Journal of Experimental Psychology: Learning, Memory, and Cognition

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Online First Publication, September 13, 2021. http://dx.doi.org/10.1037/xlm0001033

AMERICAN PSYCHOLOGICAL ASSOCIATION

Journal of Experimental Psychology: Learning, Memory, and Cognition

ISSN: 0278-7393

https://doi.org/10.1037/xlm0001033

The Elusive Effects of Incidental Anxiety on Reinforcement-Learning

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Anxiety is a common affective state, characterized by the subjectively unpleasant feelings of dread over an anticipated event. Anxiety is suspected to have important negative consequences on cognition, decision-making, and learning. Yet, despite a recent surge in studies investigating the specific effects of anxiety on reinforcement-learning, no coherent picture has emerged. Here, we investigated the effects of incidental anxiety on instrumental reinforcement-learning, while addressing several issues and defaults identified in a focused literature review. We used a rich experimental design, featuring both a learning and a transfer phase, and a manipulation of outcomes valence (gains vs losses). In two variants ($N = 2 \times 50$) of this experimental paradigm, incidental anxiety was induced with an established threat-of-shock paradigm. Model-free results show that incidental anxiety effects seem limited to a small, but specific increase in postlearning performance measured by a transfer task. A comprehensive modeling effort revealed that, irrespective of the effects of anxiety, individuals give more weight to positive than negative outcomes, and tend to experience the omission of a loss as a gain (and vice versa). However, in line with results from our targeted literature survey, isolating specific computational effects of anxiety on learning per se proved to be challenging. Overall, our results suggest that learning mechanisms are more complex than traditionally presumed, and raise important concerns about the robustness of the effects of anxiety previously identified in simple reinforcement-learning studies.

Keywords: anxiety, threat-of-shock, reinforcement-leaning, computational modeling, valence-induced bias

Supplemental materials: https://doi.org/10.1037/xlm0001033.supp

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This work was supported by startup funds from the Amsterdam School of Economics, awarded to Jan B. Engelmann. Jan B. Engelmann and Maël Lebreton are grateful for support from Amsterdam Brain and Cognition (ABC). Maël Lebreton is supported by the Swiss National Fund Ambizione Grant (PZ00P3_174127). Stefano Palminteri is supported by an ATIP-Avenir Grant (R16069JS), the Program Emergence(s) de la Ville de Paris, the Fyssen foundation, the Agence National de la Recherche (ANR; FrontCog ANR-17-EURE-0017) and a Collaborative Research in Computational Neuroscience ANR-NSF Grant (ANR-16-NEUC-0004). Maël Lebreton and Jan B. Engelmann equally contributed to this article. We are grateful to E. J. Wagenmakers for helpful discussion on Bayes Factors. We also thank Isabela Lara Uquillas for help with data collection.

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The occurrence of negative events carries important information for an organism, enabling the adjustment of future behavior (Trapp et al., 2018). Yet, unpredictable negative events can also cause prolonged anxiety and adversely impact otherwise well-adjusted behaviors, including decisions (Hartley & Phelps, 2012; Schmitz & Grillon, 2012). For example, anxiety is usually associated with higher risk-aversion (Charpentier et al., 2017; Cohn et al., 2015) as well as increased reliance on habituated behaviors (Browning et al., 2015; Schwabe & Wolf, 2009). Moreover, anxiety also impacts the cognitive processes that fundamentally support decision-making, including attention (Bar-Haim et al., 2007; Bradley et al., 2000; Cisler & Koster, 2010; MacLeod & Mathews, 1988), memory (Balderston et al., 2017; Bolton & Robinson, 2017; Robinson et al., 2013; Vytal et al., 2013), and learning (Grupe, 2017).

The ability to learn efficiently to seek reward and to avoid punishments is one of the core features of adaptive behavior. Extensive evidence suggests that humans and animals learn by trial and error using algorithms akin to reinforcement-learning, so as to repeat actions that maximize the occurrence of reward and to suppress actions that lead to punishments (Rescorla & Wagner,

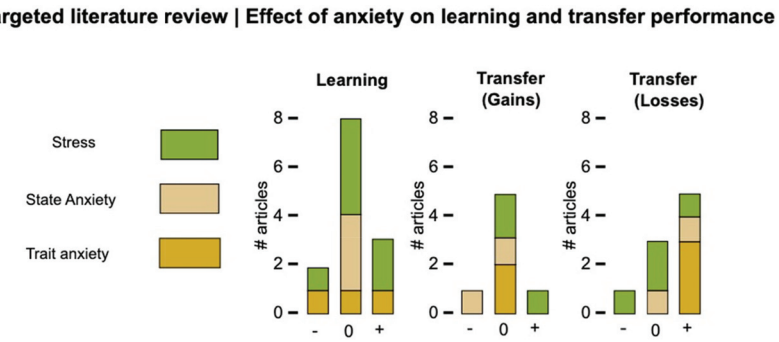
1972; Sutton & Barto, 1998). Given this pivotal role of reinforcement-learning in generating our behavior on the one hand, and the prevalence of anxiety in our daily lives on the other, it is important to garner a more detailed understanding of the effects of anxiety on learning in reward seeking and loss avoidance contexts. To accomplish this, we first review the literature investigating the impact of anxiety on learning (Berghorst et al., 2013; Browning et al., 2015; Cavanagh et al., 2019; DeVido et al., 2009; Robinson et al., 2013; Safra et al., 2018; Stevens et al., 2014; Voegler et al., 2019). While the focus of our experiments is clearly on anxiety, which we operationalize as a prolonged state of apprehension about unpredictable and aversive future events (e.g., Grillon et al., 2019; Schmitz & Grillon, 2012) in our targeted review we also draw upon the related and more extensive literature on the effects of stress on learning (Abraham & Hermann, 2015; Cavanagh et al., 2011; DeVido et al., 2009; Glienke et al., 2015; Lighthall et al., 2013; Mather & Lighthall, 2012; Otto et al., 2013; Petzold et al., 2010; Schwabe & Wolf, 2009; Treadway et al., 2017; Voegler et al., 2019; see Figure 1 and online Supplemental Materials Table S13).

An initial review of prior research suggests that to date there seems to be little consensus on the precise effect of anxiety and stress on reinforcement-learning, let al.one its potential neurobiological underpinnings (Cavanagh et al., 2019, 2011; Glienke et al., 2015; Robinson et al., 2013; Treadway et al., 2017; Voegler et al., 2019). While some studies suggest general positive effects of anxiety and stress on learning mediated by increased sensitivity to reward (Lighthall et al., 2013; Mather & Lighthall, 2012), other studies found a general detrimental effect on learning, which reportedly impair learning flexibility (Browning et al., 2015; Otto et al., 2013; Raio et al., 2017; Schwabe & Wolf, 2009).

Likewise, it is not clear how the effects of anxiety and stress on learning could depend on the valence of learning contexts (reward seeking vs loss avoidance). Again, although several studies have investigated this question, they have yielded somewhat contradictory results. For instance, Berghorst and colleagues (2013) found that threat decreased the probability of approaching a learned reward, but increased avoidance of losses. However, using the same task, other teams reported opposite results (Lighthall et al., 2013; Mather & Lighthall, 2012; Petzold et al., 2010) with some authors concluding that stress, a source of anxiety, facilitates the sensitivity to positive feedback (Lighthall et al., 2013; Mather & Lighthall, 2012).

To address these contradictory results more systematically, we conducted a targeted literature review of key studies (Figure 1, $N = 15$; see online Supplemental Materials Table S13 for inclusion/exclusion criteria) that investigate the impact of induced incidental anxiety, as well as trait anxiety on reinforcement-learning. As outlined in detail in online Supplemental Materials Table S13, our primary criterion for inclusion was the use of a two-armed bandit task commonly used to investigate reinforcement-learning The secondary inclusion criterion was the induction of incidental state anxiety. However, we also consider studies using trait measures of anxiety (that we also measure in our experiments). We clearly mark the distinction between induced anxiety (state) and trait measures of anxiety in Figure 1 and online Supplemental Materials Table S13. Moreover, we include research from a related literature on stress (Cavanagh et al., 2011; Glienke et al., 2015; Lighthall et al., 2013; Petzold et al., 2010; Schwabe & Wolf, 2009; Treadway et al., 2017). We graphically depict differences in the induction methods to clearly demarcate the effects of state and trait anxiety, as well as stress. The results from this literature review confirm the lack of consensus on the direction of the effects

Figure 1
Effects of Anxiety on Learning and Postlearning Performance Observed in Previous Studies (N = 15)



Note. The stack bars summarize previous findings about the effect of stress and anxiety on performance in learning (left panel), and transfer tasks, with the latter results further split into gains (middle-right panel) and losses (right panel). For each task category, we separately report the number of articles showing decreases (−), no changes (0) or increases (+) in performance due to stress and anxiety. The findings were categorized by stress manipulation (green) and anxiety manipulation (beige). Moreover, studies investigating the effects of anxiety were further separated into two subgroups based on whether they investigated causal effects of induced anxiety (state, light beige), or trait anxiety (dark beige). More detailed information about the exact anxiety and stress induction methods, trait measures and number of participants used in each study can be extracted from online Supplemental Materials Table S13. See the online article for the color version of this figure.

of anxiety and stress on learning performance (see Figure 1). This is particularly true for the effects of stress and anxiety on learning per se, where most studies report a null effect and an approximately equal number report positive and negative effects on learning performance. This suggests a null effect of anxiety on learning performance, which we here test using Bayesian statistics. However, in regard to transfer performance, an association between trait anxiety and better discrimination of losses seems to be emerging. These puzzling observations point to a more complex role of anxiety in learning than initially thought (Robinson, Overstreet, et al., 2013), as they show potentially differential effects of anxiety depending on task and valence.

To resolve the seemingly contradictory effects of anxiety reported in prior research, we identified three main experimental dimensions which regularly differ between studies, and whose investigation could illuminate some of the discrepancies in the effects of anxiety on learning observed previously. These three dimensions, detailed in the following sections, cover (a) the methods of anxiety induction, including the nature of the stressor, and the dynamics and intensity of the induced anxiety; (b) the measures of learning performance; and (c) the manipulation of outcome valence.

Regarding the first factor, namely anxiety induction, a large variety of methods and protocols have been used in the literature. In fact, these may in part account for the wide-ranging effects observed in our targeted literature review. A significant proportion of studies investigating the impact of stress on learning have used paradigms such as the Cold Pressor Test (CPT; Porcelli et al., 2012) and the Trier Social Stress Test (TSST; Jackson et al., 2006; Petzold et al., 2010), which suffer from some notable drawbacks: these induction techniques operate before the learning task, making the actual emotion state less contingent with the task of interest and introducing uncertainty with respect to the complex dynamics of the emotion intensity and related endocrine reactions (Hermans et al., 2014; Robinson, Vytal, et al., 2013). In fact, at about 20–30 min poststressor the initial catecholaminergic response begins to interact with a glucocortoid response (Gagnon & Wagner, 2016). At this point, corticosterone (or cortisol, a glucocorticoid stress hormone) levels peak and provide a window to observe the effects of acute stress on behavior. However, shortly after this, peak cortisol levels start declining (Hermans et al., 2014; Jackson et al., 2006) and continue to decline throughout the period during which behavioral tasks are typically conducted (30–60 min). Stress induction before the task leads to complex and dynamic interplays between different hormones that rise and decline while participants perform the task (Gagnon & Wagner, 2016). How this impacts experienced emotions is also unclear. In fact, at the level of subjective feelings, the period following a stressful event has been associated with a subjective state of relaxation, rather than a state of stress or anxiety (Takahashi et al., 2005). Moreover, these stressors are not unpredictable, which is a critical factor of anxiety (Schmitz & Grillon, 2012). A significant portion of the studies reviewed above might not investigate the effects of prolonged anxiety, but instead complex poststress recovery processes (Hermans et al., 2014). In the current experiments, we addressed this issue by using the well-established Threat of Shock (ToS) procedure to reliably induce anxiety during the learning task (Engelmann et al., 2015; Grillon, 2008; Schmitz & Grillon, 2012). ToS enables researchers to flexibly turn threat on and off (by contrasting periods during which electrical shocks are administered with periods of relative safety), which offers important advantages over other induction methods, including the ability to conduct experiments within subjects and measuring in real time the causal effects of anxiety on behavior.

Second, previous studies differ in what they refer to as *learning*. Two main experimental paradigms have been used to assess learning performance, which differ significantly in the aspect of learning they assess. More specifically, a first set of tasks (Figure 1, middle-left panel) primarily assesses the dynamic evolution of learning (*learning tasks*), while a second set of tasks (Figure 1, middle-right and right panel) mostly assesses postlearning preferences, much like extinction tests commonly used in the animal learning literature (*transfer tasks*). Learning tasks directly assess the correct response rate during probabilistic instrumental-learning (see, e.g., Pessiglione et al., 2006) and typically require participants to make repeated choices between fixed pairs of stimuli. Transfer tasks involve similar learning during an initial learning stage that provides feedback about the accuracy of participants' choices. However, learning performance is assessed after learning has already taken place in the form of an extinction test that involves novel pairings of the same stimuli and no longer includes feedback (see Frank et al., 2004). Although these tasks seem very similar, those two ways of measuring learning performance have been shown to produce qualitatively different results, for example, in the case of context-dependent learning (Klein et al., 2017; Palminteri et al., 2015). Accordingly, using different paradigms to capture the effects of anxiety on learning might not lead to comparable results across studies. We address this here by including both types of tasks in our experiments and separating these in our small-scale literature review, enabling us to assess the impact of anxiety on both learning and postlearning preferences.

