Cognitive Mechanisms, Neural Circuitry, and Individual Differences in Human Foraging Under Threat



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General Abstract

In nature, survival often requires foraging while staying vigilant for potential predators. The ability to flexibly switch between foraging and vigilance is ubiquitous across species and thought to have shaped the evolution of neural circuitry in animals. Balancing attention between rewards and threats is also relevant to contemporary human life, and changes in responding to rewarding versus threatening stimuli have been linked with symptoms of psychiatric disorders such as apathy and anxiety. However, it is not fully understood how people make these behavioural transitions. Characterising the cognitive mechanisms, neural substrate, and role of individual differences in this process would improve our knowledge of ecological decision-making and could provide insights of clinical relevance. This thesis aims to address these knowledge gaps by presenting three experiments. First, Chapter 1 introduces relevant background information including theories, methods, frameworks, and questions that inspired the design and interpretation of the following experiments. Next, Chapter 2 presents a unique ecological task for studying natural foraging and vigilance behaviours. I use a computational model to show how people solve this task by tracking information about reward and threat levels, demonstrate model validity with simulation, and show potential clinical relevance. Third, Chapter 3 describes a large online study inspired by computational psychiatry and transdiagnostic approaches. Results show that dimensions of psychiatric symptoms are characterised by distinct patterns in switching between foraging and vigilance, and suggest that emotion plays an adaptive, homeostatic role in decision-making. Chapter 4 presents a study that uses ultra-high field fMRI to map brain areas involved in behavioural transition. It shows that two distinct networks are involved in tracking reward and threat and initiating behavioural change. Finally, a general discussion considers how

this work contributes to our knowledge of fundamental cognitive and neural processes and supports emerging methodologies for studying mental health and disease.

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1. Chapter: Introduction

In everyday life we experience many different influences on our cognition and behaviour, from positive motivators such as food to negative provocations such as physical danger. To survive and thrive, we must track multiple changing sources of information and flexibly switch between different behaviours. Across species, the need to switch between foraging and vigilance is nearly ubiquitous and critical to survival. However, the neural mechanisms underlying these behavioural transitions are not well understood. In addition, individuals manage these processes differently—and in some cases this may manifest as a symptom of psychopathological disorder. Relationships between mood, psychopathology, and flexible behaviour switching are largely unexplored. In this thesis I present a series of experiments that contribute to our knowledge of how the human brain makes these behavioural transitions, as well as how this process is affected by mood and behavioural dimensions linked with psychopathology. This work is arranged in three parts: first, I present an ecological framework and computational model for studying the relevant behaviour, and demonstrate their clinical potential (Chapter 2); second, I examine how both changing moods and enduring traits affect this decision-making process (Chapter 3); and finally, I characterize the neural basis of switching between vigilance and foraging (Chapter 4). In this introduction I will present concepts relevant to this investigation, including background information about relevant cognitive processes, an overview of the computational psychiatry framework, a brief summary of methods used in computational psychiatry, and a brief discussion of relevant brain areas and ways to record their activity.

1.1. Cognitive Foundations of Switching Between Foraging and Vigilance

Many decisions concern interacting with a particular stimulus in the environment: for example, whether to persist foraging in a location, or whether to approach or avoid a potential threat. Prior to this however, a broader decision must be made: of all the stimuli in the environment, which requires attention at this moment? Animals and humans have limited cognitive resources and time, and real-world environments contain multiple features with the potential for various behavioural influences. Survival requires tracking information related to each possible behavioural mode to orient behaviour appropriately and switch behaviours based on changing circumstances (Fig. 1). Further, the need to balance foraging and vigilance merits special focus. It is nearly universal among animals, critical to survival, and therefore likely of evolutionarily ancient origin. In the clinical literature, disordered patterns of attending to threat- and reward-related stimuli are a core symptom of psychiatric disorders such as generalized anxiety disorder and obsessive-compulsive disorder. Thus, studying this type of decision-making will contribute to our understanding of fundamental naturalistic behaviour and may also provide insights of clinical relevance. In this section I will present background information about cognitive processes relevant to understanding flexible switching between reward- and threat-oriented behaviour, including information sampling and exploratory behaviour (Section 1.1.1), task switching (Section 1.1.2), vigilance and defence (Section 1.1.3), and foraging (Section 1.1.4).

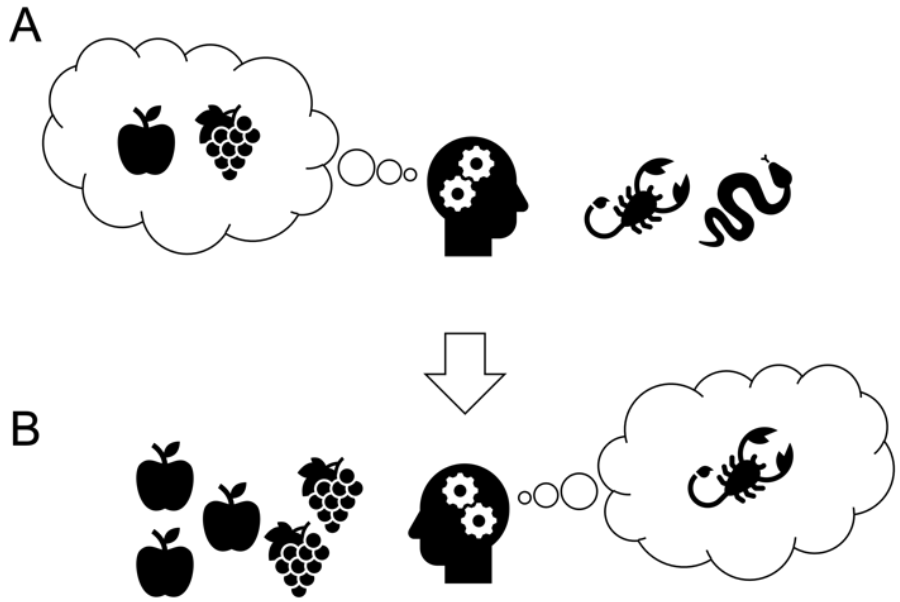


Figure 1. **Survival requires flexibly switching behaviours.** We must track information about various behavioural motivators in the environment to decide how to balance our time between different behaviours. Here a decision-making agent keeps in mind information about food quantity while attending to threats (A); when threat is reduced and food is increased, the agent switches to attending to food while keeping in mind information about threat (B).

1.1.1. Information Sampling and Exploratory Behavior

1.1.1.1. Information sampling is intrinsic. Deciding when to switch behaviours requires repeated sampling of information about the environment. Curiosity is an intrinsic behavioural driver: the desire to obtain new information tends to intensify over an interval if unsatisfied, similar to other biological drivers of behaviour like hunger (Butler, 1957; Loewenstein, 1994). However, the mechanisms underlying information seeking and its involvement in decision-making processes are not fully understood. Humans often pay an

opportunity cost to seek information about external stimuli even when the information has no direct utility or impact on reward (Loewenstein, 1994). Several theories have attempted to explain this motivation. On one hand, curiosity-drive theory proposes that decision-making agents experience uncertainty as unpleasant and find the reduction of uncertainty rewarding (Litman, 2005; Litman & Jimerson, 2004; Loewenstein, 1994; Zelick, 2007). Evidence from economic cognitive science shows that humans prefer to maintain accurate predictions about future outcomes independent of the outcomes themselves (Kreps & Porteus, 1978), and will even voluntarily sustain monetary loss in order to gain irrelevant predictive information (Bennett et al., 2016)—suggesting that humans place an intrinsic value on knowledge and are averse to uncertainty and incorrect beliefs (Grant et al., 1998; Sharot & Sunstein, 2020). Knowledge without current utility may be useful in the future, or may be directly rewarding itself: there is evidence that information prediction error signals are expressed by midbrain dopamine neurons, which may provide reinforcement for seeking information (Bromberg-Martin & Hikosaka, 2009). On the other hand, the optimal arousal model of curiosity posits that decision-making agents are driven to maintain a certain level of arousal. This model is patterned after Wundt's model of hedonic tone, which proposes that stimuli are perceived as pleasant or unpleasant according to a bell-shaped curve of stimulus intensity. Similarly, proponents of the optimal arousal theory argue that decision-making agents are repelled by the physiological arousal associated with extremely new or unusual stimuli, but when bored seek to increase their arousal by exploring their environment (Litman, 2005; Loewenstein, 1994; Zelick, 2007). More recently there have been attempts to unify these theories. The *interest/deprivation* (I/D) model of curiosity distinguishes between negative and positive motivators of information seeking behaviour and proposes that each is elicited by different contexts: I-type curiosity is aroused when an individual

has an opportunity to discover something of interest, while D-type curiosity is evoked when information seeking can reduce the unpleasant experience of uncertainty (Litman, 2005; Zelick, 2007). In sum, while the manner in which individuals are rewarded by information sampling is subjective and differs by context, curiosity remains a fundamental driver of human behaviour relevant to decision-making in complex environments.

1.1.1.2. Choosing information to sample. Moreover, deciding when to switch behaviours requires strategic sampling of information. To choose an action based on its utility relative to alternative actions, one must use information about the environment to predict how successful the action might be, and the consequences of not taking it. With limited time and cognitive resources, the individual must decide what kind of information is most valuable. A recent framework has characterized factors used to calculate the value of information (Sharot & Sunstein, 2020). One factor is the instrumental value of the information; i.e., whether it can be used to choose actions that will increase external rewards or avoid punishments/losses. Notably, instrumental value can also be negative—deliberate avoidance of this information can lead to desirable outcomes in some cases, such as impartiality or reduced responsibility (Hertwig & Engel, 2016). A second factor is the hedonic value of the information. Information sampling can lead to positive or negative emotions depending on its outcome; to regulate emotion, individuals tend to avoid information predictive of negative emotions and seek information predictive of positive emotions. Emotional regulation is important for an individual's ability to adapt to changing environments, and difficulties with emotion regulation have been linked with changes in approaching versus avoiding external stimuli (Chasiotis et al., 2021; Tull et al., 2010). A third factor affecting the perceived value of information is its cognitive value, i.e. whether the

individual feels that the information will contribute to or detract from forming a coherent mental model of their environment. Accurate mental models are useful for understanding one's current circumstances and predicting future outcomes and environmental states, and information related to concepts that feature prominently in an individual's model of the world has higher cognitive value. Integrating each of these (sometimes competing) factors to assign subjective values to different types of information is a process that individuals appear to carry out when choosing what information to sample. When choosing whether to attend to threats versus rewards, for example, a decision-maker may weigh the instrumental, hedonic, and cognitive value of checking for—and potentially encountering—a threat against the value of orienting toward potential rewards (and vice versa: the value of avoiding each type of information and the predicted consequence of doing so).

1.1.1.3. Choosing when to sample information. Equally as important as choosing what kind of information to sample is choosing when to sample it. Arranging action sequences strategically is critical for optimally exploring and surviving in a changing environment. One paradigm often used to study this behaviour is the exploration-exploitation dilemma, a situation in which a decision-maker with limited experience must decide between an option with a known value and an alternative with an unknown value. Here the individual must decide whether to accept the value of the known option or to gain information about the environment—and potentially find a higher value option—by choosing the unknown alternative at the risk of receiving less reward. Optimal performance in this scenario requires at times sampling the unknown value in order to form accurate predictions about all available options. Evidence suggests that humans use two strategies for solving this type of problem (Gershman, 2018; Hunt

et al., 2021; Trudel et al., 2021; Wilson et al., 2014). The first strategy is random exploration, in which unknown options are sampled by chance. Here the decision-maker simply adds stochasticity to their choices without making use of their knowledge of the environment. The second strategy is directed exploration, in which sampling of unknown options is biased toward options associated with greater uncertainty. Choosing the cognitively more demanding directed exploration strategy has been linked with factors such as age (Somerville et al., 2017) and temporal discounting (i.e. greater discounting of future rewards is correlated with less directed exploration) (Sadeghiyeh et al., 2019). The two strategies are also distinct in their underlying cognitive mechanisms and neural substrates (Zajkowski et al., 2017). Regardless of strategy, the extent to which decision-makers explore overall is affected by several factors. First, a longer time horizon (i.e. the number of future choice opportunities the decision-maker expects to have in the current context) is associated with more exploratory behaviour, as the decision-maker can expect to exploit the knowledge gained from exploration (Wilson et al., 2014). Second, the stage of the learning process affects exploration: early choices elicit exploration of all available information sources, while later choices are less likely to be exploratory because they are more informed by experience (Trudel et al., 2021). Overall, understanding how information sampling patterns are guided by factors such as uncertainty estimates and learning process stage provides a useful framework for analysing how people track behaviourally relevant information to flexibly reorient behaviour.

1.1.2. Task Switching

Functioning in complex environments requires the ability to shift from one task to another. Studies of human task-switching behaviour show that task switching is associated with slower

reaction times (RTs), a phenomenon referred to as a 'switch cost'. A common explanation for this is that switching tasks requires the individual to employ a 'top-down' (originating from complex decision-making instead of sensory input), voluntary process to transition between competing tasks, while repeating or continuing a task does not require this additional computation and thus can be done faster (Wylie & Allport, 2000). Breaking this down further, task switching frameworks often explain switch costs by distinguishing between cognitive processes causing behavioural rigidity versus those supporting flexibility (Allport et al., 1994; Meiran, 2010; Wylie & Allport, 2000). Cognitive processes associated with behavioural rigidity—also referred to as task-set inertia—reflect the persistence of cognition associated with the previous task (Allport et al., 1994). Evidence suggests that priming (i.e. an improvement in the ability to execute a particular cognitive process as a result of recent experience with that process; see Henson, 2003; Schacter et al., 2004) for a previous task set carries over to the next task and interferes with switch speed and/or performance on the subsequent task (Sumner & Ahmed, 2006). In other words, switch cost is partly the result of a carryover of neural activation associated with the previous task and the need to suppress it (Mayr & Keele, 2000). On the other hand, task-switching frameworks also identify cognitive processes associated with behavioural flexibility (Meiran, 2010). These are processes that help to mitigate obstacles presented by task-set inertia and facilitate performance on the new task. One such process is working memory updating: Evidence shows that burdening working memory hinders task-selection and task-switching performance (Baddeley et al., 2001; Emerson & Miyake, 2003; Kikumoto & Mayr, 2017). Another process is the suppression of activity related to the abandoned task (Masson et al., 2003; Meiran, 2010). For example, participants completing a stimuli discrimination task with shifting rules for correct discrimination exhibited longer response times when switching to a task

that had recently been abandoned, suggesting that recently discontinued tasks are linked with residual inhibition. Notably, this phenomenon persisted even when participants had prior knowledge of the upcoming sequence of required task switches, indicating that backward-inhibition of previous tasks occurs not just when task switches are governed by external cues but also when switching is initiated based on endogenous planning (Mayr & Keele, 2000). Cognitive processes such as these are at play in flexibly switching between foraging and vigilance and provide insight into experimental findings presented later in this thesis.

1.1.3. Vigilance and Defence

To understand task switching specific to the domains of reward- and threat-oriented behaviour it is necessary to consider processing associated with each behavioural mode. Organisms have a repertoire of responses to danger that range from innate reflexes to carefully planned action sequences. A hierarchical taxonomy of defensive behaviour proposed by LeDoux and Daw (2018) separates these into *reactions*, including reflexes (e.g. startling), fixed reactions (e.g. freezing), and habits (avoidant behaviours that are not updated with learning); and *goal-directed actions*, including learned avoidance behaviours and both conscious and nonconscious anticipatory threat avoidance. Transitioning from foraging to vigilance based on predictive or prior knowledge of threat reflects proactive, anticipatory threat-mitigating behaviour. This section will therefore focus on computations associated with goal-directed defensive actions.

Surviving in complex and changing environments where threats exist requires activating—and deactivating—neural circuits associated with anticipation and defence. Recent work has contributed to mapping this circuitry and characterizing its computations. Threat- and defence-related computation is mediated by a set of interconnected brain areas including the

ventromedial prefrontal cortex (vmPFC), dorsolateral and ventrolateral periaqueductal gray (dlPAG and vlPAG, respectively), hypothalamus, and various amygdala nuclei (relevant brain areas are expanded upon further in Section 1.4 of this introduction; also see Halladay & Blair, 2015; Headley et al., 2019; Mobbs et al., 2020). However, the computation executed varies and is subject to contextual factors, particularly spatiotemporal threat proximity. Fanselow and Lester (1988) proposed the threat imminence continuum model which associates defensive behaviours (e.g. worry, strategizing, fight, flight) with varying levels of threat proximity. At the 'extremely imminent' end of the continuum, the perception of proximal threat greatly constrains both the possible responses and the complexity of processing that can be carried out. A recent framework proposes several ways in which animals and humans adapt to these constraints (Mobbs et al., 2020). First, the agent can reduce computational expense by altering its decision-making algorithm. One type of algorithm that has been used as a framework for solving evasive and defensive decision-making problems is the reinforcement learning (RL) model. An RL model learns relationships between actions and environmental states to form a policy that guides action, and this policy can operate in a model-free or model-based manner depending on the extent to which it uses predictions about the environment to inform choice (Sutton & Barto, 2018). The RL model used by prey under conditions of distal or absent threat favours a computationally expensive, model-based approach that allows for prediction, planning, and risk-assessment, while under conditions of proximal threat a faster, simpler model-free architecture is optimal. Between extreme ends of the threat imminence continuum, prey may combine the advantages of both model-free and model-based approaches by simulating future outcomes to a certain extent and then using cached habitual values to reduce computation thereafter (the 'plan-until-habit' system; see Keramati et al., 2016). A second strategy for managing the cognitive constraints of

proximal threat is offline learning (i.e. making use of previously learned information at a later time when it is not the primary focus of attention). It has been proposed that in safe contexts—during appetitive behaviour, for example—decision-makers update their model-free policies with information from previous predatory interactions in order to compensate for reduced processing while under threat and to manage dangerous situations more optimally in the future (Mobbs et al., 2020). Thus, decision-making agents may process information about threat while engaging in appetitive behaviour not just to guide switching to vigilance but also to improve future threat-oriented behaviour.

1.1.4. Foraging

Like vigilance and defence, foraging efficiently is critical to survival and shared across a wide variety of organisms. Studies of animal foraging behaviour in naturalistic environments have provided insight about human reward-guided behaviour. In a version of the explore-exploit trade-off paradigm, ecological foraging tasks frame the foraging problem as a series of encounters between the decision-maker and opportunities to consume food or other rewards (often referred to as a 'patch') (Hayden et al., 2011; Hunt et al., 2021; Kolling et al., 2012; Scholl et al., 2022). At each patch encounter, the decision-maker must choose whether to engage with the current patch or leave in search of alternative patches. With limited knowledge of the environment, the decision-maker must track and integrate multiple sources of information to forage optimally. Critical among these are the value of the current opportunity, including previous encounters with the current patch and its depletion rate; the average value of the environment based on experiences with other patches; and the cost associated with searching for an alternative patch, which may entail forfeiting currently available rewards, expending energy, or a time delay

(Charnov, 1976; Hayden et al., 2011; Kolling et al., 2012; Kolling & Akam, 2017). In addition to considering information about the environment, people have been shown to consider their own likely future behavioural biases (e.g., a tendency to persevere sub-optimally) in making foraging decisions (Kolling et al., 2018).

Several frameworks demonstrate how information may be used to learn reward statistics and predict future reward trajectories. An early model of animal foraging behaviour, the marginal value theorem (MVT), stipulates that an optimal forager should search for an alternative patch when the reward rate of the current patch diminishes to the average reward rate for the environment (Charnov, 1976). Recent approaches have built on the MVT to characterize how decision-makers learn reward statistics in environments with noisy, non-monotonically decreasing patches. Rather than simply averaging patch rewards and comparing with the environment average, humans have been shown to use the recent reward rate gradient to predict future outcomes in the current patch (Wittmann et al., 2016). Such within-patch predictions appear consistent with a model-based RL strategy that may be integrated with model-free estimates of the overall environment reward rate (Kolling & Akam, 2017). However, foragers also employ strategies to reduce the computation associated with estimating future reward trajectories. Evidence suggests that foragers make predictions about multiple probabilistic future outcomes using a combination of heuristics and optimal policy calculations. Korn and Bach (2018) showed that foraging participants often used a myopic heuristic—specifically, momentary probability of foraging success—to make faster decisions, with additional choice variance explained by the use of an optimal policy that used environmental factors to compute probabilistic outcomes across the upcoming decision sequence (resembling model-based RL). Reaction times were slower when policy recommendations differed, providing evidence that

decision-makers integrated both heuristic and optimal policies in planning foraging sequences. Neurally, a key brain area by which reward statistics are used to instigate behavioural change is the dorsal anterior cingulate cortex (dACC), which has been shown to encode the average value of behavioural change (e.g. searching for alternative patches) by approximating reward statistics over multiple time scales (Kolling, Wittmann, et al., 2016) and signalling pressure to pursue riskier options (Kolling et al., 2014). Brain areas associated with reward processing are expanded upon in Section 1.4 of this introduction.

1.1.5. Relevance to the Current Work

This thesis investigates mechanisms involved in switching attention between foraging and vigilance. Tasks used in experiments presented here thus differ from those presented in this section. However, understanding principles of cognition associated with tasks that share certain aspects—such as foraging tasks, which similarly require tracking of behaviourally relevant information to make sequential decisions—is useful for forming hypotheses about how people may solve the novel problems examined here. For example, as discussed in Section 1.1.1, decision-makers navigating a reward-based explore-exploit trade-off often choose to explore more in the context of a longer time horizon. When choosing between exploring potential threats and pursuing reward, decision-makers may similarly consider time horizon. Moreover, each of the cognitive processes presented in this section—information sampling, flexible task switching, vigilance, and foraging—play a role in balancing competing appetitive and threatening behavioural influences, and the relevant cognitive models have shaped hypotheses, analyses, and interpretation of experiments presented in this thesis.

1.2. Computational Psychiatry: Pursuing a Mechanistic Understanding of Emotions, Traits, and Decision-Making

Beyond understanding the fundamental mechanisms underlying flexible switching between reward- and threat-oriented behaviour, this work also aims to characterize how these processes shape—and are shaped by—the transient influence of emotions as well as the more enduring influence of individual traits linked with symptoms of psychiatric disease. These experiments fall within the purview of computational psychiatry, a new and growing field that aims to use computational techniques such as statistical and machine learning approaches to understand and improve mental health conditions (Huys et al., 2016; Huys & Renz, 2017; Maia et al., 2017; Montague et al., 2012; Moutoussis et al., 2017; Stephan & Mathys, 2014). This field provides a framework for characterizing mental dysfunction as atypical computations that can be modelled and observed in brain activity. It is thought that computational psychiatry may help bridge the gap between biological psychiatry and cognitive science by connecting biological phenomena with individualistic models of mental function, and it may even transform diagnostics with more precise ways to measure and categorize disordered cognition. In this section I will discuss contributions from computational psychiatry relevant to this thesis, including approaches to integrating emotion into computational models of decision-making (Section 1.2.1) and theories of aberrant computation underlying psychiatric symptoms associated with vigilant and appetitive behaviour (Section 1.2.2).

1.2.1. Integrating Emotion into Decision-Making Models

Emotions have long been linked with decision-making, but the nature of their role is disputed. Despite considerable within- and between-person variability, emotions are generally identified

as distinct patterns of physiological, behavioural, and psychological processes with either positive or negative subjective valence (Huys & Renz, 2017). Increasingly, emotional states are being incorporated into computational models of behaviour. One set of theories focuses on ways in which emotion may improve computational efficiency in complex and changing environments.

One such theory proposes that during a learning process such as reinforcement learning, emotions constitute a global state that reflects the impact of multiple environmental factors and biases reward evaluation and expectation accordingly (Bennett et al., 2022; Eldar et al., 2016, 2021; Emanuel & Eldar, 2023). In a foraging example, the arrival of spring could cause food to increase across all patches simultaneously; instead of updating expectations for each patch separately, an animal could develop a happier mood as it encounters each flourishing patch, biasing subjective rewards positively and rapidly updating expectations for future patches. Although the computational implementation of this process is debated, the overall result of such a process is that expectations would come to reflect cumulative changes in the environment without the need to calculate the impact of each environmental factor individually.

A second theory conceptualises emotion as a global state that helps improve computational efficiency in selecting optimal actions. To illustrate this, first recall the discussion in Sections 1.1.3 and 1.1.4 of this thesis about the utility of algorithms that model choices informed by future outcome predictions (e.g. model-based RL algorithms). Despite their complexity, such algorithms are mere approximations of the optimal solution specified by Bayesian decision theory (BDT), which uses a generative model of all possible future environmental states to maximize long-term expected benefit (Bach & Dayan, 2017; J. O. Berger, 1985). A major problem with any approach that integrates information about future

outcomes—either BDT or its algorithmic approximations—is that the range of possible events to compute grows exponentially with the number of future time steps considered, making optimal option valuation infeasible. Sections 1.1.3 and 1.1.4 presented a few ways in which decision-making agents address this problem (e.g. integrating optimal policy with heuristics). Similarly, proponents of the idea that emotions lead to adaptive behaviour argue that emotion can be another strategy for conserving computational resources. Central to this argument is appraisal theory as a framework for understanding how emotions arise. The appraisal theory of emotion proposes that emotions arise from individuals' perceptions of situations as being either beneficial or obstructive to their personal goals; for example, a cancelled social event may elicit a negative emotion if the individual's goal was to meet new people, but may elicit a positive emotion if the individual's goal was to relax at home (Ellsworth, 2013; Frijda et al., 1989; Moors et al., 2013). From this perspective, emotions may substantially narrow the number of future outcomes considered by inducing a focus on certain behaviours deemed relevant to the individual's goals (Huys & Renz, 2017). Both of these theories represent efficient ways to adaptively allocate limited cognitive resources toward solving computationally intensive problems. Exploring ways in which mood guides decision-making behaviour is one focus of Chapter 3 of this thesis.

Another framework for linking emotion and behaviour proposes a bidirectional, homeostatic interplay between the two. In laboratory studies at shorter timescales, human behaviour tends to exhibit a pattern referred to as the hedonic principle: choices aim to minimize negative emotions and maximize positive ones (Kron et al., 2014; Taquet et al., 2016; Tice et al., 2001; Wegener & Petty, 1994). However, the hedonic principle fails to address how people are motivated to forego pleasurable activities to undertake unpleasant yet necessary tasks on a daily basis. In a study of human behaviour outside of the laboratory across an extended timescale (one

month), Taquet and colleagues (2016) found that individuals instead showed a homeostatic pattern: during low moods, they tended to engage in pleasurable activities, and conversely during good moods they pursued useful but less pleasant tasks. This is consistent with the hedonic flexibility hypothesis, a theory that emotional states function to shift priorities between long- versus short-term goals adaptively. For example, an unhappy individual may lift their mood with an enjoyable hobby—but later take advantage of their improved mood to carry out an arduous task that achieves a longer-term goal. In this way, emotions and behaviour may serve to regulate one another to maximize both present and future wellbeing. Indeed, impaired mood-behaviour homeostasis has been linked with poorer mental health outcomes in large population samples, emphasizing the importance of this mechanism for optimal function (Taquet et al., 2020, 2021). However, mood-behaviour homeostasis consistent with the hedonic flexibility hypothesis on shorter timescales has been underexplored. Investigating mechanisms by which mood and behaviour may serve to regulate one another on a momentary basis is another question addressed in Chapter 3 of this thesis.

1.2.2. Computational Accounts of Disordered Vigilant and Appetitive Behavior

Considering how animals have evolved to survive in complex environments by balancing behavioural motivators such as fear and hunger may provide insights into the roles of fear and anxiety in mental health. The field of computational psychiatry has produced insights into computation associated with disordered vigilant and appetitive behaviour. Here I will discuss a few of these accounts to illustrate the body of work that has shaped interpretation of my experimental results and to which this thesis aims to contribute.

1.2.2.1. Anxiety is characterized by changes in exploration, information sampling, and attentional bias. Anxiety is associated with a number of psychopathological disorders, including generalized anxiety disorder, obsessive-compulsive disorder (OCD), and trauma-related disorders (e.g. PTSD). In clinical practice, anxiety is often identified via self-reports about excessive worry and physical arousal (American Psychiatric Association, 2015). However, manifestations of anxiety vary among individuals, and their impact on decision-making—whether sub-optimal or adaptive—is not fully understood. Computational methods have begun to characterize the mechanisms associated with anxiety by their effect on decision-making tasks.

One line of research focuses on decisions involving risk, uncertainty, and exploration. In reward-based win/lose tasks, anxiety has repeatedly been linked with risk aversion (Bishop & Gagne, 2018; Hartley & Phelps, 2012) but not loss aversion (Charpentier et al., 2017). However, there is a lack of consensus about whether risk aversion in such tasks reflects a deficit in computing risk or an aversion to accurately assessed risk. To this point, a recent study by Fan and colleagues (2022) examined how trait somatic anxiety—a measure corresponding to the frequency at which an individual experiences physical symptoms of anxiety in their day-to-day life (Ree et al., 2008)—relates to performance on an explore-exploit problem (refer to Section 1.1.1 for an explanation of the explore-exploit dilemma). Participants exhibiting a range of anxiety scores on clinical questionnaires performed a two-armed bandit task in which they chose between options delivering either stable or fluctuating rewards. Consistent with expectations, there was an inverse relationship between trait somatic anxiety and exploration, whereby highly anxious participants were overall less likely to risk choosing uncertain (fluctuating) options. However, modelling indicated that anxious participants' choices reflected an underestimation of uncertainty in the environment (Fan et al., 2022). Together, these results suggest that trait

somatic anxiety is associated not merely with risk aversion (e.g. identifying more uncertain options and avoiding exploring them) but also with altered computation of uncertainty itself. Additional work is needed to fully characterize the nature of uncertainty estimates in anxious individuals.

Another area of investigation focuses on relationships between anxiety and information sampling behaviour. In a study of self-reported information seeking about the COVID-19 pandemic, Loosen and colleagues (2021) found that highly anxious participants showed an overall increase in information seeking behaviour. Further, Charpentier and colleagues (2022) complemented this finding by conducting a multi-part study of relationships between anxiety scores and 1) self-reported information seeking about the COVID-19 pandemic, and 2) sampling of non-instrumental information related to a virtual stock market. Here they found that trait anxiety did not affect general information seeking patterns, but instead was linked with seeking information specifically in response to substantial changes in the environment. If anxious individuals indeed experience altered learning in uncertain environments, changes in information seeking in response to external events could be either a contributing factor to impaired learning or an adaptive response to overcome it.

Further study of the relationship between anxiety and decision-making has demonstrated a link between anxiety and threat-related attentional bias. The concept of attentional bias captures the tendency for decision-makers in complex environments to strategically allocate attention toward aspects of the environment that are most motivationally relevant (Wise et al., 2019). Attentional prioritization is known to change the weighting of options considered during decision-making and is an important aspect of complex motivated behaviour (D. Pearson et al., 2022). In environments featuring rewards, option values are organized into spatial priority maps

that influence the allocation of visual attention toward high-value options relevant to the individual's current goals (B. A. Anderson et al., 2011; B. A. Anderson, 2016; Chelazzi et al., 2014). In environments dominated by aversive stimuli, visual attention tends to be allocated based on the aversive value of stimuli—and conversely, stimuli that are selected for attentional focus are given greater value estimates, suggesting that attention both influences and is influenced by the process of learning about stimuli in the environment (Wise et al., 2019). In environments presenting both rewards and threats, attentional bias has been shown to be sensitive to a number of factors including anxiety (Frewen et al., 2008). Anxiety has been linked with a number of threat-related attentional biases, including greater sensitivity to detecting threats, difficulty with disengaging from threats, and attentional avoidance (Amir et al., 2003; Cisler & Koster, 2010; Keogh et al., 2001; Mogg et al., 2000; Rinck et al., 2003). Evidence that anxiety is associated with both increased orienting toward and avoidance of threat highlights the complexity of the relationship between anxiety and threat processing. One theory that links these is the *vigilance-avoidance* theory of processing, which posits that highly anxious individuals display facilitated attention toward threat during early stages of information processing (e.g. threat detection) and then either attenuation of attentional bias or active threat avoidance during later stages (Amir et al., 2009; Mogg et al., 1987; Mogg & Bradley, 2006; Vassilopoulos, 2005). Some evidence, however, has supported an alternative: that instead of facilitated attention toward threat, anxiety is characterised by difficulty disengaging from threat (Amir et al., 2003; Koster et al., 2004; Lazarov et al., 2021; Yiend & Mathews, 2001). Eysenck and colleagues (2007) accounted for this in their attentional control theory of anxiety, which proposed that information processing in anxiety is influenced less by a goal-directed (top-down) attentional system and more by the stimulus driven (bottom-up) attentional system. Attentional biases such as these

have downstream effects on decision-making in anxious individuals. For example, anxiety has been linked with behavioural differences in tasks presenting both rewards and threats (Ball & Gunaydin, 2022; Pittig et al., 2021; Pittig & Scherbaum, 2020). In one such study, Pittig and Scherbaum (2020) investigated approach-avoidance behaviour in anxious individuals choosing between a high reward/potential threat (electric shock) option and a low-reward/safe option. They showed that highly anxious individuals often missed out on potential gains due to avoiding threats, and particularly when offered high-value rewards. Further discussion of anxiety in relation to reward- and threat-oriented behaviour appears in Chapter 3 of this thesis.

Changes in seeking and processing information about the environment—including aberrant patterns of exploration, information seeking, and selective attention—have significant consequences for learning and decision-making, and insights about mechanisms associated with anxiety have already contributed to the development of clinical interventions such as attention bias modification (Mogg & Bradley, 2016). However, more study of anxious cognition in naturalistic, complex decision-making scenarios is needed. I will now shift focus to discuss cognitive mechanisms thought to underlie disordered appetitive behaviour.

1.2.2.2. Apathy and anhedonia are characterized by altered computing of effort and reward. Balancing foraging with vigilance also elicits reward-based, appetitive behaviour, the impairment of which is a core component of apathy and anhedonia. Apathy is a psychiatric symptom that denotes lack of motivation, interest, or emotion and is characterized by a reduction in voluntary behaviours, especially in situations that would normally elicit such responses (Bonnelle et al., 2015; Husain & Roiser, 2018; Levy & Dubois, 2006). It is associated with various psychiatric disorders, including major depressive disorder (MDD) (Mulin et al., 2011),

schizophrenia (Foussias et al., 2014), and neurological conditions such as Parkinson's Disease (Pedersen et al., 2009), Alzheimer's Disease (Nobis & Husain, 2018), and traumatic brain injury (Worthington & Wood, 2018). Apathy is associated with aversion to effort. Specifically, apathetic individuals show changes in the relationship between reward magnitude and subjective estimates of effort, such that they are more likely to associate small rewards with higher subjective effort costs and forego obtaining them (Bonnelle et al., 2015). More recent work has distinguished between types of effort to which apathetic individuals are averse. In a sequential decision-making task investigated by Scholl and colleagues (2022), highly apathetic participants displayed a tendency to persist with a particular behaviour for longer than was appropriate. In this case, apathetic individuals did not avoid effort associated with action perseverance—instead, they avoided the cognitive effort of deciding on an alternative course of action. The finding that apathetic individuals appear more averse to some types of effort than others and specifically exhibit decision inertia may be an important distinction providing insight into the nature of apathy. In addition to aversion to effort, apathy—particularly the emotional dimension—has been linked with impaired social reward learning (S. Wong et al., 2023). The link with reward processing is one similarity between apathy and a related behavioural dimension, anhedonia.

Anhedonia is a psychiatric symptom that refers to a diminished ability to experience pleasure in situations that would normally elicit pleasure. Like apathy, it also features in psychiatric disorders such as MDD and neurodegenerative diseases (Treadway & Zald, 2011a; Turner & Husain, 2022). Traditionally, apathy and anhedonia were categorised into disorders of motivation and pleasure respectively; however, more recent work has demonstrated that they have overlapping characteristics including loss of motivation to pursue pleasure and difficulty using reward-related information to guide decision-making (Husain & Roiser, 2018). With

respect to anhedonia, Treadway and colleagues (2012) demonstrated that anhedonic individuals with diminished anticipation of positive future events showed attenuated willingness to work for rewards, suggesting that expending effort is linked with reward prediction. Further, anhedonia has been shown to moderate the relationship between reward expectancy and activity related to prediction errors in the ventral striatum, suggesting that anhedonic individuals may suffer impaired learning about rewards (Greenberg et al., 2015). Understanding mechanisms underlying disorders of appetitive behaviour such as apathy and anhedonia may help to interpret the behaviour of amotivated individuals participating in experiments discussed in Chapter 3 of this thesis. To complement this theoretical discussion, I will now present several methods used to form and test hypotheses about cognitive mechanisms in health and disease.

1.3. Methods for Forming and Testing Hypotheses in Computational Psychiatry

The field of computational psychiatry is young and new techniques are still emerging. Here I will discuss several approaches being used within the field, ranging from the more established practice of computational modelling to the relatively new transdiagnostic and ecological frameworks. These approaches have inspired experimental design, hypothesis formation, and analytical techniques in this thesis.

1.3.1. Computational Modelling of Cognitive Processes

Computational modelling is a technique that involves creating computer programs to simulate cognitive processes and behaviours in humans or animals. It is distinct from mathematical modelling, which uses mathematical equations to analyse the behaviour of complex systems; computational modelling instead simulates a process, providing a normative model for how the

system processes information and predicting its behaviour under different conditions (Montague et al., 2012). With computational modelling, one may form and test hypotheses about the inner workings of the mind that would be impossible to investigate through observation or experimentation alone. There are several different types of computational models. In the connectionist (neural network) approach, models use a system of connected units to approximate processes carried out by biological neural networks (Hopfield, 1984; Hopfield & Tank, 1986; O'Reilly, 2006). In contrast, the symbolic approach models problem-solving and reasoning by representing knowledge as abstract symbols and rules (Doumas & Hummel, 2012). Symbolic computation allows for high-level abstraction and the ability to represent complex systems in a simplified way. In this section I will focus on symbolic approaches to modelling decision-making. This methodology has several strengths useful for understanding cognition in health and disease: it can estimate variables that are not directly observable but which should shape decision-making, and these can then be used to analyse and simulate behaviour. Here I will explain this technique in greater detail using a simple example and highlight its utility within the current paradigm.

1.3.1.1. The importance of latent variables. Many decision-making processes are influenced by factors that cannot be directly observed. Consider an example from a naturalistic foraging paradigm: in an environment where a patch typically yields rewards after each successive foraging action, an individual may make repeated foraging actions partly as a result of reward-based computations but also partly out of habit. This tendency toward automatic repeating of actions is a well-known phenomenon that can be modelled mechanistically as an increased weighting of actions that have recently been taken (Aarts et al., 1998; Miller et al.,

2019). The degree to which an individual tends to behave habitually may not be accurately reportable by the individual or it might require assessment by a very specific test. However, a latent variable such as the repetition weighting can be estimated in many contexts and without the need for one specific task that is devoted to its examination in isolation. Not only might such a variable have a substantial impact on choices but in addition, relationships between decision-making and unobserved variables may constitute traits that are associated with symptoms of psychopathology (Hudlicka, 2017; Montague et al., 2012). Symbolic computational models rely on the assumption that these unobservable aspects of cognition can be represented as computations with abstract symbols. These symbols take the form of model parameters that are used to calculate relative action values and ultimately compute the likelihood of each decision in the task space at a given point in time.

1.3.1.2. Decision simulation. A computational model with parameters corresponding to latent variables can be used to simulate behaviour. Simulation is useful for assessing the validity of the model; i.e., providing support for the inclusion, representation, and manipulation of variables in the model. This is achieved by comparing simulated data with data produced by real humans performing the same task: the closer the resemblance between the simulated and real datasets on quantitative performance measures, the better the computational model for providing insight about the human mind (Bianchi et al., 2007; Sun, 2009). The model can then be calibrated to produce predictions that better fit the real data (Dutt & Gonzalez, 2015). A valid model can help explain human behaviour by demonstrating the types of information considered and their role in making decisions. There are many ways to simulate decisions; here I will introduce some

basic methodology by demonstrating how the subjective value of an option can be computed and how the probability of choosing it predicted.

To illustrate, consider the example given above in which a decision-maker is influenced by an intrinsic tendency toward repeating actions out of habit. In a simple implementation, one may first create a variable that is 1 when the previous action was forage and 0 otherwise. Next, this variable can be used to calculate the decision variable (DV): the accumulation of all sources of prior knowledge, evidence, and value into a quantity that can be interpreted by a decision rule to produce a choice (Gold & Shadlen, 2007). In this example, the value of foraging on the current trial can be expressed as a DV as in Equation 1:

$$DV \sim \beta_0 + \beta_1 * r + \beta_2 * m_1 + \beta_3 * m_2 \ldots \quad 1$$

where *DV* is the utility of foraging instead of the alternative, *r* is the variable signifying whether the previous action was forage, and m_i are other factors thought to influence the decision to forage (e.g. available reward magnitude, history of rewards in this patch). Weights β_i can be parameters fit to real participants' decision-making data, values drawn from the distribution of parameters fit to real participants' data, or values drawn from another distribution (e.g. gaussian). Finally, an action can be chosen by entering the DV into a decision rule. In this case a useful decision rule is the sigmoid function (for further discussion of decision rules see McFadden, 2001). A sigmoid function is a mathematical function that transforms an input value into an output ranging between 0 and 1 with a mid-point of 0.5; larger input values will produce output values closer to 1, while as the input value decreases, the output value approaches 0. This

function is useful for modelling the probability of an event occurring; in this case, it models the probability of foraging versus the alternative action as in Equation 2:

$$P(F_t) = \frac{1}{1 + e^{(T_{inv}* - DV)}} \quad 2$$

where $P(F_t)$ is the probability of foraging at timestep *t*, *e* is the mathematical constant (Euler's number), *DV* is the decision variable, and T_{inv} is the inverse temperature (a hyperparameter that scales the DV and tunes the confidence of the decision rule output). An action is then selected according to the probability output by the sigmoid.

