothesis; $F_{(2,91)}$ = 1.456, p = 0.239). In sum, we
671 found moderate evidence that HYA, HOA and PD did not differ in either the rate of win or
672 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 HGF_3 from model comparison due
677 to numerical instabilities, BMS was conducted on the HGF_2 and two reinforcement learning
678 models (RW, SK1) using the individual log-model evidence (LME) values provided by the
679 HGF toolbox. The winning model was the HGF_2, with an exceedance probability of 0.95 and
680 an expected frequency of 0.90. Of note, although the HGF_3 model was not included in BMS,
681 a qualitative comparison of LME values for the HGF_3 and HGF_2 models in the 80%
682 participants in which HGF_3 did not lead to numerical instabilities revealed extremely similar
683 values (LME differences < 1). This observation suggested that both models described
684 behaviour in our task with constant true volatility to a similar degree.
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 -
688 1.686, SEM 0.438; PD: mean -1.843, SEM 0.609; BF = 0.059; $F_{(2,91)}$ = 0.380 p = 0.685).
689 Similarly, we found strong evidence in favour of a lack of group effect on the informational
690 uncertainty about beliefs on the tendency of the action-reward contingency, σ_2 (HYA: mean
691 1.610, SEM 0.177; HOA: mean 1.663, SEM 0.158; PD: mean 1.559, SEM 0.218; BF =
692 0.045; $F_{(2,91)}$ = 0.074, p = 0.928). Last, groups exhibited a similar mapping from beliefs to
693 responses, driven by the response model parameter ζ (HYA: mean 1.735, SEM 0.191; HOA:

mean 1.523, SEM 0.176; PD: mean 2.095, SEM 0.469; BF = 0.114, demonstrating moderate evidence for the null hypothesis; $F_{(2,91)} = 1.1495$, p = 0.321).

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

Figure 3

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

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

Table 5

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

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

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.

Figure 4

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

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 intercept in the reference group, HOA, was 6.65, CI = [6.54, 6.75] (in ms, 771, CI = [693, 856]). The distribution of the differences between intercepts in HOA and HYA was centred at -0.28, CI = [-0.42, -0.13] (in ms, -188, CI = [-289, -88]), which did not overlap with zero. On the other hand, the distribution of the differences between intercepts in HOA and PD yielded a posterior point estimate of 0.09, CI = [-0.08, 0.27] (in ms, 77, CI = [-65, 231]) and included zero (**Figure 5B**). These results demonstrated that HYA initiated the sequence faster than HOA, consistent with our mIKI group results, whereas PD and HOA had a similar RT intercept.

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

Figure 5

Study 2

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 HGF_2 (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.

Figure 6

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.

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

Figure 7

Regarding RT, the predictive power for the range of RT values was weaker compared to performance tempo (**Figure 8A**), yet Gelman-Rubin statistics demonstrated an excellent chain convergence (R-hat values equal to 1.00). BLMM analyses showed no differences between $Q8_T$ and $Q8_F$ (intercepts) on RT, which is in line with our BF results **(Figure 8B**). We found no robust evidence for an association (slope) between the strength of predictions about the action-reward contingency and RT (**Figure 8C**). The 95% CI of the slope distribution ranged from -0.04 to 0.00. A closer look at 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. This outcome suggests that RT is not robustly modulated by the strength 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**).

Figure 8

Finally, we investigated the effect of differences in inferences about reward assignment on the post-performance subjective error rate. First, the subjective error rate estimation was validated by computing BF analysis on the correlation between subjective and empirical 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 differences in the subjective error rate (BF = 0.432, demonstrating anecdotal evidence for the null hypothesis; $t_{(36)} = -0.850$, p = 0.401). Thus, being not *always* sure about the causes for the lack of reward did not influence the rate of subjective number estimate of performance errors.

To conclude, our analyses provided evidence for the lack of differences between $Q8_T$ and $Q8_F$ in the evaluated parameters, suggesting that subjective inferences about task-related

credit assignment do not modulate decision-making, general motor performance or the association between expectation on reward probability and motor vigour. Thus, even if the groups in Study 1 would have had differences in credit assignment, it is unlikely that this would have led to a modulation of group effects. In addition, here we found further support for our main research hypothesis, whereby stronger predictions about the action-reward contingency enhanced motor vigour through faster movement.

Study 3

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.

For performance tempo, LOO-CV identified the most complex model (model number 4) as the best fit (mIKI, elpd_diff = -112.4178, se_diff = 15.74263; elpd_diff > 2*se_diff). The posterior predictive checks demonstrated that the observed outcome variable y overlapped 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 tempo in our sample. The BLMM analyses showed a negative association (slope) between the confidence ratings and the performance tempo, with stronger explicit beliefs about the reward tendency speeding up performance (**Figure 9B).** The slope estimate was -0.04 (95% CI 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**).

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

In a separate sanity check, we assessed whether our measure of confidence was correlated with $|\hat{\mu}_2|$ in the HGF_2. This would suggest that implicit beliefs about the tendency of the action-reward contingency—captured with computational modelling—can be a proxy for explicit ratings about the confidence of reward delivery. Indeed, a BLMM analysis demonstrated a strong association between $|\hat{\mu}_2|$ and confidence ratings. The posterior point estimate for the intercept was 0.53, CI = [0.47, 0.59]. The distribution of the fixed effect of the association between $|\hat{\mu}_2|$ and the confidence ratings had a posterior point estimate of 0.09, CI [0.04, 0.14]. R-hat values were below 1.1, indicating chain convergence (Gelman 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.

