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Anxiety, Depression, and Decision Making: A Computational Perspective

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Abstract

In everyday life, the outcomes of our actions are rarely certain. Further, we often lack the information needed to precisely estimate the probability and value of potential outcomes as well as how much effort will be required by the courses of action under consideration. Under such conditions of uncertainty, individual differences in the estimation and weighting of these variables, and in reliance on model-free versus model-based decision making, have the potential to strongly influence our behavior. Both anxiety and depression are associated with difficulties in decision making. Further, anxiety is linked to increased engagement in threat-avoidance behaviors and depression is linked to reduced engagement in reward-seeking behaviors. The precise deficits, or biases, in decision making associated with these common forms of psychopathology remain to be fully specified. In this article, we review evidence for which of the computations supporting decision making are altered in anxiety and depression and consider the potential consequences for action selection. In addition, we provide a schematic framework that integrates the findings reviewed and will hopefully be of value to future studies.

Contents

1. INTRODUCTION

1.1. Overview

Anxiety and depressive disorders are highly comorbid (Brown et al. 2001, Kessler et al. 2005) yet also distinctive in their symptomatology. Individuals suffering from both anxiety and depression show difficulties with decision making. In this article, we use the computational decision making literature to outline the component processes that inform our decisions, and consider evidence pertaining to the influence of anxiety and depression on these processes. Although previous authors have considered alterations to decision making in anxiety or depression (Hartley & Phelps 2012, Huys et al. 2015), there has been little attempt to review both in conjunction. We believe this is an important step if there is to be progress in characterizing unique, versus common, alterations to decision making in anxiety and depression and how these alterations might in turn contribute to the maintenance and distinctive features of these disorders. To this end, we also provide a schematic framework that can be used to integrate and further explore influences of anxiety and depression on both reward- and threat-related decision making. We note that, moving forward, it will be important to identify alterations in decision making specific to different subdimensions of anxiety or depression (examples of such subdimensions can be found in Bijsterbosch et al. 2014). We do not emphasize this finer differentiation in this review, given the current lack of pertinent empirical evidence. We do, however, highlight the few studies that have begun to investigate correlates of specific subdimensions of anxiety or depression.

1.2. Decision-Making Processes that Guide Reward Seeking and Threat Avoidance

Our actions, and those of other species, can be described in terms of attempts to obtain rewarding, or positive, outcomes and to avoid aversive, or negative, outcomes. Maybe we want a promotion, someone to say yes to a date, to escape being mugged, or to avoid being laid off at work. We

can rarely be certain that a given action will achieve our goal. Further, it might be the case that no single action will suffice and we need to consider how alternate action sequences will play out. Computational approaches to decision making provide us with a framework within which to understand the processes that inform our action selection.

Through our interactions with our environment, we gain information about the value of potential outcomes, the probability that those outcomes will be obtained following different actions, and the effort that different courses of action require. Multiple studies have provided evidence that such inputs are indeed used to inform action selection by humans and other animals (Camerer 1995, Chong et al. 2016, Schultz 2015). In many cases, the information needed to precisely calculate outcome value, probability, and effort costs is not fully available and these parameters must be estimated under varying levels of second-order uncertainty (Bach et al. 2011). Further, people vary in the subjective valuation of outcomes and the relative weighting of outcome probability and outcome value (i.e., risk aversion) (Kahneman & Tversky 1979). This raises the possibility that not only differences in the accuracy of parameter estimation but also differences in parameter weighting might characterize the decision making of anxious or depressed individuals.

Individuals might also vary in their reliance on different methods for estimating the potential value of alternate actions. Here, a distinction has been drawn between model-free and model-based decision-making processes (Daw et al. 2005). In model-free learning, the individual is held to use the outcome of past actions (i.e., how often a given action has been followed by a rewarding or aversive outcome and the magnitude of that outcome) to update current estimates of the value of alternate actions. In model-based decision making, the individual is held to form a model of the world that includes the probability of transitions between states and the outcomes linked to each state in question (Daw & Dayan 2014, Sutton & Barto 1998). This enables the individual to evaluate actions using the summed long-run value that would be obtained by traversing a series of states. When we think of complex real-life situations (e.g., choosing between jobs or places to live), model-based reasoning provides an intuitively appealing formulization of the decision processes involved. However, full model-based reasoning is intractable; it rapidly becomes unmanageable to evaluate every possible series of states that might follow a given initial choice. It has been argued that off-line simulation of state transitions and associated outcomes might simplify in-the-moment comparison of the long-run value of alternate actions. It has further been proposed that recall, or replay, of actual experiences of state-to-state transitions and state–outcome associations might also inform these long-run value estimates (Foster & Wilson 2006, Johnson & Redish 2005, Lin 1992, Sutton 1990). The choice of which state transitions and state–outcome associations to replay or simulate might vary across individuals, as might also the extent to which replay or simulation is engaged. Similarly, in-the-moment comparison of alternate actions might also be influenced by the effects of mood on the accessibility of different states and outcomes.