A key characteristic of simulating value-based choice behaviour is the source of randomness. Decision-making in humans and animals is marked by deviations from the optimal, value-maximizing choice; as discussed in Section 1.1.1 of this thesis, problem-solving with limited knowledge in complex and changing environments often requires exploration. Even random exploration can be useful for understanding the statistics of one's environment, and further, it has been argued that some degree of indeterminacy may be intrinsic to human and animal decision-making behaviour (Glimcher, 2005). Thus, when simulating value-based choices the source of stochasticity is considered to be internal and is modelled as part of the decision rule. Equation 2 demonstrates a probabilistic decision rule by which actions can be generated with a degree of stochasticity. Randomness attributed to the decision-maker can also be found in algorithms such as RL models, where the DV is computed deterministically based on previous reward outcomes but choice is generated by a probabilistic decision rule such as a softmax (Lau & Glimcher, 2005; Sutton & Barto, 2018; L. Zhang et al., 2020). This approach is in contrast to stochastic accumulator models of perceptual decision-making, in which the DV is

computed using stochastic external input but the decision rule—i.e. the boundary, a reference value against which the accumulated evidence is compared—is deterministic (Brody & Hanks, 2016; O'Connell et al., 2018; Purcell et al., 2010).

1.3.1.3. Linking computational models with neural substrate. One limitation of symbolic computational models is that the model does not provide any insight into how the computation it represents may be implemented biologically. However, symbolic cognitive models applied to neuroimaging data can be used to link computations with their neural substrate. In this technique, a computational model is first fit to behavioural data—for example, button presses made by a participant during recording of functional magnetic resonance imaging (fMRI) data—and then the value of model parameters at each point in time is regressed against the fMRI data (Borst et al., 2011; J. D. Cohen et al., 2017). The results of this regression may identify brain areas with activity linked to parametric variation in the variable of interest. Further, model variables can be regressed against time series data from regions of interest to test whether they are encoded in the relationship between two brain areas (O'Reilly et al., 2012). Thus, symbolic computational modelling is a tool that can link brain areas with the representation of abstract values that are difficult to quantify yet vital to the decision-making outcome. I will now turn the discussion to introducing the transdiagnostic approach, a method for investigating mental disorders that, when combined with computational modelling, holds promise for understanding and treating mental health.

1.3.2. The Transdiagnostic Approach

Despite exhaustive review of its diagnostic guidelines, psychiatry faces major challenges to the validity, sensitivity, and precision of its standards for disease classification. In contemporary psychiatry, disease categorization is still based on diagnostic interview and symptom checklists, with significant variation in symptom manifestation within existing diagnostic categories (Fried, 2017). There is a growing interest in incorporating techniques from fields such as neuroscience and cognitive science to improve psychiatric nosology. The transdiagnostic approach in psychiatry is one such effort. This approach seeks to characterize mental health using behavioural dimensions and neuroanatomical differences that cut across traditional diagnostic profiles (Cuthbert, 2014; Dalgleish et al., 2020; Mitelman, 2019; Stephan et al., 2016). Transdiagnostic studies typically do not separate participants into patient and control groups based on conventional clinical diagnosis, but instead complement these studies by examining symptoms across the spectrum from health to disease. This is in line with evidence from data-driven studies showing that aspects of poor mental health can be conceptualized as a series of continua instead of discrete categories (Dalgleish et al., 2020). Within computational psychiatry, the goal of the transdiagnostic approach is to identify core cognitive mechanisms relevant for diagnostics and characterize them with behavioural indices (Stephan et al., 2016). In a recent example, we (Scholl et al., 2022) used a cognitive model to show distinct changes in prospective decision-making linked with compulsivity and social/emotional apathy, two sub-scales of psychiatric questionnaires that correspond to unique behavioural dimensions and are not specific to any single disease classification.

Although it has potential to complement traditional clinical study paradigms, the transdiagnostic approach has limitations. One criticism is the lack of a theoretical framework to guide transdiagnostic investigation. While many agree that psychiatric nosology needs to be re-

evaluated, there is no consensus on what an alternative method for classifying psychiatric disorders should look like, or even how to conceptualize a diagnostic category (Dalgleish et al., 2020). Further work is needed for transdiagnostics to truly constitute a paradigm shift and yield translational results (see the General Discussion for more on the topic of future directions). In another criticism, Fusar-Poli and colleagues (2019) argued that transdiagnostics are simply a rediscovery of concepts that originally shaped conventional diagnostic classification. They noted that an earlier version of the Diagnostic and Statistical Manual of Mental Disorders (DSM) presented diagnostic categories as indistinct entities without clearly specified borders, and suggested that the process of translating these categories into clinical practice has led to disorders becoming more conceptually demarcated for ease of diagnosis (DSM-IV; Bell, 1994). However, whether the contemporary transdiagnostic movement is a new innovation or a rediscovery, it is valuable to re-examine existing diagnostic practices in light of recent technical advances in neuroscience and cognitive science. Key methods advancing the transdiagnostic approach include computational modelling, neuroimaging, and large-scale online behavioural research (Gillan & Daw, 2016; Mitelman, 2019; Stephan et al., 2016). In the next section, I will argue that another method critical for understanding cognition in health and disease is the ecological framework.

1.3.3. Ecological Frameworks

Laboratory-based decision-making studies in cognitive neuroscience often take the form of trial-based tasks that require participants choose within a specified time frame from a limited set of options. Such tasks have contributed a great deal to our understanding of the cognitive and neural processes underlying decision-making in the healthy brain. However, there is debate about the

extent to which these tasks are representative of everyday, real-world choices. In real life, individuals make decisions flexibly, choosing both the timing and nature of their actions with limited knowledge in a constantly changing and highly contextual environment. Thus, many classic decision-making paradigms may not be relevant to understanding natural human behaviour. This may be consequential for the study of psychiatric disorders. Computational psychiatry has yet to deliver many insights that are readily translated into clinical interventions, and some have proposed that this is due to failure in designing laboratory tasks that capture the kinds of naturalistic decision-making that is disordered in patients' everyday lives (Hitchcock et al., 2022; Moutoussis et al., 2017; Scholl & Klein-Flügge, 2018). Many symptoms of psychiatric disorders manifest over longer timescales, exhibit distinct temporal dynamics, and are highly dependent on context (Hitchcock et al., 2022; Moutoussis et al., 2017). To better study disordered cognition, studies are increasingly adopting more ecological paradigms. Natural animal behaviours such as foraging and responding to danger are critical for survival and therefore are likely to have strongly influenced the evolution of neural circuits underlying human decision-making. It has been suggested that in order to observe symptoms of a psychiatric disorder in the laboratory it is necessary to engage the processes used in responding to naturalistic scenarios relevant to the disorder (J. M. Pearson et al., 2014; Scholl & Klein-Flügge, 2018). In one example of this, performance in a naturalistic explore/exploit foraging task showed that participants who reported greater frequency of gambling—a behaviour which, in its extreme, is symptomatic of a pathological disorder—explored more and earned less money as a result of leaving patches too quickly (Addicott et al., 2015). Foraging tasks such as this may offer a way to naturally elicit behaviours relevant to a variety of psychiatric symptoms, including those related to motivation, outcome valuation, and effort. One disadvantage is that ecological tasks often entail greater

complexity. However, this challenge can be addressed through the rapidly expanding repertoire of computational models available to behavioural scientists. Inspired by these approaches, I have conducted several experiments in this thesis that use principles of behavioural ecology to elicit naturalistic decision-making behaviour.

1.4. Neural Substrate of Switching Between Foraging and Vigilance

Chapter 4 of this thesis investigates the neural basis of switching between vigilance and foraging. Various brain areas are relevant for this type of computation. In this section I will introduce the anatomy and function of two cortical regions, the anterior cingulate cortex (ACC) and anterior insular cortex (AI). I will also present several subcortical areas: the lateral habenula (LHb), a region of special relevance to threat processing; and the origins of two neuromodulatory systems, the dorsal raphe nucleus (DRN), producer mainly of serotonin; and the substantia nigra pars compacta (SNc) and ventral tegmental area (VTA), producers mainly of dopamine. For each region I will also indicate its theoretical relevance to the topic of task switching between vigilant and appetitive behaviour.

1.4.1. Anterior Cingulate Cortex (ACC)

The anterior cingulate cortex (ACC) is an anatomically and functionally distinct region in the medial part of the frontal lobes, located ventral to the superior frontal gyrus and dorsal to the corpus callosum (Fig. 2A). Brodmann (1909) was the first to parcellate this structure and identified areas 24, 25, 32, and 33 within it in his cytoarchitectonic map of the human cortex. Later work subdivided the ACC based on cytoarchitecture, connectivity, and function into two main subregions: the dorsal ACC (dACC), which occupies BA 32 and 24 and shows extensive

connectivity with pre-frontal and motor cortices; and ventral ACC (vACC; also called rostral, anterior, or genual ACC), which occupies BA 24, 25, 32, and 33 and shares connectivity with areas including the orbitofrontal cortex, amygdala, nucleus accumbens (NAc), hypothalamus, and hippocampus (Fig. 2B) (Bush et al., 2000; Hoffman, 2016; S. C. Matthews et al., 2004; Mohanty et al., 2007; Vogt et al., 2003). Further, these subregions are themselves heterogenous—the vACC in particular is often parcellated into perigenual (pgACC) and subgenual (sgACC) regions (Fig. 2B) (Y. Kim et al., 2018; Vogt, 1993).

Activity in the ACC has been linked with various signals, including search value, the updating of internal models, and behavioural change (Kolling, Behrens, et al., 2016). Its subdivisions vary in function. The dACC is particularly involved in encoding value-related information, regulating behavioural flexibility, error detection, and signalling the need for internal model updating (Kolling, Wittmann, et al., 2016). In contrast, the vACC is thought to specialize in processing of affective information and the regulation of emotional responses, owing to evidence that it directly projects to the amygdala, that it is preferentially activated in response to affective stimuli, and that it plays a role in modulating the parasympathetic nervous system (S. C. Matthews et al., 2004; Mohanty et al., 2007). Within vACC, pgACC and sgACC subdivisions appear to make different contributions via distinct patterns of projection to the amygdala and tsgACC changes have been specifically linked with major depressive disorder (Connolly et al., 2013; Gotlib et al., 2005; Rodríguez-Cano et al., 2014). In summary, signals carried by the ACC are critical components of naturalistic behaviours such as foraging and task switching and are also relevant to information processing in mood disorders. This region is therefore of great interest to the current paradigm and is hypothesised to facilitate switching between behavioural modes.

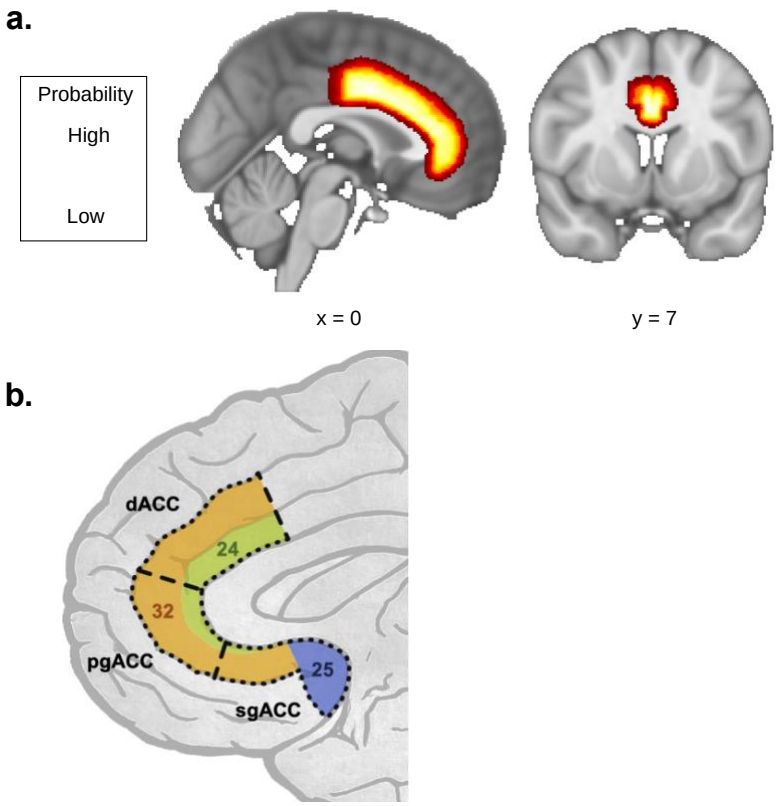


Figure 2. **Location and subdivisions of the ACC.** A) Location of the ACC demonstrated by a probability map of voxels belonging to the ACC according to the Harvard-Oxford cortical structural atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006). The map is displayed on the MNI152 standard-space T1-weighted average structural template image (Grabner et al., 2006) with MNI152 coordinates indicated. B) Subdivisions of the ACC, including dACC and vACC subregions pgACC and sgACC. Reprinted from (Alexander et al., 2021).

1.4.2. Anterior Insula (AI)

The insula in each hemisphere is a layered neocortical area situated deep within the lateral sulcus, a fissure separating the frontal and parietal lobes from the temporal lobe (Fig. 3A). Brodmann (1909) partitioned the insula into two regions based on their cytoarchitectonic features: an anterior agranular region largely characterized by pyramidal neurons and a posterior granular region characterized by granular cells, with the border corresponding roughly to the central sulcus of the insula (Nieuwenhuys, 2012; Shura et al., 2014). Later studies have refined this parcellation to specify that the anterior region includes a more ventral-anterior segment of the insula (Nieuwenhuys, 2012).

The AI has been linked with a variety of functions, including bodily self-awareness (interoception), the sense of agency and ownership, and emotional processing (Craig, 2009; Farrer & Frith, 2002; Mutschler et al., 2009; Phan et al., 2002). Functional subdivisions have also been identified within the AI. In a resting-state fMRI study, Deen, Pitskel, and Pelphrey (2011) identified 3 distinct insular subregions, two of which are in the anterior insula: a dorsal anterior subregion connected with dACC (Fig. 3B), which has been linked with cognitive control; and a ventral anterior subregion connected with pgACC (Fig. 3B), which is associated with affective-based physiological responses (Mutschler et al., 2009). Overall, AI activity has been shown to be a critical component of emotional processing and cognitive control, which has implications for the study of motivated decision-making behaviour and psychiatric disease. In the present work, it is hypothesised that the AI may play a role in monitoring internal physiological and affective states and using this information to guide decision-making about threat versus rewards.

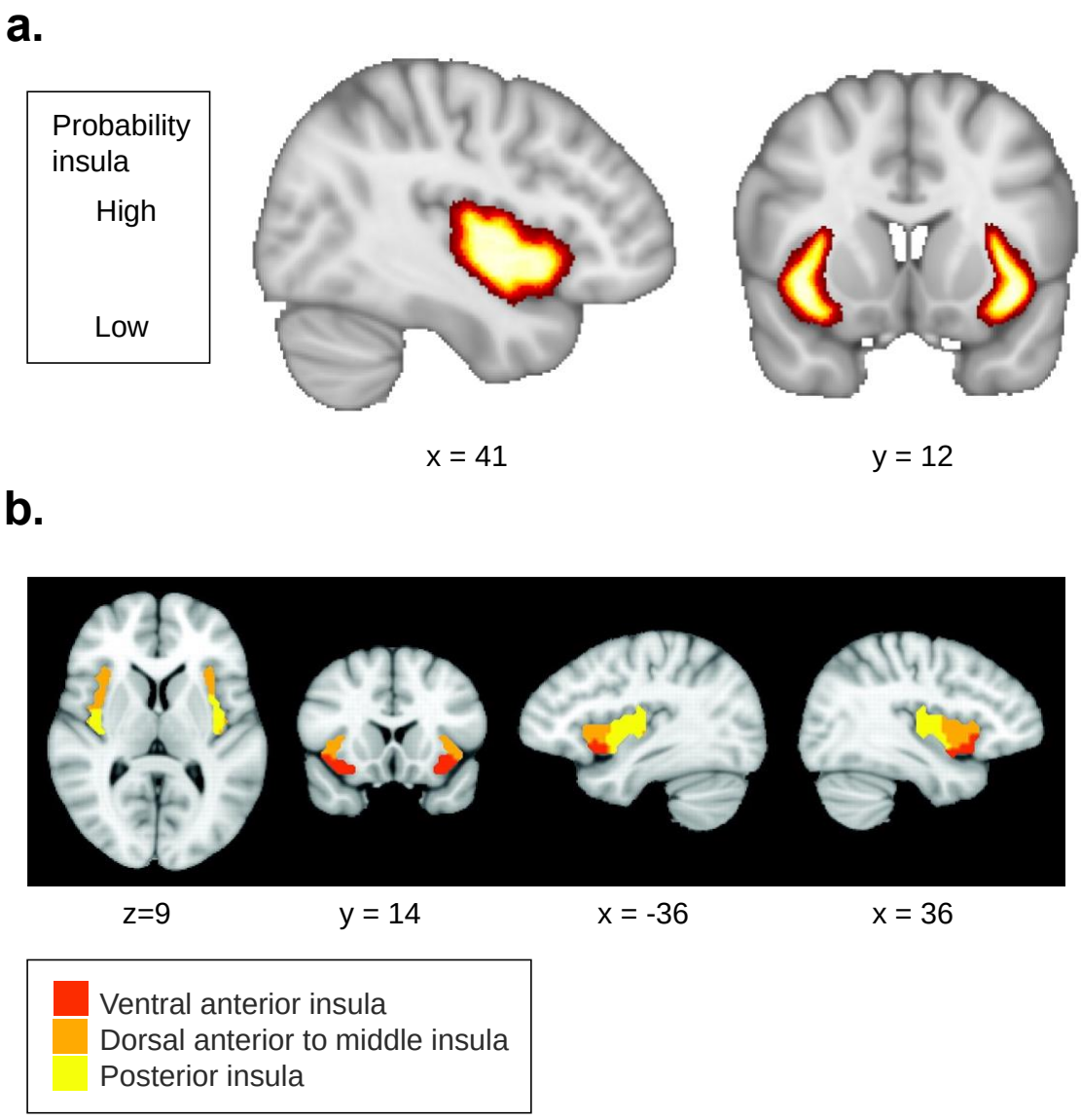


Figure 3. **Location and functional connectivity subdivisions of the anterior insula.** A) Location of the AI demonstrated by a probability map of voxels belonging to the AI according to the Harvard-Oxford cortical structural atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006). The map is displayed on the MNI152 standard-space T1-weighted average structural template image (Grabner et al., 2006) with MNI152 coordinates indicated. B) Three subregions of the right insula identified by clustering of functional connectivity patterns. Images are in radiological convention. Reprinted from (Deen et al., 2011).

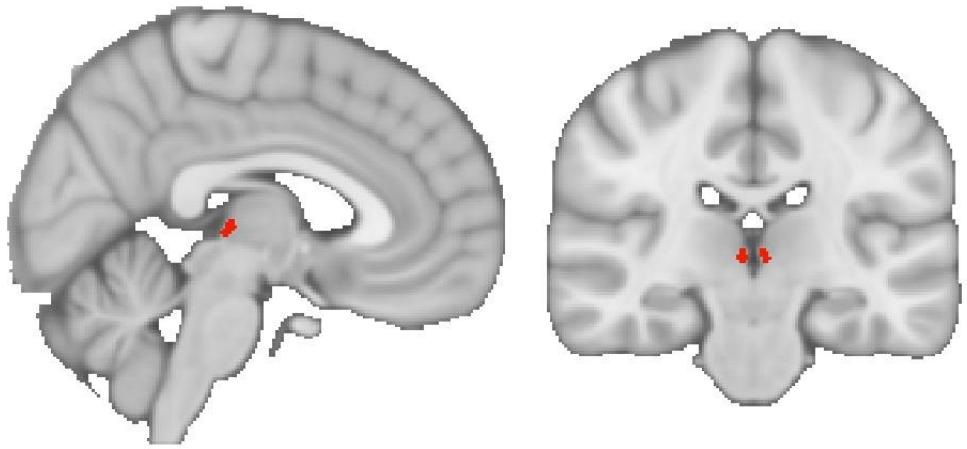
1.4.3. Lateral Habenula (LHb)

The lateral habenula (LHb) is a small, bilaterally paired and evolutionarily ancient structure located adjacent to the third ventricle and rostral to the posterior commissure in vertebrates (Fig. 4A) (Díaz et al., 2011). It is one of two heterogeneous subnuclei comprising the habenular complex (the other being the medial habenula, MHb), and is distinguished by its cell types (largely glutamatergic and GABAergic neurons) and its afferent and efferent connections. In addition to receiving afferent input from the limbic forebrain and basal ganglia that is more distributed than that received by MHb, the LHb receives afferents from areas such as the ACC, AI, globus pallidus and lateral hypothalamus (Hu et al., 2020a; Yetnikoff et al., 2015). Noteworthy among its efferents are indirect inhibitory connections with the serotonergic DRN as well as midbrain dopaminergic neurons (i.e. VTA, SNc) via the GABAergic rostromedial tegmental nucleus (RMTg; see Fig. 4B (Díaz et al., 2011; Lawther et al., 2020; Lecourtier et al., 2008; Lecourtier & Kelly, 2007).

The strategic position of LHb—connecting forebrain and midbrain regions, and controlling both the dopaminergic and serotonergic neuromodulatory systems—gives it influence over a number of physiological and motivational processes. Among these are the encoding of negative reward prediction errors (Fig. 4B), anticipation of aversive outcomes, suppression of motor activity and other behavioural changes in response to stress (Hikosaka, 2010; Hu et al., 2020a; Proulx et al., 2014). Indeed, its role in encoding aversive events and inhibiting dopamine neurons has led to it being called the ‘anti-reward centre’ and it is thought to play a role in reinforcement learning (P. M. Baker et al., 2016; Hikosaka, 2010). In the clinical literature, LHb has attracted increasing attention for its role in psychiatric disorders and

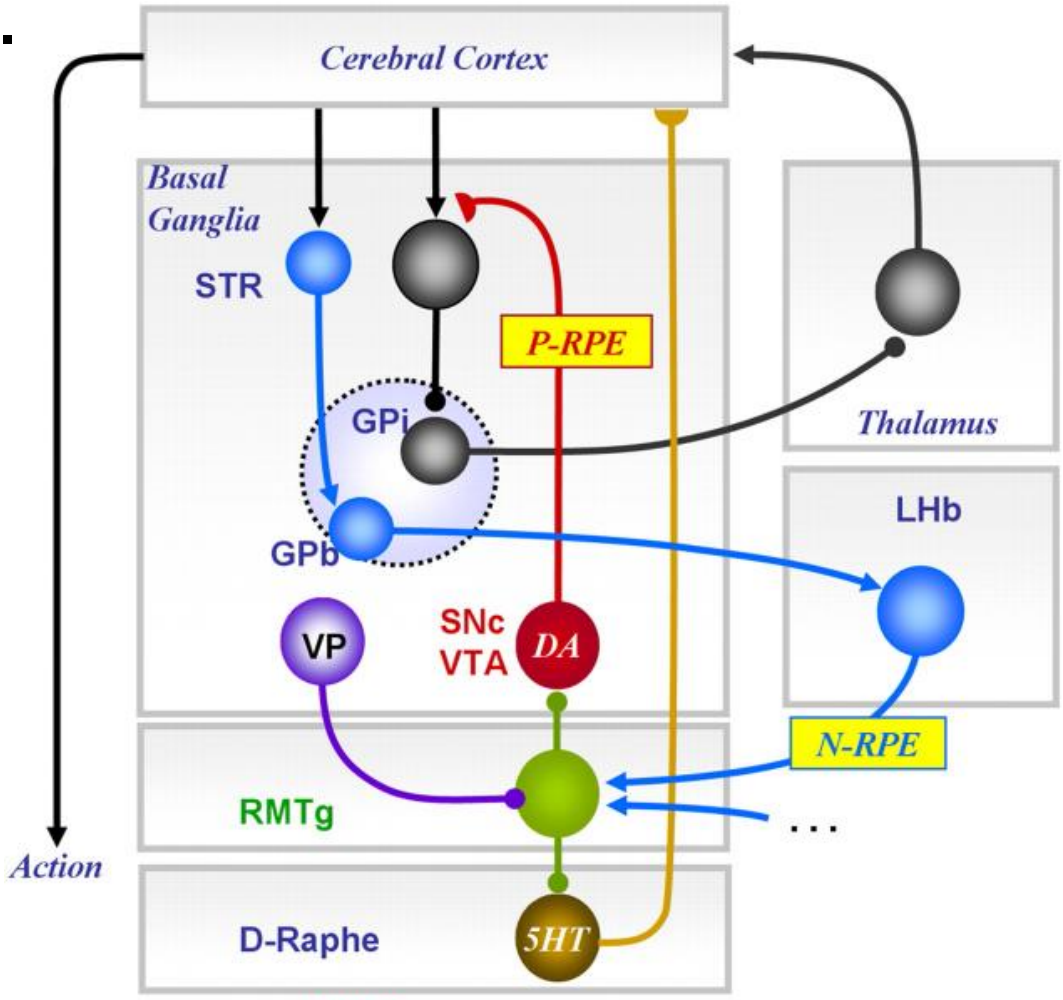
particularly in depression. Evidence emerging from animal and human studies indicates that changes in LHb activity are linked with a myriad of depressive symptoms, including helplessness, excessive negative focus, and anhedonia (Lawson et al., 2017; B. Li et al., 2011; K. Li et al., 2013). Recent experiments have demonstrated that blocking LHb burst-firing activity with the *N*-methyl-D-aspartate receptor (NMDAR) antagonist ketamine can rapidly relieve depressive symptoms in rats (Y. Yang, Cui, et al., 2018), establishing this brain area as a key target for pharmacological research. In this thesis, we hypothesize that the role of LHb in encoding aversive stimuli and acting as an 'anti-reward centre' will be relevant to tracking potential threat and motivating behavioural shift away from foraging and toward vigilance. Next I will discuss structures central to two neuromodulatory systems that are influenced by the LHb and relevant to value-based decision-making and mental health: the serotonergic and dopaminergic systems.

a.



x = 4 y = -24

b.



•*P-RPE* : positive reward prediction error
•*N-RPE* : negative reward prediction error

Figure 4. **LHb location and connectivity.** A) Location of the HB according to the Pauli atlas of human subcortical nuclei (Pauli et al., 2018), displayed on the MNI152 standard-space T1-weighted average structural template image (Grabner et al., 2006) with MNI152 coordinates indicated. B) Speculative diagram showing functional connectivity between LHb, RMTg, DRN, SNc, VTA, and other brain areas according to negative and positive reward prediction errors. N.B. Some known connections, such as the projection from the nucleus accumbens to the VP and the projections of the VP to DA neurons and to the LHb, are omitted. Abbreviations: STR, Striatum; N-RPE, negative reward prediction error; P-RPE, positive reward prediction error; D-Raphe, dorsal raphe; VP, ventral pallidum; DA, midbrain dopamine neurons; GPb, border part of the globus pallidus; GPi, globus pallidus internal segment. Reprinted from (S. Hong et al., 2011).

1.4.4. Dorsal Raphe Nucleus (DRN)

The dorsal raphe nucleus (DRN) is the most rostral subdivision of the raphe nuclei, an efferent system situated in the midline of the brainstem (Fig. 5A) (M. Berger et al., 2009). In the central nervous system, serotonin largely originates from neurons based in the raphe nuclei including the DRN. Serotonin is a neurotransmitter most often associated with functions such as mood regulation, sleep, and pain processing (De Deurwaerdère & Di Giovanni, 2020; Lucki, 1998).

The DRN is situated within a network of serotonergic projections that innervates brain areas including the basal limbic forebrain and cortex (Fig. 5B) (Commons, 2020). In addition to serotonergic neurons, however, the DRN contains a subpopulation of dopaminergic neurons, and both have been found to co-release glutamate (Lin et al., 2021; Liu et al., 2014; G. A. Matthews et al., 2016).

In humans, DRN neurons have been subdivided based on density, morphology, and projections. Baker and colleagues (1990) identified five subnuclei in their atlas and noted that the majority of DRN projections to the cortex originate from two cytoarchitecturally distinct loci: the dorsal subnucleus, being the largest but having the lowest neuronal density; and the ventrolateral subnucleus, having the highest density of neurons. Resting state functional connectivity mapping confirms that the DRN shares positive functional connectivity with cortical regions including ACC and insula as well as several subcortical areas including the amygdala, basal ganglia, and habenula (Beliveau et al., 2015; Ely et al., 2019). Of particular interest to this thesis is connectivity between DRN and the lateral habenula (LHb), another target brain area relevant for processing threat. As discussed in Section 1.4.3, LHb efferents play a role in inhibiting serotonergic neurons in the DRN (Zhao et al., 2015).

The importance of serotonin for affective regulation means that DRN activity has implications for symptoms of mood disorders, including depression and anxiety. Evidence from animal models has linked the DRN with behavioural changes in response to stress (Maier et al., 1993; Maier & Watkins, 2005), and in clinical practice the serotonergic system is considered a primary target for pharmacological intervention in anxiety disorders (Baldwin et al., 2014; M. Berger et al., 2009; Strawn et al., 2018). DRN activity is also associated with depression: its function is linked with depressive behaviours in rodents (Cui et al., 2019; K. Li et al., 2013; Lira et al., 2003; Xiu et al., 2021), post-mortem studies reveal changes in DRN neurons in depressed patients (Bach-Mizrachi et al., 2006; Baumann et al., 2002), and the serotonergic system is targeted by many antidepressant medications (Cipriani et al., 2018).

In addition to its role in affective regulation, DRN projections to the cortex give it the ability to influence many higher-level cognitive functions such as value-based decision-making.

Evidence suggests DRN activity encodes both rewarding and aversive aspects of the environment (J. Y. Cohen, 2015; Grossman et al., 2022; Khalighinejad et al., 2022; Matias et al., 2017). For example, serotonin neurons in the DRN have been shown to encode aversive stimuli, and a phasic serotonin signal in this area may function as a prediction error for future punishment (Daw et al., 2002; Dayan & Huys, 2009; Schweimer & Ungless, 2010). On the other hand, DRN serotonergic neurons co-releasing glutamate have been found to signal reward in mice, inducing rapid changes in cortical activity and having downstream effects on behaviours such as exploration and learning (Liu et al., 2014). In addition, the activity of DRN dopaminergic neurons in mice has been shown to encode diverse experiences such as the salience of behavioural incentives, acute social isolation, and moderation of pain-related behaviour (C. Li et al., 2016; Lin et al., 2021; G. A. Matthews et al., 2016). However, a cohesive understanding of the role of the DRN in decision-making is lacking. It is hypothesized that the current ecological paradigm may elicit DRN activity linked with tracking fear- and reward-related motivating factors and clarify its role in task-switching decisions.

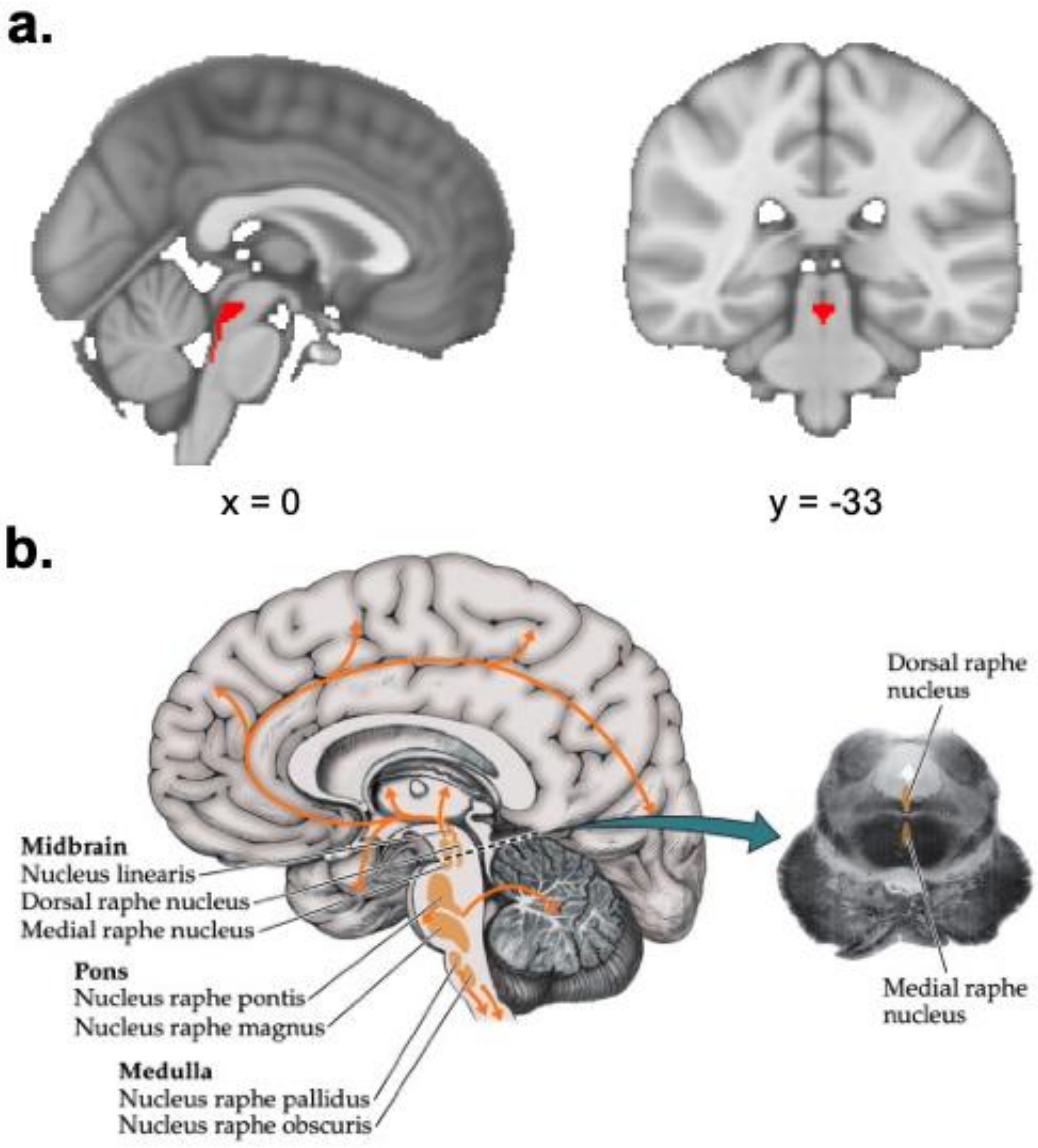


Figure 5. **Location of the DRN and position within serotonergic systems.** A) Location of the DRN adapted from (Khalighinejad et al., 2021), displayed on the MNI152 standard-space T1-weighted average structural template image (Grabner et al., 2006) with MNI152 coordinates indicated. B) DRN is situated within a network of serotonergic projections systems. DRN projects to many areas including cortical areas ACC and AI. Reproduced from (Blumenfeld, 2010).

1.4.5. Dopaminergic Midbrain: Substantia Nigra Pars Compacta (SNc) and Ventral Tegmental Area (VTA)

At various times, the dopaminergic neuromodulatory system has been implicated in a number of aspects of cognition and behaviour. Dopamine neurons are located mainly in two cell groups, the substantia nigra pars compacta (SNc) and ventral tegmental area (VTA) (a third group, the retrorubral field, also contains dopamine neurons, but its behavioural role has received comparatively less attention). The groups are situated rostral to the hindbrain and caudal to the diencephalon, with the oculomotor fibres ventromedial to the VTA (Fig. 6A) (Düzel et al., 2009; Vitošević et al., 2013). These groups are difficult to parcellate anatomically because they appear largely continuous and their small size makes it difficult to identify them with fMRI resolution (Murty et al., 2014). Masks of these regions intended to partition voxels into VTA versus SNc on an MRI often overlap, making it difficult to attribute activity definitively to one or the other. Cytoarchitectural studies in rodents have distinguished between groups based on their proportions of non-dopaminergic cells (Nair-Roberts et al., 2008). Indeed, populations of glutamatergic and GABA-ergic neurons in the SNc and VTA are notable; they comprise roughly one-third of neurons in both the SNc and VTA in rats, although the ratio is lower in humans (Düzel et al., 2009; German & Manaye, 1993; Nair-Roberts et al., 2008). These regions are more anatomically continuous in human and primates and thus are mainly partitioned with functional connectivity data (Murty et al., 2014). SNc and VTA are each integral to different neural pathways: the nigrostriatal pathway connects the SNc with the dorsal striatum, while the mesocorticolimbic pathway (comprising mesolimbic and mesocortical parts) connects projections from the VTA to the nucleus accumbens (NAc) in the ventral striatum and to frontal

and other parts of cortex (Fig. 6B) (Bezard & Gross, 1998; Braak & Del Tredici, 2008; Trutti et al., 2019).

Within the decision-making literature, dopamine neurons in the midbrain are especially important for reward-based learning and decisions. In human and non-human primates, their activity has been shown to respond to reward-predictive stimuli, encode value and confidence associated with upcoming actions, and signal reward prediction errors (Bayer & Glimcher, 2005; Düzel et al., 2009; Lak et al., 2017; Morris et al., 2006; Nomoto et al., 2010; Schultz et al., 1997). Representation of reward prediction errors in particular makes the midbrain critical for model-free RL, although there is some evidence that dopamine also plays a role in model-based RL by encoding a prediction error used to update predictive knowledge (Akam & Walton, 2021). Considered separately, SNc and VTA make different contributions to cognition and behaviour via their respective pathways. Degeneration of the nigrostriatal pathway is associated with the pathophysiology of Parkinson's Disease, leading to impairment of somatomotor function as well as diminished processing in limbic centres due to deprivation of dopamine in the striatum (Braak & Del Tredici, 2008; Trutti et al., 2019). The mesocorticolimbic pathway, on the other hand, is more functionally heterogeneous, taking part in cognition such as learning about reward and effort attributes of stimuli, behavioural motivation, and addiction (Hauser et al., 2017; Konova et al., 2013; Trutti et al., 2019; H. Yang et al., 2018). Within the context of this thesis, it is hypothesized that the dopaminergic midbrain will encode reward magnitudes and play a role in switching behaviour from vigilance to foraging.

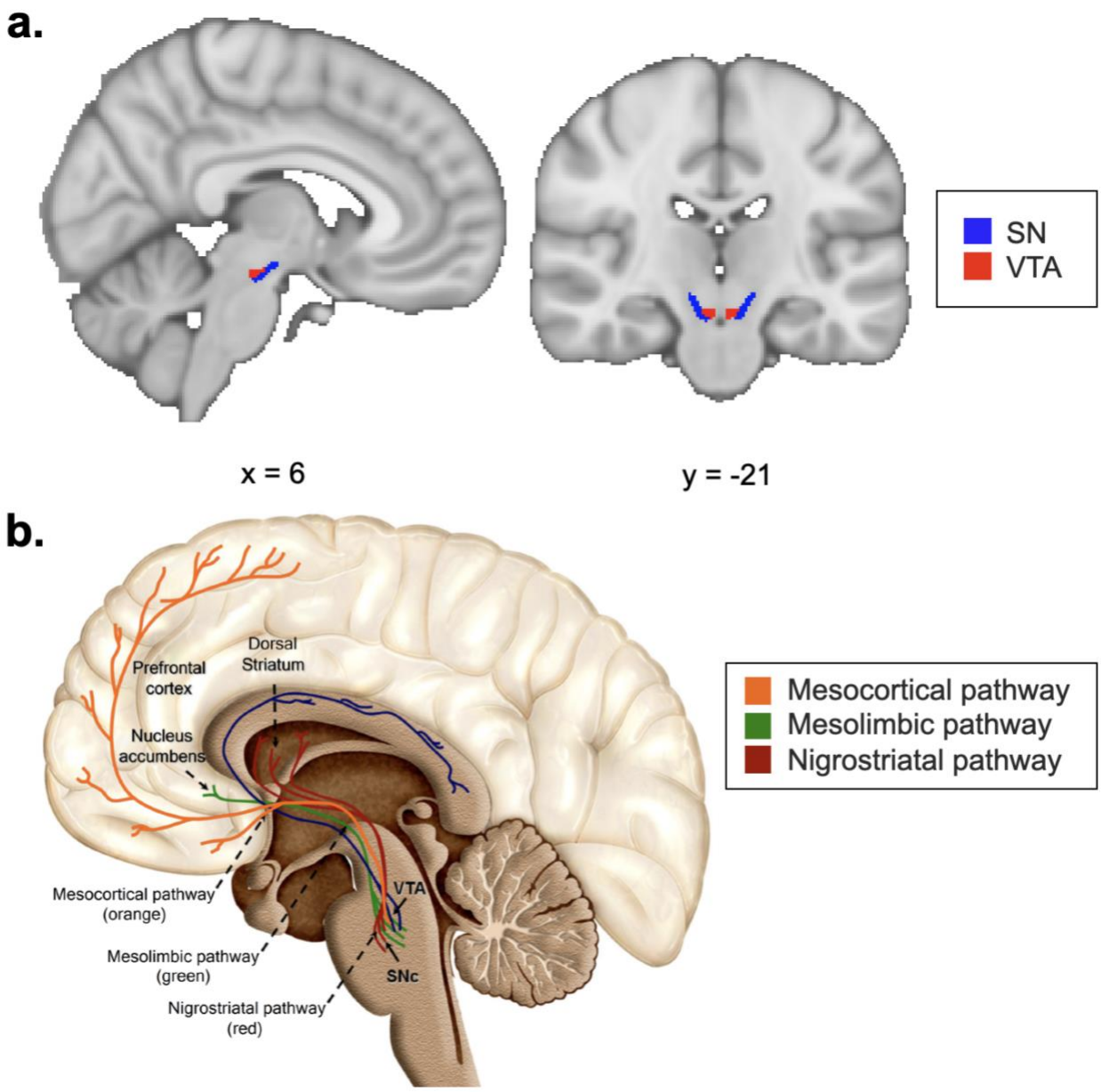


Figure 6. SNc and VTA: Locations and position within dopaminergic pathways. A) Locations of the SN and VTA according to the Pauli atlas of human subcortical nuclei (Pauli et al., 2018), displayed on the MNI152 standard-space T1-weighted average structural template image (Grabner et al., 2006) with MNI152 coordinates indicated. B) Positions of SNc and VTA within dopaminergic pathways including mesocortical, mesolimbic, and nigrostriatal pathways. Reproduced from (Arias-Carrión et al., 2010).

1.5. Methods for Measuring and Analysing Brain Activity

To translate findings in cognitive science into clinical insights, it is necessary to bridge the gap between cognitive models and biology by observing brain activity. Methods for measuring brain activity vary in the type of activity recorded as well as their spatial and temporal resolution. Recordings can capture activity ranging from the firing of a single neuron to the activity of a widely distributed network of brain areas. The technique used in Chapter 4 of this thesis is functional magnetic resonance imaging (fMRI), specifically at the 7 Tesla (7T) field strength. Here I will briefly explain this method of imaging and the advantages of using 7T.