Finally, despite the suggestions that the impact of anxiety could be valence-dependent, few studies have explicitly manipulated the valence of outcomes (gains vs losses) to contrast reward seeking and loss avoidance under conditions of anxiety (Berghorst et al., 2013; Cavanagh et al., 2011; Lighthall et al., 2013; Petzold et al., 2010). Instead, most studies have typically either limited their investigations and claims to one valence or reframed low reward probabilities as an avoidance context (Schwabe & Wolf, 2009; Stevens et al., 2014). Neither of these approaches is actually suitable to investigate potential valence-specific effects of anxiety on learning (Palminteri & Pessiglione, 2017). We address this here by including both reward and punishments in our experiments. This enables us to assess the differential impact of anxiety on reward seeking and punishment avoidance.

In the present study, we designed two experiments investigating the impact of incidental anxiety on reinforcement-learning to systematically address the shortcomings identified above. By incidental anxiety we mean task-independent state anxiety that is commonly contrasted with integral anxiety (e.g., Engelmann & Hare, 2018). Incidental emotions are caused by events that are unrelated to the decision at hand, such as the emotional state caused by the current pandemic that can influence our purchasing behavior (Laato et al., 2020). Moreover, anxiety is typically (yet controversially) distinguished from fear and stress. While fear is a phasic and intense affective reaction to immediate and identifiable threat resulting in the fight-or-flight response, anxiety is a prolonged anticipatory response to unpredictable and potentially aversive events (Duval et al., 2015; Grillon et al., 2019). Stress can be defined as the unspecific psychological and physiological reactions in response to physical challenges, cognitive demands,

and social evaluative threat (e.g., Starcke & Brand, 2012). Anxiety, fear and stress are partially distinct, but clearly related affective states that share overlapping neural circuitry (e.g., Duval et al., 2015; Hur et al., 2020) but also have distinct neural circuits and mechanisms (e.g., Grillon et al., 2019). While these concepts are clearly interrelated, our goal here was to induce incidental (state) anxiety. We follow the literature (Schmitz & Grillon, 2012) and use ToS as a well-established anxiety induction method throughout the learning task, as this method reliably and flexibly induces anxiety via unpredictable and aversive electrical shocks (Engelmann et al., 2015, 2019; Grillon, 2008; Schmitz & Grillon, 2012). Moreover, we measure trait anxiety to capture individual differences in the predisposition to feel anxious. In two different implementations of the task, we varied the dynamics and intensity of the anxiety induction, by applying ToS within relatively shorter blocks consisting of three trials or relatively longer periods consisting of the entire period of a learning session. In both experiments, shock intensity was calibrated for each individual. Second, we used a combination of tasks assessing both learning and transfer performance (Palminteri et al., 2015). Finally, we explicitly manipulated the valence of outcomes (gains and losses) to assess potential valence-specific effects of anxiety on learning (Pessiglione et al., 2006).

Regarding the analytical strategy, we first analyzed our data using standard linear mixed models that assess learning in different contexts on a trial-by-trial basis. Moreover, to more specifically assess how anxiety impacts on the underlying computations during learning and to parsimoniously make sense of this high-dimensional behavioral data, we used a recently developed computational modeling framework built around the concept of context-dependent learning (Palminteri et al., 2015, 2017). We aimed to identify the effects of anxiety on learning and its robustness across tasks and conditions: in other words, conditional on addressing what we identified as important caveats in previous studies (anxiety induction method based on ToS, explicit dissociation of learning and transfer performance, explicit gain and loss contexts), truly robust effects of anxiety should not be idiosyncratic to a specific experimental design, and should be comprehensively captured by computational modeling. We specifically hypothesized that anxiety would impact context-dependent learning and/or valence-specific learning conditioned by context-dependent-learning. Despite our rigorous, comprehensive and high-powered experimental and analytical approaches, we found no clear, specific effect of anxiety on learning. In line with the lack of apparent consensus observed in the literature, our results seem to indicate that the average effects of incidental anxiety on learning are at best elusive.

General Method

Subjects

One hundred fourteen right-handed subjects were recruited from the subject-pool of the Center for Research in Experimental Economics and Political Decision Making (CREED, www.creedexperiment.nl), and 100 subjects were analyzed in the end (Table 1; total: 51 males, aged 19–32, mean ± *SD* = 23.27 ± 3.08). We excluded four and 10 subjects from Experiment 1 and Experiment 2, respectively, either because of technical problems or average learning performance that was significantly lower than guessing level as identified via a binomial test assessing performance (i.e., requiring a 50% performance at an alpha level of .01). All subjects were prescreened via a questionnaire. Inclusion criteria consisted of (a) no history of psychiatric and neurologic disorders, (b) not taking medicine for anxiety or depression, (c) no implanted electric devices in the body (that electric shocks might interfere with), and (d) right-handedness. All subjects gave their written informed consent before participation, after being given instructions about the task, the safety of electrical stimulation and their rights as participants. All procedures were executed in compliance with relevant institutional guidelines and were approved by the Economics and Business Ethics Committee (EBEC) at the University of Amsterdam.

Table 1
Demographics and Questionnaire

Variable	Combined	Experiment 1	Experiment 2
Gender (M/F)	51/49	26/24	25/25
Age	23.27 ± 3.08	24.14 ± 3.09	22.40 ± 2.85
BAI	10.17 ± 8.61	9.90 ± 8.43	10.44 ± 8.86
STAI_T	(*N* = 85) 41.92 ± 8.88	(*N* = 40) 42.42 ± 8.76	(*N* = 50) 41.52 ± 9.05
SCR (Threat vs. Safe)	0.054 ± 0.06	0.09 ± 0.06	0.01 ± 0.04
	Self-reported emotional state toward threat condition		
Anxiety	3.53 ± 1.87	4.33 ± 2.01	2.82 ± 1.40
Fear	3.29 ± 2.04	3.95 ± 2.32	2.70 ± 1.55
Sadness	1.96 ± 1.29	2.33 ± 1.50	1.64 ± 0.96
Happiness	2.61 ± 1.65	2.62 ± 1.83	2.60 ± 1.49
Anger	2.31 ± 1.77	3.02 ± 2.06	1.68 ± 1.15
Negative feeling (Safe)	—	—	3.48 ± 1.63
Negative feeling (Threat)	—	—	4.68 ± 1.42
Calm feeling (Safe)	—	—	6.50 ± 2.15
Calm feeling (Threat)	—	—	4.86 ± 1.78

Note. BAI = Beck Anxiety Inventory; SCR = skin conductance responses; STAI_T = State–Trait Anxiety Inventory. Reported values correspond to mean ± *SD*.

Timeline of Procedure

We invited potential subjects from the CREED subject-pool, and asked them to complete a battery of questionnaires at least 1-day before the main task for an initial endowment of 10 Euros. When subjects arrived at the lab, they were asked to thoroughly read the instructions and consent form and were allowed to ask questions to ensure understanding. We then orally explained the task if necessary. Subjects' nondominant hand (i.e., left hand) was then fitted with different electrodes meant to measure SCRs and deliver electric shocks. The successful setup was then followed by a calibration of shock intensity (see Anxiety Induction), and a short training session (see Behavioral Task) while recording electrodermal activity. Subsequently the main task started and subjects completed two (four) sessions in Experiment 1 (Experiment 2). Halfway through the learning experiments (i.e., before the second session for Experiment 1, and before the third session for Experiment 2), an additional calibration session was performed to control for (de)sensitization to the electrical stimulation. After the last learning session (the second session for Experiment 1, the third and fourth session for Experiment 2), subjects completed the transfer task and an exit questionnaire. The total participant fee, including endowment amount and accumulated outcome from the learning task, was handed to subjects in cash after completion of the exit questionnaire. The whole experiment took around 90 min, including instructions, electrodes setup time, exit questionnaire, and payment (average amount earned in Experiment1: mean $\pm$ *SD* = 21.54 $\pm$ 4.21; Experiment 2: mean $\pm$ *SD* = 26.96 $\pm$ 6.4).

Experimental Paradigm

All experimental paradigms were programmed and conducted with Matlab 2017b with the Cogent library (http://www.vislab.ucl.ac.uk/cogent.php).

Learning Task

Subjects performed a probabilistic instrumental learning task adapted from previous imaging, developmental and clinical studies (Palminteri et al., 2015, 2016; Salvador et al., 2017). They were instructed that the aim of the task was to maximize their payoff, by learning to choose the best cue out of cue pairs. They were explicitly told that seeking monetary reward and avoiding monetary losses were equally important.

The experimental structure consisted of learning sessions (longer periods that contained cue pairs that were specifically associated with one condition per pair), blocks (containing three trials presented within the same experimental condition), and individual trials. Each learning session contained four novel, fixed cue pairs that were associated with one specific condition from the 2 (outcome valence: Gain vs. Loss) $\times$ 2 (anxiety: Safe vs. Threat) within-subject design. The association of each cue pair with one specific condition remained the same for the duration of one learning session (Figure 2B; Safe/Gain, Safe/Loss, Threat/Gain, Threat/Loss). New learning sessions were presented after a brief break of about 2 min and offered novel associations between previously unseen cue pairs and specific conditions. In the Gain conditions, possible outcomes were .5 or 0. Symmetrically, in the Loss conditions, possible outcomes were $-.5$ and 0. The cue-outcome associations were determined by reciprocal but independent binomial probabilities, 75% or 25% (Figure 2B). Therefore, successful learning entailed choosing the cue associated with the higher probability of reward in the gain domain, and choosing the cue associated with the lower probability of loss in the loss domain.

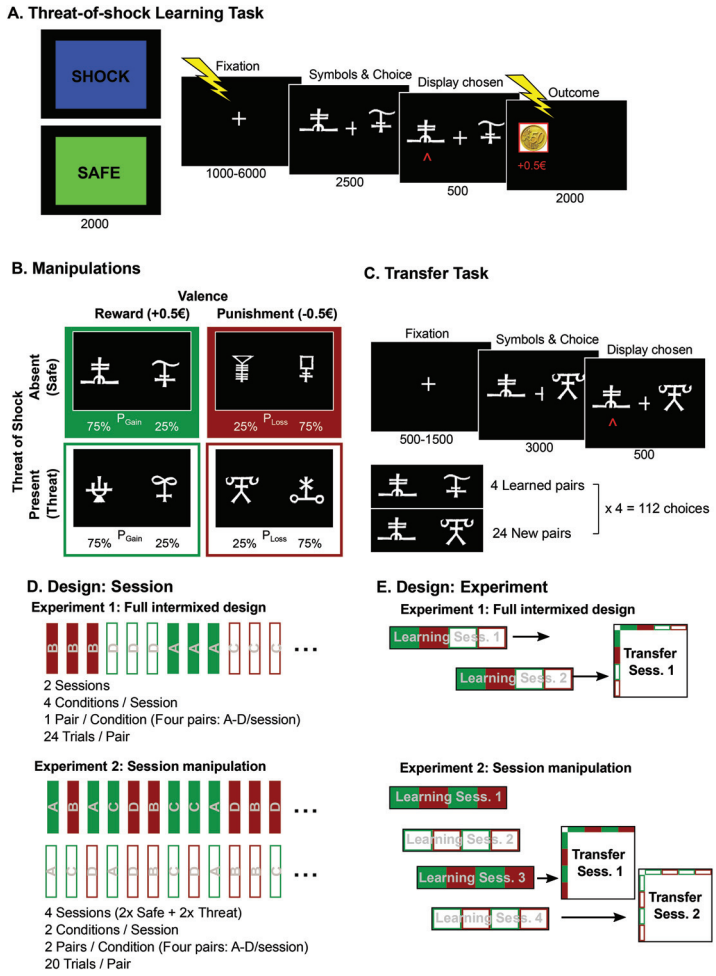
Each block in Experiment 1 (and each session in Experiment 2) started with a 1,000 ms reminder cue indicating the anxiety condition for the upcoming trials (i.e., "SHOCK" or "SAFE" associated with a frame of a particular color that was counterbalanced across subjects—see Figure 2A) that was shown before the first trial. The reminder cues were followed by a fixation cross (1,000–6,000 ms) and three trials. Each trial first featured a pair of cues (2,500 ms). During this cue display, subjects indicated their decision by pressing the left or right arrow key to choose the left or right cue, respectively. The position of the options was counterbalanced. After 2,500 ms, an arrow appeared under the chosen cue (500 ms). If subjects did not respond in the allocated 2,500 ms, this phase was omitted and subjects would get the relatively worse outcome in the feedback phase (i.e., $-.5$ in the loss domain; 0 in the gain domain). In contrast, if subjects successfully made decisions in time, the outcome associated with the chosen option was revealed (2000 ms). Both trials and miniblocks were separated by a jittered fixation cross (1,000–5,000 ms).

In Experiment 1, anxiety was induced through a ToS protocol used in previous studies (Engelmann et al., 2015, 2019). More specifically, to maintain the emotional state for a prolonged period of time, we used a blocked presentation of the ToS conditions, such that three consecutive trials of the learning task were presented either under threat, or under safety (Figure 2D). Therefore, Experiment 1 comprised two sessions, each including 96 trials (i.e., 32 blocks) and featuring a new, different set of eight cues (i.e., four pairs of cues) in each session. The Threat blocks were pseudorandomly interleaved to avoid repeating the same emotional treatment (Safe or Shock) more than two consecutive times and the order of threat-first and safety-first blocks was counterbalanced across subjects. In Experiment 2, we modified the experimental design and varied the ToS condition across separate sessions of 80 trials (with 20 repetitions of the four cue pairs; see Figure 2D). This was done to reduce the frequent switching of emotional states required by the relatively short blocks: the dynamics of emotion being notoriously slow (Williams et al., 2004), we wanted to exclude the possibility of spill-over effects of anxiety on Safe blocks. Consequently, only the valence of outcomes was manipulated within a session. Each session still featured four cue pairs, probabilistically associated with gains or losses. Experiment 2 comprised four learning sessions (two implementing the Safe condition and two implementing the Threat condition, interleaved) and the order of threat-first and safety-first blocks was counterbalanced across subjects, with 50% of subjects receiving the order (threat, safe, threat, or safe) and the other 50% the reverse order.

