

Distinct Computational Mechanisms of Uncertainty Processing Explain Opposing Exploratory Behaviors in Anxiety and Apathy

Xinyuan Yan, R. Becket Ebitz, Nicola Grissom, David P. Darrow, and Alexander B. Herman

ABSTRACT

BACKGROUND: Decision making in uncertain environments can lead to varied outcomes, and how we process those outcomes may depend on our emotional state. Understanding how individuals interpret the sources of uncertainty is crucial for understanding adaptive behavior and mental well-being. Uncertainty can be broadly categorized into 2 components: volatility and stochasticity. Volatility describes how quickly conditions change. Stochasticity, on the other hand, refers to outcome randomness. We investigated how anxiety and apathy influenced people's perceptions of uncertainty and how uncertainty perception shaped explore-exploit decisions.

METHODS: Participants ($N = 1001$, nonclinical sample) completed a restless 3-armed bandit task that was analyzed using both latent state and process models.

RESULTS: Individuals with anxiety perceived uncertainty as resulting more from volatility, leading to increased exploration and learning rates, especially after reward omission. Conversely, individuals with apathy viewed uncertainty as more stochastic, resulting in decreased exploration and learning rates. The perceived volatility to stochasticity ratio mediated the anxiety-exploration relationship post adverse outcomes. Dimensionality reduction showed exploration and uncertainty estimation to be distinct but related latent factors shaping a manifold of adaptive behavior that is modulated by anxiety and apathy.

CONCLUSIONS: These findings reveal distinct computational mechanisms for how anxiety and apathy influence decision making, providing a framework for understanding cognitive and affective processes in neuropsychiatric disorders.

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Life presents unexpected challenges, and how individuals interpret undesirable outcomes in uncertain environments shapes their actions (1). Attributing changes to environmental volatility (the speed at which the environment is changing) may encourage exploration, while attributing them to chance (stochasticity) may lead an individual to persist with existing strategies (2).

This interpretation likely interacts bidirectionally with affective states. Viewing outcomes as stochastic may protect from hurtful feedback but could lead to apathy and depression by hindering adaptation. Perceiving outcomes as volatile may motivate learning and uncertainty reduction but could increase anxiety through exposure to more adverse experiences.

Reciprocally, how individuals perceive and respond to environmental uncertainty can be influenced by underlying affective states (3). Apathy, characterized by a lack of motivation and goal-directed behavior (4,5), is an affective state associated with imprecise beliefs about action outcomes (6) and a tendency to persist with previous choices rather than explore (7). These features are mechanistically linked: imprecise outcome beliefs increase uncertainty about new actions, potentially leading individuals to choose familiar options. This computational bias is self-reinforcing because reduced

engagement limits action-outcome learning, and restricted exploration prevents exposure to diverse outcomes. Building on these observations, we hypothesize that apathetic individuals may perceive outcomes as primarily stochastic rather than controllable, potentially perpetuating a cycle of reduced exploration and helplessness (8).

In contrast, anxiety, marked by excessive worry and a heightened perception of potential threats (9,10) and uncertainty (11), may lead individuals to overestimate environmental volatility. Consequently, individuals with anxiety could be driven to seek new information to update their beliefs and reduce uncertainty (12). However, research on the link between anxiety and exploration has yielded mixed findings, with some studies showing increased exploration to mitigate uncertainty (13,14) and others showing reduced exploration to avoid unpredictable feedback under high anxiety (15,16). Notably, apathy and anxiety often coexist in clinical populations, such as individuals with Alzheimer's disease (17), Parkinson's disease (18), and depression (19), despite these diseases having distinct neural representations (20,21).

Building on these findings, we proposed 3 fundamental questions to further elucidate the relationship between affective states and decision making under uncertainty. First, we

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aimed to investigate whether apathy and anxiety exhibit distinct behavioral patterns when individuals are faced with uncertain situations. Second, we sought to examine how individual differences in levels of apathy and anxiety are associated with perceptions of different types of uncertainty, specifically volatility and stochasticity.

We posited 2 competing hypotheses:

First, apathetic individuals manifest less exploration, while individuals with anxiety engage in more exploration. Apathetic individuals weigh stochasticity over volatility and explore less, while individuals with anxiety overestimate volatility but explore more to reduce their uncertainty. This result would be consistent with previous findings suggesting that the 2 affective states have distinct neural substrates (20,22).

Second, both apathetic individuals and individuals with anxiety engage in less exploratory behavior, but through different computational mechanisms. Apathetic individuals weigh stochasticity over volatility and explore less, while individuals with anxiety overestimate volatility, leading to a sense that their actions cannot track or learn from the environment, ultimately leading to exploitation. This may provide a computational account for learned helplessness (23) and the co-occurrence of apathy and anxiety in various clinical populations, such as individuals with Parkinson's disease and Alzheimer's disease.

To address these questions, we recruited 1001 participants from a nonclinical population with measures of anxiety and apathy. Participants completed a restless 3-armed bandit task (Figure 1A), a well-established paradigm for capturing adaptive learning in volatile environments (24). We adopted a hidden Markov model (HMM) to obtain the likelihood of individuals switching between exploitation and exploration states (25,26). To further investigate how volatility and stochasticity modulate exploration, we utilized a Kalman filter (KF) model, which can dissociate 2 distinct sources of noise, volatility (process noise variance) and stochasticity (observation noise variance), during

inference (27). Our findings support the first hypothesis, revealing distinct behavioral patterns and computational mechanisms in apathetic individuals and individuals with anxiety when faced with uncertainty.

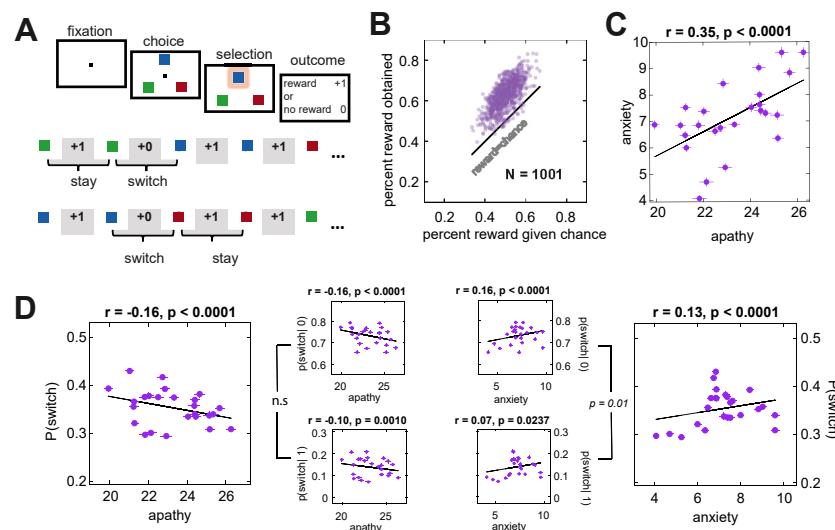
METHODS AND MATERIALS

Ethics Approval

The experimental procedures of all experiments were consistent with the standards set by the Declaration of Helsinki and were approved by the local Research Ethics Committee of the University of Minnesota, Twin Cities. Participants provided written informed consent after the experimental procedure had been fully explained and were reminded of their right to withdraw at any time during the study.

