A Theoretical Formalization of Consequence-Based Decision-Making

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ABSTRACT

Learning to make adaptive decisions depends on exploring options, experiencing their consequence, and reassessing one's strategy for the future. Although several studies have analyzed various aspects of value-based decision-making, most of them have focused on decisions in which gratification is cued and immediate. By contrast, how the brain gauges delayed consequence for decision-making remains poorly understood.

To investigate this, we designed a novel decision-making task in which each decision altered future options to decide upon. The task was organized in groups of inter-dependent trials, and the participants were instructed to maximize cumulative reward value within each group. In the absence of any explicit performance feedback, the participants had to test and internally assess specific criteria to make decisions. The absence of explicit feedback was key to specifically study how the assessment of consequence forms and influences decisions as learning progresses.

We formalized this operation mathematically by means of a multi-layered decision-making model. It uses a mean-field approximation to describe the dynamics of two populations of neurons which characterize the binary decision-making process. The resulting decision-making policy is dynamically modulated by an internal oversight mechanism based on the prediction of consequence. This policy is reinforced by rewarding outcomes. The model was validated by fitting each individual participants' behavior. It faithfully predicted non-trivial patterns of decision-making, regardless of performance level.

These findings provide an explanation to how delayed consequence may be computed and incorporated into the neural dynamics of decision-making, and to how adaptation occurs in the absence of explicit feedback.

AUTHOR SUMMARY

Decision-making often entails anticipating the consequences of one's choices over time. However, real-world choice outcomes are not always immediate, adding significant challenges to determining their long-term implications for behavior. Most previous studies on reward-driven decision-making focus on task paradigms in which the decision outcomes are immediate and explicitly cued. However, the cognitive and neurobiological mechanisms by which the brain learns about and incorporates delayed and uncertain consequences remain unclear. Consequently, the primary aim of our study was twofold. First, we designed an experimental task in which participants were instructed to maximize the reward value across sequences of trials in which some of the stimuli offers were dependent on previous choices. Crucially, participants had to learn the decision-making strategy by making exploratory decisions in the absence of any explicit feedback. We analyzed the resulting behavior to characterize individual differences in decision strategy and learning rates. Secondly, we built a model of the underlying cognitive processes involved in strategy learning and consequence-based decision-making. We formalized this by using a three-layer model which accurately reproduced the behavior of individual participants. The resulting model provides a discrete computational account of consequence-based decision-making.

1 INTRODUCTION

Adaptive behavior requires making choices that maximize long-term reward while also minimizing effort, costs and risk (1–4). This is commonly studied under the value-based wide framework of decision-making (5–7), which conceptualizes choice behavior as a trade-off between the various benefits and costs associated with different decision options. In most contexts, choice outcomes are immediate, unambiguous, and explicitly cued. These features make calculating the costs/benefits straightforward, as all the necessary information is directly and immediately available to the decision maker for calculation (8–11). However, it is significantly less clear how decision-makers can compute the time-extended costs and benefits, and thus how they learn to make adaptive choices in contexts where decision outcomes are not made explicit or depend on a prediction of future consequence. In other words, a complete account of value-based choice behavior requires understanding how the brain detects and computes the non-immediate consequences of choices, and how to use this information to guide subsequent decision strategies.

Why are consequence-based decisions more complicated than simple sensory accumulation perceptual decision-making (12,13)? Firstly, they require an increased temporal span of consideration, they are often more uncertain, since there is a greater number of factors to consider, and the environmental variability/unpredictability should be taken into account. All these aspects make option evaluation more computationally demanding, yielding longer deliberation times and a poorer decision accuracy (14,15). This is well-founded by an extensive body of previous empirical work (16–19). Secondly, because of the aforementioned factors, consequence-based decisions also depend on a much broader range of cognitive functions and brain regions than those involved in purely concurrent sensory/perceptual decisions (20), e.g., structures related to working memory (21,22) and higher cognitive processing (23,24). There is no consensus about what a minimal set of functions required for consequence-based decisions would be, and little evidence about the neural mechanisms potentially involved (7,25).

To add clarity to how these cognitive processes unfold in the human brain to achieve consequence-based decision-making, we carried out a two-part study. This consisted of a behavioral experiment with human participants and a neurally-inspired model that reproduce their decision behavior and formalize some of the potential underlying brain mechanisms. First, we designed a novel behavioral paradigm, i.e., the consequential task, in which participants had to learn an optimal strategy to maximize their cumulative reward values across groups of trials. Specifically, participants made perceptual choices between two stimuli. In some blocks, after overcoming the perceptual discrimination, decisions were one-shot, and the reward could be maximized right away by choosing the option associated with the greatest immediate amount. However, other decisions involved groups of trials in which the reward values available in later trials were dependent on choices made in earlier ones. Namely, it was designed in such a way that choosing the larger value in the first trial led to a much lesser overall amount in the next trials within the same group. Therefore, participants could not maximize the cumulative reward value by optimizing the single-trial reward value. By contrast, the optimal strategy necessarily entails learning that short-term reward value must often be sacrificed for larger subsequent reward values. This mechanism is known from studies in delay discounting (26–30), such as the marshmallow experiment (31,32), which we here apply to decision-making in a broader sense. In our task, the optimal decision policy could only be discovered via exploratory decision-making in the absence of explicit cues, i.e., the participants had to rely on subjective feedback to pick up on the delayed consequences of their decisions across successive trials. In other words, unlike previous experimental paradigms, our task is

structured such that maximum cumulative reward value can only be attained when exploiting covert dependencies across trials. This makes the consequential task uniquely well-suited to tap into the neural mechanisms specifically involved in consequence-based decisions.

In the second part of our study, we described a novel computational model designed to formalize the dynamics and strategy of decision-making, including the patterns of inhibition and of assessment of far-sighted consequence required to gain maximum cumulative reward. The model is organized in three layers, here identified as low, middle and top. The lower layer, in line with the Amari, Wilson-Cowan and Wong-Wang models (33–38), describes the average dynamics of two populations of neurons in the context of perceptual binary decision-making. The middle and top layers are needed to assess the consequence across the group of trials, incorporating complexity and consequence into the competitive dynamics of decision-making. Despite its simplicity, this model can accurately reproduce the full variety of performance observed across the different participants; in other words, the model captures the full range of processes required for real-world consequence-based decision-making. This model therefore implements the minimal core processes required for consequence-based learning and decision-making, and it is an achievement in its own right. The model describes the assessment of consequence as a complex process which may be described as an extension of value-based decision-making. The decision-making process is supervised by an oversight mechanism that monitors overall performance by means of an internal subjective mechanism of value assessment that integrates information from different sources, and after a few iterations, yields a correct prediction of consequence for each option.

2 RESULTS

2.1 Task design

In this section, we describe the consequential task, specifically designed to tap into the cognitive mechanisms involved in learning delayed consequences in the absence of feedback. In this task, 28 healthy participants were instructed to choose one of the two stimuli, depicting reward values through differently filled water containers, presented left and right on the screen. The participants reported their choices by sliding the computer mouse's cursor from the central cue to the chosen stimulus (see Figure 1 and Materials and Methods for a thorough description).

Since consequence depends on a predictive assessment of future contexts, the task was organized into two main types of trial blocks, in which the participants had to maximize the reward value. There were the blocks in which trials required one-shot decisions, purely independent from each other. As in most typical decision-making paradigms, the reward value in these trials could be maximized by picking the best available option in that instance. However, in other blocks, trials were grouped into pairs or triads of interdependent trials. We called each group of linked consecutive trials an episode to signify the boundary of interdependence between them, and defined the notion of horizon (n_H) as a metric for its quantification. The horizon of a specific episode equaled the number of dependent trials following the first trial of each episode. The nature of the dependence between trials of an episode was such that the mean reward values of the stimuli in the second/third trial were systematically increased or decreased based on the participant's choice in the preceding trial. Specifically, choosing the greater stimulus value led to a reduction of stimuli values in the subsequent trial, whereas achieving greater future value options required deliberately choosing the lesser option in the previous trial (Figure 1b).

Participants were instructed that their goal was to maximize the cumulative reward value per episode. Optimal performance across the task as a whole was achieved by choosing "big" in single trial episodes (horizon n_H=0), and deliberately choosing "small" in all trials of n_H=1 and n_H=2 episodes except the last, in which "big" should be chosen. However, learning this policy was made challenging by a number of different factors. First, perceptual discrimination, quantifying the size difference between stimuli varies within 1-20% of the container. Second, although the participants were instructed that their choices affect future trials within the episode, the nature of this dependency was not signaled in any obvious way. This means that from the perspective of the participants, the value of the reward offers might at first appear random. Third, explicit feedback after each episode was crucially omitted from the task. The reason for this is that the presence of feedback might have had the undesirable effect of participants focusing on finding the specific sequence of choices within episode yielding optimal feedback, without having to learn the relationship between their decisions and the subsequent trials. In other words, an explicit measure of performance might have reduced the task to an explicit trial-and-error test of deciding for example, "big-small", "small-big", etc., until finding the sequence of choices leading to maximum performance, rather than learning to evaluate each option's consequence in terms of their prediction of future reward value to attain the goal. In contrast, the absence of feedback made the participants not informed about their performance throughout the block, and ought to oblige them to create an internal sense of assessment, which can only rely on two mechanisms: the sensory perception of the systematic stimuli changes in the subsequent trial after each choice, and the exploration of option choices at each trial during the earlier part of each block. The resulting task essentially becomes a measure of learning about delayed consequences associated with each option in the absence of explicit feedback.

In summary, for the participants to be able to perform the task, they were informed of the episode-based organization of trials at each block, i.e., the horizon. The instruction to the participant was to find the strategy leading to the most cumulative reward value for each episode and, for the reasons mentioned previously, to actively explore their choices. Further details are shown in the Methods section, and in Figure 1.

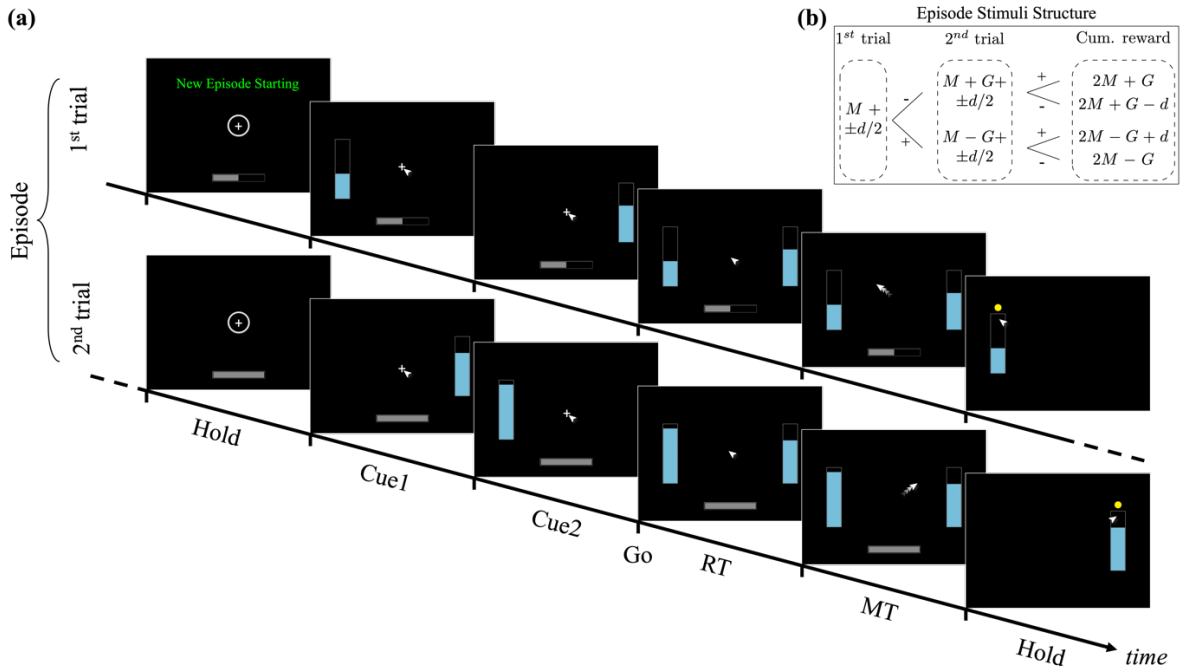

Figure 1. Time-course of a typical horizon 1 episode of the consequential decision-making task. ***(a)*** *The episode consists of two dependent trials. The first starts with the message "New Episode Starting" in the center-top of the screen, a circle surrounding a cross in the center (central target), and half full progress bar at the bottom of the screen. The progress bar indicates the current trial within the episode (for horizon 1, 50% during the first trial, 100% during the second trial). After holding for 500ms, the left or right (chosen at random) stimulus is shown, followed by its complementary stimulus 500ms later. Both stimuli are shown together 500ms later which serves as the GO signal. At GO, the participant has to slide the mouse from the central target to the bar of their choosing. Once the selected target is reached, a yellow dot appears over that target. The second trial follows the same pattern as the first. See Methods for more details.* ***(b)****: Construction scheme for the size of the stimuli in each episode. The first trial within the episode consists of 2 stimuli of size M+d/2 and M-d/2. The second trial within the episode depends on the selection made in the previous trial. If the first selected stimulus is M-d/2 (following symbol "-" in the figure), then the second trial consists of stimuli with size M+G+d/2 and M+G-d/2, otherwise M-G+d/2 and M-G-d/2 (following symbol "+" in the figure). The cumulative reward value of the episode can therefore assume 4 distinct values (ordered from best to worst): 2M+G, 2M+G-d, 2M-G+d, and 2M-G. See Methods for more details on the values of M, G, d.*