DISCUSSION

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

Study 1 showed a trial-by-trial modulation of performance tempo—commensurate with movement time—by the strength of expectations about the action-reward contingencies. The 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 predictions in our three groups. This provides compelling evidence for a preservation of motor invigoration by expectations of reward probability in HOA and PD, expanding the understanding on how reward sensitivity and reversal learning interact to modulate motor vigour in ageing and medicated PD.

Previous investigations of the beneficial effects of reward on motor behaviour (e.g., faster and more accurate motor performance; Sedaghat-Nekad et al., 2019) have been limited to manipulations of reward magnitude (presence/absence; large/small) in deterministic contexts (Codol et al., 2020; Sporn et al., 2022; Aves et al., 2021). Our findings expand on computational work that demonstrated the updating of beliefs in a perceptual task to speed RT (Marshall et al., 2016). The authors found that, as participants learned to track the transition probabilities between stimuli, different decision-making variables affected RT. Our results show that the trial-by-trial influence of motor vigour by belief updating can be 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 for between-group differences in the mean performance tempo. HYA were faster than HOA and PD, and HOA quicker than PD. The slower sequence execution in HOA is consistent with a general slowness of hand movements in later stages of life (Ketcham et al., 2002; Aves et al., 2021). Regarding PD, the slower performance is likely explained by a sequence effect (SE). SE is a common bradykinetic symptom in PD, which manifests through slower and attenuated sequential movements (Kang et al., 2010). Dopamine (DA) intake does not ameliorate symptoms associated with SE, suggesting a non-DA involvement in the pathophysiology of this effect (Bologna et al., 2016). Similar results were found for RT, with HYA displaying shorter RT than HOA and PD. Yet, RT did not dissociate between HOA and PD.

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

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

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

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

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

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

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

REFERENCES

Adkins TJ, Lee TG (2021) Reward modulates cortical representations of action. NeuroImage 228:117708.

Andraszewicz S, Scheibehenne B, Rieskamp J, Grasman R, Verhagen J, Wagenmakers E-J (2015) An Introduction to Bayesian Hypothesis Testing for Management Research. J Manag 41:521–543.

Aves P, Moreau L, Alghamdi A, Sporn S, Galea JM (2021) Age-Related Differences in Reward-Based Modulation of Sequential Reaching Performance. bioRxiv 461920. https://doi.org/10.1101/2021.09.27.461920.

Balleine BW, Delgado MR, Hikosaka O (2007) The role of the dorsal striatum in reward and decision-making. J Neurosci 27:8161-8165.

Behrens TEJ, Woolrich MW, Walton ME, Rushworth MFS (2007) Learning the value of information in an uncertain world. Nat Neurosci 10:1214–1221.

Bologna M, Leodori G, Stirpe P, Paparella G, Colella D, Belvisi D, Fasano A, Fabbrini G, Berardelli A (2016) Bradykinesia in early and advanced Parkinson's disease. J Neurol Sci 369:286–291.

Bürkner P-C (2017) brms: An *R* Package for Bayesian Multilevel Models Using *Stan*. J Stat Softw 80:1-28.

Bürkner P-C (2018) Advanced Bayesian Multilevel Modeling with the R Package brms. R J 10:395-411.

Bürkner P-C (2021) Bayesian Item Response Modeling in R with brms and Stan. J Stat Softw 100:1-54.

Carroll TJ, McNamee D, Ingram JN, Wolpert DM (2019) Rapid Visuomotor Responses Reflect Value-Based Decisions. J Neurosci 39:3906–3920.

1055 Codol O, Holland PJ, Manohar SG, Galea JM (2020) Reward-Based Improvements
1056 in Motor Control Are Driven by Multiple Error-Reducing Mechanisms. 40:
1057 3604-3620.

1058 Cools R (2001) Enhanced or Impaired Cognitive Function in Parkinson's Disease as
1059 a Function of Dopaminergic Medication and Task Demands. Cereb Cortex
1060 11:1136–1143.

1061 Cousineau D (2020) How many decimals? Rounding descriptive and inferential
1062 statistics based on measurement precision. J Math Psychol 97:102362.

1063 Dayan P, Yu AJ (2006) Phasic norepinephrine: a neural interrupt signal for
1064 unexpected events. Netw Comput Neural Syst 17:335-350.

1065 de Berker AO, Rutledge RB, Mathys C, Marshall L, Cross GF, Dolan RJ, Bestmann S
1066 (2016) Computations of uncertainty mediate acute stress responses in
1067 humans. Nat Commun 7:10996.

1068 de Boer L, Axelsson J, Riklund K, Nyberg L, Dayan P, Bäckman L, Guitart-Masip M
1069 (2017) Attenuation of dopamine-modulated prefrontal value signals underlies
1070 probabilistic reward learning deficits in old age. eLife 6:e26424.

1071 den Ouden HEM, Daunizeau J, Roiser J, Friston KJ, Stephan KE (2010) Striatal
1072 Prediction Error Modulates Cortical Coupling. J Neurosci 30:3210–3219.

1073 Diaconescu AO, Mathys C, Weber LAE, Daunizeau J, Kasper L, Lomakina EI, Fehr
1074 E, Stephan KE (2014) Inferring on the Intentions of Others by Hierarchical
1075 Bayesian Learning. PLoS Comput Biol 10:e1003810.