Transfer Task

After completing the learning task, subjects performed a transfer task (Palminteri et al., 2015). The task was built around the eight cues used in the last session(s) of the learning task. Participants were asked to choose between pairs of cues and indicate which cue they preferred. Yet, contrary to the learning sessions where cue pairs were fixed, all possible pairs were built from pairing each cue with the other seven cues, leading to 28 combinations.

Figure 2
Experimental Paradigm



Note. (A) Threat-of-Shock (ToS) learning task. Schematic representation illustrating the learning task under safe and threat conditions for both Experiment 1 and Experiment 2. A stimulus cue reminding participants of threat contingencies (SAFE/SHOCK) was presented at the beginning of each block, followed by three trials. In the threat condition, electric shocks were administered unpredictably (in timing and number of shocks) to participants inducing anxiety. (B) ToS manipulation. In the two-by-two within-subject design, anxiety (i.e., absence and presence of threat of shock for safe and threat conditions, respectively) and outcome valence (i.e., gain and loss) were associated with specific cue pairs. Each cue pair was consistently presented within a specific Valence × ToS condition for the duration of one session and not in any other condition. For illustration purposes, green and red represent gain and loss, and filled and unfilled rectangles represent safe and threat. In the experiment, blue and green backgrounds were used to remind subjects that the current condition is either safe or threat. (C) Transfer task. Twenty-four novel cue pairings were formed by pairing each cue with all others in the transfer task. These new and original pairs were repeated four times, resulting in 112 choices. (D) Experimental design for each session in Experiment 1 and Experiment 2. Each subject experienced two (Experiment 1) or four (Experiment 2) sessions in a row. Top: Experiment 1: Full intermixed design. Each session presented cues from all four conditions (Threat × Valence). Bottom: Experiment 2: Session manipulation. Threat conditions were separated by session, such that Gain or Loss cues were presented exclusively in ToS or Safe conditions within each session of 80 trials. (E) Experimental design for both learning and transfer task. Top: Experiment 1: Full intermixed design. The transfer task took place after the second session and contained cues from all four conditions. Bottom: Experiment 2: Session manipulation. The transfer task took place after the third and fourth sessions. The cues used in the transfer task were drawn from two of four conditions, depending on the emotional state of the previous session. See the online article for the color version of this figure.

Each pair was repeated four times, resulting in 112 trials (Figure 2C). Decisions were self-paced, and not followed by feedback about the decisions. Subjects were not informed about the post-learning task until they had completed the learning task, so as to avoid explicit memorization strategies.

In Experiment 1, the transfer task was conducted after the second learning session, which contained cues from both threat and safe conditions (Figure 2E, top). In Experiment 2, the transfer task was conducted after the third *and* fourth session, to elicit choices between cues from both threat and safe conditions (Figure 2E, bottom).

Monetary Compensation

In both experiments, all subjects received a payment that included an initial endowment of 10 Euros for filling in the questionnaire before the experiment, a performance-based bonus based on all trials from the learning task (including gain and loss trials), and a final bonus (.5€for each question, totally four questions) for correctly recognizing cues used in the task as part of the exit questionnaire.

Anxiety Induction

The incidental anxiety was induced by the presence of unpredictable and mildly painful electric shocks in the Threat condition (Engelmann et al., 2015, 2019; Grillon et al., 2004). The shock stimulation was generated by a DS5 Isolated Bipolar Constant Current Stimulators (Digitimer Ltd.), and delivered through two electrodes. The electrodes were attached to the wrist of the nondominant (left) hand throughout the experiment where they were taped with Velcro. Calibrations for the intensity of electric stimulation took place three times in both Experiment 1 and 2. In Experiment 1, calibration occurred before the first and second learning sessions, and before the transfer task. In Experiment 2, which consisted of four learning sessions, the calibration took place before the first and third learning sessions, and after the last transfer task. Calibration at these time points accounts for desensitization toward the shock intensity throughout the experiment (see online Supplemental Materials Figure S1).

The DS5 stimulator generated stable electric shocks with a fixed maximum input of 5V, maximum output of 25 mA and a stable duration of 50 ms across subjects and studies. Only the intensity of shocks was individually customized for each learning session to match each subject's pain threshold. This was achieved using a staircase procedure asking subjects to evaluate the painfulness of delivered electric shocks on a visual analog scaling ranging from 0 (*not painful at all*) to 10 (*extremely painful*) (Engelmann et al., 2015, 2019; Story et al., 2013). The shock intensity was initialized at 10% of the maximum output (i.e., 2.5 mA) and was then iteratively increased or decreased by 10% based on the following rules. If two consecutive ratings for the same intensity were less than 7, the intensity in the third trial would be increased by 10%. On the other hand, the intensity would be decreased when the rating was above 9. The procedure terminated as soon as the shock intensity was rated between 7 and 9 three times in a row, and we used this value in the subsequent learning sessions. During the calibration, the electric stimulations were self-triggered, that is, subjects could deliver the electric pulses by pressing the Enter key themselves. To avoid sensitization or desensitization, the intensity of electric stimulation was calibrated before and after each learning session in the Experiment 1, and was calibrated before and after every two learning sessions in the Experiment 2.

During the learning sessions, subjects were not informed about the number of shocks and the precise time point of shock stimulation to maintain the unpredictability of electrical shocks. In Experiment 1, the number of shocks for each miniblock in the Threat condition was randomly drawn from the predetermined set [1 1 3 3 3 3 5 5] without replacement, leading to an average number of three shocks per block (SD = 1.63). This approach ensures that the number and the timing of shocks within a given block remains unpredictable to participants, avoiding a period of relative safety within Threat blocks. The timing of the shock was randomized within the period of a threat block with the constraint that two consecutive shocks should be spaced more than 0.2 s apart. Subjects were explicitly notified that the shocks were unpredictable, uncontrollable and independent of their performance. Similar procedures were applied to Experiment 2 with the exception that three electric shocks were delivered at random intervals within in each Threat session.

An important advantage of the ToS anxiety induction procedure is that anxiety states can be switched on and off during the task. To make sure that subjects were subjected to this anxiety manipulation, miniblocks (Experiment 1) and sessions (Experiment 2) started with a reminder (i.e., "SAFE" or "SHOCK") and a color frame (i.e., green or blue; independent of the valence factor, Figure 2A). The color frame was displayed until the end of the miniblock (Experiment 1) or session (Experiment 2). The assignment of color frames to Safe and Threat conditions was counterbalanced across subjects.

Screening Questionnaire

Data collected with the screening questionnaire was used to (a) prescreen the subject by inclusion and exclusion criteria, and (b) assess a range of state and trait emotions. Exclusion criteria were examined first, and used to determine whether the subject qualified for the experiment (see Subjects). The screening questionnaire also included a basic demographic survey, Beck Depression Inventory (BDI: to index depression symptoms; Beck et al., 1988); Beck Anxiety Inventory (BAI: to index clinical anxious symptoms; Beck et al., 1988); State–Trait Anxiety Inventory (STAI: to index state- and trait- anxiety; Spielberger et al., 1983); and Positive and Negative affect schedule (PANAS: to index currently positive and negative affect; Watson et al., 1988). Finally, to avoid attentional biases from novel cues, the cues used in the experiment were displayed in the end of questionnaire for 60s, so that subjects have chance to explore them before the main task.

Exit Questionnaire

The exit questionnaire required subjects to retrieve and report their emotional state on a 7-point scale and to explain the strategies they used in the task. For the self-reported emotions, subjects were asked to separately rate how often they felt seven emotional-states (i.e., Anxiety, Fear, Happiness, Sadness, Anger, Surprise, and Disgust) during the threat condition (from 0 = *never* to 7 = *every time*). In Experiment 2, a few additional questions were added, where subjects reported (a) the intensity of their emotional-state

on the above emotions, and (b) their negative affect (from 0 to 7: positive to negative) and arousal level (from 0 to 7: arousal to calm) during both threat and safe conditions. In the last part of the exit questionnaire, we included a recognition task that provided a chance for subjects to earn a bonus. The recognition task presented four known cues and four novel cues that were not used in the experiment. Subjects were asked to indicate whether they have previously seen each cue in the task or not.

Skin Conductance Responses (SCRs)

SCR Acquisition

The SCRs were measured by Ag/AgCl electrodes filled with gel, and recorded via an amplifier and the software Vsrrp98 (Version 7.29). After the instruction, two electrodes were attached on the ring and third fingers of the left hand using medical tape. SCR data was collected at 1,000 Hz from the beginning to the end of the learning sessions (with the exception of 37 subjects in Experiment 1 for which a sampling rate of 500 Hz was used). SCR data was synchronized with task events based on markers that indexed block/session onsets, trial onsets and feedback onsets.

SCR Analysis

Before statistical analyses, each participant's SCR data were preprocessed using the following steps: the data underwent (a) despiking by replacing outlier signals (defined as signals $> = 3$ times the standard deviation), (b) down-sampling to 10 Hz, and (c) normalization by z-scoring the data. The SCRs were analyzed as phasic responses relative to the trial onset (Bradley et al., 2000; Clark et al., 2012). Specifically, we extracted SCRs for the time window covering 2–4 s posttrial onset and averaged the SCR response. From this we subtracted the trial-specific baseline, which was the mean SCR covering the 1-s period preceding trial onset (i.e., mean SCR during Intertrial Interval). To avoid potential confounds caused by the delivery of the electric shock, the trials including shocks were not included in the analysis. Averages for each condition were then entered into a two-way repeated measure analysis of variance (ANOVA) with outcome valence (gains vs. losses) and anxiety treatment (safe vs. threat) as within-subject factors. Note, that one (Experiment 1) and five (Experiment 2) subjects were excluded from the SCR analysis, because of the low quality of the recorded SCR signal.

Behavioral Analysis

Learning Task Analysis

Correct choices from the learning task were extracted and served as a binary outcome variable (coded 1/– respectively 0 – for a choice of the cue associated with the highest—respectively lowest—objective expected value). Averaged correct choice rates were computed per condition and per subject, and analyzed via a repeated-measures two-way ANOVA with (a) valence and (b) anxiety as factors, subject ID as a random effect, and a full interaction structure. To assess the effect of the differences in design between our two experiments on the different effects, we also added experiment number as between-subjects factor in the original ANOVA. Paired t-test were used to evaluate post hoc comparisons between specific conditions.

As a complementary—and presumably more powerful—analysis, we also analyzed trial-by-trial data using a generalized linear mixed-effect (GLME) model. GLME models included independent variables accounting for the trial number (computed per condition, i.e., Experiment 1: trial = 0:1:23; Experiment 2: trial = 0:1:19), feedback valence (gain= 1; loss = −1), anxiety (threat = 1; safe = −1), and their two- and three-way interaction terms (Valence × Anxiety × Trial). These variables were used in both the fixed-effects and the random-effects structure. The random effects structure accounted for the differences in experimental setups (coded 1 or 2 for Experiment 1 and Experiment 2, respectively) and interindividual variations (subject's ID), which is nested within experiments. In Wilkinson-Rogers notation, this GLME writes as follows:

$$\begin{aligned}\mathrm{GLME1}_{\mathrm{Learning}} : \ & \mathrm{Correct} \sim (\mathrm{Intercept}) + \mathrm{Valence} \times \mathrm{Anxiety} \\ & \times \mathrm{Trial} + (1 + \mathrm{Valence} \times \mathrm{Anxiety} \\ & \times \mathrm{Trial} \,|\, \mathrm{Experiment}/\mathrm{Subject});\end{aligned}$$

Given that the dependent variable was binary (the correctness of the choice) we used a logistic link function.

To directly assess the potential effects of the experimental designs on the manipulation effects, we also estimated the following GLMEs:

$$\begin{aligned}\mathrm{GLME2}_{\mathrm{Learning}} : \ & \mathrm{Correct} \sim (\mathrm{Intercept}) + \mathrm{Valence} + \mathrm{Anxiety} \\ & \times \mathrm{Experiment} \times \mathrm{Trial} \\ & + (1 + \mathrm{Valence} + \mathrm{Anxiety} \\ & \times \mathrm{Experiment} \times \mathrm{Trial} \,|\, \mathrm{Subject}).\end{aligned}$$

Transfer Task Analysis

Similar to the learning task, the data from the transfer task was analyzed with both a repeated-measures ANOVA and GLME model. To impose similar data structures in Experiment 1 and in Experiment 2, we limited our analysis of Experiment 1 transfer pairs to trials where both cues were presented in the same Anxiety condition (i.e., both Safe or both Threat). Average choice rates for each cue were computed, and analyzed using a three-way repeated-measures ANOVA with (a) option valence, (b) quality (option expected value: coded 1 if cue was the best of its pair during learning, 0 otherwise), and (c) anxiety manipulation as within-subjects factors, subject ID as a random effect, and a full interaction structure. Again, we added experiment number as between-subjects factor to the original ANOVA to account for the potential effects of design differences between our two experiments.

Because the preference relationship between intermediate values (i.e., Gain 25%—referred to as G25—and Loss 25%—referred to as L25) provide information about contextual learning (Palminteri et al., 2015), we ran additional analyses that focused on those cues. We submitted the choice rate of cues G25 and L25 to a two-way ANOVA with (a) option valence and (b) emotion manipulation. Afterward, we separately analyzed them for each comparison using a one-sample t-test.