1.3. Structure of the Review

In Section 2, we review the evidence for whether anxiety or depression influences the rate of model-free learning. In Section 3, we consider the evidence for whether anxiety or depression influences the accessibility of particular states and outcomes during simulation and recall, given the proposed role of these processes in model-based decision making. We also consider whether the extent of engagement in simulation or recall might be altered in anxiety or depression. In the remaining sections, we review findings pertaining to the influence of anxiety and depression on the subjective valuation and weighting of parameters that likely inform both model-free and model-based decision making. Specifically, we review the evidence for whether anxiety or depression is associated with altered valuation of rewarding or aversive stimuli (Section 4), and with different

willingness to engage in various levels of effort to achieve the desired outcome (Section 5). We also consider studies of risk aversion and the evidence for whether anxiety or depression is associated with differential weighting of outcome magnitude versus probability (Section 6). In Sections 7 and 8, we conclude with the provision of a schematic framework that can be used to characterize and further investigate the influences of anxiety and depression on the component computational processes that guide our decision making.

2. INFLUENCES OF ANXIETY AND DEPRESSION ON THE RATE OF MODEL-FREE LEARNING

One way that anxiety and depression might affect action values is through model-free learning and the rate at which estimates of action values are updated following an unexpected outcome. Activity in the dopamine system and brain regions innervated by this system, including the striatum and regions within the frontal cortex, signals how much outcomes received diverge from outcomes expected (Schultz 1998, Schultz et al. 1997). This signal is called a prediction error, and changes in both outcome probability and outcome magnitude influence the size of this signal in the context of reward (Rushworth & Behrens 2008). Similar prediction error signals are generated when aversive outcomes differ from expectation (Li et al. 2011, Mirenowicz & Schultz 1996, Seymour et al. 2004) (though see Schultz 2016 for caveats regarding the interpretation of dopaminergic prediction errors for aversive outcomes and Dayan & Huys 2009 for the potential role of serotonergic systems in aversive prediction errors).

The extent to which we use prediction errors to update our estimates of expected value depends on our current rate of learning. For optimal performance, we need to take into account levels of second-order uncertainty (Bach et al. 2011). The more confident we are in our value estimates, the slower we should be to change them. One source of second-order uncertainty is contingency volatility. If action–outcome contingencies are noisy but stable, such as when a given action leads to a given outcome three-quarters of the time, the lower the learning rate that is adopted, the less likely an actor is to suboptimally change behavior following intermittent unexpected outcomes. In contrast, when the probability or magnitude of outcome linked to a given action is rapidly changing, a high learning rate is required for the actor to avoid becoming stuck in a pattern of behavior that is no longer optimal. It might seem a tall order for individuals to be able to differentiate contingency volatility from contingency noise and adjust their behavior by moderating their learning rate accordingly. However, in the cases of both reward and aversive learning, healthy participants are remarkably accurate in their ability to do this (Behrens et al. 2007, Browning et al. 2015). Findings from the human and basic neuroscience literature implicate the anterior cingulate cortex (ACC) and the amygdala in the use of contingency volatility to modulate rate of learning (Behrens et al. 2007, Li et al. 2011, Roesch et al. 2012).

In contrast to low-trait anxious individuals, high-trait anxious individuals struggle to adapt their learning rate to current levels of volatility, especially in the case of aversive outcomes (Browning et al. 2015). There is no difference between high- and low-anxious individuals in mean learning rate, and high-anxious individuals do not show impaired prediction error generation—modulation of both pupil dilation and next-trial reaction time by outcome surprise (i.e., the unsigned prediction error) is unaffected by trait anxiety (Browning et al. 2015). The association between anxiety and impoverished adaptation of learning rate has been shown to also hold in the case of reward loss but not reward gain (Pulcu & Browning 2017).

Turning to depression, a recent meta-analysis concluded that there was little evidence that learning rate differs between patients with major depressive disorder (MDD) and controls or varies as a function of level of anhedonic depression (Huys et al. 2013). However, the task used in the

studies reviewed did not manipulate contingency volatility. Hence, this leaves open the question of whether depression, like anxiety, might be linked to a specific deficit in ability to adjust learning rate to contingency volatility. In the study reported by Browning et al. (2015), both the anxious arousal and the anhedonic depression subscales of the Mood and Anxiety Symptom Questionnaire showed the same inverse relationship to adjustment of learning rate as that reported for the State Trait Anxiety Inventory trait subscale (C. Gagne & S. Bishop, unpublished data). Further analysis revealed that learning rate adjustment was linked primarily to the shared variance of these two subscales. Given the high correlations ($r \geq 0.6$) between scores on the different scales, we need to establish whether this result replicates in a larger sample. For now, this finding provides tentative evidence that impoverished adjustment of learning rate to match environmental volatility might represent a common vulnerability linked to both anxiety and depression.

An inability to adapt learning rate to current levels of volatility is likely to result in individuals being less able to determine the best course of action when faced with unexpected outcomes. That this can affect high-trait anxious individuals' decision making even when contingencies are stable is supported by existing findings (Browning et al. 2015). One potential response may be to simply treat all environments as highly volatile; indeed, there is evidence that anxious participants do sometimes select this approach (Huang et al. 2017). If individuals either incorrectly treat stable environments as volatile or have high levels of uncertainty around their estimates of volatility (high meta-volatility), the breadth of distribution of potential values of a given action derived from model-free learning will be increased. This in turn might reduce subjective confidence in action value estimates.

3. EVIDENCE FOR INFLUENCES OF ANXIETY AND DEPRESSION ON SIMULATION AND RECALL PROCESSES

Tversky and Kahneman (Kahneman & Tversky 1982, Tversky & Kahneman 1974) introduced the idea that individuals might use availability heuristics when judging the probability of future events. Here, the contention is that the more instances we can recall of a given event having happened in the past, or the easier we find it to simulate the given event happening in the future, the higher our subjective judgment of the event's probability will be. When an event type is rare, we are generally less likely to recall or simulate instances of the event's occurrence; hence, we judge the event as less probable. In terms of current theories of model-based decision making, our judgment of the probability of a given outcome is influenced by the number of state sequences sampled that result in that outcome.