Participants

Sample size was determined through a priori power analysis. To detect correlations of $r = 0.1$ (typical for individual differences research; see *Supplementary Text S1*) with 80% power at $\alpha = 0.05$, we required a minimum sample of 782 participants. We recruited 1500 participants to account for expected exclusions based on previous large-sample online studies (7,15) and our own pilot work, expecting to achieve a sample of between 900 and 1100 participants, thus allowing for a buffer above the minimum sample size. Our final sample of 1001 participants provided 98% power to detect a correlation of $r = 0.1$. We recruited a sample of 1512 participants (nonclinical sample) via Prolific (Prolific Co.); exclusion criteria included a current or history of neurological or psychiatric disorders. Participants were excluded if they did not complete all questionnaires (3.57% of initial sample) or did not complete the bandit task (30.22% of initial sample) (*Table S1*). A total of 1001 participants completed all questionnaires and the bandit task (age range 18–54 years, mean [SD] = 28.446 [10.354] years;



bins based on the x-axis), with lines representing the standard error. Note that these may be smaller than the symbol. Statistical analyses were performed on raw data. For plots with all data points, see *Figure S4*. n.s., not significant.

Figure 1. Three-armed restless bandit task and distinct behavioral patterns associated with apathy and anxiety. (A) Three-armed restless bandit task. Participants chose one option from among the 3 targets to receive reward or nonreward feedback. Each target was associated with a hidden reward probability that randomly and independently changed throughout the task. The lower panel indicates the example choice and reward sequence and the definition of stay and switch. Specifically, stay was defined as choosing the same target as in the previous trial, while switch was defined as choosing a different target. “+1” denotes reward feedback, and “+0” denotes reward omission. (B) Most participants earned more rewards than expected by chance. (C) Apathy and anxiety were positively correlated. (D) Apathy was negatively correlated with switch behaviors, while anxiety was positively correlated with switch behaviors. Individuals with anxiety were more sensitive to undesired feedback (no reward) and exhibited more switch behaviors than reward feedback. [Panels (C) and (D) utilize binned correlation plots (25 quantile

493 female). All participants were compensated for their time in accordance with the minimum wage.

Questionnaire Measurement

Anxiety and apathy were assessed using the General Anxiety Disorder Screener (28) and the Apathy Motivation Index (AMI) (29), respectively. Higher scores indicate greater anxiety or apathy. See [Table S2](#) for details.

Three-Armed Restless Bandit Task

We assessed exploration-exploitation behavioral dynamics using a 300-trial 3-armed restless bandit task (25) ([Figure 1A](#)). Task parameter settings can be found in [Supplementary Method S1](#). We assessed performance by comparing the total number of rewarded trials to the number of rewarded trials expected by chance. Of the 1001 participants, 985 accrued more rewarded trials than would be expected by chance ([Figure 1B](#)).

Model-Free Analyses

We defined a trial as a switch trial if the chosen option was different from the last trial and as a stay trial if the choice was the same as the last trial. We adopted some widely used model-free measures, including win-stay and lose-shift (30,31), as the direct measurement for this learning task.

$p(\text{switch})$ is calculated as the proportion of trials in which participants selected a different option from their previous choice. Win-stay is defined as the percentage of times that the choice in trial $t-1$ was repeated on trial t following a reward. In contrast, lose-shift equals the percentage of trials for which the choice was shifted or changed when the outcome of trial $t-1$ was nonreward.

Model-free results can be found in [Table S3](#).

Complementary Computational Approaches: Process Model and Latent Space Model

To comprehensively characterize decision making under uncertainty, we used 2 complementary computational approaches: a KF process model capturing the individual differences in how to learn and process uncertainty and an HMM revealing trial-by-trial differences in exploration and exploitation across individuals. These models provide distinct but complementary insights (for more details, see [Supplementary Text S2](#)).

Hidden Markov Model

We fit an HMM to the behavior to decode the hidden state of each trial for each participant. We fit the HMM via expectation-maximization using the Baum-Welch algorithm and decoded hidden states from observed choice sequences by the Viterbi algorithm (32). From this analysis, we extracted 2 types of measures. The first measure, $p(\text{explore})$, quantifies the overall proportion of trials classified as exploratory states for each participant. The second measure, the transition probabilities, which characterize the temporal dynamics of state switching: $p(\text{explore} \rightarrow \text{explore})$, indicates the probability of maintaining an exploratory state between consecutive trials, with higher values reflecting more sustained exploration periods; $p(\text{exploit} \rightarrow \text{exploit})$ represents the probability of maintaining an

exploitative state, with higher values indicating more persistent exploitation of chosen options. Model details are provided in [Supplementary Method S2](#). HMM results can be found in [Figure 2](#) and [Table S4](#). For details on parameter recovery for the HMM, see [Supplementary Method S7](#).

KF Model

The KF model has been widely applied in psychology and neuroscience to study various aspects of learning and decision making (33,34). Details to explain the KF model are provided in [Supplementary Method S3](#).

Extended KF for Three-Armed Bandit Task

The KF model can be extended to capture the effects of both volatility and stochasticity in a multiarmed bandit task (27,35). In the current study, process noise variance (ν) and observation noise variance (σ^2) represent volatility and stochasticity, respectively. A traditional assumption of the KF is that ν and σ^2 are constant.

Reward means update is as follows:

$$m_t = m_{t-1} + k_t(O_t - m_{t-1})$$

where m_t is the estimated mean or value of the chosen arm at trial t and O_t is the observed reward at trial t .

The mean update is driven by the prediction error, which is the difference between the observed reward and the previous estimate.

Kalman gain is defined as follows:

$$k_t = (w_{t-1} + \nu) / (w_{t-1} + \nu + \sigma^2)$$

Here, k_t represents the Kalman gain or learning rate, which adjusts the weight given to new information based on the relative uncertainty of the prior estimate (w_{t-1}) and the total noise ($\nu + \sigma^2$). When the stochasticity (σ^2) is high relative to the volatility (ν), the Kalman gain (learning rate) will be small, and the model will rely more on its prior beliefs and less on the observations. Conversely, when the volatility (ν) is high relative to the stochasticity (σ^2), the Kalman gain (learning rate) will be large, and the model will update its beliefs more strongly based on the observed rewards.