Like for the learning task data, the transfer task data was further analyzed more comprehensively at the trial-by-trial level using a GLME approach. The model included independent variables accounting for differences between right and left cues, such as Diff_valence (difference in valence during learning) and Diff_quality (difference in the likelihood of avoiding a loss/attaining a gain during learning), and whether cues were learned in the context of threat (threat = 1, safe =0) and their interactions. These variables were entered into a logistic linear mixed model to predict binary choice based on the same structure of fixed- and random-effects, and also accounting for experiment (coded 1 or 2 for Experiment 1 and Experiment 2, respectively) and interindividual variations (subject's ID), which is nested within experiment. In Wilkinson-Rogers notation, this GLME writes as follows:

$$\begin{aligned}\text{GLME1}_{\text{Transfer}} : \text{ChooseRight} \sim (\text{Intercept}) &+ \text{Diff\_Valence} \\ &\times \text{Diff\_Quality} \times \text{Anxiety} \\ &+ (1 + \text{Diff\_Valence} \times \text{Diff\_Quality} \\ &\times \text{Anxiety} \mid \text{Experiment/Subject});\end{aligned}$$

Additional GLMEs added experiment number as fixed effect to assess its effect on experimental manipulation effects:

$$\begin{aligned}\text{GLME2}_{\text{Transfer}} : \text{ChooseRight} \sim (\text{Intercept}) &+ \text{Diff\_Valence} \\ &+ \text{Diff\_Quality} \times \text{Anxiety} \times \text{Experiment} \\ &+ (1 + \text{Diff\_Valence} + \text{Diff\_Quality} \\ &\times \text{Anxiety} \times \text{Experiment} \mid \text{Subject});\end{aligned}$$

All statistical analyses were performed using Matlab R2015a. GLME models were estimated using the function fitglme.

Computation of Bayes Factors

To quantify evidence in favor of the null hypothesis that anxiety does not have an effect on learning performance and postlearning preferences we computed Bayes factors, which we report as BF_{01} to reflect support for the null hypothesis. For ANOVAs, we use the software package JASP to compute Bayes Factors. Specifically, we used the Bayesian repeated-measures ANOVA function within JASP. First, JASP identifies the best model by computing the posterior probability among all possible models represented within the full model. Next, each model is compared with the best model to compute model-specific Bayes factors. For the analysis of learning effects, across all data sets, the best model is the null model. For the transfer task data, the best model differs across experiments: in Experiment 1, the model including the Valence × Quality interaction won. In contrast, the best model in Experiment 2 and the combined dataset is the model with main effects for valence and quality.

For GLMEs we follow the approach by Wagenmakers (2007). Specifically, for all models listed above, we estimated a reduced model that excludes the anxiety fixed-effect, but maintains the anxiety random-effect. We then computed the Bayesian information criterion (BIC) for the full and reduced model. Finally, we computed the Bayes Factor values using the following equation (Equation 10 in Wagenmakers, 2007):

$$BF_{01} \approx exp\left(\frac{BIC(H_1) - BIC(H_0)}{2}\right)$$

where BF_{01} represents the Bayes factor in favor of the null hypothesis, while BIC(H1) and BIC(H0) denote the fit of the models with and without the anxiety fixed-effect (Wagenmakers, 2007).

Computational Modeling

Step 1: Identifying the Best Computational Architecture. In a first modeling stage, we aimed to identify the general algorithm governing learning, regardless of the anxiety condition. Following a previous approach (Rescorla & Wagner, 1972), we first built a nested model-space (model Space 1), including six increasingly complex RL models. The six models are referred to as ABS, REL, REL_w, ABS_a and REL_a, and $REL_{a,w}$, where REL and ABS, respectively, referred to ABSOLUTE and RELATIVE, 'a' to asymmetric, and 'w' to weighted counterfactual outcome. The ABSOLUTE and RELATIVE models were introduced in (Palminteri et al., 2015).

In the ABSOLUTE model, at each trial t, the chosen option c of the current context s is updated with the Rescorla-Wagner rule (Rescorla & Wagner, 1972):

$$Q_{t+1}\ (s,c) = Q_t(s,c) + \ \alpha \times \delta_t \tag{1}$$

In Equation 1, Q refers to option value, α is the learning rate for the chosen option and $\delta_t$is the prediction error term calculated as follows:

$$\delta_t = R_t(s) - Q_t(s,c) \tag{2}$$

where R denotes outcome of the chosen option.

In the RELATIVE model, a choice context value ($V(s)$) is also learned and used as the reference point to which an outcome should be compared before updating option values.

$$\delta_t = R_t(s) - V_t(s) - Q_t(s,c) \tag{3}$$

Context value is also learned via a delta rule:

$$V_{t+1}\ (s) = V_t(s) + \ \alpha_V \times \ \delta_{V,t} \tag{4}$$

where α_V is the context value learning rate and δ_V is a prediction error-term calculated as follows:

$$\delta_{V,t} = (R_t(s) + \neg R_t(s))/2 - V_t(s) \tag{5}$$

$\neg R_t(s)$ indexes the outcome of the counterfactual option, which is unknown to subjects, in context s, and is computed as follows:

$$\neg R_t(s) = \begin{cases} 0 \ \textit{if} \ R_t(s) = -0.5 \ \textit{or} \ 0.5 \\ 0 \ \textit{if} \ R_t(s) = 0 \ \textit{and} \ V_t(s) = 0 \\ 0.5 \ \textit{if} \ R_t(s) = 0 \ \textit{and} \ V_t(s) > 0 \\ -0.5 \ \textit{if} \ R_t(s) = 0 \ \textit{and} \ V_t(s) < 0 \end{cases} \tag{6}$$

Therefore, $\neg R_t$ captures the fact that participants infer that the nonselected cue is associated with the complementary outcome to

the one they actually received. The formulation of $\neg R_t$ depends on the context value $V_t(s)$ because context values have to be disambiguated (i.e., gain or loss context) before participants can infer the outcome that is complementary to 0. Note that this specification slightly differs from the original model proposed in (Palminteri et al., 2015), which writes:

$$\delta_{V,t} = (R_t(s) + Q_t(s,u))/2 - \mathrm{V}_t(s) \tag{7}$$

where $Q_t(s,u)$ is the Q-value of the unchosen option u.

The proposed modifications to the RELATIVE model (Equations 4 and 5) are meant to account for the significant context dependency observed in our data, evidenced in the Transfer task data (see Results, model-based analysis indicates that learning is asymmetric and context-dependent). In addition, this formulation provided a better fit of the data than the original one in a formal model-comparison.

In the asymmetric models ($\mathrm{ABS_a}$, $\mathrm{REL_a}$, or $\mathrm{REL_{a,w}}$), we additionally introduced different learning rates after positive versus negative prediction errors. This follows from several studies using similar probabilistic learning paradigms (i.e., two-armed bandit, no reversal and one-stage) showing that individuals tend to give more weight to positive, confirmatory feedback than to negative, dis-confirmatory feedback (Lefebvre et al., 2017; Palminteri et al., 2017).

In those models, Equation 1 becomes

$$\begin{cases} Q_{t+1}\ (s,c) = Q_t(s,c) + \ \alpha^+ \times \delta_t \ \ if\, \delta_t > 0 \\ Q_{t+1}\ (s,c) = Q_t(s,c) + \ \alpha^- \times \delta_t \ \ if\, \delta_t < 0 \end{cases} \tag{8}$$

In the weighted models ($\mathrm{REL_w}$, $\mathrm{REL_{a,w}}$), the inference on the unchosen outcome $\neg R_t(s)$was modulated by a weight w as follows:

$$\delta_{V,t} = (R_t(s) + \mathbf{w}(\neg R_t(s)))/2 - V_t(s) \tag{9}$$

In all models, the probability of choosing option A over B was derived from a softmax function with temperature parameter β:

$$P(choice = A) = \ (1 + \exp(\beta(v(A) - v(B))))^{-1} \tag{10}$$

In the learning task at trial t, we have, for an option i of a context s: $v(i) = \ Q_t\ (s,i)$

In the transfer task, we have, $v(i) = Q_{end}\ (s,i)$, where $Q_{end}\ (s,i)$ indicate the Q-values of option i at the end of the learning session.

Step 2: Modeling the Effects of Anxiety. After having identified the general algorithm governing learning, we next investigated if and how incidental anxiety—as induced by threat of shocks—affects specific subprocesses of learning. We defined a second model space (model Space 2) by systematically allowing each parameter (the temperature parameter, each of the three learning-rates, and the weighting parameter) of the winning model (i.e., model $\mathrm{REL_{a,w}}$) to differ between the safe and the threat condition. This produced a five-models model-space, to which was added a base model where all parameters were identical between the safe and the threat condition.

Initialization

Option (Qs) and context (Vs) values were initialized at 0 in each condition.

Parameter Optimization

For each model M, and regardless of the criterion used for model comparison (see below), the parameters $\theta_M$were optimized by minimizing the negative logarithm of the posterior probability (LPP) over the free parameters:

$$\mathrm{LPP} = -\log(P(\theta_M|D,M)) \propto -\log(P(D|M,\theta_M)) - \log(P(\theta_M|M))$$

Here, $P(D|M,\theta_M)$is the likelihood of the data (i.e., the observed choice) given the considered model M and parameter values θ_M, and $P(\theta_M|M)$is the prior probability of the parameters.

Following (Daw et al., 2011) the prior probability distributions were defined as a gamma distribution (shape parameter (κ) = 1.2, scale parameter (θ) = 5) for the choice temperature, and as beta distributions (shape parameter (α) = 1.1, shape parameter (β) = 1.1) for learning rates and weight.

This procedure was conducted using Matlab's fmincon function with different initialized starting points of the parameter space (i.e., $0 < \beta <$ Infinite, $0 < \alpha < 1$; Palminteri et al., 2015). Note that both the learning and transfer task data were used for the parameter optimization.

Model Comparison Criteria

We computed three model comparison criteria, which measure the ability of each model to explain the experimental data, by trading-off their goodness-of-fit and complexity: the BIC, the Akaike's information criteria (AIC) and the Laplace approximation to the model evidence (LAME).

Defining $\hat{\theta}_M$ the model parameters identified in the optimization procedure, df the number of model parameters, and n the number of data-points (i.e., trials), AIC, BIC, and LAME were computed as follows:

$$\mathrm{BIC} = \log\left(P\left(D|M,\hat{\theta}_M\right)\right) - \frac{df}{2}\log(n)$$

$$\mathrm{AIC} = \log\left(P\left(D|M,\hat{\theta}_M\right)\right) - df$$

$$\mathrm{LAME} = \log\left(P\left(D|M,\hat{\theta}_M\right)\right) + \log\left(P\left(\hat{\theta}_M|M\right)\right) + \frac{df}{2}\log(2\pi) - \frac{1}{2}\log H$$

where $H$is the determinant of the Hessian.

These three criteria were compared in their ability to correctly identify model simulations (see Model Identifiability and Parameter Recovery section below). Because LAME gave the most satisfactory results, only model comparisons using this criterion are reported in the main text. LAME generated identifiability confusion matrices that were closer to the ideal ones (i.e., full diagonal) than AIC or BIC in our simulation exercise. This was first

evaluated visually, and then confirmed by computing the Euclidean distance (ED) between the identifiability confusion matrices (obtained with LAME, AIC, and BIC) and the (ideal) diagonal matrix, which was smaller with LAME (ED to ideal matrix for each method: LAME = 75.6, AIC = 132.6, BIC = 172.1, smaller value is better).

Bayesian Model Comparison

To identify the model most likely to have generated a certain data set, AIC, BIC, and LAME were computed at the individual level for each model in the respective model-space, and fed to random-effects Bayesian model comparison using the mbb-vb-toolbox (http://mbb-team.github.io/VBA-toolbox/; Daunizeau et al., 2014). This procedure estimates the expected frequencies (denoted PP) and the exceedance probability (denoted XP) for each model within a set of models, given the data gathered from all subjects. XP quantifies the belief that the model is more likely than all the other models of the model-space. An XP > 95% for one model within a set is typically considered as significant evidence in favor of this model being the most likely. Expected frequency (PP), on the other hand, quantifies the posterior probability, that is, the probability that the model generated the data for any randomly selected subject.

Model Identifiability and Parameter Recovery

To assess the reliability of our modeling approach, we performed model identifiability and parameter recovery simulations (Palminteri et al., 2017; see Correa et al., 2018, for a similar approach). Choices from synthetic subjects were generated for each task and each model by running our computational models with model parameters sampled in their prior distribution: softmax temperature β were drawn from gamma distribution (random ('Gamma',1.2,5)) and learning rates and weights were drawn from beta distributions (random('beta,1.1,1.1)), as outlined above. Option values Qs and context values Vs were initialized from 0 for four conditions. For each model, we ran 10 simulations including 50 synthetic subjects ($N = 500$).

Model identifiability was assessed by running the Bayesian model comparison on the synthetic data. Results are pictured as confusion matrices, where perfect recovery would result in matrices with diagonal elements equal to 1, and off-diagonal elements close to 0. Parameter recovery was assessed by evaluating the correspondence between the parameters used in the simulation, and the parameters recovered by the parameter optimization procedure (online Supplemental Materials Table S12). We used two main assessment criteria: first, we performed a linear regression analysis between the parameters used for simulations and the estimated parameters, using data from all simulations ($n = 500$). In this case, perfect recovery would result in intercepts close to 0 and slopes close to 1, and would be pictured as a 500 dots scatter plot aligned on the identity line. Then, we performed correlation analyses between the parameters used for simulations and the estimated parameters on individual simulations (each with $n = 50$ synthetic data). Correlation coefficients were averaged over the 10 simulations, and displayed as correlation matrices. In this case, perfect recovery would result in matrices with diagonal elements equal to 1, and off-diagonal elements close to 0.