2.2 Behavioral Results

The metrics extracted from the participants' behavioral data were their performance (PF), reported choices (CH), reaction time (RT), and visual discrimination (VD) sensitivity. The PF is a single-episode metric assuming values from 0 (worst) to 1 (best), and is calculated as the percentage of reward value obtained throughout the episode normalized by the maximum and minimum that could have been obtained. CH was the choice made by the participant in each trial, in terms of small or large reward stimulus. The RT was calculated as the time difference between the simultaneous presentation of both stimuli (the GO signal), and the onset of the movement. The VD is the ability to visually discriminate between stimuli, i.e., identifying which one is the bigger/smaller (see Methods for further details). As shown below, when the difference between stimuli (DbS) is small, participants were not able to accurately distinguish between stimuli. The DbS varies within 1-20% of the size of the container.

The absence of explicit performance-related feedback at the end of each episode made the task more difficult, and, consequently, not all participants were able to find the optimal strategy. For horizon $n_H=0$, all twenty-eight participants but one learned and applied the optimal strategy, i.e., repeatedly selecting the larger stimulus. By contrast, only twenty-two participants learned the optimal strategy during horizon $n_H=1,2$ blocks, i.e., selecting the larger stimulus in

the last trial only. Most participants who did not learn the optimal strategy for n_H=1,2 repeatedly chose the larger stimulus for all trials.

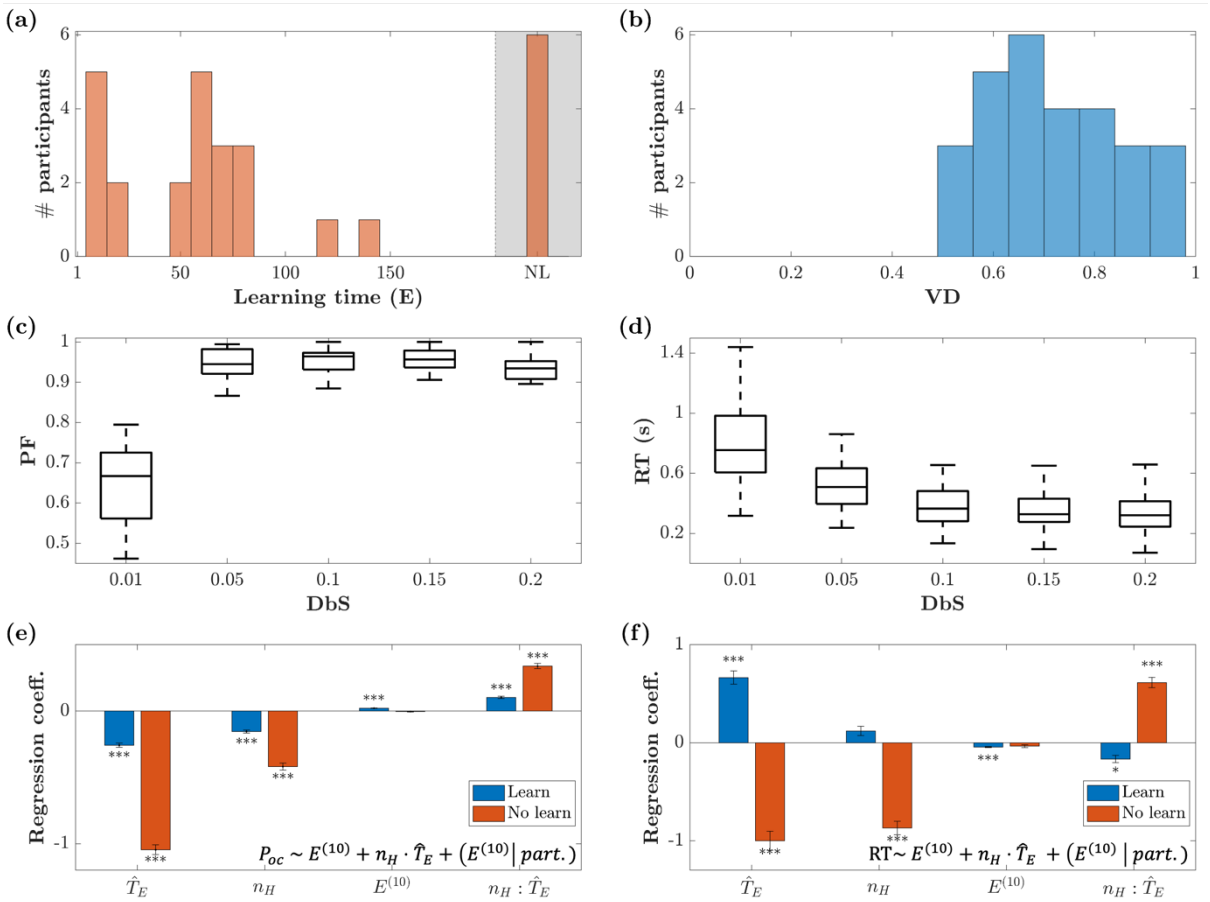

Figure 2. Summary results across participants. ***(a)*** *Histogram of learning times, in terms of episodes (E). The learning time is defined as the first episode throughout the whole session in which the optimal strategy was applied repeatedly (see Methods). We identified four groups of participants: fast, medium and slow learners, and participants who did not discover the optimal strategy (NL – No Learning).* ***(b)*** *Histogram of the visual discrimination (VD) calculated by computing the percentage of correct selections of the last 80 episodes, in the horizon 0 block, for only the most difficult trials (DbS = 0.01).* ***(c)*** *Performance as a function of DbS, for the trials after the optimal strategy was applied.* ***(d)*** *Reaction Time (RT) versus DbS. The more similar the stimuli, the longer participants needed to make a decision. (e-f) Regression coefficients for the linear mixed-effects models* $P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + (E^{(10)}|part.)$ *and* $RT \sim E^{(10)} + n_H \cdot \hat{T}_E + (E^{(10)}|part.)$*, where* P_{oc} *is the percentage of optimal choices, RT is the reaction time,* $E^{(10)}$ *is the moment in time (counting episodes in groups of 10), nH is the horizon number,* $\hat{T}_E$ *is the trial within episode counting backwards from last to first, and part. is the participant. We used maximum likelihood to estimate the model parameters. Participants were divided into two groups: those who learned the optimal strategy (blue) and those who did not (red), see Panel (a).*

Figure 2 shows the summary results for all twenty-eight participants. In Panel (a) we show the histogram of their learning time in terms of episodes (*E*), defined as the first episode of the session in which the optimal strategy was assimilated. Namely, we defined the time at which the strategy was assimilated as the moment after which the optimal strategy was used in at least 9 out of the following 10 episodes. To ensure that a low success rate was not caused by perceptual discrimination errors (during low VD), we excluded the most difficult episodes in terms of DbS to calculate the learning time. The last histogram bar in Figure 2a (shown as NL – No Learning), shows the aggregate of the 6 participants who never learned the optimal strategy. We can identify four types of participants as a function of their learning speed: slow, medium, fast learners, and those participants who did not ever learn the strategy. Figure 2b shows the VD, for all difficult trials (smallest DbS) and participants, where VD was calculated

as the percentage of correct choices over the last 80 episodes in the horizon $n_H=0$ block. On average, stimuli were discriminated correctly in 71% of the most difficult trials. Thus, despite having learned the optimal strategy, because of the low VD, most participants continued making some errors. This is reported in Figure 2c, showing the grand average and standard error of the PF across subjects as a function of the difficulty level of the episode, for all episodes following each participant's learning time (Mixed effects model fit; AIC = -168.88, BIC = -158.442, Log-likelihood = 88.442, p = 7.11E-11). Note that the RT gradually increased with growing difficulty to discriminate the stimuli (Figure 2d), thus exhibiting a gradual and significant sensitivity to VD (Mixed effects model fit; AIC=-101.61, BIC=-89.85, Log-likelihood = 54.81, p =7.67E-25).

While both PF and RT vary with VD, their dependency on other variables must be established statistically. To assess the learning process, we quantified the relationship of PF and RT with horizon n_H, trial within episode T_E, and episode E. To obtain consistent results, we adjusted these variables as follows: the trial within episode is reversed, from last to first, because the optimal choice for the last T_E (large) is the same regardless of the horizon number. The variable representing the trial within episode counted backwards is denoted as $\hat{T}_E$. Furthermore, we grouped the episodes in blocks of 10 and used their average. This new variable is called $E^{(10)}$. Finally, to consider trials within episode independently, we adapted the notion of PF (defined as a summary measure per episode) to an equivalent of PF per trial, i.e., the percentage optimal choices P_{oc}. We then used a linear mixed effects model (39,40) to predict PF and RT. The independent variables for the fixed effects are horizon n_H, trial within episode $\hat{T}_E$ (counted backwards), and the passage of time expressed as groups of 10 episodes $E^{(10)}$ each. We set the random effects for the intercept and the episodes grouped by participant. The resulting models are: $P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$ and $RT \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$. The independent variables for the fixed effects are horizon n_H, trial within episode $\hat{T}_E$ (counted backwards), and the passage of time expressed as groups of 10 episodes $E^{(10)}$ each. We set the random effects for the intercept and the episodes grouped by participant. The resulting models are: $P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$ and $RT \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$. The regression coefficients, with their respective group significance, are shown in Figure 2e-f. The results of the statistical analysis are reported in the Supplementary Materials Table 2-3. Here, we made the distinction between the group of participants that learned the optimal strategy and the ones who did not, according to Figure 2a. In panel (e), P_{oc} decreases with $\hat{T}_E$, suggesting that the first trial(s) within the episode are less likely to be guessed right, i.e., favoring the smaller of both stimuli. This makes sense, since only the early trials within the episode required inhibition. Moreover, looking at the amplitude of the regression coefficients, we can state that this has a larger impact in the no-learning case. The same argument can be made for the dependency with n_H. The difference between learning and no-learning can be realized when considering the time dependence: for the learners' group P_{oc} increases as time goes by, i.e., $E^{(10)}$ increases, while it is not significant for the group that did not learn the optimal strategy. In panel (f), RT shows converse effect directions between learning and no-learning groups for both dependencies on $\hat{T}_E$ and n_H. The participants who learned the optimal strategy exhibited longer RT for the earlier trials within the episode, consistently with the need of inhibiting the selection of the larger stimulus.

Although we analyzed the data from all twenty-eight participants, in Figure 3 we show the data from four participants whose behavior was representative of the four groups we defined as a function of their learning speed (no learning, slow, medium, & fast learning). Figure 3 shows their associated PFs, CHs, and RTs metrics. Each column corresponds to a participant and each

row to a different horizon level. Note that all four participants performed the $n_H=0$ task correctly (Figure 3a,b). The first three participants also performed $n_H=1$ correctly, while participant 4 did not learn the correct strategy until he executed $n_H=2$. Note that participant 2 performed $n_H=2$ before $n_H=1$, they learned during $n_H=2$, and then applied the same strategy for $n_H=1$. Because of this, no learning process can be detected during the $n_H=1$ block. In Figure 3c, note that some RTs are negative. In these cases, the participant did not wait for the presentation of the GO signal to start the movement.