Variance update equation is as follows:

$$w_t = (1 - k_t)(w_{t-1} + \nu)$$

This equation updates the posterior variance (w_t), which represents the estimate's uncertainty after observing O_t .

Alternative Models

We also fitted our data with alternative models including volatile KF model ([Supplementary Method S4](#)) and Rescorla-Wagner model ([Supplementary Method S5](#)).

Model Fitting and Comparison

We employed hierarchical Bayesian inference (HBI) to fit models to choice data (36) (for details, see [Supplementary Method S6](#)). For model comparison, we used Bayesian model selection (37), specifically employing the protected exceedance probability (PXP) to select the winning model. The

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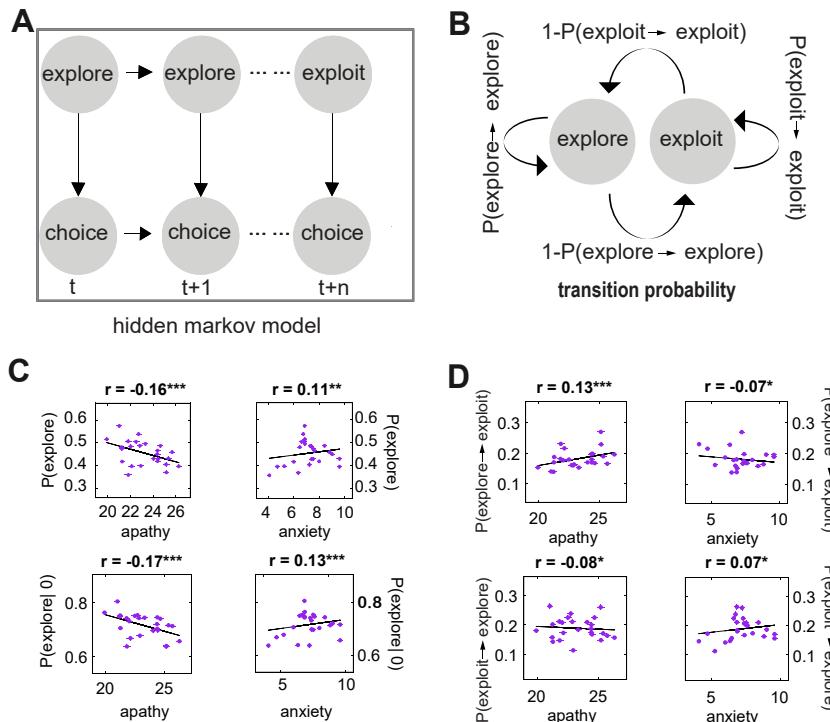


Figure 2. Apathy and anxiety have opposing relationships with exploration and explore and exploit state dynamics. **(A)** Unrolled structure of the hidden Markov model (HMM) that was used to infer the explore and exploit states' underlying behavior. **(B)** The transition probabilities within and between states in the HMM. **(C)** The probability of exploration, plotted as a function of apathy (top left) and anxiety (top right). The probability of exploration following a reward omission is plotted as a function of apathy (bottom left) and anxiety (bottom right). **(D)** The transition probability from explore to exploit, plotted as a function of apathy (top left) and anxiety (top right); the transition probability from exploit to explore plotted as a function of apathy (bottom left) and anxiety (bottom right). [Panels **(C)** and **(D)** utilize binned correlation plots (25 quantile bins based on the x-axis), with lines representing the standard error. Note that these may be smaller than the symbol. Statistical analyses were performed on raw data. For plots with all data points, see [Figure S5](#). * $p < .05$, ** $p < .01$, *** $p < .001$. All p values remained significant after false discovery rate $p < .05$ correction.

detailed results of our model comparison, including PXP and Bayesian information criterion (BIC) values for all models, can be found in [Table S5](#).

Model Validation

We validated our modeling procedure using 2 approaches. First, we assessed parameter recovery by refitting data simulated from the winning model and comparing the resulting parameter estimates to their ground truth. We simulated 50 agents' choices and observations, repeating this process 50 times. Second, we tested the accuracy of the model prediction. We calculated the correlation between behavioral output predicted by model and real choices. The details for validation analyses can be found in [Supplementary Method S8](#) and [Figures S1 and S2](#).

Split-Half Reliability

To assess the split-half reliability of our task, we examined the consistency of overall choices and model parameters from the winning model between the first and second halves of trials. Analyses details are provided in [Supplementary Method S9](#) and [Figure S3](#).

RESULTS

Apathy and Anxiety Predicted Distinct Exploratory Behaviors

As expected, anxiety and apathy showed a significant positive correlation ($r = 0.35, p < 10^{-29}$) ([Figure 1C](#)), which is consistent

with previous findings on their co-occurrence ([17](#)). We found that apathy negatively predicted p(switch) ($r = -0.16, p < .001$) regardless of feedback type (reward or no reward), while anxiety positively correlated with p(switch) ($r = 0.13, p < .001$). Intriguingly, the relationship between anxiety and switch behaviors was greater after nonreward feedback ($r = 0.16, p < .001$) compared with reward feedback ($r = 0.07, p = .024$) (their difference, z score = 2.40, $p = .01$). Although coexisting in this population, these 2 affective states predicted distinct switch behaviors under uncertainty ([Figure 1D](#)). The stronger relationship between anxiety and p(switch) after undesirable feedback indicates that highly anxious individuals are more sensitive to negative feedback, which may lead them to disengage.

Next, we fitted the behavior with an HMM to decode the hidden states, explore and exploit ([Figure 2A](#)) ([24,25,38,39](#)). Each arm is associated with a hidden reward probability that randomly and independently changes throughout the task ([Figure 2A](#)). We calculated the percentage of explore states, i.e., p(explore). Consistently, apathy correlated negatively with p(explore) ($r = -0.16, p < .001$) and the percentage of exploration after reward omission [$p(\text{explore} | 0)$] ($r = -0.17, p < .001$), while anxiety positively correlated with p(explore) ($r = 0.11, p = .003$) as well as $p(\text{explore} | 0)$ ($r = 0.13, p < .001$) ([Figure 2C](#)).

In addition to the overall frequency with which hidden states occur, examining the transitions between these states can further illuminate the dynamics of decision making. Therefore, we investigated how apathy and anxiety manifest in the transition probability ([Figure 2B](#)) between explore and exploit. As

predicted, apathy had a positive correlation with the transition probability from explore to exploit ($r = 0.13, p < .001$) but a negative correlation with the transition probability from exploit to explore ($r = -0.08, p = .011$). In contrast, anxiety had a negative correlation with the transition probability from explore to exploit ($r = -0.07, p = .035$) but a positive correlation with the transition probability from exploit to explore ($r = 0.07, p < .022$) (Figure 2D). All significant results reported in the study survived false discovery rate (FDR) ($p < .05$) correction.