1076 Domenech P, Rheims S, Koechlin E (2020) Neural mechanisms resolving
1077 exploitation-exploration dilemmas in the medial prefrontal cortex. Science
1078 369:eabb0184.

1079 Eppinger B, Hämmerer D, Li S-C (2011) Neuromodulation of reward-based learning
1080 and decision making in human aging: Eppinger et al. Ann N Y Acad Sci
1081 1235:1–17.

1082 Euteneuer F, Schaefer F, Stuermer R, Boucsein W, Timmermann L, Barbe MT,
1083 Ebersbach G, Otto J, Kessler J, Kalbe E (2009) Dissociation of decision-
1084 making under ambiguity and decision-making under risk in patients with
1085 Parkinson's disease: A neuropsychological and psychophysiological study.
1086 Neuropsychologia 47:2882–2890.

1087 Fahn S, Elton RL (1987) The unified Parkinson's disease rating scale. In: Recent
1088 developments in Parkinson's disease, Vol 2 (Fahn S, Marsden CD, Calne
1089 DB, Goldstein M, eds), pp 153–163, 293–304. Florham Park, NJ. Macmillan
1090 Health Care Information.

1091 Feldman H, Friston KJ (2010) Attention, Uncertainty, and Free-Energy. Front Hum
1092 Neurosci 4:215.

1093 Fera F (2005) Neural Mechanisms Underlying Probabilistic Category Learning in
1094 Normal Aging. J Neurosci 25:11340–11348.

1095 Frank MJ, Seeberger LC, O'reilly RC (2004) By carrot or by stick: cognitive
1096 reinforcement learning in parkinsonism. Science 306:1940-1943.

1097 Frässle S, Aponte EA, Bollmann S, Brodersen KH, Do CT, Harrison OK, ... Stephan
1098 KE (2021) TAPAS: An Open-Source Software Package for Translational
1099 Neuromodeling and Computational Psychiatry. Front Psychiatry 12:68081.

1100 Frömer R, Nassar MR, Bruckner R, Stürmer B, Sommer W, Yeung N (2021)
1101 Response-based outcome predictions and confidence regulate feedback
1102 processing and learning. Elife 10.

1103 Friston KJ, Stephan KE, Montague R, Dolan RJ (2014) Computational psychiatry: the
1104 brain as a phantastic organ. Lancet Psychiatry 1:148–158.

1105 Galaro JK, Celnik P, Chib VS (2019) Motor Cortex Excitability Reflects the Subjective
1106 Value of Reward and Mediates Its Effects on Incentive-Motivated
1107 Performance. J Neurosci 39:1236–1248.

1108 Gelman A, Rubin DB (1992) Inference from Iterative Simulation Using Multiple
1109 Sequences. Stat Sci 7:457-472.

1110 Haarsma J, Fletcher PC, Griffin JD, Taverne HJ, Ziauddeen H, Spencer TJ, Miller C,
1111 Katthagen T, Goodyer I, Diederen KM, Murray GK (2021) Precision weighting
1112 of cortical unsigned prediction error signals benefits learning, is mediated by
1113 dopamine, and is impaired in psychosis. Mol Psychiatry 26:5320-33.

1114 Hayden BY, Heilbronner SR, Pearson JM, Platt ML (2011) Surprise signals in
1115 anterior cingulate cortex: neuronal encoding of unsigned reward prediction
1116 errors driving adjustment in behavior. J Neurosci 31: 4178–4187.

1117 Hein TP, de Fockert J, Ruiz MH (2021) State anxiety biases estimates of uncertainty
1118 and impairs reward learning in volatile environments. NeuroImage
1119 224:117424.

1120 Hein TP, Herrojo Ruiz M (2022) State anxiety alters the neural oscillatory correlates
1121 of predictions and prediction errors during reward-based learning.
1122 NeuroImage 249:118895.

1123 Herrojo Ruiz M, Jabusch H-C, Altenmüller E (2009) Detecting Wrong Notes in
1124 Advance: Neuronal Correlates of Error Monitoring in Pianists. Cereb Cortex
1125 19:2625–2639.

1126 Herrojo Ruiz M, Maess B, Altenmüller E, Curio G, Nikulin VV (2017) Cingulate and
1127 cerebellar beta oscillations are engaged in the acquisition of auditory-motor
1128 sequences. Hum Brain Mapp 38:5161–5179.

1129 Hird EJ, Beierholm U, De Boer L, Axelsson J, Backman L, Guitart-Masip M (2022)
1130 Dopamine and reward-related vigor in younger and older adults. Neurobiol
1131 Aging 118:34-43.

1132 Iglesias S, Mathys C, Brodersen KH, Kasper L, Piccirelli M, den Ouden HEM,
1133 Stephan KE (2013) Hierarchical Prediction Errors in Midbrain and Basal
1134 Forebrain during Sensory Learning. Neuron 80:519–530.

1135 Kang SY, Wasaka T, Shamim EA, Auh S, Ueki Y, Lopez GJ, Kida T, Jin S-H, Dang
1136 N, Hallett M (2010) Characteristics of the sequence effect in Parkinson's
1137 disease: Sequence Effect in Parkinson's Disease. Mov Disord 25:2148–2155.