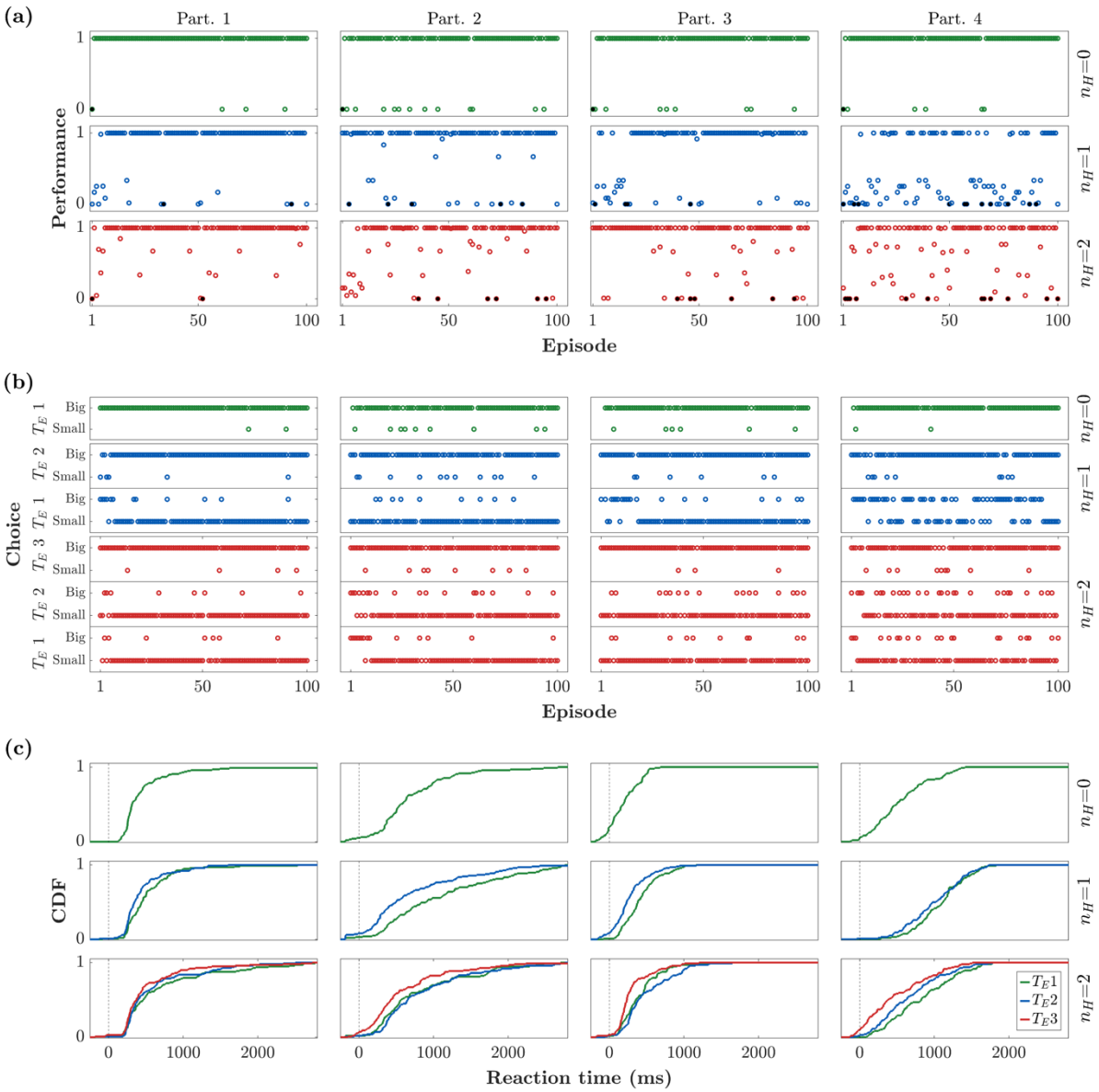

Figure 3. Behavioral results for four representative participants. Rows and columns refer to horizons (n_H) and participants, respectively. (a) Performance per episode. (b) Choice behavior per trial, in terms of selecting the bigger or smaller stimulus. Results are gathered by horizon (n_H) and respective trial within episode (T_E). (c) Cumulative density function (CDF) of reaction times. The color code indicates the trial within episode (green for $T_E=1$, blue for $T_E=2$, and red for $T_E=3$).

2.3 A Neurally-inspired Model of Consequential Decision-Making

In this section, we describe our mathematical formalization of consequential decision-making, incorporating a variable foresight mechanism, adaptive to the specifics of how reward is distributed across trials of each episode. We formalized these processes using a three-layer neural model, described next.

2.3.1 Layer 1: Neural dynamics

To describe the neural dynamics at each trial, we used a mean-field approximation of a biophysically based binary decision-making model (38,41–43). This approximation has been often used to analytically study neuronal dynamics, through analysis of population averages. This included a simplified version that reproduced most features of the original spiking neuron model while using only two internal variables (33).

The core of the model consists of two populations of excitatory neurons: one sensitive to the stimulus on the left-hand side of the screen (L), and the other to the stimulus on the right (R). The intensity of the evidence is the size of each stimulus, which is directly proportional to the amount of reward displayed. In the model this is captured by the parameters λ_L, λ_R, respectively. Although in the interest of our task we distinguish between the bigger and smaller stimulus values, in the formulation of the model it is convenient to characterize stimuli based on their position, i.e., left/right. The reason here is that the information on which target is bigger is already conveyed by the respective stimuli values, i.e., the parameters λ_L, λ_R. Moreover, this allows to introduce an extra degree of freedom in the model, without increasing the number of variables. The equations

$$\begin{cases} \tau \dfrac{dr_L(t)}{dt} = -r_L(t) + f\big(\lambda_L + \omega_+ r_L(t) - \omega_- r_R(t)\big) + \sigma\xi_L(t) \\ \tau \dfrac{dr_R(t)}{dt} = -r_R(t) + f\big(\lambda_R + \omega_+ r_R(t) - \omega_- r_L(t)\big) + \sigma\xi_R(t) \end{cases} \qquad \text{Eq. 1}$$

describe the temporal dynamics of the firing rates (r_L, r_R) for each of the two populations, and may be interpreted as originating from a neural network as shown in Figure 4a. Each pool has recurrent excitation (ω_+), and mutual inhibition (ω_-). Although the schematic indicates that both excitation and inhibition emanate from a single population of excitatory neurons, this connectivity could be achieved with an equivalent network of excitatory and inhibitory subpopulations (33,35,42,44,45). In particular, we refer to the work by Wong and Wang (33), where they reduced a spiking neural network of both excitatory and inhibitory neurons to a two-variable system describing the firing rate of the mean-field dynamics of two populations of excitatory neurons. We opted for this simplified architecture because they are equivalent under some conditions and provide a more compact formulation. Furthermore, the network shares a basic feature with many other models of bi-stability: to ensure that only one population is active at any time (mutual exclusivity; (46,47)), mutual inhibition is exerted between the two populations ((48–50)). The overall neuronal dynamics are regulated by the time constant τ, and Gaussian noise ξ with zero mean and standard deviation σ. The sigmoidal function f is defined as $f(x) = F_{max}/\left(1 + exp\left(-(x-\theta)/\tilde{k}\right)\right)$, with F_{max} denoting the firing rate saturation value.

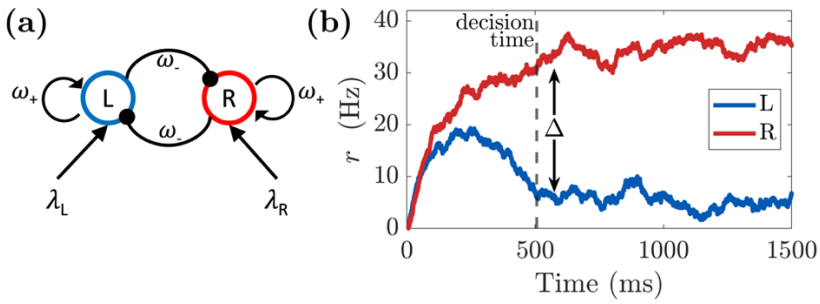

Figure 4. ***(a)*** *Network structure of binary decision model of mean-field dynamics. The L pool is selective for the stimulus L (λ_L), while the other population is sensitive to the appearance of the stimulus R (λ_R). The two pools mutually inhibit each other (ω_-) and have self-excitatory recurrent connections (ω_+).* ***(b)*** *Firing rate of the two populations (L, R) of excitatory neurons according to the dynamics in Eq. 1. A decision is taken at time 506 ms (vertical dashed line) when the difference in activity between L and R pools passes the threshold of Δ =25Hz. The strengths of the stimuli are set to λ_L = 0.0203 and λ_R = 0.0227. The time constant and the noise are set to τ = 80 and σ = 0.003, respectively.*

The neural dynamics described in this section refer to the time-course of a single trial, and is related to the discrimination of the two stimuli. The model commits to a perceptual decision when the difference between the L and R pool activity crosses a threshold Δ (51), see Figure 4b. This event defines the trial's decision time. Note that the decision time and the likelihood of picking the larger stimulus are conditioned by the evidence associated with the two stimuli (λ_L, λ_R), i.e., how easy it is to distinguish between them. Namely, the larger the difference between the stimuli is, the more likely and quickly it is that the larger stimulus is selected.

This type of decision-making model is made such that the larger stimulus is always favored. Although the target with the stronger evidence in Eq. 1 is the most likely to be selected, this behavior becomes a particular case when this first layer interacts with the middle layer of our model, as described in the next section.

2.3.2 Layer 2: Intended decision

While most decision-making models consider only information involving one-shot decisions (33,51–54), the increased temporal span consideration and the uncertainty due to the consequence of the decision-making processes involved in the consequential task require additional elements for our model. The second layer of our model is devoted to build a mechanism capable of dynamically shifting from the natural (perceptual based) impulse of choosing the larger stimulus, to inhibiting that preference and choosing the smaller one. We implemented such a mechanism by means of an inhibitory control pool, which regulates, when desired, the reversal of the selection criterion towards the smaller or larger stimulus. We called this mechanism *intended decision*, as it defines the intended target to select at each trial. This constitutes the layer enabling the model to switch preference as a function of the context (see layer 3 description).

Specifically, the intended decision mechanism at each trial is represented as a two-attractor dynamical system. If the state of the model may be interpreted as the continuous expression of its tendency for one over another choice, an attractor is the state towards which the dynamics of the system naturally evolve. Since we have two choices, to implement this we considered the energy function $E(\psi) = \psi^2(\psi - 1)^2$ that has two basins of attraction at 0 and 1, associated to the small and big stimulus, respectively (see Figure 5a). Hence, the dynamics of ψ are regulated by

$$\tau_\psi \frac{d\psi(t)}{dt} = -4\psi(t)(\psi(t)-1)(\psi(t)-1/2) + \frac{1}{t^2}\sigma_\psi \xi_\psi(t) \qquad \text{Eq. 2}$$

where τ_ψ is a time constant. The Gaussian noise $\xi_\psi(t)$ is scaled by a constant (σ_ψ) and decays quadratically with time. Thus, the noise exerts a strong influence at the beginning of the process and becomes negligible as one of both basins of attraction is reached.

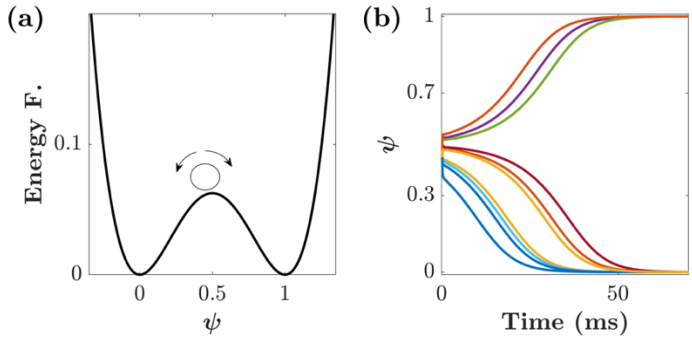

Figure 5. Dynamics of the second layer of the model. a) Energy function $E(\psi) = \psi^2(\psi-1)^2$ with two basins of attraction in 0 and 1, associated with the small/big targets, respectively. The small circle represents a possible initial condition for the dynamics of ψ. (b) Ten simulated trajectories for $\psi(t)$ according to Eq. 2 with initial condition $\psi(0) = 0.45$ and noise amplitude $\sigma_\psi = 0.4$.

If we set the initial condition to $\psi_0 = 0.5$ and let the system evolve, the final state would be either 0 or 1 with equal probability. Shifting the initial condition towards one of the attractors results in an increased likelihood of leaning towards that same attractor, and ultimately its fixed point, i.e., the basin of attraction that was reached. For example, Figure 5b shows 10 simulated trajectories of $\psi(t)$ where the initial condition was set to $\psi_0 = 0.45$. Since the initial condition is smaller than 0.5, most of the trajectories have a fixed point of 0. Nevertheless, due to the initial noise level, the fewer of them reach 1 as their final state.

