

1 **Altered decision-making under uncertainty in unmedicated mood and anxiety disorders**

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12

1 **Abstract**

2 In daily life we are constantly faced with decisions that have uncertain outcomes. This  
3 uncertainty can lead to feelings of anxiety. However, the reciprocal role that anxiety plays in  
4 altering the decisions made under uncertainty is not fully understood. This is important, because  
5 psychological treatments for anxiety disorders attempt to alter anxiety-related decision-making.  
6 In this study we therefore probed the computational basis of decision-making under uncertainty  
7 in individuals with high levels of mood and anxiety symptoms. Specifically, healthy individuals  
8 (N=88) and individuals with mood and anxiety disorders (N=44) were asked to choose between  
9 four competing slot machines ('four armed bandit') with fluctuating, uncertain, outcomes (i.e.  
10 rewards and/or punishments, or neither). Decisions were made during periods of safety and  
11 environmental stress (threat of unpredictable shock). We predicted that anxious individuals  
12 under stress would learn faster about punishments, and exhibit choices that were more affected  
13 by them. We formalized these hypotheses in terms of parameter values – punishment learning  
14 rate and punishment sensitivity respectively - in reinforcement learning accounts of behaviour.  
15 We found no evidence for an effect on punishment choice sensitivity in the pathological group,  
16 even under elevated stress. However individuals with high anxiety symptoms did have higher  
17 learning rates for punishment across all conditions. The behaviour of the pathological group was  
18 also apparently more random, with a greater influence of a lapse parameter in the model across  
19 conditions. Overall, these data suggest that anxious individuals do not weigh negative outcomes  
20 more heavily; rather they are quicker to update their behaviour in response to negative (but not  
21 positive) outcomes. This suggests that, when treating anxiety, we should not seek to blunt  
22 responses to negative outcomes, but instead encourage anxious individuals to integrate  
23 information over longer horizons when bad things happen. As such, these findings provide a  
24 formal mathematical framework for developing psychological treatment strategies for mood and  
25 anxiety disorders.

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## 1 **Introduction**

2 Mood and anxiety disorders are the most common mental health problems in the developed  
3 world accounting for 4% of all years lived with disability<sup>1</sup>. Despite this, we have very little  
4 understanding of the mechanisms driving pathological feelings of anxiety, and the associated  
5 alterations to cognitive processes, such as decision-making, when people are anxious. This  
6 hinders our ability to improve treatments<sup>2</sup>.

7 Altered psychological, behavioural and neural responses to uncertainty are thought to be key to  
8 the manifestation of anxiety<sup>3</sup>. Firstly, anxious individuals report finding uncertain situations  
9 distressing<sup>4-6</sup>. Secondly, anxious individuals have been shown to be averse to uncertain  
10 decisions – preferring less profitable but more predictable options over more profitable but  
11 uncertain ones<sup>7</sup>. Finally, in translational research, a well-established dissociation is made  
12 between the processing of predictable and unpredictable threats<sup>8</sup>, with unpredictable threats  
13 used as a pre-clinical model of anxiety. Critically, in humans, the neural signatures of  
14 unpredictable threat responding<sup>9</sup> overlap with those engaged by pathological anxiety<sup>10</sup>.

15 Decision-making under uncertainty is nevertheless ubiquitous in daily life<sup>11</sup>. ‘Multi-armed bandit’  
16 tasks can probe this decision making under uncertainty by asking individuals to select one of  
17 multiple slot machines (i.e. bandits) with slowly fluctuating payoffs. On any given trial, the best  
18 option might be one that you chose recently (and so have some knowledge about), or it might  
19 be one you haven’t chosen (and so do not have up-to-date information about). Computationally  
20 it has been demonstrated that the balance of decision-making about which bandit to choose can  
21 be captured through reinforcement-learning algorithms, which approximately optimise decisions  
22 based on the history of feedback from the bandits<sup>11,12</sup>. Specifically, decisions are made  
23 according to the relative weights afforded to rewards and punishments (i.e. sensitivity – how  
24 much one anticipates liking being rewarded or disliking being punished), and how quickly  
25 information is integrated over time (i.e. learning rates – how quickly one might switch bandits  
26 following a punishment, or how long one persists in choosing a previously rewarded bandit). If  
27 altered response to uncertainty were a core feature of anxiety symptoms, we would predict that  
28 the mechanisms parameterised by reinforcement-learning models should differ in individuals  
29 with high levels of anxiety symptomatology. Specifically, given that anxiety is associated with a  
30 bias towards aversive processing – i.e., negative affective bias<sup>14-16</sup>- we might predict that  
31 anxiety will selectively increase the weights of aversive-specific parameters in reinforcement-  
32 learning algorithms: i.e., punishment sensitivity and punishment learning rate.

