Approach-avoidance reinforcement learning as a translational and computational model of anxiety-related avoidance

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Abstract

Although avoidance is a prevalent feature of anxiety-related psychopathology, differences in existing measures of avoidance between humans and non-human animals impede progress in its theoretical understanding and treatment. To address this, we developed a novel translational measure of anxiety-related avoidance in the form of an approach-avoidance reinforcement learning task, by adapting a paradigm from the non-human animal literature to study the same cognitive processes in human participants. We used computational modelling to probe the putative cognitive mechanisms underlying approach-avoidance behaviour in this task and investigated how they relate to subjective task-induced anxiety. In a large online study, participants (n = 372) who experienced greater task-induced anxiety avoided choices associated with punishment, even when this resulted in lower overall reward. Computational modelling revealed that this effect was explained by greater individual sensitivities to punishment relative to rewards. We replicated these findings in an independent sample (n = 627) and we also found fair-to-excellent reliability of measures of task performance in a sub-sample retested one week later (n = 57). Our findings demonstrate the potential of approach-avoidance reinforcement learning tasks as translational and computational models of anxiety-related avoidance. Future studies should assess the predictive validity of this approach in clinical samples and experimental manipulations of anxiety.

1   Introduction

Avoiding harm or potential threats is essential for our well-being and survival, but it can sometimes lead to negative consequences in and of itself. This occurs when avoidance is costly, that is, when the act to avoid harm or threat requires the sacrifice of something positive. When offered the opportunity to attend a job interview, for example, the reward of landing a new job must be weighed against the risk of experiencing rejection and/or embarrassment due to fluffing the interview. On balance, declining a single interview would likely have little impact on one's life, but routinely avoiding job interviews would jeopardise one's long-term professional opportunities. More broadly, consistent avoidance in similar situations, which are referred to as involving *approach-avoidance conflict*, can have an increasingly negative impact as the sum of forgone potential reward accumulates, ultimately leading one to missing out on important things in life. Such excessive avoidance is a hallmark symptom of pathological anxiety (Barlow, 2002) and avoidance biases during approach-avoidance conflict are thought to drive the development and maintenance of anxiety-related (Aupperle & Paulus, 2010; Hayes, 1976; Mkrtchian et al., 2017; Stein & Paulus, 2009; Struijs et al., 2018) and other psychiatric disorders (Aldao et al., 2010; Kakoschke et al., 2019).

How is behaviour during approach-avoidance conflict measured quantitatively? In non-human animals, this can be achieved through behavioural paradigms that induce a conflict between natural approach and avoidance drives. For example, in the 'Geller-Seifter conflict test' (Geller et al., 1962), rodents decide whether or not to press a lever that is associated with the delivery of both food pellets and shocks, thus inducing a conflict. Anxiolytic drugs typically increase lever-presses during the test (Treit et al., 2010), supporting its validity as a model of anxiety-related avoidance. Consequently, this test, along with others inducing approach-avoidance conflict are often used as non-human animal tests of anxiety (Griebel & Holmes, 2013). In humans, on the other hand, approach-avoidance conflict has traditionally been measured using questionnaires such as the Behavioural Inhibition/Activation Scale (Carver & White, 1994), or cognitive tasks that bear little semblance to those used in the non-human literature (Guitart-Masip et al., 2012; Kirlic et al., 2017; Mkrtchian et al., 2017).

Translational approaches, specifically when equivalent tasks are used to measure the same cognitive construct in humans and non-human animals, benefit the study of avoidance and its relevance to mental ill-health for two important reasons (Bach, 2021; Pike et al., 2021). First, precise causal manipulations of neural circuitry such as chemo-/optogenetics are only feasible in non-human animals, whereas only humans can verbalise their subjective experiences – it is only by using translational measures that we can integrate data and theory across species to achieve a

comprehensive mechanistic understanding. Second, translational paradigms can make the testing of

novel anxiolytic drugs more efficient and cost-effective, since those that fail to reduce anxiety-

related avoidance in humans could be identified earlier during the development pipeline.

Since the inception of non-human animal models of psychiatric disorders, researchers have

recognised that it is infeasible to fully recapitulate a disorder like generalised anxiety disorder in

non-human animals due to the complexity of human cognition and subjective experience. Instead,

the main strategy has been to reproduce the physiological and behavioural responses elicited under

certain scenarios across species, such as during fear conditioning (Craske et al., 2006; Milad & Quirk,

2012). Computational modelling of behaviour (Kriegeskorte & Douglas, 2018), allows us to take a

step further and probe the *mechanisms* underlying such physiological and behavioural responses,

using a mathematically principled approach. A fundamental premise of this approach is that the

brain acts as an information-processing organ that performs computations responsible for

observable behaviours. With respect to translational models, it follows that a valid translational

measure of some behaviour not only matches the observable responses across species, but also

their underlying computational mechanisms. This criterion, which has been termed *computational*

validity, has been proposed as the primary basis for evaluating the validity of translational measures

(Redish et al., 2022).

To exploit the advantages of translational and computational approaches, there has been a recent

surge in efforts to create relevant approach-avoidance conflict tasks in humans based on non-human

animal models (referred to as back-translation; Kirlic et al., 2017). One stream of research has

focused on exploration-based paradigms, which involve measuring how participants spend their

time in environments that include potentially anxiogenic regions. Rodents typically avoid such

regions, which can take the form of tall, exposed platforms as in the elevated plus maze (Pellow et

al., 1985), or large open spaces as in the open-field test (Hall, 1934). Similar behaviours have been

observed in humans when virtual-reality was used to translate the elevated plus maze (Biedermann

et al., 2017), and when participants were free to walk around a field or around town (Walz et al.,

2016). These translational tasks have excellent face validity in that they involve almost identical

behaviour compared to their non-human analogues, and their predictive validity is supported by

findings that individual differences in self-reported anxiety are associated with greater avoidance of

the exposed/open regions of space (Biedermann et al., 2017; Walz et al., 2016). But what of their

computational validity? The computations underlying free movement are difficult to model as the

action-space is large and complex (consisting of 2-dimensional directions, velocity, etc.), which

makes it difficult to understand the precise cognitive mechanisms underlying avoidance in these

tasks.

Other studies have designed tasks that emulate operant conflict paradigms in which non-human

participants learn to associate certain actions with both reward and punishment, such as the Geller-

Seifter and Vogel conflict tests (Geller et al., 1962; Vogel et al., 1971). These studies used decision-

making tasks in which participants choose between offers consisting of both reward and punishment

outcomes (Aupperle et al., 2011; Sierra-Mercado et al., 2015). The strengths of such decision tasks

lie in the simplicity of their action-space (accept/reject an offer; choose offer A or B), which

facilitates the computational modelling of decision-making, through for example value-based logistic

regression models (Ironside et al., 2020) or drift-diffusion modelling (Pedersen et al., 2021).

However, these tasks have less face validity compared to exploration-based tasks, as explicit offers

('Will you accept £1 to incur an electric shock?') are incomprehensible to the majority of non-human

animals (although non-human primates can be trained to do so, see: Ironside et al., 2020; Sierra-

Mercado et al., 2015). Instead, non-human participants such as rodents typically have to learn the

possible outcomes given their actions, for example that a lever-press is associated with both food

pellets and electric shocks. Critically, this means that humans performing offer-based decision-

making are doing something *computationally dissimilar* to non-human participants during operant

conflict tasks, and the criterion of computational validity is unmet.

Therefore, in the current study, we developed a novel translational task that was specifically

designed to mimic the computational processes involved in non-human operant conflict tasks, and

was also amenable to computational modelling of behaviour. During the task, participants chose

between options that were asymmetrically associated with rewards and punishments, such that the

more rewarding options were more likely to result in punishment. However, in contrast to previous

translations of these tests using purely offer-based designs, participants had to learn the likelihoods

of receiving rewards and/or punishments from experience, thus ensuring computational validity.