Results

Manipulation Checks: Successful Induction of Anxiety

To ensure that our anxiety manipulation was successful, we inspected self-reported emotion and physiological responses. In both experiments, self-reported anxiety during the threat condition was significantly higher than other (negative and high arousal) emotions, including sadness (Experiment 1: $t_{44} = 6.78$, $p < .001$, $d = 1.01$; Experiment 2: $t_{49} = 6.17$, $p < .001$, $d = .87$) and anger (Experiment 1: $t_{44} = 3.56$, $p < .001$, $d = .53$; Experiment 2: $t_{49} = 4.98$, $p < .001$, $d = .70$), but was similar to fear (Experiment 1: $t_{44} = 1.57$, $p = .1235$; $d = .23$; Experiment 2: $t_{44} = .67$, $p = .5024$; $d = .09$). While self-reported anxiety levels were significantly greater than 0 in both experiments (see Table 1), anxiety levels were significantly higher in Experiment 1 compared with Experiment 2 ($t_{93} = 4.28$, $p < .001$, $d = .87$). This indicates that presenting ToS in miniblocks, as done in Experiment 1, induced greater levels of anxiety compared with the more prolonged ToS presentation in Experiment 2.

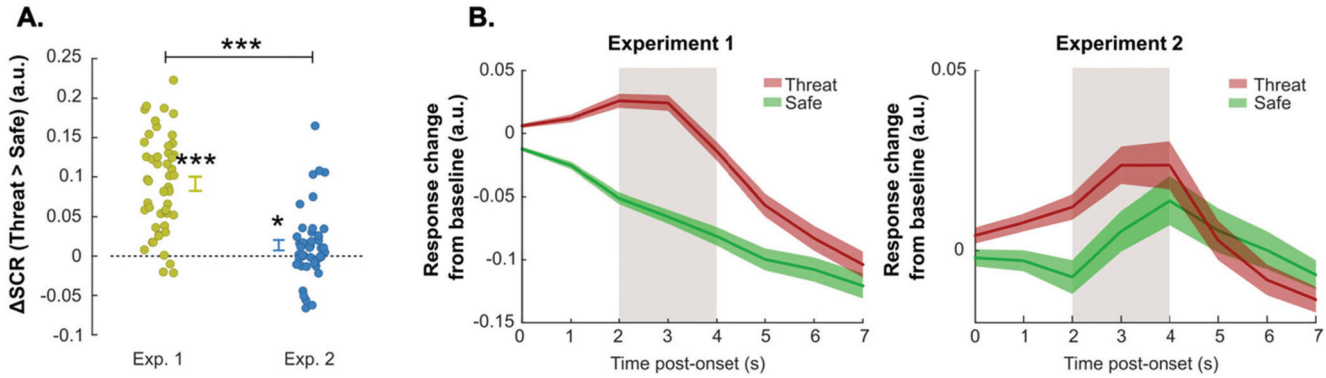
The self-report results are paralleled by the SCR results, which showed significantly higher phasic responses during anxious compared with safe trials (see Figure 3). An ANOVA showed a main effect of anxiety (Experiment 1: $F(1, 47) = 130.35$, $p < .0001$, $\eta_p^2 = .69$; Experiment 2: $F(1, 44) = 4.28$, $p = .0444$, $\eta_p^2 = .08$). This effect was not modulated by outcome valence (Experiment 1: $F(1, 47) = .08$, $p = .7719$, $\eta_p^2 = .02$; Experiment 2: $F(1, 44) = .00$, $p = .9901$, $\eta_p^2 = .00$). While SCR levels were significantly greater during threat compared with safe trials in both experiments (Experiment 1: $t_{48} = 10.44$, $p < .0001$; $d = 1.49$; Experiment 2: $t_{44} = 2.06$, $p = .0444$; $d = .30$), arousal levels during threat (vs. safe) conditions were also significantly greater on average in Experiment 1 compared with Experiment 2 (Experiment 1 > Experiment 2: $t_{92} = 6.94$, $p < .0001$; $d = .35$). Finally, self-reports of anxiety correlate with the effect of anxiety on SCR ($r = .26$, $p = .0151$), while this is not the case for self-reports of fear ($r = .18$, $p = .1003$; bivariate correlations reported in online Supplemental Materials Table S1). Jointly, results from SCR and self-report indicate that ToS successfully induced anxiety in both experiments.

Model-Free Analyses

Model-Free Analysis of Learning Task: No Effects of Valence and Anxiety on Learning Performance

To investigate the overall effects of our experimental manipulations (valence: gain vs. loss; anxiety: safe vs. threat) on learning performance, we first analyzed the probability of correct responses averaged per condition, using a two-way repeated-measures ANOVA. We expected Valence and Anxiety to jointly influence learning, such that anxiety showed differential effects on learning performance for gain compared with loss learning. This would be reflected by a significant interaction effect between Valence and Anxiety. However, our analysis revealed no significant main effects of—nor significant interactions between—our experimental factors on learning performance (Experiment 1: $ps > .12$; Experiment 2: $ps > .14$; see Figure 4A and online Supplemental Materials Table S3 and S4). In fact, Bayes factors lend positive support for the null hypothesis, with all $BF_{01} > 1.79$ (online

Figure 3
Electrophysiological Results



Note. (A) Skin conductance responses (SCR) were significantly higher in the threat condition compared with the safe condition (Experiment 1: t_{48} = 10.44, $p < .0001$, d = 1.49; Experiment 2: t_{44} = 2.06, p = .0444, d = 0.30). Moreover, this effect was stronger in Experiment 1 than Experiment 2 (Experiment 1 > Experiment 2: t_{92} = 6.94, $p < .0001$, d = 0.35). Separate columns indicate results from different experiments. Each dot represents each subject, means are plotted next to distributions of individual responses with error bars reflecting the standard error of the mean. (B) Electrodermal response functions showing the temporal evolution of responses in the threat (red) and no threat (green) conditions after onset of the stimulus screen at 0 s across Experiment 1 (left) and Experiment 2 (right). Gray bars reflect period that was used for statistical analyses shown in A. See the online article for the color version of this figure.
~ $0.05 < p < 0.1$. * $0.01 < p < 0.05$. ** $0.001 < p < 0.01$. *** $p < 0.001$.

Supplemental Materials Table S3). While the two variants of the ToS procedure had a marginally different impact on average learning performance (Experiment 1 = 74.12%, Experiment 2 = 71.60%; $F(1, 99) = 2.66$, p = .1057, η_p^2 = .02, BF_{01} = 2.99), they did not induce significantly different effects of anxiety on learning ($F(1, 99)$ = .008, p = .9271, η_p^2 = .00, BF_{01} = 84.60). As subsequent analyses focus on identifying the effect of anxiety, we combined the data from the two experiments (but we additionally continue to report individual experiment results for all main analyses).

Combining the two experiments in a single ANOVA, we replicate the absence of significant main and interaction effects on learning performance (all $ps > .20$: see Figure 4A and online Supplemental Materials Table S3), as reported above. Although the lack of valence effects replicates previous findings (Fontanesi et al., 2019; Lebreton et al., 2019; Palminteri et al., 2015), the absence of significant effects of anxiety might seem surprising at first glance, as it contradicts several previous studies suggesting anxiety affects learning per se (DeVido et al., 2009; Glienke et al., 2015; Treadway et al., 2017). However, our findings agree with our literature review of 15 studies on the effects of experimentally induced anxiety on instrumental learning, which also failed to identify a consensual, robust effect of anxiety on learning (Figure 1 and online Supplemental Materials Table S13).

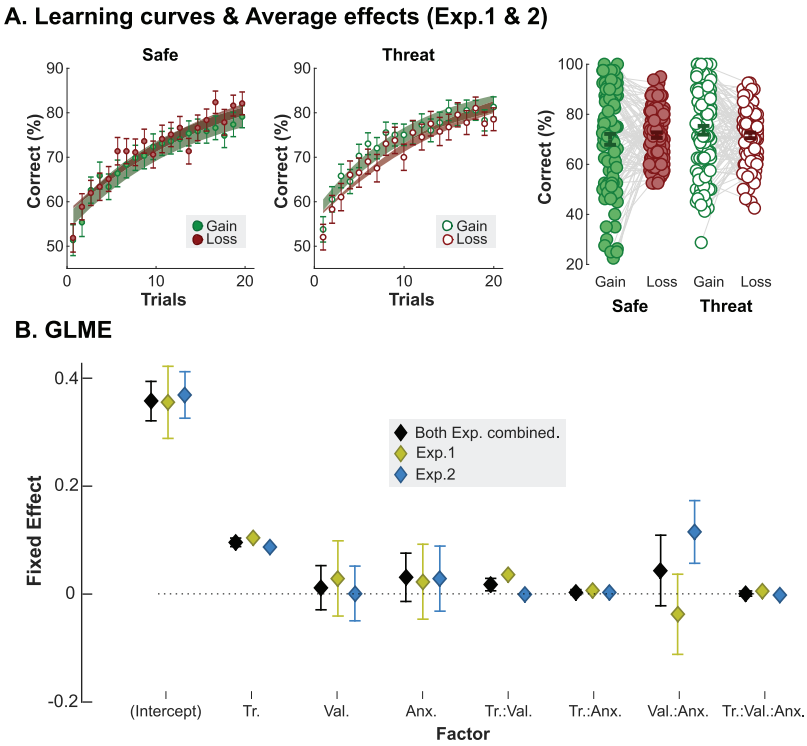
To ensure that our initial analysis strategy did not miss potential effects due to averaging over individual trials, we next turned to a more flexible statistical analysis framework using a GLME model. This approach allows us to inspect our data trial-by-trial to capture learning effects and may be more powerful than ANOVAs in the presence of unbalanced or missing data (Matuschek et al., 2017; Pinheiro & Bates, 2000). Although the GLME revealed a main effect of trial on performance, capturing the dynamics of learning (Figure 4B and online Supplemental Materials Table S4), no other significant main effects and/or interaction with the experimental manipulations were detected. Confirming the ANOVA results, this indicates that threat of shock might have a limited impact on learning processes, with Bayes factors lending very strong support in favor of the null hypothesis (all $BF_{01} > 2.103 \times 107$, online Supplemental Materials Table S5). Moreover, we also did not find differential effects of experimental designs on learning (β_{exp} = −.00 ± .03, t_{25276} = −.14, p = .8834; $\beta_{Exp \times Anxiety}$ = .03 ± .04, t_{25276} = .82, p = .4082; see online Supplemental Materials Robustness tests and Figure S2A).

Model-Free Analysis of Transfer Task: Nonspecific Effects of Anxiety on Transfer task Performance Reflecting Learned Values

Participants' choices in the transfer task provide additional information about the value of the cues that they have learned throughout the learning task. Following our hypothesis for learning performance, we also expected joint influences of Anxiety and Valence on postlearning preferences. To test this, we first computed the preference for each cue as the probability of choosing the cue over all other cues (Figure 5; and see Palminteri et al., 2015, for a similar approach). The three-way repeated-measures ANOVA (see online Supplemental Materials Table S6 and Method–Behavioral analysis) identified an interaction between cue quality and anxiety (interaction of anxiety and quality; $F(1, 99)$ = 6.37, p = .0131, η_p^2 = .06, $BF_{01} = 1.55 \times 10^{48}$). Post hoc tests were performed to characterize the interaction between anxiety and quality. Results indicate that the interaction is driven by subjects choosing the better symbols (G75 and L25) over the worse symbols (G25 and L75) significantly more often in the threat compared with the safe condition (Better-Worse in threat > Better-Worse in safe: t_{99} = 2.41, p = .0165; d = .17; see also online Supplemental Materials Table S10). These results indicate that anxiety boosts participants' preference for higher quality cues.

Figure 4

Learning Performance and Results From Generalized Linear Mixed-Effect Model



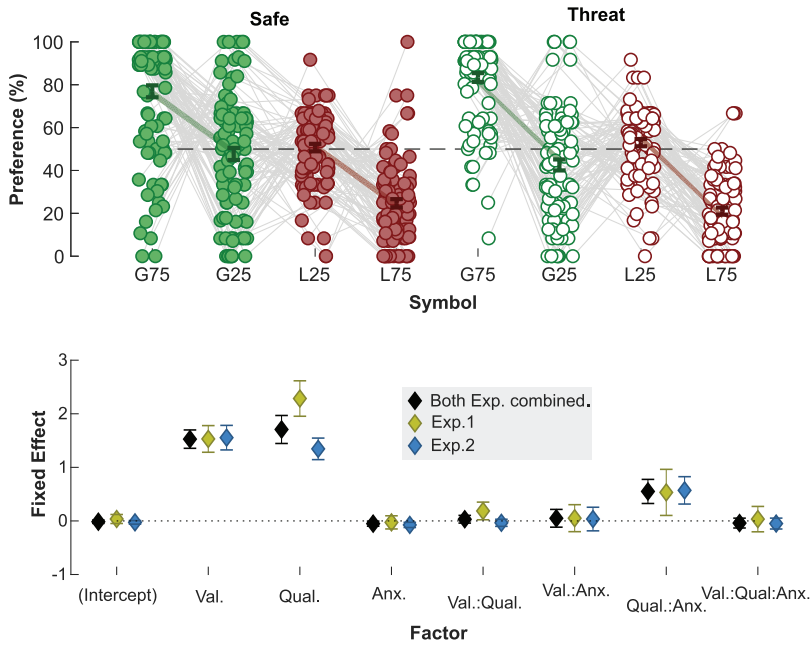
Note. (A) Left and middle panels: learning curves representing the fraction of correct choices in the safe (left; filled dots) and the threat (middle; unfilled dots) conditions. Error bars indicate the standard error of the mean (*SEM*), and shaded areas represent the mean ± *SEM* of GLME predictions. Right panels: average correct rate across four conditions. Each gray line indicates individual's choice patterns across the conditions. (B) Generalized linear mixed-effect model (i.e., $GLME1_{Learning}$) with choice accuracy as dependent variable. The *y*-axis represents the estimated standardized coefficient (*t*-value), and the *x*-axis represents each factor in the GLME model. Dot colors indicate results from different dataset. Tr. = Trial; Val. = outcome valence; Anx. = anxiety manipulation. See the online article for the color version of this figure.