The initial condition (ψ_0) and the noise intensity (σ_ψ) are interdependent. The closer an initial condition is to one of the attractors, the larger the noise is required to escape that basin of attraction. Behaviorally, the role of the initial condition is to capture the a-priori bias of choosing the smaller/bigger target. Though this is true, please note that a strong initial bias towards one of the targets does not guarantee the final decision, especially when the level of uncertainty is large. Because of this behavioral effect, we refer to the noise intensity σ_ψ as *decisional uncertainty.*

The evolution of the dynamical system in Eq. 2 describes the intention of the decision-making process, at each trial *T*, of choosing the smaller/bigger target. Once a fixed point is reached, the intention is established. We call $\tilde{\psi}(T)$ the fixed point reached at trial *T*, i.e.,

$$\tilde{\psi}(T) = \lim_{t\to\infty} \psi(t) = \begin{cases} 0 \\ 1 \end{cases}$$

is the intended decision of choosing the smaller (0) or bigger (1) stimulus.

Although the small/big stimulus may be favored at each trial, the final decision still depends on the stimuli intensity ratio. More specifically, if the evidence associated with the small/large stimulus is higher/lower than that of its counterpart, the dynamics of the system will evolve as described in the previous section, see Eq. 1. For this reason, we incorporated the *intention* term

$\tilde{\psi}(T)$ into Eq. 1, connecting the *intended decision layer* with the *neural dynamics layer*. This yields a novel set of equations

$$\begin{cases} \tau \dfrac{dr_L(t)}{dt} = -r_L(t) + f\left(\tilde{\psi}(\mathrm{T})\lambda_L + \left(1 - \tilde{\psi}(T)\right)\lambda_R + \omega_+ r_L(t) - \omega_- r_R(t)\right) + \sigma\xi_L(t) \\ \tau \dfrac{dr_R(t)}{dt} = -r_R(t) + f\left(\tilde{\psi}(\mathrm{T})\lambda_R + \left(1 - \tilde{\psi}(T)\right)\lambda_L + \omega_+ r_R(t) - \omega_- r_L(t)\right) + \sigma\xi_R(t) \end{cases} \quad \text{Eq. 3}$$

which exhibit the competence of switching preference between the large and small stimulus. If $\tilde{\psi}(T) = 1$, the larger stimulus is favored (and the equations reduce to Eq. 1); however, if $\tilde{\psi}(T) = 0$ the smaller is preferred.

To summarize, this *intended decision* layer endows the dynamics of decision-making hereby described with the ability of directing their preference towards either the smaller or bigger stimulus in a dynamical fashion. This inhibitory control plays the role of the regulatory criterion (size-wise) with which a decision is made in the consequential task, as described by Eq. 2.

2.3.3 Layer 3: Learning the Strategy

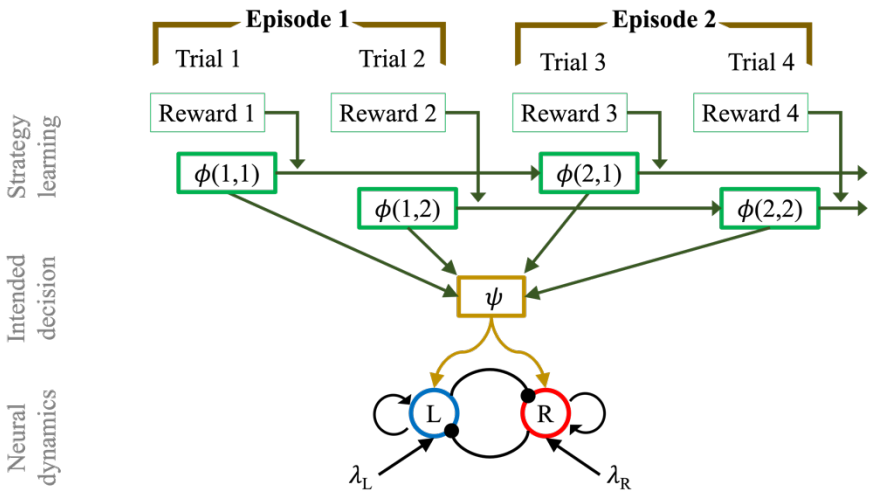

Figure 6. Multi-layer network structure of mean-field model of consequence-based decision making, in the case of a horizon 1 experiment. From the bottom: Neural dynamics layer: pool L is selective for the stimulus L (λ_L), while the other population is sensitive to the appearance of the stimulus R (λ_R). The two pools mutually inhibit each other (ω_-) and have self-excitatory recurrent connections (ω_+). The dynamics of the firing rate of the two populations is regulated by Eq. 3. Intended decision layer: the function ψ represents the intention, in terms of decision process, made at each trial T, of aiming for the smaller or bigger target. The dynamics of the intended decision is regulated by Eq. 2. Strategy learning layer: after each trial the strategy is revised, in a reinforcement learning fashion, depending on the magnitude of the gained reward value. The strategy is updated according to Eq. 4.

Although the previously described intended decision layer endowed our model with the ability of targeting a specific type of stimulus at each trial, a second mechanism to internally oversee performance and to promote only beneficial strategies is a requirement. The overall goal for each participant of the consequential task is to maximize the cumulative reward value throughout an episode. As shown by previous analyses, most participants attained the optimal strategy after an exploratory phase, gradually improving their performance until the optimum is reached. Inspired by the same principle of exploration and reinforcement, we incorporated the strategy learning layer to our model.

The internal dynamics of an episode are such that selecting the small/large stimulus in a trial implies an increase/decrease of the mean value of the presented stimuli in the next trial (Figure 1). Consequently, the strategy to maximize the reward value must vary as a function of the position of the trial within episode (T_E). For clarity, we labelled each trial T via the episode E and the number of trial within episode T_E, i.e., $T=(E,T_E)$. We use both notations interchangeably.

The strategy learning implemented for the model abides by the general principle of reinforcing beneficial strategies and weakening unprofitable ones, much like a reinforcement learning algorithm (55). At each episode E, the strategy function $\phi = \phi(E, T_E)$ is updated by considering the intended choice $\tilde{\psi}(T)$ and the reward value $R(T)$ obtained. In our case, this reward value originates from subjective evaluation for each individual participant in the absence of explicit feedback. This internal assessment yields a positive or negative perception of reward, i.e., a subjective reward. Learning implies that the preference for the selected strategy is reinforced if the subjective reward is considered beneficial. Namely, with a positive reward ($R(T)>0$), ϕ is increased if the larger stimulus was chosen ($\tilde{\psi}(T) = 1$) and decreased otherwise ($\tilde{\psi}(T) = 0$). Notice that a negative reward discourages the current strategy but promotes the exploration of alternative strategies and makes possible, eventually, to learn the optimal one over time. Mathematically, we describe the dynamics of learning as

$$\phi(E+1, T_E) = \phi(E, T_E) + kR(E, T_E)\big(2\tilde{\psi}(E, T_E) - 1\big)(\phi(E, T_E) - 1)^2\big(\phi(E, T_E)\big)^2 \quad \text{Eq. 4}$$

where k is the learning rate. Note that if $k=0$, $\phi(E, T_E)$ remains constant, i.e., there is no learning. The term $(\phi(E, T_E) - 1)^2\big(\phi(E, T_E)\big)^2$ is required to gradually reduce the increment to zero the closer ϕ gets to either zero or one, thus bounding ϕ in the interval [0,1]. The reward function $R(E, T_E)$ represents the subjective reward. The only requirement for this function is that $R(E, T_E)$ must be positive/negative if the subjective reward is considered beneficial or not. In the absence of explicit feedback, as is the case in the current task, participants must look for clues that convey some indirect information about their performance that could feed their internal criterion of assessment. In our case, the correct clue to look for was the change in the mean $M(T)$ stimuli between consecutive trials within an episode. For this reason, in our simulations we use $R(E, T_E) = M(E, T_E + 1) - M(E, T_E)$ in Eq. 4.

Complementary to the lower layers, the strategy layer operates at a slower-pace, adaptive at a time scale of episodes. At the end of each episode, the strategy is updated by reinforcing/weakening the policy that has yielded a positive/negative reward. Mathematically, as mentioned before, this means that with a positive reward ($R(T)>0$), ϕ is increased if the larger stimulus was chosen ($\tilde{\psi}(T) = 1$) and decreased otherwise ($\tilde{\psi}(T) = 0$). In the long term, in the case that both the larger stimulus is repeatedly chosen and positive rewards obtained, then ϕ converges to 1. Otherwise, if both the smaller stimulus is repeatedly chosen and positive rewards obtained, then ϕ converges to 0. This update manifests in the next episode as a change in the initial condition for the intended decision ψ (Eq. 2), i.e., suggesting the direction for the intended decision to go. As shown in Figure 5, shifting the initial condition towards one of the two basins (0 or 1) increases the likelihood of reaching it. In other words, the closer the initial condition to zero/one, the more likely the intended decision will be small/big. Mathematically, this can be implemented by setting $\psi(0) = \phi(T)$ for each trial. In other words, the connection between the intended decision and the strategy layers lays in the influence the strategy learning exerts at each decision.

To conclude, our model consists of a three concurrent layer structure. The dynamics of each layer are defined by Eq. 3 (neural dynamics), Eq. 2 (intended decision), and Eq. 4 (strategy learning). Figure 6 shows a schematic of the model here described. The bottom part depicts the neural dynamics originated from two pools of neurons encoding the responses to two external stimuli (*L, R*). The middle (in yellow) shows the intended decision layer at every trial. Finally, the top (in green) presents the strategy learning layer, which evolves at a much slower timescale; the combined information of the intended decision and the subjective reward drives the learning of the strategy.

2.4 Model Simulations

We performed a parameter space analysis to assess the influence of the model parameters on the main behavioral metrics of interest: reaction time (RT) and performance (PF). To obtain meaningful biophysical results for the neuronal dynamics, we simulated our model varying the time constant τ, the noise amplitude σ, and the decision threshold Δ (in Eq. 3) in the following ranges: $\tau \in [25,95]$, $\sigma \in [10^{-3}, 10^{-2}]$, and $\Delta \in [0.01,0.035]$ (see (35)). Also, we set F_{max}= 0.04 ms^{-1}, θ = 0.015 ms^{-1}, $\tilde{k}$ = 0.022 ms^{-1}, ω_+ = 1.4, ω_- = 1.5. We decided to keep most of the parameters fixed (as in (35)), i.e., the ones defined within the function *f* (see Eq. 3) and the strengths of connection between pools of neurons (ω_+ and ω_-). As we will see below, by only varying τ, σ, and Δ we can simulate a wide range of different behaviors. In Eq. 2, we set τ_ψ=10 such that the dynamics of Eq. 2 is faster than the dynamics of Eq. 3 while remaining the same order of magnitude. Figure 7 a-d shows how RT is affected by τ and Δ. By increasing the time constant τ, the RT increases both in mean and standard deviation (panel a). The same trend occurs when increasing the threshold Δ (panel b), as expected. When varying the noise σ, we did not find a substantial difference in the RT (panel c). Panel (d) shows the joint influence of τ and Δ on the RT for a fixed value of σ. By fixing τ, σ, and Δ, we studied the influence of the learning rate *k* and the decisional uncertainty σ_ψ on the PF, and, consequently, on the learning time t_L. Figure 7e shows that learning time decreases as learning rate *k* increases, and as decisional uncertainty σ_ψ decreases. Note that for these simulations we used $n_H=1$ with 50 episodes, therefore any t_L bigger than 50 means that the optimal strategy was not learned.