1138 Ketcham CJ, Seidler RD, Van Gemmert AWA, Stelmach GE (2002) Age-Related
1139 Kinematic Differences as Influenced by Task Difficulty, Target Size, and
1140 Movement Amplitude. J Gerontol B Psychol Sci Soc Sci 57:P54–P64.

1141 Kjær SW, Damholdt MF, Callesen MB (2018) A systematic review of decision-making
1142 impairments in Parkinson's Disease: Dopaminergic medication and
1143 methodological variability. Basal Ganglia 14:31–40.

1144 Levy-Gigi E, Haim-Nachum S, Hall JM, Crouse JJ, Winwood-Smith R, Lewis SJ,
1145 Moustafa AA (2019) The interactive effect of valence and context on reversal
1146 learning in individuals with Parkinson's disease. Neurosci Lett 692:216-224.

1147 Lewandowski D, Kurowicka D, Joe H (2009) Generating random correlation matrices
1148 based on vines and extended onion method. J Multivar Anal 100:1989–2001.

1149 Mantziara M, Ivanov T, Houghton G, Kornysheva K (2021) Competitive state of
1150 movements during planning predicts sequence performance. J Neurophysiol
1151 125:1251-68.

1152 Manohar SG, Muhammed K, Fallon SJ, Husain M (2019) Motivation dynamically
1153 increases noise resistance by internal feedback during movement.
1154 Neuropsychologia 123:19–29.

1155 Marshall L, Mathys C, Ruge D, de Berker AO, Dayan P, Stephan KE, Bestmann S
1156 (2016) Pharmacological Fingerprints of Contextual Uncertainty. PLOS Biol
1157 14:e1002575.

1158 Mathys C (2011) A Bayesian foundation for individual learning under uncertainty.
1159 Front Hum Neurosci 5:1-20.

1160 Mathys CD, Lomakina EI, Daunizeau J, Iglesias S, Brodersen KH, Friston KJ,
1161 Stephan KE (2014) Uncertainty in perception and the Hierarchical Gaussian
1162 Filter. Front Hum Neurosci 8:1-24.

1163 MATLAB and Statistics Toolbox Release 2020b, The MathWorks, Inc., Natick,
1164 Massachusetts, United States.

1165 McDougle SD, Boggess MJ, Crossley MJ, Parvin D, Ivry RB, Taylor JA (2016) Credit
1166 assignment in movement-dependent reinforcement learning. Proc Natl Acad
1167 Sci 113:6797–6802.

1168 Metitieri T, Geroldi C, Pezzini A, Frisoni GB, Bianchetti A, Trabucchi M (2001) The
1169 Itel-MMSE: An Italian telephone version of the mini-mental state examination.
1170 Int J Geriatr Psychiatry 16:166-167.

1171 Moran RJ, Campo P, Symmonds M, Stephan KE, Dolan RJ, Friston KJ (2013) Free
1172 energy, precision and learning: the role of cholinergic neuromodulation. J
1173 Neurosci 33:8227-36.

1174 Nassar MR, Bruckner R, Gold JI, Li S-C, Heekeren HR, Eppinger B (2016) Age
1175 differences in learning emerge from an insufficient representation of
1176 uncertainty in older adults. Nat Commun 7:11609.

1177 Padmala S, Pessoa L (2011) Reward Reduces Conflict by Enhancing Attentional
1178 Control and Biasing Visual Cortical Processing. J Cogn Neurosci 23:3419–
1179 3432.

1180 Powers AR, Mathys C, Corlett PR (2017) Pavlovian conditioning–induced
1181 hallucinations result from overweighting of perceptual priors. Science
1182 357:596–600.

1183 R Core Team (2022). R: A language and environment for statistical computing. R
1184 Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-
1185 project.org/.

1186 Reed EJ, Uddenberg S, Suthaharan P, Mathys CD, Taylor JR, Groman SM, Corlett
1187 PR (2020) Paranoia as a deficit in non-social belief updating. eLife 9:e56345.

1188 Rescorla RA, Wagner AR (1972) A theory of Pavlovian conditioning: variations in the
1189 effectiveness of reinforcement and nonreinforcement. Curr Res Theory 2:64–
1190 99.

1191 Rolls ET, Deco G, Huang CC, Feng J (2022) The human orbitofrontal cortex,
1192 vmPFC, and anterior cingulate cortex effective connectome: emotion,
1193 memory, and action. Cereb Cortex.

1194 Rouault M, Drugowitsch J, Koechlin E (2019) Prefrontal mechanisms combining
1195 rewards and beliefs in human decision-making. Nat Commun 10:301.

1196 Rouder JN, Morey RD, Speckman PL, Province JM (2012) Default Bayes factors for
1197 ANOVA designs. J Math Psychol 56:356–374.

1198 Ryterska A, Jahanshahi M, Osman M (2013) What are people with Parkinson's
1199 disease really impaired on when it comes to making decisions? A meta-
1200 analysis of the evidence. Neurosci Biobehav Rev 37:2836–2846.

1201 Sedaghat-Nejad E, Herzfeld DJ, Shadmehr R (2019) Reward Prediction Error
1202 Modulates Saccade Vigor. J Neurosci 39:5010–5017.

1203 Shadmehr R (2010) Control of movements and temporal discounting of reward. Curr
1204 Opin Neurobiol 20:726-730.

1205 Sheffield JM, Suthaharan P, Leptourgos P, Corlett PR (2022) Belief Updating and
1206 Paranoia in Individuals with Schizophrenia. Biol Psychiatry Cogn Neurosci
1207 Neuroimaging.