1.5.1. Functional magnetic resonance imaging (fMRI)

Magnetic resonance (MR) signal is generated by applying a strong magnetic field to biological tissue to align its protons in a certain direction, perturbing those protons with radio waves, and measuring their return to resting state when the radio waves are switched off (A. Berger, 2002). Neural activation within the tissue is accompanied by changes in cerebral blow flow (CBF) and blood oxygenation which affects the local MR signal. Blood oxygenation level dependent (BOLD) functional MRI (fMRI) is a technique for recording neural activity by mapping these metabolic changes. In fMRI, the neurovascular coupling between local neural activity and its corresponding BOLD signal is often modelled with the hemodynamic response function (HRF), a mathematical transfer function (Rangaprakash et al., 2021). One advantage of fMRI is that the BOLD signal can be recorded with comparatively good spatial resolution (typically 1-2mm^2). This allows for the simultaneous recording of many different brain areas with relative specificity. In event-related experiments, the value of experimental variables at each point in time can be

regressed against the BOLD signal (usually with a general linear model) to identify brain activity correlated with each variable. The experiment in Chapter 4 of this thesis uses this approach to identify brain areas with activity linked to parametric variation in computational model variables.

One limitation of fMRI is the poor temporal resolution. Hemodynamic response time—i.e. the time needed to deliver blood to active cells—constrains BOLD signal to a width of roughly 3s and a peak at ~5-6s after the onset of a stimulus (Glover, 2011). This is very slow in comparison to the response time of single neurons, so BOLD signal measurements constitute only a rough approximation of the underlying neural activity.

1.5.2. 7T Field Strength

In MRI, the image's signal-to-noise ratio (SNR) increases with greater magnetic field strength. The magnetic field strength used to collect fMRI data in this thesis was 7 Tesla (7T). This is substantially higher than field strengths typically used for clinical and experimental imaging, which tend to be 1.5T or 3T. The SNR boost in 7T fMRI allows for imaging structural and functional details at higher spatial resolution (Yacoub et al., 2001). In this thesis, 7T field strength was chosen in order to better record BOLD signal in subcortical brain areas of interest—including LHb, DRN, VTA, and SNc—which are usually too small to parcellate accurately in lower field strength fMRI. As a result, the fMRI analysis presented here can provide insight into the contributions of these subcortical regions to task-switching between foraging and threat-oriented behaviour.

1.6. Summary

In summary, this thesis investigates how the human brain transitions between reward- and threat-oriented behaviours and looks at ways in which mood and psychopathology may affect this process. In this chapter I introduced concepts that have guided this investigation, including the computational psychiatry, transdiagnostic, and ecological frameworks; models of cognition in health and disease; brain areas underlying vigilant and appetitive behaviour; and relevant methodologies. However, gaps in existing knowledge remain. This thesis aims to address several open questions by presenting three experiments. 1) First, recall that Sections 1.3.2 and 1.3.3 discussed the need for tasks that emulate everyday decision-making processes and probe mechanisms associated with mental illness. Such tasks may have potential to form new diagnostic tools, but how best to develop and test them is still an open question. **Chapter 1** addresses this by presenting the design and validation of an ecological task and computational model and showing their potential for producing clinical insights. 2) Second, as demonstrated in Section 1.2, reward- and threat-oriented behaviour is highly idiosyncratic and can be characteristic of mental disorder. The mechanisms associated with symptoms such as anxiety, compulsive checking, apathy, and anhedonia, however, are not fully known. **Chapter 2** presents an experiment that aims to characterise these symptoms by linking them with distinct behavioural patterns. It also contributes to gaps in knowledge about the role of emotion in decision-making. 3) Third, an open question is how switching between foraging and vigilance is implemented in the brain. Section 1.4 discussed several brain areas involved in processing reward and threat as well as general decision making, including the ACC, AI, LHb, DRN, SNc, and VTA. However, it is not known how these areas work together to track behaviourally relevant information and initiate transitions between appetitive and vigilant states. **Chapter 3** of this thesis uses 7T fMRI to characterise the neural substrate of these processes. Overall, it is hoped that this work will

produce methodological, clinical, and biological insights about human foraging under threat that may be useful for future studies.

2. Chapter: An Ecological Task and Computational Model Capture Individual Differences in Foraging Under Threat with Potential Clinical Relevance

2.1. Abstract

Flexibly switching attention between rewards and potential threats is important for animal survival and is also relevant to everyday human decision-making. However, it is not well understood how people make these decisions; what kind of information is used to guide behaviour, and how this behaviour is affected by individual differences such as mood and symptoms of mental illness, are open questions. Here I present an ecological task designed to elicit naturalistic decision-making about foraging under threat and probe cognitive mechanisms associated with disordered reward- and threat-oriented behaviour. An online experiment used this task to collect behavioural, self-report, and clinical questionnaire data from 300 participants. We used a computational model to explore the types of information people used to complete the task and validated this model with behavioural simulations. Finally, we analysed correlations between all collected measures and showed that the task has potential to detect measures of clinical significance.

2.2. Introduction

To survive in complex and changing environments, animals must use information about their surroundings to guide their behaviour. In particular, foraging while detecting and evading potential predators requires balancing attention between rewards and threats appropriately according to current circumstances. This kind of decision-making is also relevant to modern human life, where environments often contain many potential behavioural motivators across both rewarding and aversive domains. For instance, to win a competition an athlete may need to

switch their attention between finding opportunities to score points and monitoring competitors. Understanding the process by which people decide to forfeit rewards in favour of monitoring threat, and conversely how we decide to take risks to gain rewards, is thus helpful for understanding natural human behaviour in a variety of contexts.

Further, understanding these behaviours may be clinically relevant. Disordered response to threatening stimuli is a key component of a number of psychopathologies, including anxiety-related disorders and obsessive-compulsive disorder (American Psychiatric Association, 2015; Corchs & Schiller, 2019). For example, a common symptom of OCD is repetitive behaviours that aim to reduce risk or harm (Abramowitz & Jacoby, 2014). In addition, pathologies such as apathy and anhedonia have been linked with impairment in the way the brain processes reward to motivate behaviour (Husain & Roiser, 2018). Thus, studying decisions to reorient toward rewarding versus threatening stimuli may contribute to our understanding of disordered anxious, fearful, and appetitive behaviours by characterising the relevant cognitive mechanisms. Despite relevance to everyday life in both health and disease, however, it is not fully understood how people make these decisions, and there is a need for clinical tools that can capture individual differences in these processes. In this study, we addressed this by designing a task and computational model and applying these to a large online sample.

One important aspect of our task is its ecological design. The study of cognitive mechanisms underlying reward- and threat-oriented behaviour has been advanced by paradigms in which single-event decisions are presented to participants at discrete intervals. However, recently a new framework has emerged for observing natural, everyday decision-making with ecological tasks. In computational ethology, experimental paradigms are framed as ecological virtual environments thought to probe decision-making processes relevant to daily life (Kolling

et al., 2012; Kolling & Akam, 2017; Mobbs et al., 2021; J. M. Pearson et al., 2014; Scholl & Klein-Flügge, 2018). One paradigm that has contributed to understanding natural, reward-based decision-making is the ecological foraging task. In these tasks, the foraging problem is framed as a series of encounters between a decision-maker and opportunities to gather rewards ('patches'): at each encounter, the decision-maker must choose whether to engage with the current patch or search for an alternative patch in hopes of greater reward. Previous studies have described cognitive and neural mechanisms associated with foraging in environments with fluctuating rewards (Hayden et al., 2011; Hunt et al., 2021; Kolling et al., 2012, 2018; Kolling & Akam, 2017). However, it is not well understood how decision-makers manage foraging in the context of predatory threat. Risk of predation is a critical constraint on animal foraging behaviour, and survival requires foraging strategically to evade threat. Animal studies have modelled the predatory risk versus foraging trade-off and characterised the effects of environmental conditions on evasive behaviour and value-based decision-making (Abrahams & Dill, 1989; Mangel et al., 1988; Stankowich & Blumstein, 2005), but few studies have explored these mechanisms in humans and their relationship with mental health. In a recent study, Bach and colleagues (2020) described individual differences in human foraging behaviour under predatory threat based on behavioural measures such as participants' location relative to threat versus safety when foraging. The role of vigilance in foraging under predatory threat, however, is largely unexplored. The current study addressed this gap in the literature by observing participants' decisions to forage versus check for predators in a naturalistic virtual environment.

Ecological tasks may be particularly useful for studying behaviour that is impaired in poor mental health. Symptoms of psychiatric illness are more often observed in the context of individuals' everyday lives than in conventional laboratory tasks, making the ecological

approach a useful tool for probing mechanisms associated with atypical behaviour. We designed our study with this in mind. To emulate a real-world decision-making context, our task allowed participants to choose both the timing and nature of their actions freely and continuously. In addition, our task and analyses focused on the balance between fearful and appetitive behaviours, an ability that is impaired in many psychological illnesses. We studied behavioural dimensions relevant to these illnesses including anxiety, compulsive checking, apathy, and anhedonia. Further, several features of our task were designed to capture individual differences specific to these behavioural dimensions.

Our task allowed us to examine two attentional biases associated with anxiety by requiring participants to perform two different types of checking behaviour. The first type of checking behaviour occurred when there was potentially a hidden, undiscovered predator in the environment. This situation encouraged participants to conduct sequences of checks to scan their surroundings for threats. The second type of checking behaviour occurred when a predator had been observed in the surrounding area. In this scenario, participants occasionally checked on the predator's location to assess its proximity. Analysing these behaviours separately allowed us to probe distinct attentional biases associated with anxiety. Previous work has linked anxiety with two divergent attentional biases: hypervigilance and attentional bias toward threat, which can manifest in the absence of actual threat and involves excessive scanning of the environment and greater sensitivity to threat detection. In addition, however, it can also involve threat avoidance; this might even entail apparently diminution in vigilance because a person is actually worried about encountering the threatening item (Amir et al., 2009; Cisler & Koster, 2010; Richards et al., 2014; Rinck et al., 2003). To link these apparently contradictory biases, the *vigilance-avoidance* theory posits that anxious individuals display the former attentional bias

(hypervigilance) in early stages of threat processing and the latter (avoidance) in later stages. Our task design was suited to observing behaviours potentially related to these biases.

Our task also contained elements relevant to other behavioural dimensions studied here, including apathy, anhedonia, and compulsive checking. Apathy has been associated with changes in subjective estimates of reward and effort; apathetic individuals have been shown to forego expending effort to obtain even small rewards (Bonnelle et al., 2015), and to display decision inertia, inappropriately persevering with an action to avoid reorienting behaviour (Scholl et al., 2022). In addition, anhedonia has been linked with difficulty in using reward-related information to guide decision-making (Treadway et al., 2012). Our task studied the use of reward- related information to flexibly reorient behaviour, a context in which aspects of apathy and anhedonia might manifest. The task was also suited to observe compulsive checking. Individuals diagnosed with obsessive-compulsive disorder (OCD), and particularly the subset of patients scoring highly on the checking scale of the Obsessive-Compulsive Inventory (OCI-R; Foa et al., 2002), tend to check repeatedly and distrust their memory for checking (Giele et al., 2015; van den Hout & Kindt, 2004; van Uijen & Toffolo, 2015). However, the expression of vigilance in OCD is complex. Recent evidence has suggested that these patients attend to threat-related stimuli less often than controls, suggesting a strategic avoidance of threat to prevent costly checking processes (Bucarelli & Purdon, 2016; Merritt, 2018). Our task is able to measure multiple aspects of checking behaviour, potentially providing a tool to observe complex, atypical vigilance.

To examine these possibilities, we designed an ecological task in which participants flexibly switched between foraging for food rewards and monitoring and evading predatory threat in a virtual environment with the goal of earning as much reward as possible. We collected

task behaviour and self-report responses (including questions related to psychiatric symptoms, mood, and task experience) from a large online sample and analysed their behaviour in four stages. First, we looked at how observable task factors such as threat and reward levels influenced participants' behaviour. Second, to explore what latent information people take into account when choosing freely among foraging, checking, and hiding behaviours, we fit a computational model and tested links between its parameters and task behaviour. Third, we validated this model by simulating decisions and comparing task performance in simulated versus real participants' data. Finally, we tested relationships between task behaviour, fitted model parameters, and self-report measures with correlations.

Our analysis was guided by the following hypotheses. First, in **Hypothesis 1** we predicted that high anxiety participants would show increased sensitivity to threat-related task factors **(Hypothesis 1a)** and decreased interest in foraging **(Hypothesis 1b)**. Second, apathy and anhedonia affect the willingness to expend effort to obtain reward and the use of reward value in decision-making respectively; we therefore hypothesised that these clinical measures would be associated with lower sensitivity to reward **(Hypothesis 2).** In **Hypothesis 3** we predicted that compulsive checking would be associated with prolonged and thorough checking behaviour **(Hypothesis 3a)** but also avoidance of this time-consuming ritual through infrequent initiation of checking **(Hypothesis 3b)**.

Overall, results showed that participants tracked behaviourally relevant information in several domains and used this information to make decisions about how to orient their task behaviour. In addition, the behavioural dimensions anxiety, apathy, anhedonia, and compulsive checking were characterised by distinct patterns of task behaviour: anxiety was linked with greater sensitivity to threat-related task factors, apathy and anhedonia were associated with

insensitivity to reward, and compulsive checking was related to strategic avoidance of threat. These findings suggest that our task indeed probed decision-making processes relevant to symptoms of poor mental health, and that our computational model captured information that guided these decisions. This task and model may be useful tools for future clinical investigations.

2.3. Methods

2.3.1. Participants

We recruited 300 participants from the online platform Prolific.ac that fulfilled the inclusion criteria listed below. Ethics approval for the study was given by Oxford University Central University Research Ethics Committee (CUREC) (Ref-number: R54722/RE001). All participants provided informed consent before taking part.

2.3.2. Task

We designed a gamified online foraging task in which participants freely made a series of choices with the goal of earning as much money as possible. During the task participants controlled an animated fish in an ocean environment where there was rewarding food (later translated to money), threatening predators (leading to large point loss if they 'caught' the fish), and a hiding space (where participants could hide from the predators) (Fig. 7). Participants could choose freely between three actions: 'forage' for food, 'check' for predators, and 'hide' in a safe space.

2.3.2.1. Forage. The average amount of food available varied randomly and participants could always see how much food was available. If participants 'foraged' by pressing a button the fish dived down to obtain food, thereby increasing its supply of energy (Fig. 7B); when an

energy bar at the top of the screen was full, the fish gained a ‘life’ which corresponded to extra payment.

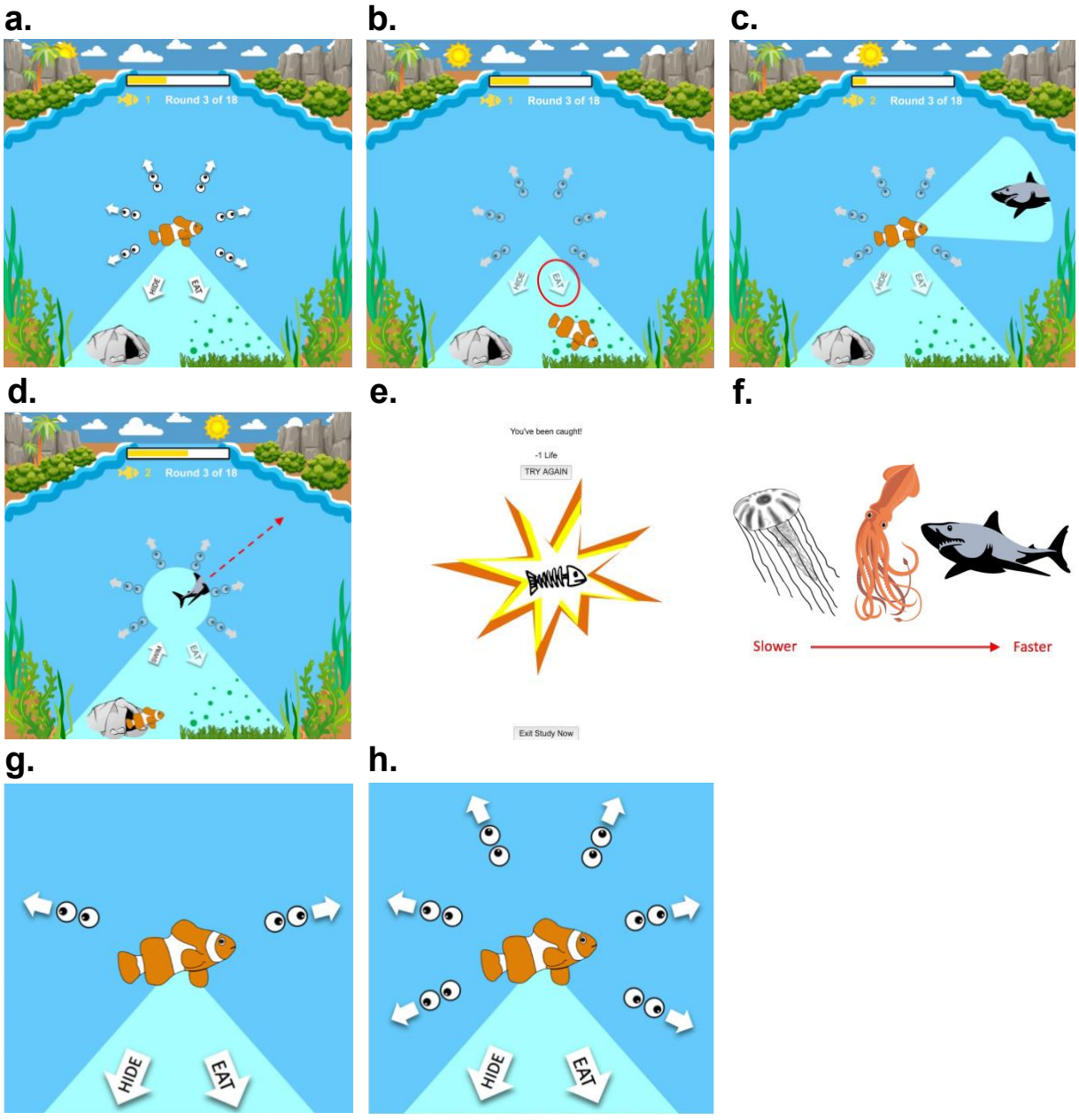


Figure 7. **Illustration of the environment layout and the three possible actions during an example block.** A) At the start of a block the fish begins in the centre position. In this block the

surrounding area is divided into four sections that must be searched to determine whether there is a predator in the area. B) By clicking 'EAT' the fish dives down to the patch of food and the yellow energy bar at the top increases by the amount of reward gained. C) By clicking one of the eye icons the fish checks in a particular direction. In this example the fish discovers that there is a predator in that area. D) By clicking 'HIDE' the fish dives into a small cave and is safe from the predator. It can see the predator reach the screen centre and then retreat, and by clicking 'SWIM' the fish can return to the original centre position. E) If the fish fails to hide in time, it is 'caught' by the predator and loses one 'life' (equivalent to a full bar of collected energy). D) The three types of predators, in order of speed. G-H) Each block differed in the number of segments in which participants could check for predators. G) shows an example block divided into two directions for checking, while H) shows an example block divided into six directions for checking.

2.3.2.2. Check. Predators were hidden from participants' view unless they 'checked' a specific portion of the surrounding area (Fig. 7C). Predators appeared at the edge of the screen and moved toward the fish's location at the screen centre. When the predator reached the centre of the screen it would either catch the fish (causing the participant to lose one 'life') or, if the fish was in hiding (see below), the predator would quickly exit the environment. By checking, participants could see whether a predator was in a specific area of the environment and how close it was (Fig. 7C). There were three types of predators that differed in speed: (1) the jellyfish was slowest (20s to reach the screen centre), (2) the squid was medium speed (15s), and (3) the shark was fastest (10s) (Fig. 7F). Each block (see below) had only one type of predator, appearing one at a time, and participants were informed which before the block start. There was a random delay

(1-10s) between the environment start or previous predator disappearance and the appearance of the subsequent predator.

2.3.2.3. Hide. Pressing ‘hide’ caused the fish to escape to a safe space in a corner of the screen where it could not be caught by the predator. While hiding the ‘hide’ button transformed into a ‘swim’ button that the participant could click to return the fish to the screen centre (Fig. 7D).

2.3.2.4. Blocks. Each of 18 blocks lasted 90s and had a different combination of (1) predator type (i.e. predator speed, three levels, see above) and (2) number of segments in which participants could check for predators (range 1-6; see Fig. 7G, H). With fewer segments, more of the environment was visible during each check action and therefore fewer checks were required to survey the entire surrounding area. Blocks were visually distinguished from one another by the sky changing between the appearance of night and day, but this had no impact on predators or rewards.

After each block, participants answered four questions about how they perceived the block: (1) “How much food was available in the last round?” (2) “In the last round, how difficult was it to balance between eating food and checking for predators?” (3) “How stressful was the last round?” (4) “How exciting was the last round?” (see Fig. 8 for response options).

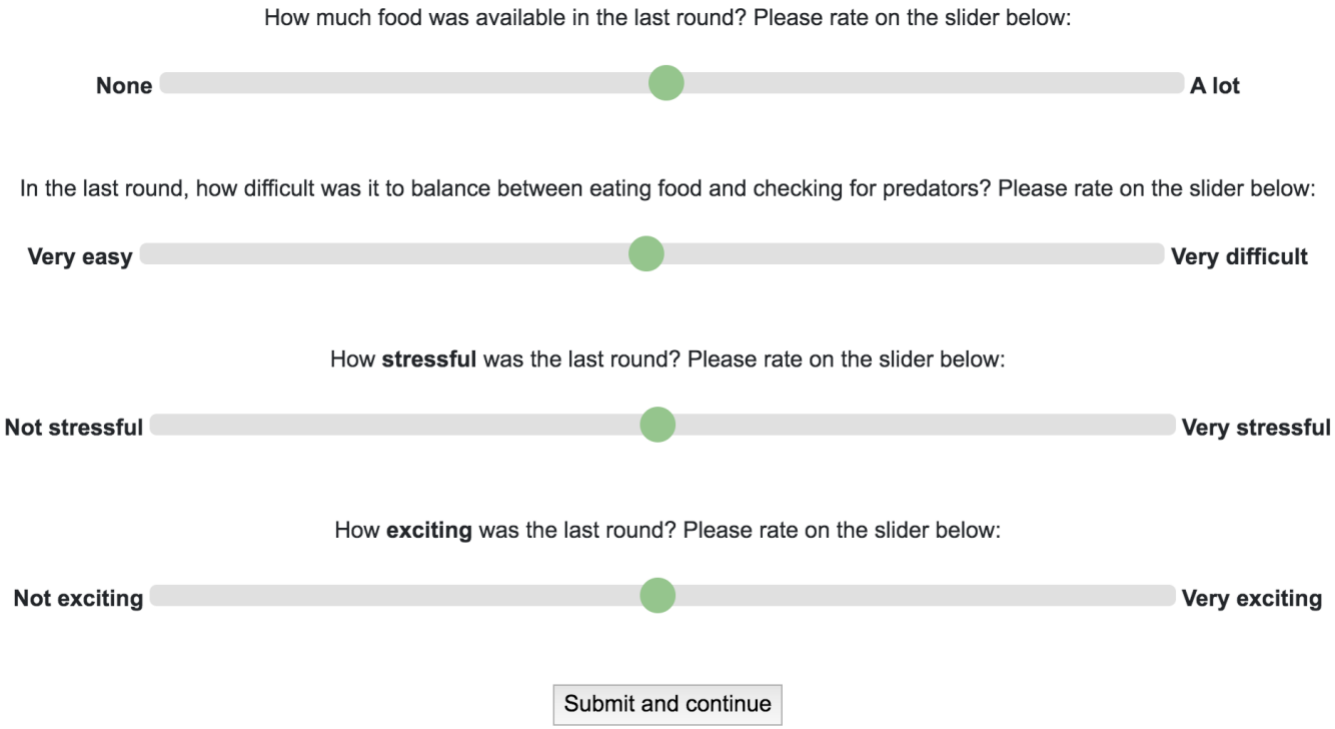


Figure 8. **Post-block ratings.** After each block participants were presented with four questions to rate their subjective perceptions of the block.

2.3.2.5. Timings. Each action involved a time cost: foraging took 1.5s, checking took 0.5s, hiding took 0.5s, and returning from hiding took 2s. Block duration was 90s, and time in between blocks was variable. The scheduled delay before appearance of a new predator was random and varied between 1-10s. Reward magnitude fluctuated randomly at each second.

2.3.2.6. Training. Before entering the experimental blocks participants clicked through a series of instructions for the task (Table A1). They then completed two practice blocks and completed a multiple-choice quiz testing their understanding of the task (Table A2), which they had to answer correctly in order to advance.

2.3.3. Questionnaires

After the task participants completed previously validated questionnaires to measure psychiatric symptoms: the Apathy Motivation Index (Ang et al., 2017) (AMI), State-Trait Inventory for Cognitive and Somatic Anxiety (Grös et al., 2007) (STICSA), Snaith-Hamilton Pleasure Scale (Snaith et al., 1995) (SHAPS), and the OCI-R checking scale (Foa et al., 2002) (OCI-R). One question from each of the three AMI, SHAPS, and OCI-R questionnaires was repeated on each of the other two questionnaires (totalling three presentations of the same question) to screen for quality data ('consistency questions'; see below for exclusion criteria).

Questionnaire scores were grouped for analysis by pathology. First, for anxiety the STICSA Trait subscale was analysed separately as it is the subscale for which a diagnostic threshold has been validated. We also included in anxiety analysis the difference between STICSA Trait and State Somatic subscale scores for participants who completed the questionnaires after the task. Second, we averaged the AMI and SHAPS scores, as apathy and anhedonia show overlapping phenomena (Husain & Roiser, 2018). OCD was included as a third pathology of interest.

Participants also completed a debrief questionnaire in which they reported their metacognitive awareness of their task behaviour (see Table A3). For this they responded to a series of statements about the task by marking how often each statement was true for them. Response options were presented as a seven-point scale from 0 ('Never') to 6 ('Very often').

2.3.4. Participant Screening and Exclusion Criteria

Participant screening criteria included age (18+) and English language comprehension, but not psychiatric scores. To ensure data quality, participants were excluded if their data suggested inattentiveness, incompleteness, or otherwise a lack of engagement in the task or questionnaires. Specifically, participants were excluded if their submission took less than the minimum amount of time necessary to complete all steps of the experiment. Participants were excluded based on behaviour if they earned zero or negative 'extra lives', suggesting that the participant was not pursuing rewards. Exclusion criteria also included questionnaire incompleteness and divergent answers on consistency questions.

2.3.5. Behavioural Analysis

Data analyses were performed in R (R Core Team, 2022) using RStan (Carpenter et al., 2017). To pre-process data, we removed epochs that contained no check actions from both real and simulated data because these epochs were not informative for predicting this behaviour. Across all participants this resulted in an average of 6.03 ± 12.39 epochs omitted per participant in the pre-threat discovery phase (hereafter pre-discovery phase) and an average of 7.06 ± 12.89 epochs omitted per participant in the post-threat discovery phase (hereafter post-discovery phase).

Before analysis we split the time from the start of the delay period to the arrival of each predator ('predator epochs') into two segments: the 'pre-discovery phase' and the 'post-discovery phase'. On average each participant's data set yielded 409.02 ± 99.82 actions in the pre-discovery phase and 128.40 ± 54.52 actions in the post-discovery phase. Then we created a series of 34 behavioural measures across both phases to characterise behaviour within the task (Table 1).

To analyse the effect of observable contextual variables such as predator speed on behaviour we conducted two-tailed independent samples t-tests of participant data from selected

behavioural measures. To analyse relationships between task behaviour, fitted model parameters, and self-report measures, we calculated Pearson's R correlations and assess significance with *p*-values using cor.test from the stats package in R. Correlations were used instead of regressions because psychiatric measures are often highly correlated and preliminary analyses showed no effects of clinical measures when controlling for all other clinical measures.

Table 1

All Model-Free Behavioural Measures Computed

No.	Disc. Phase	Name	Description
1	Pre	timeUntilFirstSearch_slow_TS	Average time between epoch start and the first check (slow condition only)
2	Pre	timeSincePrevSearch_s2_slow_TS	Time between start of first cluster of searches and the start of the second cluster of searches (slow condition only)
3	Pre	varianceInWaitTime_2Min1_slow_TS	Variable 2 minus variable 1 (see above)
4	Pre	timeUntilFirstSearch_med_TS	Average time between epoch start and the first check (medium speed condition only)
5	Pre	timeUntilFirstSearch_fast_TS	Average time between epoch start and the first check (fast condition only)

6	Pre	numChecksPerTp_lowestThirdPrevRew	How many checks are conducted in the lowest third of reward bins (time points are binned by the reward during the previous action) for each time point? (slow condition, after 10s only)
7	Pre	numChecksPerTp_midThirdPrevRew	How many checks are conducted in the middle third of reward bins (time points are binned by the reward during the previous action) for each time point? (slow condition, after 10s only)
8	Pre	numChecksPerTp_highestThirdPrevRew	How many checks are conducted in the highest third of reward bins (time points are binned by the reward during the previous action) for each time point? (slow condition, after 10s only)
9	Pre	freqFullChecks_all	How frequently did participants conduct full (i.e. searching in all directions without stopping) vs partial checks of the environment? (all conditions included)
10	Pre	freq_singleChecks_all	How frequently did participants conduct single checks of the environment? (all conditions included)
11	Pre		Variable 9 minus variable 10 (see above)

12	Pre	rateChecks_cluterEnd2s_NoMinYes	Rate of checking for when a check cluster did NOT end in the past 2 seconds minus the rate of checking for when a check cluster DID end in the past 2 seconds
13	Pre	rateChecks_cluterEnd3s_NoMinYes	Rate of checking for when a check cluster did NOT end in the past 3 seconds minus the rate of checking for when a check cluster DID end in the past 3 seconds
14	Pre	rateChecks_cluterEnd5s_NoMinYes	Rate of checking for when a check cluster did NOT end in the past 5 seconds minus the rate of checking for when a check cluster DID end in the past 5 seconds
15	Post	checkRate_1stThird_TM	Rate of checking in the first third of the monitoring period (time segments based on proximity; i.e. how many seconds away the predator arrival was)
16	Post	checkRate_2ndThird_TM	Rate of checking in the middle third of the monitoring period (time segments based on proximity; i.e. how many seconds away the predator arrival was)

17	Post	checkRate_lastThird_TM	Rate of checking in the last third of the monitoring period (time segments based on proximity; i.e. how many seconds away the predator arrival was)
18	Post	checkRate_last3rdMinFirst3rd_slow	Variable 17 minus variable 15
19	Post	timeUntilFirstSearch_slow_TM	Average time between monitoring period start and the first check (slow condition only)
20	Post	timeSincePrevSearch_s2_slow_TM	Average time between the first check and second check in the monitoring period (note that the first check is considered the first check *after* the predator has been discovered) (slow condition only)
21	Post	varianceInWaitTime_2Min1_slow_TM	Variable 20 minus variable 19
22	Post	avgHideTime	Average time at which participant hides (recorded as proximity of predator during the hide action)
23	Post	percForage_lowestThirdRew	Percentage of foraging actions (relative to all actions) in the lowest third of rewards (note that rewards are binned across epochs by individual time point)

24	Post	percForage_midThirdRew	Percentage of foraging actions (relative to all actions) in the middle third of rewards (note that rewards are binned across epochs by individual time point)
25	Post	percForage_highestThirdRew	Percentage of foraging actions (relative to all actions) in the highest third of rewards (note that rewards are binned across epochs by individual time point)
26	Post	rateChecks_noCheckLast2s	Rate of checking when there was NO check in the last 2 seconds
27	Post	rateChecks_checkLast2s	Rate of checking when there was a check in the last 2 seconds
28	Post	rateChecks_noCheckLast3s	Rate of checking when there was NO check in the last 3 seconds
29	Post	rateChecks_checkLast3s	Rate of checking when there was a check in the last 3 seconds
30	Post	rateChecks_noCheckLast5s	Rate of checking when there was NO check in the last 5 seconds

31	Post	rateChecks_checkLast5s	Rate of checking when there was a check in the last 5 seconds
32	Post	diff_checkFreq_1stMin2ndThird_TM	Frequency of checking across monitoring period: difference between frequencies in the 1st third and 2nd third of the monitoring period
33	Post	diff_forageFreq_1stMin2ndThird_TM	Frequency of foraging across monitoring period: difference between frequencies in the 1st third and 2nd third of the monitoring period
34	Post	diff_hideFreq_1stMin2ndThird_TM	Frequency of hiding across monitoring period: difference between frequencies in the 1st third and 2nd third of the monitoring period

2.3.6. Computational Modelling and Simulations

We created a computational model to analyse task behaviour. This model allowed us to discover what information people used to guide their decisions and to compare individual differences in the decision-making process. Data from each epoch phase—pre- and post-discovery—were fit to separate models to test how the relevant task components affected participants' behaviour. Model parameters represented different types of task-related information available to the participant. Two types of information were modelled: observations or expectations about potential motivating factors in the environment (such as available reward or threat proximity) and information about the participant's own actions and experiences (such as what action they

had recently taken). Some variables were simple heuristics, while others were updated moment-by-moment based on new information. Model parameters for each phase are described below.

Model parameters were fit to participants' choice data using hierarchical Bayesian regression in RStan (Carpenter et al., 2017) with 1000 samples per chain and 3 chains. Choices were modelled binomially with the Bernoulli_logit link function. Absence of divergent samples was verified using the shinystan diagnostic toolbox (Gabry, 2015) and convergence of the model fit was assessed using the Rhat <1.1 criterion (Gelman et al., 2013).

To assess model validity—i.e., to evaluate the extent to which model variables captured information actually used by task participants and justify their inclusion in the model—we simulated the behaviour artificial participants. In one simulation (N=300), each artificial dataset used parameters fitted to a real participant's data to simulate decisions based on changing contextual factors. Then we compared the simulated and real datasets on model-free behavioural measures. We specifically selected behavioural measures that, while computed in a manner unrelated to any of the model parameters, nevertheless demonstrated the importance of a particular parameter. For example, to examine whether people and simulations used the parameter *continue checking* similarly, we plotted the average frequency with which participants conducted full scans of the entire environment versus the frequency of single checks (Fig. 11G, H). Behavioural similarities were considered evidence that the model parameters provided a good approximation of the information used in decision-making.

Further, we conducted another simulation (N=1000) to examine the role of each model variable in the behavioural measures selected for real/simulated data comparison. In this simulation, each artificial dataset used parameters drawn randomly from the range of parameters fit to real participants' data. We extracted binomial behavioural measures from the simulated

data and entered each of these into a separate hierarchical logistic regression to predict the relationship between model variables and the likelihood of the test category. For example, in Figure 11I, we counted instances of switching to checking and categorised them according to whether the check was followed by a full scan of the environment or whether it occurred in isolation; then we used logistic regression to test the relationship between the likelihood that a check would be followed by a complete scan of the environment and the variables *predator probability, continue checking, reward, time pressure,* and the randomly drawn hyperparameter T_{inv}. Regressions were run in RStan (Carpenter et al., 2017) using the same settings described above.

2.3.6.1. Pre-discovery phase. To model this part of the epoch we used four variables (Fig. 9A). First, *reward* corresponded to the amount of reward available (always visible on-screen). Second, *predator probability* represented the probability that a hidden predator had entered the environment; its value started at 0 and increased linearly from the minimum delay period (1s) to the maximum delay period (10s), at which point it reached and remained at its maximum value of 1. Equation 3 demonstrates how to compute *predator probability* for a given time point *t* (in seconds):

Predator probability:

$$f(t) = \begin{cases} 0, & t \leq 1 \\ \dfrac{t-1}{9}, & 1 < t < 10 \\ 1, & t \geq 10 \end{cases} \qquad 3$$

Thus, *predator probability* was a heuristic based on the participant's knowledge of the task and was not updated with experience. In contrast, the variable *time pressure* represented the amount

of time since the participant had last been certain that there was no predator present and was updated with experience. Equation 4 demonstrates how *time pressure* was computed for a given time point *t* (in seconds) in block *b*:

$$\textit{Time pressure:} \qquad f(t) = \left(\frac{1}{minDelay + speed_b}\right) * (t - lastFullCheck_t) \qquad 4$$

where *minDelay* is the minimum possible delay for all predators in this task (2.5s), $speed_b$ is the number of seconds that the predator type in block *b* takes to reach the centre of the screen, and $lastFullCheck_t$ indicates, for timepoint *t*, the timepoint at which the participant most recently completed checking all areas of the environment (i.e., when they could be certain that no predator was present). Finally, *continue checking* represented the tendency for participants to check in all directions to ascertain whether a predator was present; the value started at 0, and once an initial check had been made it changed to 1 until the participant had checked all surrounding areas.

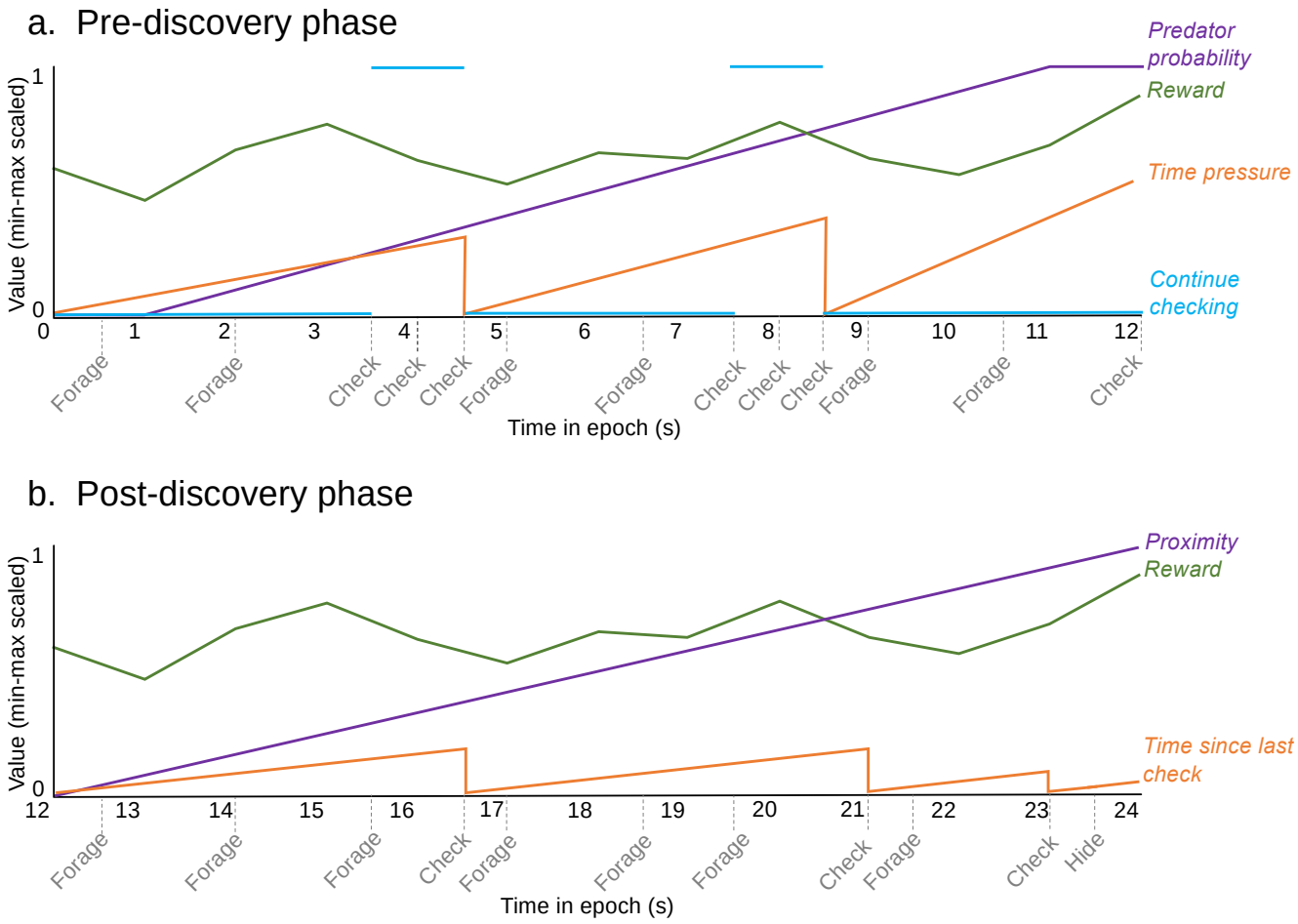


Figure 9. **Illustration of how model variables changed across an example epoch.** The value of model variables changed from moment to moment depending on factors such as time elapsed and participant behaviour. The example epoch illustrated here has a scheduled delay of 9s, medium predator speed (15s before arrival), and 3 directions for checking, and the predator was discovered at 12s. Variables are min-max scaled relative to all epochs. **A) Pre-discovery phase:** The values of *predator probability* and *reward* were independent of participant behaviour. In contrast, *time pressure* was updated after a full scan of the environment revealed no predator, and *continue checking* indicated whether a scan of the environment was incomplete. **B) Post-discovery phase:** The values of *proximity* and *reward* were independent of participant behaviour, while *time since last check* indicated how long it had been since the participant had

last seen the predator's location and therefore varied between participants depending on precise details of their behaviour.

To simulate decisions in the pre-discovery phase, we first calculated a decision variable (DV, the accumulation of all sources of prior knowledge, evidence, and value into a quantity that can be interpreted by a decision rule; refer to Section 1.3.1) expressing the value of checking using the variables described above. Equation 5 demonstrates how the DV was calculated:

$$DV = \beta_1 reward + \beta_2 predatorProbability + \beta_3 timePressure + \beta_4 continueChecking \quad (5)$$

where *DV* represents the utility of checking instead of foraging at a given timestep, other variables are as described above, and β_i corresponded to parameters fit to the real participants' data. Then the DV was entered into a sigmoid function with the inverse temperature (T_{inv}, a hyperparameter that scales the DV and tunes the confidence of the sigmoid output) to get the probability of checking as expressed in Equation 6:

$$P(C) = \frac{1}{1 + e^{(T_{inv}* - DV)}} \quad (6)$$

where *P(C)* is the probability of checking instead of foraging at a given timestep, *e* is the mathematical constant (Euler's number), T_{inv} is the inverse temperature (in this case, a parameter fit to the real participants' data), and *DV* is the decision variable calculated for the given timestep.

An action—forage or check—was then selected according to the probability output by the sigmoid function.