1 In this study, we therefore sought to formalise the differences in decision-making under  
2 uncertainty between healthy individuals and those with high levels of anxiety in terms of  
3 differences in the parameters of reinforcement-learning models. Moreover, given that the  
4 diathesis-stress hypothesis<sup>13</sup> predicts that some symptoms of mood and anxiety disorders are  
5 only revealed when an individual is under stress<sup>14</sup>, we also transiently induced stress in  
6 participants using threat of unpredictable shock. We predicted, therefore, that anxiety symptoms  
7 would selectively increase punishment sensitivity and punishment learning rate in the  
8 reinforcement-learning algorithm, and that this would be exaggerated under acute stress.

## 1 **Methods**

2 We recruited 132 participants, N=88 healthy controls (50 female; age=23±5) and N=44 with  
3 unmedicated mood and anxiety symptoms (28 female; age=28±9) from the local community.  
4 Although our focus was on anxiety symptoms, we recruited a mixed sample because mood and  
5 anxiety disorder symptoms show considerable overlap, and the disorders are strongly comorbid  
6 indicating that they may not be mechanistically dissociable. The majority of our pathological  
7 sample (N=28) had a mixed diagnosis of Generalised Anxiety Disorder (GAD) and Major  
8 Depressive Disorder (MDD); eight had GAD diagnosis alone; three had panic disorder with  
9 MDD; and five had MDD alone (according to the Mini International Neuropsychiatric Interview  
10 (MINI))<sup>17</sup>. The average number of depressive episodes was 5 (SD±7), with the average onset of  
11 first episode 20±8 years. All were currently unmedicated, but N=18 had tried psychiatric  
12 medication more than 6 months prior to the experiment, and N=21 had undergone some form of  
13 psychological treatment. Exclusion criteria were any form of psychiatric medication within the  
14 last 6 months, any current psychiatric diagnosis (other than major depression or anxiety  
15 disorder), neurological disorder, or pacemaker. Continuous measures of anxiety  
16 symptomatology were obtained using the State-Trait Anxiety Inventory (STAI) and recent  
17 depression symptoms using the Beck depression inventory (BDI). All participants provided  
18 written informed consent and were reimbursed £7.50/hour for participation. The study obtained  
19 ethical approval from the UCL Research Ethics Committee (Project ID Numbers: 1764/001 and  
20 6198/001).