1208 Sivula T, Magnusson M, Matamoros AA, Vehtari A (2022) Uncertainty in Bayesian
1209 Leave-One-Out Cross-Validation Based Model Comparison. arXiv
1210 2008.10296. https://doi.org/10.48550/arXiv.2008.10296.

1211 Soch J, Allefeld C (2018) MACS – a new SPM toolbox for model assessment,
1212 comparison and selection. J Neurosci Methods 306:19–31.

1213 Spielberger CD, Gorsuch RL, Lushene R, Vagg PR, Jacobs GA (1983). Manual for
1214 the State-Trait Anxiety Inventory. Palo Alto, CA: Consulting Psychologists
1215 Press.

1216 Sporn S, Chen X, Galea JM (2022) The dissociable effects of reward on sequential
1217 motor behavior. J Neurophysiol 128:86-104.

1218 Stefanics G, Heinzle J, Horváth AA, Stephan KE (2018) Visual Mismatch and
1219 Predictive Coding: A Computational Single-Trial ERP Study. J Neurosci
1220 38:4020–4030.

1221 Summerside EM, Shadmehr R, Ahmed AA (2018) Vigor of reaching movements:
1222 reward discounts the cost of effort. J Neurophysiol 119:2347–2357.

1223 Sutton RS (1992) Gain adaptation beats least squares? Paper presented at the 7th
1224 Yale Workshop on Adaptive and Learning Systems, New Haven, CT, May.

1225 Valton V, Wise T, Robinson OJ (2020) Recommendations for Bayesian hierarchical
1226 model specifications for case-control studies in mental health. arXiv
1227 2011.01725. https://doi.org/10.48550/arXiv.2011.01725.

1228 Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using
1229 leave-one-out cross-validation and WAIC. Stat Comput 27:1413–1432.

1230 Weber LA, Diaconescu AO, Mathys C, Schmidt A, Kometer M, Vollenweider F,
1231 Stephan KE (2020) Ketamine Affects Prediction Errors about Statistical
1232 Regularities: A Computational Single-Trial Analysis of the Mismatch
1233 Negativity. J Neurosci 40: 5658-5668.

1234 Yoon T, Jaleel A, Ahmed AA, Shadmehr R (2020) Saccade vigor and the subjective
1235 economic value of visual stimuli. J Neurophysiol 123:2161-2172.

1236 Zigmond AS, Snaith RP (1983) The hospital anxiety and depression scale. Acta
1237 Psychiatr Scand 67:361-370.

1238

FIGURES

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

Figure 2. The Hierarchical Gaussian Filter (HGF) for binary outcomes. ***A,*** Illustration of the 3-level HGF model (HGF_3) with relevant parameters modulating each level (adapted from Hein et al., 2021). Level x_1 represents the binary categorical variable of the

experimental stimuli on each trial *k*; x_2 reflects the true value of the tendency of the stimulus-outcome contingency, and x_3 the true volatility of the environment. In our experiment, ω_2, ω_3 and ζ were free parameters and were estimated by fitting individual responses and observed inputs with the HGF. κ represents the strength of coupling between level 2 and 3 (fixed to 1 in our study; not shown in the text; see Mathys et al., 2014 for the model equations). ***B,*** Belief trajectories for the HGF_3 across the total 180 trials in a representative participant in Study 1. At the lowest level, black dots (*u*) represent the outcomes, denoting whether seq1 was rewarded or not (1 = seq1 wins [seq2 loses]; 0 = seq2 wins [seq1 loses]); orange dots (*y*) represent the participant's choices (1 = seq1 is played; 0 = seq2 is played); orange crosses depict performance execution errors; the black line is a subject-specific learning rate about stimulus outcomes (α; see Mathys et al. 2014 for the full HGF equations). At the second level, μ_2 (σ_2) is the trial-by-trial trajectory of beliefs (mean and variance) about the tendency of the stimulus-outcome contingencies (x_2). A mean estimate μ_2 shifted towards positive values on the y-axis indicates that the participant had a greater expectation that seq1 was rewarded relative to seq2. In addition, larger (absolute) μ_2 values on that axis denote a stronger expectation that given the correct sequence choice a reward will be received. The trajectory of beliefs about phasic (log)volatility (μ_3 [σ_3]) is displayed at the top level. The true volatility in our task, x_3, was constant, as the stimulus-outcome contingencies changed every 25-35 trials. Participants could, however, express individual differences in their log-volatility estimates, which could be captured by the HGF_3 (e.g., Powers et al., 2017). In our three studies, the winning model was the 2-level HGF (HGF_2), in which volatility was fixed across participants. Blue circles on the y-axis denote the upper and lower priors of the posterior distribution of beliefs, $\mu_i^{(0)} \pm \sigma_i^{(0)}$, $i = 2,3$.

Figure 3. Markers of general task performance and decision making across groups. Data presented for healthy younger adults (HYA; in light blue), healthy older adults (HOA; in dark blue) and patients with Parkinson's Disease (PD; in purple) in Study 1. ***A***, Performance

tempo (mIKI, mean inter-keystroke-interval, in ms); ***B***, Reaction time (RT, in ms); ***C***, Rate of win trials (percWin); ***D***, Rate of performance execution errors (percError); ***E***, Tonic volatility (ω_2); ***F***, Informational uncertainty on level 2 (σ_2); ***G***, Response model parameter (ζ). Values mIKI, RT and σ_2 are averaged across 180 trials within each participant. mIKI and RT values 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) the individual data points in each group are shown to visualise group population variability.