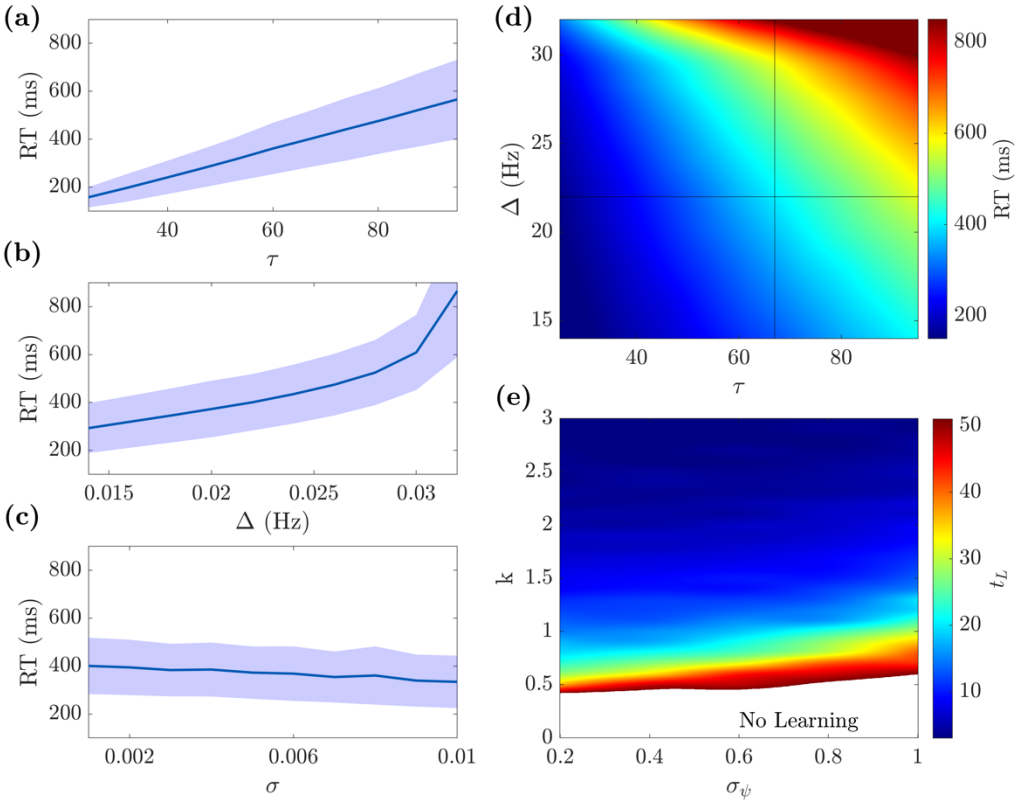

Figure 7. Parameter space analysis. Both the mean and standard deviation of the reaction time increase consistently with both ***(a)*** *the time constant* τ *and* ***(b)*** *the threshold* Δ. ***(c)*** *The noise intensity* σ *does not have a substantial influence on the reaction time.* ***(d)*** *Mean RT varying* τ *and* Δ *for a fixed value of* σ*. The horizontal and vertical black lines indicate the values for* Δ *and* τ *used for (a-c).* ***(e)*** *The learning time* t_L *decreases when increasing the learning rate k and decreasing the decisional uncertainty* σ_ψ *. – For all panels we used* τ*=67,* σ*=0.001, and* Δ*=22 Hz, when not varied for the plot.*

To demonstrate the behavior of the model, Figure 8 shows the results of a typical simulation of a horizon $n_H = 1$ experiment. Figure 8a shows the example dynamics of the neural dynamics layer of our model together with the stimuli used in the simulation during the first three episodes. More specifically, the bottom row shows the time course of the two population firing rates (Eq. 3) encoding the stimuli L, R depicted in the top row. To better understand the progression of this process over time, Figure 8b gives an outlook of 36 episodes. The top row shows the performance and difficulty (in terms of difference between stimuli DbS) metrics. Note that the optimal strategy in this simulation was learned and applied from the 17th episode onward. After this point, only the most difficult episodes (smallest DbS) managed to diminish the performance. The same conclusions can be drawn by looking at the middle inset, indeed after the 17th episode, the intended decision metric exhibits the same pattern (small for $T_E=1$, and big for $T_E=2$) repeatedly. The bottom row shows the strategy learning. For the first trial within episode ($T_E=1$), ϕ tends to 0, i.e., it pushes the intended decision to choose the smaller stimulus. For the second trial within episode ($T_E=2$), the trend is reversed, capturing indeed the optimal policy.

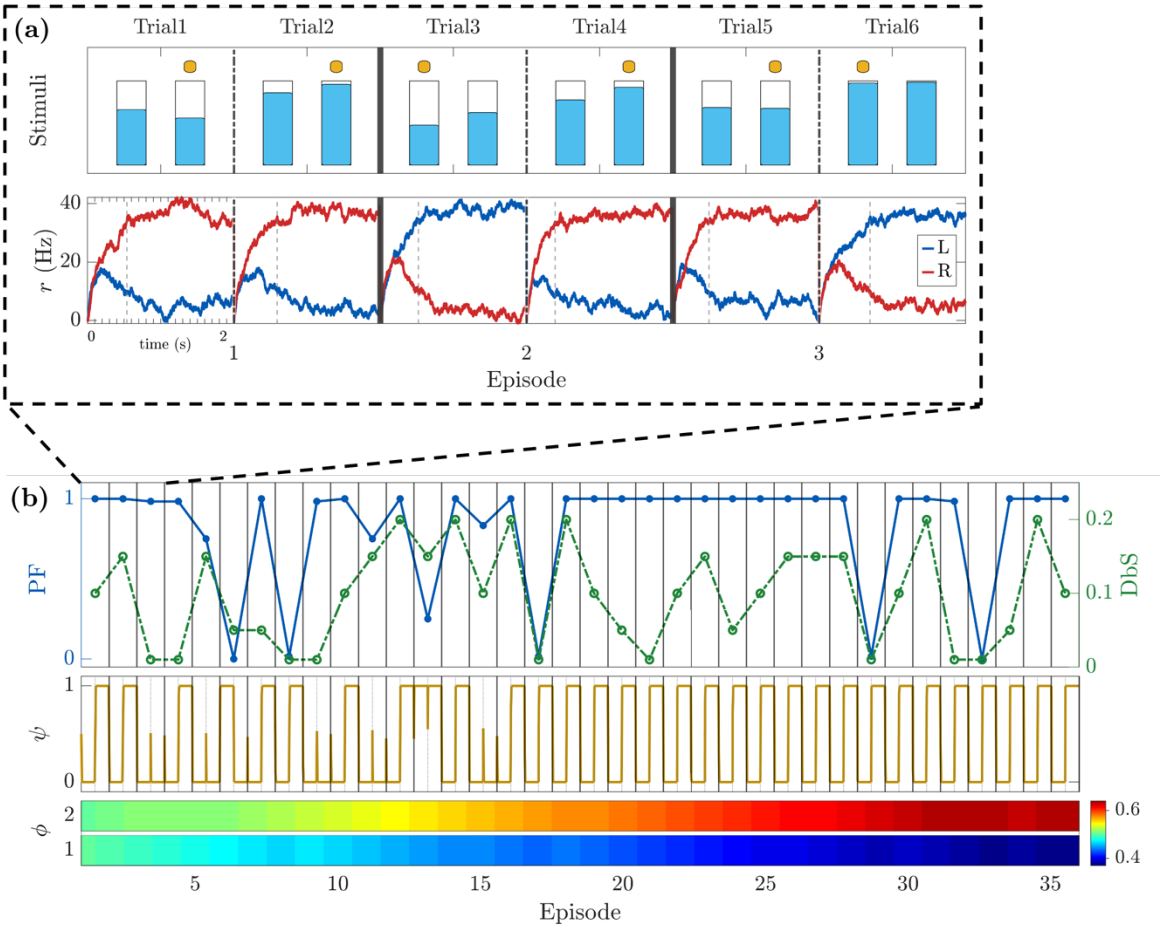

Figure 8. Model example simulations for a horizon 1 block. (a) Simulation of the first 3 episodes. Top row: Stimuli presentation with respective selection made in each trial displayed with a yellow dot. Bottom row: firing rate of the two populations of neurons encoding the left (in blue) and right (in red) stimuli (Eq. 3). Vertical dashed bars indicate the time the decision threshold was crossed. (b) Simulation of 36 consecutive episodes. First row: Performance (blue - solid) and difference between stimuli DbS (green - dashed). Second row: intended decision dynamics of choosing the bigger (1) or smaller (0) stimulus. Third row: evolution of strategy learning for each trial within episode (T_E). Parameters used for the simulations: G=0.3, Δ=0.025, τ=80, σ=0.006, $\phi_0(1, T_E) = 0.5$ for T_E=1,2, k=0.4, σ_ψ=0.4.

2.5 Individual Participants' Behavioral Fit

This section describes the fit of the model parameters to the participants' individual behavioral metrics. The fitting process is described as a pipeline process. In the first step, the goal is to find the best fit for the neural dynamics by fitting the reaction time (RT) and the visual discrimination (VD), i.e., fit the parameters τ, σ, Δ, α and β involved in Eq. 3. We then focus on the behavioral part. The second step consists of calculating the initial preferential bias ϕ_0. Finally, in the third step, we ran the model using the previously established parameters, and found the best fit for σ_ψ and k, i.e., the decisional uncertainty and the learning rate. The reason why we fit the parameters in a sequential fashion is the following. The estimates of both RT and VD depend uniquely on Eq. 3. In order to evaluate the dynamics of the perceptual processes, RT and VD are fit using horizon $n_H=0$ only. Once these have been established, we focus on the behavioral part, by fitting the initial preferential bias, the learning rate and the decisional uncertainty.

2.5.1 Reaction Times and Visual Discrimination

The fitting of the model parameters to each of the participant's behavioral metrics was performed in stages. First, we started by considering the neural dynamics layer, and fitting each

parameter of Eq. 3. The first metric to fit is each participant's RT. Note that due to response anticipation of the GO signal, the experimental RTs could be negative in a few cases (see Figure 3c). A free parameter was incorporated into the model to control for this temporal shift.

The second metric to fit is the VD, i.e., the ability to distinguish between stimuli. We assumed VD to be specific to each participant, and constant across blocks of each session. As a means of assessment, we checked how often the larger stimulus had been selected over the last 50 correct trials of the $n_H=0$ block for each level of difficulty. The only case where accuracy was low was the highest difficulty level (DbS = *0.01)*. For our model to capture this aspect, we used a linear transformation $\tilde{s} = \alpha + \beta s$ to re-scale the stimuli s, ranging from 0 (empty) and 1 (full), to a range of meaningful stimuli for the model ($\lambda_{L,R} \sim 10^{-2}$, [22]). Furthermore, additional constraints were set for α and β, such that this transformation did not swap the intensities between stimuli (i.e. if $s_L \geq s_R$ then $\tilde{s}_L \geq \tilde{s}_R$), and that the input stimuli were always positive ($\tilde{s}_{L,R} > 0$). Abiding by these conditions, we varied α and β and ran a grid-search set of simulations of Eq. 3 (with DbS $|s_L - s_R| = 0.01$). We calculated the frequency with which the firing rate of the population encoding the larger stimulus was bigger than the alternative. The result depends not only on α and β, but also on τ, σ, and Δ (see Supplementary Figure 2). Thus, to capture the large variety of results encompassed by the ranges of τ, σ, and Δ (see Sec. Model simulations for the respective ranges of values), while abiding by the aforementioned constraints, we let α vary between -0.03 and 0, and β vary between 0 and 0.055-2.5α. These ranges allowed for proper exploration of the parameter space.