Considerable evidence indicates that the emotional salience of events affects their recall (Cahill et al. 1996, Dolcos et al. 2017). Within the anxiety and depression literatures, it has been argued that mood-congruent biases might affect the relative ease with which individuals recall or simulate negative and positive events and that this in turn might influence judgments of the future probability of events. In the terminology of model-based decision making, anxiety and depression might influence the states and outcomes we consider when we engage in simulation and recall processes and when we use these processes to inform long-run estimates of the probability of various outcomes and the consequent summed value of a given course of action. We break down the empirical evidence in support of this claim below.

First, anxious and depressed individuals do indeed show altered judgments of the future probability of real-world emotional events. Patients with generalized anxiety disorder (GAD) and MDD and individuals with high subclinical levels of anxiety and depression show elevated estimates of the probability that they will experiences negative events (Butler & Mathews 1983, MacLeod et al. 1996, Muris & van der Heiden 2006). Here, there is some evidence that estimates of the future

probability of negative events are more strongly linked to anxiety than to depression when the two are teased apart (Muris & van der Heiden 2006). Depression is also strongly linked to reduced estimates of the future probability of positive events, with evidence indicating this association is specific to depression rather than shared with anxiety (MacLeod et al. 1996, Muris & van der Heiden 2006).

Other findings meanwhile link both ease of simulation and ease of recall to judgments of the future probability of real-world events. Macleod et al. (1991) reported that participants' ability to generate reasons why events might or might not occur significantly predicted their estimates of the probability of both future negative and future positive events. Similarly, ease of recall of past negative or past positive events has also been found to predict estimates of the probability of future events (MacLeod & Campbell 1992). In addition, studies of simulation and recall in anxiety and depression have revealed valence-specific biases. When asked to generate, in a limited time, events that might happen in the future, anxious individuals show increased generation of negative events relative to control participants (MacLeod & Byrne 1996). Meanwhile, groups characterized by depressed mood show reduced generation of positive events (Bjärehed et al. 2010, MacLeod & Byrne 1996, MacLeod & Salaminiou 2001, Moore et al. 2006). Multiple studies have also linked elevated depression levels to heightened recall of negative events and stimuli (Bradley & Mathews 1983, Clark & Teasdale 1982, Teasdale et al. 1980), with some additional evidence for depression being linked to reduced recall of positive events and stimuli (Bishop et al. 2004). We note that in the studies reviewed, it is difficult to dissociate the influence of mood-congruent biases on recall or simulation from the influences of differences in life experiences on recall or simulation. However, putting aside the origin of these biases, it does appear that anxiety and depression are associated with differences in the output of the recall and simulation processes central to model-based decision making. In relation to negative events, in particular, there is some suggestion that recall biases might be more evident in depression and future-oriented simulation biases might be more evident in anxiety. However, the robustness of this dissociation and the relative influence of recall processes versus simulation processes on judgments of the future probability of negative events remain to be established.

Additional potential evidence of alterations to simulation and recall processes in anxiety and depression comes from clinical studies of the role of repetitive cognitions, specifically worry and rumination, in anxiety and depressive disorders. Although both rumination and worry tend to be focused on negative outcomes, rumination is largely a past-oriented form of repetitive thought and worry is future-oriented in its focus (Watkins et al. 2005). Multiple cross-sectional and longitudinal studies have linked extent of rumination to levels of both current and future depressive symptomatology; worry has similarly been linked to both current and future anxiety symptomatology (for a comprehensive review of this literature, see Watkins 2008). However, many of these studies focused selectively on depression and rumination or on anxiety and worry. One exception was a study by Hong (2007). Here, the author found that worry predicted both future depressive and anxiety-related symptomatology, whereas rumination was more uniquely associated with future risk for depression. It has since been proposed that rumination and worry might be different facets of a transdiagnostic risk factor (McEvoy et al. 2013). In line with this, Kircanski et al. (2015) reported that rumination and worry were equally elevated across patients with GAD, patients with MDD, and patients comorbid for GAD and MDD, relative to healthy control participants.

Rumination and worry have been interpreted by some as maladaptive attempts at problem solving (Szabó & Lovibond 2006, Treynor et al. 2003, Watkins 2008). In particular, the worry literature throws light on how simulation processes might become pathological in nature. Here, a focus on negative outcomes has been linked to both elevated reported frequency and uncontrollability of worrying (Szabó & Lovibond 2006). Difficulty with terminating the simulation process

also appears to be of importance. In model-based decision making terms, this difficulty might reflect failure to achieve a given stopping criterion. Szabó & Lovibond (2006) reported that worry characterized as uncontrollable was associated with failure to settle on a good solution to the problem being worried about. In addition, children with clinically significant levels of anxiety were more likely to report an inability to stop worrying until the perceived threat was removed (Szabó & Lovibond 2004). In adults, anxiety has also been linked to an increased number and duration of periods spent worrying (Verkuil et al. 2007). These findings suggest that anxiety, and possibly depression, given its similar association with worry and rumination (Kircanski et al. 2015), might be characterized by a perceived or actual failure to successfully complete attempts at model-based decision making, leading to prolonged engagement in simulation and replay.