Figure 4. Invigoration of performance tempo by beliefs is preserved in healthy ageing 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 group in Study 1. ***A***, Illustration of the posterior predictive checks where the distribution of the observed outcome variable (y, in our case performance tempo) is compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). ***B***, Distributions of the difference in ms between performance tempo (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, 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.

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 ~ 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.

Figure 6. Effect of retrospective credit assignment on general task performance and decision making. Markers of general task performance and decision making in participants that replied True to Question 8 ($Q8_T$; in dark brown) and participants that replied False to

Question 8 ($Q8_F$; in light brown) in the post-performance questionnaire (see **Table 2**) in Study 2. ***A***, Performance tempo (mIKI, mean inter-keystroke-interval; in ms, $Q8_T$: mean 287, SEM 13.2; $Q8_F$: mean 307, SEM 27.2); ***B***, Reaction times (RT; in ms, $Q8_T$: mean 564, SEM 30.5; $Q8_F$: mean 555, SEM 68.7); ***C***, Rate of win trials (percWin; $Q8_T$: mean 0.574, SEM 0.013; $Q8_F$: mean 0.555, SEM 0.024); ***D***, Rate of performance execution errors (percError; $Q8_T$: mean 0.077, SEM 0.010; $Q8_F$: mean 0.102, SEM 0.020); ***E***, Tonic volatility, (ω_2;$Q8_T$: mean -1.624, SEM 0.510; $Q8_F$: mean -0.715, SEM 0.357); ***F***, Informational uncertainty on level 2 (σ_2; $Q8_T$: mean 1.740, SEM 0.203; $Q8_F$: mean 2.057, SEM 0.237); ***G***, Response model parameter, (ζ; $Q8_T$: mean 1.599, SEM 0.237; $Q8_F$: mean 1.271, SEM 0.206). Values mIKI, RT and σ_2 are averaged across 180 trials within each participant. mIKI and RT values 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 group to visualise group population variability.

Figure 7. No effect of retrospective credit assignment on motor vigour: performance tempo. Bayesian Linear Mixed Models (BLMM; model number 6, y ~ 1 + group * x + [1 + x|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 performance tempo) is compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). ***B***, Distribution of the difference in ms between performance tempo (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 performance tempo separately for $Q8_T$ (in dark brown) and $Q8_F$ (in light brown). 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, which replicates our findings in the main experiment (see **Figure 4C**). ***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 motor performance tempo. Thus, the sensitivity of performance tempo to the strength of predictions about the reward mapping is not differently 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 ~ 1 + group * x + [1 + x|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.

Figure 9. Explicit confidence ratings invigorate performance tempo. Bayesian Linear Mixed Models (BLMM; model number 4, y ~ 1 + x + [1 + x|subject] + [1|trial]) in Study 3 for performance tempo (left) and reaction times (RT; right). ***A***, Illustration of the posterior predictive checks where the distribution of the observed outcome variable (y, in our case performance tempo) is compared to simulated datasets (y_{rep}) from the posterior predictive distribution (100 draws). ***B***, Results of the BLMM analysis. We analysed how explicit beliefs about the reward tendency (confidence ratings) modulate performance tempo. Here, mIKI (performance tempo: mean inter-keystroke-interval) values are represented in the log-scale. The negative slope had a point estimate of -0.04 (95% credible interval [CI] from -0.08 to -0.001, including three decimal digits in the upper bound). The 95% CI did not include zero. This suggest that being more certain about receiving a reward outcome is associated with faster performance tempo, which replicates our findings with the computational parameter $|\hat{\mu}_2|$ (see **Figure 4C** and **Figure 7C**). ***C***, Distribution of the slope. The grey vertical bar indicates the posterior point estimate, while the grey area under the curve represents the 95% CI. The vertical red line denotes zero. ***D***, 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). ***E***, Results of the BLMM analysis. 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 (95% CI from -0.20 to 0.01). ***F***, Distribution of the slope. The grey vertical bar indicates the posterior point estimate, while the grey area under the curve represents the 95% CI. The vertical red line denotes zero.

TABLES

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	B	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	T	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	T	SX	100	652	Benserazide, Levodopa, Pramipexole, Selegiline
10	69	7	21	45	5	6	3	B	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	B	SX	437	470	Benserazide, Levodopa, Ropinirole, Selegiline
17	65	5	21	26	1	7	16	R/B	SX	360	100 + 3.9	Levodopa, Opicapone, Pramipexole, Trihexyphenidyl

											ml/h 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

1433 MMSE predicted score = 1.01 x ITEL-MMSE score + 5.16; HADS_A = anxiety score; HADS_D = depression score; R = rigidity, B =
1434 bradykinesia, LE = lack of energy, T = tremor, D = dyskinesia.

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]

Post-performance questionnaire included in Study 2. Question 8 (Q8) is aimed at evaluating subjective inferences about the task-related credit assignment.

Table 3. Means and variances of the priors on perceptual parameters and starting values of the beliefs of the winning HGF_2 model

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

Free parameter ω_2 was estimated in its unbounded (linear) space. The prior values on ω_2 (mean [variance]) were: -2.17 (16), -2.16 (16) and -2.22 (16) for Study 1, 2 and 3, respectively. These prior values were obtained using an ideal observer model that received the input that each participant had experienced. The response model parameter, ζ, was log-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 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 prior variances are given in the space in which the parameters are typically estimated.