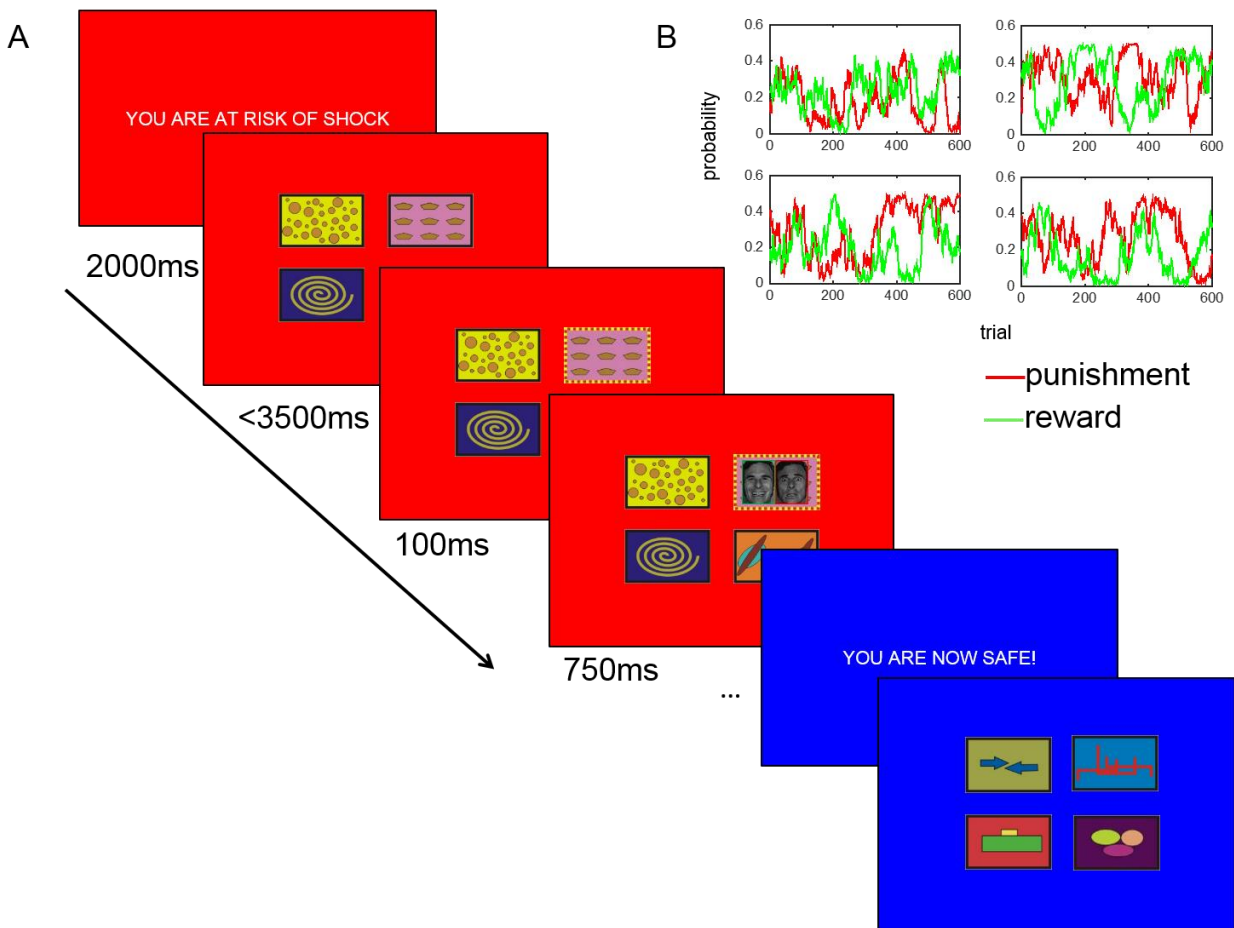
### 21 ***Four-armed bandit task***

22 The task was adapted from Seymour et al<sup>12</sup>. Positive feedback was a happy face, and negative  
23 feedback was a fearful face (consistent with our prior work<sup>14,18</sup>) The task was completed under  
24 alternating conditions of safe and threat (see *Stress manipulation* section below), with a different  
25 set of four bandits in each stress condition.

26 On each trial, subjects were asked to select one of the four bandits (within 3.5s) and were then  
27 provided (for just the selected bandit; **Figure 1A**) with one of: 1) no feedback, 2) positive  
28 feedback, 3) negative feedback, or 4) both positive and negative feedback. The probabilities of  
29 these outcomes fluctuated independently and slowly across bandits, such that the bandit that  
30 was most rewarding changed over time (**Figure 1B**). The participants were instructed to “try to  
31 get happy faces! avoid fearful!”. The bandits remained in the same spatial location on every trial.

### 32 ***Stress manipulation***

1 State anxiety was induced via threat of unpredictable electric shocks delivered with two  
2 electrodes attached to the non-dominant wrist using a Digitimer Constant Current Stimulator  
3 (Digitimer Ltd, Welwyn Garden City, UK). The appropriate shock level was established using a  
4 shock work-up procedure prior to testing. Up to five shocks of increasing intensity were  
5 administered, and participants rated each one on a scale from 1 (barely felt) to 5 (unbearable),  
6 with the final shock level set to 4. The experimental task was programmed using the Cogent  
7 toolbox for MATLAB 2014, presented on a laptop and administered under alternating safe and  
8 threat blocks. At the start of the safe block, the background colour changed to blue and  
9 proceeded by a 2000ms message stating: "YOU ARE NOW SAFE!" At the start of the threat  
10 block, the background colour changed to red and the message: "YOU ARE AT RISK OF  
11 SHOCK" was presented for 2000ms. Participants were told that they might receive a shock only  
12 during the threat condition but that the shocks were not dependent on their performance. As a  
13 manipulation check, participants retrospectively rated how anxious they felt during the safe and  
14 threat conditions on a scale from 1 ("not at all") to 10 ("very much so"). This manipulation has  
15 been shown to have high reliability<sup>18</sup>.



1  
2 **Figure 1: Task schematic** A) Participants were asked to select one of four bandits on each  
3 trial. Following selection (here illustrated as top right under the threat condition), the bandit  
4 border changed colour, followed by the outcome (here illustrated as a combined reward and  
5 punishment) overlaid on the selected bandit. The task proceeded in the same manner under the  
6 safe condition, but with a different set of bandits. B) Example of the independent fluctuation of  
7 reward and punishment probabilities across four bandits. At the start of a new condition, the  
8 bandits started with the probabilities they finished with at the end of the previous condition. I.e.  
9 the bandits at the end of one safe block paused during the subsequent threat block.

10 **Manipulation check and model agnostic task analysis**

11 The retrospective manipulation check was analysed in a 2 (block) x 2 (condition) x 2 (diagnosis)  
12 repeated measures ANOVA. For model agnostic task analysis, we calculated stay probability  
13 following win only and loss only trials (excluding trials in which both wins and losses were given)  
14 and included them in a 2 (outcome) x 2 (condition) x 2 (diagnosis) repeated measures ANOVA.