Preserving the element of learning in our translational task did not necessarily risk confounding the

study of approach-avoidance behaviour. Rather, a critical advantage of our approach was that we

could model the cognitive processes underlying approach-avoidance behaviour using classical

reinforcement learning algorithms (Sutton & Barto, 2018), and then use these algorithms to

disentangle the relative contributions of learning and value-based decision-making to anxiety-

related avoidance. Specifically, using the reinforcement learning framework; we accounted for

individual differences in learning by estimating learning rates, which govern the degree to which

recently observed outcomes affect subsequent actions; and we explained individual differences in

value-based decision-making using outcome sensitivity parameters, which model the subjective

values of rewards and punishments for each participant.

We therefore aimed to develop a new translational measure of approach avoidance conflict. Based

on previous findings that anxiety predicts avoidance biases under conflict (Biedermann et al., 2017;

Walz et al., 2016), we predicted that anxiety would increase avoidance responses (and conversely

decrease approach responses) and that this would be reflected in changes in computational

parameters. Having found evidence for this in a large initial online study, we retested the prediction

that anxiety-related avoidance is explained by greater sensitivity to punishments relative to rewards

in in a pre-registered independent replication sample.

137 2 Results

138 2.1 The approach-avoidance reinforcement learning task

We developed a novel approach-avoidance conflict task, based on the "restless bandit" design (Daw

et al., 2006), in which participants' goal was to accrue rewards whilst avoiding punishments (Figure

1a). On each of 200 trials, participants chose one of two options, depicted as distinct visual stimuli,

to obtain certain outcomes. There were four possible outcomes: a monetary reward (represented by

a coin); an aversive sound consisting of a combination of a female scream and a high-pitched sound;

both the reward and aversive sound; or no reward and no sound (Figure 1b). The options were

asymmetric in their associated outcomes, such that one option (which we refer to as the 'conflict'

option) was associated with both the reward and aversive sound, whereas the other (the 'safe'

option) was only associated with the reward (Figure 1c). In other words, choosing the conflict option

could result in any of the four possible outcomes on any given trial, but the safe option could only

lead to either the reward or no reward, and never the aversive sounds.

The probability of observing the reward and the aversive sound at each option fluctuated randomly

and independently over trials, except the probability of observing the aversive sound at the safe

option, which was set to 0 across all trials (Figure 1c). On average, the safe option was less likely to

produce the reward compared to the conflict option across the task (Figure 1d). Therefore, we

induced an approach-avoidance conflict between the options as the conflict option was generally

more rewarding but also more likely to result in punishment. Participants were not informed about

this asymmetric feature of the task, but they were told that the probabilities of observing the reward

or the sound were independent and that they could change across trials.

We initially investigated behaviour in the task in a discovery sample (n = 369) after which the key

effects-of-interest were retested in a pre-registered study (https://osf.io/8dm95) with an

independent replication sample (n = 629). Since our findings were broadly comparable across

samples, we primarily report findings from the discovery sample and discuss deviations from these

 findings in the replication sample. A detailed comparison of statistical findings across samples is

163 reported in the Supplement.

Figure 1. The approach-avoidance reinforcement learning task. a, Trial timeline. A fixation cross initiates the trial. Participants are presented with two options for up to 2 s, from which they choose one. The outcome is then presented for 1 s. **b**, Possible outcomes. There were four possible outcomes: 1) no reward and no aversive sound; 2) a reward and no aversive sound; 3) an aversive sound and no reward; or 4) both the reward and the aversive sound. **c**, Probabilities of observing each outcome given the choice of option. Unbeknownst to the participant, one of the options (which we refer to as the 'conflict' option - solid lines) was generally more rewarding compared to the other option (the 'safe' option – dashed line) across trials. However, the conflict option was also the only option of the two that was associated with a probability of producing an aversive sound (the probability that the safe option produced the aversive sound was 0 across all trials). The probabilities of observing each outcome given the choice of option fluctuated randomly and independently across trials. The correlations between these dynamic probabilities were negligible (mean Pearson's r = 0.06). **d**, Distribution of outcome probabilities by option and outcome. On average, the conflict option was more likely to produce a reward than the safe option. The conflict option had a variable probability of producing the aversive sound across trials, but this probability was always 0 for the safe option.

164 2.2 Choices reflect both approach and avoidance

First, we verified that participants demonstrated both approach and avoidance responses during the

task through a hierarchical logistic regression model, in which we used the latent outcome

probabilities to predict trial-by-trial choice. Overall, participants learned to optimise their choices to

accrue rewards and avoid the aversive sounds. As expected, across trials participants chose (i.e.

approached) the option with relatively higher reward probability ($\beta = 0.98 \pm 0.03$, $p < 0.001$; Figure

2a, c). At the same time, they avoided the conflict option when it was more likely to produce the

punishment ($\beta = -0.33 \pm 0.04$, $p < 0.001$; Figure 2a, d). These effects were also clearly evident in our

replication sample (effect of relative reward probability: $\beta = 0.95 \pm 0.02$, $p < 0.001$; effect of

punishment probability: $\beta = -0.52 \pm 0.03$, $p < 0.001$; Supplementary Table 1).

2.3 Task-induced anxiety is associated with greater avoidance

Immediately after the task, participants rated their task-induced anxiety in response to the question, 'How anxious did you feel during the task?', from 'Not at all' to 'Extremely' (scored from 0 to 50). On average, participants reported a moderate level of task-induced anxiety (mean rating of 21, SD = 14; Figure 2b).

Task-induced anxiety was significantly associated with multiple aspects of task performance. At the most basic level, task-induced anxiety was correlated with the proportion of conflict/safe option choices made by each participant across all trials, with greater anxiety corresponding to a preference for the safe option over the conflict option (permutation-based non-parametric correlation test: Kendall's τ = - 0.074, p = 0.033), at the cost of fewer rewards on average.

To investigate this association further, we included task-induced anxiety into the hierarchical logistic regression model of trial-by-trial choice. Here, task-induced anxiety significantly interacted with punishment probability (β = -0.10 ± 0.04, p = 0.022; Figure 2a), such that more anxious individuals were proportionately less willing to choose the conflict option during times it was likely to produce the punishment, relative to less-anxious individuals (Figure 2e). This explained the effect of anxiety on choices, as the main effect of anxiety was not significant in the model, although it was when the interaction effects were excluded. The analogous interaction between task-induced anxiety and

Figure 2. Predictors of choice in the approach-avoidance reinforcement learning task. a, Coefficients from the mixed-effects logistic regression of trial-by-trial choices in the task. On any given trial, participants chose the option that was more likely to produce a reward. They also avoided choosing the conflict option when it was more likely to produce the punishment. Task-induced anxiety significantly interacted with punishment probability. Significance levels are shown according to the following: $p < 0.05$ - *; $p < 0.05$ - **; $p < 0.001$ - ***. **b**, Subjective ratings of task-induced anxiety, given on a scale from 'Not at all' (0) to 'Extremely' (50). **c**, On each trial, participants were likely to choose the option with greater probability of producing the reward. **d**, Participants tended to avoid the conflict option when it was likely to produce a punishment. **e**, Compared to individuals reporting lower anxiety during the task, individuals experiencing greater anxiety showed greater avoidance of the conflict option, especially when it was more likely to produce the punishment. *Note*. For visualisation purposes, the continuous predictors (based on the latent outcome probabilities or task-induced anxiety) were categorised into discrete bins. Mean probabilities of choosing the conflict arm across the sample are plotted with standard errors.

relative reward probability was non-significant (β = -0.06 ± 0.03, *p* = 0.074, Figure 2a).

These associations with task-induced anxiety were again clearly evident in the replication sample

(correlation between task-induced anxiety and proportion of conflict/safe option choices: τ = -0.075,

p = 0.005; interaction between task-induced anxiety and punishment probability in the hierarchical

model: β = -0.23 ± 0.03, *p* < 0.001; Supplementary Table 1).