Table 4. Models of increasing complexity used for Bayesian Linear Mixed Models analyses

Study #	Model #	Model
1 - 2		
	1	y ~ 1 + (1|subject)
	2	y ~ 1 + group + (1|subject)
	3	y ~ 1 + group + x + (1|subject)
	4	y ~ 1 + group * x + (1|subject)
	5	y ~ 1 + group * x + (1 + x|subject)
	6	y ~ 1 + group * x + (1 + x|subject) + (1|trial)
3		
	1	y ~ 1 + (1|subject)
	2	y ~ 1 + x + (1|subject)
	3	y ~ 1 + x + (1 + x|subject)
	4	y ~ 1 + x + (1 + x|subject) + (1|trial)

Models of increasing complexity used in Study 1 and 2 (top) and Study 3 (bottom). In Study 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 ($|\hat{\mu}_2|$_c). This parameter represents the strength of the predictions. In model 1, y is explained by a fixed effect of the intercept and a random effect of intercept by subject (the latter accounts for repeated measurements); model 2 adds a fixed effect of group; model 3 includes the fixed effect of x, which allows to assess the sensitivity (slope) of performance tempo or RT to $|\hat{\mu}_2|$_c in the reference group; model 4 incorporates the interaction term between group and x, which allows to investigate the between-group differences in the sensitivity (slope) of performance tempo or RT to $|\hat{\mu}_2|$_c; model 5 includes the random effect of $|\hat{\mu}_2|$_c by subject; last, model 6 includes a random effect of intercept by trial. In Study 3, y corresponds to the

motor performance (log_mIKI or log_RT); x is the confidence rating. In model 1, y is explained by a fixed effect of the intercept and a random effect of intercept by subject (the latter accounts for repeated measurements); model 2 adds a fixed effect of x, which allows to assess the sensitivity (slope) of performance tempo or RT to confidence ratings; model 3 includes the random effect of confidence ratings by subject; last, model 4 includes a random effect of intercept by trial.

1472 **Table 5. Summary of the posterior distributions for the fixed effects of the best fitting**