1 We implemented frequentist and Bayesian (adopting a default Cauchy prior) repeated measures  
 2 ANOVAs using JASP<sup>19</sup> (for data and associated JASP analyses see link: [osf.io/2jx87/](https://osf.io/2jx87/))

### 3 **Computational Modelling**

4 We fitted four different models<sup>12</sup> using the hBayesDM\* package for R<sup>20</sup> (for code see  
 5 <https://osf.io/2jx87/>). This toolbox simplifies the implementation of hierarchical Bayesian  
 6 parameter estimation using STAN. For more details please refer to<sup>20</sup>. Previous studies showed  
 7 that hierarchical parameter estimation outperforms individual parameter estimation in parameter  
 8 recovery<sup>21</sup>. We fit four models, show in **Table 1**.

Model	NP	Parameters				
bandit4arm_4par	4	Reward Sensitivity	Punishment Sensitivity	Reward Learning Rate	Punishment Learning Rate	
bandit4arm_lapse	5	Reward Sensitivity	Punishment Sensitivity	Reward Learning Rate	Punishment Learning Rate	Lapse
igt_pvl_decay	4	Decay Rate	Shape	Consistency	Loss Aversion	
igt_pvl_delta	4	Learning Rate	Shape	Consistency	Loss Aversion	

9 **Table 1: Model specification.** We fitted four different models using the hBayesDM package.  
 10 NP= number of parameters. Model = model names implemented in the hBayesDM package.

11 The bandit4arm models were calculated according to:

12 (1)  $Value_{t(i)}^{rew} = Value_{t(i)}^{rew} + LearningRate_{rew} \cdot PredictionError_{t(i)}^{rew}$

13 (2)  $Value_{t(i)}^{pun} = Value_{t(i)}^{pun} + LearningRate_{pun} \cdot PredictionError_{t(i)}^{pun}$

14 (3)  $PredictionError_{t(i)}^{rew}$   
 15 =  $Sensitivity_{rew} \cdot RewardOutcome(t) - Value_{t-1(i)}^{rew}$  if  $i = chosen$   
 $- Value_{t-1(i)}^{rew}$  if  $i = unchosen$

16 (4)  $PredictionError_{t(i)}^{pun}$   
 17 =  $Sensitivity_{pun} \cdot PunishmentOutcome(t) - Value_{t-1(i)}^{pun}$  if  $i = chosen$   
 $- Value_{t-1(i)}^{pun}$  if  $i = unchosen$

18

\* <https://github.com/CCS-Lab/hBayesDM>



1 Choice probability was determined by passing the reward and punishment values through a  
2 softmax function in the ‘\_4par’ model:

$$3 \quad (5) \quad \text{Choice Probability}_{t(i)} = \frac{\exp\left(\text{Value}_{t(i)}^{\text{rew}} + \text{Value}_{t(i)}^{\text{pun}}\right)}{\sum_j \exp\left(\text{Value}_{t(j)}^{\text{rew}} + \text{Value}_{t(j)}^{\text{pun}}\right)}$$

4 For the ‘\_lapse’ model, the addition of an irreducible noise parameter (i.e. ‘lapse’) allowed for  
5 the possibility of decisions made at random, irrespective of the inferred values of the bandits  
6 (sometimes referred to as ‘trembling hand’ decisions)<sup>22</sup>

$$7 \quad (6) \quad \text{Choice Probability}_{t(i)} = \frac{\exp\left(\text{Value}_{t(i)}^{\text{rew}} + \text{Value}_{t(i)}^{\text{pun}}\right)}{\sum_j \exp\left(\text{Value}_{t(j)}^{\text{rew}} + \text{Value}_{t(j)}^{\text{pun}}\right)} \cdot (1 - \text{Lapse}) + \frac{\text{Lapse}}{4}$$

8 For the two ‘IGT\_pvl’ models, readers are referred to<sup>20,23</sup>, but briefly they are ‘prospect valence  
9 learning’ models which integrate aspects of reinforcement learning and prospect theory learning  
10 models.

### 11 **Model selection**

12 Parameters for all models were initially fit under four separate hierarchical priors: 1)  
13 anxious/depressed individuals under threat; 2) healthy controls under threat; 3)  
14 anxious/depressed individuals under safe; 4) healthy controls under safe. The winning model  
15 was defined as the model with the lowest Leave-One-Out Information Criterion (LOOIC)  
16 summed across these four priors.

17 We then followed up initial model selection with a subsequent exploration of all four  
18 combinations of group/condition priors (1: all four, 2: two representing each condition, 3: two  
19 representing each group and 4: one pooling everyone together) on the winning model. We then  
20 compared parameter estimates from the winning model across the two groups using 95%  
21 highest density intervals (HDI). Specifically, for each comparison, we calculated the difference in  
22 the hyper parameters and reported the 95% HDI of the difference. If this HDI did not overlap  
23 zero, we consider there to be a meaningful difference between the groups<sup>24,25</sup>. Note that we are  
24 not testing if we can reject the null hypothesis (i.e., that two groups are the same on a given  
25 parameter), but instead whether the hyper parameters differ between the groups/conditions<sup>24,25</sup>.  
26 To illustrate group differences we plotted the individual mean posterior parameter estimates  
27 using raincloud plots<sup>26</sup>.