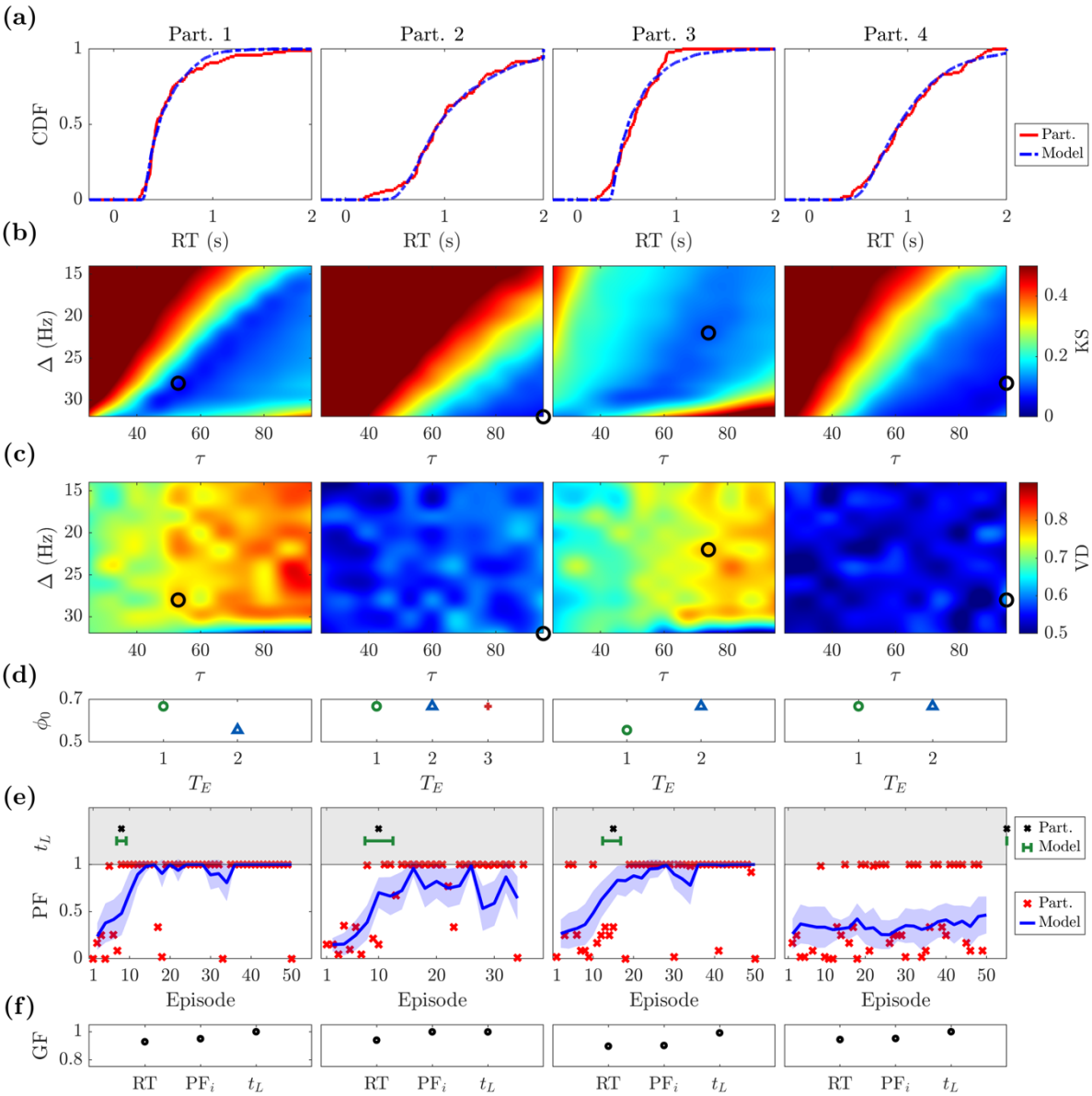

Figure 9. Model fit to four sample participants' behavioral metrics. Data used: one block of horizon 1 for participants 1, 3 and 4; one block of horizon 2 for participant 2. The specific parameter values of the fit are displayed in Table 1. ***(a)*** *Cumulative distribution function (CDF) of the reaction times (RT) for the participant data (solid red) and model simulation (dashed blue).* ***(b)*** *Kolmogorov-Smirnov distance (KSD) between the participant and the model's RT varying τ and Δ for the best fitting values of σ, α and β. The black circle refers to the best fit.* ***(c)*** *Visual discrimination (VD) extracted from model simulations varying τ and Δ for the best fitting values of σ, α and β. The black circle refers to the best fit.* ***(d)*** *Initial bias ϕ_0 of the participant at the beginning of the block for each trial within episode (T_E). The more the preferred choice tends towards choosing the larger (smaller) stimulus, the bigger (smaller) ϕ_0 is.* ***(e)*** *Bottom: Performance of the participant (red crosses) and of the model's simulations (blue line: mean, shaded area: confidence interval). Top: Learning time for the participant (black cross) and model simulations (green error bar).* ***(f)*** *Goodness of fit (GF) for three metrics: reaction time (RT), initial performance (PF_i), and learning time (t_L). Goodness of fit is calculated as follows: RT = 1- Kolmogorov-Smirnov distance between CDF, PF_i = 1- mean square error, t_L: 1- difference between learning times of participant and model's mean divided by the total number of episodes.*

We ran 100-trial simulations of a horizon $n_H=0$ block for each combination of the parameters τ, σ, Δ, α and β. We then calculated the empirical cumulative distribution functions (CDF) of the RTs for all trials, and the VDs only for the difficult trials, i.e., when the DbS is *0.01*. The distribution of simulated RTs were then compared with the distributions of experimental RTs by means of the Kolmogorov-Smirnov distance (KSD) between CDFs (56–59). Since both RTs

and VDs strongly depend on all parameters, both were fit simultaneously. Namely, we consider the error metric $\widehat{M} = KSD + c\,|VD^{sim} - VD^{real}|$, with c being a constant and VD^{sim}, VD^{real} being the VD from the simulated and real data, respectively. The value of c is discussed at the end of the Results Section. The parameters τ, σ, Δ, α and β that minimize $\widehat{M}$ are selected for the fit.

Panels (a-c) in Figure 9 show the optimal parameters for the RT and VD of the four sample participants introduced in the Behavioral Results Section. Figure 9a depicts the CDF of the RT for the participants and for the best-fit model simulation. Figure 9b presents the KSD between the model and shifted-participant CDFs varying τ and Δ, for a fixed (best-fit) σ. Likewise, Figure 9c shows the mean VD for the model simulations. In both panels (b-c) the circle mark indicates the combination of parameters that gives the best fit.

To summarize, in the first step of the fit, we focused on the neural dynamics layer fit all the free parameters of Eq. 3, i.e., τ, σ, Δ, α and β, concerned with the visual discrimination. The following steps will consider the behavioral component of the data.

2.5.2 Initial Preferential Bias

Each participant performing our current task might have an initial choice preference, i.e., a natural bias towards the larger (or smaller) stimulus. In our model this is captured by the parameter ϕ_0 in Eq. 4. In the absence of bias ϕ_0 equals 0.5. The greater the preference towards the bigger choice, the closer to 1 ϕ_0 will be.

We set a vector of initial conditions $\phi(E = 1, T_E) = \phi_0(T_E)$ for each trial within episode (T_E). To quantify ϕ_0, we selected the first 3 episodes for each participant, and calculated the frequency f with which the larger stimulus was selected. The parameter ϕ_0 works as an initial condition for the intended decision process (see Eq. 2). In agreement with the attractor dynamics, if the initial condition coincides with one of the basins of attraction, the system will be locked in that state. To prevent this (since ϕ_0 should only be an initial bias), we rescaled the frequency of the selected choices f to make the value closer to 0.5, i.e., $\phi_0 = (1 + f)/3$ (other rescaling factors could be used and would not change the results). Figure 9d shows the values obtained for ϕ_0 for each trial within episode T_E. Note that we have selected one block from $n_H=2$ for participant 2 and $n_H=1$ for the others.

2.5.3 Learning Rate and Decisional Uncertainty

Finally, to fit the remaining parameters σ_ψ and k to each participant's data, we ran the model using the previously established parameters (τ, σ, Δ, α, β, and ϕ_0) and fitted its resulting performance to that of each participant. For each set of σ_ψ and k, we ran 50 simulations and extracted the performance mean and standard deviation. To compare model and participant performances, we considered different metrics such as goodness-of-fit and likelihood, e.g., Bayesian (BIC) and Akaike information criterions (AIC) (57,59–62). While these are accurate methods to compare model performance, these metrics disregard the specific time dependency throughout each block, which is a key factor to characterize the learning process of the participant. To fill in this gap, we designed an ad-hoc novel metric consisting of two factors that determine the best fit of the learning process. The first is the initial condition, obtained by calculating the mean-square error of the performance between the model and the data during the first five episodes. By minimizing the mean-square error, we ensured that the learning

process began under similar conditions for the model and for the participant. The second factor is the time required to learn the strategy. As already introduced in the Behavioral Results Section, we defined the time at which the strategy was learned as the moment after which the optimal strategy was employed in at least 9 out of the following 10 episodes. To ensure that a low success rate was not due to errors caused by visual discrimination, we excluded the episodes with DbS *0.01* from this part of the fit. In summary, by combining the results for the initial conditions (I) and the learning time (L), we could extrapolate the best fit for σ_ψ and k by minimizing the linear combination $L + 0.1 \cdot I$.

Figure 9e shows the participants' performance (red marks) as well as the associated best-fit model performance (the blue line is the mean, and the colored area is the 95% confidence interval). The top part of the plots depicts the learning time (t_L) calculated for the participant (black mark) as well as for the best fit model simulations (green error-bar). Table 1 shows the best-fit parameter values per participant.

All participants except one learned the strategy yielding maximum reward value. Specifically, participant 1 learned very fast (in 8 episodes). This was fitted by the model with the highest learning rate ($k=2.6$). Interestingly, even if participant 4 did not learn the correct strategy, the parameters obtained from the fitting process still reported a slow learning process ($k=0.2$). In addition to this, we noticed that a slightly higher learning rate was reported for participant 3, even if the strategy in this case was learned after 15 episodes only. The reason the learning rates for these two participants are similar, even though they reflect two distinct strategies, lays in the initial condition. Namely, participant 4 began the task with a stronger bias towards choosing the larger stimulus ($\phi_0(T_E) = \{0.67,0.67\}$ against $\{0.56,0.67\}$ for participant 3). Moreover, the noise amplitude for participant 4 is higher for both the neural dynamics σ and the decisional uncertainty σ_ψ. When combining high noise and disadvantageous initial conditions, a weak learning rate is not enough for the strategy to be learned in a block of 50 episodes.

Figure 9f shows the goodness of fit for the two main behavioral metrics we aimed to reproduce: the reaction time (RT), and the performance, in terms of initial performance (PF_i) and learning time (t_L). To measure the goodness of fit, while remaining consistent with our fitting procedure, we used the following measures. For RT we calculated the KSD, for PF_i we evaluated the mean-square error, and for t_L we took the difference between the participant's data and the model's mean divided by the total number of episodes.

To summarize, we have first found the best fit for the RT and the VD by minimizing the metric $\widehat{M} = KSD + c\,|VD^{sim} - VD^{real}|$ obtained by varying all the free parameters of Eq. 3, i.e., τ, σ, Δ, α and β. Then, we calculated the subjective initial bias ϕ_0. Finally, employing these parameters, we found the best fit for the decisional uncertainty σ_ψ, and the learning rate k. The very last value that needs to be set, is the constant c in $\widehat{M} = KSD + c\,|VD^{sim} - VD^{real}|$. To this end, we repeated all the simulations described so far, varying c from 0.1 to 1 in step of 0.1 and selecting the value of c that minimize the global goodness of fit. Namely, we minimize the norm of the three-dimensional vector that has as elements the goodness of fit for the reaction time (RT), and the performance, in terms of initial performance (PF_i) and learning time (t_L). Figure 9 (and Figure 10) shows the results for the best value of c.

Finally, we show summary results for all 28 participants. To illustrate that the model is able to capture all participants' behavioral results, Figure 10 shows the goodness of fit for the RT,

initial performance PF_i, and learning time t_L for the entire set of 28 participants. For all three metrics, we show the scatter plot including each participant, the respective distribution, and the boxplot depicting the median and the 25th/75th percentile. For reference, we superposed colored markers on the results of the four sample participants shown in the previous figure.

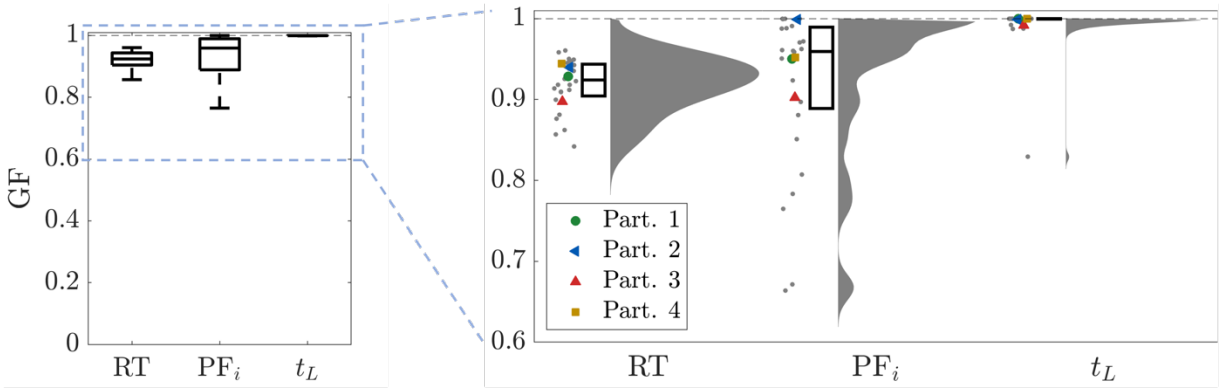

Figure 10. Goodness of fit. For RT we calculated KSD, for PF_i we evaluated the mean-square error, and for t_L we took the difference between the participant's data and the model's mean divided by the total number of episodes. For all three metrics, we show the scatter plot of each single participant, the respective distribution, and the boxplot depicting the median and the 25/75 percentile. For reference, we superposed (colored markers) the results for the four participants shown in the previous figure.