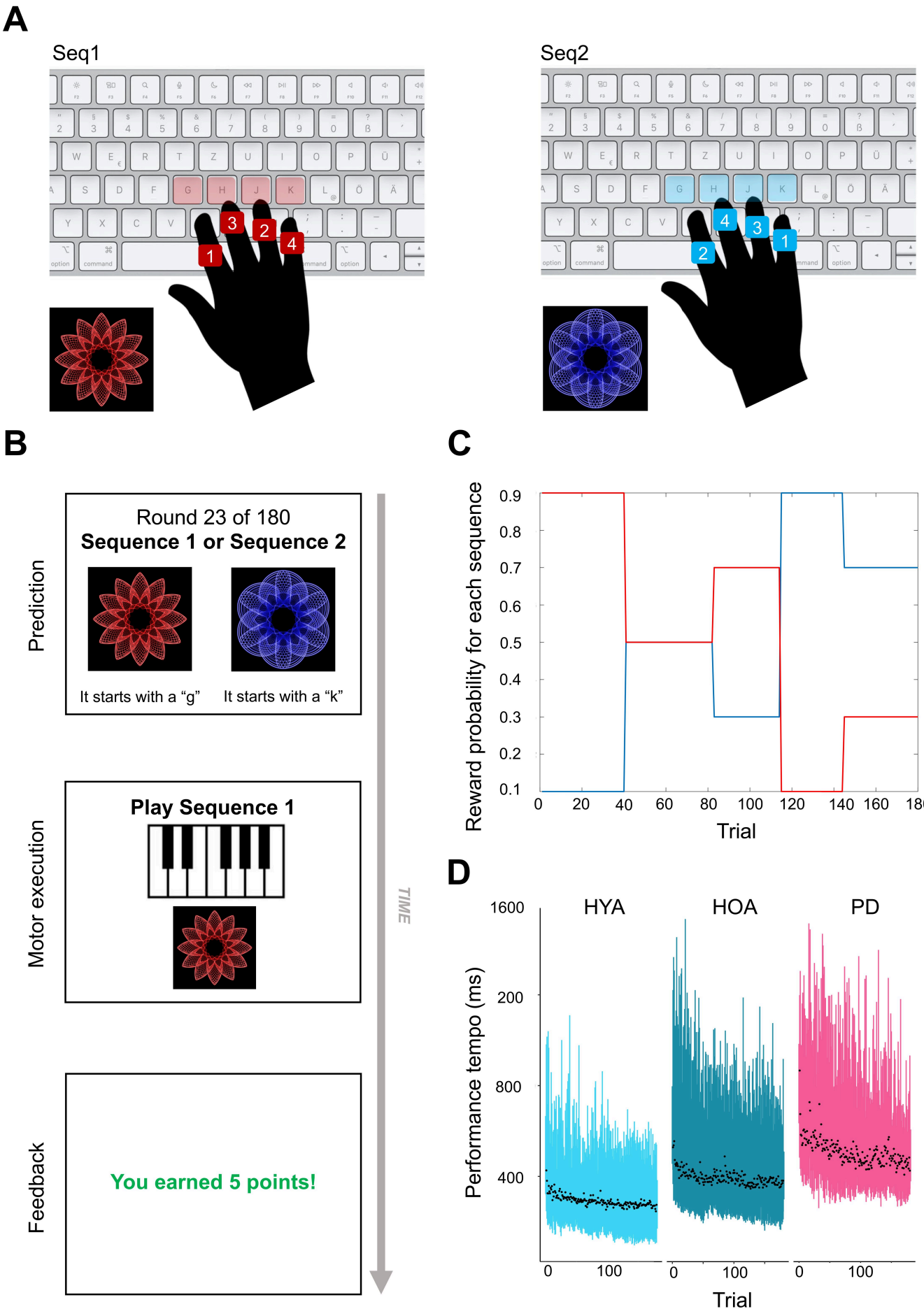
1473 **Bayesian Linear Mixed Models**

Study #	Dependent Variable	Fixed Effect	Estimate	l-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: $Q8_T$ 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: $Q8_T$ vs $Q8_F$	0.01	-0.03	0.04	1.00
3						

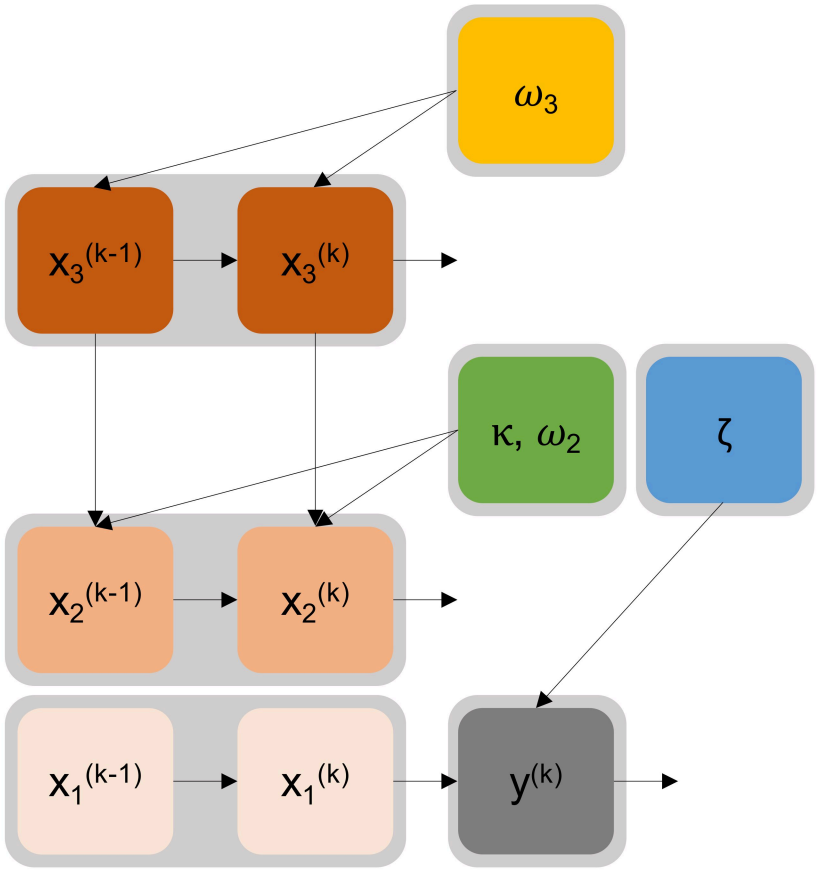
Performance tempo					
	y	5.82	5.73	5.91	1.00
	x	-0.04	-0.08	-0.001	1.00
Reaction times					
	y	6.47	6.37	6.58	1.00
	x	-0.10	-0.20	0.01	1.00

Estimates, credible intervals (CIs) and R-hat values for the fixed effects of the best fitting models in Study 1, 2 (model number 6: y ~ 1 + group * x + [1 + x|subject] + [1|trial]) and in Study 3 (model number 4: y ~ 1 + x + [1 + x|subject] + [1|trial]). In Study 1, y: HOA refers to the posterior estimate for the intercept in the reference group (healthy older adults, HOA). y: HOA vs HYA and y: HOA vs PD reflect the posterior distributions of the differences between intercepts (HOA vs healthy younger adults [HYA]; HOA vs Parkinson's patients [PD], respectively). x: HOA is the posterior distribution of the association (slope) between motor performance (either performance tempo or reaction times) and the strength of predictions about the action-reward contingency in the reference group. group * x: HOA vs HYA and group * x: HOA vs PD are the posterior distributions of slope differences between HOA and HYA and between HOA and PD, respectively. In Study 2, y: $Q8_T$ refers to the posterior estimate for the intercept in the reference group (participants that replied True to Question 8, $Q8_T$). y: $Q8_T$ vs $Q8_F$ reflects the posterior distribution of the difference between intercepts ($Q8_T$ vs participants that replied False to Question 8 [$Q8_F$]). x: $Q8_T$ is the posterior distribution of the association (slope) between motor performance (either performance tempo or reaction times) and the strength of predictions about the action-reward contingency in the reference group. The upper bound of the CI for the slope effect in the BLMM analyses for RT is given with three decimal digits to demonstrate that 0 was included in the 95% CI. group * x: $Q8_T$ vs $Q8_F$ is the posterior distribution of slope difference between $Q8_T$ and $Q8_F$. In Study 3, y refers to the posterior estimate for the intercept. x is the posterior distribution of the association (slope) between motor performance (either performance tempo or reaction times) and the 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, l-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).



A



B