28 Finally, parameter estimates from the winning model/prior combination were used to simulate  
29 choices for each individual and then compared to each individual’s real choices to confirm that

1 this model was not only the best model of those tested, but also a realistic model of the data (we  
2 required a correlation of greater than 0.7). Finally, we confirmed that simulated data  
3 recapitulated patterns observed in the model agnostic task analysis.

4 ***Continuous symptom analysis***

5 Individual parameters (mean posterior estimates) for the overall winning model were extracted  
6 and correlated with individual trait anxiety and depression scores in Bayesian and Frequentist  
7 correlation matrices using JASP<sup>19</sup>.

8

1 **Results**

2 **Self-report analysis**

3 As expected the mood and anxiety group demonstrated higher levels of trait anxiety (data  
4 missing from 1 subject in each group;  $t(128)=8.7$ ,  $p<0.001$ ,  $d=1.6$ ), and recent depression  
5 symptoms (data missing from 3 patients; 4 controls;  $t(124)=9.0$ ,  $p<0.001$ ,  $d=1.7$ ), relative to  
6 healthy controls (Table 2). Moreover, participants reported feeling more anxious under the  
7 threat relative to the safe conditions (data missing for the second block for 1 patient;  
8  $F(1,129)=319$ ,  $p<0.001$ ,  $\eta^2=0.7$ ) but this did not differ according to group (group\*condition  
9 interaction:  $F(1,129)=0.04$ ,  $p=0.8$ ,  $\eta^2<0.001$ ).

	<b>Control</b>	<b>Symptomatic</b>
<b>Total N</b>	88	44
<b>% female</b>	57	64
<b>Age</b>	23±5	28±9
<b>Anxiety</b>	41±11	57±8
<b>Depression</b>	7±7	20±9

10

11 **Table 2: Demographics and clinical information:** *The symptomatic patients had higher mean*  
12 *anxiety (trait anxiety from the State-Trait Anxiety Inventory) and depression (Beck Depression*  
13 *Inventory) scores than the healthy control participants ( $\pm$  represents standard deviation).*

14 **Model agnostic task analysis**

15 As expected, participants were more likely to repeat a choice following a win than a loss  
16 ( $F(1,130)=78$ ,  $p<0.001$ ,  $\eta^2=0.4$ ). However this was not modulated by group (group x outcome  
17 interaction:  $F(1,130)=0.18$ ,  $p=0.68$ ,  $\eta^2=0.001$ ) or stress condition (stress condition x outcome  
18 interaction:  $F(1,130)=2.6$ ,  $p=0.11$ ,  $\eta^2=0.019$ ), and the three-way interaction narrowly missed  
19 significance ( $F(1,130)=3.6$ ,  $p=0.061$ ,  $\eta^2=0.026$ ).

20 A Bayesian version of the same analysis confirmed that the winning model included only  
21 outcome ( $\log BF_{10}=91$ ), which scored 8 times better than the next best model (main effects of  
22 outcome and stress condition;  $\log BF_{10}=89.3$ ).

23 **Modelling results**

24 The winning model fit with the full prior specification was the five-parameter model that included  
25 a lapse parameter (**Table 3a**). We then fit this winning model with the different combinations of

1 group/condition hierarchical priors and demonstrated that this model is actually best fit using  
 2 only two priors; one for each group (**Table 3b**).

<b>a) Model</b>	<b>LOOIC</b>
<i>bandit4arm</i>	128456
<i>bandit4arm_lapse</i>	<b>128198</b>
<i>igt_pvl_decay</i>	132008
<i>igt_pvl_delta</i>	131774

<b>b) Prior (<i>bandit4arm_lapse</i>)</b>	<b>LOOIC</b>
<i>Diagnosis and Condition Priors (4)</i>	128198
<i>Diagnosis Priors (2)</i>	<b>128166</b>
<i>Condition Priors (2)</i>	128225
<i>Single Prior (1)</i>	128174

3  
 4 **Table 3: Model and prior fits.** a) The winning model is that with the lowest Leave-One-Out  
 5 Information Criterion (LOOIC). The lowest number (for model *bandit4arm\_lapse*) is displayed in  
 6 bold. b) The lowest LOOIC is then obtained when the winning (*bandit4arm\_lapse*) model is fit  
 7 with two priors: one for symptomatic and one for healthy individuals (*Diagnosis priors*)