Apathy and Anxiety Are Associated With Distinct Computational Processes Underlying Exploration

Then we asked whether differing perceptions of the environment might explain the distinct patterns of exploration predicted by apathy and anxiety we observed.

To address this question, we utilized a KF model (Figure 3A), which can dissociate sources of uncertainty into perceived volatility and stochasticity (27). We also fitted the behavioral

data to alternative models including volatile KF (for model details, see *Supplementary Method S4*) (27), Rescorla-Wagner models single (RW1) (*Supplementary Method S5*) (40) and dual learning rates (RW2) (*Supplementary Method S5*) to weigh positive and negative learning rates (31). The KF served as the best model for our population, and we examined the resulting distribution of volatility and stochasticity (Figure 3B).

We conducted correlation analyses using all data points. Specifically, we found that apathy was positively correlated with stochasticity ($r = 0.08, p = .010$) but negatively correlated with volatility ($r = -0.08, p = .008$). Conversely, anxiety negatively correlated with stochasticity ($r = -0.12, p = .0001$) and had a positive correlation with volatility ($r = 0.11, p = .0003$). These correlations highlight the distinct cognitive biases associated with apathy and anxiety in processing environmental uncertainties (Figure 3C).

To aid the visualization for these effects, we then categorized participants into distinct groups based on their apathy and anxiety levels. For apathy, we identified the high apathy

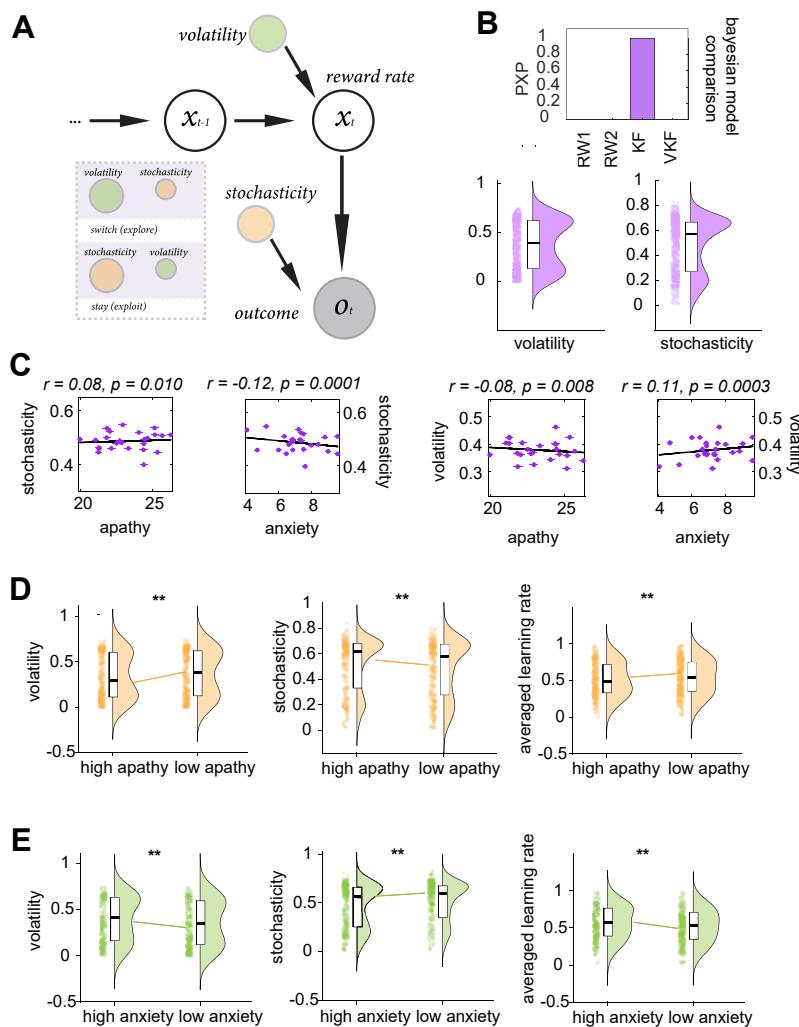
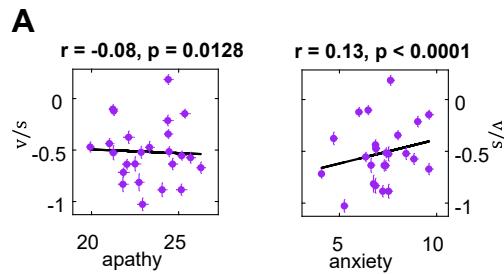


Figure 3. Apathy and anxiety have opposing relationships with volatility and stochasticity. **(A)** The schematic of the Kalman filter model that was used in our analysis. The diagram illustrates how this model can differentiate between volatility (process noise variance) and stochasticity (observation noise variance), providing insights into the underlying decision-making processes. **(B)** Bayesian model comparison and the parameter ranges of volatility and stochasticity. **(C)** Apathy was positively correlated with stochasticity but negatively correlated with volatility estimation. Conversely, anxiety showed a negative correlation with stochasticity and a positive correlation with volatility (for plots with all data points, see Figure S6). **(D)** Individuals with a high level of apathy overestimated stochasticity but underestimated volatility, resulting in a lower learning rate. **(E)** In contrast, individuals with a high level of anxiety overestimated volatility but underestimated stochasticity, resulting in a higher learning rate. ** $p < .01$. All p values remained significant after false discovery rate $p < .05$ correction. [Note that violin plots in panels **(D)** and **(E)** are provided for visualization purposes only. For details on the grouping methodology and statistical analyses, refer to Table S6 and *Supplementary Text S3*.]

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analyses were performed on raw data. For plots with all data points, see Figure S7]. $**p < .01$, $***p < .001$. All p values remained significant after false discovery rate $p < .05$ correction.

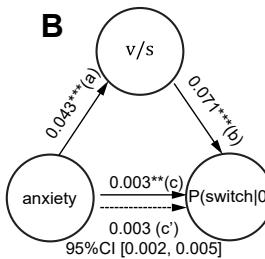


Figure 4. Distinctions between apathy and anxiety on the ratio of volatility to stochasticity (v/s) and its mediation effect. **(A)** The ratio of volatility to stochasticity plotted as a function of apathy (left) and anxiety positively (right). **(B)** Mediation analysis showing the mediating effect of the ratio of volatility to stochasticity on the relationship between anxiety and switch behavior after reward omission. [Panels in **(A)** utilize binned correlation plots (25 quantile bins based on the x-axis), with lines representing the standard error. Note that these may be smaller than the symbol. Statistical

group ($n = 223$) as those scoring in the top 25% (total score, mean [SD] = 34.879 [4.055]) on the AMI, which assesses apathy in behavioral and social domains (29). Conversely, the low apathy group ($n = 251$) comprised individuals scoring in the bottom 25% (12.912 [3.695]) of apathy scores (Figure 3D). Similarly, for anxiety, the high anxiety group ($n = 228$) included participants within the top 25% of scores (15.395 [2.819]) on the 7-item General Anxiety Disorder scale (28), while the low anxiety group ($n = 250$) consisted of those in the bottom 25% (0.844 [0.852]) (Figure 3E). Statistical details examining the group differences are provided in Table S6. To ensure our findings were not dependent on arbitrary cutoffs, we also validated our results using a standard deviation approach (± 1 SD from the mean); the results were the same (see Supplementary Text S3).