Additional results from this ANOVA revealed that a cue is more likely to be preferred if it was associated with gains compared with losses (main effect of option valence; $F(1, 99) = 212.85$, $p < .0001$, $\eta_p^2 = .68$, $BF_{01} = 1.23 \times 10^{71}$), regardless of the anxiety condition ($F(1, 99) = .31$, $p = .5756$, $\eta_p^2 = .00$, $BF_{01} = 1.43 \times 10^{73}$). A cue is also more likely to be preferred if it was the best cue (G75 and L25) of the pair during the learning task (main effects of Option quality; $F(1, 99) = 241.60$, $p < .0001$, $\eta_p^2 = .70$, $BF_{01} = 2.15 \times 10^{47}$). However, there were no valence-dependent effects of anxiety on preferences in the transfer task ($F(1, 99) = .55$, $p = .4587$, $\eta_p^2 = .00$, $BF_{01} = 155.542$), as well as no main and interaction effects of anxiety with the factor experiment ($ps > .19$). The latter result suggests that the two anxiety induction methods did not differentially impact preference in the transfer task. Bayes factors were computed for all main and interaction effects, which lend substantial support for the null hypothesis with all $BF_{01} \geq 19.14$ (online Supplemental Materials Table S6). This means that anxiety likely has no true effect. Moreover, Bayesian analyses indicated that models including interaction (Experiment 1) and main (Experiment 2) effects of quality and valence can best explain performance in the transfer task, better than any model that includes anxiety (online Supplemental Materials Table S6). Taken together, anxiety during learning improved recognition of cue quality in the transfer task independent of valence.

Those results were confirmed in a more comprehensive GLME approach (see Method–Behavioral Analysis), which modeled transfer task choices between two cues as a function of (a) the difference between the cues' valence (gains vs. losses), (b) the difference between the cues' quality (better option in learned pair vs. worse option in learned pair), and (c) whether cues were learned in the anxiety condition (safe vs shock). The GLME model also accounted for differences in experimental designs (Experiment 1 vs. Experiment 2) and subject ID, which was nested within each experiment (see Method–Behavioral Analysis). The results (online Supplemental Materials Figure 5B and Table S7) showed that subjects' decisions were influenced by valence ($t_{13592} = 8.90$; $p < .0001$), quality ($t_{13592} = 6.53$; $p < .0001$) and the interaction between anxiety and quality ($t_{13592} = 2.44$; $p = .0144$). Comparable with the ANOVA results above, we did not find a main effect of

Figure 5

Choice Pattern in Transfer Task and Corresponding Results From Generalized Linear Mixed Effect Model



Note. (A) Averaged choice rate for each cue. Grey lines reflect individual choice patterns. The filled dots represent cues learned under the safe condition, the unfilled dots indicate cues learned during the threat condition. Error bars indicate the standard error of the mean (*SEM*), and shaded areas represent the mean ± *SEM* of the GLME predictions (B) Generalized linear mixed-effect model (i.e., $GLME1_{Transfer}$) with cue selection as dependent variable. The *y*-axis represents the estimated standardized coefficient (*t*-value), and the x-axis represents each factor in the GLME model. Dot colors indicate results from different dataset. G75 = 75% of gain; G25 = 25% of gain; L25 = 25% of loss; G75 = 75% of loss; Val. = outcome valence; Qual. = quality of cue (i.e., higher expected value in its pair during learning); Anx. = anxiety manipulation. See the online article for the color version of this figure.

experiment ($\beta_{exp} = -.02 \pm .06$, $t_{13591} = -.42$, $p = .6681$) nor an interaction between experiment and anxiety ($\beta_{Exp \times Anxiety} = -.03 \pm .12$, $t_{13591} = -.24$, $p = .8041$; see online Supplementary Materials Robustness tests and Figure S2B), indicating that the experimental design had little effect on the impact of anxiety on postlearning performance.

Post hoc analyses showed that cue discrimination (G75 + L25 > G25 + L75) was significantly improved in the threat compared with the safe condition ($t_{99} = 2.41$, $p = .0165$; $d = .17$). Note that this effect was not significant in Experiment 1 ($t_{49} = 1.27$, $p = .2058$; $d = .12$), but the direction was the same as observed in Experiment 2 ($t_{49} = 2.42$, $p = .0171$; $d = .24$). The results indicate that anxiety might enhance subjects' ability to identify the higher quality symbol some time after learning, even though it does not affect average learning performance at the learning stage (see online Supplemental Materials Figure 5).

Following previous studies (Palminteri et al., 2015, 2017) we conducted an additional analysis that focused on cues that were associated with intermediate values (i.e., G25 and L25) and tested if subject displayed rational preferences to choose cues based on expected value (online Supplemental Materials Table S9). The two-way ANOVA with valence and anxiety as factors showed a significant main effect of valence ($F(1, 99) = 5.96$, $p = .0163$, $\eta_p^2 = .05$), but no significant main effect of anxiety ($F(1, 99) = .55$, $p = .4586$, $\eta_p^2 = .00$) nor its interaction ($F(1, 99) = 2.63$, $p = .1077$, $\eta_p^2 = .02$).

Model-Free Analysis of Trait Anxiety: No Joint Effects of State and Trait Anxiety

While our threat of shock manipulation successfully manipulated state anxiety as indicated by our self-reported affect and SCR results, an open question is whether participants that differ in their propensity to feel anxious also show an increased effect of induced incidental anxiety on learning behavior. That trait anxiety can modulate the impact of induced anxiety on learning has been shown in previous studies (Cavanagh et al., 2011). We predicted here that subjects who reported high levels of anxiety might react more strongly to a threatening environment than subjects with low levels of anxiety. To assess these potentially interactive effects between trait and state anxiety, we ran the additional GLME regressions that included trait anxiety (i.e., BAI scores) as a fixed factor for decisions in the learning and transfer tasks (see online

supplemental materials for additional information on regression models). Our results show that BAI did not moderate the effects of state anxiety on learning ($ps > .25$) and postlearning performance ($ps > .65$). Moreover, there were no main effects of BAI on learning nor higher-order interactions (Figure 6, online Supplemental Materials Tables S14 and S15).

Model-Based Analysis

Identifying Model Architecture: Learning is Asymmetric and Context-Dependent

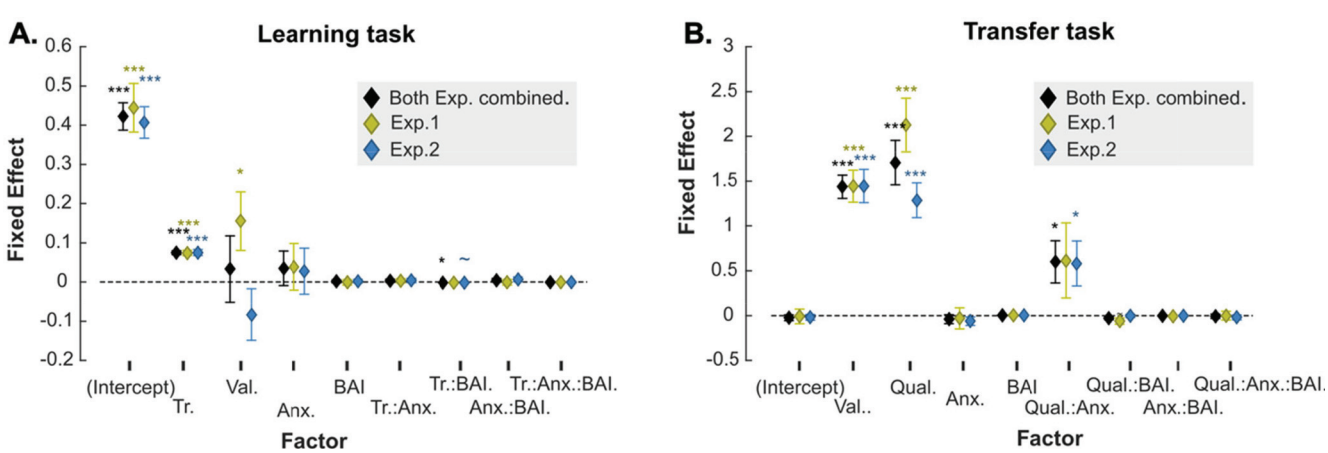
Our analysis of the general effects of anxiety in our factorial design (see previous sections) points toward nonspecific, elusive effects of anxiety in reinforcement-learning. Two concurrent hypotheses might explain this observation: on the one hand, it is possible that anxiety affects specific latent mechanisms of reinforcement-learning, that may be subtle and difficult to identify via model-free factorial design analyses; alternatively, it may be that anxiety indeed does not affect reinforcement-learning processes in a strong and specific way.

To tease apart these competing explanations, we next turned to computational modeling. By explicitly modeling the computations giving rise to participants' behavior, computational modeling can efficiently combine data from both learning and transfer task (Palminteri et al., 2015) and can identify latent operations that would be specifically impacted by anxiety (Bishop & Gagne, 2018; Mkrtchian et al., 2017; Treadway et al., 2017). As a first step, we aimed at identifying a core architecture that would capture the learning behavior regardless of anxiety (i.e., in both safe and threat conditions). Following decades of research on the modeling of similar tasks (Pessiglione et al., 2006; Rescorla & Wagner, 1972; Sutton & Barto, 1998), we assumed that participants learned the value of available options using an algorithm akin to Q-learning.

Yet, several features of the observed behavioral pattern suggest that simple Q-learning would not be sufficient to comprehensively capture our participants' learning dynamics. First, the fact that subjects generally express higher preference for the L25 than for the G25 cue in the transfer task is a signature of context-dependent learning (Klein et al., 2017; Lebreton et al., 2019; Palminteri et al., 2015, 2017). Briefly, in addition to standard Q-learning computations, context-dependent learning explicitly computes a context-value, which approximates the average expected value from a specific context. Obtained outcomes are then reframed relatively to this context value, allowing for example, minor losses encountered in a loss context to be experienced as relative gains and vice-versa. This explains why small losses (L25) are preferred to small gains (G25) post learning in the transfer task. Second, the apparently higher variability of performance observed in the gain compared with the loss domain could be a signature of asymmetric learning. Briefly, if positive prediction errors are weighted more heavily than negative ones, individuals can quickly diverge in response rates (Lefebvre et al., 2017). Considering these two potential additional features of reinforcement-learning models, we built a model space comprising six computational models presenting different combinations of those features (see Method and Figure 7A and B). Using simulations, we verified that those models were identifiable, and that their parameters could be satisfactorily estimated (online Supplemental Materials Figure 7C and D).

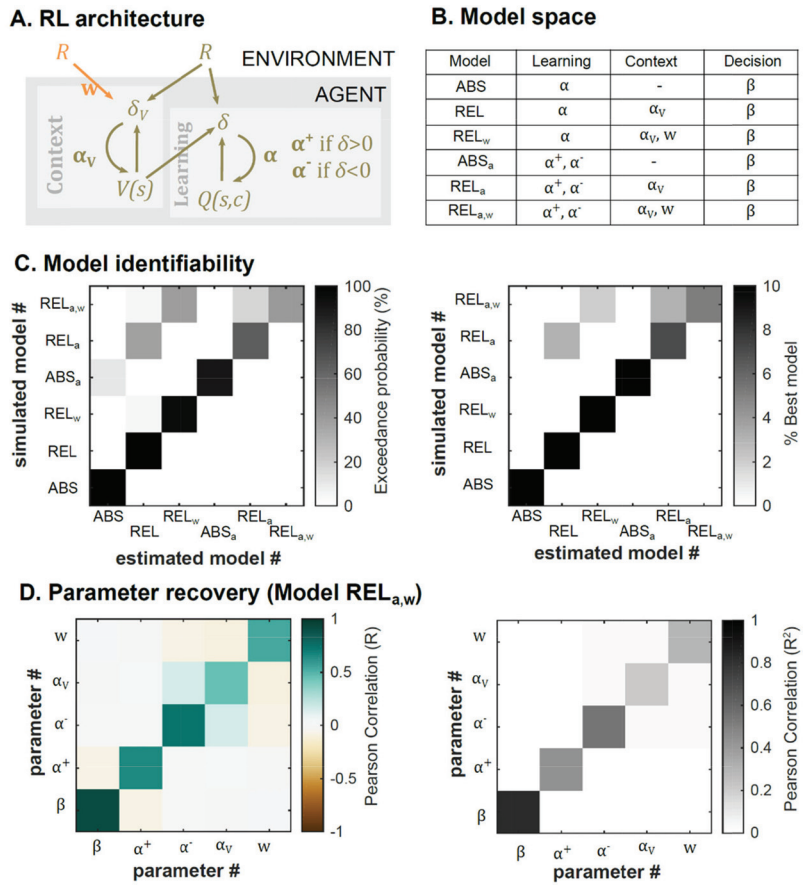
We then fitted those models to our data, and ran a full Bayesian model comparison procedure, aiming at identifying the best and most parsimonious computational architecture. In line with the behavioral signatures identified in the beginning of this section, the Bayesian model comparison identified the RL model including both learning-rate asymmetry and context-dependency ($REL_{a,w}$) as the best explanation of our data (exceedance probability: 93%; Figure 8A). Note that $REL_{a,w}$ also won the BMC procedure based on data restricted to Experiments 1 and 2 (exceedance probability: 76% and 88%; Figure 8A). Average estimated parameter values were very similar to previous studies (Palminteri et al., 2015) and were also very similar between

Figure 6
Effects of Trait Anxiety (BAI) on Learning and Transfer Task Choices



Note. (A) Generalized linear mixed-effect model (i.e., $GLME1_{Learning}$) with choice accuracy as dependent variable. (B) Generalized linear mixed-effect model (i.e., $GLME1_{Transfer}$) with cue selection as dependent variable. The *y*-axis represents the estimated standardized coefficient (*t*-value), and the *x*-axis represents each factor in the GLME model. Dot colors indicate results from different dataset. BAI = Beck Anxiety Inventory. See the online article for the color version of this figure.