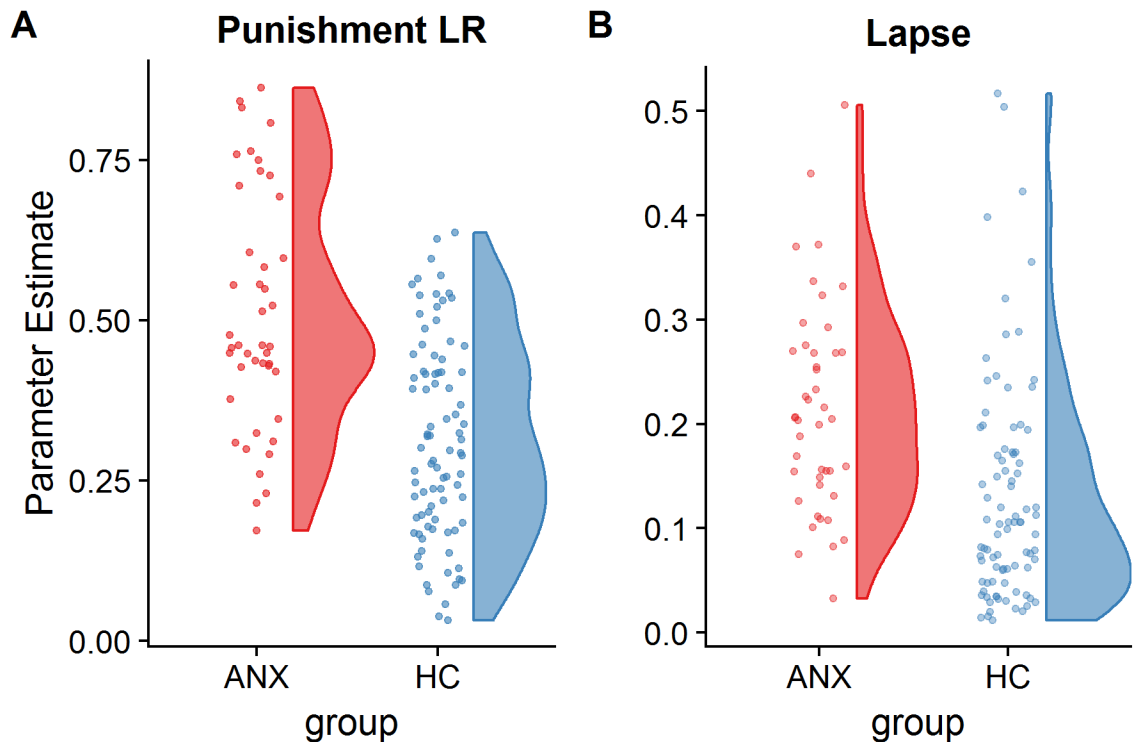
8 Extracting the parameters from the model fit using two priors (one for each group) demonstrated  
 9 elevated punishment learning rate and lapse parameters in symptomatic relative to control  
 10 individuals (HDI for the comparison across groups does not overlap zero; **Table 4; Figure 2**). Of  
 11 note, this same pattern (main effect of group on punishment learning rate and lapse parameters  
 12 only) was seen when parameters were extracted from the 4 prior model, and there was no effect  
 13 of condition on any parameter (see supplement).

14  
 15  
 16  
 17

	Symptomatic	Control	Group HDI
<b>Reward Sensitivity</b>	7.47 (2.91)	9.61 (4.87)	-4.55 0.65
<b>Punishment Sensitivity</b>	7.41 (7.21)	6.67 (4.83)	-4.95 2.24
<b>Reward Learning Rate</b>	0.31 (0.30)	0.25 (0.22)	-0.11 0.17
<b>Punishment Learning Rate</b>	0.51 (0.18)	0.31 (0.15)	<b>0.08 0.38</b>
<b>Lapse</b>	0.21 (0.10)	0.13 (0.11)	<b>0.02 0.2</b>

1

2 **Table 4: Parameter estimates and group comparison on the winning model and prior**  
3 **combination.** Values represent the mean (standard deviation) of the final estimated posterior  
4 mean estimates for each individual. The 'Group HDI' column comprises the upper and lower  
5 bounds of the 95% highest density intervals (HDI) of the comparison between the symptomatic  
6 and control groups. If the HDI does not encompass zero, we consider there to be a meaningful  
7 difference between the groups/conditions. We find a main effect of group on the punishment  
8 learning rate and lapse parameters only (in bold).