2.4   A reinforcement learning model explains individual choices

Next, we investigated the putative cognitive mechanisms driving behaviour on the task by fitting

standard reinforcement learning models to trial-by-trial choices. The winning model in both the

discovery and replication samples included reward- and punishment-specific learning rates, and

reward- and punishment-specific sensitivities (i.e. four parameters in total; Figure 3a, b). Briefly, it

models participants as learning four values, which represent the probabilities of observing each

outcome (reward/punishment) for each option (conflict/safe). At every trial, the probability

estimates for the chosen option are updated after observing the outcome(s) according to the

Rescorla-Wagner update rule. Individual differences in the rate of updating are captured by the

learning rate parameters (α^r, α^p), whereas differences in the extent to which each outcome impacts

choice are captured by the sensitivity parameters (β^r, β^p).

To assess how well this model captured our observed data, we simulated data from the model given

each participant's parameter values, choices and observed outcomes. These synthetic choice data

Figure 3. Computational modelling of approach-avoidance reinforcement learning. a, Model comparison results. The difference in integrated Bayesian Information Criterion scores from each model relative to the winning model is indicated on the x-axis. The winning model included specific learning rates for reward (α^R) and punishment learning (α^p), and specific outcome sensitivity parameters for reward (β^R) and punishment (β^P). Some models were tested with the inclusion of a lapse term (ξ). **b**, Distributions of individual parameter values from the winning model. **c**, The winning model was able to reproduce the proportion of conflict option choices over all trials in the observed data with high accuracy (observed vs predicted data r = 0.97). **d**, The distribution of the reward-punishment sensitivity index – the computational measure of approach-avoidance bias. Higher values indicate approach biases, whereas lower values indicate avoidance biases.

were qualitatively similar to the actual choices made by the participants (Figure 3c). Parameter

recovery from the winning model was excellent (Pearson's r between data generating and recovered

parameters ≈ 0.77 to 0.86; Supplementary Figure 3).

To quantify individual approach-avoidance bias computationally, we calculated the ratio between

the reward and punishment sensitivity parameters (β^r / β^p). As the task requires simultaneously

balancing reward pursuit (i.e., approach) and punishment avoidance, this composite measure

provides an index of where an individual lies on the continuum of approach vs avoidance, with

higher and lower values indicating approach and avoidance biases, respectively. We refer to this

measure as the 'reward-punishment sensitivity index' (Figure 3d).

2.5   Computational mechanisms of anxiety-related avoidance

We assessed the relationship between task-induced anxiety and individual model parameters

through permutation testing of non-parametric correlations, since the distribution of task-induced

anxiety was non-Gaussian. The punishment learning rate and reward-punishment sensitivity index

were significantly and negatively correlated with task-induced anxiety in the discovery sample

(punishment learning rate: Kendall's τ = -0.088, *p* = 0.015; reward-punishment sensitivity index : τ = -

0.099, *p* = 0.005; Figure 4a-e). These associations were also significant in the replication sample

(punishment learning rate: τ = -0.064, *p* = 0.020; reward-punishment sensitivity index : τ = -0.096, *p* <

0.001), with an additional positive correlation between punishment sensitivity and anxiety (τ =

0.076, *p* = 0.004; Supplementary Table 1) which may have been detected due to greater statistical

power. The learning rate equivalent of the reward-punishment sensitivity index (i.e., α^r/α^p) did not

significantly correlate with task-induced anxiety (discovery sample: τ = 0.048, *p* = 0.165; replication

sample: τ = 0.029, *p* = 0.298).

Given that both the punishment learning rate and the reward-punishment sensitivity index were

significantly and reliably correlated with task-induced anxiety, we next asked whether these

computational measures explained the effect of anxiety on avoidance behaviour. We tested this via

structural equation modelling, including both the punishment learning rate and reward-punishment

sensitivity index as parallel mediators for the effect of task-induced anxiety on proportion of choice

for conflict/safe options. This suggested that the mediating effect of the reward-punishment

sensitivity index (standardised β = -0.009 ± 0.003, *p* = 0.003) was over four times larger than the

mediating effect of the punishment learning rate, which did not reach the threshold as a significant

mediator (standardised β = -0.002 ± 0.001, *p* = 0.052; Figure 4f). A similar pattern was observed in

the replication sample (mediating effect of reward-punishment sensitivity index: standardised β = -

0.009 ± 0.002, *p* < 0.001; mediating effect of punishment learning rate: standardised β = -0.001 ±

Figure 4. Relationships between task-induced anxiety, model parameters and avoidance. a, Task-induced anxiety was negatively correlated with the punishment learning rate. **b**, Task-induced anxiety was also negatively correlated with reward-punishment sensitivity index. Kendall's tau correlations and approximate Pearson's r equivalents are reported above each figure. **c**, The mediation model. Mediation effects were assessed using structural equation modelling. Bold terms represent variables and arrows depict regression paths in the model. The annotated values next to each arrow show the regression coefficient associated with that path, denoted as *coefficient (standard error)*. Only the reward-punishment sensitivity index significantly mediated the effect of task-induced anxiety on avoidance. Significance levels in all figures are shown according to the following: *p* < 0.05 - *; *p* < 0.05 - **; *p* < 0.001 - ***.

0.0003, p = 0.132; Supplementary Table 1. Supplementary Figure 2).

This analysis reveals two effects: first, that individuals who reported feeling more anxious during the

task were slower to update their estimates of punishment probability; and second, more anxious

individuals placed a greater weight on the aversive sound *relative to the reward* when making their

decisions, meaning that the potential for a reward was more strongly offset by potential for

punishment. Critically, the latter but not the former effect explained the effect of task-induced

anxiety on avoidance behaviour, thus providing an important insight into the computational

mechanisms driving anxiety-related avoidance.

2.6   Psychiatric symptoms predict task-induced anxiety, but not avoidance

We assessed the clinical potential of the novel measure by investigating how model-agnostic and

computational indices of behaviour correlate with self-reported psychiatric symptoms of anxiety,

depression and experiential avoidance; the latter indexes an unwillingness to experience negative

emotions/experiences (Hayes et al., 1996). We included experiential avoidance as a direct measure

of avoidance symptoms/beliefs, given that our task involved avoiding stimuli inducing negative

affect. Given that we recruited samples without any inclusion/exclusion criteria relating to mental

health, the instances of clinically-relevant anxiety symptoms, defined as a score of 10 or greater in

the Generalised Anxiety Disorder 7-item scale (Spitzer et al., 2006), were low in both the discovery

(16%, 60 participants) and the replication sample (20%, 127 participants).

Anxiety, depression and experiential avoidance symptoms were all significantly and positively

correlated with task-induced anxiety (p < 0.001; Supplementary Table 1). Only experiential

avoidance symptoms were significantly correlated with the proportion of conflict/safe option

choices (τ = -0.059, p = 0.010; Supplementary Table 1), but this effect was not observed in the

replication sample (τ = -0.029, p = 0.286). Experiential avoidance was also significantly correlated

with punishment learning rates (Kendall's τ = -0.09, p = 0.024) and the reward-punishment sensitivity

index (τ = -0.09, p = 0.034) in the discovery sample. However, these associations were non-significant

in the replication sample (p > 0.3), and no other significant correlations were detected between the

psychiatric symptoms and model parameters (Supplementary Table 1).

2.7   Test-retest reliability

We assessed the test-retest reliability of the task by retesting 57 participants from the replication

sample at least 10 days after they initially completed the task. The retest version of the task was

identical to the initial version, except for the use of new stimuli to represent the conflict and safe

options and different latent outcome probabilities to limit practise effects. The test-retest reliability

of model-agnostic effects was assessed using the intra-class correlation (ICC) coefficient, specifically

ICC(3,1) (following the notation of Shrout & Fleiss, 1979). Test-retest reliability of the model

parameters was assessed by calculating Pearson correlations derived from the parameter covariance

matrix with both sessions included in the model, following a previous approach recently shown to

accurately estimate parameter reliability (Waltmann et al., 2022). We interpreted indices of

reliability based on conventional values of < 0.40 as poor, 0.4 - 0.6 as fair, 0.6 - 0.75 as good, and >

0.75 as excellent reliability (Fleiss, 1986).