4. SENSITIVITY TO THREAT AND REWARD IN ANXIETY AND DEPRESSION

Alterations to model-free or model-based decision making in anxiety and depression might interact with altered subjective valuation of rewarding or aversive outcomes. The main evidence pertaining to whether subjective valuation of aversive and rewarding outcomes is altered in anxiety and depression comes from studies of sensitivity to threat and sensitivity to reward. We review these in turn.

It has long been suggested that anxiety is linked to increased threat sensitivity, potentially as a result of amygdala hyperresponsivity to threat (Etkin et al. 2004, Mathews & Mackintosh 1998). However, an increasing number of studies are beginning to challenge this assumption. Blair & Blair (2012) reviewed studies examining both physiological and neural responses to visual threat stimuli in patients with GAD relative to healthy control subjects. Most studies reviewed reported either no difference in threat responsivity between groups or reduced threat responsivity in the GAD group. In other anxiety disorders, amygdala hyperresponsivity has been reported most consistently in response to disorder-related stimuli (e.g., social stimuli in social anxiety disorder, trauma-related cues in post-traumatic stress disorder). In these cases, it is difficult to dissociate elevated threat sensitivity from differential prior Pavlovian learning of conditioned responses to the stimuli in question (Blair & Blair 2012, Shin & Liberzon 2010). Within the pain literature, researchers have addressed whether sensitivity to primary aversive stimuli is altered in individuals with preexisting anxiety or depression. However, here, investigations of whether individuals with anxiety and depressive disorders show altered pain sensitivity have also produced inconsistent findings including both hyper- and hyposensitivity to pain (Wiech & Tracey 2009).

The studies reviewed above examine the response to aversive stimuli upon presentation. The effects of anxiety on threat responsivity have also been studied during expectation of aversive stimuli. Studies of both rodents and humans have reported anxiety-related increases in the magnitude of physiological responses while subjects are waiting for the occurrence of aversive stimuli, especially when the delivery of these stimuli is unpredictable (Davis et al. 2010, Grillon et al. 2008). Further, anxiety has been linked to elevated estimates of the aversiveness, as well as of the probability, of potential future real-life negative events (Butler & Mathews 1983). One possible explanation for these findings is that anxiety influences expectations about the subjective value of aversive outcomes, as opposed to modulating the immediate response to outcomes of a given magnitude. If this is the case, we would need to address why nonpathological responses to experienced outcomes do not lead to successful updating of expected outcomes. Arguably, this might arise from a combination of deficits in model-free learning (see Section 2) and heightened accessibility of aversive outcomes during model-based simulation (see Section 3). We further explore this possibility in Section 7.

Alterations in reward sensitivity have been studied primarily in relation to depression rather than anxiety. Self-reported anhedonia, the inability to derive pleasure from normally rewarding activities, is a diagnostic feature of MDD (Am. Psychiatr. Assoc. 2013) and a major dimension of depressive symptomatology. However, experimental studies have found little evidence for reductions in primary reward sensitivity in MDD. For example, several studies have failed to find reductions in pleasantness ratings of sucrose, or chocolate, in patients with MDD relative to control participants (Amsterdam et al. 1987, Potts et al. 1997, Scinska et al. 2004). Although we need to be cautious when interpreting null results, one possibility is that depression is associated primarily with altered processing of social rewards. This would still fit with depressed patients' reduced participation in normally rewarding activities as these tend to be social in nature. However, studies have also failed to find an influence of depression on perceived intensity of socially rewarding stimuli (Branco et al. 2017, Schaefer et al. 2010). An alternate possibility is that, in parallel to anxiety and threat, depression might be linked to biases in estimation of future reward value, as opposed to altered responsivity to actual outcomes. In line with this possibility, MacLeod & Salaminiou (2001) found that patients with MDD gave lower estimates of the pleasure they would experience from various life events than did control participants, whereas Peeters et al. (2003) found that patients with MDD actually reported greater increases in positive affect after experiencing positive events than did control participants. This pair of findings is consistent with depression being linked to a lower expectation of reward value and a positive prediction error upon reward receipt. Here, again, the natural question is why would a positive prediction error not lead to updating of expected reward value over time. In parallel to the argument for anxiety and threat sensitivity outlined above, this could arise as a result of impaired model-free learning in conjunction with reduced sampling of states linked to highly rewarding outcomes during model-based simulation and recall. As reviewed in Section 2, there is less evidence for altered model-free updating in the case of depression and rewarding outcomes than in the case of anxiety and aversive outcomes. An alternative possibility is that, in depression, elevated subjective valuation of effort costs might reduce engagement in actions aimed at obtaining reward and decrease opportunities for model-free updating based on actual experiences of reward. In line with this, Peeters et al. (2003) report that MDD patients experience fewer positive events than do controls. We further consider the evidence for altered valuation of effort in depression versus anxiety in the next section.

5. VALUATION OF EFFORT: OPPOSING EFFECTS OF ANXIETY AND DEPRESSION

In depression, reduced participation in normally rewarding activities might reflect increased subjective valuation of the effort costs involved in pursuing these activities. Findings suggest that depression is associated with reduced preference for high-magnitude rewards that require high-effort expenditure over low-magnitude rewards that require low-effort expenditure (Treadway et al. 2009, 2012). However, these findings might reflect either altered subjective effort costs or altered subjective valuation of rewarding outcomes.