2.3.6.2. Post-discovery phase. Three variables were included in the post-discovery phase model (Fig. 9B). First, *reward* again corresponded to the amount of reward available. Next, *time since last check* represented how long it had been since the participant had last seen the predator's location, as a percentage of the total time the predator was in the environment during that epoch (its speed). Equation 7 demonstrates how *time since last check* was computed for a given timepoint *t* in block *b*:

Time since last check: $$f(t) = \frac{t - lastCheck_t}{speed_b} \quad (7)$$

where $lastCheck_t$ indicates, for timepoint *t*, the timepoint when the participant last saw the predator, and $speed_b$ is the speed of the current predator type at block *b*. Third, another threat-related variable, *proximity*, represented the amount of time until the predator would arrive and increased linearly with the predator's approach. Equation 8 demonstrates how *proximity* was computed for a given timepoint *t* within epoch *e* in block *b*:

Proximity: $$f(t) = t - (delay_e + speed_b) \quad (8)$$

where $delay_e$ is the scheduled delay for the predator in epoch *e* and $speed_b$ is the speed of the current predator type at block *b*. Theoretically, measures of threat proximity should affect a wide variety of vigilant and defensive behaviours (Fanselow & Lester, 1988), so we expected that

proximity would influence both the probability of checking and of hiding. For this reason, the *proximity* variable was fit to separate regression weights for checking and hiding, and was entered into decision variables representing the utilities of both actions.

To simulate decisions in the post-discovery phase, we calculated the values of the three possible actions separately using the variables described above. Equations 9, 10, and 11 (Table 2) demonstrate how DVs for checking, foraging, and hiding respectively were computed:

Table 2

Computation of Decision Variables for Post-Discovery Phase

Decision variable	Formula	Equation No.
Check:	$DV_1 = \beta_1 proximity + \beta_2 timeSinceLastCheck$	9
Forage:	$DV_2 = \beta_1 reward$	10
Hide:	$DV_3 = \beta_1 proximity$	11

Then we entered these decision variables (DV_1, DV_2, DV_3) into a softmax function with the inverse temperature (T_{inv}) to get the probability of selecting each action at a given timepoint (Eq. 12):

$$s(DV_i) = \frac{e^{(T_{inv} * DV_i)}}{\sum_{j=1}^{3} e^{(T_{inv} * DV_j)}} \quad 12$$

where T_{inv} again corresponded to a parameter fit to the real participants' data. An action—forage, check, or hide—was then selected according to the probability output by the softmax function.

2.4. Results

Our sample included 300 online participants (age: 26.88 ± 5.92; gender: 141 female, 159 male; most common education levels: A-levels/high school diploma, N=123; and bachelor's degree, N=103). Participants completed an online foraging task in which they freely and continuously made choices with the aim of earning as much bonus money as possible. In all 18 blocks of this task, participants controlled an animated fish in an ocean environment where there was rewarding food (leading to bonus payment at the end), threatening predators (leading to a large reward loss if they were 'caught' by the predator), and a hiding space where they would be safe from predators (Fig. 7; see Methods for more details on properties of blocks). Participants chose between three actions: foraging for food, checking the surrounding area for hidden predators, and hiding in the safe space. Predators travelled at various speeds from the edge of the screen toward the fish's location and were hidden from view until participants performed a check on the area of the environment where a predator was located. Environments were divided into a variable number of directions in which the predator could hide ('check directions'). In between blocks, participants answered questions about how they perceived aspects such as food availability, the difficulty of balancing foraging with checking, stress, and excitement in the previous block (Fig. 8; see Methods for details). After the task participants completed a series of psychiatric questionnaires measuring symptoms of anxiety, apathy, anhedonia, and obsessive-compulsive checking behaviour, as well as a debrief questionnaire that asked participants to assess their metacognition about their task behaviour (see Methods for questionnaire details).

For analysis, task blocks were separated into epochs starting from the delay before a predator appeared and ending when the predator arrived at the fish's location (at which point it would 'catch' the fish if it was not in the safe space). Each epoch was analysed as two separate segments: (1) the 'pre-discovery phase' corresponding to the time when participants knew there was the possibility of a predator being in the area, but had not yet seen one and did not know its location; and (2) the 'post-discovery phase' corresponding to the time in the epoch when participants had discovered the predator (i.e., checked the area of the environment where a predator was located) but before it was necessary to hide to avoid predation. These two segments were considered distinct because they were associated with different patterns of checking: During the pre-discovery phase participants had to search the entire surrounding area for potential threats, resulting in clustered series of checks; in contrast, during the post-discovery phase participants checked only the location of the predator, resulting in single, sporadic checks. Thus, our task enabled us to observe vigilance for potential threats as well as monitoring of known threats. Participants behaved differently in the pre- and post-discovery phases, as well as behaved differently from one another, showing distinct, idiosyncratic behavioural patterns (Fig. 10).

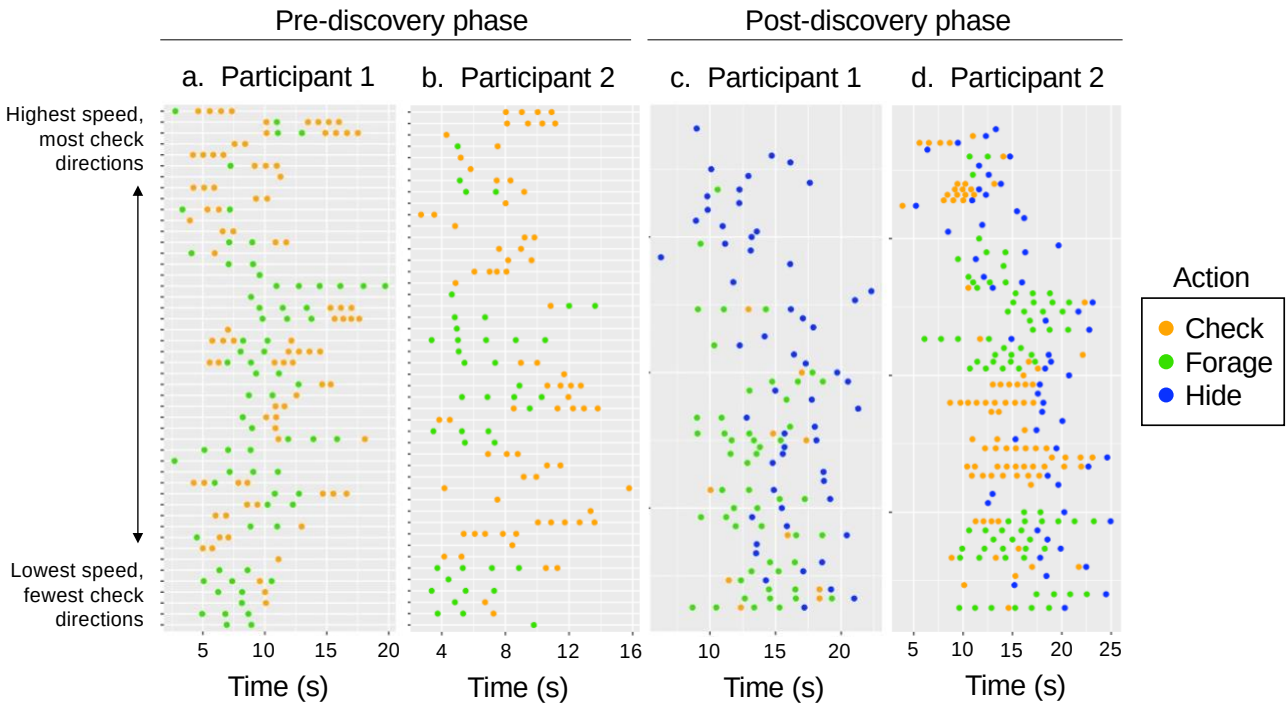


Figure 10. **Individuals had distinct behavioural patterns.** Raster plots displaying the choice data of two example participants (IDs 10 and 15) who adopted different behavioural strategies. Plots are separated into pre-discovery phase (A, B) and post-discovery phase (C, D). Y-axes index epochs by increasing threat/difficulty, starting with slowest speed/1 check direction, then increasing to slowest speed/2 check directions, and so on up to fastest speed/6 check directions. Both participants checked sequentially when there were more directions to check in the environment (A, B), and both foraged less at higher threat levels. In the pre-discovery phase (A, B), participant 10 (A) often interspersed checking and foraging, while participant 15 (B) had more epochs where they only performed one action and often did not forage at all. In the post-discovery phase (C, D), participant 10 (C) rarely checked and tended to hide after just a few foraging actions, while in contrast participant 15 (D) foraged more often at higher threat levels and frequently checked on the predator before hiding.

2.4.1. Pre-Discovery Phase

Analyses of pre-discovery phase data allowed us to assess how sensitive participants were to behaviourally relevant information during the time when they were under potential—but not confirmed—threat. Participants' choices were influenced by contextual factors. First, participants were influenced by predator speed: they began checking the environment sooner in epochs with a fast predator than in epochs with a slow predator (two-tailed independent samples t-test of average check times, $t(404.10)=11.69$, $p < 0.001$; Fig. 11A; see Methods for details about epochs). In addition, participants were sensitive to reward magnitude: they were less vigilant when presented with a high reward than when the reward was among the lowest third of rewards (two-tailed independent samples t-test of average number of checks in each condition, $t(541.01)=9.68$, $p < 0.001$; Fig. 11D). Participants also showed sensitivity to the number of directions for checking in the environment by performing more checks in blocks where the environment had six areas where a predator could be hidden ($M = 52.52 \pm 20.43$ checks across epochs) than when the environment had only one area where a predator could hide ($M = 17.33 \pm 5.61$ checks across epochs; two-tailed independent samples t-test, $t(343.9)=28.77$, $p < 0.001$; not shown in Fig. 11 because it is unrelated to selected behavioural measures which are the focus of Fig. 11). Further, participants were more likely to conduct a full scan of the environment than to check only a single direction (two-tailed independent samples t-test of average full scan frequencies, $t(367.60)=26.33$, $p < 0.001$; Fig. 11G), and shortly after conducting a full scan without discovering a predator—confirming that no threat was present—participants checked at a lower rate ($t(510.73) = 40.45$, $p < 0.001$; Fig. 11J).

We fit a computational model to gain insight into both observed and latent variables affecting behaviour. The pre-discovery phase model included four variables: *reward*, the amount

of reward available; *predator probability*, the probability that there was a hidden predator in the surrounding area; *time pressure*, the amount of time since the participant had last been certain that there was no predator present; and *continue checking*, representing the tendency for participants to repeat checks until they had scanned the entire surrounding area (see Methods for details of how variables were computed). A graphical illustration of how the values of these variables changed across an example epoch is shown in Fig. 9A. To validate this model, we conducted simulations (see Methods).

In one simulation (N=300), we used exact parameters fit to real participants' data to compute decisions. Simulated data (Fig. 11B, E, H, K) was then compared to real data (Fig. 11A, D, G, J) on key behavioural measures selected for their ability to demonstrate the use of model parameters. In Figure 11, each row shows results from a behavioural measure relevant to a parameter from the pre-discovery phase model. For example, panels J and K explore whether participants considered *time pressure* by plotting their check rate directly after a completed scan of the environment; since *time pressure* was reduced to zero after a completed series of checks, the decrease in check rate after a completed series of checks suggests that *time pressure* was indeed a factor in participants' decision-making. Results showed that simulated data produced behavioural measures resembling those from real data, suggesting that participants indeed used factors such as our model variables to guide their behaviour.

To further investigate the involvement of each parameter in the selected behaviours (i.e., the behaviours plotted in Fig. 11A, D, G, J), we conducted another simulation (N=1000) using weights drawn from the range of parameters fit to real data. For each behaviour of interest, we extracted a relevant binomial measure from the simulated data and performed logistic regression to examine how model parameters influenced its odds of occurring (see Methods for modelling

details). Results showed that behavioural measures were often influenced by a mix of parameters, not just one (Fig. 11C, F, I, L). For example, the odds of conducting a full scan of the environment instead of a single check—a measure supporting the inclusion of the parameter *continue checking*—was indeed positively associated by the parameter *continue checking* (*M*=1.92, 95% CI [1.33 – 2.49]), but also by *predator probability* (*M* =1.53, 95% CI [1.42 – 1.64]), *reward* (*M*=1.87, 95% CI [1.75 – 1.99]), and *time pressure* (*M* = 0.30, 95% CI [0.15 – 0.45]; Fig. 11I). Overall, simulation results validate the use of the pre-discovery phase model for characterising information used to make decisions about foraging and checking.

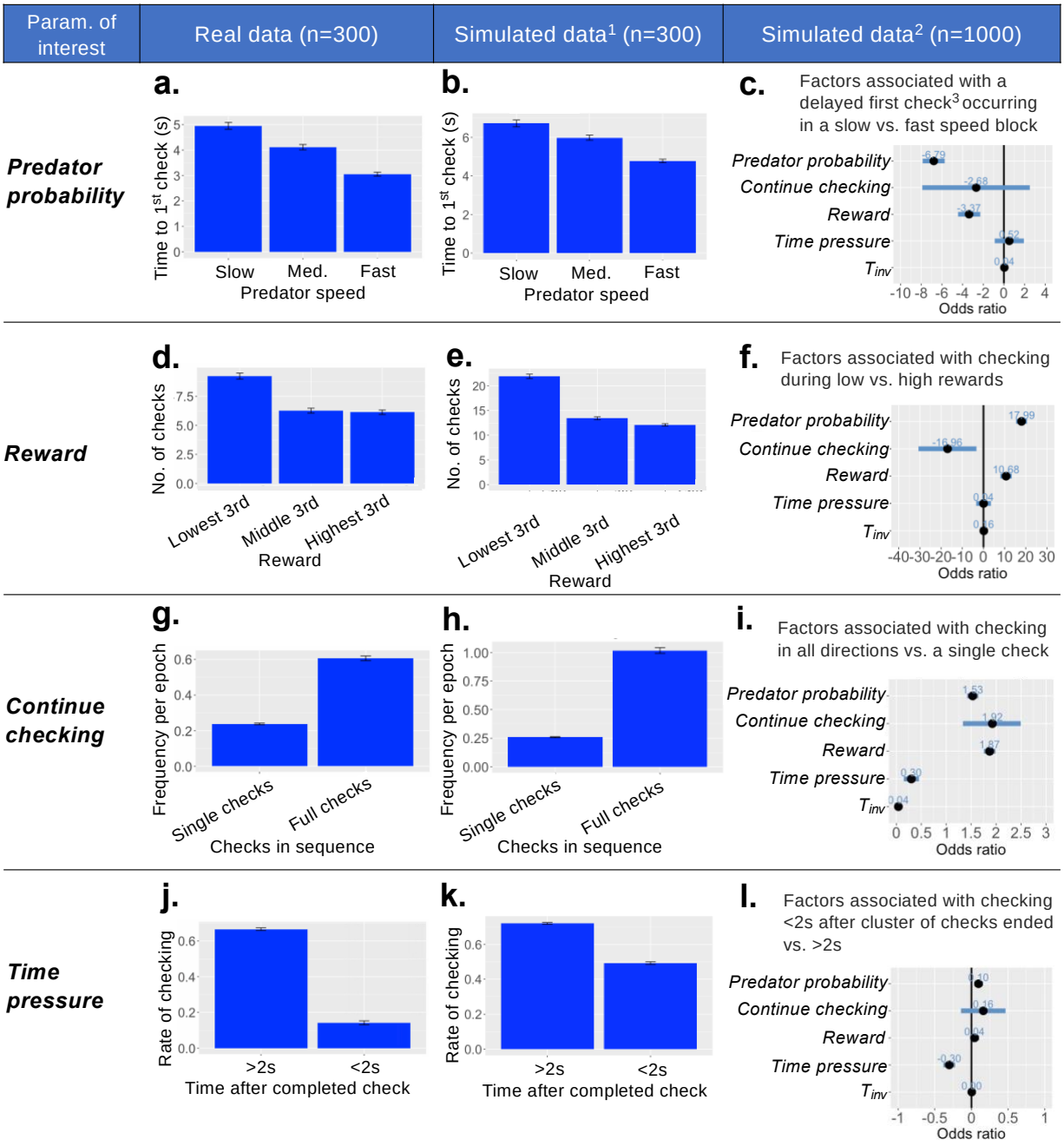


Figure 11. **Pre-discovery phase: Measures of real and simulated behaviour.** Participants' checking behaviour was influenced by contextual variables including A) predator speed, D) reward, G) the need to scan multiple directions in the environment, and J) having recently completed checking (all $p < 0.001$). To support the inclusion of each pre-discovery model parameter, measures of real participants' behaviour **(Left column: A, D, G, J)** were compared

with measures of simulated behaviour (N=300; **middle column: B, E, H, K)**. **Right column: C, F, I, L)** Group-level estimates of how model variables affected the odds of behaviours in each test category (listed first in plot titles) in a simulation (N=1000). Estimates shown with two-tailed 95% Bayesian credible intervals; significance indicated by credible intervals not including 1. **A, B, C)** Real and simulated participants started checking sooner during an epoch with fast predator speed, suggesting they used *predator probability* in the decision to check (A, B). In a large simulation (C), both *predator probability* and *reward* significantly attenuated the tendency to delay checking in an epoch with a slow predator (relative to a fast predator epoch; both 95% CI excluding 1). **D, E, F)** Real and simulated participants checked more when offered lower rewards, suggesting they considered *reward* (D, E). In a large simulation (F), *reward* and *predator probability* were positively associated with the odds of checking during lower rewards, while *continue checking* was negatively associated (all 95% CI excluding 1). **G, H, I)** Real and simulated participants more frequently checked the entire surrounding area than conducted single checks, suggesting participants considered the *continue checking* variable (G, H). In a large simulation (I), *predator probability*, *continue checking*, and *reward* were all positively associated with the odds of conducting a full scan instead of a single check, while *time pressure* was negatively associated (all 95% CI excluding 1). **J, K, L)** Real and simulated participants checked at a higher rate when more than 2s had elapsed since their last full scan of the environment, suggesting they considered *time pressure* (a variable reduced to zero after a full scan) (J, K). In a large simulation (I), *predator probability*, *reward*, and *time pressure* were all negatively associated with the odds of checking when <2s had elapsed. [1]Simulations created by using exact fitted parameters from real data as weights for simulated parameters. [2]Simulations created by drawing weights from the range of fitted parameters in the real data. [3]A first check

was considered "delayed" if it occurred after the minimum delay (1s) plus 50% of the predator's total journey time (i.e., the time when theoretically the predator could be halfway to the centre of the screen).

We also fit this model to participants' pre-discovery phase behaviour. We found that checking was positively associated with both *time pressure* (M=0.23, 95% CI [0.23 – 0.24]; Fig. 12A) and *continue checking* (mean=0.33, 95% CI [0.32 - 0.34]; Fig. 12A), showing that participants considered how recently they had checked and whether a scan of the environment was incomplete when deciding whether to check. In addition, checking was inversely with *reward* (mean=-0.40, 95% CI [-0.41 - -0.39]; Fig. 12A), demonstrating that participants' foraging behaviour was sensitive to available reward. However, surprisingly, the probability that a hidden predator had entered the environment (*predator probability)* contributed negatively to the decision to check (mean=-0.03, 95% CI [-0.04 - -0.02]; Fig. 12A). This suggests that participants tended to rely more on their updated experience (indexed as *time pressure)* than on a heuristic (indexed as *predator probability)* as an indicator of when to be vigilant.

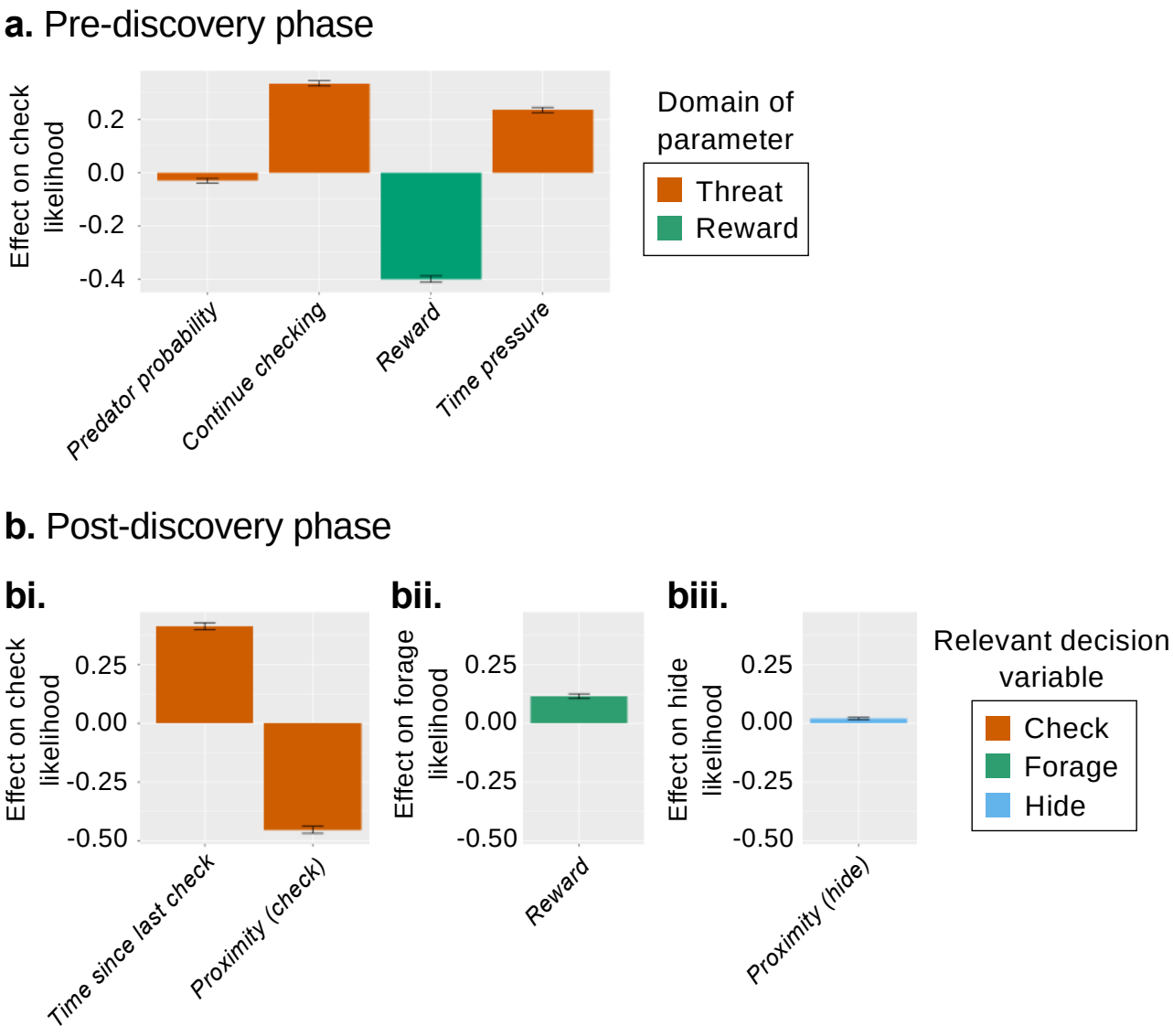


Figure 12. **Model parameters fit to real participants' data.** Hierarchical logistic regressions were performed to estimate the effects of model parameters on the action for which they were used to calculate the decision variable (DV, or action utility; see decision variable calculations in Section 2.3.6). Plots show group-level coefficient estimates fit to choice data from the pre- (A) and post-discovery (B) phase. A) Predictors in this regression model were the variables used to calculate the DV for checking in the pre-discovery phase (see Eq. 5). Predictors *continue checking* and *time pressure* were positively associated with checking, while *reward* and *predator*

probability were negatively associated (i.e., linked with foraging; all 95% CI excluding zero). Bi, Bii, and Biii) Each panel shows results from a regression model with predictors selected from the variables used to calculate the DV for checking, foraging, and hiding, respectively (see Table 2). Bi) Predictor *time since last check* was positively associated with checking (instead of forage or hide), while the opposite was true of *proximity_check* (both 95% CI excluding zero). Bii) Predictor *reward* was positively associated with foraging instead of checking or hiding (95% CI [0.10 – 0.13]). Biii) Predictor *proximity_hide* was positively associated with hiding instead of foraging or checking (95% CI [0.016 – 0.025]). Error bars show Bayesian 95% credible intervals (two-tailed) and significance is shown by credible intervals not including zero.

2.4.2. Post-Discovery Phase

We analysed the post-discovery phase to assess how sensitive participants were to different types of behaviourally relevant information after they had discovered a threat. At a glance, behavioural data demonstrated strategic differences between individuals; for example, some participants focused on foraging during the post-discovery phase (Fig. 10C) while others tended to repeatedly check on the predator's location until hiding (Fig. 10D). Across participants, tests of behavioural measures showed that behaviour was influenced by contextual variables in this phase. First, participants were sensitive to threat level represented by predator speed: they tended to forage more during slow predator blocks (M = 3.19 ± 1.19 forages per epoch) than fast predator blocks (M = 0.95 ± 0.49 forages per epoch; $t(392.61) = 29.88$, $p < 0.001$), and hid sooner in fast predator blocks (M = 6.40s ± 1.61s until predator arrival) than slow predator blocks (M = 3.33s ± 0.63s until predator arrival; $t(383.90)=30.57$, $p < 0.001$; not shown in Fig. 13 because unrelated to the selected behavioural measures featured in that figure). Check behaviour was also sensitive to

threat level. Participants' rate of checking was affected by how close the predator was (independent samples t-test of average checking rates in the most distal versus proximal third of the predator journey, $t(336.06) = 3.67$, $p < 0.001$; Fig. 13A), and participants checked less frequently when they had recently checked within the last 3s ($t(553.94) = 23.12$, $p < 0.001$; Fig. 13D). In addition, higher rewards encouraged foraging: participants foraged more in response to the highest third of rewards relative to the lowest third of rewards ($t(579.29) = 5.11$, $p < 0.001$; Fig. 13G). Finally, a histogram of hiding times suggests that participants tended not to wait until the last second before predator arrival before escaping to the safe space; the most frequent time for hiding was between 3-4s before predator arrival (Fig. 13J).

We fit a computational model to gain insight into both observed and latent variables affecting decisions to forage, check, or hide. As parameters, we included *reward*, *time since last check*, and *proximity* (used to calculate the utility of both check and hide actions; *proximity_check* and *proximity_hide*) (see Methods for details; also see Fig. 9B for an illustration of how values of model variables changed in response to epoch circumstances and participant actions). To validate this model, we again conducted simulations (see Methods).

In one simulation (N=300), each artificial participant used exact parameter weights fit to a real participant's data. Simulated data (Fig. 13B, E, H, K) was then compared to real data (Fig. 13A, D, G, J) on key behavioural measures selected for their ability to demonstrate the use of model parameters. In Figure 13, each row shows results from a behavioural measure relevant to a parameter from the post-discovery phase model. For example, panels D and E explore whether participants considered *time since last check* by plotting their check rate <3s after a previous check; since the variable *time since last check* was reduced to zero after each check, the decrease in check rate 3s after a check suggests that participants indeed considered a factor similar to *time*

since last check when deciding whether to check again. Results showed that simulated data produced behavioural measures resembling those from real data (Fig. 13), suggesting that participants used factors such as those in our model to guide their behaviour in the post-discovery phase.

In a second simulation (N=1000), we took a closer look at how each post-discovery model variable influenced the selected behaviours (i.e., the behaviours depicted in Fig. 13A, D, G, J). To make decisions, this simulation used weights drawn from the range of parameters fit to real participants' data. For each behaviour of interest, we then extracted a relevant binomial measure from the simulated data and performed logistic regression to test how model parameters influenced its odds of occurring (see Methods for modelling details). Results showed that behavioural measures were often influenced by multiple parameters, not just one (Fig. 13C, F, I, L). For example, checking less then 3s after a previous check (a behavioural measure selected for its relevance to the parameter *time since last check*) was indeed inversely related with *time since last check* (*M*=-0.26, 95% CI [-0.49 – -0.02]; Fig. 13F), showing that simulated checks were more likely to reoccur after >3s had elapsed. This odds of this behaviour were also negatively associated with *proximity_check* (*M* =-0.32, 95% CI [-0.54 – -0.10]) and *reward* (*M*=-0.48, 95% CI [-0.78 – -0.19]), however, demonstrating that the timing of simulated checks was sensitive to predator proximity and reward levels as well. It is notable that not all simulations returned the predicted results; for example, model predictors were not significantly related to hiding. This suggests that our simulation did not optimally capture typical behaviour in the post-discovery phase. With respect to hiding, one reason for this could be that the simulation used a softmax function to probabilistically select between forage, check, and hide at each timestep. This means that there was a possibility of hiding even immediately after discovering a distant

predator. In contrast, real participants may not have considered hiding as an option until later in the epoch, when the predator was close. Thus our simulations are too simplistic to consider the entire range of factors considered by real participants. However, our model does capture several types of information used by participants, and thus can be of use in approximating participants' decision-making processes and studying individual differences in task performance.

After validation we fit this model to real participants' post-discovery phase behaviour. Participants' foraging and hiding behaviour was influenced by model variables as expected: greater reward was positively associated with foraging (mean=0.11, 95% CI [0.10 – 0.13]; Fig. 12Bii), and predator proximity (weighted for hiding, modelled as *proximity_hide)* was positively associated with hiding (mean=0.02, 95% CI [0.016 – 0.025]; Fig. 12Biii). Checking was influenced by two factors. We found that the time since the predator had been last seen (indexed as *time since last check*) was positively associated with checking (mean=0.41, 95% CI [0.40 – 0.43]; Fig. 12Bi). This suggests that checking was driven by the feeling of not having seen the predator's location for some time, which potentially created uncertainty about one's current level of danger. In contrast, predator proximity (weighted for checking, modelled as *proximity_check)* had a negative relationship with checking (mean=-0.45, 95% CI [-0.47 - -0.44]; Fig. 12Bi), indicating that close predator proximity was associated more with decisions to forage and hide than with checking. This suggests that, like in the discovery phase, participants relied on their updated experience of threat level (indexed as *time pressure* in the pre-discovery phase and as *time since last check* in the post-discovery phase) to decide when to check instead of on a heuristic (indexed as *predator probability* in the pre-discovery phase and *proximity* in the post-discovery phase; see Methods for details of how variables were calculated). Correlations among fitted parameters, behavioural measures, and debrief questions further revealed that low values

for *proximity_check* were associated with fewer check actions in the last third of the post-discovery phase (r = 0.48, p < 0.001), an overall greater number of foraging actions than checking actions (r = -0.26, p < 0.001), and the tendency to hide earlier than necessary due to stress (r = -0.14, p < 0.05) (Tables A6 and A8). This suggests that during proximal threat participants tended to adopt a strategy of conducting last-minute foraging and then hiding.

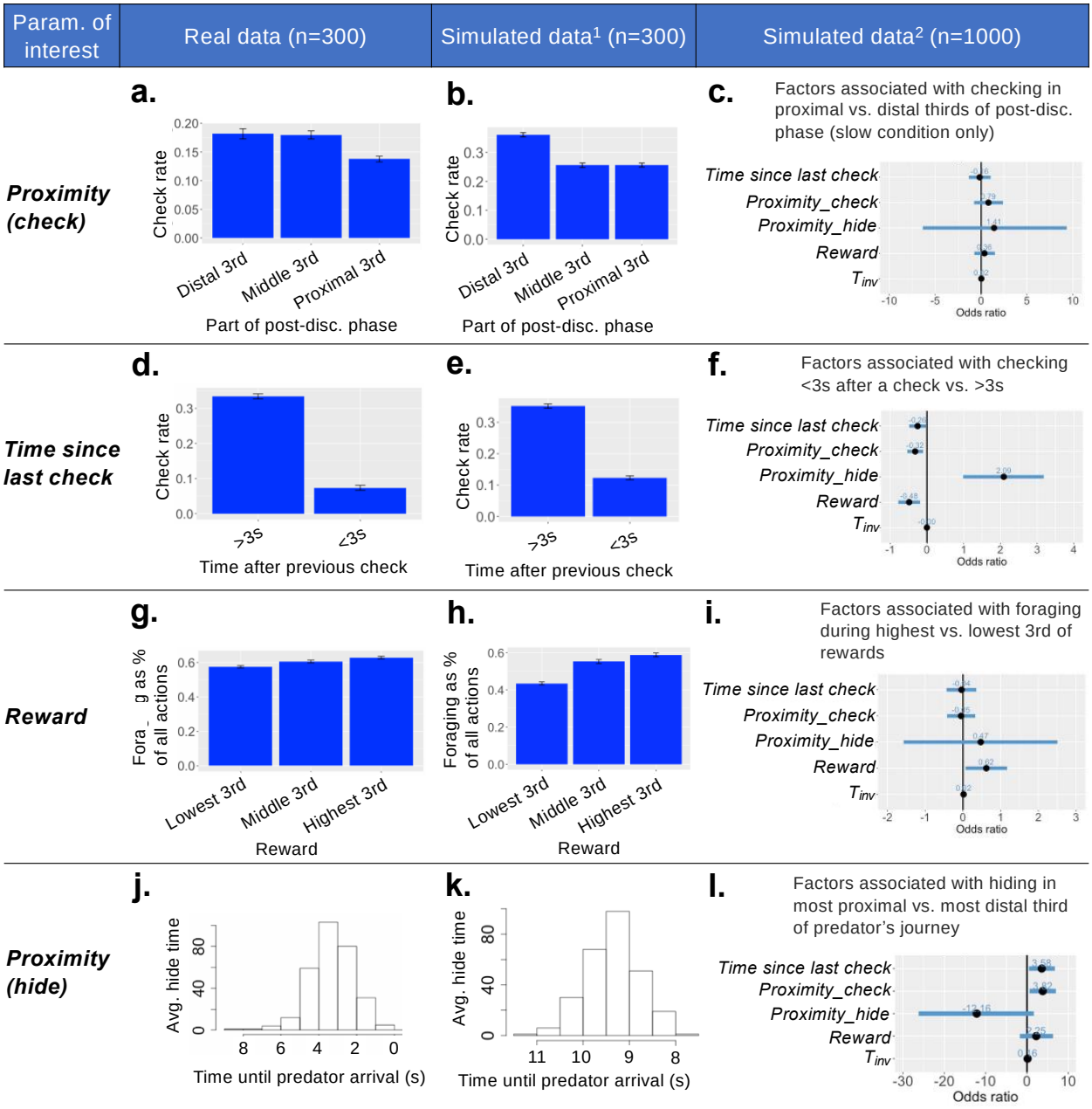


Figure 13. **Post-discovery phase: Measures of real and simulated behaviour.** Participants' behaviour was influenced by contextual variables. Vigilance was sensitive to A) threat proximity and D) having checked recently (both $p < 0.001$). Foraging was sensitive to G) rewards ($p < 0.001$). Participants did not wait until the last second to hide (J). To support the inclusion of each post-discovery model parameter, measures of real participants' behaviour **(Left column: A, D,**

G, J) were compared with measures of simulated behaviour (N=300; **middle column: B, E, H, K)**. **Right column: C, F, I, L)** Group-level estimates of how model variables affected the odds of behaviours in each test category (listed first in plot titles) in a simulation (N=1000). Estimates shown with two-tailed 95% Bayesian credible intervals; significance indicated by credible intervals not including 1. **A, B, C)** Real and simulated participants checked at a lower rate in the most proximal third of the post-discovery phase than the most distal third (A, B). This suggests the use of *proximity* in the decision to check and shows that participants typically preferred to do last-minute foraging or hiding when the predator was close. However, *proximity_check* did not significantly affect the odds of checking in the most proximal third of the post-discovery phase (C). **D, E, F)** Real and simulated participants checked at a lower rate when they had checked in the past 3s, suggesting the use of *time since last check* as a factor in deciding to check (D, E). Indeed, *time since last check* was associated with a decrease in the odds of checking again within 3s in a large simulation (F; 95% CI excluding 1). **G, H, I)** Real and simulated participants foraged more as a percentage of all actions when offered higher rewards, suggesting the use of *reward* in choosing to forage (G, H). In a large simulation (I), the odds of foraging during high rewards were significantly decreased by *time since last check* and *proximity_check* (both 95% CI excluding 1) but unaffected by *reward*. **J, K, L)** Real and simulated participants typically did not wait until the last second to hide (J, K). However, model predictors did not affect the likelihood of hiding in a large-scale simulation (L). [1]Simulations created by using exact fitted parameters from real data as weights for simulated parameters. [2]Simulations created by drawing weights from the range of fitted parameters in the real data.

2.4.3. Psychiatric Measures, Post-Block Ratings, and Debrief Questionnaires

Psychiatric questionnaires showed a range of scores, both clinically significant and sub-clinical (see Methods for questionnaire details). The average STICSA Trait scale score was 35.14 ± 10.00, with 20% of participants at or above the clinical threshold of 43 (Dam et al., 2013). The average difference between STICSA Trait and State Somatic subscales for participants who completed the questionnaires after the task (see Methods for details) was 0.32 ± 4.39, average score on the apathy and anhedonia combined scale was 8.00 ± 7.99, and average score on the OCI-R Checking subscale was 4.63 ± 3.23; see Methods for details on psychiatric measures).

Responses to post-block questions asking participants to rate their perception of the environment (see Methods for details; Fig. 8) showed that differences in block conditions changed participants' perceptions of task difficulty. Participants found that both faster predators and greater directions for the predator to hide made it more difficult to perform the task effectively, as their average rating for the question "In the last round, how difficult was it to balance between eating food and checking for predators?" was higher for fast predator blocks (all ratings on a scale of 0-100; M = 56.07 ± 16.41) than slow predator blocks (M = 27.60 ± 15.60), and higher for blocks with 5 or 6 areas for the predator to hide (M = 46.51 ± 16.16) than blocks with only 1 or 2 areas (M = 34.67 ± 16.18). In addition, participants found blocks with fast predators and blocks with more areas for a predator to hide more stressful; they rated "How stressful was the last round?" higher for fast predator blocks (M = 55.50 ± 19.92) than slow predator blocks (M = 29.16 ± 18.11; $t(592.67) = 16.95$, $p < 0.001$), and higher for blocks with 5 or 6 areas for the predator to hide (M = 45.15 ± 18.46) than blocks with only 1 or 2 areas (M = 37.39 ± 18.60; $t(596.93) = 5.12$, $p < 0.001$). However, participants also found fast predator blocks more exciting, as they rated "How exciting was the last round?" higher for fast predator blocks (M = 60.49 ± 18.56) than slow predator blocks (M = 49.86 ± 21.91; $t(578.48) = -6.39$, $p < 0.001$),

and overall they tended to interpret their perception of fast blocks positively, as the average rating of excitement for fast blocks was higher than stress ($t(593.63) = 3.16$, $p < 0.01$). This was despite their perception that less food was available in fast blocks ($t(593.79) = 4.78$, $p < 0.001$). The number of areas for the predator to hide did not affect perception of food availability or perception of excitement, suggesting that predator speed posed a greater perceived challenge than the number of areas a predator could hide.

Debrief questionnaires on a scale of 0 ('None of the time') to 6 ('All of the time') indicated that participants thought they spent the most time foraging ($M = 4.59 \pm 0.97$), followed by checking for a predator ($M = 3.56 \pm 1.34$), and the least time hiding ($M = 3.00 \pm 1.32$). Results from the 28 debrief questions are presented below. Psychiatric measures, post-block ratings, debrief questionnaires, behaviour, and fitted parameters were linked using Pearson's r correlations (results detailed in Tables A4-A13).

2.4.4. Hypothesis 1: Anxiety was Linked with Greater Sensitivity to Threat-Related Factors and Lower Sensitivity to Reward

Our first hypothesis was that participants scoring highly on measures of anxiety would demonstrate a heightened and persistent state of defence by behaving with greater sensitivity to threat-related task factors (Hypothesis 1A) and less sensitivity to reward-related factors (Hypothesis 1B). We found evidence for this by examining relationships among behavioural measures, questionnaire responses, and model parameters.

2.4.4.1. Hypothesis 1A. First, participants scoring highly on the STICSA Trait scale were less reassured about the absence of threat by having recently checked, as they showed a higher

rate of checking during the pre-discovery phase when they had checked in the past 2s ($r = 0.15$, $p < 0.05$). Moreover, participants were aware of this as they reported that they often "checked again for a predator even though I had just finished checking in all directions" ($r = 0.41$, $p < 0.01$). This indicates the cognizant maintenance of a heightened state of vigilance that is not mitigated by gaining information about threat. Further, high trait anxiety participants rather paradoxically tended to report that "I tried not to check on the predator when it was very close because it felt threatening" ($r = 0.35$, $p < 0.05$. They also reported hiding to avoid threat: they indicated that they often "hid for longer than necessary because I was afraid to leave the hiding place" ($r = 0.23$, $p < 0.001$) and "hid earlier than necessary because I was stressed" ($r = 0.33$, $p < 0.001$). Together, these results indicate that anxious participants scanned the environment more frequently when they didn't know the location of a threat, but after seeing one they avoided exposure to it by checking less and hiding for longer.

In addition, post-block ratings showed that high trait anxiety participants found the task more stressful on average ($r = 0.16$, $p < 0.01$), during fast predator blocks ($r = 0.18$, $p < 0.01$), and during blocks with both a high and low number of directions in which the predator could hide ($r = 0.16$ and $r = 0.15$ respectively, both $p < 0.01$). These participants were also more likely to interpret their arousal as stress rather than excitement ($r = 0.13$, $p < 0.05$), and more likely to report that it was hard to focus on gathering food in a block with a fast predator ($r = 0.33$, $p < 0.001$). Similarly, participants with high somatic anxiety after task performance reported being challenged by the task by finding it more difficult on average to balance foraging and vigilance, $r = -0.14$, $p < 0.05$. These findings suggest that participants with high anxiety, whether trait or somatic, experienced more stress during the task which caused them to perceive the task as more challenging.

2.4.4.2. Hypothesis 1B. Participants with high anxiety showed decreased appetitive behaviour in response to increased threat. Increased predator speed was associated with less foraging among those scoring highly on somatic anxiety after task performance, as they foraged at a lower rate during fast predator blocks than slow predator blocks in the pre-discovery phase ($r = 0.13$, $p < 0.05$). Debrief questions indicated that predatory threat interfered with the ability to gather food in participants with high trait anxiety: these participants reported that "it was hard to focus on gathering food in a block with a fast predator" ($r = 0.33$, $p < 0.001$), they often "didn't try hard to gain more lives" because a round was too stressful ($r = 0.19$, $p < 0.01$), and they "only dove for food when there was no predator in the area" ($r = 0.15$, $p < 0.05$).