Task-induced anxiety, overall proportion of conflict option choices and the model parameters

demonstrated fair to excellent reliability (reliability indices ranging from 0.4 to 0.77; Supplementary

Figure 4), except for the punishment learning rate which showed a model-derived reliability of r = -

0.45. Practise effects analyses showed that task induced anxiety and the punishment learning rate

were also significantly lower in the second session (anxiety: t_{56} = 2.21, p = 0.031; punishment

learning rate: t_{56} = 2.24, p = 0.029), whilst the overall probability of choosing the conflict option and

the other parameters did not significantly change over sessions (Supplementary Figure 5). As the

dynamic (latent) outcome probabilities were different across the test *vs.* retest sessions, in other

words participants were not performing the exact same task across sessions, we argue that even

'fair' reliability (i.e., estimates in range of 0.4 to 0.6) is encouraging, as this suggests that model

parameters generalise across different environments if the required computations are preserved.

However, potential within-subjects inferences based on the punishment learning rate may not be

justified in this task.

294   3   Discussion

To develop a translational and computational model of anxiety-related avoidance, we created a

novel task that involves learning under approach-avoidance conflict and investigated the impact of

anxiety on task performance. Importantly, we show that individuals who experienced more task-

induced anxiety avoid actions that lead to aversive outcomes, at the cost of potential reward.

Computational modelling of behaviour revealed that this was explained by relative sensitivity to

punishment over reward. However, this effect was limited to task-induced anxiety, and was only

evident on a self-report measure of *general* avoidance in our first sample. Finally, test-retest

analyses of the task indicated fair-to-excellent reliability indices of task behaviour and model

parameters. These results demonstrate the potential of approach-avoidance reinforcement learning

tasks as translational measures of anxiety-related avoidance.

We can evaluate the translational validity of our task based on the criteria of face, construct,

predictive and computational validity (Redish et al., 2022; Willner, 1984). The task shows sufficient

face validity when compared to the Vogel/Geller-Seifter conflict tests; the design involves a series of

choices between an action associated with high reward and punishment, or low reward and no

punishment, and these contingencies must be learned. One potentially important difference is that

our task involved a choice between two active options, referred to as a two-alternative forced choice

(2AFC), whereas in the Vogel/Geller-Seifter tests, animals are free to perform an action (e.g. press

the lever) or withhold the action (don't press the lever; i.e. a go/no-go design). The disadvantage of

the latter approach is that human participants can and typically do show motor response biases (i.e.

for either action or inaction), which can confound value-based response biases with approach or

avoidance (Guitart-Masip et al., 2012). Fortunately, there is ample evidence that rodents can

perform 2AFC learning (Metha et al., 2020) and conflict tasks (Glover et al., 2020; Oberrauch et al.,

2019; Simon et al., 2009). That avoidance responses were positively associated with task-induced

anxiety also lends support for the construct validity of our measure, given the theoretical links

between anxiety and avoidance under approach-avoidance conflict (Aupperle & Paulus, 2010; Hayes,

1976; Stein & Paulus, 2009). However, we note that the empirical effect size was small ($|r| \sim 0.13$) -

we discuss potential reasons for this below.

The predictive and computational validity of the task needs to be determined in future work.

Predictive validity can be assessed by investigating the effects of anxiolytic drugs on task behaviour.

Reduced avoidance after anxiolytic drug administration, or indeed any manipulation designed to

reduce anxiety, would support our measure's predictive validity. Similarly, computational validity

would also need to be assessed directly in non-human animals by fitting models to their behavioural

data. At the same time, we are encouraged by our finding that the winning computational model in

our study relies on a relatively simple classical reinforcement learning strategy. There exist many

studies showing that non-human animals rely on similar strategies during reward and punishment

learning (Mobbs et al., 2020; Schultz, 2013); albeit to our knowledge this has never been modelled in

non-human animals where rewards and punishment can occur simultaneously.

One benefit of designing a task amenable to the computational modelling of behaviour was that we

could extract model parameters that represent individual differences in precise cognitive

mechanisms. Our model recapitulated individual- and group-level behaviour with high fidelity, and

mediation analyses revealed a mechanism of how anxiety induces avoidance, namely through the

relative sensitivity to punishment compared to reward. This demonstrates the potential of

computational methods in allowing for mechanistic insights into anxiety-related avoidance. Further,

we found satisfactory test-retest reliability of the reward-punishment sensitivity index in test-retest

analyses, suggesting that the task can be used for within-subject experiments (e.g. on/off

medication) to assess the impact of interventions on the mechanisms underlying avoidance.

The composite nature of the reward-punishment sensitivity index may be important for

contextualising prior results of anxiety and outcome sensitivity. The traditional view has long been

that anxiety is associated with greater automatic sensitivity to punishments and threats (i.e. that

anxious individuals show a negative bias in information processing; Bishop, 2007), due to amygdala

hypersensitivity (Hartley & Phelps, 2012; Mathews & Mackintosh, 1998). However, subsequent

studies have found inconsistent findings relative to this hypothesis (Bishop & Gagne, 2018). We

found that, rather than a straightforward link between anxiety and punishment sensitivity, the

relative sensitivity to punishment over reward provided a better explanation of anxiety's effect on

behaviour. This effect is more in keeping with cognitive accounts of anxiety's effect on information

processing that involve higher-level cognitive functions such as attention and cognitive control,

which propose that anxiety involves a global reallocation of resources away from processing positive

and towards negative information (Beck & Clark, 1997; Cisler & Koster, 2010; Robinson et al., 2013),

possibly through prefrontal control mechanisms (Carlisi & Robinson, 2018). Future studies using

experimental manipulations of anxiety will be needed to test the causal role of anxiety on relative

sensitivities to punishments versus rewards.

Since we developed our task with the primary focus on translational validity, its design diverges from

other reinforcement learning tasks that involve reward and punishment outcomes. One important

difference is that we used distinct reinforcers as our reward and punishment outcomes, compared

to many studies which use monetary outcomes for both (e.g. earning and losing £1 constitute the

reward and punishment, respectively; Aylward et al., 2019; Pizzagalli et al., 2005; Sharp et al., 2022).

Other tasks have been used that induce a conflict between value and motor biases, relying on

prepotent biases to approach/move towards rewards and withdraw from punishments, which

makes it difficult to approach punishments and withdraw from rewards (Guitart-Masip et al., 2012;

Mkrtchian et al., 2017). However, since translational operant conflict tasks typically induce a conflict

between different types of outcome (e.g. food and shocks), we felt it was important to implement

this feature. One study used monetary rewards and shock-based punishments, but also included

four options for participants to choose from on each trial, with rewards and punishments associated

with all four options (Seymour et al., 2012). This effectively requires participants to maintain eight

probability estimates (i.e. reward and punishment at each of the four options) to solve the task,

which may be too difficult for non-human animals to learn efficiently. Notably, although a recent

computational meta-analysis of reinforcement learning studies showed that symptoms of anxiety

and depression are associated with elevated punishment learning rates (Pike & Robinson, 2022), we

did not observe this pattern in our data. Indeed, we even found the contrary effect in relation to

task-induced anxiety, specifically that anxiety was associated with lower punishment learning rates,

as has previously been reported in relation to state somatic anxiety (Wise & Dolan, 2020). The

reason for this difference is likely that parameter values are highly dependent on task design

(Eckstein et al., 2022) and that studies to date have optimised designs that are sensitive to learning

rate differences (Pike & Robinson, 2022).

One potentially important limitation of our findings is that the effect size of the correlation between

task-induced anxiety and avoidance was small. This may have been due to the aversiveness of the

punishment outcomes (aversive sounds) used in our study, compared to other studies which

included aversive images (Aupperle et al., 2011), shocks (Talmi et al., 2009), or used virtual reality

(Biedermann et al., 2017) to provide negative reinforcement. Using more salient punishments would

likely produce larger effects. Further, whilst we included tests to check whether participants were

wearing headphones for this online study, we could not be certain that the sounds were not played

over speakers and/or played at a sufficiently high volume to be aversive. Finally, it may simply be

that the relationships between psychiatric symptoms and behaviour are small due to the inherent

variability of individuals, the lack of precision of self-reported symptoms or the unreliability of

mental health diagnoses (Freedman et al., 2013; Wise et al., 2022). Despite these limitations, an

advantage of using web-based auditory stimuli is their efficiency in scaling with sample size, as only a

web-browser is needed to complete the task. This is especially relevant for psychiatric research,

given the need for studies with larger sample sizes in the field (Rutledge et al., 2019).