In recent work on apathy, Husain and colleagues have used computational modeling to tease apart the influences of reward magnitude and required effort. Findings from these studies suggest that apathy is linked primarily to increased valuation of effort, as opposed to differential sensitivity to the magnitude of reward (Bonnelle et al. 2015, 2016; Chong et al. 2016). Given that individuals with MDD often show high levels of apathy, an important question is how much do apathy levels mediate differences in willingness to exert effort to obtain reward in patients with depression relative to healthy controls. Moving forward, larger-scale studies are required to disentangle the

relationship between overall levels of depressive symptomatology, specific levels of apathy and of anhedonia, and effort valuation versus reward sensitivity. Investigation of the influences of anxiety on effort–reward trade-offs is also much needed.

At the neural level, ACC dysfunction is a strong potential candidate for contributing to altered effort–reward trade-offs in depression. ACC lesions, disconnection of the ACC and NAc core, and disconnection of the amygdala and ACC have all been demonstrated to result in a shift in behavior toward lower-effort, lower-reward options (Floresco & Ghods-Sharifi 2007; Hauber & Sommer 2009; Walton et al. 2003, 2009). Human neuroimaging findings have also reported altered ACC structural and functional connectivity in individuals with high levels of apathy (Bonnelle et al. 2016).

With regard to aversive outcomes, increased willingness to exert effort to avoid aversive outcomes is commonly observed in animal models of anxiety (Servatius et al. 2008). The forced swim test, more commonly associated with animal models of depression, measures exertion of physical effort when subjects are placed in water without the ability to reach a platform (Porsolt et al. 1977). Reduced time spent immobile in the forced swim test is a predictor of antidepressant effectiveness (Cryan et al. 2005, Porsolt et al. 1977), suggesting that neurochemical changes determining recovery from depression may be linked to alterations in the level of effort that an individual is willing to exert. Recent work has revealed that elevated anxiety leads to above-baseline levels of locomotion in the forced swim test and that this is reduced by anxiolytic agents (Lee et al. 2017). These findings are of interest because they reveal opposing effects of anxiolytics and antidepressants. This suggests that willingness to exert effort to avoid aversive outcomes might be a domain where differential correlates of depression and anxiety will potentially be observed in humans. Research, in human participants, into the trait correlates of willingness to deploy effort to avoid aversive outcomes is in its early stages. Initial findings suggest that negative affect is linked to increased deployment of effort (Nord et al. 2017). Further studies are required to tease apart the effects of anxiety and depression as well as to control for potential intersubject differences in outcome valuation both prior to action selection and upon receipt.

6. INCREASED RISK AVERSION IN ANXIETY

Differences in the relative valuation of outcome magnitude versus outcome probability might also lead to differences in how individuals weigh competing options. One area where this has been studied is in relation to risk aversion and its association with anxiety. Patients with anxiety disorders report fewer risk-taking behaviors than patients with depressive disorders or healthy control participants (Maner et al. 2007). In the context of reward-based decision making, risk aversion has been studied by assessing participants' preferences for higher-probability, lower-value outcomes over lower-probability, higher-value outcomes. Although many individuals show some degree of risk aversion, several studies have reported that risk aversion is more pronounced in individuals with high levels of anxiety (for a review, see Hartley & Phelps 2012).

When analyzing risk aversion findings, it is important to consider the computations that might give rise to apparent risk aversion. Individual differences in risk aversion might reflect preference for actions with high-probability outcomes, altered subjective valuation of low-magnitude versus high-magnitude outcomes, or a combination of both. In addition, if participants need to estimate outcome probability, individual differences in learning rate, or adaptation of learning rate to second-order uncertainty (both volatility and level of information available with which to estimate outcome probability), might come into play. Finally, if there is the possibility for loss of reward, then individual differences in valuation of reward gain versus reward loss are also likely to be pertinent.

Raghunathan & Pham (1999) investigated risk aversion using a simple paradigm in which information about outcome probability was directly provided. Participants chose between a high-risk (i.e., low-probability), high-magnitude reward option and a low-risk (i.e., high-probability), low-magnitude reward option using a simple gamble matched on expected value (i.e., the product of outcome probability by outcome magnitude). Raghunathan & Pham (1999) found that induced anxiety led to increased selection of the low-risk, low-reward option, in contrast to induced sadness, which was associated with greater selection of the high-risk, high-reward option. One limitation of this study is that participants were presented with only a single gamble. In contrast, recent studies have typically adopted more complex paradigms with multiple trials.

One task commonly used to investigate risk aversion is the balloon analog risk task. Participants choose how far to pump up a virtual balloon, increasing their financial payout with each pump but losing all their winnings for a given balloon if they reach the unknown point at which the balloon explodes (Lauriola et al. 2014). Individuals with elevated levels of anxiety and worry tend to have earlier stopping points (Maner et al. 2007). This finding is taken as indicative of increased risk aversion. In this task, participants can use their experience with prior balloons to update their estimates of how likely a balloon is to pop at any given point. This popping point is unknown and variable (often drawn from two or more probability distributions); hence, the probability that the balloon will pop at any point needs estimating and there is considerable second-order uncertainty around this estimate. If anxious individuals are less able to choose an appropriate learning rate under such circumstances, as discussed in Section 2, one possible heuristic might be to adopt a safe early stopping point. Hence, risk aversion in this task might reflect either a deficit in learning or a preference for low risk despite uncompromised learning. This is difficult to disentangle. Further, the amount of money already gained and that will be lost if the balloon explodes increases with each pump. It is well established that many individuals weight potential losses more than potential gains (Tversky & Kahneman 1992; for a review, see Schultz 2015). Individual differences in risk aversion versus loss aversion are also difficult to differentiate within the balloon analog risk task.