Figure 7
Modeling Approach (Step 1)



Model	Learning	Context	Decision
ABS	α	-	β
REL	α	α_V	β
REL_w	α	α_V, w	β
ABS_a	α^+, α^-	-	β
REL_a	α^+, α^-	α_V	β
$REL_{a,w}$	α^+, α^-	α_V, w	β

Note. (A) Depiction of the model architecture basis. (B) Model Space. (C) Model identifiability analysis. Data from 100 synthetic participants were simulated (50 with Experiment 1 design, 50 with Experiment 2 design) with each of our six models. Bayesian model selection was used to identify the most probable model generating the data, using the Laplace approximation to model evidence. This procedure was repeated 10 times. Left: average exceedance probability confusion matrix. Right: Best model selection confusion matrix. (D) Parameter recovery analysis. The confusion matrices represent summary statistics of the correlations between parameters, estimated over 100-subjects simulations, and averaged over the 10 simulations. Diagonal: correlations between simulated and estimated parameters. Off diagonal: cross correlation between estimated parameters. Left: Pearson correlation (R). Right: explained variance (R2). See the online article for the color version of this figure.

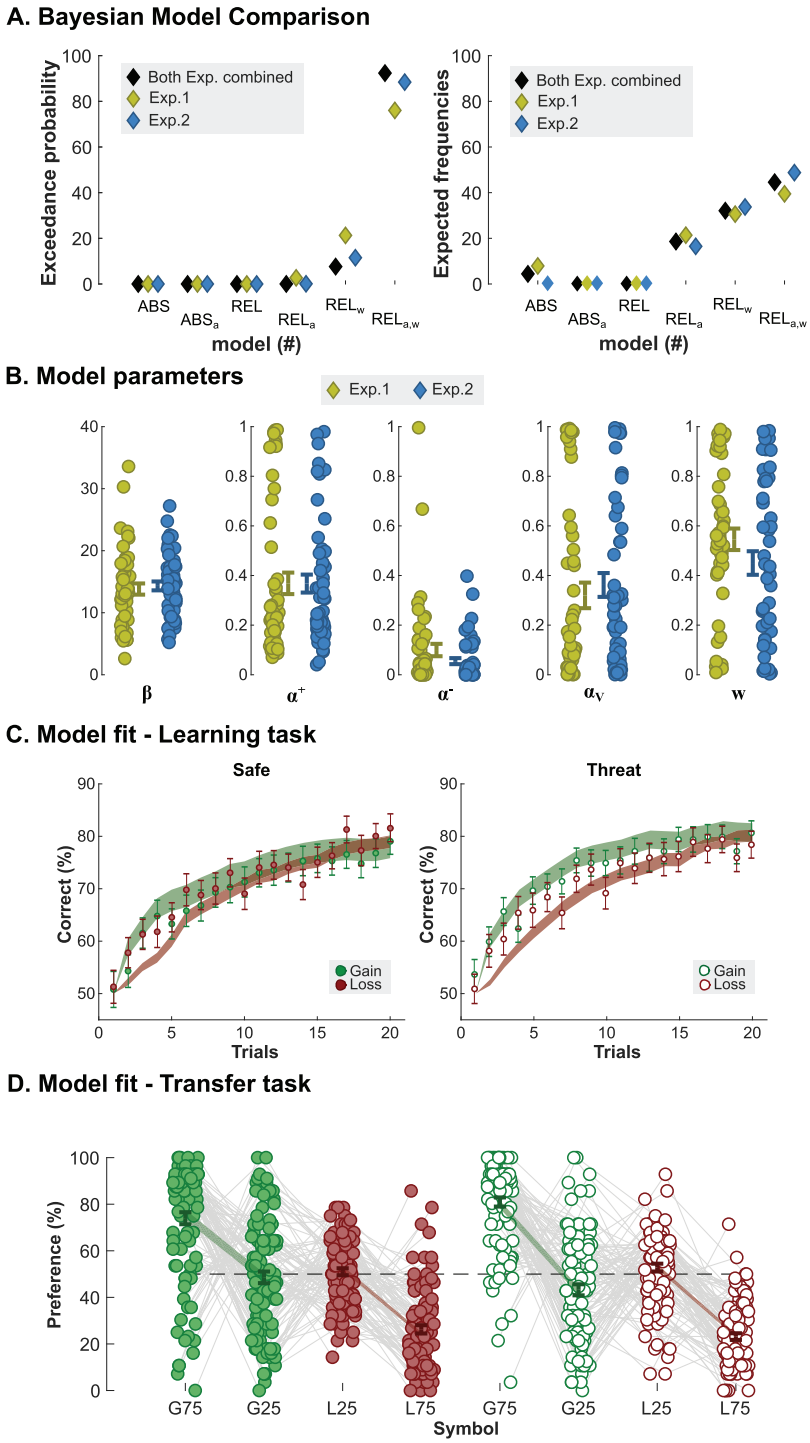
Experiments 1 and 2 (Figure 8B). The modeling results notably replicate the learning asymmetry reported in previous studies (Lefebvre et al., 2017; Palminteri et al., 2017) with positive learning rates being significantly larger than negative learning rates ($\alpha^+ = .37 \pm .02$; $\alpha^- = .07 \pm .01$; $t_{99} = 10.26$, $p < .0001$, $d = 1.06$). Overall, this model provided a very good fit of both learning and transfer task data (Figure 8 C–D).

Identifying Model-Based Effects of Anxiety: The Effects of Anxiety on Learning Are Inconclusive

To investigate the effects of anxiety on learning, we next built a second model space, where all models were derived from the $REL_{a,w}$, but additionally allowed parameters to vary between the Safe and Threat conditions. Given that $REL_{a,w}$ possesses five parameters (the choice temperature, three learning rates, and the unchosen outcome weighting parameter), the second model space featured six models (see Method). Similar to the first modeling step, we ran model identifiability and parameter recovery analyses (Figure 9B). Results show that some models cannot be perfectly identified: Models 4 and 6, which, respectively, feature differential learning rates for negative PE (α^-) and differential weighting parameters (w) between anxiety and safe conditions both tended to be identified as the simplest model.

Despite those limitations, we still compared those models in their ability to account for the observed data (see Method). The Bayesian model comparison with LAME failed to identify a clear best model (Figure 9C), indicating that allowing important model parameters to vary as a function of anxiety does not improve model fit.

Figure 8
Modelling Results for the General Learning Architecture (Step1)



Note. A. Model comparison results. These panels depict the results of a Bayesian model comparison analysis on our participants data, for experiment 1 (yellow diamonds), experiment 2 (blue diamonds) and both experiments combined (black diamonds). Left: exceedance probability of each model. Right: expected frequencies of each model. B. Model parameters of the winning model (RELa,w) for experiments 1 (yellow) and 2 (blue). Filled dots represent individual parameters

(Continued on next page)

Discussion

Summary of Design, Results, and Contributions

In two experiments, we investigated the impact of incidental anxiety on both learning performance during a probabilistic instrumental task (Pessiglione et al., 2006; Palminteri et al., 2015) and on postlearning transfer preferences (Frank et al., 2004; Palminteri et al., 2015) using a well-established ToS paradigm (Engelmann et al., 2015, 2019; Grillon, 2008; Schmitz & Grillon, 2012). Two variants of the anxiety induction method were used during learning: threat and safety trials were either alternated in blocks of three trials (Experiment 1), which induced relatively higher levels of anxiety, or in sessions of 80 trials (Experiment 2), which induced relatively lower levels of anxiety. Behavioral results from two experiments consistently showed that anxiety and outcome valence had little to no effect on learning performance per se At first glance, these results may be somewhat surprising given that they seem to contradict several previous studies suggesting that anxiety alters learning performance (DeVido et al., 2009; Schwabe & Wolf, 2009; Stevens et al., 2014; Treadway et al., 2017). However, a small-scale literature review agrees with our main result as it also failed to identify consensual and robust main effects of anxiety on learning across 15 papers (Figure 1 and online Supplemental Materials Table S13).

Our results nonetheless suggest that transfer preferences were significantly altered by the safe/anxiety manipulation. Specifically, postlearning preferences indicate that participants were better able to identify the quality of cues when these cues were learned in a threatening compared with a safe context. Note again that this effect was observed in the absence of any effects of anxiety on average learning performance and is indicative of anxiety exhibiting somewhat delayed effects on postlearning preferences and recall (see also Discussion–Transfer Task). Similar improvements in the ability to identify cues during a postlearning transfer task have been observed in one other prior study (Cavanagh et al., 2011).

Considering the possibility that anxiety effects differ when individuals seek reward versus avoid punishments, our experiment did not reveal any valence-dependent effects during both learning and postlearning performance. These results agree with our targeted literature review, which also failed to identify a robust consensus on this question. Specifically, other studies have reported inconsistent valence dependent effects of stress or anxiety on postlearning performance (Abraham & Hermann, 2015; Berghorst et al., 2013; Cavanagh et al., 2019, 2011; Lighthall et al., 2013; Petzold et al., 2010; Voegler et al., 2019): for learning performance in the domain of gains 5/7 results reported a null effect, 1/7 reported improvements and 1/7 reported reduced performance. In the domain of losses, 5/9 studies reported improved performance, while 1/9 reported reduced performance in the domain of losses and 3/9 reported a null effect (see Figure 1). Jointly, the current and previous results indicate that anxiety likely does not have differential effects on learning to seek reward and to learning to avoiding punishments.

A primary goal of the current experiments was to assess multiple experimental factors that could skew results from prior experiments in one experimental setup. To this end, our experiments were carefully designed to assess the differential effects of anxiety on learning and postlearning preferences, as well as on punishment and reward learning, while simultaneously reducing the effects of potential confounding factors using multiple methods. First, by adapting a ToS paradigm to induce anxiety, each subject learned action-outcome associations separately under a threatening context and under safety. Moreover, the ToS procedure allowed us to customize the intensity of the negative event (i.e., electric shock) to each participant's pain threshold, and to successfully create significant threat levels for all subjects across two experiments (as assessed by SCR responses and self-reports). The ability to turn threat on and off at specific time points throughout the experiments allowed us to directly assess the effects of anxious states on learning in a within-subject design. This is important to assess the causal effects of anxiety on learning (Engelmann et al., 2015, 2019) and addresses a major limitation of traditional emotion and stress induction techniques, the common delay between the induction time point and behavioral task. Second, we induced anxiety for two different periods including relatively short blocks of three trials (Experiment 1) and relatively long periods lasting for full session of 96 trials (Experiment 2). This was done for two reasons; (1) it allowed us to assess potential biases induced by the repeated switching of emotional states and associated stimuli in Experiment 1, and (2) it allowed us to assess the effect of different threat level intensities, with Experiment 1 creating a relatively more intense emotional state compared with Experiment 2. Third, we assessed the effects of anxiety on learning over gains and losses by crossing the ToS manipulation with an outcome valence manipulation. This allowed us to directly assess the effects of anxiety on learning to seek gains and to avoid losses separately (Palminteri & Pessiglione, 2017). Finally, we differentiated the effects of anxiety on learning and postlearning performance by including both a learning stage and a postlearning task in the same study. Despite these methodological advances, we find only limited effects of anxiety on learning per se, but significant enhancements of the ability to identify better quality cues in a post learning transfer task.

Discussion: Learning

We consider three explanations for the limited effects of incidental anxiety on learning, observed in the current two experiments. These include the hypotheses that (a) only trait, but not

Figure 8 ***(Continued)***

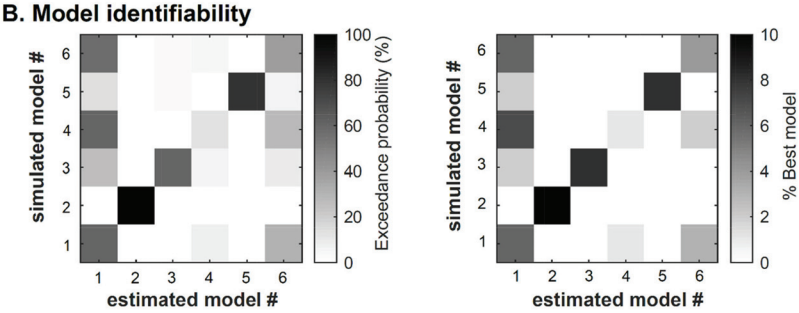
while error bars represent population mean±SEM. C. Learning curves, representing the fraction of correct choices in the safe (left; filled dots) and the threat (middle; unfilled dots) conditions. Error bars indicate the standard error of the mean (SEM), and shaded areas represent the mean ± SEM of the RELa,w predictions. D. Transfer choice rate for each cue. Grey lines reflect individual choice patterns. The filled dots represent cues learned under the safe condition, the unfilled dots indicate cues learned during the threat condition. Error bars indicate the standard error of the mean (*SEM*), and shaded areas represent the mean ± *SEM* of the RELa,w predictions. See the online article for the color version of this figure.