Furthermore, the punishment learning rate was severely unreliable given a model-derived

correlation across sessions of r = -0.45, whereas the other indices of task performance showed fair-

to-excellent reliability. This might be a result of practise effects, where participants learned about

the punishments differently across sessions, but not about the rewards. However, given that the

sensitivity parameters were more important for explaining how anxiety affected avoidance, the low

observed reliability of the punishment learning rate may not present a barrier for future use of this

task in repeated-measures designs.

We also did not find any significant correlations between task performance and clinical symptoms of

anxiety, which raises questions around the predictive validity of the task. Since we recruited

participants without imposing any inclusion/exclusion criteria relating to mental health, this may be

due to the low level of clinically-relevant symptoms in the data. Further studies in samples with high

levels of anxiety or examining individuals at the extreme ends of symptom distributions may be

more sensitive in assessing predictive validity.

4 Conclusion

Avoidance is a hallmark symptom of anxiety-related disorders and there is a need for better translational models of avoidance. In our novel translational task designed to involve the same computational processes as those involved in non-human animal tests, anxiety was reliably induced, associated with avoidance behaviour, and linked to a computational model of behaviour. We hope that similar approaches will facilitate progress in the theoretical understanding of avoidance and ultimately aid in the development of novel anxiolytic treatments for anxiety-related disorders.

5 Methods

5.1 Participants

We recruited participants from Prolific (www.prolific.co). Participants had to be aged 18-60, speak English as their first language, have no language-related disorders/literacy difficulties, have no vision/hearing difficulties/have no mild cognitive impairment or dementia, and be resident in the UK. Participants were reimbursed at a rate of £7.50 per hour, and could earn a bonus of up to an additional £7.50 per hour based on their performance on the task. The study had ethical approval from the University College London Research Ethics Committee (ID 15253/001).

We first recruited a discovery sample to investigate whether anxiety was associated with avoidance in the novel task. We conducted an a priori power analysis to detect a minimally-interesting correlation between anxiety and avoidance of r = 0.15 (alpha$_{\text{two-tailed}}$ = 0.05, power = 0.80), resulting in a required sample size of 346. We aimed to replicate our initial finding (that task-induced anxiety was associated with the model-derived measure of approach-avoidance bias) in a replication sample. In the initial sample, the size of this effect was Kendall's tau = 0.099, which approximates to a Pearson's r of 0.15 - this was the basis for the power analysis for the replication sample. Therefore, the power analysis was configured to detect a correlation of r = 0.15 (alpha$_{\text{one-tailed}}$ = 0.05, power = 0.95), resulting in a required sample size of n = 476. A total of 423 participants completed the initial study (mean age = 38, SD = 10, 59% female), and 726 participants completed the replication study (mean age = 34, SD = 10, 51% female).

5.2 Headphone screen and calibration

We used aversive auditory stimuli as our punishments in the reinforcement learning task, which consisted of combinations of female screams and high-frequency tones that were individually rated as highly aversive in a previous online study (Seow & Hauser, 2022). The stimuli can be found online at https://osf.io/m3zev/. To maximise their aversiveness, we asked participants to use headphones whilst they completed the task. All participants completed an open-source, validated auditory

discrimination task (Woods et al., 2017) to screen out those who were unlikely to be using

headphones. Participants could only continue to the main task if they achieved an accuracy

threshold of five out of six trials in this screening task.

To further increase the aversiveness of the punishments, we wanted each participant to hear them

at a loud volume. We initially used a calibration task to increase the system volume and

implemented attention checks in the main task to ensure that participants had kept the volume at a

sufficiently high level during the task (see below). Before beginning the calibration task, participants

were advised to set their system volume to around 10% of the maximum possible. Then, we

presented two alternating auditory stimuli: a burst of white noise which was set to have the same

volume as the aversive sounds in the main task, and a spoken number played at a lower volume to

one ear ('one', 'two' or 'three'; these stimuli are also available online at https://osf.io/m3zev/). We

instructed participants to adjust their system volume so that the white noise was loud but

comfortable. At the same time, they also had to press the number key on their keyboard

corresponding to the number spoken between each white noise presentation. The rationale for the

difference in volume was to fix a lower boundary for each participant's system volume, so that the

volume of the punishments presented in the main task was locked above this boundary. We used

the white noise as a placeholder for the punishments to limit desensitisation.

5.3   The approach-avoidance reinforcement learning task

We developed a novel task on which participants learned to simultaneously pursue rewards and

avoid punishments. On each trial, participants had 2 s to choose one of two option, depicted as

distinct visual stimuli (Figure 2a), using the left/right arrow keys on their keyboard. The chosen

option was then highlighted by a white border, and participants were presented with the outcome

for that trial for 2 s. This could be one of 1) no outcome, 2) a reward (an animated coin image), 3) a

punishment (an aversive sound), or 4) both the reward and punishment. We incentivised

participants to collect the coins by informing them that they could earn a bonus payment based on

the number of coins earned during the task. If no choice was made, the text 'Too slow!' was shown

for 2s and the trial was skipped. Participants completed 200 trials which took 10 mins on average

across the sample. Each option was associated with separate probabilities of producing the

reward/aversive sound outcomes (Figure 2B), and these probabilities fluctuated randomly over

trials. Both options were associated with the reward, but only one was associated with the

punishment (i.e., the 'conflict' option could produce both rewards and punishments, but the 'safe'

option could produce only rewards and never punishments). When asked to rate the unpleasantness

of the punishments from 'Not at all' to 'Extremely' (scored from 0 to 50, respectively), participants

gave a mean rating of 31.7 (SD = 12.8).

The latent outcome probabilities were generated as decaying Gaussian random walks in a similar

fashion to previous restless bandit tasks (Daw et al., 2006), where the probability, p, of observing

outcome, o, at option, i, on trial, t, drifted according to the following:

$$p_{i,o}(t + 1) = \lambda p_{i,o}(t) + (1 - \lambda)\theta + e$$

$$e \sim N(0, 0.04^2)$$

The decay parameter, λ, was set to 0.97, which pulled all values towards the decay centre θ, which

was set to 0.5. The random noise, e, added on each trial was drawn from a zero-mean Gaussian with

a standard deviation of 0.04. All probabilities of observing the reward at the safe option were scaled

down by a factor of 0.7 so that it was less rewarding than the conflict option, on average. We

initialised each walk at the following values: conflict option reward probability – 0.7, safe option

reward probability – 0.35, conflict option punishment probability – 0.2. We only used sets of latent

outcome probabilities where the cross-correlations across each probability walk was below 0.3. A

total of four sets of outcome probabilities were used across our studies – they are available online at

https://osf.io/m3zev/.

We implemented three auditory attention checks during the main task, to ensure that participants

were still using an appropriate volume to listen to the auditory stimuli. As participants could

potentially mute their device during the outcome phase of the trial only (i.e. only when the aversive

sounds could occur), the timing of these checks had to coincide with moment of outcome

presentation. Therefore, we implemented these checks at the outcome phase of two randomly

selected trials where the participants' choices led to no outcome (no reward or punishment), and

also once at the very end of the task. Specifically, we played one of the spoken numbers used during

the calibration task (see above) and the participant had 2.5 s to respond using the corresponding

number key on their keyboard.

Immediately after the task and the final attention check, we obtained subjective ratings about the

task using the following questions: "How unpleasant did you find the sounds?" and "How anxious did

you feel during the task?". Responses were measured on a continuous slider ranging from 'Not at all'

(0) to 'Extremely' (50).