In a recent elegant computational study, Charpentier et al. (2017) teased apart the effects of risk aversion from those of loss aversion while investigating the correlates of both anxiety and depression. Patients with GAD showed elevated risk aversion relative to healthy control participants but did not differ from controls in how much they valued losses relative to gains. Patients with GAD and a concurrent diagnosis of MDD showed a level of risk aversion that fell in between that of patients with GAD alone and that of control participants. Analyses using continuous measures of trait anxiety and depression revealed that anxiety levels were positively correlated with risk aversion when controlling for depression, but depression levels showed no significant relationship with risk aversion when controlling for anxiety. The experimental power of these analyses was relatively low, and replication of these results is needed. However, taken together with the other findings reviewed here, these results suggest that anxiety is linked to increased preference for low-risk options. In contrast, there appears to be little evidence of a unique relationship between depression and risk aversion.

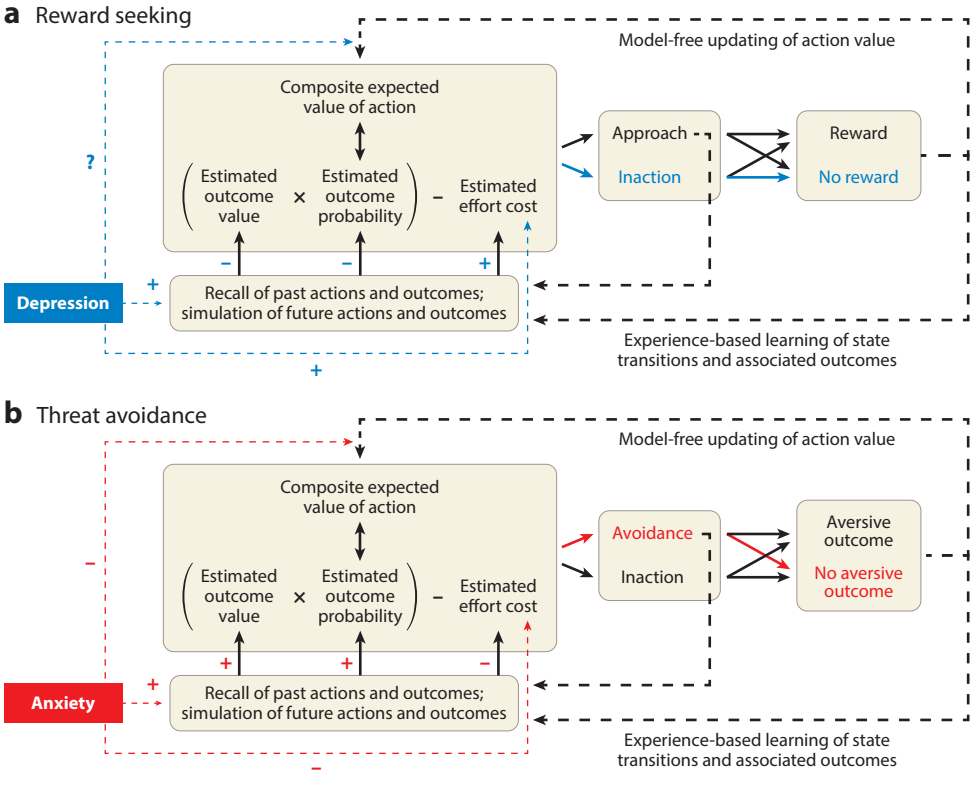
7. A SCHEMATIC FRAMEWORK OF ALTERED COMPUTATIONS UNDERLYING DECISION MAKING IN ANXIETY AND DEPRESSION

In the sections above, we have reviewed findings pertaining to the influences of anxiety and depression on the component processes involved in decision making. In this penultimate section of the article, we put forward a schematic framework of altered decision making in anxiety and depression. Our intention is to both integrate the findings reviewed above and provide a framework of potential value to future computational psychiatry studies. In **Figure 1**, we illustrate how

the altered computations underlying decision making (ACDM) framework can be applied to account for reduced engagement in rewarding activities in depression and increased engagement in avoidance behaviors in anxiety and the vicious circles that might consequently ensue and contribute to maintenance of psychopathology. We expand our discussion of this framework within the rest of this section and in Section 8. We note that the ACDM framework is easily extended to address altered decision making in other forms of psychopathology.

The ACDM framework illustrates how model-free and model-based decision making processes might interact to contribute to altered action selection in both anxiety and depression. Some of the choices we face in everyday life reoccur only intermittently. This influences the potential frequency of model-free updating of action values following actual outcomes. Further, if we choose not to act, we gain no new evidence about outcome value or probability or the effort that would be required and hence do not have the opportunity to update our action values. Similarly, if we act to avoid a given outcome, we gain no new information about how bad or probable that outcome would have been in the absence of the action taken. The potential consequences of such path dependency for anxiety and depression are outlined in **Figure 1** and further considered below.