The Ratio of Volatility to Stochasticity Distinguished Apathy and Anxiety

To clarify the differential impacts of apathy and anxiety on decision making under uncertainty, we computed the ratio of volatility to stochasticity (v/s) to represent the balance between these 2 types of uncertainties. A higher v/s indicates a perception of greater volatility relative to stochasticity, while a lower ratio suggests a perception of more stochasticity relative to volatility. We applied a logarithmic transformation to the ratio to manage extreme values (e.g., cases where individuals might perceive very high volatility but very low stochasticity). Consistently, our findings revealed a clear distinction: v/s correlated negatively with apathy ($r = -0.08$, $p = .0128$) but positively with anxiety ($r = 0.13$, $p < .001$) (Figure 4A).

The Ratio of Volatility and Stochasticity Mediated the Relationship Between Anxiety and the Exploration After Negative Feedback

To examine potential associations between individual differences in the perception of uncertainty, exploratory behavior, and affect, we conducted a mediation analysis (see Supplementary Method S10) with anxiety, switching after reward omission [$p(\text{switch} | 0)$], and v/s . The results demonstrate that the relationship between anxiety and the tendency to switch after receiving no reward is significantly mediated by v/s (Figure 4B). This mediation was also significant for the analogous HMM-based measures (see Figure S9). This is consistent with expectations given the strong correlation between $p(\text{switch})$ and $p(\text{explore})$ ($r = 0.916$, $p < .0001$)

(Figure S10). No significant mediation effect was found for apathy.

A Low Dimensional Manifold Unifies Exploration, Perceptions of Uncertainty, and Affective State

The HMM state model of exploration-exploitation and the KF process model of uncertainty estimation represent complementary ways of understanding adaptive behaviors (see Supplementary Text S2). We hypothesized that a latent structure underlying adaptive behavior on this task might unify these descriptions of behavior. We utilized advanced dimensionality reduction methods to uncover such a latent structure in the raw task behavior.

First, we formatted each participant's trial-by-trial task data into sequences of choices to stay (repeat the choice on the last trial) or switch (choose a different option) and reward outcome for 2 consecutive trials (choice_{t-1} , outcome_{t-1} , choice_t) (Figure 5A, B). The behavioral data for each participant were then transformed into counts for each of these 8 unique sequences. Then we applied Uniform Manifold Approximation and Projection (UMAP) (41) to learn the 2-dimensional manifold underlying the 8-dimensional behavioral data (Figure 5C; see Supplementary Method S11 for more algorithm details). Including additional reward history and applying other dimensionality reduction methods such as principal component analysis and t-distributed stochastic neighbor embedding did not change the results (Figure S11 and Table S7).

Our analysis using UMAP revealed distinct correlations within the derived dimensions. Specifically, the dimension 1 score (the horizontal axis) exhibited a very strong significant negative correlation with exploratory behavior [$p(\text{explore})$] ($r = -0.90$, $p < 10^{-200}$), but it showed no significant relationship with v/s ($r = 0.03$, $p = .35$) (Figure 5D, E). In contrast, the dimension 2 score (the vertical axis) demonstrated a strong negative correlation with v/s ($r = -0.72$, $p < 10^{-185}$), which was significantly more pronounced than its correlation with $p(\text{explore})$ ($r = -0.19$, $p < 10^{-10}$) (Figure 5F, G). This suggests that dimension 1 primarily represents exploratory behavior, while dimension 2 primarily reflects the computational factors: volatility and stochasticity.

Furthermore, both dimensions also showed correlations with affective states; the dimension 1 score was positively correlated with apathy ($r = 0.14$, $p < .001$) and negatively correlated with anxiety ($r = -0.11$, $p < .001$). Similarly, the dimension 2 score had a positive correlation with apathy ($r =$