5.4   Data cleaning

As the task was implemented online where we could not ensure the same testing standards as we

could in-person, we used three exclusion criteria to improve data quality. Firstly, we excluded

participants who missed a response to more than one auditory attention check (see above) – as

these occurred infrequently and the stimuli used for the checks were played at relatively low

volume, we allowed for incorrect responses as long as a response was made. Secondly, we excluded

those who responded with the same response key on 20 or more consecutive trials (> 10% of all

trials). Lastly, we excluded those who did not respond on 20 or more trials. We excluded 51 out of

423 (12%) in the discovery sample, and 98 out of 725 (14%) in the replication sample. We conducted

all the analyses with and without these exclusions (Supplementary Table X). These exclusions had no

effects on the main findings reported in the manuscript, and differences before and after excluding

data are reported in the Supplement.

5.5 Mixed-effects regressions of trial-by-trial choice

We specified two hierarchical logistic regression models to test the effect of the dynamic outcome

probabilities on choice. Both models included predictors aligned with approach and avoidance

responses, based on the latent probabilities of observing an outcome given the chosen option at trial

t, $P(outcome \mid option)_t$. First, if individuals were learning to choose maximise their rewards earned,

they should generally be choosing the option which was relatively more likely to produce the reward

on each trial. This would result in a significant effect of the difference in reward probabilities across

options, as given by:

$\delta P(reward)_t = P(reward \mid conflict)_t - P(reward \mid safe)_t$.

Second, if individuals were learning to avoid punishments, they should generally be avoiding the

conflict option on trials when it is likely to produce the punishment. This would result in a significant

effect of the difference in punishment probabilities across options, as given by:

$\delta P(punishment)_t = P(punishment \mid conflict)_t$,

where $P(punishment \mid safe)$ is omitted as it was always 0 across trials.

The first regression model simply included these two predictors and random intercepts varying by

participant to predict choice:

$Choice \sim \delta P(reward) + \delta P(punishment) + (1 \mid participant)$.

The second model tested the effect of task-induced anxiety on choice, by including anxiety as a main

effect and its interactions with $\delta P(reward)_t$ and $\delta P(punishment)_t$:

$Choice \sim \delta P(reward) + \delta P(punishment) + Anxiety +$

$Anxiety * \delta P(reward) + Anxiety * \delta P(punishment) + (1 \mid participant)$.

5.6 Computational modelling using reinforcement learning

5.6.1 Model specification

We used variations of classical reinforcement learning algorithms (Sutton & Barto, 2018), specifically

the 'Q-learning' algorithm (Watkins & Dayan, 1992), to model participants' choices in the main task

(Table 1). Briefly, our models assume that participants estimate the probabilities of observing a

reward and punishment separately for each punishment, and continually update these estimates

after observing the outcomes of their actions. Consequently, participants can then use these

estimates to choose the option which will maximise subjective value, for example by choosing the

option which is more likely to produce a reward, or avoiding an option if it is very likely to produce a

punishment. By convention, we refer to the probability estimates as 'Q-values'; for example, the

estimated probability of observing a reward after choosing the conflict option is written as

$Q^r(\text{conflict})$, whereas the probability of observing a punishment after choosing the safe option

would be written as $Q^p(\text{safe})$.

In all models, the probability estimates of observing outcome, $o = \{r, p\}$, of the chosen option,

$a = \{\text{conflict, safe}\}$, on trial, t, were updated via:

$Q^o_{t+1}(a) = Q^o_t(a) + \alpha \cdot [o^t - Q^o_t(a)]$,

where the learning rate is controlled by $\alpha \in (0,1)$. In some models (Table X), the learning rate was

split into reward- and punishment-specific parameters, α^r and α^p.

On each trial, the probability estimates for observing rewards and aversive sounds are integrated

into action weights, W, via:

$W = \beta \cdot (Q^r - Q^p)$,

where individual differences in sensitivity to the outcomes (how much the outcomes affect value-

based choice) are parameterised by the outcome sensitivity parameter, β. In models with a single

sensitivity parameter, participants were assumed to value the reward and punishment equally, such

that obtaining a reward had the same subjective value as avoiding a punishment. However, as

individual differences in approach-avoidance conflict could manifest in asymmetries in the valuation

of reward/punishment, we also specified models (Table X) where β was split into reward- and

punishment-specific parameters, β^r and β^p:

$W = \beta^r \cdot Q^r - \beta^p \cdot Q^p$.

The action weights are then the basis on which a choice was made between the options, which was

modelled with the softmax function:

$P(a) = \frac{W(a)}{\sum_i W(i)}$.

We also tested all models with the inclusion of a lapse term, which allows for choice stochasticity to

vary across participants, but since this did not improve model fit for any model, we do not discuss

this further.

Table 1. Model specification

Model	Parameters			
Reward learning only	α^r		β^r	
Symmetrical learning	α		β	
Asymmetric learning rates	α^r	α^p	β	
Asymmetric sensitivities	α		β^r	β^p
Asymmetric learning rates and sensitivities	α^r	α^p	β^r	β^p

All custom model scripts are available online at https://osf.io/m3zev/.

5.6.2   Model fitting and comparison

We fit the models using a hierarchical expectation-maximisation algorithm (Huys et al., 2011) – the

algorithm and supporting code is available online at www.quentinhuys.com/pub/emfit. All prior

distributions of the untransformed parameter values were set as Gaussian distributions to regularise

fitting and to limit extreme values. Parameters were transformed within the models, via the sigmoid

function for parameters constrained to values between 0 and 1; or exponentiated for strictly positive

parameters. We compared evidence across models using integrated Bayesian Information Criterion

(iBIC; Huys et al., 2011) which integrates both model likelihood and model complexity into a single

measure for model comparison.

5.7   Mediation analysis of anxiety-related avoidance

To investigate the cognitive processes underlying anxiety-related avoidance, we tested for potential

mediators of the effect of task-induced anxiety on avoidance choices in the approach-avoidance

reinforcement learning task. Mediation was assessed using structural equation modelling with the

'lavaan' package in R (Rosseel, 2012). This allowed us to test multiple potential mediators within a

single model. We used maximum-likelihood estimation with and without bootstrapped standard

errors (using 2000 bootstrap samples) for estimation. The potential mediators were any parameters

from our computational model that significantly correlated with task-induced anxiety. Therefore, the

model included the following variables: task-induced anxiety, avoidance choices (computed as the

proportion of safe option choices for each participant), and model parameters which correlated with

task-induced anxiety. The model was constructed such that the model parameters were parallel

mediators of the effect of task-induced anxiety on avoidance choices. The model parameters were

allowed to covary across one another.

5.8   Symptom questionnaires

Psychiatric symptoms were measured using the Generalised Anxiety Disorder scale (GAD-7; Spitzer et al., 2006), Patient Health Questionnaire depression scale (PHQ-8; Kroenke et al., 2009) and the Brief Experiential Avoidance Questionnaire (BEAQ; Gamez et al., 2014).

5.9   Test-retest reliability analysis

We retested a subset of our sample (n = 57) to assess the reliability of our task. We determined our sample size via an *a priori* power analysis using GPower (Faul et al., 2007), which was set to detect the smallest meaningful effect size of r = 0.4, as any lower test-retest correlations are considered poor by convention (Cicchetti, 1994; Fleiss, 1986). The required sample size was thus 50 participants, based on a one-tailed significance threshold of 0.05 and 90% power. Participants were recruited from Prolific. We invited participants from the replication study (providing they had not excluded on the basis of data quality) to complete the study again, at least 10 days after their first session. The retest version of the approach-avoidance reinforcement learning task was identical to that in the first session, except for the use of new stimuli to represent the conflict and safe options and different latent outcome probabilities to limit practise effects.