Experience-based learning also informs model-based estimates of state-to-state transition probabilities and state–outcome associations. However, during both off-line simulation and recall and in-the-moment selection between alternate actions, the relative ease with which different states and outcomes are accessed is held to be susceptible to fluctuations in mood state and affected by mood-congruent biases linked to both anxiety and depression (findings linking anxiety to increased accessibility of negative outcomes when simulating future events and depression to decreased



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

The altered computations underlying decision making (ACDM) schematic framework: accounting for reduced reward-seeking behaviors in depression and increased threat-avoidance behaviors in anxiety. (*a*) Engagement in potentially rewarding activities. Model-free estimates of action value are updated over time on the basis of the individual's experiences. These estimates are influenced by the frequency with which the action in question has a positive outcome, how subjectively rewarding the outcome is, and the level of subjective effort required. Model-based recall and simulation mechanisms enable off-line updating of estimates of the probability that a given action will directly, or indirectly, result in one or more outcomes, as well as of the relative subjective value of those outcomes and the level of effort that achieving them, directly or indirectly via the action in question, will entail. These model-based estimates are also updated over time as a result of the individual's experience. However, in addition, current mood affects which state transitions and state–outcome associations are sampled during off-line simulation and recall and in-the-moment evaluation of alternate actions. An interplay between model-free and model-based processes occurs, with the relative influence of these processes on action selection varying across individuals and situations. Depressed mood is predicted to reduce availability of simulated states associated with future positive outcomes, especially those of high value, resulting in decreased estimates of the probability and value of rewarding outcomes. Difficulties recalling past experiences of reward following engagement in similar activities are also expected to affect these estimates. We speculate that depressed mood might similarly increase recall or simulation of state transitions involving high effort costs. On the basis of the forced swim test literature, we also propose a direct effect of depression on maximal effort levels that an individual is willing to exert. Together these influences are expected to lead to reduced engagement in actions that have the potential to result in rewarding outcomes. As a result, experience-based updating of model-free and model-based estimates will decrease, leaving calculations of action value increasingly susceptible to the influences of depressed mood state on simulation and recall processes. For now, we remain agnostic about whether depression also affects confidence in action value estimates through failure to adjust model-free learning rates to environmental volatility. (*b*) Avoidance of aversive outcomes. Many of the aversive outcomes that we worry about are relatively rare. Hence, we are likely to have low certainty in our estimates of their probability and severity. This leaves room for simulation processes to have a strong influence on these estimates. Anxiety is hypothesized to modulate this influence through increased simulation of future states associated with feared outcomes, leading to overestimation of aversive outcome probability and magnitude. Anxiety is also predicted to increase the effort an individual is willing to commit to avoidance behaviors. Given the relative infrequency of aversive events, engagement in avoidance behaviors is likely to be reinforced by the nonoccurrence of aversive outcomes, especially if effects of anxiety on simulation processes have upwardly biased estimates of aversive outcome probability and magnitude. In addition, opportunities will be missed for learning an association between inaction and aversive outcome nonoccurrence. Finally, anxiety also affects the adjustment of the rate of learning to match the stability, or volatility, of the current environment, potentially also impairing the ability to learn from actual experience. Both engagement in avoidance behaviors and disrupted learning from actual outcomes are predicted to leave calculations of action value increasingly susceptible to influences of anxiety on simulation processes, enabling a vicious circle to develop.

accessibly of positive outcomes when simulating future events are reviewed in Section 3). This might contribute to biases in model-based estimates of both outcome probability and value (see Sections 3 and 4) and potentially also affect model-based estimates of effort costs. We note that the ACDM framework includes a reciprocal influence between model-free and model-based estimates of action value. This reflects the contention that output from simulation- and recall-based processes influences model-free estimates of action value (Sutton 1990), as well as evidence that model-free action value estimates are integrated into model-based calculations under certain circumstances (Keramati et al. 2016).

In **Figure 1**, we illustrate how influences of anxiety at various stages of the decision-making process might lead to increased engagement in actions aimed at avoiding aversive outcomes. Learning theorists have long argued that avoidance behaviors play a key role in maintaining anxiety disorders (for a review, see Krypotos et al. 2015). Within the ACDM framework, selection of avoidance-related actions reduces opportunities for updating estimates of the value of aversive outcomes, or their probability of occurrence in the absence of the avoidance behavior engaged, on the basis of

actual experiences. This maintains high levels of second-order uncertainty around these estimates, which is likely to be compounded by anxious individuals' difficulty in using second-order uncertainty to inform learning rate (Browning et al. 2015). The predicted consequence is that estimates of action value will be highly susceptible to influences of mood-congruent biases on simulation processes. As reviewed in Section 3, anxiety is linked to increased time spent worrying about potential future negative outcomes (Verkuil et al. 2007). In the ACDM framework this translates to heightened engagement in simulation processes, especially ones focused on the occurrence of aversive outcomes. This heightened engagement is expected to lead to an increasing imbalance between model-free and model-based influences on decision making and to a vicious circle of greater valuation, and selection, of avoidance behaviors, worsening anxiety, and increased time spent worrying, with estimates of the probability and severity of future possible aversive events becoming increasingly reliant on mood-congruent simulations and decreasingly based on actual experience.

The ACDM framework also illustrates how a distinct vicious circle may maintain the association between depression and reduced pursuit of rewarding activities. On the basis of the findings reviewed in Sections 3–5, depression is proposed to be associated with both increased valuation of effort costs and decreased estimates of the expected value of potentially rewarding outcomes. The latter might initially reflect effects of low positive affect on the ability to simulate experiencing and enjoying future rewarding outcomes (MacLeod & Salaminiou 2001, MacLeod et al. 1996). Decreased estimates of expected value and increased estimates of effort costs are expected to decrease the choice to pursue reward. This in turn reduces opportunities for updating the action value of engaging in potentially rewarding activities on the basis of actual experience. As a result, action values may become increasingly reliant, across time, on output from simulation processes susceptible to mood-congruent biases.