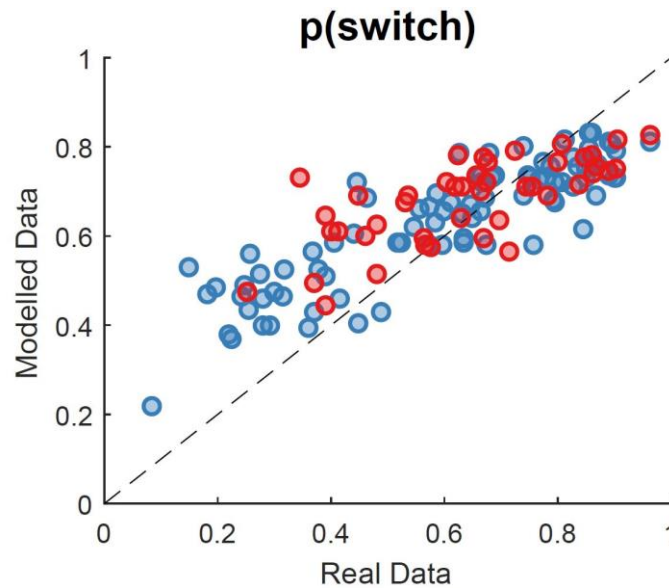


9

10 **Figure 2: Group difference in parameters.** Higher A) punishment learning rates (LR) and B)  
11 lapse rates in the mood and anxiety group (ANX) relative to the healthy controls (HC). Here we  
12 plot the final estimated posterior mean of each parameter for each individual.

1 **Model check**

2 Finally, we simulated data for this model for each subject based on their parameter estimates.  
3 For both the simulated and real data we calculated the proportion of all trials on which subjects  
4 switched bandits. Real and simulated data showed close correspondence ( $r=0.84$ ; **Figure 3**).



5

6 **Figure 3: Sensitivity plot.** Simulated data for each individual shows close correspondence with  
7 real data on a simple metric ‘ $p(\text{switch})$ ’ – i.e. the proportion of trials in which the individual (or  
8 simulated agent) selected a different bandit from the previous trial. Healthy controls plotted in  
9 blue, patients in red; dashed line represents the identity.

10 Moreover, simulated data recapitulated the model-agnostic analysis. There was a main effect of  
11 outcome ( $F(1,130)=434$ ,  $p<0.001$ ,  $\eta^2=0.8$ ) driven by greater stay probability following wins than  
12 losses, which did not interact with diagnosis ( $F(1,130)=0.003$ ,  $p=0.95$ ,  $\eta^2<0.001$ ).

13 **Continuous symptom analyses**

14 Extracting each individual’s posterior mean estimated parameters supported the existence of  
15 positive correlations between trait anxiety and the lapse parameter ( $r(130)=0.32$ ,  $\log\text{BF}_{10}=4.5$ ,  
16  $p<0.001$ ) and punishment learning rate ( $r(130)=0.28$ ,  $\log\text{BF}_{10}=2.9$ ,  $p=0.001$ ), with no supported  
17 correlations for any of the other parameters (all  $\text{BF}_{10}<1.5$ ). Trait anxiety was, as expected,  
18 strongly correlated with recent depression symptoms (BDI;  $r(126)=0.8$ ,  $\log\text{BF}_{10}=60$ ,  $p<0.001$ ),  
19 and so similar correlations were observed between BDI scores and model parameters.

## 1 Discussion

2 Partly consistent with our hypotheses, we found that higher mood and anxiety symptoms were  
3 associated with altered decision-making in the aversive domain; specifically greater  
4 punishment-learning rates. However, contrary to our hypotheses, this was independent of  
5 stress, and we did not detect any difference in punishment sensitivity. Moreover, the higher  
6 learning rate for punishments occurred in combination with lower reliance on the modelled  
7 reinforcement-learning parameters in general (as evidenced by an increased influence of the  
8 lapse parameter in the symptomatic group).

9 A greater punishment learning rate means that individuals with mood and anxiety symptoms  
10 learn faster about punishments, and will therefore be inclined to make decisions weighted more  
11 heavily by negative outcomes in the recent past. This is also reflected in the lower stay  
12 probabilities immediately following punishment in the model agnostic analysis (which was  
13 recapitulated in the model simulations). Importantly, this was seen independent of a difference  
14 between the groups in punishment sensitivity, which suggests that anxious individuals do not  
15 over-weigh punishments *per se*. This is consistent with our prior work with reinforcement  
16 learning paradigms<sup>14</sup>, as well as work indicating similar loss aversion between anxious and  
17 healthy individuals (albeit in the context of higher risk aversion)<sup>7</sup>. Taken together these results  
18 indicate that it is not that anxious individuals weigh negative outcomes more heavily in  
19 themselves; rather they use that information differently. Specifically, a greater punishment  
20 learning rate implies that individuals with anxiety integrate information about threats over fewer  
21 trials, will over-estimate the probability of bad outcomes, and hence engage in avoidance  
22 behaviours. Clinically this might result in overestimating negative events. For example, in the  
23 aftermath of a heavily reported plane crash an anxious individual might overestimate the risk of  
24 it re-occurring and therefore avoid flying<sup>16</sup>. In the long run, such avoidance behaviour will reduce  
25 an anxious individual's ability to update learning and hence over-estimation persists, and  
26 avoidance behaviour is upheld.