2.4.5. Hypothesis 2: Apathy and Anhedonia were Associated with Lower Sensitivity to Reward

Our second hypothesis was that participants scoring highly on measures of apathy and anhedonia would show lower appetitive motivation through insensitivity to reward-related factors. We found evidence for this by linking psychiatric measures with behaviour: the foraging behaviour of participants scoring highly on the apathy/anhedonia average measure was less influenced by reward, as they had lower values fit to the *reward* parameter in the pre-discovery phase ($r = -0.12$, $p < 0.05$). This occurred despite apathetic/anhedonic participants reporting that they did not feel more nervous after seeing a predator ($r = -0.15$, $p < 0.05$) and was also associated with participants feeling that the task was less exciting on average ($r = -0.18$, $p < 0.01$). This suggests that although apathetic/anhedonic participants were not distracted by excitement or nervousness imposed by threat, they were still unmotivated to pursue rewards.

We further analysed apathetic/anhedonic participants' vigilance behaviour and found that they were less influenced by threat. These participants spent less time hiding from a predator, as they returned from hiding and performed the first action in an epoch sooner on average (r = -0.14, $p < 0.05$) and reported spending little of their time hiding from predators (r = 0.32, $p < 0.05$). Further, their fitted parameters showed they were less likely to perform a whole scan of the environment, as they had lower values for the fitted parameter *continue checking* (r = -0.16, $p < 0.01$).

2.4.6. Hypothesis 3: Obsessive-Compulsive Symptoms are Associated with Less Frequent but Prolonged Checking

Our third hypothesis was that participants scoring highly on the OCI-R checking subscale would exhibit prolonged checking accompanied by a strategic avoidance of threat, which would be shown through less frequent (Hypothesis 1A) but more exhaustive searches of the environment (Hypothesis 1B) during the pre-discovery phase.

2.4.6.1. Hypothesis 3A. We found evidence from questionnaire and behavioural data that participants scoring highly on the OCI-R Checking subscale performed strategic avoidance of threat. These participants waited longer to begin checking in the pre-discovery phase ($r = 0.18$, $p < 0.01$) and tended to report during debrief that they avoided checking for a predator because they were afraid to see one ($r = 0.23$, $p < 0.01$). Although these participants did not check more or less overall, they foraged more in fast predator epochs than in slow predator epochs ($r = -0.14$, $p < 0.05$) even though they were more likely to rate fast epochs as stressful than slow epochs ($r = 0.16$, $p < 0.05$), suggesting a counterintuitive focus on appetitive behaviour during

high-threat environments. In the post-discovery phase, fitted model parameters showed that the hiding behaviour of participants with high OCD checking subscale scores was more influenced by predator proximity, as they had higher values fit to *proximity_hide* ($r = 0.25$, $p < 0.001$); and further, on the debrief questionnaire they tended to report hiding earlier than necessary because they felt stressed ($r = 0.27$, $p < 0.001$). Overall these results indicate strategic avoidance of threat in the pre-discovery phase through increased appetitive behaviour during perceived stressful situations, and increased threat evasion in the post-discovery phase through earlier hiding.

2.4.6.2. Hypothesis 3B. We did not find behavioural evidence that participants scoring highly on the OCI-R Checking subscale checked more thoroughly by performing more full checks of the environment. However, their responses on post-block ratings suggested that they found checking more areas for a predator to be a more arduous task, as they tended to report that blocks where there were more directions a predator could be hidden were more stressful ($r = 0.14$, $p < 0.05$).

2.5. Discussion

Switching between vigilance and foraging is exhibited across species and is common in daily human life, but nonetheless varies considerably between individuals. Understanding the mechanisms underlying this process and its idiosyncrasies may be particularly relevant for the study of mental illness given the prominence of disordered reward- and threat-oriented attention in many psychiatric symptoms. Here we investigated this decision-making process by collecting a large online sample of behavioural data using an ecological task. We analysed this data with two aims: first, to examine the types of information used in reorienting between foraging and

vigilance we developed a computational modelling approach and explored its validity with simulation; second, to determine whether clinical measures were associated with distinct behavioural patterns in our dataset we tested correlations among task behaviour and self-report data. Several key findings resulted from each.

Participants' behaviour was influenced by a variety of factors. First, as expected, behaviour was sensitive to readily observed contextual variables (e.g., reward levels, number of directions for checking, and predator speed). In addition, behaviour was influenced by latent variables included in our computational model. As expected, reward level was linked with foraging and proximity was linked with hiding (Fig. 12). However, relationships between threat-related variables and checking behaviour were more complex. Checking was driven by variables that required effortful updating based on experience (i.e., *time pressure*, a pre-discovery phase measure which was recalculated after a participant confirmed there was no predator present; and *time since last check,* a post-discovery phase measure which was updated at every check), but had an inverse relationship with simple estimates of threat based on static task knowledge (i.e., *predator probability* and *proximity*) (Fig. 12). This finding might be interpreted in light of Fanselow and Lester's (1988) theory of the threat imminence continuum. This theory proposes that defensive behaviours can be mapped onto a continuum based on threat proximity, and that the reason for this mapping is that proximal threat greatly constrains the complexity of processing that can be carried out. According to this model, participants' decision-making capacity in our task would be greatly diminished in moments of proximal threat. However, the majority of behaviour in our task occurred under circumstances of distal threat. Before predator discovery, each participant's data set yielded on average 409.02 ± 99.82 actions compared to an average of 128.40 ± 54.52 actions after predator discovery; even after predator discovery, little

data was collected in the final moments before predator arrival (participants tended to hide 3-4s before predator arrival; see Fig. 13J). Thus, it is sensible that participants generally opted for a resource-intensive yet more precise method of estimating threat level across both phases.

Further analyses relating clinical scores with task behaviour and other self-report measures (including questions related to mood, and task experience) suggested that the behavioural dimensions anxiety, apathy, anhedonia, and compulsive checking were associated with distinct response patterns. Self-report data about participants' experiences of the task were particularly useful. For example, responses from highly anxious participants supported the vigilance-avoidance theory of anxiety: they reported that they often "checked again for a predator even though I had just finished checking in all directions" but also "tried not to check on the predator when it was very close because it felt threatening". If replicable, this would indicate that anxious participants displayed heightened attention toward potential threat and sensitivity to threat detection, but subsequently avoided a threat after identifying it. Other behavioural dimensions were also linked with distinct responses: apathy and anhedonia were associated with insensitivity to reward, supported by findings such as having lower values fit to the *reward* parameter in the post-discovery phase. Participants scoring highly on compulsive checking did not check more overall as expected, but did exhibit suboptimal vigilance, as shown by behaviours such as focusing on appetitive behaviour in high threat contexts by foraging more in fast predator epochs.

It is important to note the limitations of this study. First, it does not provide evidence that the observed relationships between task and clinical measures exist in the general population. Even though our sample size was large (N=300), we conducted analyses in a largely exploratory manner, without preregistering hypotheses or attempting to replicate results in an independent

sample. Behavioural research suffers from replication challenges, and strategies such as preregistration or the split-sample approach function to limit false discoveries and can have a significant impact on the conclusions (M. L. Anderson & Magruder, 2017; Fafchamps & Labonne, 2017). In addition, despite conducting many tests, we did not conduct additional corrections for multiple comparisons. Thus, we cannot say, for example, that our results showing significant relationships between task measures and anxiety add to our general knowledge about cognitive mechanisms and behaviours in anxious individuals. However, the results presented here are useful because they demonstrate that this task has potential to detect behaviours characteristic of various symptoms of mental disorders. Future studies—including the next chapter of this thesis—may seek to use this task as a tool for probing idiosyncratic and atypical cognitive mechanisms related to reorienting between foraging and vigilance. Developing and validating new tools for clinically relevant research are important for better understanding of cognition in health and disease.

2.6. Summary

This study developed, validated, and explored the clinical potential of an ecological task and computational model. The task was designed to address a gap in the foraging literature: cognitive mechanisms associated with foraging under threat. Although foraging under risk of predatory threat is a natural behaviour found across species, it is not well understood how decision-makers flexibly trade off between pursuing rewards and checking for predators. Understanding this decision-making process may also be clinically relevant, because changes in attending to rewarding versus threatening stimuli is a feature of many psychiatric symptoms including anxiety, compulsive checking, apathy, and anhedonia. It is thought that an ecological task may

be particularly suited to exploring these questions. According to the emerging field of computational ethology, it is necessary to study naturalistic, unrestrained behaviour to advance our understanding of cognition relevant to daily life; further, tasks allowing for unrestrained behaviour may be uniquely positioned to produce clinical insights by probing cognitive mechanisms associated with mental illness. In this experiment, we asked 300 participants to play an online task in which they flexibly switched between foraging for food rewards and monitoring and evading predatory threat. We used a computational model to explore the types of information people used to make decisions about when to forage, check, and hide, and we validated this model by simulating data and comparing simulated with real behaviour. Finally, we showed that this task has potential to produce clinical insights by testing links between task measures and self-report responses (including psychiatric questionnaires). In summary, we have produced a task and model that have potential to be useful tools in future clinical studies.

3. Chapter: Emotions and individual differences shape foraging under threat

3.1. Abstract

Animals and humans in natural environments often balance their time between vigilance and foraging. We investigated individual differences in this behaviour and linked them to mood ratings and psychiatric symptoms in a large online sample (discovery: N=374, replication: N=702). Participants completed a novel decision-making task in which they gathered rewards while monitoring and evading predatory threats. Mood was related to environmental factors and showed a homeostatic relationship with task behaviour. Compulsive checking was linked with increased, sub-optimal vigilance, while anxiety was associated with decreased vigilance and worry. Apathy was related to reduced vigilance and frequent foraging, potentially reflecting reluctance to switch behaviours. Anhedonia was linked with a reduction in self-reported task engagement. In sum, behavioural traits associated with psychological illness corresponded to distinct, replicable patterns of behaviour in an ecological context. This task is a good candidate for inclusion in future clinical studies involving threat- and reward-oriented behaviour.

3.2. Introduction

In naturalistic environments, animals often must balance their time between threats and rewards to survive. Humans also rely on this type of decision-making in contemporary life: for example, cooking may require monitoring a hot burner while preparing a delicious meal. However, people's responses to appetitive and threatening behavioural motivators are highly individualistic and our decisions depend on circumstances, personal traits, and current mood. Thus, examining people's decisions to switch between foraging and vigilance may help us

understand not only a fundamental decision-making process that is ubiquitous across species but also how it is shaped by individual human traits and emotions. As discussed in previous chapters, switching between reward- and threat-oriented behaviour is an ability that is often impaired in psychiatric illnesses characterised by disordered responses to appetitive and/or threatening stimuli, including generalised anxiety disorder, obsessive compulsive disorder (OCD), and conditions involving apathy and anhedonia. In this study we analysed distinct, transdiagnostic behavioural dimensions of these illnesses, including anxiety, compulsive checking, apathy, and anhedonia.

The impact of anxiety on decision-making is not fully understood. Computational methods have characterised anxiety as a tendency toward threat avoidance, threat-related attentional bias, and changes in information sampling (Bishop & Gagne, 2018; Charpentier et al., 2022; Cisler & Koster, 2010; Fan et al., 2022; Hartley & Phelps, 2012; Keogh et al., 2001; Mogg et al., 2000; Rinck et al., 2003). In particular, Pittig and Scherbaum (2020) showed that highly anxious participants avoided aversive stimuli at the cost of high potential rewards, suggesting a weaker impact of rewards on behaviour when competing with threat. However, it is not known how anxiety affects behaviour in the context of predatory threat, when vigilance can reveal danger but also help evade it. Similar knowledge is lacking for symptoms of disordered appetitive behaviour such as apathy and anhedonia. Apathetic individuals show changes in subjective estimates of effort such that they tend to associate small rewards with higher subjective effort costs and forego pursuing them (Bonnelle et al., 2015). However, recent evidence has linked apathy with decision inertia—over-persevering with an action to avoid switching behaviours—suggesting some types of effort are more aversive to apathetic individuals than others (Scholl et al., 2022). In contrast, anhedonia is associated with impairment

in using reward-related information to guide decision-making (Treadway et al., 2012). It is not known how the reward valuation, threat assessment, and effort required to switch between foraging and vigilance will be affected by apathy and anhedonia. With a unique naturalistic paradigm, we observed these behavioural transitions and found that distinct behavioural patterns were associated with dimensions of psychiatric symptoms.

In addition to the influence of individual traits, everyday behaviour is subject to changing moods. There are several ways by which emotion is thought to play an adaptive role in learning and decision-making. First, emotion might improve computational efficiency in complex and changing environments. According to one theory, during a learning process such as reinforcement learning, an emotion comes to reflect the impact of multiple environmental factors (e.g., multiple positive encounters with fruitful foraging patches) and biases reward evaluation and expectation accordingly (Bennett et al., 2022; Eldar et al., 2016, 2021; Emanuel & Eldar, 2023). This causes expectations to reflect cumulative changes in the environment without the need to calculate the impact of each factor individually. Another theory proposes that emotions make action selection more efficient: to narrow the number of future outcomes considered, an emotion may induce a focus on behaviours deemed relevant to one's personal goals (Huys & Renz, 2017). Both strategies represent a way to allocate limited cognitive resources when solving computationally intensive problems. Second, there may be a bidirectional, homeostatic relationship between emotion and behaviour. Evidence suggests that emotional states help to shift priorities between long- and short-term goals adaptively; for example, individuals engage in pleasurable activities during low moods and shift to useful but less pleasant tasks during good moods (Taquet et al., 2016). This balance seems clinically important: history of mental illness has been associated with impaired mood-behaviour homeostasis (Taquet et al., 2020, 2021).

However, mood-behaviour homeostasis on shorter timescales has been underexplored. This study examines moment-to-moment relationships between mood and behaviour to better understand the role of emotion in everyday decision-making.

To investigate links between psychiatric symptoms, mood, and switching between foraging and vigilance, we asked a large online sample of participants to complete the ecological task described in Chapter 1: a task in which they freely and continuously foraged for rewards while monitoring and evading predatory threat (with some task changes; see Fig. 14). From this dataset we obtained behavioural measures capturing how participants differed in strategy and response to task factors: for example, we observed how often individuals foraged under high risk of predation, and conversely how often they were vigilant for threats during a highly rewarding opportunity. We also asked participants to rate their moods at task intervals, collected their responses to validated psychiatric questionnaires measuring anxiety, compulsive checking, apathy, and anhedonia, and asked them to introspect about their own behaviour by self-reporting on their task performance. This rich dataset allowed us to explore associations between many aspects of threat- and reward-related behaviour, mood, and clinical symptoms.

Importantly, we did not screen our participants based on clinical diagnosis or separate participants into patient and control groups: instead, our large sample allowed us to include participants with a wide range of psychiatric symptoms. This allowed us to pursue a transdiagnostic dimensionality-based approach. This approach diverges from the more conventional grouping of individuals based on established symptom descriptions, and instead seeks to characterize behavioural dimensions that are not bound by traditional diagnostic profiles (Cuthbert, 2014; Stephan et al., 2016; Wise et al., 2023). We expected our investigative approach to be useful in distinguishing transdiagnostic behavioural dimensions for three reasons. First, our

ecological task was specifically designed to evoke behaviour associated with fear, anxiety, and rewards. These states and their behavioural manifestations are features of many psychiatric disorders, and comorbidity among anxiety disorders is high (Koyuncu et al., 2019). Additionally, seeking versus avoiding information is known to vary across individuals and relates to psychopathology (Kelly & Sharot, 2021). Thus, a transdiagnostic approach here may provide unique insight into behavioural dimensions related to anxiety and information seeking. Second, we collected questionnaires used in diagnosing a variety of psychiatric conditions. This allowed us to further address issues of comorbidity in psychiatric diagnosis and capture behaviours shared across disorders that are conventionally considered distinct. Third, previous work in this area has shown the usefulness of analysing not only task behaviours but also metacognitive self-report data in understanding decision-making processes (Scholl et al., 2022). Our approach combined behavioural, metacognitive self-report, and questionnaire data with these goals in mind.

We used a split-sample strategy for data collection to allow both data exploration and statistical rigour (Fig. 15) (M. L. Anderson & Magruder, 2017; Fafchamps & Labonne, 2017; Scholl et al., 2022): first we collected an initial ('discovery') sample from which we established hypotheses based on significant results. We pre-registered these hypotheses (OSF link: https://osf.io/3gb8n). Finally, we then collected an independent replication sample to test the preregistered hypotheses. In summary, we formed hypotheses about the association between task-related measures and 1) mood, 2) clinical scores, and 3) gender. First, we hypothesized that ratings of mood and stress would be affected by task factors, and further that we would find evidence of homeostatic relationships between participants' moods and behaviour. If confirmed, this would support an emerging view of emotion as not just reactive but also as a global cognitive state that helps an individual adapt to their circumstances (Huys & Renz, 2017). Second, we

hypothesized that we would be able to predict clinical and demographic measures based on distinct profiles of task-based behaviour and self-reports. We expected that these sub-scales—each expressing a transdiagnostic behavioural dimension—would be characterized by unique metacognitive and task behaviour.

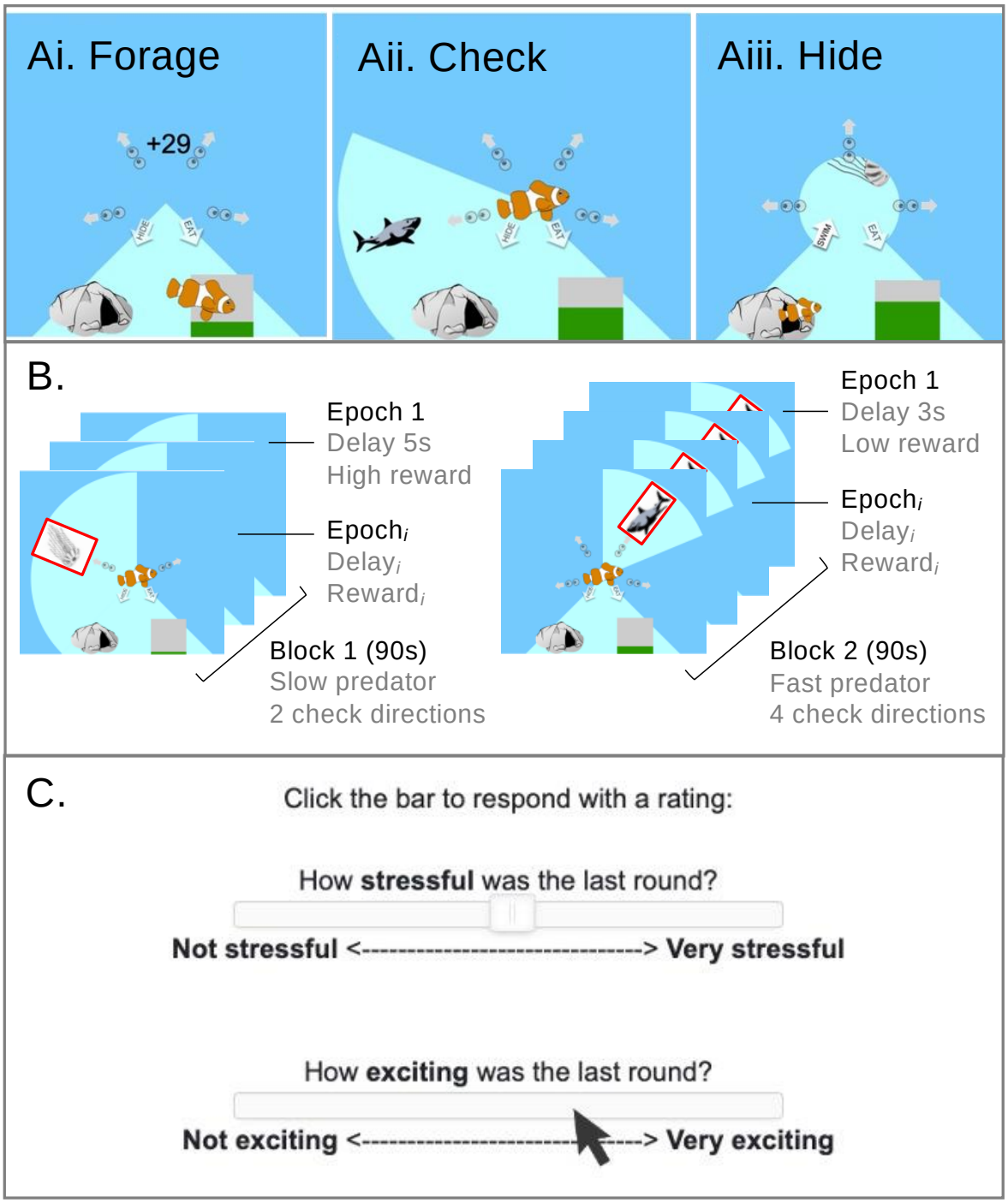


Figure 14. **Experimental task.** At the start of a block the fish begins in the centre position. The surrounding area is divided into four sections that must be searched to determine whether there is a predator in the area. Participants could freely choose the timing and nature of their actions (forage, check, or hide). Ai) When foraging, the fish dives down into the patch of food and the

energy bar increases by the amount of reward gained. Aii) When checking, the fish checks in a particular direction. In this example the fish discovers that there is a predator in the area being checked. Predators appeared at a randomized location and time and moved toward the fish until either catching it or retreating. Aiii) When hiding, the fish dives into a cave and is safe from the predator. It can see the predator reach the screen centre and then retreat, and with another button press the fish can return to the original centre position. B) Task timeline. Blocks lasted 90s and varied by predator threat level (speed) and number of directions for checking. Blocks contained multiple epochs (i.e., time from start of delay to predator arrival), which varied by delay duration and average reward level. C) In between blocks, participants used sliding scales to rate their level of excitement and stress during the previous block.

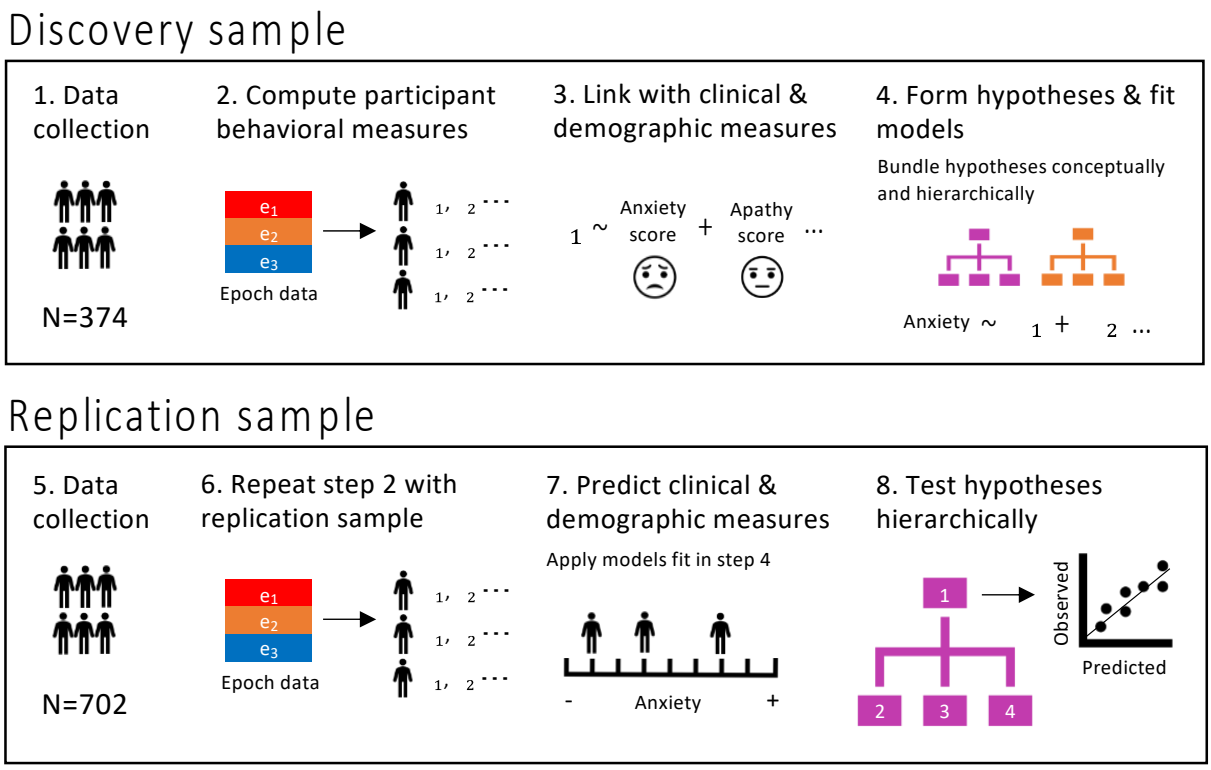


Figure 15. **Principles of individual difference analyses.** 1) We included 374 participants in a discovery sample after data quality checks. 2) To extract behavioural measures for each participant, we used epoched task data to regress environment factors (e.g. reward, predator speed) against task behaviour (e.g. rate of foraging before discovery of the predator). 3) To identify unique links, we entered the behavioural measures computed in step 2 as regressors in models where the independent variables were clinical scores, demographic measures, and mood ratings. 4) To establish hypotheses, we bundled significant findings from step 3 by concept and arranged them hierarchically (from general to increasingly specific predictions). We expressed these hypotheses as regression models (clinical scores as dependent variables) and pre-registered them. 5) To replicate hypothesis tests, we collected an independent sample and included 702 participants after data quality checks. 6) To extract behavioural measures from the replication sample, we repeated step 2 by computing for each participant each behavioural measure that was

part of a hypothesis. 7) To predict clinical scores and demographics for each person, we applied the models fit in step 4 to the replication sample. 8) We tested our hypotheses in a hierarchical manner (starting with the most general hypothesis first and proceeding to test its sub-hypotheses only if the general hypothesis was significant) by testing the goodness of our predictions.

3.3. Methods

All methods were consistent with preregistration with the exception of a variation of statistical testing (described in Section 3.3.6).

3.3.1. Participants

We recruited participants (Discovery sample: N=419 collected, N=374 included, age range 29.8 ± 6.16 years; Replication sample: N=780 collected, N=702 included, age range 35.4 ± 11.0 years; see Table 3 and Table 4 for replication sample descriptive statistics and reported medications respectively) using the online platform Prolific.co (*Prolific*, 2022) that fulfilled inclusion criteria (see below). Web applications JATOS (Lange et al., 2015) and Pavlovia (Peirce et al., 2019) and the jsPsych library (de Leeuw, 2015) were used for experiment hosting and data collection. Ethics approval for the study was given by Oxford University Central University Research Ethics Committee (CUREC) (Ref-numbers: R54722/RE001 and R77387/RE003). All participants provided informed consent before taking part.

Table 3

Replication Sample Demographics and Clinical Scores

Measure	Count (SD or % of N)*	N
Age	35.4 (11.0)	702
Education level		702
GCSE	79 (11.3%)	
A-levels	195 (27.8%)	
Bachelor	304 (43.3%)	
Masters	103 (14.7%)	
Doctorate	21 (2.99%)	
Gender:		702
Female	355 (50.6%)	
Male	337 (48.0%)	
Other	10 (1.42%)	
Clinical anxiety (STICSA)[1]		702
Clinical anxiety probable	188 (26.8%)	
No clinical anxiety	514 (73.2%)	
Psychoactive medication (%yes)[2]		702
FALSE	586 (83.5%)	
TRUE	116 (16.5%)	
Experiment duration (min)	58.4 (12.3)	702
Questionnaire duration (min)	8.84 (4.02)	702
Task Duration (min)	34.9 (6.90)	702
Training Duration (min)	9.84 (4.28)	702

[1]Clinical scores are shown only for the STICSA as it is the only questionnaire for which a validated clinical threshold (>43 for the trait scale; Van Dam et al., 2013) is available. [2]Percentage of participants reporting using any psychoactive medication is shown here; see Table 4 for a more detailed breakdown.

Table 4

Psychoactive Medication Reported in Replication Sample

Medication	Count
ADHD medication	5
Antidepressant	105
Antipsychotic	10
Anxiolytic	23
Epilepsy or Bipolar Disorder	4
Other	10

Note. This table shows a total count of medications reported (it was possible for participants to report more than one medication). Overwhelmingly, antidepressants were the most commonly taken medication. Antidepressants included selective serotonin re-uptake inhibitors (e.g. citalopram, fluoxetine, sertraline), tricyclic antidepressants (e.g. amitriptyline), serotonin-norepinephrine reuptake inhibitors (e.g. venlafaxine) and atypical antidepressants (e.g. buproprion). Antipsychotic medication included quetiapine. Anxiolytic medication included beta blockers (propranolol), benzodiazepines (lorazepam, diazepam, alprazolam), anticonvulsant/anxiolytic (pregabalin). ADHD medication included amphetamines (Adderall).

3.3.1.1. Sample size. After discovery sample analysis, replication sample size was computed for each clinical hypothesis using the WebPower package (Z. Zhang & Yuan, 2018) in R. For this, we computed Cohen's f^2 for each hypothesis (Figure B1). We computed the number of participants required for power between 0.8 and 0.95. This suggested that 580 participants should provide 95% power for all analyses for $p < 0.05$, one-tailed. We planned to collect 830 participants due to available funds for this project. Of these, 402 were recruited under ethics approval R77387/RE003 and the rest were recruited under approval R54722/RE001. Our planned replication sample size exceeded the number dictated by power analysis in order to use the remainder of money set aside for data collection.

3.3.2. Task

The task used for this study was based on the task presented in Chapter 2 but differed slightly. We designed a gamified online foraging task in which participants freely made a series of choices with the goal of earning as much money as possible. During the task participants used arrow keys to control an animated fish in an ocean environment where there was rewarding food (later translated to money), threatening predators (leading to large point loss if they 'caught' the fish), and a hiding space (where participants could hide from the predators) (Fig. 14A). Participants could choose freely between three actions: 'forage' for food (Fig. 14Ai), 'check' for predators (Fig. 14Aii), and 'hide' in a safe space (Fig. 14Aiii).

3.3.2.1. Forage. The average amount of food available varied randomly (range: 0-90 units; samples were drawn from a normal distribution around the mean with $\sigma=2$) by predator epoch (i.e. the time starting from either block start or previous predator exit, and ending with

either the fish being caught or the predator exiting the environment). Participants could always see how much food was available. If participants 'foraged' by pressing the right arrow key the fish dove down to obtain food, thereby increasing its supply of energy (Fig. 14Ai); when an energy bar at the left of the screen was full, the fish gained a 'life' which corresponded to extra payment.

3.3.2.2. Check. Predators were hidden from participants' view unless they 'checked' a specific portion of the surrounding area (Fig. 14Aii). Predators appeared at the edge of the screen and moved toward the fish's location at the screen centre. When the predator reached the centre of the screen it either caught the fish (causing the participant to lose one 'life') or, if the fish was in hiding (see below), it quickly exited the environment. By checking, participants could see whether a predator was in a specific area of the environment and how close it was. To check, participants pressed the up arrow key. If the current predator was undiscovered, the section being checked advanced clockwise to the next section of the environment at each key press; after the participant discovered the predator's location, successive up arrow key presses revealed the predator's location. There were three types of predators that differed in speed (10s, 15s, and 20s to reach the screen centre). Each block (see below) had only one type of predator, appearing one at a time, and participants were informed which before the block start (Fig. 14B). There was a random delay (2-10.5s) between the block start or previous predator disappearance and the appearance of the subsequent predator.

3.3.2.3. Hide. Pressing the left arrow key caused the fish to escape to a safe space in a corner of the screen where it could not be caught by the predator. While hiding the participant could press the left arrow key again to return the fish to the centre (Fig. 14D).

3.3.2.4. Blocks. Each of 20 blocks lasted 90s and had a different combination of (1) predator speed and (2) number of segments in which participants could check for predators (range 1-4) (Fig. 14B). With fewer segments, more of the environment was visible during each check action and therefore fewer checks were required to survey the entire surrounding area. Each participant received one of two schedules (due to a coding error, schedules were distributed to 1/3 and 2/3 of participants respectively), each having block and reward conditions randomly generated with the absolute value of all correlations between block variables kept below $r = 0.3$.

After each block, participants answered two questions about how they perceived the block: (1) “How stressful was the last round?” and (2) “How exciting was the last round?”. Participants responded to each question by moving a slider to indicate a score between 0 and 100 (Fig. 14C).

3.3.2.5. Timings. Each action involved a time cost: foraging took 1.5s, checking took 0.5s, hiding took 0.5s, and returning from hiding took 2s. Block duration was 90s, and time in between blocks was variable. The delay before appearance of a new predator was random and varied between 2-10.5s. Reward magnitude fluctuated at each second.

3.3.2.6. Training. Before entering the experimental blocks, participants clicked through a series of instructions for the task (Table B1). They then completed two practice blocks and

completed a multiple-choice quiz testing their understanding of the task (Table B2), which they had to answer correctly in order to advance.

3.3.3. Questionnaires

Before the task, participants were asked for demographic information. Demographics were coded as follows: gender was coded as 1 for male, 2 for female, and 1.5 for 'other' (in regression analyses where gender was a covariate of no interest, 'other' was coded as 1.5; when predicting gender, 'other' was omitted and gender was binary); and education was coded linearly ascending (options: GCSE or middle school graduation (education up to age 15/16); A-Levels or high school diploma; Bachelor's degree; Master's degree; Doctorate or similarly advanced qualification). To screen for quality data, one question from each of the three AMI, SHAPS, and OCI-R questionnaires was repeated at the end of the questionnaire session ('consistency questions'; see above for exclusion criteria).

After the task, participants completed previously validated questionnaires to measure psychiatric symptoms and traits: the Apathy Motivation Index, including its two subscales, Behavioural and Emotional (AMI; Ang et al., 2017), State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA; Grös et al., 2007), Snaith-Hamilton Pleasure Scale (SHAPS; Snaith et al., 1995), the Obsessive Compulsive Inventory (Revised) 'Checking' subscale (OCI-RC; Foa et al., 2002), the decentering subscale of the Experiences Questionnaire (D-EQ; Fresco et al., 2007), and the Intolerance of Uncertainty Scale, Short Form (IUS-12; Carleton et al., 2007), including its two subscales, prospective (P-IU) and inhibitory (I-IU; see Hong & Lee, 2015; all questionnaires screened for attentiveness as described below, Section 3.3.4.2). During analysis, all questionnaire subscales were analysed separately.

Participants also completed a 29-item debrief questionnaire in which they reported their metacognitive awareness of their task behaviour. For this they responded to a series of statements about the task by marking how often each statement was true for them (response options were presented as a seven-point scale from 0/Never to 6/Very often).

3.3.4. Screening, Pre-processing, and Data Quality Checks

3.3.4.1. Pre-screening. Participants were at least 18 years old and were native English speakers. For the replication sample, participants recruited under ethics approval R77387/RE003 were pre-screened based on attentiveness and data quality in two unrelated online tasks as part of a larger study. They were also pre-screened using measures of anxiety from the STICSA questionnaire (Grös et al., 2007), measures of apathy from the AMI questionnaire (Ang et al., 2017), and measures of anhedonia from the Temporal Experience of Pleasure Scale (TEPS; Gard et al., 2006). Participants were selected such that scores in the final sample were evenly distributed across the lowest, middle, and highest thirds of the possible score range for both anxiety and apathy/anhedonia averaged.

3.3.4.2. Inattentiveness and poor performance. Participants were excluded if they had too many (> 6) epochs in the experiment without any actions, if they checked too rarely (< 40 times), if they were caught too often (> 9 times), and if they earned less than 5 extra lives. To check attentiveness to questionnaires, three questions were repeated and participants were excluded if the average absolute difference in repeated question scores was larger than one.

In addition, epochs were screened for measures of inattentiveness. Problematic epochs were either excluded from certain behavioural measures or excluded altogether. Epochs were excluded

entirely if participants stayed in hiding at the beginning of the epoch for more than 2.2s, or if participants hid more than once. Behavioral measures were computed from epochs depending on the epoch outcome: if participants discovered the predator and successfully hid, epoch data was used to compute all behavioural measures; if participants discovered the predator but the block ended before they could hide, epoch data was used to compute all pre-discovery behavioural measures; if participants did not discover the predator in an incomplete epoch with at least 10s of data, epoch data was used to compute the 'rate of inactive button presses' and 'time to first action' measures; if participants did not discover the predator in an incomplete epoch with less than 10s of data, epoch data was used to compute only 'time to first action'; if participants were caught by the predator, all within-epoch behavioural measures were computed but the data was not used to compute measures across epochs (e.g. time to first action after the predator leaves). See Figure B2 for the amount of data omitted per criterion.

3.3.4.3. Technical errors. Participants were excluded if they reported technical problems with the task, including the predator or the reward animations showing incorrectly. In addition, data was screened for unreported technical errors. If errors were detected in a predator epoch, that epoch and all subsequent ones in that block were removed from data analysis. If too many epochs were removed, the participant was excluded. The cut-off for what was considered too many removed epochs was determined based on the replication sample, such that at most 2.5% of participants were removed by a single behavioural measure.

Two indicators of technical errors were used to exclude data: 1) Any actions that happened in an epoch after a predator caught the participant were removed (as these did not lead to outcomes for participants). 2) After each action, there was an enforced delay before the buttons

became active again (1.5 sec for forage, 0.5 sec for check). Technical problems sometimes meant that this was not respected. We used a difference by more than 100 msec as a cut-off for exclusion.

3.3.5. Discovery Sample Analyses

Discovery sample analyses were preregistered in detail (OSF link: https://osf.io/3gb8n). In summary, we computed a set of 33 behavioural measures for each epoch (e.g. rate of checking before the predator was discovered). Then we performed regressions (fit using maximum likelihood estimation) relating behaviours, task features, and self-reported mood separately for each participant. The types of measures computed were the same as reported in 'Statistical Tests of Pre-registered Hypotheses' (Section 3.3.6).

The discovery sample analysis differed from the replication sample analysis in the following way. After all measures were computed, we performed a final series of analyses relating the results to clinical and demographic measures. To identify links between subscales and task-based measures, we performed linear, non-Bayesian regressions predicting each task-based measure based on clinical variables of interest, while controlling for demographics and clinical variables of no interest. For example, for analyses where the main variable of interest was any of the anxiety subscales, we controlled for all apathy, anhedonia, and compulsivity subscales and demographical measurements (age, gender, education). For analyses where the main interest was any apathy or anhedonia subscales, we controlled for all anxiety and compulsivity subscales (for IUS-12, only the P-IU subscale was used as a control because it highly correlated with the I-IU anxiety subscale in the discovery sample) and demographics. For analyses focused on OCI-RC score we controlled for all apathy, anhedonia, and anxiety subscales

as well as demographics. For analyses focused on demographics, we controlled for all anxiety, apathy, anhedonia, and compulsivity subscales, as well as all other demographics. When conducting regressions involving debrief questions 1-25, we additionally controlled for the sum of the participant's response to debrief questions 27-29 ("How much time did you spend performing each of these actions?" Q27: "Eating food", Q28: "Checking for a predator", Q29: "Hiding from a predator"); this was to account for an individual's tendency to use the right- or left-hand side of the scale more often. Significant results from these regressions were grouped by concept, arranged hierarchically from general to specific, and pre-registered as hypotheses. See Tables B3-B6 for a hierarchical presentation of all pre-registered hypotheses.

Regression models fit to the discovery sample were saved for future use with the replication sample as RData files in the preregistered Models folder (N.B. The RData files are numbered differently than the hypothesis tables; refer to the clinical/demographic label on the RData file to check to which hypotheses it pertains; OSF link: https://osf.io/3gb8n).

3.3.6. Statistical Tests of Preregistered Hypotheses

Data analysis was performed in R (R Core Team, 2022) using RStan (Carpenter et al., 2017), Tidyverse (Wickham et al., 2019), ggpubr (Kassambara, n.d.), compareGroups (Subirana et al., 2021), fuzzyjoin (Robinson, 2020), data.table (Dowle & Srinivasan, 2022), ggcorrplot (Kassambara, 2019), sjPlot (Lüdecke, 2022), psych (Revelle, 2022), brms (Bürkner, 2017, 2018), Stan (Stan Development Team, 2019), projpred (Projection Predictive Variable Selection; Piironen et al., 2023), and BayesFactor (Morey et al., 2022). To generate hypotheses, we first tested all possible links among collected measures in the discovery sample with regression. Then we grouped significant findings by concept and pre-registered these as hypotheses. Hypothesis

tests formed three groups relating task behaviour with 1) mood states (Table B3), 2) clinical scores (Table B4), and 3) gender (Table B5) (see 'Discovery Sample Analysis', Section 3.3.5). A fourth group containing miscellaneous hypotheses was also preregistered (Table B6) and tested (Table B7).

Next we tested whether we could replicate each of these hypotheses (see Fig. 15; Hypotheses test results are listed in Table 5 and Table 6). First, we extracted the behavioural measures involved in each of the hypothesis tests from the replication sample. To capture the interplay between emotions, environment, behaviour, and psychiatric traits, we extracted six types of behavioural measures: 1) impact of task features (e.g. speed) on behaviour; 2) impact of task features on mood; 3) impact of mood on behaviour; 4) impact of behaviour on mood; 5) post-task self-reports; 6) behavioural measures pertaining to the overall experiment (non-blockwise). Details of each measurement type are as follows:

3.3.6.1. Impact of task features on behaviour. We ran regression analyses as non-hierarchical Bayesian analyses, linking behavioural measures to task features. A regression model for any behavioural measure v that was obtained in each epoch before predator detection was formulated as in Equation 13:

$$v = \beta_0 + \beta_1 * reward + \beta_2 * mo(speed) + \beta_3 * mo(checkDirections) + \beta_4 * delay + \beta_5 * block + \beta_6 * firstEpoch \quad (13)$$

where measures of interest included *reward,* indicating average epoch reward magnitude; *mo(speed),* indicating predator speed modelled as a monotonic variable (see Bürkner, 2018);

mo(checkDirections), indicating the number of directions for checking modelled as a monotonic variable; and the intercept. Measures of no interest included *delay*, indicating the random delay before the predator entered the environment in each epoch; *block*, corresponding to block number; and *firstEpoch*, indicating whether the epoch was the first in the block. A regression model for any behavioural measure obtained in each epoch after predator detection was formulated similarly but with the addition of another regressor of no interest corresponding to how much time in seconds remained until predator arrival at the time of predator discovery in that epoch (where a higher value indicates earlier predator detection). In later analyses relating these measures to questionnaire scores, we additionally included the mean of each behavioural measure.