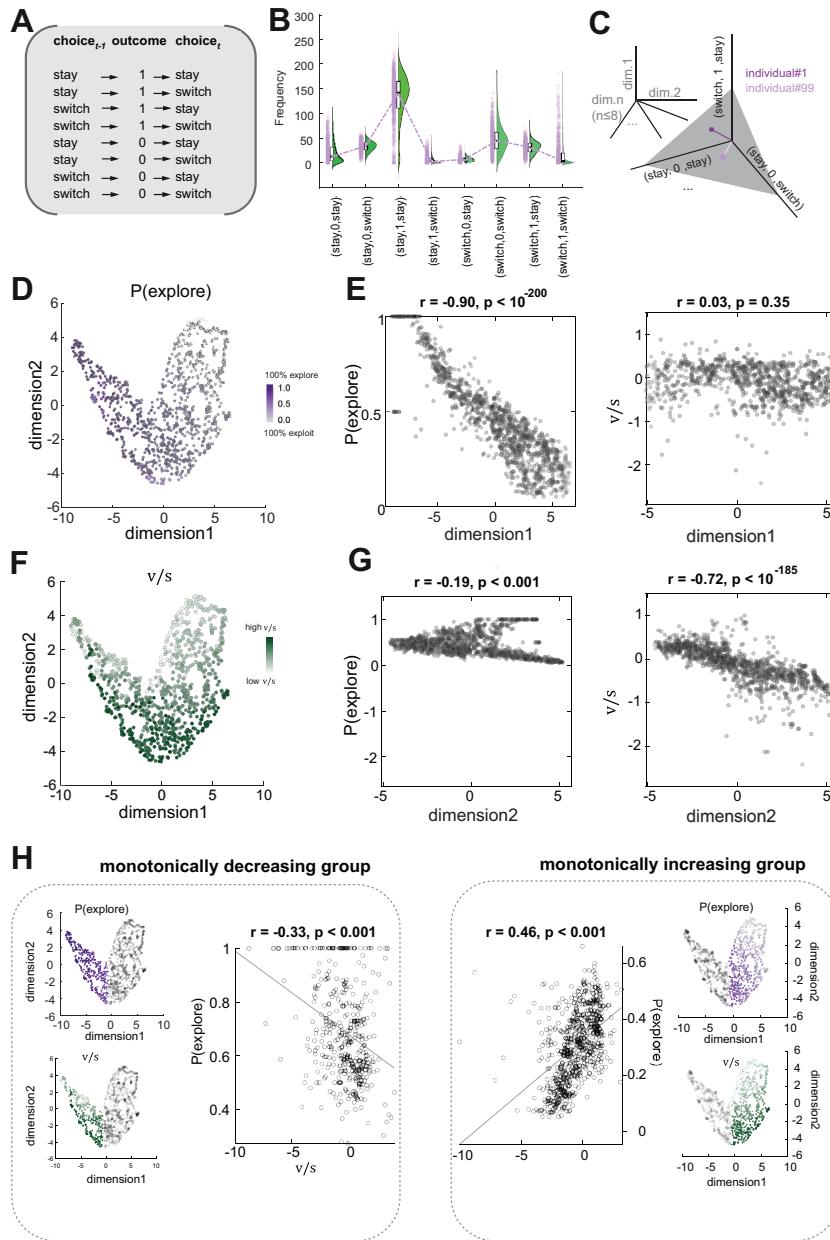


Figure 5. Visualizing the complex relationships in decision making through low-dimensional space. **(A)** All possible sequences of choices and rewards that participants could make during the experiment. **(B)** The frequency distribution of individual decision-making patterns. The black line in the box plot represents each pattern's mean value, highlighting participants' typical behaviors. **(C)** Schematic high-dimensional space of participants' decision-making pattern. **(D)** The 2-dimensional space representation of exploration by using the Uniform Manifold Approximation and Projection (UMAP) (different dimensionality reduction methods such as principal component analysis [PCA] and t-SNE lead to a similar space). **(E)** Dimension 1 exclusively represents $p(\text{exploration})$ but does not represent the ratio of volatility to stochasticity. **(F)** The 2-dimensional space representation of the ratio of volatility to stochasticity behavior by using UMAP (PCA and t-SNE lead to similar results, Figure S11 and Table S7). **(G)** Dimension 2 mainly represents the ratio of v/s but not $p(\text{exploration})$. **(H)** We divided the manifold into the monotonically decreasing group (the left-most panel) and monotonically increasing group (the far-right panel). The decreasing group exhibited higher overall exploration rates and was characterized by slightly higher anxiety levels and lower apathy levels. Within this group, higher v/s ratios were associated with decreased exploration. In contrast, the increasing group showed lower overall exploration rates, lower anxiety levels, and higher apathy levels, with higher v/s ratios being correlated with increased exploration. All p values remained significant after false discovery rate (FDR) $p < .05$ correction (for details about FDR correction, see Supplementary Method S13).

0.097, $p = .002$) and a negative correlation with anxiety ($r = -0.088, p = .004$).

To better understand the structure of the manifold, we examined its relationship with affective states and exploration patterns. Using a critical dimension 1 score of -0.671 as the dividing point (see Supplementary Method S12 and Figure S12), we identified 2 distinct groups: a monotonically decreasing group ($n = 390$) and a monotonically increasing group ($n = 611$). These groups showed markedly different characteristics. The decreasing group exhibited higher overall exploration rates and was characterized by slightly higher

anxiety levels ($t_{999} = 2.08, p = .037$) and lower apathy levels ($t_{999} = -3.56, p = .0003$), with higher v/s being associated with decreased exploration. In contrast, the increasing group showed lower overall exploration rates, lower anxiety levels, and higher apathy levels, with higher v/s correlating with increased exploration.

These patterns reveal complexity that is not captured by traditional analyses. When using simple quartile splits of anxiety and apathy groups, higher v/s consistently predicts increased exploration regardless of group membership. However, the manifold approach integrates multiple behavioral

aspects, including affective states (anxiety and apathy), exploration behaviors, and uncertainty processing (v/s), thereby allowing us to identify interaction patterns that would be missed when examining each factor in isolation. This integration also captures the nonlinear relationship between (v/s) and exploration (Figure S13).

It is worth noting that we only found linear relationships between apathy, anxiety, and exploration, as well as between these affective states and the ratio of volatility to stochasticity (our analysis using higher-order effects among these variables did not yield significant results; more details can be found in Table S8).

DISCUSSION

The distinct patterns of exploratory behavior observed in individuals with anxiety and apathetic individuals highlight the role of affective states in shaping responses to uncertainty. Individuals with anxiety, who generally display a heightened sensitivity to potential threats and environmental changes, exhibited a bias toward perceiving greater volatility and exploring more after negative outcomes. Our mediation analysis revealed that the perception of volatility relative to stochasticity partially mediated the relationship between anxiety and exploratory behavior after reward omission. The apparent relationship between anxiety and a higher weighting of volatility relative to stochasticity may be linked to increased information-seeking behavior. This may reflect a strategy aimed at reducing uncertainty and managing perceived risks more effectively (42). Although such a strategy may be beneficial for adaptation in genuinely volatile environments, it may also contribute to excessive worry and stress, especially if the perceived level of volatility exceeds actual environmental volatility (9,11). Consequently, individuals with anxiety may find themselves in a prolonged state of heightened arousal and uncertainty, leading to suboptimal decision making and diminished well-being.

On the other hand, apathetic individuals, who generally exhibit diminished motivation and responsiveness (43), tended to attribute outcomes more to stochasticity in our study. This perception may underlie their reduced exploratory behavior, reflecting a disengagement from active learning and adaptation. If outcomes seem random and beyond our control, expending energy to explore may seem futile, and focusing on what we know seems rational. While this approach may conserve energy, the inflexibility can perpetuate a cycle of disengagement and maintain apathetic symptoms (44,45). Apathetic individuals may fail to recognize the potential benefits of exploration and remain stuck in suboptimal decision-making patterns, further reinforcing their disengagement from the environment (4).

The dimensionality reduction of the behavioral sequence data using UMAP allowed us to examine the relationship between exploration and the estimation of volatility and stochasticity. Despite the intuitive connection between these 2 behavior models, their relationship has not been directly examined. Our results showed that exploration and uncertainty estimation were closely related to the 2 axes of a parabolic latent structure of explore-exploit trade-off in our task. As a result, both model-based metrics were necessary to characterize the spectrum of individual differences fully. Segmenting

the data on the manifold further illuminated the fine-grained interplay between affective states and exploratory behavior. The monotonically decreasing group ($n = 390$) (Figure 5H), characterized by relatively higher anxiety and lower apathy, showed higher overall exploration rates than the monotonically increasing group ($n = 611$), who had lower anxiety and higher apathy. Intriguingly, these groups exhibited opposing relationships between uncertainty estimation and exploration: within the decreasing group (left), higher (v/s) ratios were associated with decreased exploration, while within the increasing group (right), higher (v/s) ratios predicted increased exploration. This pattern suggests that the relationship between uncertainty estimation and exploratory behavior depends on an individual's mixed mental states. The shape from UMAP captures the nonlinear relationship between the ratio of volatility to stochasticity and exploration (Figure S13), raising important questions about how environmental volatility and stochasticity may affect exploration and its implications for mental health.