27 The clarity that it is the learning rate, rather than sensitivity to punishment, which is elevated in  
28 mood and anxiety disorders<sup>15,18</sup> is important in relation to potential interventions that could  
29 mitigate such a negative bias. Specifically, we may not need to 'blunt' aversive responses  
30 through treatment – rather treatments should seek to modify how negative information is used.  
31 Indeed, changing the way individuals use the same information is one principle underpinning  
32 psychological interventions for mood and anxiety disorders, such as Cognitive Behavioural  
33 Therapy. One specific recommendation here is that therapists might encourage patients to hold

1 off on implementing decisions on the basis of negative experiences so that they can learn how  
2 infrequent they are. This is implemented already in exposure therapy, but the present work  
3 takes us a step towards formalising the behavioural effect at a trial-by-trial cognitive level.

4 The altered punishment learning rates in the symptomatic group do, however, need to be  
5 considered in the context of an accompanying increased reliance on the lapse parameter. In the  
6 model, this parameter quantifies dependence on a form of 'unexpected' responding. This could  
7 occur from subjects losing concentration on a trial and choosing at random, or possibly  
8 increasing their tendency towards undirected exploration in an attempt to avoid unpredictable  
9 punishments<sup>27</sup>. Future experiments should test the substantial difference between these two  
10 explanations. However, the lapse parameter also captures aspects of decision-making that are  
11 not encompassed by the model. In other words, what we have consigned to categories of  
12 irreducible uncertainty might actually be reduced by more sophisticated and proficient models.  
13 Our data are available online for future exploration of different models as the field and literature  
14 develop<sup>†</sup>.

15 Finally, it is worth noting that the modelled effects were not, in this instance, affected by acute  
16 stress. We predicted that they would be because the diathesis-stress hypothesis predicts that  
17 symptoms of anxiety will be exacerbated in stressful circumstances<sup>13</sup>. Indeed, our prior work  
18 indicated that reliance on Pavlovian avoidance biases in anxiety disorders is exacerbated by the  
19 same stress manipulation adopted here<sup>14</sup>. Of note, there was a trend towards a group\*stress  
20 condition interaction in the model agnostic task analysis, but this did not reach significance in  
21 this relatively large sample. Nevertheless it remains possible that such an effect exists, but it is  
22 weak relative to the strong effects of diagnosis and outcome, and the current study was simply  
23 underpowered to detect it.

24 These findings extend our prior work attempting to formalise the behavioural alterations seen in  
25 anxiety disorders in terms of computational models<sup>7,14</sup>. Such models aim to bridge the gap  
26 between observable symptoms (which form the basis of current diagnostic categories) and the  
27 underlying cognitive computations in the brain. Ultimately, the experience of debilitating anxiety  
28 emerges from interactions between an individual and their environment; and fully optimised  
29 treatments are unlikely to emerge without a clearer understanding of how these symptoms  
30 emerge mechanistically. Formally specifying some of the behavioural changes that occur in  
31 clinical anxiety takes us a step closer to this goal.

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† Data, analyses and scripts available here [osf.io/2jx87](https://osf.io/2jx87)



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8

1 **Supplement**

2

3 Examining the individual parameters from the four prior model, we found a main effect of  
 4 diagnosis only on the lapse and punishment learning rate parameters (**Table 4**) reiterating the  
 5 same pattern seen in the winning two prior model. Of note, a similar pattern was seen on  
 6 punishment learning rates in the model without the lapse parameter under threat (punishment  
 7 learning rate under threat HDI 0.05-0.3); but, interestingly, not in the safe condition (HDI -0.19-  
 8 0.27), although this model was not favoured in the model-comparison.

	Symptomatic – Control				Threat - safe			
	Threat		Safe		Anxious		Healthy	
<b>Reward Sensitivity</b>	-5.71	1.63	-1.31	10.69	-12.00	0.76	-2.33	3.57
<b>Punishment Sensitivity</b>	-4.83	6.72	-4.48	21.52	-21.51	7.40	-1.80	3.32
<b>Reward Learning Rate</b>	-0.13	0.25	-0.14	0.26	-0.27	0.28	-0.07	0.11
<b>Punishment Learning Rate</b>	<b>0.11</b>	<b>0.45</b>	<b>0.08</b>	<b>0.55</b>	-0.30	0.25	-0.08	0.10
<b>Lapse</b>	<b>0.01</b>	<b>0.23</b>	<b>0.12</b>	<b>0.34</b>	-0.25	0.02	-0.07	0.08

9

10 **Table S1: Group and condition effects on the full model** Values represent 95% highest  
 11 density intervals (HDI) lower bound and upper bound). If the HDI does not encompass zero, we  
 12 consider there to be a meaningful difference between the groups/conditions. We find a main  
 13 effect of group on the punishment learning rate and lapse parameters (in bold).

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