P.	**c**	***GF (RT, PF$_i$, t$_L$)***	***t$_L$***	***k***	σ_ψ	τ	σ	Δ	α	β	ϕ_0 ***(T$_E$)***
1	0.1	{0.93,0.95,1}	8	2.8	0.4	53	0.001	0.028	0	0.036	{0.67,0.56}
2	0.2	{0.94,1,1}	10	2.7	0.4	95	0.005	0.032	-0.006	0.045	{0.67,0.67,0.67}
3	0.2	{0.90,0.90,1}	15	0.5	0.2	74	0.001	0.022	0	0.030	{0.56,0.67}
4	0.2	{0.94,0.95,1}	-	0.4	0.4	95	0.006	0.028	0	0.024	{0.67,0.67}

Table 1 – Parameter values obtained when fitting data from 1 block for each of the 4 participants. The parameters τ, σ, Δ, α, and β refer to Eq. 3; ϕ_0 and k belong to Eq. 4; σ_ψ is deployed in Eq. 2. The learning time (t_L) and the goodness of fit (GF) are shown in the last 2 columns.

To summarize, we performed an individual fit to each of the participant's behavioral metrics. We first used the RT distribution and VD of each participant to fit the parameters in Eq. 3. Once these parameters were fixed, we moved on to calculate the initial bias, and ran simulations of the model. Finally, we compared the results of the simulations with the performance of the participants and found the best fit for the behavioral parameters, i.e., the learning rate and decisional uncertainty.

3 DISCUSSION

Here we studied decision-making as a process in which options may be assessed in terms of their future consequence, and provided a computational account of their associated cognitive processes and of their dynamics for adaptive decision-making. To this end, we designed a novel experimental task in which trials were grouped into episodes of one to three trials, and the decisions at a trial influence the subsequent stimuli to select upon in the same episode. In brief, the stimuli during the trials of an episode were deliberately varied to promote inhibitory choices in the initial trial(s) and incentive ones in the last one. To specifically study how a consequence-

based assessment forms and influences decisions as learning progresses, we provided the participant with the instruction to explore his/her decisions to find the strategy yielding the most cumulative reward value per episode, while depriving them of any performance feedback. In this manner, our purpose was to promote the participant to develop his/her own subjective assessment of performance, based on the observation of stimuli changes in trials after performing each decision. Although the participants acted in a variety of ways, for the most part they explored the space of choices and learned the optimal strategy after a few episodes. This demonstrates that they had grasped the relationship between actual decisions and consequences, incorporated that information to their internal assessment of performance, and modified their decisions-making policies to maximize the reward value.

In addition to the experimental analyses, this manuscript also introduces a novel mathematical model encompassing the cognitive processes required for consequence-based decision-making in a joint framework. The model is organized in three-layers. The bottom layer describes the average dynamics of two neural populations, representing each the preference for one option, competing against each other until their difference in activity reaches a threshold. The middle layer encompasses the definition of the so-called intended decision, which implements the participant's preference of choosing the bigger or smaller stimulus at each specific trial. The top layer describes the strategy learning process, which oversees the model's performance, adapts by reinforcement to maximize the cumulative reward value, and drives the intended decision layer. We argue that this oversight mechanism, combined with the modulation of preference, is consistent with an internal process of consequence assessment and subsequent policy update. As part of a global validation process, the model parameters were fit to each participant's behavioral data (reaction time distribution, visual discrimination, initial bias, and performance). The model predictions faithfully reproduced these metrics along with the learning time for each participant, regardless of their level of accuracy throughout the session.

3.1 Rule-Based vs Far-Sighted Assessment of Consequence

The optimal strategy to attain maximum cumulative reward value may be reduced to a set of decision rules: choose small, then big in horizon 1 episodes; choose small, then small, then big, in horizon 2 episodes. Although these sequential choices were expected once the learning was complete and the decision strategy leading to maximum reward value established, the main focus of this study was on how consequence-based assessment forms and influences the learning of decision strategies. Thus, it was crucial to run a task design devoid of any explicit external feedback, which could potentially inform the participant of his/her performance throughout each episode and ultimately promote a rule-based strategy from the very beginning.

For the same purpose, and to promote exploration, the participants were left in the uncertainty of neither having a clear criterion to decide upon nor the knowledge about which aspect of the stimuli to prioritize to obtain bigger reward values in the trial next and across the episode. Note that, in addition to the height of the bars (proportional to reward value), the stimuli at each trial were presented on the right and left of the screen, and were shown sequentially, randomly alternating their order of presentation across trials. Although meaningless from the perspective of gaining the most of reward value, both the position and order of presentation contributed to increase the uncertainty as to which dimension of the stimuli were relevant to attain the goal during the learning phase. In fact, under these conditions, the participants were left with a single element that could aid them build their internal criterion to assess performance: perceiving the relationship between their choice at a trial, and the stimuli being subsequently presented in the next. If noticed, over a few episodes, this piece of evidence could then be used to predict the consequence associated with choosing each option at each trial within episode. To this end,

participants had to rely on their own subjective perception of performance, fed alone by their observations of the stimuli presented after each decision, and by their own internal assessment criterion, based on their skill at estimating the sum of water (reward value) throughout the trials of each episode. Importantly, learning the optimal strategy could only be achieved via exploration, either purposely or randomly, testing the pairing between the stimuli presented at each trial, the choice made, and, most importantly, the stimuli of the trial next.

To summarize, the problem of having explicit feedback is that the learning of the optimal strategy could be reduced to testing rule-based sequences until the one that gives the optimal feedback is found. Although the optimal strategy consists of the same rule-based sequence, the crucial element of the task is that, to reach that stage, the participant must first forego a phase of exploration in which learning is driven by exploration and assessment of the reward-based consequence associated with each option. Until then, the learning depends on a computation of reward value encompassing the consideration of far-sighted effect of each decision within episode, on the grounds of an internal subjective assessment criterion that makes this learning possible, and the results hereby presented non-trivial.

3.2 Building a Subjective Assessment Criterion

The crucial element of the aforementioned process is that, in the absence of explicit performance feedback, learning depends on first building up a subjective criterion of reward. This criterion necessarily depends on cognitive processes implementing an oversight mechanism of whether the correct decision criterion is being used, and whether the proper association between the choice and subsequent stimuli is being correctly perceived (63–66). Moreover, despite the participants being able to find the optimal strategy and diminishing the uncertainty of their behavior to reach the optimal strategy, the fact they never get an explicit external confirmation forces them to bear the doubt of whether their strategy is indeed the optimal one. The discussion of the theoretical formalization presented next suggests a minimal implementation for these mechanisms. This suggests a plausible strategy for this subjective mechanism to capture the relationship between stimuli and subsequent stimuli are established on a single trial basis, within the wider decision-making strategy of maximizing cumulative reward value.

3.3 Computational models of consequence

The analyses described in the results section demonstrate that the consequential task is an appropriate framework to study how consequence-based option assessment forms and influences decision-making. In parallel, the model we developed has the goal of reaching a formal characterization of the cognitive processes underlying the operations necessary to perform this task. As for most value-based decision-making models (41,51,67–70), learning in our model is operationalized by a reinforcement comparison algorithm, scaled by the difference between predicted vs. obtained reward value (71,72), measured accordingly to the participant's subjectively perceived scale. For simplicity, we assumed a fixed function across participants to quantify reward value (R(T) function in Eq. 4). Furthermore, to provide the necessary flexibility for the model to capture the full range of participants' learning dynamics, the model included a free parameter of learning rate, to be fit to the participant's behavior. The result is a model that could faithfully reproduce the full range of behaviors of each participant: RT distribution, pattern of decision-making, and learning time.

The structure of the model, organized in three layers, responds to the requirements of a minimal implementation of consequence-based decision-making within the context of our experimental

task. The lower layer (neural dynamics) represents the average activity of two neural populations competing for the selection, each representing one of the two stimuli to decide upon. The commitment for one of the two options is taken when the difference in firing rate between the two populations crosses a given threshold (35,41,67). These processes, with small variations, have been used to model decision-making in a broad set of tasks (33,35,73,74) and can describe most types of single-trial, binary decision-making, including value-based and perceptual paradigms. Although is outside of the scope of this investigation, we would like to mention that this type of model can subserve working memory (33,75); a transient input can bring the system from the resting state to one of the two stimulus-selective persistent activity states, which can be internally maintained across a delay period. However, modelling consequence-based decision-making requires at least two additional mechanisms beyond binary population competition. The first one is to define hypothetical criteria to prioritize a specific policy for decision-making. The second one is to create an internal mechanism of performance to evaluate these criteria, based on the difference between predicted and obtained reward value. Accordingly, the role of the middle layer (intended decision) is precisely the implementation of specific criteria, which in our case depends on the relative value of the stimuli and on the number of trial within episode. Finally, the top layer (strategy learning) implements the learning via reinforcement comparison (55) and temporal difference (71,76). The results and predictions depicted in the model descriptive section show that the dynamics of the three layers combined can accurately reproduce the behavior of each single participant, including those who did not attain the optimal strategy. The low number of equations in the model, together with the low number of free parameters, makes this model a simple, yet powerful tool able to reproduce a large variety of behavioral results. Moreover, unlike the basic reinforcement learning agents or models for evidence accumulation, our model is biologically plausible and therefore able to fit individual behavioral metrics. Furthermore, it allows to extract model-based features of participants, e.g., their initial bias, visual discrimination and learning rate.

4 Conclusion and Future Work

In this manuscript we have introduced a novel minimalistic formalism of the brain dynamics of consequence-based decision-making and its associated learning process. We validated this formalism with the behavioral data gathered from twenty-eight human participants, which the model could accurately reproduce. By extension of the classic single-trial binary decision-making, we designed a mechanism of oversight based on the assessment of the effect of prior decisions on subsequent stimuli, and a reinforcement rule to modify behavioral preferences. As part of the same project, we also designed the consequential task, a novel experimental framework in which gaining the most of reward value required learning to assess the consequence associated with each option during the decision-making process. Both the experimental results and the model predictions review consequence-based decision-making as an extended version of value-based decision-making in which the computation of predicted reward value may extend over several trials. The formalism introduces the necessary notions of oversight of the current strategy and of adaptive reinforcement, as the minimal requirements to learn consequence-based decision-making.

Although our model has been designed and tested in the consequential task described here, we argue that its generalization to similar paradigms in which optimal decisions require assessing the consequence associated to the options presented, or sequences of multiple decisions, may be relatively straightforward. Specifically, we envision three possible extensions to facilitate

its generalization. First, the model could incorporate several preference criteria simultaneously or combinations thereof to the intended decision layer: left vs. right or first vs. second, instead of small vs. big, to be determined in a dynamical fashion. This could be achieved with a multi-dimensional attractor model, with as many basins of attraction as the number of preference criteria to be considered.

The second extension we propose is a re-definition of the reward function R(T) according to the subjective criterion of preference. Namely, if not clearly specified, a reward value can be perceived differently by different subjects, i.e., people operate optimally according to their own subjective perception of the reward value. Because of this, a possible extension is to incorporate an individual reward value function per participant (R(T) in Eq. 4). For simplicity, in this manuscript we set R(T) to be fixed and to be the objective reward value function. In case a participant did not perceive what was the optimal reward value, he/she performed sub-optimally according to objective reward function, and the model responded by allowing the learning constant k to be zero. This holds since the optimal strategy was never reached, and the fitting of the participant's performance was correct. Nevertheless, it remains a standing work of significant interest to investigate different subjective reward mechanisms and their implementation in the model.

Finally, the third enhancement we propose for our model is making the learning rate time dependent, i.e., $k(E)$. This would facilitate reproducing learning processes starting at different times throughout the session. For example, it is possible that participants initiate the session having in mind a possible (incorrect) strategy and they stick to it without looking for clues, and therefore without learning the optimal policy. Nevertheless, after many trials they may change their mind and begin to explore different strategies. In this case the learning rate $k(E)$ would be set to zero for all the initial trials when indeed there is no learning.

Again, we want to emphasize that even if this model is built ad-hoc for the task we designed, it can be easily adapted to reproduce other tasks of sequential consequence-based decision-making. Note that the strategy learning mechanism is already general enough to adapt to tasks where the optimal policy is not fixed throughout the experiment. Indeed, if the optimal policy would change suddenly at some point during the block, the learning mechanism would be able to detect a change and adapt accordingly. Finally, we want to stress that our model could be applied to other decision-making paradigms, such as a version of the consequential random-dot task (77) or other multiple-option paradigms. Moreover, our model can be employed not only in human experiments, but also with non-human primates or rodents.