These results reconcile previously inconsistent findings regarding exploratory behavior in individuals with anxiety, with some studies showing more exploitative behavior (15,16) and others finding that higher anxiety predicted more exploratory behaviors (13,14). The relationship between perceived volatility and exploration is modulated by the degree of anxiety, with more severe anxiety potentially suppressing exploration as a form of avoidance. Conversely, moderate anxiety may drive exploration to gather information and reduce uncertainty, potentially easing discomfort. This dual response to perceived volatility underscores the complex interplay between anxiety levels, environmental perceptions, and behavioral strategies in managing emotional responses.

Our findings have implications for personalized behavioral interventions in mental health. For individuals with anxiety, therapies focusing on recalibrating volatility perceptions and improving uncertainty management may reduce worry and enhance decision making (46,47). Encouraging longer-term information integration could also benefit anxiety management (48). For apathetic individuals, strengthening perceived control and action efficacy may counteract stochasticity attribution. Incorporating these strategies into existing therapies such as behavioral activation and motivational interviewing (49) could promote balanced environmental perceptions and exploration.

The behavioral manifold (Figure 5) could predict and monitor treatment responses in patients. By tracking an individual's position on the manifold before and during treatment, clinicians may infer changes in anxiety, apathy, and associated behaviors. Key questions remain about the predictability of individual trajectories and whether clinical populations conform to the same manifold. Answering these questions could advance personalized neuropsychiatric care by offering a more nuanced approach to assessment and treatment based on individual behavioral patterns (50).

The observed effect sizes in the current study ($r \approx 0.10-0.16$) are consistent with recent recalibrations of effect size interpretation in individual differences research, where $r = 0.10$ is considered meaningful (51). These effects are comparable to well-established phenomena such as the effectiveness of antihistamines on allergy symptoms ($r = 0.11$) (52). While modest in isolation, such effects on exploratory decisions can

accumulate substantially over time, potentially contributing to the maintenance of anxiety or apathetic behaviors through persistent influence on decision making.

Conclusions

While our findings provide valuable insights into uncertainty processing mechanisms, we acknowledge that our sample may not fully represent individuals with clinical levels of anxiety and apathy, potentially limiting generalizability to diagnosed populations. Future research with clinical samples will be crucial to validate and extend these findings, strengthening their translational impact.

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The source scripts that were used to do data analysis are available on GitHub (https://github.com/hermandarrowlab/uncertainty_apathy_anxiety).

Data are available upon request.

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ARTICLE INFORMATION

From the Department of Psychiatry and Behavioral Sciences, University of Minnesota, Minneapolis, Minnesota (XY, ABH); Department of Neuroscience, Université de Montréal, Montreal, Quebec, Canada (RBE); Department of Psychology, University of Minnesota, Minneapolis, Minnesota (NG); and Department of Neurosurgery, University of Minnesota, Minneapolis, Minnesota (DPD).

DPD and ABH contributed equally to this work.

Address correspondence to Alexander B. Herman, M.D., Ph.D., at herma686@umn.edu.

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REFERENCES

1. Soltani A, Izquierdo A (2019): Adaptive learning under expected and unexpected uncertainty. *Nat Rev Neurosci* 20:635–644.
2. Piray P, Daw ND (2021): A model for learning based on the joint estimation of stochasticity and volatility. *Nat Commun* 12:6587.
3. Pulcu E, Browning M (2019): The mismeasurement of uncertainty in affective disorders. *Trends Cogn Sci* 23:865–875.
4. Husain M, Roiser JP (2018): Neuroscience of apathy and anhedonia: A transdiagnostic approach. *Nat Rev Neurosci* 19:470–484.
5. Marin RS (1996): Apathy: Concept, syndrome, neural mechanisms, and treatment. *Semin Clin Neuropsychiatry* 1:304–314.
6. Hezemans FH, Wolpe N, Rowe JB (2020): Apathy is associated with reduced precision of prior beliefs about action outcomes. *J Exp Psychol Gen* 149:1767–1777.
7. Scholl J, Trier HA, Rushworth MFS, Kolling N (2022): The effect of apathy and compulsion on planning and stopping in sequential decision-making. *PLoS Biol* 20:e3001566.
8. Huys QJM, Dayan P (2009): A Bayesian formulation of behavioral control. *Cognition* 113:314–328.
9. Browning M, Behrens TE, Jocham G, O'Reilly JX, Bishop SJ (2015): Anxious individuals have difficulty learning the causal statistics of aversive environments. *Nat Neurosci* 18:590–596.
10. Buhr K, Dugas MJ (2009): The role of fear of anxiety and intolerance of uncertainty in worry: An experimental manipulation. *Behav Res Ther* 47:215–223.
11. Gagne C, Zika O, Dayan P, Bishop SJ (2020): Impaired adaptation of learning to contingency volatility in internalizing psychopathology. *Elife* 9:e61387.
12. Hirsh JB, Mar RA, Peterson JB (2012): Psychological entropy: A framework for understanding uncertainty-related anxiety. *Psychol Rev* 119:304–320.
13. Aberg KC, Toren I, Paz R (2022): A neural and behavioral trade-off between value and uncertainty underlies exploratory decisions in normative anxiety. *Mol Psychiatry* 27:1573–1587.
14. Witte K, Wise T, Huys QJ, Schulz E (2024): Exploring the Unexplored: Worry as a Catalyst for Exploratory Behavior in Anxiety and Depression. *PsyArXiv* <https://doi.org/10.31234/osf.io/td8xh>.
15. Fan H, Gershman SJ, Phelps EA (2023): Trait somatic anxiety is associated with reduced directed exploration and underestimation of uncertainty. *Nat Hum Behav* 7:102–113.
16. Smith R, Taylor S, Wilson RC, Chunig AE, Persich MR, Wang S, Killgore WDS (2021): Lower levels of directed exploration and reflective thinking are associated with greater anxiety and depression. *Front Psychiatry* 12:782136.
17. Holthoff VA, Beuthien-Baumann B, Kalbe E, Lüdecke S, Lenz O, Zündorf G, et al. (2005): Regional cerebral metabolism in early Alzheimer's disease with clinically significant apathy or depression. *Biol Psychiatry* 57:412–421.
18. Wen MC, Chan LL, Tan LCS, Tan EK (2016): Depression, anxiety, and apathy in Parkinson's disease: Insights from neuroimaging studies. *Eur J Neurol* 23:1001–1019.
19. Steffens DC, Fahed M, Manning KJ, Wang L (2022): The neurobiology of apathy in depression and neurocognitive impairment in older adults: A review of epidemiological, clinical, neuropsychological and biological research. *Transl Psychiatry* 12:525.
20. Dan R, Ružička F, Bezdecik O, Ružička E, Roth J, Vymazal J, et al. (2017): Separate neural representations of depression, anxiety and apathy in Parkinson's disease. *Sci Rep* 7:12164.
21. Tinaz S, Kamel S, Aravala SS, Sezgin M, Elfil M, Sinha R (2021): Distinct neural circuits are associated with subclinical neuropsychiatric symptoms in Parkinson's disease. *J Neurol Sci* 423:117365.
22. Oosterwijk CS, Vriend C, Berendse HW, van der Werf YD, van den Heuvel OA (2018): Anxiety in Parkinson's disease is associated with reduced structural covariance of the striatum. *J Affect Disord* 240:113–120.
23. Seligman MEP (1975): Helplessness: On depression, development, and death. *A series of books in psychology*.
24. Chen CS, Knep E, Han A, Ebitz RB, Grissom NM (2021): Sex differences in learning from exploration. *Elife* 10:e69748.
25. Ebitz RB, Albaran E, Moore T (2018): Exploration disrupts choice-predictive signals and alters dynamics in prefrontal cortex. *Neuron* 97:450–461.e9.
26. Kask EA, Chen CS, Meyer C, Yang F, Ebitz B, Grissom N, et al. (2023): Prolonged physiological stress is associated with a lower rate of exploratory learning that is compounded by depression. *Biol Psychiatry Cogn Neurosci Neuroimaging* 8:703–711.
27. Piray P, Daw ND (2020): A simple model for learning in volatile environments. *PLoS Comput Biol* 16:e1007963.
28. Löwe B, Decker O, Müller S, Brähler E, Schellberg D, Herzog W, Herzberg PY (2008): Validation and standardization of the Generalized