We used different types of link functions available in brms depending on the distribution of the behavioural measures, including normal, bernoulli, shifted log normal and poisson (see Table B8). All regressors were z-score normalized and weak priors were set (normal distribution with mean 0 and standard deviation 3). Predicted variables were not z-scored to allow the intercept to capture individual differences (e.g. main effect in rate of checking). Four chains were run with 4000 iterations and adapt_delta set to 0.8. Model fit was checked using Rhat < 1.1 and the absence of divergent samples. If this was not the case, the number of samples and adapt_delta were increased (adapt delta up to 0.9875 and number of samples up to 64,000). If Rhat or divergence were still not appropriate, the data were excluded from further analyses. Regressions were only run if at least one epoch was available for all conditions of predator speed and directions for checking, if more than 15 epochs were available, and if the behaviour was not always the same (as could be the case for e.g. having been caught, which might have never happened).

3.3.6.2. Impact of task features on mood. Participants rated mood (stress and excitement) after each 90s block. We fit regressions separately for each participant predicting mood ratings. For example, stress ratings given after each block *s* were modelled as Equation 14:

$$s = \beta_0 + \beta_1 * rewardMax + \beta_2 * rewardMin + \beta_3 * mo(speed) + \beta_4 * mo(checkDirections) + \beta_5 * livesGained + \beta_6 * block + \beta_7 * caught \quad (14)$$

where *rewardMax* and *rewardMin* indicate range of reward in the block, *mo(speed)* indicates predator speed modelled as a monotonic variable, *mo(checkDirections)* indicates the number of directions for checking modelled as a monotonic variable, *livesGained* indicates extra 'lives' gained by foraging, *block* corresponds to block number, and *caught* indicates whether the fish was caught by the predator at any point during the block. Note that this is different from the formula reported in the pre-registration document, which was accidentally reported wrongly. The formula here was used in both the discovery and the replication sample. Other mood ratings (e.g. post-block excitement) were modelled similarly to Equation 14. All regressors were z-scored across participants. Settings for brms models were as above (see '1. Impact of task features on behaviour').

3.3.6.3. Impact of mood on behaviour. We analysed the influence of pre-block mood on task behaviour. For this, we predicted the residuals of regressions predicting behaviour based on task features (described above). These were averaged within each block to match the number

of behavioural measures and mood ratings. We included as predictors mood ratings before the block from which the behaviour was taken coded in different ways: 1) including only stress or excitement; and 2) including both stress and excitement (i.e. measuring the independent contributions to behaviour), as this approach was found to yield significant results in the discovery sample. By using the residuals of the regression of task features to behaviour, we ensured that the mood effects were not confounded with task features. For example, the residual y of a regression predicting a behavioural measure based on task features was modelled as a dependent variable explained by pre-block stress and excitement as in Equation 15:

$$y = \beta_0 + \beta_1 * preblockStress + \beta_2 * preblockExcitement \quad (15)$$

All predictors were z-score normalized across all participants. Settings for the brms fitting procedure were as defined above.

3.3.6.4. Impact of behaviour on mood. We examined the impact of behaviour on post-block mood ratings using two analyses. First, we related behaviour during each block to the mood rating given right after each block. Specifically, we predicted the residuals of regressions predicting mood based on block variables described above (see '2. Impact of task features on mood'). As predictor, we included in a separate analysis each behavioural measure (e.g. rate of foraging). The analyses were run as separate regressions for each person (settings for brms as above). Regressions took the form of Equation 16:

$$r = \beta_0 + \beta_1 * m_i \quad (16)$$

where r is the residual of a regression predicting mood based on block variables as in Equation 14 and m_i is a behavioural measure such as foraging rate.

3.3.6.5. Post-task self-reports. After the end of the experiment, participants completed 29 questions about their behaviour in the task. These were extracted without further pre-processing and related to participants' questionnaire answers. See 'Questionnaires' section of Methods.

3.3.6.6. Behavioural measures pertaining to the overall experiment. Some behavioural measures, such as total payment at the end of the experiment, could not be computed in a block-wise manner. Those were extracted without further pre-processing and related to participants' questionnaire answers.

Once each behavioural measure had been extracted, we tested hypotheses in a hierarchical manner: we first tested general hypotheses (e.g. compulsive checking is related to task behaviour) before then testing the more specific sub-hypotheses, if the overall hypothesis was significant (with this hierarchical method we addressed the problem of multiple comparisons).

3.3.6.7. Mood hypothesis testing. We tested whether there were interactions between the task, evoked mood states, and task-related behaviour. Regressions were run separately for each participant (resulting in separate regression weights for each person per regressor per

behavioural measure analysed). Each hypothesis and sub-hypothesis were then tested using one-sided t-tests or Wilcoxon tests (test type noted in Table B3 for each hypothesis) with significance determined at $p < 0.05$. In some cases, a hypothesis test involved several regression weights (e.g., see Hypothesis 1A from Table B3, which is comprised of three regression weights). In this case, the weights were added together before testing, taking into account whether their signs needed to be flipped due to how the variables were coded. The only exception from this approach was Hypothesis 1C, which specified that stress and excitement were affected in opposite ways by having been caught: That statistic was computed as the least significant p-value of the two individual components (one-tailed).

3.3.6.8. Clinical and demographic hypothesis testing. Clinical hypotheses were tested by applying the regression models fit to the discovery sample to the replication sample, generating clinical score predictions for each person. Regression models used to make predictions were of the form (see Eq. 17):

$$y \sim \beta_0 + \beta_1 * m_1 + \beta_2 * m_2 + \beta_3 * m_3 \ldots \quad 17$$

where y is a clinical, demographic, or mood-related measure and m_i are task-related measures. These models were fit in BRMS in Stan (Bürkner, 2017, 2018; Stan Development Team, 2019) with 2000 iterations, 4 chains, weak priors (normal(0,1) for intercept and parameters), z-scored parameters, and family function Gaussian.

Note that these models diverged from the pre-registered statistical tests in one aspect. Our preregistered analysis plan specified that both the experimental and control models would

also include demographics variables and other clinical measures as predictors. While we did carry out those tests as planned, the results reported here are instead derived from models without those additional predictors (models formulated as in Eq. 17). This is because the omission of the clinical and demographic control predictors changed the results significantly, indicating that even though the clinical scales measure different constructs they are strongly interrelated and interfere with predicting each other.

Model predictions were compared against control model predictions (control regression models included only the intercept β_0) to compute out-of-sample R^2 (R^2_{OOS} ; see Campbell & Thompson, 2008), as in Equation 18:

$$R^2_{OOS} = 1 - \frac{MSE_m}{MSE_{null}} \qquad 18$$

where MSE_m is mean squared error of the model of interest ($(true\ score - predicted\ score)^2$) and MSE_{null} is the same for the control model. When a hypothesis encompassed several regressions (e.g. hypothesis 6B encompasses regressions predicting different clinical subscales), the R^2_{OOS} terms were averaged. R^2_{OOS} significance was assessed with permutation testing (N=10,000 shuffles of the clinical scores; see Berry et al., 2019). Significance was defined as one-tailed 95% (i.e., null hypothesis was rejected if the true R^2_{OOS} was larger than 95% of R^2_{OOS} derived from predicting the permuted scores). As a measure of goodness of the prediction we compared predicted and true clinical scores by computing correlations (Pearson's R). For nested hypotheses involving more than one clinical subscale, we computed the average correlation with Fisher's Z Transformation. Correlation significance was determined using permutation testing (N=10,000, significance level defined as one-tailed 95%). Finally, Bayes factor was computed

for each model to quantify evidence for and against the null model (Morey et al., 2022; Rouder et al., 2009). For models with clinical score as the dependent variable, a one-tailed Bayes factor test for linear correlation was conducted with Jeffreys prior associated with the Beta distribution (R. Yang & Berger, 1996) and rscale=1.

Hypothesis tests linking demographics with task-related behaviour in the replication sample were conducted in a similar way to the clinical tests (see above). However, the only dependent variable tested in demographics hypotheses was gender. Participants reporting 'other' as gender were omitted and the variable was treated as binary. Regression models were fit with family function Bernoulli.

Out-of-sample R^2 (R^2_{OOS}) for models predicting gender was computed as in Equation 19:

$$R^2_{OOS} = 1 - \frac{LL_m}{LL_{null}} \quad 19$$

where LL_m is the log-likelihood of the model of interest and LL_{null} is the same for the control model. To measure goodness of the prediction in these models, we compared predicted and true clinical scores by computing accuracy (% correct classification). Significance for R^2_{OOS} and accuracy was assessed with permutation testing as in the clinical models described above. Bayes factor was computed using a one-tailed Bayes factor test of single proportions on the number of correct classifications made by each model (Morey et al., 2022).

3.3.7. Exploratory Analyses

We used a machine learning approach, regularized Bayesian regression with predictor selection, to further explore whether task behaviour could predict clinical scores/demographics. To fit the

best possible model, models here were trained on the larger (replication) sample. The discovery sample was used as an independent hold-out dataset.

For this method we built three types of models: 1) A model including all behavioural measures (including post-task self-reports) as predictors, which allowed us to test overall ability to predict clinical subscales or gender. 2) A model including all measures collected (including behavioural, self-report, clinical, and demographic measures) as predictors. We compared this against performance of a model only including clinical scales and demographics. This allowed us to test whether our task added predictive power beyond the other clinical questionnaires. 3) A model including all non-clinical and non-demographics measures as predictors except the post-task self-reports (i.e., behavioural measures only). This allowed us to measure how much behaviour in the task itself was predictive. For each model type, goodness of fit and significance were determined through permutation testing as above.

Data contained missing values. For example, if a participant never discovered the predator, measures such as rate of foraging after discovery could not be computed. Behavioural measures significant on the group-level were extracted, and these were further constrained to only the set of measures that allowed keeping ~95% of participants with full data (N=663). For the Bayesian models, all predictors were z-score normalized. To summarise the method, a regularized model was fit and the most predictive features were selected.

3.3.7.1. Modelling details. BRMS and Stan together were used to fit a regularized Bayesian regression, implemented with a horseshoe prior (Carvalho et al., 2009; with expected significant parameter ratio set to 20%). We built a separate regression model that included all task measures described in the main methods section after cleaning. The variable to be predicted

was a single clinical/demographic feature (e.g. compulsive checking, a questionnaire measure). Other BRMS settings were: 4000 iterations, 4 chains, parameters to reduce divergence: target average acceptance probability (adapt delta) = 0.99, max tree depth = 12. Models were checked for fit (Rhat < 1.1), while we note that a very low number of divergences persisted (< 20), which is expected given the large number of regressors. In the replication sample, fit of this model was compared to a null model (containing intercept only) using efficient approximate leave-one-out cross validation (loo, Vehtari et al., 2017). Moment matching was used when Pareto k diagnostic values were high (k > 0.7).

Only if the model showed a better fit than the control model based on expected log predictive density (elpd_loo; Vehtari et al., 2017) was predictor selection done. For predictor selection, we used the projpred package (Piironen et al., 2020, 2023). Predictor selection was necessary because, while a regularised model might overall show a better fit than a null model to the data, none of the individual predictors might be significant. For this, we ran predictor selection twice (following the manual): first approximative (without cross validation) to get a rough estimate of the appropriate number of terms to include, then with cross-validation, allowing the number of maximum terms from the approximate fit + 5 as total number of terms to include. If this was not successful (either the best number of features was at least as large as the maximum allowed or fit measures (elpd) suggested problematic fit (elpd did not smoothly approach the fit of the full model), we reran the predictor selection (up to 3 times), each time increasing the maximum number of allowed features by 5 and changing the fit method to 'forward'.

3.4. Results

A total of 1,199 participants took part in this online-based preregistered study (OSF link: https://osf.io/3gb8n). Data quality checks excluded 123 participants due to inattentiveness, incompleteness, or otherwise low-quality data (see 'Screening, Pre-processing, and Data Quality Checks', Section 3.3.4). This resulted in 1,076 participants included across the preregistered discovery sample (N=374 included) and replication sample (N=702 included; demographics in Table 3 and psychoactive medication reported in Table 4). Here we report results from testing the replication sample with both preregistered and exploratory analyses (Fig. 16); results from the discovery sample can be found in the preregistration.

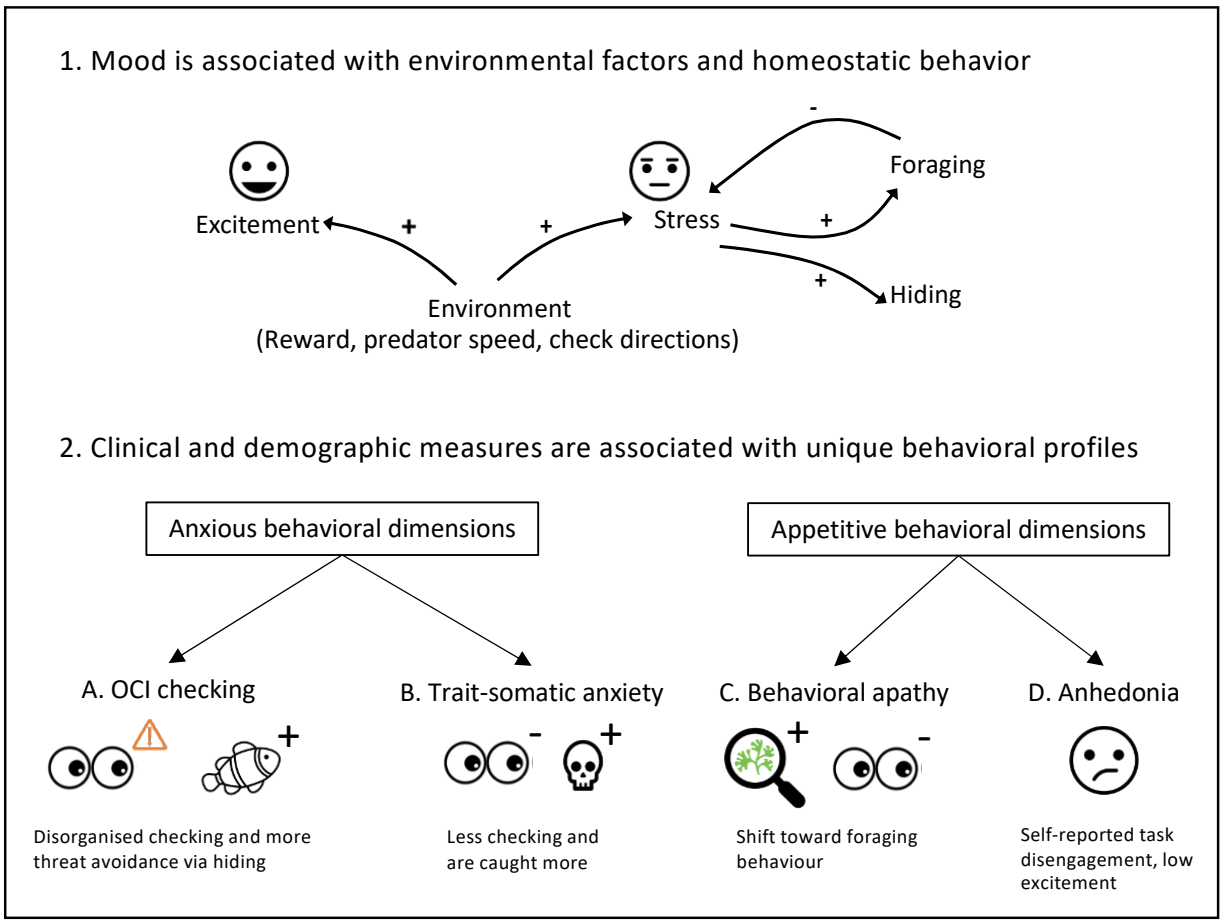


Figure 16. **Results summary.** An online task in which participants foraged for rewards under threat of predation evoked behaviour and self-report data that predicted mood (stress/excitement), clinical scores, and gender. 1) Task-related environmental factors (e.g. reward, predator speed, check directions) were linked with evoked mood states. Stress was associated with homeostatic behaviours: for example, pre-block stress was linked with increased foraging, and increased foraging was subsequently related to lower stress ratings. 2) Clinical and demographic measures were associated with unique behavioural profiles. A) Compulsive checking (OCI-RC score) was linked with disorganized and sub-optimal checking, greater threat avoidance via hiding and task disengagement, and higher arousal. B) Trait-somatic anxiety (STICSA Trait-somatic score) was related to less checking due to threat-related worry, self-reported checking avoidance, and being caught by the predator more. C) Behavioural apathy (AMI Behavioural score) was associated with a shift in behaviour towards foraging and self-reported emotional sensitivity to threat. D) Anhedonia (SHAPS score) was linked with self-reported task disengagement and lower excitement.

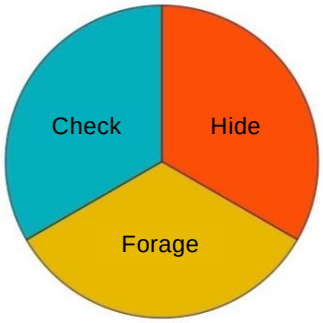
During each of twenty 90s blocks, participants played a fish in an underwater environment in which they continuously and freely chose between foraging for rewarding food (later translated into bonus payment; Fig. 14Ai), checking for threatening predators (being 'caught' by a predator decreased bonus payment; Fig. 14Aii), and hiding in a safe space (Fig. 14Aiii). Their goal was to gain as much reward as possible without being caught by any predators. Predators appeared at a randomized location and time and moved toward the fish until either catching it or retreating. Blocks varied by predator threat level and the number of checks required to scan the surrounding area for predators (Fig. 14B). In between blocks, participants used sliding scales to rate their

level of excitement and stress during the previous block (Fig. 14C). After the task, participants completed previously validated psychiatric questionnaires measuring symptoms of apathy (Ang et al., 2017), anhedonia (Snaith et al., 1995), anxiety (Grös et al., 2007), intolerance to uncertainty (Carleton et al., 2007) and compulsive checking (Foa et al., 2002) and answered questions that required them to introspect about their task performance (see Methods).

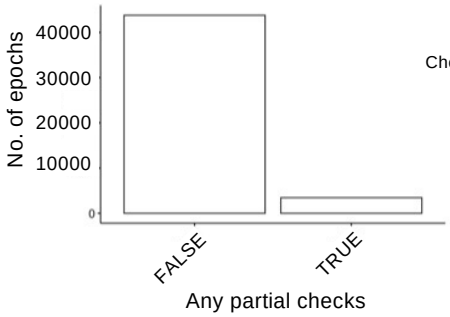
3.4.1. Testing Preregistered Hypotheses in the Replication Sample

We tested three groups of preregistered hypotheses relating task behaviour with 1) mood states (Table B3), 2) clinical scores (Table B4), and 3) gender (Table B5) (summary in Figure 15; see Methods Section 3.3 and preregistration). Example behavioural measures selected from replicated hypothesis tests are shown in Figure 17.

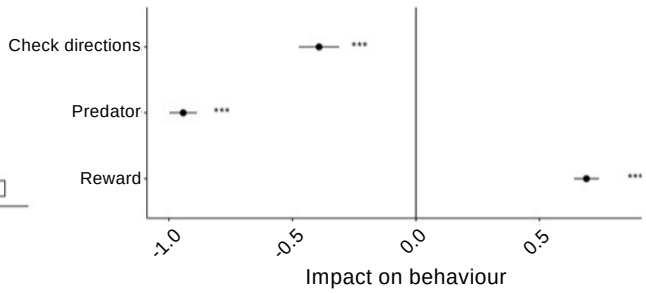
A.



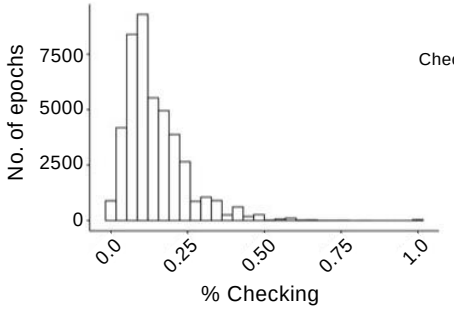
Bi. Any partial checks (Pre-disc. phase)



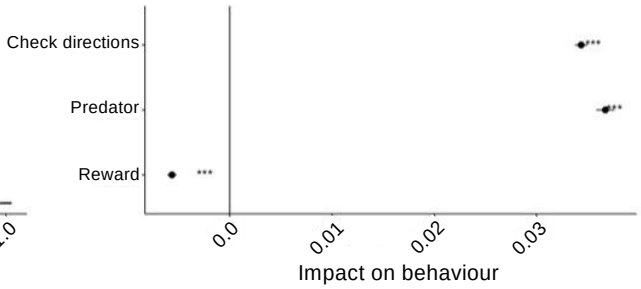
Bii.



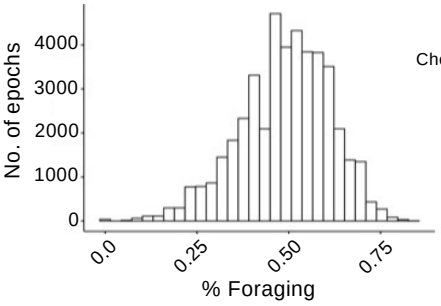
Ci. Checking, as % of all checks and forages in the epoch



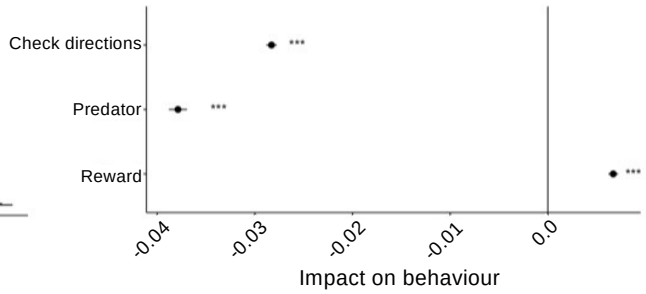
Cii.



Di. Foraging, as % of all checks and forages in the epoch



Dii.



E. Self-report: “I tried to gather food as long as possible before hiding”

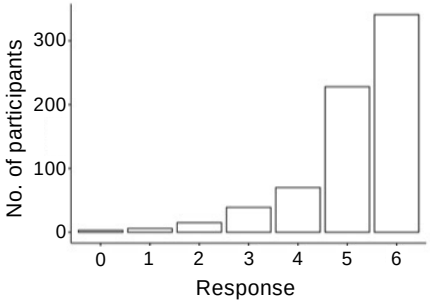


Figure 17. **Selected behavioural measures.** Performance of replication sample participants on selected behavioural measures that each form part of a hypothesis test. A) Pie chart showing percentages of epoch time spent foraging, checking, and hiding averaged across participants. B-E) Results for behavioural measures including B) the number of epochs in which a 'partial check' (a series of checks that did not scan the full environment) was conducted (formed part of H4Aii), C) checks (formed part of H5B) and D) forages (formed part of H5B) as percentages of all checks and forages in the epoch, and E) responses to the self-report question "I tried to gather food as long as possible before hiding" (options ranged from 0/Never to 6/Very often; formed part of H6Bii). Bi, Ci, Di, and E show histograms indicating frequency of responses across the range. Bii, Cii, and Dii show relationships between each corresponding behavioural measure and environmental factors (check directions, predator, and reward), displayed as means and standard errors of the mean for estimated parameters. Significance is for one-sample t-tests (two-tailed); *p<0.05, **p<0.01, ***p<0.001.

3.4.2. Mood Hypothesis Test Results

3.4.2.1. Mood is influenced by environment. It is intuitive that one's environment and mood state may have some influence on one another, but it is not clear whether this relationship exists in the context of an online experiment. Our first set of hypothesis tests confirmed that task-related environmental factors (e.g., threat level, reward) were linked with evoked mood states (H1; Z = -15.37 p < 0.0001; Table 5, Fig. 18). Examining this further, we found that environmental factors were significantly linked with excitement (H1A; Z = -11.21, p < 0.0001; Table 5) and stress (H1B; Z = -19.97 p < 0.0001): for both moods, higher ratings were coupled with higher rewards, faster predator speed (threat level), and greater number of directions to

check for predators. However, being caught by a predator was associated with stress and excitement in different ways (H1C; least significant *p*-value of two component measures was $p < 0.001$; Table 5): virtual death was linked with increased stress and decreased excitement. Of interest here is the finding that some threat-related factors affected arousal regardless of valence (e.g., faster predator speed increased both stress and excitement) while others had a valence-specific effect (e.g., virtual death). Further work is needed to understand how general arousal versus distinct emotions may affect decision-making differently.

3.4.2.2. Mood and behaviour are homeostatic. We next wondered whether we could characterize a relationship between task behaviour and mood. Given that task factors affected mood, we asked whether participants adapted behaviour in response to their changing moods—and conversely, whether certain behaviours resulted in altered moods. A second set of hypothesis tests investigated possible homeostatic interactions between stress and task-related behaviour; i.e., whether an interdependent relationship exists between stress and behaviour by which each contributes to regulating the other. We found general evidence of such interactions (H2; $Z = -4.90$, $p < 0.0001$; Table 5) and conducted sub-hypothesis tests to characterize this relationship. First, we confirmed a homeostatic relationship between stress and foraging behaviour before predator discovery (H2A; $Z = -4.85$, $p < 0.0001$; Table 5). There was a significant link between increased stress and behaviours such as increased foraging and more efficient checking before predator discovery (H2Ai; $Z = -3.46$, $p = 0.0003$; Table 5), suggesting that stress could play an adaptive role in some contexts by optimizing the balance between reward- and threat-oriented behaviours. Conversely, we found significant links between reduced stress, foraging, and efficient checking—for example, earlier predator discovery was associated with reduced stress

(H2Aii; Z = -6.98, $p < 0.0001$; Table 5). In addition, greater stress was linked with a behavioural shift toward hiding rather than activity (H2B; Z = -3.45, $p = 0.0003$; Table 5). These behaviours—foraging, more effective checking, and hiding—appeared to play a role in regulating stress.

We failed to replicate a positive feedback loop exists between excitement and action vigour (H3, $t(688) = 1.15$, $p = 0.125$; Table 5), so we do not report tests of its sub-hypotheses in line with our strategy for correction for multiple comparisons. Statistics for all mood-related hypothesis tests are reported in Table 5.

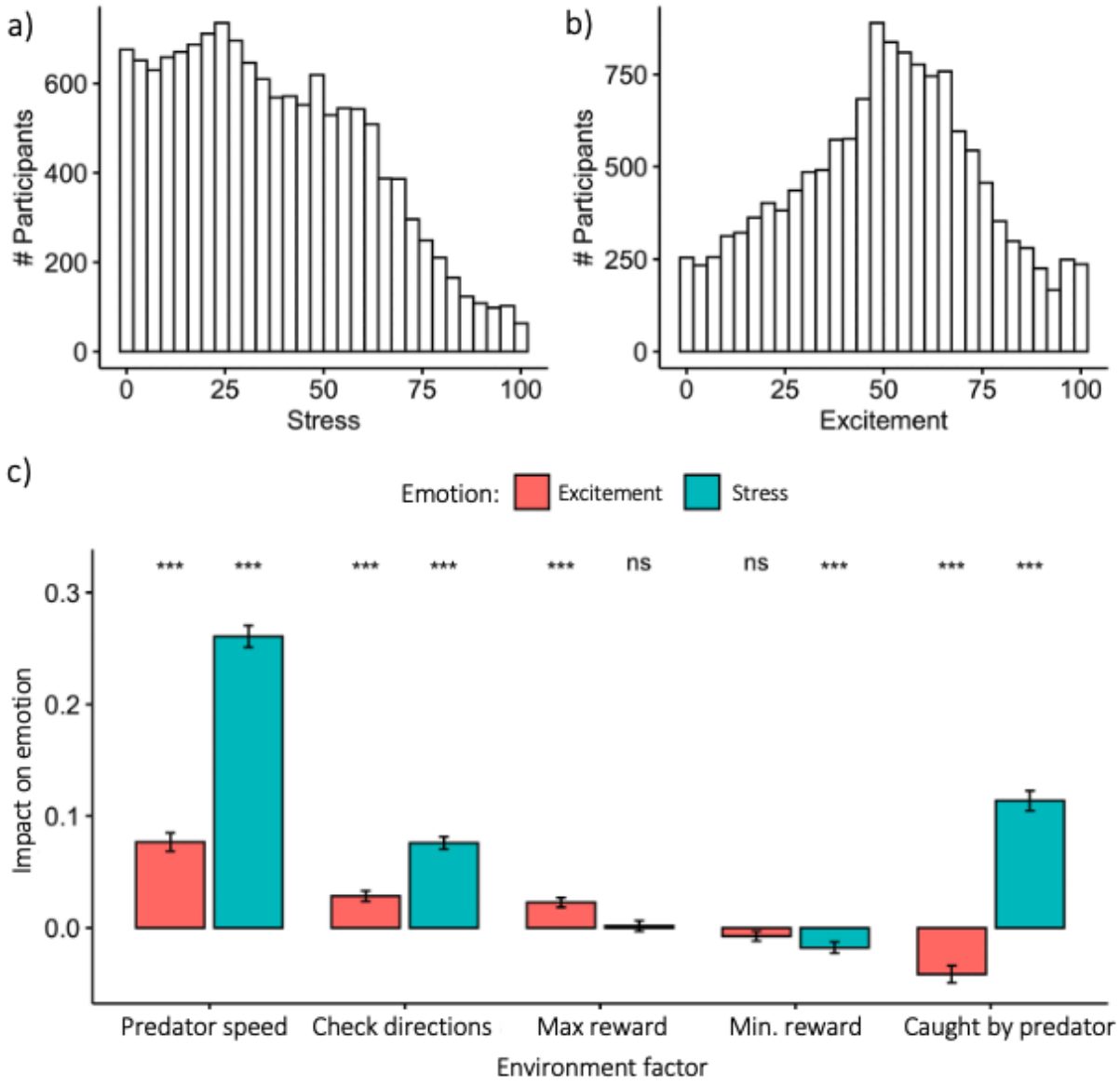


Figure 18. **Distribution of mood ratings and environmental influences.** Histograms show the frequency of A) stress ratings and B) excitement ratings across the sliding scale for all participants (binned). C) Bar chart showing the relationship between environmental factors and mood ratings (mean and standard error). 'Predator speed' = Fast, medium, or slow speed, an indicator of threat level; 'Check directions' = the number of possible directions to check; 'Max. reward' = maximum reward in the block; 'Min. reward' = minimum reward in the block; 'Caught

by predator' = whether or not the participant was caught by the predator at any point in the block. Significance stars are from two-tailed one-sample t-tests. ***p<0.001, ns = not significant.

Table 5

Mood-Related Hypothesis Test Results (H1-3)

Hypothesis	Measures included[1]	Est.	Stat.[2]	Z[3]	Effect[4]	*p*[5]	N	Test[6]
1. Environment is linked with mood	NA	0.55	68176	-15.37	0.79	<0.001	377	Wil.
1A. Environment affects excitement	Exc.*#Dir; Exc.*Threat level; Exc.*Reward	0.10	182190	-11.21	0.42	<0.001	699	Wil.
1B. Environment affects stress	Stress*# Dir; Stress*Threat level; Stress*Max. reward; Stress*Min. reward	0.33	228984	-19.97	0.76	<0.001	699	Wil.

1C. Having been caught affects stress and excitement in opposite ways	Stress*Fish caught; Exc.*Fish caught	-0.03	NA	NA	0.23	<0.001	377	Least sig. p^7
2. Stress and behaviour have homeostatic interactions	NA	0.20	115222	-4.90	0.20	<0.001	612	Wil.
2A. Stress has a homeostatic relationship with foraging behaviour before discovery of the predator	NA	0.15	133611	-4.85	0.19	<0.001	662	Wil.
2Ai. Stress is linked with increased foraging and	Stress->Predator proximity at disc. (s); Stress->Pre-disc.	0.10	139623	-3.46	0.13	<0.001	696	Wil.

more efficient checking before the predator is seen	foraging rate; Stress->Checking as % of all actions; Stress->Time to first forage							
2Aii. Foraging and efficient checking are linked with reduced stress (both pre- and post-discovery)	Pre-disc. check frequency->Stress; Predator prox. at disc. (s)->Stress; Foraging as % of all actions*Stress; Foraging as % of all actions->Stress; Any foraging post-disc.->Stress; Forage is last action before hiding->Stress; Pre-disc. forage	0.04	144076	-6.98	0.27	<0.001	662	Wil.

	rate->Stress; Max. repeated forages pre-disc.->Stress							
2B. Stress is linked with a behavioural shift toward hiding rather than activity	Stress->Predator prox. at hide (s); Any checks post-disc.*Stress; Stress->Any checks post-disc.; Stress->Max. repeated forages post-disc.	0.06	119065	-3.45	0.14	<0.001	641	Wil.
3. Excitement and action vigour are in a positive feedback loop	NA	0.01	1.15	NA	0.04	0.125	689	T
3A. Excitement is linked with increased	Stress->#inactive checks	0.00	-0.33	NA	-0.01	0.629	699	T

response vigour									
3B. Response vigour is linked with increased excitement	# inactive hides->Exc.; Rate of inactive forages->Exc.	0.01	3.01	NA	0.11	0.001	690	T	

[1]#Dir = Number of directions for checking; Exc.=Excitement rating; disc. = discovery; prox. = proximity.

[2]Either T statistic for t-tests or W statistic for Wilcoxon signed rank tests.

[3]Z value for Wilcoxon signed rank tests (based on one-tailed *p* value).

[4]Effect size: Cohen's d for t-tests and Wilcoxon effect size for Wilcoxon signed-rank tests.

[5]*p* values are one-tailed.

[6]Wil. = Wilcoxon signed-rank test; T = T-test.

[7]Least significant *p*-value of the two tests.

3.4.3. Clinical Hypothesis Test Results

Psychiatric symptoms manifest behaviourally in many ways; in particular, anxiety-related and apathetic/anhedonic disorders are known to alter various vigilance, threat avoidance, and appetitive behaviours. In our study participants completed post-task psychiatric questionnaires with subscales representing distinct behavioural dimensions (see Fig. 19 for subscale correlations). We investigated whether there was a replicable relationship between participants' scores on psychiatric questionnaires based on their (self-reported) task behaviour, and found that

we could predict scores for each of compulsivity, anxiety, apathy, and anhedonia clinical subscales (all $p < 0.05$; see Table 6). Statistics for all clinical hypothesis tests are reported in Table 6.

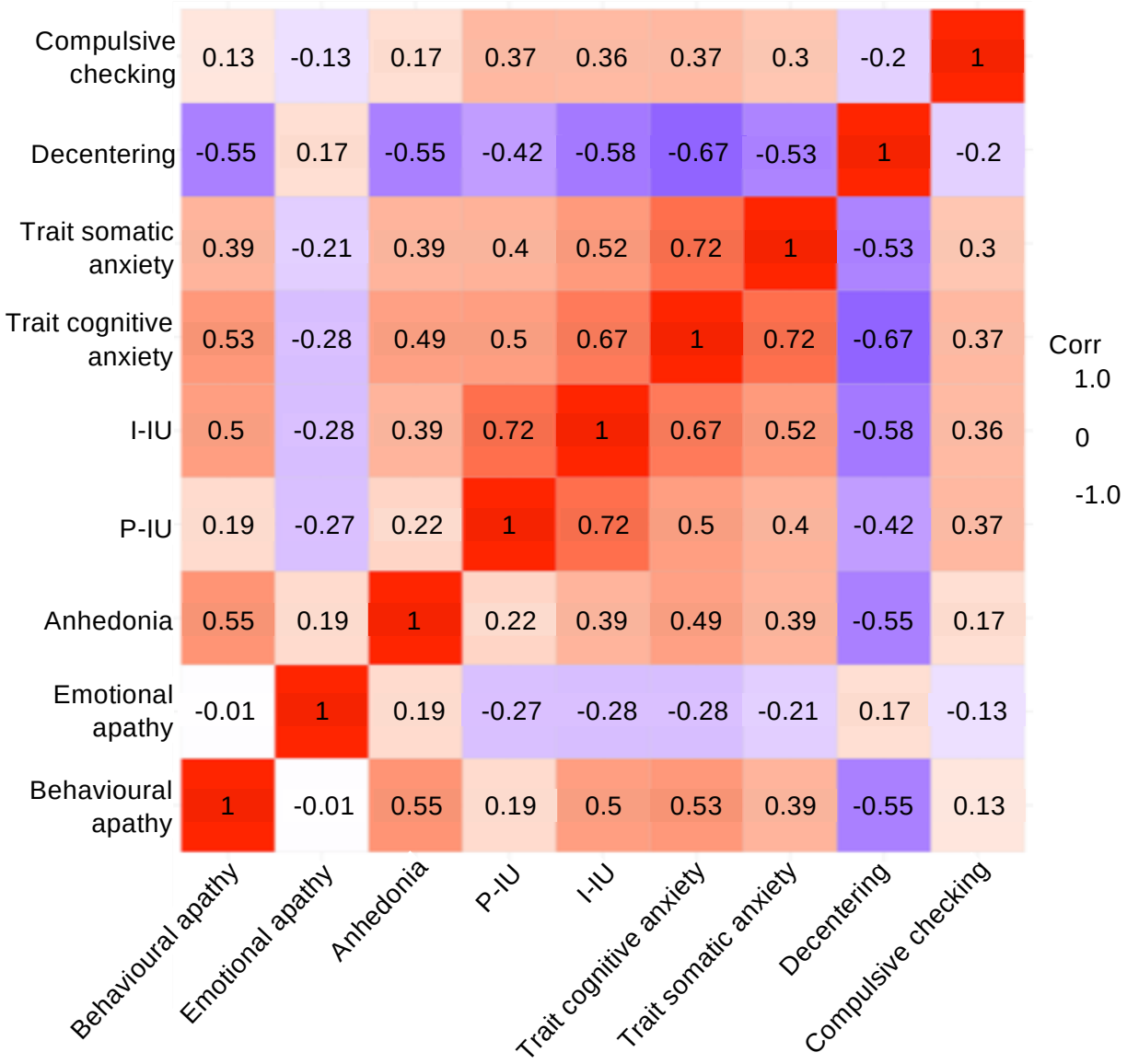


Figure 19. Correlations between subscales of psychiatric questionnaires.

3.4.3.1. Compulsive checking is associated with a disordered relationship to threat. First, we confirmed that compulsive checking (as measured by the Obsessive Compulsive Inventory (Revised) 'Checking' subscale score, or OCI-RC; Foa et al., 2002) changed selected task behaviour and self-report measures overall (H4; out-of-sample R^2 (R^2_{OOS}) = -0.05, p < 0.0001, Pearson's r = 0.16). Specifically, compulsive checking was associated with increased vigilance and decreased foraging—but in a disorganised manner (H4A; R^2_{OOS} = -0.02, p < 0.001; Pearson's r = 0.14, p < 0.001). This was driven by multiple measures of sub-optimal checking behaviour (H4Aii; R^2_{OOS} = 0.04, p < 0.0001). One possible interpretation is that individuals who scored highly on compulsive checking felt less reassured by confirming the absence of threat and remained unnecessarily vigilant. Indeed, one of the measures included in H4Aii is a link between high OCI-RC score and responding positively to the question "I sometimes checked again for a predator even though I had just finished checking in all directions".

At the same time, compulsive checking was associated with greater threat avoidance: OCI-RC was predicted by six measures of hiding and threat-related task disengagement (H4B; R^2_{OOS} = -0.01, p < 0.0001; Pearson's r = 0.16, p < 0.0001). A possible interpretation for this is that highly compulsive participants felt more emotionally perturbed by the task and specifically by predators, leading to longer breaks from threat engagement. In another test, we confirmed that OCI-RC was related to higher reported arousal (both stress and excitement), in general and in anticipation of predator arrival (H4C; R^2_{OOS} = -0.02, p = 0.001; Pearson's r = 0.11, p = 0.001).

3.4.3.2. Anxiety is linked with decreased vigilance and impaired task performance. A test across sub-hypotheses related to anxiety (as measured by the State-Trait Inventory for Cognitive and Somatic Anxiety, or STICSA; Grös et al., 2007) and intolerance of uncertainty

(as measured by the Intolerance of Uncertainty Scale Short Form, or IUS-12; Carleton et al., 2007) scores indicated a general association with task behaviour (H5; Pearson's r = 0.072, p = 0.032), although the sub-hypothesis related to intolerance of uncertainty did not replicate (H5A, p = 0.478; likely contributing to the low correlation in H5) so we did not carry out more specific related tests. However, we confirmed that anxiety was linked with decreased vigilance due to threat-related worry and avoidance—leading anxious participants to be caught by the predator more often (H5B; R^2_{OOS} = 0.04, p < 0.0001). Regressors predicting trait-somatic anxiety included behavioural measures of vigilance and virtual death as well as self-report measures, showing that anxious participants were aware of being perturbed by threat both emotionally and behaviourally.

3.4.3.3. Apathy and anhedonia alter appetitive behaviour and task engagement. Behavioural apathy (as measured by Apathy Motivation Index, or AMI, Behavioural subscale; Ang et al., 2017) was generally associated with task-related behaviour (H6; Pearson's r = 0.12, p < 0.001), and we proceeded to characterize this relationship. Consistent with our hypothesis, behavioural apathy was associated with a reduction in both vigilant and threat-avoidant behaviour in favour of foraging (H6A: R^2_{OOS} = -0.07, p = 0.006, Pearson's r = 0.10, p = 0.006; H6Ai: R^2_{OOS} = -0.04, p = 0.024, Pearson's r = 0.08, p = 0.023), despite increased emotional sensitivity to threat (H6Aii; R^2_{OOS} = -0.03, p = 0.022; Pearson's r = 0.08, p = 0.023). One possible interpretation of this finding is that apathetic participants switched between different behavioural modes with less frequency, over-persevering with foraging instead of balancing their behaviour between foraging and vigilance.

We next tested the general hypothesis that anhedonia (as measured by the Snaith-Hamilton Pleasure Scale, or SHAPS; Snaith et al., 1995), was associated with greater reward

sensitivity but a reduced feeling of task engagement. While this was confirmed (H6B: R^2_{OOS} = -0.03, $p < 0.001$, Pearson's r = 0.14, $p < 0.0001$), the only sub-hypothesis that replicated was the reduced feeling of task engagement (H6Bii; R^2_{OOS} = 0.03, $p < 0.0001$), suggesting that the predictive power of test H6B was driven not by reward motivation but primarily by self-report measures indicating reduced task engagement.

3.4.4. Demographic Hypothesis Test Results

In addition to psychiatric scores, we wondered whether demographics such as gender, education, and age affected participants' task behaviour. Hypotheses based on the discovery sample focused on the influence of gender. Here we show that classifying gender using task behaviour outperformed control models, and we characterize this relationship in several ways. Statistics for all demographic hypothesis tests are reported in Table 6.