We calculated intra-class correlations coefficients to assess the reliability of our model-agnostic measures. Specifically, we used consistency-based ICC(3,1) (following the notation of Shrout & Fleiss, 1979). To estimate the reliability of the model-derived measures, we estimated individual- and session-level model parameters via a joint model in an approach recently shown to improve the accuracy of estimating reliability (Waltmann et al., 2022). Briefly, this involved fitting behavioural data from both test and retest sessions per participant in a single model, but specifying unique parameters per session. Since our fitting algorithm assumes parameters are drawn from a multivariate Gaussian distribution, information about the reliability of the parameters can be derived from the covariance of each parameter across time. These covariance values can subsequently be converted to Pearson's r values, and thus indices of reliability.

6 Data and code availability

The data and code required to replicate the data analyses are available online at

https://osf.io/m3zev/.

7 Competing interests

YY has no financial or non-financial interests to declare. OJR's MRC senior fellowship is partially in collaboration with Cambridge Cognitive Ltd (who plan to provide in-kind contribution) and he is running an investigator-initiated trial with medication donated by Lundbeck (escitalopram and placebo, no financial contribution). He also holds an MRC-Proximity to discovery award with Roche (who provide in-kind contributions and have sponsored travel for ACP) regarding work on heart-rate variability and anxiety. He also has completed consultancy work for Peak, IESO digital health, Roche and BlackThorn therapeutics. OJR sat on the committee of the British Association of Psychopharmacology until 2022. In the past 3 years, JPR has held a PhD studentship co-funded by Cambridge Cognition and performed consultancy work for GH Research and GE Ltd. These disclosures are made in the interest of full transparency and do not constitute a conflict of interest with the current work.

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844   9   Supplementary material

845   9.1   Comparison of results in the discovery and replication samples, with and without

846   data cleaning exclusions

Supplementary Table 1. Statistical results across the discovery and replication samples, and the effect of data cleaning exclusions			
Statistical test/model	**Sub-test**	**Sample (*without data cleaning*)**	
		Discovery	**Discovery**
Hierarchical logistic regression; no task-induced anxiety	Reward coefficient	β = 0.98 ± 0.03, p < 0.001	β = 0.95 ± 0.02, p < 0.001
		β = 0.95 ± 0.03, p < 0.001	*β = 0.90 ± 0.02, p < 0.001*
	Punishment coefficient	β = -0.33 ± 0.04, p < 0.001	β = -0.52 ± 0.03, p < 0.001
		β = -0.29 ± 0.04, p < 0.001	*β = -0.50 ± 0.03, p < 0.001*
Distribution; task-induced anxiety		Mean = 21, SD = 14	Mean = 22, SD = 13
		Mean = 21, SD = 14	*mean = 22, SD = 14*
Correlation; task-induced anxiety and choice		τ = -0.074, p = 0.033	τ = -0.075, p = 0.005
		τ = -0.068, p = 0.036	*τ = -0.081, p = 0.002*
Hierarchical logistic regression; with task-induced anxiety	Reward coefficient	β = 0.98 ± 0.03, p < 0.001	β = 0.95 ± 0.02, p < 0.001
		β = 0.95 ± 0.03, p < 0.001	*β = 0.90 ± 0.02, p < 0.001*
	Punishment coefficient	β = -0.33 ± 0.04, p < 0.001	β = -0.52 ± 0.03, p < 0.001
		β = -0.29 ± 0.04, p < 0.001	*β = -0.50 ± 0.03, p < 0.001*
	Task-induced anxiety coefficient	β = -0.04 ± 0.04, p = 0.304	β = 0.02 ± 0.03, p = 0.637
		β = -0.03 ± 0.04, p = 0.377	*β = 0.003 ± 0.03, p = 0.925*
	Interaction of task-induced anxiety and reward	β = -0.06 ± 0.03, p = 0.074	β = -0.003 ± 0.02, p = 0.901
		β = -0.05 ± 0.03, p = 0.076	*β = -0.006 ± 0.02, p = 0.774*
	Interaction of task-induced anxiety and punishment	β = -0.10 ± 0.04, p = 0.022	β = -0.23 ± 0.03, p < 0.001
		β = -0.10 ± 0.04, p = 0.011	*β = -0.23 ± 0.03, p < 0.001*
Hierarchical logistic regression; with task-induced anxiety, no interaction	Reward coefficient	β = 0.99 ± 0.03, p < 0.001	β = 0.95 ± 0.02, p < 0.001
		β = 0.95 ± 0.03, p < 0.001	*β = 0.89 ± 0.02, p < 0.001*
	Punishment coefficient	β = -0.33 ± 0.04, p < 0.001	β = -0.52 ± 0.03, p < 0.001
		β = -0.29 ± 0.04, p < 0.001	*β = -0.50 ± 0.03, p < 0.001*
	Task-induced anxiety coefficient	β = -0.09 ± 0.03, p = 0.012	β = -0.08 ± 0.03, p = 0.005
		β = -0.08 ± 0.03, p = 0.016	*β = -0.10 ± 0.03, p < 0.001*
Computational model comparison	Winning model	2 learning rate, 2 sensitivity	2 learning rate, 2 sensitivity
		2 learning rate, 2 sensitivity	*2 learning rate, 2 sensitivity*
Correlation; task-induced anxiety and model parameters	Reward learning rate	τ = -0.019, p = 0.596	τ = -0.010, p = 0.749
		τ = -0.006, p = 0.847	*τ = -0.012, p = 0.637*
	Punishment learning rate	τ = -0.088, p = 0.015	τ = -0.064, p = 0.019
		τ = -0.073, p = 0.026	*τ = -0.074, p = 0.003*
	Learning rate ratio	τ = 0.048, p = 0.175	τ = 0.029, p = 0.282
		τ = -0.037, p = 0.276	*τ = 0.045, p = 0.072*
	Reward sensitivity	τ = -0.038, p = 0.286	τ = -0.028, p = 0.285
		τ = -0.047, p = 0.149	*τ = -0.023, p = 0.345*
	Punishment sensitivity	τ = 0.068, p = 0.051	τ = 0.076, p = 0.004*

		$\tau = 0.047, p = 0.153$	$\tau = 0.094, p < 0.001$
	Reward-punishment sensitivity index	τ = -0.099, p = 0.005 $\tau = -0.084, p = 0.011$	τ = -0.096, p < 0.001 $\tau = -0.103, p < 0.001$
Mediation	Punishment learning rate	β = -0.002 ± 0.001, p = 0.052 $β = -0.001 ± 0.001, p = 0.222$	β = -0.001 ± 0.003, p = 0.132 $β = -0.001 ± 0.003, p = 0.031†$
	Reward-punishment sensitivity index	β = 0.009 ± 0.003, p = 0.003 $β = 0.006 ± 0.002, p = 0.011$	β = 0.009 ± 0.002, p < 0.001 $β = 0.009 ± 0.002, p < 0.001$
Correlation; psychiatric symptoms and choice (overall proportion of conflict option choices)	GAD7	τ = -0.026, p = 0.458 $\tau = 0.005, p = 0.894$	τ = -0.001, p = 0.988 $\tau = -0.002, p = 0.919$
	PHQ8	τ = -0.02, p = 0.579 $\tau = 0.014, p = 0.684$	τ = -0.013, p = 0.639 $\tau = -0.012, p = 0.646$
	BEAQ	τ = -0.059, p = 0.010 $\tau = -0.048, p = 0.151†$	τ = -0.029, p = 0.286* $\tau = -0.020, p = 0.423$
Correlation; psychiatric symptoms and task-induced anxiety	GAD7	τ = 0.256, p < 0.001 $\tau = 0.267, p < 0.001$	τ = 0.222, p < 0.001 $\tau = 0.231, p < 0.001$
	PHQ8	τ = 0.233, p < 0.001 $\tau = 0.244, p < 0.001$	τ = 0.184, p < 0.001 $\tau = 0.194, p < 0.001$
	BEAQ	τ = 0.15, p < 0.001 $\tau = 0.172, p < 0.001$	τ = 0.176, p < 0.001 $\tau = 0.17, p < 0.001$
Correlation; GAD7 and model parameters	Reward learning rate	τ = -0.06, p = 0.076 $\tau = -0.061, p = 0.074$	τ = -0.03, p = 0.304 $\tau = -0.028, p = 0.264$
	Punishment learning rate	τ = -0.07, p = 0.077 $\tau = -0.037, p = 0.265$	τ = -0.01, p = 0.621 $\tau = -0.017, p = 0.534$
	Learning rate ratio	τ = -0.001, p = 0.999 $\tau = -0.032, p = 0.35$	τ = -0.034, p = 0.229 $\tau = -0.026, p = 0.301$
	Reward sensitivity	τ = -0.01, p = 0.802 $\tau = -0.005, p = 0.877$	τ = -0.01, p = 0.745 $\tau = -0.009, p = 0.718$
	Punishment sensitivity	τ = 0.05, p = 0.154 $\tau = 0.022, p = 0.513$	τ = 0.003, p = 0.907 $\tau = 0.012, p = 0.633$
	Reward-punishment sensitivity index	τ = -0.05, p = 0.149 $\tau = -0.023, p = 0.496$	τ = 0.01, p = 0.746 $\tau = 0.007, p = 0.797$
Correlation; PHQ8 and model parameters	Reward learning rate	τ = -0.03, p = 0.396 $\tau = -0.04, p = 0.239$	τ = -0.03, p = 0.219 $\tau = -0.035, p = 0.17$
	Punishment learning rate	τ = -0.06, p = 0.100 $\tau = -0.022, p = 0.504$	τ = -0.01, p = 0.630 $\tau = -0.025, p = 0.348$
	Learning rate ratio	τ = 0.008, p = 0.809 $\tau = -0.038, p = 0.259$	τ = -0.033, p = 0.231 $\tau = -0.016, p = 0.521$
	Reward sensitivity	τ = -0.012, p = 0.610 $\tau = -0.009, p = 0.801$	τ = 0.01, p = 0.729 $\tau = 0.004, p = 0.901$
	Punishment sensitivity	τ = 0.05, p = 0.179 $\tau = 0.008, p = 0.802$	τ = -0.002, p = 0.948 $\tau = 0.012, p = 0.619$
	Reward-punishment sensitivity index	τ = -0.06, p = 0.123 $\tau = -0.01, p = 0.773$	τ = 0.02, p = 0.557 $\tau = 0.005, p = 0.867$
Correlation; BEAQ and	Reward learning rate	τ = -0.06, p = 0.085	τ = -0.02, p = 0.394