Figure 9
Modelling Approach (Step 2)

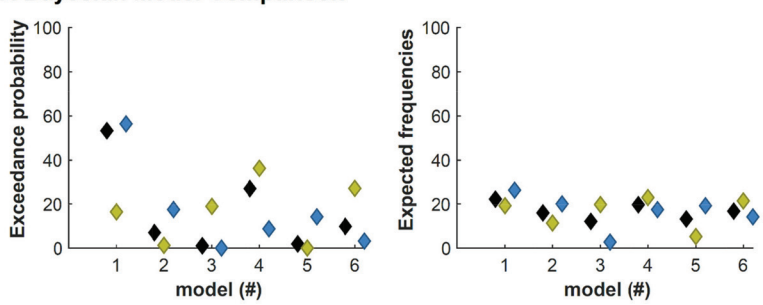
A. Model space

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
β	S = T	S ≠ T	S = T	S = T	S = T	S = T
α^+	S = T	S = T	S ≠ T	S = T	S = T	S = T
α^-	S = T	S = T	S = T	S ≠ T	S = T	S = T
α_V	S = T	S = T	S = T	S = T	S ≠ T	S = T
w	S = T	S = T	S = T	S = T	S = T	S ≠ T

B. Model identifiability



C. Bayesian Model Comparison



Note. A. Model Space. S and T represent safe and threat condition, respectively. S = T indicates safe and threat condition share the same parameter. B. Model identifiability analysis. Data from 100 synthetic participants were simulated (50 with experiment 1 design, 50 with experiment 2 design) with each of our 6 models. Bayesian model selection was used to identify the most probable model generating the data, using the Laplace approximation to model evidence. This procedure was repeated 10 times. Left: average exceedance probability confusion matrix. Right: Best model selection confusion matrix. C. Model comparison results. These panels depict the results of a Bayesian model comparison analysis on our participants data, for experiment 1 (yellow diamonds), experiment 2 (blue diamonds) and both experiments combined (black diamonds). Left: exceedance probability of each model. Right: expected frequencies of each model. See the online article for the color version of this figure.

state anxiety may have an impact on learning; (b) anxiety reduces the available cognitive resources and its effects can only be revealed in more difficult settings; and (c) anxiety causes an inflexibility in learning, which can only be revealed using more complex task designs that require planning and adaptation.

First, a prominent hypothesis suggests that state and trait anxiety might impact different underlying learning mechanisms (Robinson, Vytal, et al., 2013). Specifically, Robinson, Vytal, et al., 2013 argue that state anxiety in response to unpredictable threat is "adaptive" as it prepares flexible physiological responses and behaviors to cope with negative events that may ensure survival (Robinson, Vytal, et al., 2013). Elevated and prolonged levels of trait anxiety on the other hand can become "maladaptive" and interfere with normal day-to-day functioning (Robinson, Vytal, et al., 2013). A number of previous studies showed behavioral effects of trait and pathological anxiety on learning that generally support this hypothesis (Figure 1, dark beige bars; Abraham & Hermann, 2015; Browning et al., 2015; DeVido et al., 2009; Robinson et al., 2015; Stevens et al., 2014; Voegler et al., 2019). However, this idea has recently been challenged by research revealing more limited effects of both trait and state anxiety on learning performance (Berghorst et al., 2013; Cavanagh et al., 2011; Lighthall et al., 2013; Petzold et al., 2010; Schwabe & Wolf, 2009; Voegler et al., 2019), even in more complicated settings (model-based learning: Gillan et al., 2019; social learning: Safra et al., 2018). To resolve this disagreement on the relative importance of state compared

with trait anxiety, we assessed the effects of trait anxiety in our current data set by conducting additional analyses focusing on individual differences in BAI scores on learning and postlearning performance (see Figure 6 and Table S14 and S15 in online supplemental materials). Note that our approach allows us to identify both main effects of state and trait anxiety, but also their interaction. Our results did not identify any main effects of BAI in the learning and postlearning task, indicating that high and low anxious subjects learned to seek gains and avoid losses equally well. Moreover, we did not observe an interaction effect between state and trait anxiety during learning and postlearning. Our results, together with the inconsistent findings of prior research identified by our literature review, suggest that both trait and state anxiety have little main and interactive effects on learning and postlearning performance.

Second, according to attentional control theory (Eysenck et al., 2007), performance might be intact if cognitive demands of the task do not exceed cognitive resources. Therefore, if the probability of a positive or negative outcome differs substantially between the stimuli during the learning phase (i.e., 75% vs. 25%), the task might be too easy to reveal the impact of anxiety given the experimental setup in current study. Specifically, subjects might have sufficient cognitive resources to deal with such a relatively simple task, even when learning under conditions of anxiety. Although this explanation is partially rejected by previous studies that found no significant interactions between difficulty and anxiety manipulations, the tasks used in previous experiments might also not have sufficiently challenged participants (Abraham & Hermann, 2015; Berghorst et al., 2013; Cavanagh et al., 2019, 2011; Lighthall et al., 2013; Petzold et al., 2010; Voegler et al., 2019). To address this potential explanation, we inspected our data by focusing on a subset of participants that showed evidence for finding this task relatively difficult. We identified these subjects via cluster analysis (k-means; online supplemental materials–Robustness test, Section 3) and split our subject pool into two groups, one showing relatively lower average performance (57% accuracy) throughout the learning task and another with relatively higher average performance (76% accuracy). If the predictions from attentional control theory apply to our results, we should observe larger effects of anxiety on learning and postlearning performance in the subject group with lower average performance that likely found the task more difficult. Our results did not support this potential interpretation and were consistent with previous findings (Abraham & Hermann, 2015; Berghorst et al., 2013; Cavanagh et al., 2019, 2011; Lighthall et al., 2013; Petzold et al., 2010; Voegler et al., 2019; see also Robinson et al., 2013). Specifically, while we found a significant main effect of performance group on predicting correct choice in the learning task, this effect was not modulated by anxiety (see online Supplemental Materials–Robustness test, Section 3 and Figure S3). The result in the transfer task also showed nonsignificant two- and three-way interactions of anxiety with performance group and quality. These results further support the notion that anxiety has limited effects on learning performance. Moreover, the effects we observe here are likely not modulated by task-dependent availability of cognitive resources (see also Engelmann et al., 2015).

In a similar vein, the anxiety condition might specifically increase cognitive task load. We inspected this possibility by analyzing reaction times across the two conditions, which is generally considered one of the hallmark measures of cognitive load (Pashler, 1994). We did not find slower reaction times under conditions of anxiety (online Supplemental Materials Table S11), indicating that subjects did not face greater cognitive load in the threat condition.

Finally, the effects of anxiety have previously been associated with inflexibility in learning, which might be caused by either difficulty in switching between habit and goal-directed decisions (Browning et al., 2015; Otto et al., 2013; Raio et al., 2017; Schwabe & Wolf, 2009) or intolerance for uncertainty (Browning et al., 2015; Christian & Florian, 2020). Therefore, our one-stage reinforcement-learning task with stable contingency of action and outcome might not be able to detect these anxiety-related changes in behavior. Taken together, the impact of anxiety on learning might be varied and depend on the type of anxiety and the task's difficulty and their interactions. Yet, again, the robustness of the effects of anxiety on learning flexibility have been challenged by recent high-powered studies (Gillan et al., 2019) and our small-scale review.

Discussion: Transfer Task

The significant general improvement in the ability to identify better options during the transfer task when these were learned under anxiety is consistent with a growing literature showing that a threatening environment can significantly impact memory processes under specific conditions (Bolton & Robinson, 2017; Vytal et al., 2012, 2013). In light of this, the current results might indicate that anxiety enhances memory retrieval for the value of cues encoded under anxiety (Mather & Lighthall, 2012; Porcelli & Delgado, 2017).

Note that the presence of anxiety effects observed in the transfer task in the absence of any effects of anxiety on average learning performance could also indicate that the transfer task is more sensitive to capture anxiety effects, whereas average learning effects dilute them. We tested this possibility, by analyzing separately the early and late phase of learning (see online supplemental materials–Robustness test, Section 5 and 6). Our results suggest that the learning performance in the late learning stage, rather than early or overall performance, might be more susceptible to the effect of incidental anxiety—although these effects are still very marginal and would need to be replicated.

The absence of detectable valence-specific effects of anxiety on performance in the transfer task in the present study might at first glance contradict previous results on the effects of anxiety on learning (Berghorst et al., 2013; Cavanagh et al., 2019; Lighthall et al., 2013; Petzold et al., 2010; Voegler et al., 2019). However, our targeted literature review, suggests that prior results are rather inconsistent with no detectable trends in the domain of gains (null effect: ∼70%, improvement: ∼15%, decline: ∼15%) and suggest a slight improvement in average performance in the domain of losses (null effect: ∼35%, improvement: ∼55%, decline: ∼10%).

Discussion: Modeling

Besides model-free analyses, we also used computational modeling as a more formal tool to characterize the specific influence(s) of anxiety on the learning process. Our modeling approach, validated by simulation-based parameter recovery and model indentifiability procedures, identified a winning model that updates expected values using a context-dependent and asymmetric

learning rule (Palminteri et al., 2017; Wilson & Collins, 2019). Context-dependency implies that option values are updated with respect to a reference point, which approximate the average expected value of a pair, and which is learned on a trial-by-trial basis with a specific contextual-learning rate (Palminteri et al., 2015). Factually, this allows to reframe small losses as reward in a loss context and small reward as losses in a gain context. Learning asymmetry was featured by different learning rates to update values after positive vs negative prediction errors. Similarly to previous reports, we found that learning asymmetry captures a confirmation bias, with positive learning rate parameters taking values twice as big as negative learning rate parameters (Lefebvre et al., 2017; Palminteri et al., 2017).

These results have important implications: they suggest that human learning incorporates more features (context-dependency, learning asymmetry) than typically thought, even in simple, traditional instrumental learning tasks that have been used for years (Frank et al., 2004; Pessiglione et al., 2006). Because interpreting parameter fits from models that provide incomplete descriptions of behavior is problematic (Nassar & Gold, 2013), this suggests that some simple modeling approaches that omit those features could have converged on erroneous conclusions about the effects of experimental manipulations or neuro-psychiatric pathologies on learning parameters.

After having identified the model that best and most comprehensively accounts for the general learning behavior of our participants, we aimed to evaluate the impact of anxiety on its parameters. Yet, we found that models including extra parameters to capture the effect of anxiety cannot be robustly identified. This misidentification issue suggests that those parameters have such a subtle (i.e., small) effect on the general behavior observed in the learning and transfer tasks, that the current task design (with its conditions, number of sessions, and number of trials) is not powerful enough to detect them. Given that our experimental design favorably compares to previous ones in terms of power (number of subjects, trials, etc.), this indicates that most designs (including ours) might not be powerful enough to allow the detection of the potential effects of anxiety, once all the complex features of learning that can be detected in human learning behavior (context dependency, learning asymmetry) are taken into account.

Limitations

While the current article largely discusses average effects that persist across both experiments, and are robustly observed across different anxiety and task parameters, a number of experiment-specific effects were also observed that deserve mention. These additional effects include (a) an Anxiety × Valence interaction for average learning in Experiment 2, but not Experiment 1 (Figure 4B and online Supplemental Materials Table S4), and (b) an Anxiety × Cluster interaction in control analyses of relatively good compared with bad learners in Experiment 1, but not Experiment 2 (online Supplemental Materials Figure S3A). These differences most likely reflect the effects of different anxiety intensities induced by the changes in ToS manipulations across experiments, as indexed by increased SCR arousal and self-reported anxiety in Experiment 1. While these effects might indicate that anxiety can have specific effects, our goal here was to identify results that robustly persist across experiments. Future research is required to identify similar specific effects of anxiety and the exact contextual variables that might cause them.

One limitation that deserves further discussion is that we observed relatively low variability in trait anxiety (BAI scores) within our sample (range of scores = 0–38). While our distribution (M = 10.17, SD = 8.61), compares quite well with previous studies (e.g., Bowman et al., 2019; Lawrence et al., 2014), the BAI scores reflect that our sample consisted of a relatively healthy population with mostly mild to moderate self-reported anxiety. This limited range of BAI scores might limit our ability to identify state by trait interactions. Moreover, a low representation of moderate to highly anxious people might also make it more difficult to identify more general effects of state anxiety on learning in our study (e.g., Berghorst et al., 2013). One potential reason for these relatively low levels of anxiety in our sample may be due to the (very reasonable) requirement of our ethics committee to clearly advertise the use of electric shocks in our experiments during recruitment. This might lead to a selection bias, attracting mostly participants that are generally less anxious, or at least less afraid of electrical shocks, compared with other studies. This limitation might equally impact other studies investigating stress and anxiety, and it is difficult to remedy such selection biases (e.g., Charpentier et al., 2020).

Conclusion

The current study investigated the effects of anxiety on learning, while addressing several concerns about experimental designs and analytical choices that might have led to discrepancies in the identification of such effects in previous studies. Despite our relatively powerful approach that simultaneously assessed learning and post-learning performance, as well as reward and punishment learning in the context of a within-subject anxiety induction, and contrary to some previous studies, our experiments failed to reveal clear and specific effects of anxiety on learning per se. While surprising at first glance, our null results agree with findings from a small-scale review that shows little to no effects of anxiety on learning and postlearning performance on average and they add to recent results, which have started to challenge the role of anxiety in experience-based decision-making (Bishop & Gagne, 2018; Gillan et al., 2019).

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Received May 23, 2020
Revision received February 9, 2021
Accepted March 15, 2021 ■