8. CAVEATS AND CONCLUSIONS

The schematic portrayal of the effects of anxiety and depression on decision-making processes provided in **Figure 1** is inevitably highly simplified. The studies reviewed in this article support differential influences of anxiety versus depression on threat avoidance versus reward seeking. However, the evidence is far from clear-cut and our ability to draw conclusions is hampered by the relative lack of studies, in humans, addressing influences of anxiety on decision making about rewarding outcomes and influences of depression on decision making about aversive outcomes. It would be of value for future studies to seek to remedy this imbalance.

One area where evidence is mixed concerns whether depression, and not just anxiety, is linked to elevated estimates of the probability and subjective value of real-world aversive outcomes. Here, we note that clinical studies have revealed that patients with MDD show levels of worry similar to those shown by patients with GAD (Kircanski et al. 2015). Further, depression is also highly associated with rumination (Kircanski et al. 2015, Watkins 2008) and increased recall of negative events and stimuli (Bradley & Mathews 1983, Clark & Teasdale 1982, Teasdale et al. 1980). However, even if elevated levels of rumination or worry exert an influence on depressed individuals' estimates of the expected value of aversive outcomes, an important predicted difference between anxiety and depression pertains to the willingness to exert effort to avoid aversive outcomes. Within the ACDM framework, influences of depression on estimated effort costs are predicted to reduce engagement in the active avoidance behaviors that are thought to play a key role in the maintenance of anxiety disorders. Effectively, in depression, a bias toward inaction may counteract a bias toward overvaluation of aversive future outcomes, facilitating learning about the nonoccurrence of the feared event when avoidance behaviors are not engaged.

In **Figure 1**, we also do not consider how the ACDM framework can encompass effects of anxiety on reward-related decision making. As reviewed in Section 6, anxious individuals are more risk averse than healthy control participants when pursuing reward. This effect appears to be unique to anxiety, as opposed to shared with depression (Charpentier et al. 2017). In the context of our ACDM framework, risk-averse behavior is predicted to increase feedback about, and hence decrease uncertainty about, the expected value of low-risk reward outcomes. In other words, over time, low-risk options will also become more information rich (i.e., lower in estimation uncertainty) than high-risk options. Both unpublished empirical data from our laboratory and findings from the clinical literature (Dugas et al. 1998) suggest that anxiety is associated with avoidance of information-poor options. Hence, increases in the relative information level of low-risk versus high-risk options might potentially augment anxious individuals' engagement in risk-averse behaviors.

Inevitably, this review is not exhaustive in its scope. Availability-based heuristics are unlikely to be the only heuristics to influence decision making regarding rewarding and aversive outcomes. In addition, we have not covered the literature on Pavlovian learning or on the influences of Pavlovian-to-instrumental transfer on willingness to engage in approach or avoidance behaviors (Talmi et al. 2008). The role of temporal discounting in decision making is an additional topic that we have not had space to discuss. Finally, we have focused largely on how depression and anxiety influence the component processes supporting decision making, as opposed to discussion of the underlying brain mechanisms. Whereas computational neuroscience studies have advanced our understanding of the neural substrate of decision-making component processes in healthy subjects (for reviews, see Rushworth & Behrens 2008, Schultz 2015), there is currently limited evidence pertaining to the specific influences of anxiety and depression on this neural circuitry, especially in humans. Over the next few years, the burgeoning field of computational psychiatry will hopefully provide further insight into the neural substrate of anxiety- and depression-related deficits in decision making. In particular, we look forward to being able to draw more concrete conclusions about the relative role of cingulate, striatal, and amygdala dysfunction.

To conclude, our review had two primary objectives. The first was to bring together studies that provide insight into which of the computations supporting decision making are altered in anxiety and depression as well as to highlight areas in which our knowledge is lacking. The second was to provide a schematic framework of how these alterations might lead to decreased engagement in potentially rewarding activities in depression and increased engagement in threat-avoidance behaviors in anxiety. Our review of the literature produced little compelling evidence for altered valuation of primary rewarding or aversive outcomes in anxiety or depression upon outcome receipt. In contrast, anxiety, and possibly depression, appears linked to increased estimates of the future probability and value of aversive outcomes, with depression also being linked to lower estimates of the future probability and value of rewarding outcomes. Findings from studies of rumination and worry and of recall and simulation in anxiety and depression suggest that increased engagement in recall and simulation processes, and mood-congruent influences on state and outcome accessibility, might contribute to these estimate biases. Differential effects of anxiety and depression on willingness to exert effort might additionally contribute to increased engagement in avoidance behaviors in anxiety and reduced engagement in potentially rewarding activities in depression. This in turn might affect opportunities for updating action value estimates on the basis of actual outcomes in a manner that sustains these maladaptive behavioral patterns. Problems with adjusting learning rate to match levels of second-order uncertainty in anxiety might further impair learning from actual outcomes.

Additional research is needed to establish whether depression also affects use of second-order uncertainty to adjust learning rate for either aversive or rewarding outcomes. It would also be of

value to better understand the potential three-way trade-offs of outcome value, outcome probability, and effort costs and whether these trade-offs vary as a function of anxiety or depression levels. Finally, further research is needed to determine whether the effects of anxiety or depression on specific components of decision-making processes are mediated by levels of worry, rumination, apathy, or anhedonia, as well as other dimensions of interest. Results from such research might enable us to better predict patterns of difficulties with decision making and behavioral symptoms across patients with different profiles on these dimensional measures. We hope that the framework we have put forward will be of value in guiding such future studies and in interpreting their findings.

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