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Anxiety Disorder Screener (GAD-7) in the general population. *Med Care* 46:266–274.

29. Ang Y-S, Lockwood P, Apps MAJ, Muhammed K, Husain M (2017): Distinct subtypes of apathy revealed by the apathy motivation index. *PLoS One* 12:e0169938.

30. Bari A, Theobald DE, Caprioli D, Mar AC, Aidoo-Micah A, Dalley JW, Robbins TW (2010): Serotonin modulates sensitivity to reward and negative feedback in a probabilistic reversal learning task in rats. *Neuropsychopharmacology* 35:1290–1301.

31. den Ouden HEM, Daw ND, Fernandez G, Elshout JA, Rijpkema M, Hoogman M, et al. (2013): Dissociable effects of dopamine and serotonin on reversal learning. *Neuron* 80:1090–1100.

32. Coelho JP, Pinho TM, Boaventura-Cunha J (2019): Hidden Markov Models: Theory and Implementation Using MATLAB®. Boca Raton, FL: CRC Press.

33. Cheng S, Zhou Y, Zhang W, Wu D, Yang C, Li B, Wang W (2022): Uncertainty-aware and multigranularity consistent constrained model for semi-supervised hashing. *IEEE Trans Circuits Syst Video Technol* 32:6914–6926.

34. Dayan P, Kakade S, Montague PR (2000): Learning and selective attention. *Nat Neurosci* 3:1218–1223.

35. Chakroun K, Mathar D, Wiesler A, Ganzer F, Peters J (2020): Dopaminergic modulation of the exploration/exploitation trade-off in human decision-making. *Elife* 9:e51260.

36. Piray P, Dezfouli A, Heskes T, Frank MJ, Daw ND (2019): Hierarchical Bayesian inference for concurrent model fitting and comparison for group studies. *PLoS Comput Biol* 15:e1007043.

37. Stephan KE, Penny WD, Daunizeau J, Moran RJ, Friston KJ (2009): Bayesian model selection for group studies. *Neuroimage* 46:1004–1017.

38. Hampton AN, Bossaerts P, O'Doherty JP (2006): The role of the ventromedial prefrontal cortex in abstract state-based inference during decision making in humans. *J Neurosci* 26:8360–8367.

39. Schlagenhauf F, Huys QJM, Deserno L, Rapp MA, Beck A, Heinze HJ, et al. (2014): Striatal dysfunction during reversal learning in unmedicated schizophrenia patients. *Neuroimage* 89:171–180.

40. RA Rescorla and Wagner (1972): A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: Black AH, Prokasy WF, editors. *Classical Conditioning II: Current Research and Theory*. New York: Appleton-Century-Crofts, 64–99.

41. McInnes L, Healy J, Saul N, Großberger L (2018): UMAP: Uniform Manifold Approximation and Projection. *J Open Source Softw* 3:861.

42. Grupe DW, Nitschke JB (2013): Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nat Rev Neurosci* 14:488–501.

43. Fahed M, Steffens DC (2021): Apathy: Neurobiology, assessment and treatment. *Clin Psychopharmacol Neurosci* 19:181–189.

44. Pagonabarraga J, Kulisevsky J, Strafella AP, Krack P (2015): Apathy in Parkinson's disease: Clinical features, neural substrates, diagnosis, and treatment. *Lancet Neurol* 14:518–531.

45. Pessiglione M, Vinckier F, Bouret S, Daunizeau J, Le Bouc R (2018): Why not try harder? Computational approach to motivation deficits in neuro-psychiatric diseases. *Brain* 141:629–650.

46. Beck JS (2011): *Cognitive Behavior Therapy: Basics and Beyond*. New York, NY: Guilford Press.

47. Craske MG, Mystkowski JL (2006): Exposure therapy and extinction: Clinical studies. In: Craske MG, Hermans D, Vansteenwegen D, editors. *Fear and Learning: From Basic Processes to Clinical Implications*. Washington: American Psychological Association, 217–233.

48. Aylward J, Valton V, Ahn WY, Bond RL, Dayan P, Roiser JP, Robinson OJ (2019): Altered learning under uncertainty in unmedicated mood and anxiety disorders. *Nat Hum Behav* 3:1116–1123.

49. Alexopoulos GS, Arean P (2014): A model for streamlining psychotherapy in the RDoC era: The example of "Engage". *Mol Psychiatry* 19:14–19.

50. Cuthbert BN, Insel TR (2013): Toward the future of psychiatric diagnosis: The seven pillars of RDoC. *BMC Med* 11:126.

51. Gignac GE, Szodorai ET (2016): Effect size guidelines for individual differences researchers. *Pers Individ Dif* 102:74–78.

52. Funder DC, Ozer DJ (2019): Evaluating effect size in psychological research: Sense and nonsense. *Adv Methods Pract Psychol Sci* 2:156–168.