model parameters		$\tau = -0.047, p = 0.147$	$\tau = -0.017, p = 0.503$
	Punishment learning rate	$\tau = -0.08, p = 0.024$	$\tau = -0.03, p = 0.337*$
		$\tau = -0.071, p = 0.032$	$\tau = -0.031, p = 0.228$
	Learning rate ratio	$\tau = 0.018, p = 0.618$	$\tau = -0.005, p = 0.883$
		$\tau = 0.002, p = 0.938$	$\tau = 0.007, p = 0.759$
	Reward sensitivity	$\tau = -0.01, p = 0.739$	$\tau = 0.01, p = 0.753$
		$\tau = -0.036, p = 0.29$	$\tau = 0.002, p = 0.927$
	Punishment sensitivity	$\tau = 0.07, p = 0.061$	$\tau = 0.02, p = 0.477$
		$\tau = 0.05, p = 0.127$	$\tau = 0.025, p = 0.308$
	Reward-punishment sensitivity index	$\tau = 0.02, p = 0.034$	$\tau = -0.01, p = 0.745*$
		$\tau = -0.073, p = 0.028$	$\tau = -0.015, p = 0.548$

Note. All correlations tests were conducted using permutation-based Kendall's tau correlations, using 10,000 permutations per test. Symbols represent the following: * - Inconsistent findings across discovery replication samples. † - Inconsistent findings before and after data cleaning exclusions. Abbreviations: GAD7 – Generalised Anxiety Disorder 7-item scale; PHQ8 – Patient Health Questionnaire 8-item depression scale; BEAQ – Brief Experiential Avoidance Questionnaire.

A sensitivity analyses of the effect of implementing or not implementing our data cleaning exclusions
showed that the significant and negative correlation between experiential avoidance symptoms and
overall proportion of conflict option choices ($\tau = -0.059$, $p = 0.010$) was not significant when the data
cleaning exclusions were not implemented ($\tau = -0.029$, $p = 0.286$), however since this effect was not
replicated in the independent sample (with and without data exclusions), we do not discuss this
further. The mediating effect of the punishment learning rate was also significant in the replication
sample only before excluding data, however the effect sizes were small and similar before and after
excluding data, and so we also do not discuss this further.

9.2 Computational modelling

Supplementary Figure 1. Model comparison and parameter distributions across studies. a, Model comparison results. The difference in integrated Bayesian Information Criterion scores from each model relative to the winning model is indicated on the x-axis. The winning model in both studies included specific learning rates for reward (α^R) and punishment learning (α^p), and and specific outcome sensitivity parameters for reward (β^R) and punishment (β^P). Some models were tested with the inclusion of a lapse term (ξ). **b**, Distributions of individual parameter values from the winning model across studies.

9.3   Mediation analyses

Supplementary Figure 2. Mediation analyses across studies. Mediation effects were assessed using structural equation modelling. Bold terms represent variables and arrows depict regression paths in the model. The annotated values next to each arrow show the regression coefficient associated with that path, denoted as *coefficient (standard error)*. Only the reward-punishment sensitivity index significantly mediated the effect of task-induced anxiety on avoidance. Significance levels in all figures are shown according to the following: $p < 0.05$ - *; $p < 0.05$ - **; $p < 0.001$ - ***.

 ## 9.4   Parameter recovery

 To establish how well we could recover our parameters from the best fitting model, we simulated

 data from each study (discovery, replication) and refitted these new datasets with the identical

 model fitting procedure used for the empirical data. We matched the number of participants,

 number of trials per participant, and latent outcome probabilities in the simulated datasets to the

 empirical data, and used the best-fitting parameters for each participant to generate their choices.

 Trial-by-trial outcomes were generated stochastically according to the latent outcome probabilities,

 which meant that the simulated participants did not necessarily receive the same series of outcomes

 to our real participants. To average over this stochasticity in the outcomes, we repeated the

 simulations 100 times for each study. After fitting our best-fitting model to the simulated data, we

 computed Pearson's correlation coefficients across the data-generating parameters and the

 recovered parameters. Across all parameters, the Pearson's r values between data-generating and

 recovered parameters ranged from 0.77 to 0.86, indicating excellent recovery (Supplementary Figure

 3).

Supplementary Figure 3. Parameter recovery. Pearson's r values across the data-generating and recovered parameters by parameter. Coloured points represent Pearson's r values for each of 100 simulation iterations, and black points represent the mean value across simulations.

   9.5   Test-retest reliability of the task

Figure 5. Test-retest reliability of the task. Correlations of measures across the test and retest sessions are shown with their estimates of reliability. Reliability estimates for the model-agnostic measures (task-induced anxiety, proportion of conflict option choices) were estimated using intra-class correlation coefficients. Reliability estimates for the computational measures from the winning computational model were computed by first fitting both sessions' parameters within a single model, then using the parameter covariance matrix to derive a Pearson's correlation coefficient ($r_{Model\text{-}derived}$) for each parameter across sessions to be calculated from their covariance. Dotted lines represent the reference line, indicating perfect correlation. Red lines show lines-of-best-fit.

878   ## 9.6   Practise effects

879   We checked for practise effects in the behavioural data by comparing the behavioural measures and

880   computational model parameters across sessions via paired t-tests. These tests were all non-

881   significant ($p > 0.07$) except for task-induced anxiety ($t_{56} = 2.21$, $p = 0.031$) and the punishment

882   learning rate ($t_{56} = 2.24$, $p = 0.029$; Supplementary Figure 4).

883

Supplementary Figure 5. Task practice effects. Comparison of behavioural measures and model parameters across time. Lines represent individual data, red points represent mean values, and red lines represent standard error bars. P-values of paired t-tests are annotated above each plot. Task-induced anxiety and the punishment learning rate was significantly lower in the second session, whilst the other measures did not change significantly across sessions.