3.4.4.1. Gender is linked with vigilance, stress, and response vigour. We found an overall link between gender and task performance (H7; R^2_{OOS} = 0.03, $p < 0.0001$) and confirmed several aspects of this relationship. First, women generally performed worse, tending to forage less (H7A: R^2_{OOS} = 0.08, $p < 0.0001$; H7Ai: R^2_{OOS} = 0.09, $p < 0.0001$), check more frequently and sooner, and yet were caught by the predator more often (H7Aii; R^2_{OOS} = 0.05, $p < 0.0001$). Second, we found that women reported feeling more stressed in general and particularly in response to threat (H7B; R^2_{OOS} = -0.03, p = 0.015; Accuracy = 54% correct, p = 0.010). Third, women showed lower response vigour (i.e., rapid button pressing while buttons were inactivated), particularly in situations where it was usually increased. Overall, women's behaviour was generally more threat-oriented, and women were less successful in balancing

between threat- and reward-oriented behaviours. Contributing factors could be emotional perturbation as a result of threat, task engagement, and physical arousal.

Table 6

Clinical and Demographic Hypothesis Test Results (H4-7)

Hypothesis	1-tailed *p* value	Pearson's r or % correct	Bayes Factor	R^2_{OOS}*	$p\ (R^2_{OOS})$	N
4. OCI-RC score is associated with measures of task-related behaviour	0.00001	0.16	464.02	-0.05	2.00E-05	652
4A. OCI-RC score is associated with increased vigilance and decreased foraging, but in a disorganized pattern	0.00022	0.14	52.5	-0.02	0.00019	655
4Ai. OCI-RC score is associated with increased vigilance	0.39845	0.01	0.06	-0.05	0.42364	690
4Aii. OCI-RC score is associated with increased disorganized checking	p<1e-05	0.22	2136432.77	0.04	0	701

4Aiii. OCI-RC score is associated with decreased foraging, particularly when reward is low	0.20654	0.03	0.11	-0.06	0.20024	663
4B. OCI-RC score is associated with greater threat avoidance	0.00002	0.16	684.84	-0.01	2.00E-05	702
4C.OCI-RC score is related to higher reported arousal (stress and excitement), in general and in anticipation of predator arrival.	0.00137	0.11	8.31	-0.02	0.00134	699
5. Anxiety and intolerance to uncertainty are related to measures of task-related behaviour	0.03195	0.07	NA	NA	NA	660
5A. Intolerance to uncertainty (IU) is associated with a change in the balance of check/forage/hide actions in response to both environment and mood	0.47781	0.002	NA	NA	NA	660

5Ai. Prospective IU is associated with a reduction in the tendency for reward to shift behaviour toward foraging instead of vigilance	0.20089	0.03	0.11	-0.06	0.20928	663
5Aii. Inhibitory IU is linked with changes in the effect of predator speed and stress on hiding behaviour	0.69767	-0.02	0.03	-0.06	0.70962	698
5Aiii. Prospective IU and cognitive/somatic anxiety are associated with increased emotional responses to reward and threat	0.66602	-0.02	0.03	-0.04	0.69741	699
NA	0.26775	0.02	0.09	-0.09	0.27521	660
5B. Trait-somatic anxiety is linked with decreased vigilance due to threat-related worry and	p<1e-05	0.21	529597.08	0.04	0	697

avoidance, resulting in being caught more often						
6. Apathy and anhedonia are linked with measures of task-related behaviour	0.00095	0.12	NA	NA	NA	695
6A. Behavioural apathy is associated with a reduction in vigilant and threat-avoidant behaviour in favour of foraging, despite increased emotional sensitivity to threat	0.0064	0.10	2.12	-0.07	0.00606	695
6Ai. Behavioural apathy is associated with a reduction in vigilant and threat-avoidant behaviour in favour of foraging (resulting in higher final score)	0.02258	0.08	0.66	-0.04	0.02413	697
6Aii. Behavioural apathy is linked with increased self-reported emotional sensitivity to threat	0.02301	0.08	0.66	-0.03	0.02241	700

6B. Anhedonia and emotional apathy are linked with the foraging/vigilance trade-off being more sensitive to reward, while reducing the subjective feeling of task engagement	0.00006	0.14	91.22	-0.03	0.00013	695
6Bi. Anhedonia and emotional apathy are linked with the foraging/vigilance trade-off being more sensitive to reward	0.08629	0.05	0.22	-0.06	0.09249	698
6Bii. Anhedonia and emotional apathy are associated with a reduction in the self-reported feeling of task engagement	p<1e-05	0.18	7101.94	0.03	0	699
7. Gender is linked with task performance	p<1e-05	65%	1.74E+14	0.03	0	641
7A. Women overall perform worse. They tend	p<1e-05	66%	1.42E+15	0.08	0	644

to favour vigilance over foraging						
7Ai. Women forage less	p<1e-05	67%	1.34E+17	0.09	0	653
7Aii. Women check more and sooner, but also get caught more often	p<1e-05	59%	466076.79	0.05	0	678
7B. Women are more stressed in general and particularly by threat	0.00952	54%	95.64	-0.03	0.01546	689
7C. Women show lower response vigour, particularly in situations where it is usually increased	p<1e-05	63%	1.08E+12	0.06	0	691

Note. Measures included in each model, including their count and significance, are listed in Table B9. *Some reported R^2_{OOS} values are negative but the corresponding *p*-value are positive. This occurred when the R^2_{OOS} value associated with the permuted clinical scores was even more negative than that of the true R^2_{OOS}; thus, the target model still performed significantly better than the control model even though its R^2_{OOS} value is negative.

3.4.5. Exploratory Analyses

The preregistered hypothesis tests examined relationships between task and clinical measures based on a conceptual grouping. An alternative, more exhaustive approach is to explore which

task behaviours best predict clinical and demographic measures with machine learning. For this we fit regularized Bayesian regression models on the replication sample, reserving the discovery sample as a test set (see Methods). We then used this strategy to answer three questions. First, we wanted to know whether our task had predictive power beyond that of the other clinical questionnaires. If true, this would have important implications for future clinical studies: a task that has unique predictive power to predict dimensions of mental illness could be a useful tool for diagnosis or further study. Second, we asked how strong this predictive power might be. Third, we tested the importance of the post-task debrief questions by assessing the task's predictive power with and without these data. A task that has clinical predictive power independent of self-report questions—that is, one based purely on objective behavioural measures—would represent a diagnostic strategy distinct from all other assessments currently used in psychiatry. In each corresponding set of analyses, we found that we could predict several clinical and demographic measures significantly better than a null model. A summary of results is as follows.

3.4.5.1. Task-related measures added power to predict anxiety, apathy, anhedonia, and gender beyond clinical measures and demographics alone. To test whether our task added predictive power beyond clinical questionnaires alone, we fit models including all measures collected (including behavioural, self-report, other clinical and demographic) as predictors, and compared their performance against that of control models with only clinical and demographic predictors. We found that the inclusion of task-related measures significantly improved model performance for predicting gender, AMI Behavioural scores, P-IU scores, STICSA Trait Cognitive scores, and SHAPS scores (see Table 7for statistics). This showed that

measures from our task added unique predictive power exceeding that of clinical measures and demographics alone.

3.4.5.2. Task behaviour and self-report data predicted all clinical subscales and gender. Next we tested our overall ability to predict clinical subscales and gender using models that included all behavioural measures (including post-task self-reports) as predictors. We compared the goodness of these models' predictions against those of a null model (including intercept only) and found that we could significantly predict every clinical subscale, including STICSA Trait Cognitive, D-EQ, P-IU, STICSA Trait Somatic, AMI Behavioural, AMI Emotional, SHAPS, OCI-RC, and I-IU (see Table 7for statistics and Table B10 for selected predictors). We could also significantly classify gender with 70% accuracy ($p < 0.0001$). This demonstrated that our task-related measures had predictive power without any support from clinical or demographic predictors.

3.4.5.3. Task behaviour alone predicted clinical and demographic measures. Last, we asked to what extent the task behaviour itself—without any self-report, clinical, or demographic measures—was predictive of clinical scores and gender. We fit models with behavioural predictors and compared their goodness of prediction against those of a null model (intercept only). We could significantly predict every clinical scale except OCI-RC, including SHAPS, D-EQ, AMI Behavioural, AMI Emotional, P-IU, STICSA Trait Cognitive, I-IU, and STICSA Trait Somatic (see Table 7 for statistics and Table B10 for selected predictors). We could also significantly classify gender with 67% accuracy ($p < 0.0001$). These findings showed that participants' task behaviour alone had power to predict both clinical and demographic

measures. We subsequently tested the performance of models with only self-report measures for comparison (see Table 7).

Table 7

Results from Bayesian Regularized Regression with Predictor Selection

	R^2_{OOS} (*p* value)	Pearson's r or % accuracy (*p* value)		
Independent variable	All measures vs. control with only clinical/dem. measures	Model with task and self-report measures vs. null model	Model with task measures only vs. null model	Model with self-report measures only vs. null model
Compulsive checking	-0.065 (p=0.07)	0.24 (p<1e-05)	0.087 (p=0.05)	0.34 (p<1e-05)
Behavioural apathy	0.044 (p<1e-05)	0.29 (p<1e-05)	0.239 (p<1e-05)	0.22 (p<1e-05)
Emotional apathy	-0.017 (p=0.12)	NA (NA)	0.242 (p<1e-05)	0.30 (p<1e-05)
Anhedonia	0.000 (p=0.03)	0.27 (p<1e-05)	0.269 (p<1e-05)	0.10 (p=0.03)
Prospective intolerance of uncertainty	0.014 (p=0.03)	0.31 (p<1e-05)	0.217 (p<1e-05)	0.30 (p<1e-05)

Inhibitory intolerance of uncertainty	0.005 (p=0.22)	0.24 (p<1e-05)	0.174 (p<1e-05)	0.22 (p<1e-04)
Trait-cognitive anxiety	0.002 (p=0.02)	0.37 (p<1e-05)	0.200 (p<1e-05)	0.32 (p<1e-05)
Trait-somatic anxiety	0.007 (p=0.15)	0.29 (p<1e-05)	0.089 (p=0.04)	0.29 (p<1e-05)
Decentering	-0.008 (p=0.75)	0.32 (p<1e-05)	0.290 (p<1e-05)	0.26 (p<1e-05)
Gender	0.118 (p<1e-05)	70% (p<1e-05)	67% (p<1e-05)	59% (p<0.001)

3.5. Discussion

3.5.1. Summary

In this paper, we examined links between behaviour in a risky foraging task and psychiatric scores, demographic traits, and self-reported mood. We explored relationships between many variables in a discovery sample, pre-registered a series of hierarchical hypotheses and sub-hypotheses based on significant discovery sample tests, and then attempted to replicate these tests in an independent replication sample.

3.5.1.1. Transdiagnostic approach. We used a transdiagnostic dimensionality-based approach that analysed behavioural patterns beyond conventional diagnostic boundaries (Cuthbert, 2014; Stephan et al., 2016). Our large sample of participants exhibited scores ranging from healthy to clinically significant on psychiatric questionnaires (with a sizable portion of

participants in the clinically significant range, e.g. 26.8% for anxiety; see Table 3), allowing us to investigate partially correlated behavioural patterns that may be a feature of many psychiatric disorders. Our results also demonstrate that task-related behaviour and metacognitive self-report measures add power to predict behavioural dimensions beyond clinical and demographic measures alone.

We found links between task factors ('environmental factors'), behaviour, and mood; between clinical measures and task behaviour; and between gender and task performance.

3.5.2. Mood was linked with environment and homeostatic behaviour

We pre-registered our hypotheses based on a discovery sample (N=374) before testing them on a replication sample (N=702) here (though with a small divergence in statistical approach, see Methods Section 3.3.6). Consistent with expectations, analyses of participants' mood ratings showed that task environment was linked with mood (H1). Specifically, environmental factors including available reward, predator speed, and number of check directions moderated both excitement and stress ratings (H1A, H1B). In addition, virtual death affected stress and excitement in opposite ways (H1C), with participants tending to report greater stress and less excitement after being caught by a predator.

Although human emotional responses to stimuli are variable within and between subjects (Huys & Renz, 2017), evidence points to a broad link between situational factors and emotion across people. Appraisal theory posits that the nature and intensity of an emotional response to a situation is dependent on how the individual interprets the circumstances relative to their goals; an appraisal of a situation as particularly rewarding or punishing, for example, has been shown to relate to mood across participants (Ortony et al., 2022; Roseman, 1991). Through this lens,

the link between mood and block variables suggests that these variables effectively moderated participants' appraisals of being able to accomplish their goals.

From another perspective, emotions may be not just reactive but also useful for behavioural adaptation: an emotion may be considered a global cognitive state that helps manage limited cognitive resources by preparing an individual to behave appropriately according to their circumstances (Huys & Renz, 2017). Consistent with a view of emotions as adaptive, we found evidence of homeostatic interactions between stress and behaviour (H2). Specifically, stress had a homeostatic relationship with both reward- and threat-oriented behavioural modes (H2A): stress was linked with increased foraging and more efficient checking before predator discovery (H2Ai), and conversely, foraging and efficient checking were linked with reduced stress both before and after predator discovery. Evidence that stress was linked with a behavioural shift toward hiding rather than activity further indicated that behaviour and mood may serve to regulate one another (H2B). These findings are aligned with evidence of homeostatic relationships between mood and behaviour in humans. Such relationships, in which emotions both guide and are guided by behaviour, may help individuals keep mood fluctuations within more comfortable bounds, pursue positive affective states, and make advantageous decisions (Coricelli et al., 2007; Forgas & Ciarrochi, 2002; Gros, 2010; Hess et al., 2006; Naqvi et al., 2006; Taquet et al., 2020, 2021). One possible process for this is that pairing a behaviour with a positive mood transition leads to reinforcement of the behaviour, establishing a mechanism by which the behaviour then serves to regulate the emotion (Gros, 2009, 2010). Our findings fit with this theory: participants who gained energy through foraging and evaded threat through efficient checking were better able to achieve their task-related goals, and reported less stress; conversely, after reporting increased stress, participants pursued those same behaviours (H2A).

In addition, behavioural adaptation to mood is evidenced by the negative relationship between stress and any activity other than hiding (H2B). Humans under acute stress shift from goal-directed to habitual choices (Phelps et al., 2014; Schwabe & Wolf, 2009) and take fewer risks when faced with risk of reward loss (Pabst et al., 2013; Porcelli & Delgado, 2017), which may explain why stressed participants in our task engaged less with reward pursuit or threat monitoring and instead defaulted to hiding. While this behavioural response to stress may simply reflect a shift in cognitive resources from goal-directed, effortful decision-making to fear-related cognition (Hermans et al., 2014; Porcelli & Delgado, 2017), it may also serve to regulate mood by protecting stressed participants from further stressful experiences such as virtual death.

3.5.3. Clinical and demographic measures were linked with unique behavioural profiles

Analyses involving clinical and demographic measures showed behavioural links with compulsive checking (H4), anxiety (H5), intolerance of uncertainty (IU; H5), apathy (H6), anhedonia (H6), and gender (H7). Importantly, we found that dimensions that are often found together in disorders (compulsivity, anxiety – apathy, anhedonia) can be revealed to have unique behavioural signatures.

3.5.3.1. Compulsive checking. Compulsive checking (as measured by the OCI-RC subscale) was associated with increased vigilance and decreased foraging (H4A), although this general finding was primarily supported by evidence of particularly disorganized, sub-optimal checking (H4Aii). Compulsivity was also related to greater threat avoidance (H4B). Notably, the positive links between compulsive checking and both vigilance and avoidance are not at odds: hypotheses linking compulsive checking with increased and disorganized vigilance (H4A,

H4Aii) are supported by evidence of increased checking, while the hypothesis linking compulsive checking with threat avoidance (H4B) is supported by evidence of increased hiding (including hiding earlier, longer, and in response to threat). Together, these results provide a nuanced picture of behaviour characterized by trait compulsivity. One explanation for these findings is the 'vigilance-avoidance' theory of processing, which proposes that information processing in anxious individuals (including individuals diagnosed with Obsessive-Compulsive Disorder, or OCD) is marked by attentional bias toward threat during early, automatic stages of processing and avoidance of threat during later stages (Amir et al., 2009; Bar-Haim et al., 2007; Mogg et al., 1987; Mogg & Bradley, 2006). This pattern of information processing could serve to maintain anxiety by first amplifying anxiety through threat detection, then subsequently prolonging anxiety by preventing any further threat evaluation that could reduce anxiety (Bar-Haim et al., 2007). In our task, this could explain why participants scoring highly on compulsive checking paid more attention to threat by checking often, but then avoided re-engaging with threat by transitioning to prolonged hiding.

Another possible interpretation of the disordered nature of highly compulsive participants' checking behaviour is that anxiety delays attentional disengagement from threat (Bar-Haim et al., 2007; Fox et al., 2001, 2002; Yiend & Mathews, 2001). This theory would suggest that participants checked repeatedly on a known threat because they had difficulty shifting their attention away from threat search. It would also frame compulsive participants' disorganized checking—which included checking again immediately after ascertaining that there was no present threat, and conducting more partial scans of the environment—as prolonged attentiveness to threat and difficulty managing the vigilance/foraging trade-off.

Finally, compulsive checking was associated with changes in arousal: participants reported higher arousal (both stress and excitement) in general as well as in anticipation of predator arrival (4C). While the behaviour of highly compulsive participants may fit with existing theories of disordered information processing, evidence of their higher reported mood ratings (both stress and excitement) is less easily interpreted. Evidence of higher arousal may be linked to general difficulties in emotion regulation observed in patients diagnosed with OCD (Yap et al., 2018), but more work is needed to understand links between mood and compulsive checking when managing risk-reward trade-offs.

3.5.3.2. Anxiety. We replicated the link between the STICSA trait-somatic anxiety subscale and task-related measures (5B). Participants with high somatic anxiety were less vigilant due to self-reported threat-related worry and avoidance (H5B). One possible interpretation is that anxious participants had difficulty managing negative emotions in response to both real (seen) and imagined (unseen) threat, and this skewed the balance of their reward- and threat-oriented behaviour away from threat monitoring. This fits with a model of anxiety that frames anxious individuals' attentional avoidance as a strategy to regulate negative emotion (Amstadter, 2008; Cisler & Koster, 2010; Koster et al., 2006), particularly when exposed to threatening stimuli at longer (multi-second) durations (Mogg et al., 2004). A contributing factor could be that anxious participants checked less due to overestimating their knowledge about the environment. Evidence shows that trait somatic anxiety in particular is linked with underestimation of the relative uncertainty in an environment, leading to reduced information seeking (Fan et al., 2022; R. Smith et al., 2022).

In a previous study, Bach and colleagues (2020) did not find evidence that self-reported anxiety was associated with behaviour in a rodent-style approach-avoid conflict task where participants balanced reward pursuit with evading predatory threat. However, their task did not measure checking for threat, a behaviour that was integral to our anxiety-related findings. This highlights attention to threat as an important mechanism in anxiety pathology. Threat-related attentional biases have been repeatedly observed in anxious individuals, and recent work has begun to characterise downstream effects of visual attention on aversive learning—suggesting that attentional biases could have complex and wide-ranging consequences in anxious individuals' decision-making (Cisler & Koster, 2010; Frewen et al., 2008; Keogh et al., 2001; Mogg et al., 2000; Rinck et al., 2003; Wise et al., 2019). Our results demonstrate not just how anxiety affects attention to threat but more broadly how it impacts individuals' ability to balance their time between attention to threat versus reward.

3.5.3.3. Apathy and anhedonia. We found that behavioural apathy was associated with a shift from vigilance and threat-avoidant behaviour toward foraging, resulting in a higher final score (H6A, H6Ai). Notably, this behaviour was not linked with reward magnitude: apathetic participants were inclined to choose foraging over checking generally, without sensitivity to reward size. This is surprising given that individuals with behavioural apathy are thought to be highly sensitive to the effort cost of an action, biasing cost-benefit decision-making away from reward pursuit (Bonnelle et al., 2015). One interpretation of our results could be that apathetic participants may have been unwilling to switch between behavioural modes, perceiving behavioural switching as an effort to be avoided. Apathy has been linked with decision inertia—persevering with a behaviour for longer than is optimal in order to avoid making a decision about

redirecting behaviour (Scholl et al., 2022). In our task, foraging is in one sense a 'default' action (i.e., it is easier to decide when to forage than when to check, because threats are unseen while potential rewards are always visible); observing that apathetic participants persevered with foraging and avoiding switching to vigilance therefore reinforces a link between apathy and decision inertia. It is important to highlight here that in this case behavioural apathy benefitted task performance, showing that the apathetic dimension does not always entail dysfunction. This is consistent with the ecological view that atypical computation styles are not bad by definition and their utility depends on the individual's goals and circumstances.

Another possible interpretation is that apathetic participants were averse to the emotional perturbation of threat-oriented behaviour. Apathy has largely been studied in the context of effortful reward gain (Heron et al., 2019), and to our knowledge no previous work has explored the effects of apathy in the context of risk-reward decisions in which both actions require similar effort. We speculate that when choosing how to act, behavioural apathy may affect the subjective perception of effort associated with different behavioural modes. Given that apathetic participants reported increased emotional sensitivity to threat (e.g. they reported feeling more stressed after seeing a predator, see H6Aii in Table B4), apathetic participants may have perceived the arousal associated with vigilance as a cost to be avoided.

In another finding, we linked anhedonia with a self-reported decrease in the feeling of task engagement (H6, H6Bii); for example, anhedonic participants were less likely to report foraging as long as possible before hiding, and they reported lower excitement (see H6Bii, Table B4). Anhedonic individuals demonstrate an inability to enjoy and lack of motivation toward typically rewarding activities (Husain & Roiser, 2018; van Roekel et al., 2019), and have difficulty using reward-related information to guide decisions (Kieslich et al., 2022; Treadway

et al., 2012; Treadway & Zald, 2011b). Our findings fit with this characterization of anhedonia and highlight that this persists even when reward gain is in direct contrast with threat-related experiences.

Importantly, the behavioural patterns associated with apathy and anhedonia underscore the distinction between the two behavioural dimensions. Although they share some aspects (e.g., loss of motivation to pursue pleasure, and being symptomatic of overlapping groups of psychiatric disorders), it is clear from evidence such as this that the two arise from different cognitive mechanisms.

3.5.3.4. Gender. Our main finding from analyses of demographic variables was a link between gender and task behaviour (H7). Women performed worse overall: they tended to favour vigilance over foraging (H7Ai), but despite checking more often and sooner, women also experienced virtual death more often, indicating their checking behaviour was suboptimal (H7Aii). This is aligned with a body of literature demonstrating greater and more successful risk-taking in men (Byrnes et al., 1999). Men have been shown to be less cautious and more successful in managing risk-reward trade-offs involving predatory threat (Bach et al., 2020), and males are more tolerant of financial risk (Fisher & Yao, 2017; Khor et al., 2020). Our findings broadly replicate this and add that female participants' cautious behaviour was specifically characterized by excessive information seeking. Women started checking earlier when threat was minimal, checked more often, and discovered threats earlier; despite having more threat-related information, however, they were less successful in using this information to gain reward and avoid being caught. One explanation for the gender differences in cautiousness and information seeking is differences in subjective probability estimation. Subjective estimates of probability

are influenced by factors including event utility and severity (Harris et al., 2009), and women have been shown to be more pessimistic about objective probabilities when gains are at stake (Fehr-Duda et al., 2006; Sarin & Wieland, 2016). In our task, the probability of predator presence increases linearly in the first 10s of the epoch; with reward at stake, women may have been more pessimistic about the duration of predator-free time they had in the epoch, and thus may have begun monitoring for threat sooner.

Another explanation for women's cautiousness may be that women preferentially process threat at higher levels of arousal. Women have been shown to rate unpleasant visual stimuli as more unpleasant and arousing than men (Bradley et al., 2001), exhibit greater cortical processing of threatening stimuli (E. Y. Kim et al., 2013), and report stronger emotions associated with economic risk (Eriksson & Simpson, 2010). Further, Lighthall et al. (2009) found that stress increased risk-taking behaviour in men but decreased it in women. In our task, women reported feeling more stressed in general and particularly in response to threat (H7B). Thus, preferential processing of threatening stimuli and greater stress in response to threat could help explain women's preoccupation with checking over foraging and their risk-avoidant behaviour.

Interestingly, however, greater emotional arousal did not manifest as greater response vigour (measured as the rate of pressing buttons that were still inactivated from recent button presses). Women's behaviour demonstrated lower response vigour—particularly in situations where it was typically increased (such as during high threat or high reward conditions; see H7C in Table 6). Thus, despite experiencing greater subjective arousal in response to threat, women displayed more cautiousness in action selection. This may reflect gender-based differences in response time to visual stimuli, in line with evidence that women respond slower to neutral-valence visual stimuli (Conroy & Polich, 2007; Shan et al., 2022) and emotional words (Sass et

al., 2010). Overall, our findings emphasize gender-based differences in risk-taking behaviours and demonstrate how these differences manifest in behavioural mode switching task.

3.5.4. Exploratory analyses showed the unique predictive power of our task

To complement our tests of conceptually grouped hypotheses, we conducted a comprehensive set of machine learning analyses to determine which of our measures were most predictive of clinical scores and gender. Analyses comparing models with task-related measures versus those without (i.e., testing against a control model containing only clinical and demographic measures) demonstrated that our task had predictive power beyond that of clinical and demographic measures alone. This indicates the potential for this and similar tasks to be a valuable addition to psychiatric clinicians' diagnostic toolbox. Further, behavioural task measures had predictive power independent of post-task self-report data. An assessment of mental illness based only on objective behavioural measures such as these would represent a significant departure from conventional self-report based psychiatric diagnosis. Thus, our task has not only contributed to our understanding of several distinct dimensions of mental health—it also has shown itself to be a valuable tool for identifying unique behavioural patterns associated with mental illness.

3.6. Summary

In conclusion, a large-scale online task requiring participants to switch between foraging and vigilance for predatory threat provided behavioural, self-report, and questionnaire data that we used to predict measures of compulsive checking, anxiety, apathy, anhedonia, and gender. We used pre-registered hypothesis tests to link clinical measures and demographics with unique

behavioural profiles and showed that task-related measures provided significant predictive power beyond clinical measures alone.

4. Chapter: An ancient subcortical circuit regulates the switching and re-orienting of behaviour to threat in humans

4.1. Abstract

Many psychiatric symptoms affect an individual's ability to balance their time effectively between threat- and reward-related behaviours. However, the process by which people decide to orient their behaviour toward threats versus rewards is poorly understood. We investigated neural activity associated with switching between foraging and vigilance with 7T fMRI. In a virtual naturalistic environment, participants freely switched between gathering rewards and monitoring and evading predatory threats. The activity of distributed neural network encoded threat level and transitioning to vigilance, including ACC, AI, LHb, DRN, SN, and VTA. Cortical and sub-cortical areas communicated about action selection and expected threat level and sub-cortical areas responded to threat discovery. A distributed neural network also encoded reward and reorienting toward foraging, including ACC, precentral gyrus, striatum, and DRN. Areas involved in both networks may be important in tracking behaviourally relevant information and flexibly reorienting behaviour.

4.2. Introduction

Anxiety and fear are prominent when mental health is poor. They are central features of psychological illnesses including generalized anxiety disorder, social anxiety, panic and obsessive-compulsive disorder. The understanding of cognitive and neural mechanisms related to fear and anxiety has benefitted from experimental paradigms in which the impact of fear-inducing stimuli on behaviour and neural activity can be investigated in the laboratory. Despite

their elegance and critical importance, such paradigms do not capture an important feature of fear-related behaviour in the everyday lives of humans and other animals: the balancing of attention between threat and reward. In everyday life people must attend vigilantly to stimuli that presage adverse events but also to the stimuli predictive of positive events. To thrive they must identify and respond adaptively to stimuli predictive of positive outcomes while ensuring that their pursuit is not curtailed by dangerous threats. For the modern office worker this might mean balancing pursuit of promotion and a higher salary while avoiding the depredations of difficult colleagues. For animals in natural environments the situation is analogous; daily life entails careful balancing between foraging for food while maintaining vigilance for predatory threats.

Focussing on the types of decisions that animals have evolved to make while foraging in natural environments has provided new insights into human reward-guided behaviour and brain mechanisms (Hunt et al., 2021; Kolling, Wittmann, et al., 2016; Kolling & Akam, 2017; Korn & Bach, 2018; J. M. Pearson et al., 2014; Rushworth et al., 2012). Similarly, it has been argued that considering how animals have evolved to deal with environmental threats may provide insights into fear and anxiety mechanisms both in normal and poor mental health (Bach et al., 2020; Mobbs et al., 2018, 2020; Scholl & Klein-Flügge, 2018). Here we examine how human participants balance attention between reward- and threat-related stimuli focussing on moments of transition between two behaviours – foraging for reward and checking for threats and; the first occasion on which checking led to actual threat detection. We do this in a gamified but carefully controlled task in which both reward and threat stimuli were presented in a quantified manner. We measured when participants either foraged for rewards or checked for predators. Thus, we measured behaviour when it was predominantly guided by reward (foraging) and when it was

predominantly guided by threat (checking) and in both behavioural contexts we quantified the environmental feature that drove the behaviours (rate of reward and rate of threat).

The type of behaviour examined—the focus on transition between threat-guided behaviour and reward-guided behaviour—is one important feature of the present study. The second is that we used 7T functional magnetic resonance imaging (fMRI) to identify the neural mechanisms mediating the transitions. The ubiquity of the need to balance reward-guided foraging and threat-guided vigilance and checking across all animals suggests an evolutionarily ancient origin and its possible mediation by some of the first cephalic neural circuits to have evolved. These are, however, of comparatively small size in humans, often overlooked, and difficult to measure without ultra-high field imaging. We focus here on one such candidate neural circuit centred on the lateral habenula nucleus (LHb) and dorsal raphe nucleus (DRN). While this circuit is present in primates it is unusual in that it is present in many vertebrates including even cyclostomes – jawless fish – that diverged from other vertebrates 550 million years ago (Freudenmacher et al., 2020; S. Hong & Hikosaka, 2008; Matsumoto & Hikosaka, 2007a; Stephenson-Jones et al., 2013, 2016). The DRN is an important source of serotonergic innervation and like other neuromodulatory systems, such as the dopaminergic system with its origins in the ventral tegmental area (VTA) and substantia nigra pars compacta (SN), its activity is under LHb control.

An important reason for looking at DRN and LHb is that both nuclei have been linked to depression and one way of conceptualizing depression is that a core feature is an inability to focus on rewarding stimuli (anhedonia) and a sustained focus on negative events. A series of recent studies have linked LHb to depression-like symptoms in rodent models (Cui et al., 2019; Hu, 2016; K. Li et al., 2013; Y. Yang, Wang, et al., 2018). The serotonergic system is also considered the first line pharmacological target in both depression and anxiety disorders

(Baldwin et al., 2014; M. Berger et al., 2009; Cipriani et al., 2018; Strawn et al., 2018). An additional reason, however, is that, while there is debate about which aspects of the environment and behaviour are linked to DRN activity, there is evidence that it includes both positive (reward) and negative (punishment) events (Cohen et al., 2015; Grossman et al., 2022; Khalighinejad et al., 2022; Matias et al., 2017). Therefore, to assess whether DRN has a role in tracking aversive features of the environment that drive anxiety-related behaviours such as checking, and balancing these against reward-driven behaviours such as foraging, we examined LHb and DRN activity and interactions and compared them with the activity of midbrain dopaminergic nuclei (SN, VTA).

Of course, the presence of cortex in the mammalian brain and its importance for many aspects of behaviour suggest that LHb-DRN interactions are likely to be influenced by cortical activity. The routes by which this might happen are, however, limited. There is little direct information about LHb connections in primates but only two cortical areas, anterior cingulate cortex (ACC) and anterior insula (AI) cortex have been shown to project to LHb in rodents (Ely et al., 2019; Torrisi et al., 2017; Yetnikoff et al., 2015). We therefore consider the role and interactions of these two areas. Intriguingly, in macaques, these two cortical areas—ACC and AI—have been shown to carry signals related to those seen in DRN (Khalighinejad et al., 2021, 2022; Meder et al., 2017; Wittmann et al., 2016, 2020). Further, AI and DRN have been shown to share functional connectivity related to harm avoidance behaviours (Meylakh & Henderson, 2016) and anxiety pathology (M. Kim et al., 2019). However, surprisingly little is known about these areas' activity in many situations including predatory threat and checking behaviour.

4.3. Methods

4.3.1. Subjects

24 healthy adult participants (15 females), aged 18 to 35, completed the study. Participants were paid £10 and £15 per hour for the online and scan sessions respectively, plus a performance-dependent bonus (£5.10 ± 0.86). Ethical approval was given by the Oxford University Central University Research Ethics Committee (Ref-Number MSD-IDREC-R55856/RE006). One participant was excluded from all analyses because they did not make enough 'check' actions to compute all regressors of interest in the model. Behavioural data from all other participants were included in analyses.

4.3.2. Task

We designed a gamified foraging task in which participants freely made a series of choices with the goal of earning as much money as possible. During the task participants used arrow keys to control an animated fish in an ocean environment where there was rewarding food (later translated to a bonus payment), threatening predators (leading to large point loss if they 'caught' the fish), and a hiding space (where participants could hide from the predators) (Fig. 20). Participants chose freely between three actions: 'forage' for food, 'check' for predators, and 'hide' in a safe space. Participants were trained on the task in an online session before the scan (Table C1) and tested on their knowledge with a multiple-choice quiz (Table C2). Each participant received one of two task schedules, each having the same scheduled blocks but in a different, randomised order.

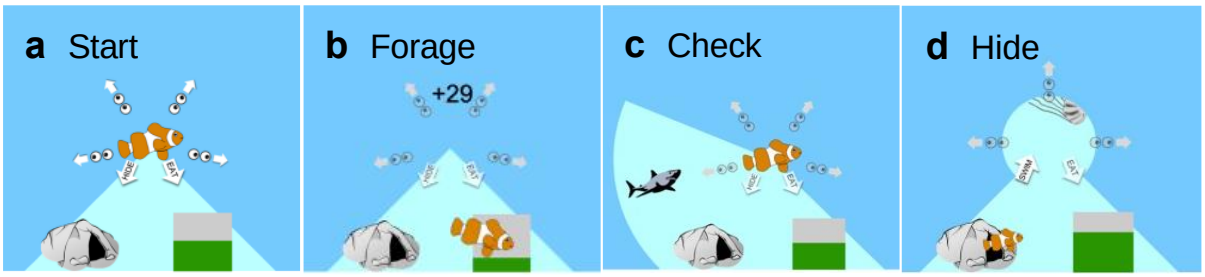


Figure 20. **Experimental task.** A) At the start of a block the fish begins in the centre position. In this block the surrounding area is divided into four sections that must be searched to determine whether there is a predator in the area. At left (not shown here) participants are shown their collected energy, number of lives gained (each 'life'=1 bar of energy), and time remaining in the current block (grey/black wheel). B) When foraging the fish dives down into the patch of food and the energy bar increases by the amount of reward gained. C) When checking, the fish checks in a particular direction. In this example the fish discovers that there is a predator in the area being checked. D) When hiding, the fish dives into a cave and is safe from the predator. It can see the predator reach the screen centre and then retreat, and with another button press the fish can return to the original centre position.

4.3.2.1. Forage. The average amount of food available varied randomly per second (range: 0-90 units). Participants could always see how much food was available. When foraging the fish dived down to obtain food (translated later into money; see Fig. 1B).

4.3.2.2. Check. Predators were hidden from participants' view unless participants pressed a button to 'check' a specific portion of the surrounding area (Fig. 1C). Predators appeared (after a random delay, 2-10.5s) at the edge of the screen and moved toward the fish's location at the screen centre. When the predator reached the centre of the screen it either caught the fish (causing the participant to lose one 'life') or, if the fish was in hiding (see below), the

predator quickly exited the environment (ending one 'predator epoch'). If the current predator was undiscovered, the section being checked advanced clockwise to the next section of the environment at each key press; after the participant discovered the predator's location, successive key presses re-checked the same location. Predator types (e.g. shark) differed in speed (10s, 15s or 20s to reach screen centre). Each block (see below) had only one type of predator, appearing one at a time, and participants were informed which before the block start.

4.3.2.3. Hide. Pressing the 'hide' button caused the fish to escape to a safe space where it could not be caught by the predator; a subsequent button press would return the fish to the centre (Fig. 1D).

4.3.2.4. Blocks. Each of 27 experimental blocks lasted 90s and had a different combination of (1) predator type (i.e. predator speed, three levels, see above) and (2) number of segments in which participants could check for predators (range 1-4). With fewer segments, more of the environment was visible during each check action and therefore fewer checks were required to survey the entire surrounding area. Each participant received one of three schedules, each having block and reward conditions randomly generated with the absolute value of all correlations between block variables kept below $r = 0.3$.

After each block, participants answered two questions about how they perceived the block: (1) "How stressful was the last round?" and (2) "How exciting was the last round?". Participants respond to each question by moving a slider to indicate a score between 0 and 100.

4.3.2.5. Timings. Each action involved a time cost: foraging took 1.5s, checking took 0.5s, hiding took 0.5s, and returning from hiding took 2s. Pressing a button inactivated all buttons for the duration of that action's time cost.

4.3.3. Questionnaires

In the online session, participants were asked for demographic information (age, gender, education level, English fluency, and visual acuity). They also completed previously validated questionnaires to measure psychiatric symptoms and traits: the Apathy Motivation Index (AMI; Ang et al., 2017), the State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA; Grös et al., 2007), the Snaith-Hamilton Pleasure Scale (SHAPS; Snaith et al., 1995), and the Obsessive Compulsive Inventory (Revised) 'Checking' subscale (OCI-RC; Foa et al., 2002). One question from each of the three AMI, SHAPS, and OCI-R questionnaires was repeated as an indicator of consistency.

After the experimental session, participants completed a 29-item debrief questionnaire in which they reported their metacognitive awareness of their task behaviour. They responded to a series of statements about the task by marking how often each statement was true for them. Response options were presented as a seven-point scale from 0 ('Never') to 6 ('Very often').

4.3.4. Behavioural Analysis

4.3.4.1. Choice analyses. We analysed participants' behaviour as a function of contextual factors. Separate models were fit to button presses occurring before the predator had been discovered ('pre-discovery phase') and after ('post-discovery phase').

For button presses occurring in the pre-discovery phase, we analysed the probability that each action was a check versus a forage given a combination of two contextual factors: reward magnitude, an indication of the amount of reward available that was always visible on-screen; and *time pressure,* a variable representing the amount of time since the participant had last been certain that there was no predator present which was updated with experience. Equation 20 demonstrates how *time pressure* was computed for a given time point *t* (in seconds) in block *b*:

$$\textit{Time pressure:} \qquad f(t) = \left(\frac{1}{minDelay + speed_b}\right) * (t - lastFullCheck_t) \qquad 20$$

where *minDelay* is the minimum possible delay for all predators in this task (2.5s), $speed_b$ is the number of seconds that the predator type in block *b* takes to reach the centre of the screen, and $lastFullCheck_t$ indicates, for timepoint *t*, the timepoint at which the participant most recently completed checking all areas of the environment (i.e., when they could be certain that no predator was present).

For button presses occurring after the predator had been discovered ('post-discovery phase'), we analysed 1) the probability that each action was a check or not, 2) the probability that each action was a forage or not, and 3) the probability that each action was a hide or not, based on three contextual factors: first, reward magnitude available at the time of each action. Second, a variable, *time since last check*, representing how long it had been since the participant had last seen the predator's location, as a percentage of the total time the predator was in the environment during that epoch (its speed). Equation 21 demonstrates how *time since last check* was computed for a given timepoint *t* in block *b*:

Time since last check: $$f(t) = \frac{t - lastCheck_t}{speed_b} \quad (21)$$

where $lastCheck_t$ indicates, for timepoint t, the timepoint when the participant last saw the predator, and $speed_b$ is the speed of the current predator type at block b. Third, a variable, *proximity,* that represented the amount of time until the predator would arrive and increased linearly with the predator's approach. Equation 22 demonstrates how proximity was computed for a given timepoint t within epoch e in block b:

Proximity: $$f(t) = t - (delay_e + speed_b) \quad (22)$$

where $delay_e$ is the scheduled delay for the predator in epoch e and $speed_b$ is the speed of the current predator type at block b. Variables *time since last check* and *proximity* were both included because they provided measurements of different threat-related information: *proximity* was an expectation of predator arrival based on task knowledge that was not updated (a kind of heuristic), while *time since last check* was an estimate of threat level that was updated based on experience and thus more difficult to compute. All analyses of choice data were computed as non-hierarchical Bayesian regression models using the package brms (Bürkner, 2017, 2018) with bernoulli(link='logit') link function. Regressions for both pre- and post-discovery phases were formulated as in Equation 23:

$$y_a \sim \beta_0 + \beta_1 reward_a + \beta_2 * t_{1a} \ldots \quad (23)$$

where y_a is a binary variable indicating whether each action a in the relevant phase was the target action (either check, forage, or hide), $reward_a$ is the reward available at the time of action a, and t_{ia} are the relevant threat-related variables computed for action a (see Table C3 for results and exact formulations). Regressors were z-score normalized and weak priors were set (normal distribution with mean 0 and standard deviation 3). Four chains were run with 4000 iterations and adapt_delta set to 0.8. Model fit was checked using Rhat < 1.1 and the absence of divergent samples. Model fits that did not meet these criteria were re-run with increased samples and adapt_delta. After computing each model non-hierarchically for each participant, we conducted two-tailed single-sample *t* tests across participants' coefficient estimates to determine the parameter's effect on choice data. Where outliers existed, test statistics are only reported as significant if the test was also significant with outliers excluded.

4.3.4.2. Reaction time analyses. We also analysed participants' inter-response times (IRTs) with respect to contextual factors such as action sequence. IRT was computed as the time in milliseconds between either the start of the block or the conclusion of the previous action (after the time cost associated with that action, when buttons were inactivated) and the next action. During analysis we found that participants often pressed buttons while they were inactivated (during the time cost of the most recent action) and we included these 'inactive' button presses in our IRT analyses. To the raw IRT values we applied a within-participant min-max transformation and across-participant outlier removal: Outlier values lower than the 25th quartile minus 1.5 times the interquartile range (IQR) and greater than the 75th quartile plus 1.5 times IQR across all participants were omitted. These analyses were computed as non-

hierarchical Bayesian regressions using the package brms (Bürkner, 2017, 2018) with 'shifted_lognormal' link function. Regressions were formulated as in Equation 24:

$$IRT_a \sim \beta_0 + \beta_1 reward_a + \beta_2 time_a + \beta_3 block_a + \beta_4 x_{1a} + \beta_5 x_{2a} \ldots \quad 24$$

where $reward_a$ is the current reward magnitude at action a, $time_a$ is the amount of time elapsed in the experiment at action a, $block_a$ is the block index for action a, and x_{ia} are contextual variables specific to each model (e.g., behavioural transition type) for action a. See Tables C5-C7 for specific model formulations and results. Modelling settings, model fit criteria, and parameter testing methods were the same as those used for the button press analysis (Section 4.3.4.1).