5 MATERIALS AND METHODS

5.1 Participants

A total of 28 participants (15 males, 13 females; age range 18-30 years; all right hand dominant) participated in the experimental task. All participants were neurologically healthy, had normal or corrected to normal vision, were naive as to the purpose of the study, and gave informed consent before participating. The study was approved by the local Clinical Research Ethics Committee (CEIm Ref. #2021/9743/I) and was conducted in accordance with relevant guidelines and regulations. Participants were paid a €10 show-up fee.

5.2 Experimental Setup

Participants were situated in the laboratory room at the Facultat de Matemàtica i Informàtica, Universitat de Barcelona, where the task was performed. The participants were seated in a chair, facing the experimental table, with their chest approximately 10cm from the table edge and their right arm resting on its surface. The table defined the plane where reaching movements were to be performed by sliding a light computer mouse (Logitech Inc). On the table, approximately 60cm away from the participant's sitting position, we placed a vertically-oriented, 24" Acer G245HQ computer screen (1920x1080). This monitor was connected to an Intel i5 (3.20GHz, 64-bit OS, 8 GB RAM) portable computer that ran custom-made scripts, programmed in MATLAB with the help of the MonkeyLogic toolbox, to control task flow (NIMH MonkeyLogic, NIH, USA; https://monkeylogic.nimh.nih.gov). The screen was used to show the stimuli at each trial and the position of the mouse in real time.

As part of the experiment, the participants had to respond by performing overt movements with their arm along the table plane while holding the computer mouse. Their movements were recorded with a Mouse (Logitech, Inc), sampled at 1 kHz, which we used to track hand position. Given that the monitor was placed upright on the table and movements were performed on the table plane (horizontally, approximately from the center of the table to the left or right target side), the plane of movement was perpendicular to that of the screen, where the stimuli and finger trajectories were presented. Data analyses were performed with custom-built MATLAB scripts (The Mathworks, Natick, MA), licensed to the Universitat de Barcelona.

Each participant was required to maintain posture at a fixed distance from the table and to place his/her chin on the chinrest. Pupil diameter from both eyes were tracked and recorded with an EyeTribe oculometer (Oculus, Menlo Park, CA, USA), sampling at 60Hz. We used a chinrest to stabilize posture and to fix the head position at approximately 60cm from the screen and from the oculometer. The signals delivered by the oculometer were recorded by the OpenFrameworks custom-made code, along with the movement trajectories and other behavioral data. Behavioral data from each session were transferred to a MySQL community server database (Oracle, Redwood Shores, CA, USA) for further analysis using custom-designed MATLAB scripts (Mathworks, Natick, MA, USA). External pulses, generated by the custom made Openframeworks v1.1 code, were used to synchronize the recordings from both computers at each trial.

5.3 Consequential Decision-Making Task

This section describes the consequential decision-making task, designed to assess the role of consequence on decision-making while promoting prefrontal inhibitory control (78). Since consequence depends on a predictive evaluation of future contexts, we designed a task in which trials were grouped together into episodes (groups of one, two or three consecutive trials), establishing the horizon of consequence for the decision-making problem within that block of trials.

The number of trials per episode equals the horizon n_H plus 1. In brief, within an episode, a decision in the initial trial influences the stimuli to be shown in the next trial(s) in a specific fashion, unbeknown to our participants. Although a reward value is gained by selecting one of the stimuli presented in each trial, the goal is not to gain the largest amount as possible per trial, but rather per episode.

Each participant performed 100 episodes for each horizon n_H = 0, 1, and 2. In the interest of comparing results, we have generated a list of stimuli for each n_H and used it for all participants. To avoid fatigue and keep the participants focused, we divided the experiment into 6 blocks, to be performed on the same day, each consisting of approximately 100 trials. More specifically, there was 1 block of $n_H=0$ with 100 trials, 2 blocks of $n_H=1$ each with 100 trials, and 3 blocks of $n_H=2$ with two of them of 105 trials and one of 90. Finally, we have randomized the order in which participants performed the horizons.

Figure 1 shows the timeline of one horizon 1 episode (2 consecutive trials). At the beginning of the trial, the participant was required to move the cursor onto a central target. After a fixation time (500 ms), the two target boxes were shown one after the other (for 500 ms each) to the left and right of the screen, in a random order. Targets were rectangles filled in blue by a percentage corresponding to the reward value associated with each stimulus (analogous to water containers). Next, both targets were presented together. This served as the GO signal for the participant to choose one of them (within an interval of 4s). Participants had to report their choice by making a reaching movement with the computer mouse from the central target to the target of their choice (right or left container). If the participant did not make a choice within 4 s, the trial was marked as an error trial. Once one of the targets had been reached for and the participant had held that position (500ms), the selection was recorded, and a yellow dot appeared above the selected target, indicating successful selection and reward value acquisition. In case of horizons larger than 0, the second trial started following the same pattern, although with a set of stimuli that depended on the previous decision (see next section).

5.4 Episode Structure

The participants were instructed to maximize the cumulative reward value throughout each episode, namely the sum of water contained by the selected targets across the trials of the episode. If trials within an episode were independent, the optimal choice would be to always choose the largest stimulus. Since one of the major goals of our study was to investigate delayed consequence assessment involving adaptive choices, we deliberately created dependent trial contexts in which making incentive decisions (selecting the larger stimulus) would not necessarily lead to the most cumulative reward value within episode.

To promote inhibitory choices, the inter-trial relationship was designed such that selecting the small (large) stimulus in a trial, yielded an increase (decrease) in the mean value of the options presented in the next trial. For this reason, always choosing the larger stimulus did not maximize cumulative reward value for $n_H=1, 2$.

Trials were generated according to 3 parameters: horizon's depth n_H, perceptual discrimination (in terms of difference d between the stimuli), and the gain/loss G in mean size of stimuli for successive trials. The stimuli $s_{1,2}$ presented on the screen could take values ranging from 0 to 1. Trials were divided into five difficulty levels by setting the difference between stimuli (DbS) $d \in \{0.01, 0.05, 0.1, 0.15, 0.2\}$.

For horizon $n_H=0$, for each trial the stimuli $s_{1,2}$ are generated as to have mean M and difference d between them, i.e., $s_{1,2} = M \pm d/2$. To have stimuli ranging from 0 to 1, the mean M is randomly generated using a uniform distribution with bounds $[d_{max}/2, 1 - d_{max}/2]$, where $d_{max} = 0.2$ is the maximum DbS. In horizon $n_H=1$, each episode consists of 2 dependent trials. Specifically, the stimuli presented in the second trial depend on the selection reported in the previous trial of that same episode. More specifically, the rule is such that if the choice of the

first trial is the smaller/larger stimulus, the mean of the pair of stimuli in the second trial will be increased/decreased by a specific gain G. In practice, the first trial of an $n_H=1$ episode is generated in the same way as for horizon $n_H=0$, i.e., the two stimuli equal $s_{1,2} = M \pm d/2$. The stimuli in the second trial within the same episode could be either $s_{1,2} = M + G \pm d/2$ or $s_{1,2} = M - G \pm d/2$, depending on the previous decision. Note that the difficulty of the trial remains constant within episode. A schematic for the trial structure is shown in Figure 1. Again, to have stimuli ranging from 0 to 1, the mean M is randomly generated using a uniform distribution with bounds $[G + d_{max}/2, 1 - G - d_{max}/2]$. In horizon $n_H=2$, episodes consist of three trials. The trial generation is structured as for horizon $n_H=1$. Namely, the first trial has stimuli $s_{1,2} = M \pm d/2$, the second $s_{1,2} = M \pm G \pm d/2$, and the third $s_{1,2} = M \pm G \pm G \pm d/2$. To have stimuli ranging from 0 to 1, the mean M is randomly generated from a uniform distribution with bounds $[2G + d_{max}/2, 1 - 2G - d_{max}/2]$. We set the gain/loss parameter to $G=0.3$ and $G=0.19$ for horizon $n_H=1$ and $n_H = 2$, respectively. Our choice was motivated by the fact that G should be big enough to let the participants perceive the gain/loss between trials, while simultaneously allowing some variability for the randomly generated means M.

5.5 Statistical analysis

We are interested in testing the relationship of the performance (PF) and the reaction time (RT) with the horizon n_H, trial within episode T_E, and episode E. To have coherent and meaningful results we have adjusted these variables as follows. The trial within episode is counted backwards from last to first, for the reason that the optimal choice for the last T_E is the same for any horizon. The variable representing the trial within episode counted backwards is denoted $\hat{T}_E$. The other adjustment we made is clustering the episodes in groups of 10. This new variable is called $E^{(10)}$. Finally, in order to consider trials within episode independently, we had to adapt the concept of PF since, by definition, it is a measure defined per episode. The equivalent of PF for a single trial is the percentage of selected optimal choices P_{oc}. We used a linear mixed effects model (39,40) to predict PF and RT. The independent variables for the fixed effects are horizon n_H, trial within episode $\hat{T}_E$ (counted backwards), and the evolution in time expressed as blocks of 10 episodes $E^{(10)}$, and we set the random effects for the intercept and the episodes grouped by participant. The resulting formulae are $P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + (E^{(10)} | part.)$ and $RT \sim E^{(10)} + n_H \cdot \hat{T}_E + (E^{(10)} | part.)$.

The statistics were run separately for the group of participants that learned the optimal strategy and the ones who did not, according to **Error! Reference source not found.**a. In addition, the R T were z-scored to run the analysis. The results of the statistical analysis are reported in Table 2. The regression coefficients, with respective significance, are shown in **Error! Reference source not found.**e-f.

$P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$												
	Group Learn						**Group No-Learn**					
AIC	-299.61						75.41					
BIC	-253.81						110.38					
Log-likel.	158.8						-28.7					
Fixed effects	**Estimate**	**SE**	**tStat**	**pVal**	**Lower**	**Upper**	**Estimate**	**SE**	**tStat**	**pVal**	**Lower**	**Upper**
Intercept	1.14	0.05	23.7	10^{-102}	1.05	1.24	1.19	0.10	20.4	10^{-62}	1.77	2.14
$\hat{T}_E$	-0.26	0.03	-7.8	10^{-14}	-0.32	-0.19	-1.05	0.07	-14.0	10^{-36}	-1.19	-0.90
n_H	-0.16	0.02	-6.7	10^{-11}	-0.20	-0.11	-0.42	0.05	-8.1	10^{-14}	-0.52	-0.32
$E^{(10)}$	0.02	0.00	7.1	10^{-12}	0.02	0.03	-0.00	0.01	-0.6	0.58	-0.02	0.01
$\hat{T}_E : n_H$	0.10	0.02	5.8	10^{-9}	0.07	0.14	0.34	0.04	8.6	10^{-16}	0.26	0.42

Table 2 – Linear mixed effects model with formula $P_{oc} \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$ for the percentage of optimal choices selected (P_{oc}), horizon nH, trial within episode $\hat{T}_E$ (counted backwards), and the evolution in time expressed as blocks of 10 episodes $E^{(10)}$.

$RT \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$												
	Group Learn						**Group No-Learn**					
AIC	3105						780					
BIC	3151						815					
Log-likel.	-1544						-381					
Fixed effects	**Estimate**	**SE**	**tStat**	**pVal**	**Lower**	**Upper**	**Estimate**	**SE**	**tStat**	**pVal**	**Lower**	**Upper**
Intercept	-0.70	0.20	-3.6	10^{-4}	-1.08	-0.31	1.58	0.41	3.85	10^{-4}	0.77	2.38
$\hat{T}_E$	0.66	0.14	4.9	10^{-6}	0.40	0.93	-1.00	0.20	-5.09	10^{-7}	-1.39	-0.61
n_H	0.12	0.09	1.3	0.20	-0.06	0.31	-0.87	0.14	-6.34	10^{-10}	-1.14	-0.60
$E^{(10)}$	-0.04	0.01	-4.0	10^{-5}	-0.06	-0.02	-0.03	0.03	-1.21	0.23	-0.09	0.02
$\hat{T}_E : n_H$	-0.17	0.07	-2.3	0.02	-0.31	-0.02	0.61	0.10	5.88	10^{-9}	0.41	0.82

Table 3 – Linear mixed effects model with formula $RT \sim E^{(10)} + n_H \cdot \hat{T}_E + \left(E^{(10)} \middle| part.\right)$ for the percentage of optimal choices selected (P_{oc}), horizon nH, trial within episode $\hat{T}_E$ (counted backwards), and the evolution in time expressed as blocks of 10 episodes $E^{(10)}$.

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