4.3.5. Neural Recording and Analysis

We used ultra-high field functional magnetic resonance imaging (7T fMRI) to identify brain activity corresponding to task behaviour.

4.3.5.1. Data acquisition. We used a Siemens 7T MRI scanner to collect structural and functional MRI. High-resolution functional data were acquired using a multiband gradient-echo T2* echo planar imaging (EPI) sequence with a 1.5 x 1.5 x 1.5mm resolution; multiband acceleration factor 3; repetition time (TR) 1962ms; echo time (TE) 20ms; flip angle 68°; and a GRAPPA acceleration factor 2. Field of view (FOV) covered the whole brain with axial orientation and a fixed angulation of -30° (anterior-to-posterior phase encoding direction; 96 slices). In addition, a single-measurement, whole-brain, functional image with similar orientation

(expanded functional image) was acquired prior to the main functional image and later used to improve registration of the main functional image. Structural data were acquired with a T1-weighted MP-RAGE sequence with a 0.7 x 0.7 x 0.7mm resolution; GRAPPA acceleration factor 2; TR 2200ms; TE 3.02ms; and inversion time (TI) 1050ms. To correct for magnetic field inhomogeneities a field map was acquired with a 2 x 2 x 2mm resolution; TR 620ms; TE1 4.08ms; TE2 5.10ms. Finally, cardiac and respiratory measurements were collected using pulse oximetry and respiratory bellows to regress out the effect of physiological noise in the functional data.

4.3.5.2. Data processing. Pre-processing was carried out using tools from FMRIB Software Library (FSL) (Jenkinson et al., 2012; S. M. Smith et al., 2004; Woolrich et al., 2009). Functional images were normalised, spatially smoothed (Gaussian kernel with 3mm full-width half-maximum), and temporally high-pass filtered (cut-off of 100s). Motion correction was performed using MCFLIRT (Jenkinson et al., 2002) and separation of brain from non-brain matter was performed using the Brain Extraction Tool (BET) (Jenkinson et al., 2005). Registration of functional images into Montreal Neurological Institute (MNI) space was carried out in three stages: first, the main functional image was registered to the expanded functional image using FMRIB's Linear Image Registration Tool (Jenkinson et al., 2002; Jenkinson & Smith, 2001) with three degrees of freedom (translation only); second, the main functional image was registered to the individual structural image using Boundary-Based Registration (BBR) (Greve & Fischl, 2009), incorporating Fieldmap correction; and third, the individual structural image was registered to standard space by using FMRIB's Non-linear Image Registration Tool (FNIRT) (Andersson et al., 2010).

4.3.5.3. Whole-brain analyses. Whole-brain statistical analyses were performed at two-levels as implemented in FSL FEAT (Woolrich et al., 2001, 2004). At the first (individual) level, we used a univariate general linear model (GLM) framework for each participant to estimate parameters. To account for temporal autocorrelations, first-level data were pre-whitened before group-level analysis (Woolrich et al., 2001). The contrast of parameter and variance estimates from each participant were then combined at the second (group) level in a mixed-effects analysis (FLAME 1+2). The results were cluster-corrected with the voxel inclusion threshold Z=3.1 and cluster significance threshold of p = 0.0001.

First-level analyses searched across the whole brain for voxels in which BOLD signal was associated with parametric variation in model variables. Our analysis split the time from the start of the delay period to the arrival of each predator ('predator epochs') into two phases: before the predator was discovered ('pre-discovery phase') and after ('post-discovery phase'). Model variables (see Fig. C1 for correlation matrix) were computed separately for each phase. For the pre-discovery phase (GLM1), model variables included (see behavioural regressions): *reward* and *time pressure* (see Eq. 20), formulated as in Equation 25:

$$GLM1\text{: } BOLD = \beta_0 + \beta_1 reward + \beta_2 timePressure \qquad 25$$

where *BOLD* is a column vector of time series data for a given voxel. For the post-discovery phase (GLM2), model variables included: *reward*; *time since last check* (see Eq. 21), and *proximity* (see Eq. 22), formulated as in Equation 26:

$$GLM2: BOLD = \beta_0 + \beta_1 reward + \beta_2 timeSinceLastCheck + \beta_3 proximity \quad (26)$$

where *BOLD* is again voxel time series data. Variables *time since last check* and *proximity* were both included because they measured distinct threat-related information (correlated at $r = 0.45$ for transitions to checking, $r = 0.41$ for transitions to foraging, and $r = 0.04$ for transitions to hiding; see correlations in Fig. C1). Regressors were modelled as stick functions (i.e., duration of zero), convoluted with a double-gamma hemodynamic response function (HRF). To reduce noise in the BOLD signal we added several task-unrelated confound regressors, including head motion parameters estimated by MCFLIRT in pre-processing; voxel-wise regressors created by physiological noise modelling (PNM) (Brooks et al., 2008) to model the effects of cardiac and respiratory noise; and regressors to remove timepoints corrupted by large motion that could not be corrected with MCFLIRT.

Whole-brain analyses were time-locked to actions that represented behavioural transitions (e.g., the first check after a series of forages). Time-locking to behavioural transitions allowed enough time to separate events for analysis. Effect Required statistics provided by lower-level FSL FEAT (Woolrich et al., 2001), a measure of each contrast's efficiency/estimability, indicated that the average BOLD percent signal change required for any contrast of interest in the pre-discovery phase across all participants was 1.83 ± 0.58 (maximum 2.595). Due to participants conducting fewer checks after discovering a predator, contrasts in the post-discovery phase were more difficult to estimate; average BOLD percent signal change required across post-discovery contrasts was 2.46 ± 0.91 (maximum 3.64). Consequently, tests

of post-discovery phase data (below) used only data from participants whose first-level statistics reported Effect Required below 2% for contrasts of interest (N=13).

4.3.5.4. ROI time course analyses. To study the activity of regions of interest (ROIs), anatomical masks were created for each ROI in the MNI standard space using a conversion of the Talairach structural atlas (transformed into MNI space; Lancaster et al., 2000, 2007; Talairach, 1988), mask templates from similar studies (Khalighinejad et al., 2021; Klein-Flügge et al., 2020), and cluster-corrected activations identified via whole-brain analysis. Next, masks were transformed from standard space to each participant's structural space by applying a standard-to-structural warp field, transformed from structural to functional space by applying a structural-to-functional affine matrix, and binarised.

These masks were used to extract time-series data for analysis. First, a first-level whole-brain analysis was conducted for each participant with only regressors of no interest (all forages and all pre-discovery checks). Time-series data from each voxel within each ROI were then extracted from the residual functional data. Next, time-series data were averaged across the voxels within each ROI, normalised, up-sampled 20 times with cubic spline interpolation, and epoched in 17s windows starting from 2s before the button press to 15s after. Finally, GLMs were fit to each time step of the epoched data.

Given that the delay in hemodynamic response means that a BOLD signal change reflects neural activity ~6s earlier (S. M. Smith et al., 2004), we partitioned the ROI time courses into two phases for analysis: an early phase (0-5s post-action) when neural activity associated with the action of interest first becomes observable, and a late phase (5-10s post-action) that may reflect secondary neural processes associated with the action of interest. In support of this, a two-way repeated-measures ANOVA showed a main effect of phase on group peaks [$F(1, 132)$ =

11.20, p = 0.001, η_p^2 = 1.44] such that parametric variation in *time pressure* was linked with greater BOLD response in the early phase (M = 0.10, SE = 0.01) than in the later phase (M = 0.04, SE = 0.01) across VTA, SN, and DRN ROIs while controlling for time elapsed. Some tests were carried out on only the early or late phase depending on the expected timing of the effect.

For each psychophysiological interaction (PPI) analysis, time courses were time-locked to action transitions in the pre-discovery phase and regressions were formulated as in Equation 27:

$$\begin{aligned} BOLD \sim\ & \beta_0 + \beta_1 transition_i + \beta_2 time_i + \beta_3 reward_i \\ & + \beta_4 timePressure_i + \beta_5 ROI2_i \\ & + \beta_6 (ROI2_i * transition_i) + \beta_7 (ROI2_i * v_i) \\ & + \beta_8 (transition_i * v_i) + \beta_9 (ROI2_i * transition_i * v_i) \end{aligned} \quad 27$$

where *BOLD* is a i x t (i button press action, t time samples) matrix containing the time-series data from a given ROI; $transition_i$ is a binary variable indicating the behavioural transition (switch to check or forage) associated with action i, with the transition of interest coded positively; $time_i$ is the time elapsed in the experiment at action i; $reward_i$ is the reward magnitude available at the time of action i; $timePressure_i$ is a measure of threat level at action i (see Eq. 20); *ROI2* is the time course for another area of interest at action i; and v_i is either *reward* or *timePressure* from action i depending on the effect of interest. To test for significance, we searched for peaks (or troughs) in each phase (early and late; see above) using a leave-one-out procedure to avoid any temporal selection biases: for a parameter of interest, a β weight value was selected for each participant from the time point identified as the peak average signal for the

group minus that participant (similar to the approach used in Khalighinejad et al., 2020). Selected values were tested via two-tailed single sample *t* tests. Further correction for multiple comparisons was considered unnecessary because ROIs were chosen based on their significance in cluster-corrected whole-brain analysis ($p < 0.0001$), which itself performs rigorous correction for multiple comparisons.

To test for overall effects of factors such as ROI location (cortical versus sub-cortical) and behavioural transition type on functional connectivity, we performed ANOVAs on fitted parameter peak values selected using the same method (see Tables C11-C19).

4.3.5.5. Replication analyses. To test whether key findings from our fMRI analysis replicated, we regressed variables of interest against ROI time course data with models formulated as in Equation 28:

$$ROI \sim \beta_0 + threat_i + \beta_2 reward_i + \beta_3 time_i \qquad 28$$

where *ROI* is the time course data processed as in the PPI analyses; $threat_i$ is a measure of threat level at action *i* as indexed by either *time pressure* or *proximity* for the pre- and post-discovery phases respectively; $reward_i$ is the reward available at action *i*; and $time_i$ is the time elapsed at action *i*. Models were fit for each ROI in the distributed neural circuits presented in the main text (ACC, AI, DRN, LHb, SN, and VTA for the threat-related circuit, and ACC, precentral gyrus, striatum, and DRN for the reward-related circuit), with separate models for the pre- and post-discovery phase data. Peaks were selected from parameters fit to pre-discovery phase data using the leave-one-out procedure (above). Here the peak search was constrained to a time window

dictated by significant PPI results reported in Table 9: For tests involving ROIs in the threat-related circuit, we used the range of mean peak times reported for all PPIs associated with action commission within that circuit; and the same for the reward-related circuit (excluded from this were mean peak times associated with very early action selection as in Fig. 24Aii and action outcome as in Fig. 25D-F). Selected peaks were tested with two-tailed single sample t-tests. Tests significant at the $p < 0.05$ level were then replicated using the equivalent parameters fit to post-discovery phase data. Peaks were selected from these parameters by searching within the time range that contained 95% of the selected peaks from the equivalent pre-discovery phase test. Selected peaks were then tested with a one-tailed single-sample t-test, with the tail corresponding to the direction of effect in the pre-discovery phase test. Results of replication tests are in Table C4 and Figure C2.

4.4. Results

We designed a task in which humans freely and continuously chose between foraging for reward or checking for predatory threat in a virtual environment. A third action – hiding – was also available and was taken on occasions when the threat was imminent. Participants attempted to gain as much reward as possible while avoiding being caught by a predator (an outcome that resulted in losing the accumulated reward of many foraging actions and therefore a partial bonus payment). Actions entailed time costs, so participants had to manage their time strategically to maximize reward. We show that activity in a distributed circuit centred on LHb and DRN continually reflects threat and, moreover, additional interactions occur across the circuit at the moment that the potential for threat comes to guide behaviour and participants started to engage

in checking. Activity in a partially overlapping network of cortical and subcortical structures encodes reward-related information during transitions back to foraging.

During the task (Fig. 21A-D) participants used arrow keys to control an animated fish in an ocean environment where there was rewarding food (later translated to a bonus payment), threatening predators (leading to large point loss if they 'caught' the fish), and a hiding space (where participants could hide from the predators). Participants chose freely between three actions: 'forage' for food, 'check' for predators, and 'hide' in a safe space. Here we focus on the two most frequent actions – foraging and checking – and the environmental variables – reward rate and threat level that drove the behaviours. Participants were trained on the task in an online session before the scan. The average amount of food available varied randomly per second (range: 0-90 units). Participants could always see how much food was available. When participants took the foraging action, the fish dived down to obtain food. Predators were hidden from participants' view unless participants pressed a button to 'check' a portion of the surrounding area (Fig. 21C). Predators appeared (after a random delay, 2-10.5s) at the edge of the screen and moved toward the fish's location at the screen centre. When the predator reached the centre of the screen it either caught the fish (causing the participant to lose one 'life', equivalent to 100 points collected via foraging and a partial bonus payment) or, if the fish was in hiding (see below), the predator quickly exited the environment (ending one 'predator epoch'). When participants took the checking action, if the current predator was undiscovered, the section being checked advanced clockwise to the next section of the environment at each key press; after the participant discovered the predator's location, subsequent check responses re-checked the same location. Predator types (jellyfish, squid, shark) differed in speed (10s, 15s or 20s) to reach screen centre. Each block had only one type of predator and participants were informed which

might appear before the block start. Pressing the ‘hide’ button caused the fish to escape to a safe space where it could not be caught by the predator; a subsequent button press returned the fish to the centre (Fig. 21D).

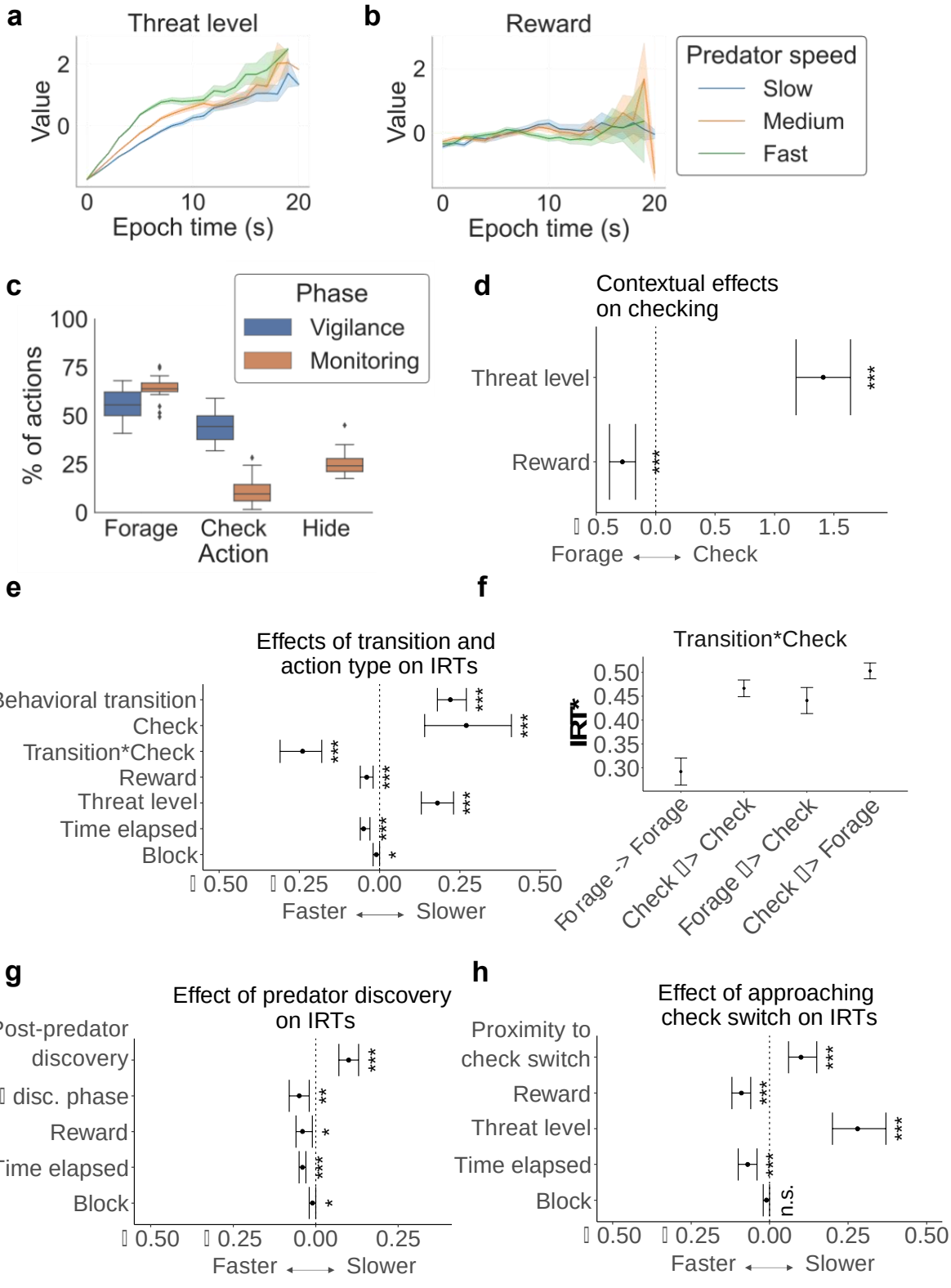

a
Threat level
Value
2
0
0
10
20
Epoch time (s)
b
Reward
Value
2
0
0
10
20
Epoch time (s)
Predator speed
Slow
Medium
Fast
c
Phase
Vigilance
Monitoring
% of actions
100
75
50
25
0
Forage
Check
Hide
Action
d
Contextual effects on checking
Threat level
Reward
***
***
0.5
0.0
0.5
1.0
1.5
Forage
Check
e
Effects of transition and action type on IRTs
Behavioral transition
Check
Transition*Check
Reward
Threat level
Time elapsed
Block
***
***
***
***
***
***
*
0.50
0.25
0.00
0.25
0.50
Faster
Slower
f
Transition*Check
IRT*
0.50
0.45
0.40
0.35
0.30
Forage -> Forage
Check -> Check
Forage -> Check
Check -> Forage
g
Effect of predator discovery on IRTs
Post-predator discovery
Pre- disc. phase
Reward
Time elapsed
Block
***
**
*
***
*
0.50
0.25
0.00
0.25
Faster
Slower
h
Effect of approaching check switch on IRTs
Proximity to check switch
Reward
Threat level
Time elapsed
Block
***
***
***
***
n.s.
0.50
0.25
0.00
0.25
0.50
Faster
Slower

Figure 21. Contextual factors influenced participants' decisions, including time pressure (A) and reward (B; reward appears flat because it is averaged here across all epochs); mean standardized value and 95% CI shown in 1s bins across the pre-discovery phase of the epoch. C-H) Contextual factors influenced pre-discovery phase action selection (forage or check) and IRTs. C) Box plots showing action type as a percentage of all actions. D) Group mean estimates and 95% confidence intervals from two-tailed single sample t-tests showing effects of model parameters on the probability that an action was a check. E, G, H) Group mean estimates and 95% confidence intervals from two-tailed single sample t-tests showing effects of model parameters on IRTs. E) There were main effects of behavioural transition, checking, and threat level (indexed as *time pressure*) on IRTs such that each significantly slowed reaction time (all $p < 0.001$). IRTs were significantly faster during higher rewards ($p < 0.001$). There was also a significant interaction between behavioural transition and checking ($p < 0.001$). F) Group mean and standard error for the average IRTs associated with each action sequence within each participant (*IRT values standardized). IRTs were slowest when switching from checking to forage and fastest when repeating foraging. F) There was a significant main effect of whether an action occurred immediately after discovering a new predator, such that discovering a predator slowed IRTs ($p < 0.001$; both pre- and post-discovery phase data analysed). H) IRTs between forages became significantly slower as they approached an upcoming switch to checking ($p < 0.001$). *p <0.05, **p <0.01, ***p <0.001, n.s.=not significant.

4.4.1. Participants Used Task-Relevant Information to Guide Behaviour

On average, participants' actions before predator discovery consisted of an approximately equal amount of checks and forages (44.68 ± 7.80% 55.32 ± 7.80% respectively; Fig. 21C) but once

the predator had been detected, behaviour changed; revelation of predator position was followed by participants focusing more on foraging (64.01 ± 6.14%) with only occasional checks that were now directed towards the known predator direction (10.75 ± 6.95%) and hiding actions (25.24 ± 6.15%; see Fig. 21C). The initial analyses, therefore, examined the 'pre-discovery phase' – the time period before the threatening stimulus was first seen when two actions, foraging and checking, were made with a similar frequency.

The moment-to-moment balance between the two behaviours – checking and foraging – was a function of two key features of the environment, the *time pressure* reflecting a predator's approach (the more time elapsed after the start of the block, the more likely the predator was to appear; see Eq. 20 in Methods Section 4.3.4; Fig. 21A) and the reward rate (Fig. 21B). Regression analyses (GLM1; see Methods Section 4.3.5) showed that before discovering a predator, participants were more likely to check instead of forage as *time pressure* increased ($t(22) = 12.94$, $p < 0.0001$, $M = 1.41 \pm 0.52$) and conversely as *rewards* decreased ($t(22) = -5.38$, $p < 0.0001$, $M = -0.28 \pm 0.25$; Fig. 21D; all t-tests in Table C3). A replication analysis using post-discovery phase data confirmed that participants behaved similarly in response to a comparable threat-related variable, *time since last check*; see Methods for modelling details and Table C3 and Figure C3 for results.

We analysed inter-response times (IRTs) to gain insights into the process of transitioning between behaviours. IRT was significantly affected by contextual factors: it was slower in response to threat level (*time pressure*; $t(22) = 7.30$) and faster in response to reward level ($t(22) = -4.56$, $p < 0.001$; Fig. 21E, Table C5). In addition, IRTs were influenced by the nature and order of actions: they were slowed when initiating a check ($t(22) = 4.23$; all $p < 0.001$; see Fig. 21E, Table C5) and when making a behavioural transition ($t(22) = 10.16$), with a significant

interaction between transition and checking ($t(22) = -8.07$, $p < 0.001$; Fig. 21E, Table C5). A closer look at this interaction revealed that mean IRT was slowest when switching from checking to forage and fastest when repeating foraging (Fig. 21F). These findings indicate that switching between behavioural modes requires greater cognitive resources and that, in particular, it is especially effortful to focus behaviour away from the pursuit of reward to monitoring the environment for threats.

We also looked at IRTs for evidence of additional cognitive processes occurring in preparation of a behavioural switch as well as after a switch to vigilance revealed a new threat. In support of this, IRT was significantly slowed by the discovery of a new predator ($t(22) = 6.18$, $p < 0.001$; Fig. 21G, Table C6). Finding that IRTs were slowed by predator discovery suggests that encountering a new threat requires additional processing relative to a check that does not reveal new information. In addition, IRT was sensitive to upcoming behavioural change. IRTs between forages became significantly slower as they approached a switch to checking ($t(22) = 4.4$, $p < 0.001$; Fig. 21H, Table C7). The gradual lengthening of IRTs prior to the transition indicates that preparations to switch began several seconds before actually switching, and further that these preparations required additional cognitive resources.

IRTs are widely thought to be an indicator of the time needed to compute not just response execution but also response selection (Sternberg, 1969; Sternberg et al., 1978, 1990; A. L. Wong et al., 2017). When sequences of actions are made, an especially long reaction time (RT) prior to the first movement suggests that not just the first movement, but also several subsequent responses, are planned before the sequence is begun (Sternberg, 1969; Sternberg et al., 1978, 1990). Similarly, a particularly long RT or IRT when switching tasks is indicative of prominent behavioural reconfiguration at the start of the new mode of responding (referred to as

'switch costs' in the task switching literature) (Monsell, 2003; Rogers & Monsell, 1995; Wylie & Allport, 2000). Main effects of behavioural transition proximity and the transition itself on IRTs suggests participants may have prepared for an upcoming transition by planning several actions ahead. Here long IRTs also indicate recruitment of greater cognitive resources associated with task switching and processing a threat discovery. In subsequent neural analyses we focus on understanding these behavioural transitions.

4.4.2. A Distributed Neural Network for the Monitoring of Threat and the Transition to Checking

The fMRI analysis was used to identify the neural circuits in which activity was differentially related to the two key behaviours – switching to checking and switching to foraging – and the two key environmental features that drove these behaviours – threat level (as indexed by *time pressure*) and reward. In addition to examining activity in the ROIs we also conducted a whole-brain analysis. We used GLM2 to analyse fMRI data, structured analogously to GLM1 used to analyse behaviour, to search for brain areas with activity linked to parametric variation in threat level and reward level during each key behaviour, and activity linked to the first instance of each behaviour – foraging or checking – on each occasion that participants switched between behaviours (referred to, respectively, as forage switch and check switch, modelled as constants in GLM2).

Variation in threat level at the time that participants switched to checking was linked to significant increases in activity across all six ROIs (ACC, AI, LHb, SN, VTA, and DRN), moreover the effect was so strong that this was apparent even in the whole brain cluster-corrected results ($p < 0.0001$; $Z > 3.1$; Fig. 22; Table 8; all clusters reported in Table C8) providing initial

evidence that these brain areas might constitute a distributed circuit spanning cortex and subcortical nuclei for orienting behaviour towards potential threats. The act of switching to check was also associated with significant activation in ACC (Fig. 22; Table 8).

While we focus here on ACC, AI, LHb, SN, VTA, and DRN, it was also apparent (Fig. 22; Table 8) that threat level during checking and the act of switching to checking was also associated with activity in superior colliculus (SC), pulvinar nucleus of the thalamus (PUL), and dorsal and ventrolateral parts of the periaqueductal grey (PAGd and PAGvl). This is consistent with the suggestion that these brain structures may mediate fast responses to threat stimuli (Kragel et al., 2021).

Plotting parameter estimates from our whole-brain analysis across the ROIs and contrasts (Fig. 22C, D) provided a broad picture of how ROIs encoded task-related variables. In general, threat encoding in all six ROIs was more prominent as participants switched to checking – the behaviour promoted by higher threat level (Fig. 22C)—as opposed to during switches to foraging it – the behaviour that declined with threat level (Fig. 22D). This difference was especially prominent in the two cortical regions, ACC and AI, and LHb. By contrast, switching to foraging was associated with decreased activity in all regions (Fig. 22D; Fig. 25A). In addition, activity related to reward levels, which promoted foraging, as opposed to checking, was negligible at the time of checking (Fig. 22D). Below we discuss reward rate-related activity at the time of switching to foraging, but at the time of checking the complete absence of reward-related activity throughout the brain suggested a strong attentional focus only on threat.

To examine relationships between DRN, LHb and the other ROIs, we conducted further analyses of how activity coupling between the areas evolved with threat level and the checking

behaviour it promoted using psychophysiological interaction (PPI) analyses (O'Reilly et al., 2012).

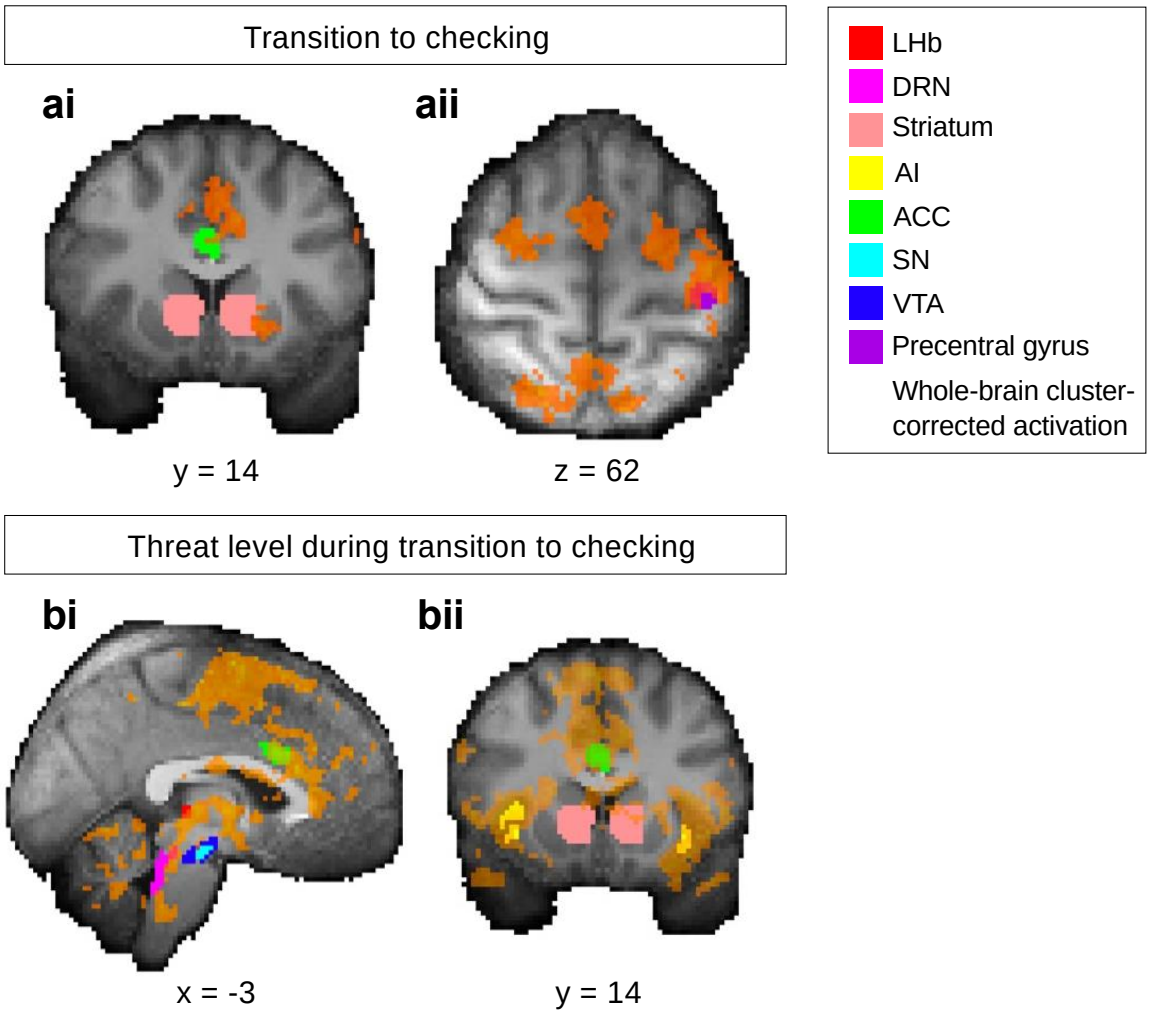

Transition to checking
ai
aii
y = 14
z = 62
LHb
DRN
Striatum
AI
ACC
SN
VTA
Precentral gyrus
Whole-brain cluster-corrected activation
Threat level during transition to checking
bi
bii
x = -3
y = 14
c
Switch to check: Threat circuit activity
Parameter estimate
4
2
0
−2
ACC
AI
LHb
DRN
VTA
SN
ROI
Contrast
Threat level during switch to check
Switch to check
d
Switch to forage: Threat circuit activity
Parameter estimate
2
0
−2
−4
ACC
AI
LHb
DRN
VTA
SN
ROI
Contrast
Reward during switch to forage
Switch to forage

Figure 22. **Activity related to transitions to checking and threat level.** A) Activity in ACC, striatum, and precentral gyrus is correlated with transitioning to check. Whole-brain analysis showed voxels where activity was positively associated with checking in ACC (Ai), striatum (Ai), and precentral gyrus (Aii). B) Activity in LHb, DRN, striatum, AI, ACC, SN, and VTA is correlated with *time pressure* (an indicator of threat level) during transitioning to check. Whole-brain analysis showed voxels with significant, cluster-corrected effects in LHb (Bi), DRN (Bi), striatum (Bii), AI (Bii), ACC (Bi, Bii), SN (Bi), and VTA (Bi). Whole-brain cluster-based correction, $Z > 3.1$, $p < 0.0001$. All results are from analyses of pre-discovery phase data. Legend indicates color-coding of ROI masks and whole-brain cluster corrected activation. C-D) Parameter estimates (mean and standard error) in ROIs associated with threat level as indexed by *time pressure*, reward level, and the effect of switching to checking or switching to foraging. C) The set of a priori ROIs (also activated in Figure 22) encode switching to check and threat level. D) The same areas are not activated by reward and they are deactivated by switching to foraging. Full ROI statistics from whole-brain analysis are reported in Table C9.

Table 8.

Whole-Brain Cluster-Corrected Activations and their Peak Values within ROIs

Time-locked action	Parameter	Cluster type	ROI	Peak MNI coord.	Peak Z	No. of voxels*	Cluster index
Check switch	Constant	Act.	Pulvinar	(-14, -22, 12)	4.44	38	1
Check switch	Constant	Act.	Striatum	(-16, 14, -2)	3.67	4	3

Check switch	Constant	Act.	ACC	(-2, 12, 32)	3.94	21	7
Check switch	Constant	Act.	Precentral gyrus	(-40, -24, 64)	4.54	23	7
Check switch	Threat level	Act.	ACC	(0, 16, 28)	5.30	95	2
Check switch	Threat level	Act.	DRN	(2, -30, -16)	4.43	22	2
Check switch	Threat level	Act.	LHb	(-4, -24, 0)	4.35	26	2
Check switch	Threat level	Act.	AI	(30, 22, -10)	6.00	422	2
Check switch	Threat level	Act.	PAG	(6, -30, -10)	4.28	37	2
Check switch	Threat level	Act.	Pulvinar	(8, -24, 14)	4.81	88	2
Check switch	Threat level	Act.	SC	(4, -28, -4)	4.61	50	2
Check switch	Threat level	Act.	SN	(-6, -20, -12)	4.19	57	2
Check switch	Threat level	Act.	Striatum	(-14, 18, 4)	4.18	24	2
Check switch	Threat level	Act.	VTA	(-4, -20, -14)	3.86	5	2

Forage switch	Constant	Act.	Precentral gyrus	(-40, -30, 64)	6.19	44	4
Forage switch	Constant	Deact.	Striatum	(8, 12, 2)	6.17	168	9
Forage switch	Constant	Deact.	DRN	(0, -32, -20)	4.46	34	12
Forage switch	Constant	Deact.	LHb	(-4, -24, 0)	4.97	31	12
Forage switch	Constant	Deact.	PAG	(4, -30, -6)	4.65	48	12
Forage switch	Constant	Deact.	Pulvinar	(10, -24, 0)	4.69	15	12
Forage switch	Constant	Deact.	SC	(-4, -30, -4)	5.51	77	12
Forage switch	Constant	Deact.	SN	(8, -26, -16)	4.26	58	12
Forage switch	Constant	Deact.	VTA	(-4, -12, -10)	3.76	6	12
Forage switch	Constant	Deact.	AI	(-30, 20, 10)	6.11	419	13
Forage switch	Constant	Deact.	ACC	(-2, 16, 24)	5.41	97	14
Forage switch	Threat level	Act.	LHb	(6, -24, 0)	3.74	6	1
Forage switch	Threat level	Act.	PAG	(4, -30, -10)	4.24	18	1
Forage switch	Threat level	Act.	Pulvinar	(10, -24, 0)	3.92	3	1
Forage switch	Threat level	Act.	SC	(4, -30, -4)	3.92	13	1
Forage switch	Threat level	Act.	AI	(32, 28, 4)	4.78	144	8

Forage switch	Threat level	Deact.	Striatum	(10, 12, -4)	4.54	57	6
Forage switch	Reward	Act.	Striatum	(-12, 14, 4)	4.24	63	2
Forage switch	Reward	Act.	Precentral gyrus	(-40, -24, 64)	3.85	8	3
Forage switch	Pre-disc. reward plus post-disc. reward	Act.	Striatum	(-16, 10, 0)	4.51	199	3
Forage switch	Pre-disc. reward plus post-disc. reward	Act.	Precentral gyrus	(-40, -22, 64)	3.93	10	5

Note. All Z > 3.1, $P < 0.0001$. All time-locked actions are from the pre-discovery phase unless otherwise specified.

*Where the cluster activation/deactivation overlaps with the ROI.

4.4.3. Interactions Across the Distributed Network for Threat Monitoring and Transition to Checking

We extracted the time course of neural activity within ROIs and examined interactions between LHb, DRN and the cortical ROIs – ACC and AI – as a function of threat level (*time pressure*), the transition from foraging to checking (as opposed to the transition from checking to foraging. As noted, these areas are anatomically connected with LHb and DRN and, in some cases, known to exhibit correlated activity that is measurable with fMRI (Ely et al., 2019; Hikosaka, 2010; Hu et al., 2020b; Linley et al., 2013; Torrisi et al., 2017; Yetnikoff et al., 2015). We found two types of interactions. The first occurred as a function of whether or not participants were going to switch from foraging to checking. The second also occurred as a function of whether or not participants were going to switch from foraging to checking but, in addition, this interaction also varied with the threat level determined by time pressure.

The first pattern of interaction, which occurred as a function of the switch to checking, was evident between ACC and LHb (two-sided Wilcoxon signed rank test, $Z = 3.28$, $p = 0.001$; Fig. 23Aii, Table 9; full PPI analyses results reported in Table C10). Stronger ACC activity was associated with stronger LHb activity when switching to check as opposed to switching to foraging (when, if anything the interaction pattern was in the opposite direction; Figs. 23iii and 23Aiv illustrate how the ACC-LHb relationship differed depending on switch direction, foraging-to-checking versus checking-to-foraging). Notably, the average peak time of this effect was shortly prior to the first checking button press. Given that the fMRI peak effect is delayed by the haemodynamic response function, the PPI effect probably reflects neural events that were occurring several seconds before the actual switch to checking. This is consistent with the behavioural evidence (Fig. 21H) that suggested that participants were preparing to switch to checking several seconds before actually making the transition. This pattern is specific to these areas; no evidence was found for similar interactions involving AI and DRN (Fig. C4A-C). To

demonstrate the specificity of the ACC-LHb pathway we carried out a factorial style analysis in which we examined interactions between two cortical regions, ACC and AI, and two subcortical regions, LHb and DRN. A two-way ANOVA revealed a main effect of cortical region (ACC and AI) on the extent to which switching to check moderated functional connectivity with subcortical ROIs LHb and DRN ($F(1, 180) = 7.03$, $p = 0.009$); Fig. 23Ai; Table C11); post-hoc Tukey HSD test found that peak values were greater on average for ACC than AI (p adj. = 0.012; 95% CI = [-0.04, -0.01]; Table C12). There was also a significant interaction between cortical and sub-cortical region (two-way ANOVA, $F(1, 180) = 16.13$, $p < 0.001$; Fig. 23Ai; Table C11), with mean peak values being highest for the interaction between ACC and LHb as a function of checking which, as reported above, was significant when tested in isolation.

The second pattern of interaction, encoding of threat level and switching to check between AI and DRN, is summarized in (Fig. 23Bii). It was similar to the first in that it was an interaction between a cortical and subcortical region that occurred as a function of switching to checking but now the interaction was between AI and DRN and it occurred as a function of an additional factor – *time pressure* – the environmental variable that drove participants to switching. Analysis of functional connectivity between AI and DRN revealed a significant three-way interaction between AI activity, threat level, and switching to check that modulated DRN activity ($Z = 1.98$, $p < 0.048$; Fig. 23Bii, Table 9; Table C10), such that stronger AI activity was associated with stronger DRN activity as a function of the transition to checking and as a function of *time pressure* (see Fig. 23Biii, 23Biv for depictions of how AI activity and *time pressure* affected DRN activity differently depending on the direction of transition). Again, this pattern of activity was a very specific one, and no evidence of similar interactions were found for similar interactions involving ACC and LHb (Fig. C4D-F). To demonstrate the specificity of the pattern

found in the activity of the AI-DRN pathway we again carried out a factorial style analysis in which we examined interactions between the two cortical regions, ACC and AI, and the two subcortical regions, LHb and DRN. There was a main effect of sub-cortical ROI (LHb and DRN; two-way ANOVA, $F(1, 180) = 11.11$, $p = 0.001$; Table C13) and a main effect of cortical ROI (ACC and AI; $F(1, 180) = 4.22$, $p = 0.04$; Table C13) on the extent to which switching to check and threat level moderated functional connectivity between the four regions. Post-hoc Tukey HSD tests found that peak values were on average greater for analyses with DRN as the sub-cortical ROI (p adj. = 0.001, 95% CI = [-0.06, -0.01]; Table C14) and greater for analyses with AI as the cortical ROI (p adj. = 0.047, 95% CI = [0.0003, 0.05]; Table C15).

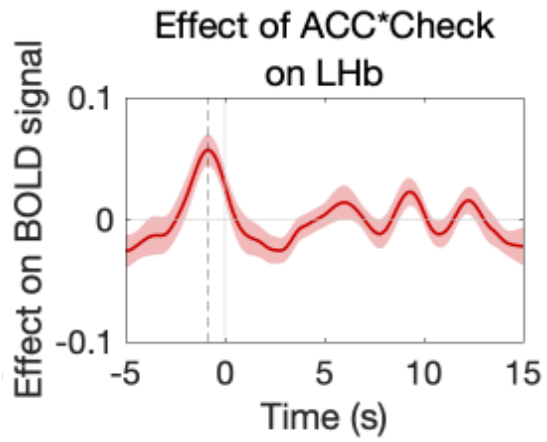
ai

2-Way ANOVA

		Cortical region[1,2]	
		ACC	AI
Sub-cortical region[2]	DRN	ACC*Check ↔ DRN	AI*Check ↔ DRN
	LHb	ACC*Check ↔ LHb	AI*Check ↔ LHb

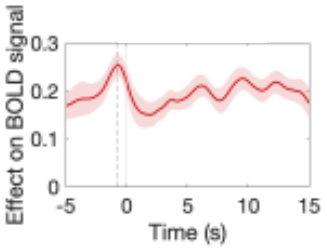
[1]Main effect ($p < .01$)
[2]Interaction effect ($p < .001$)

aii

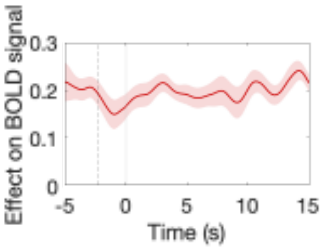


Effect of ACC on LHb:

aiii Switching to check



aiv Switching to forage



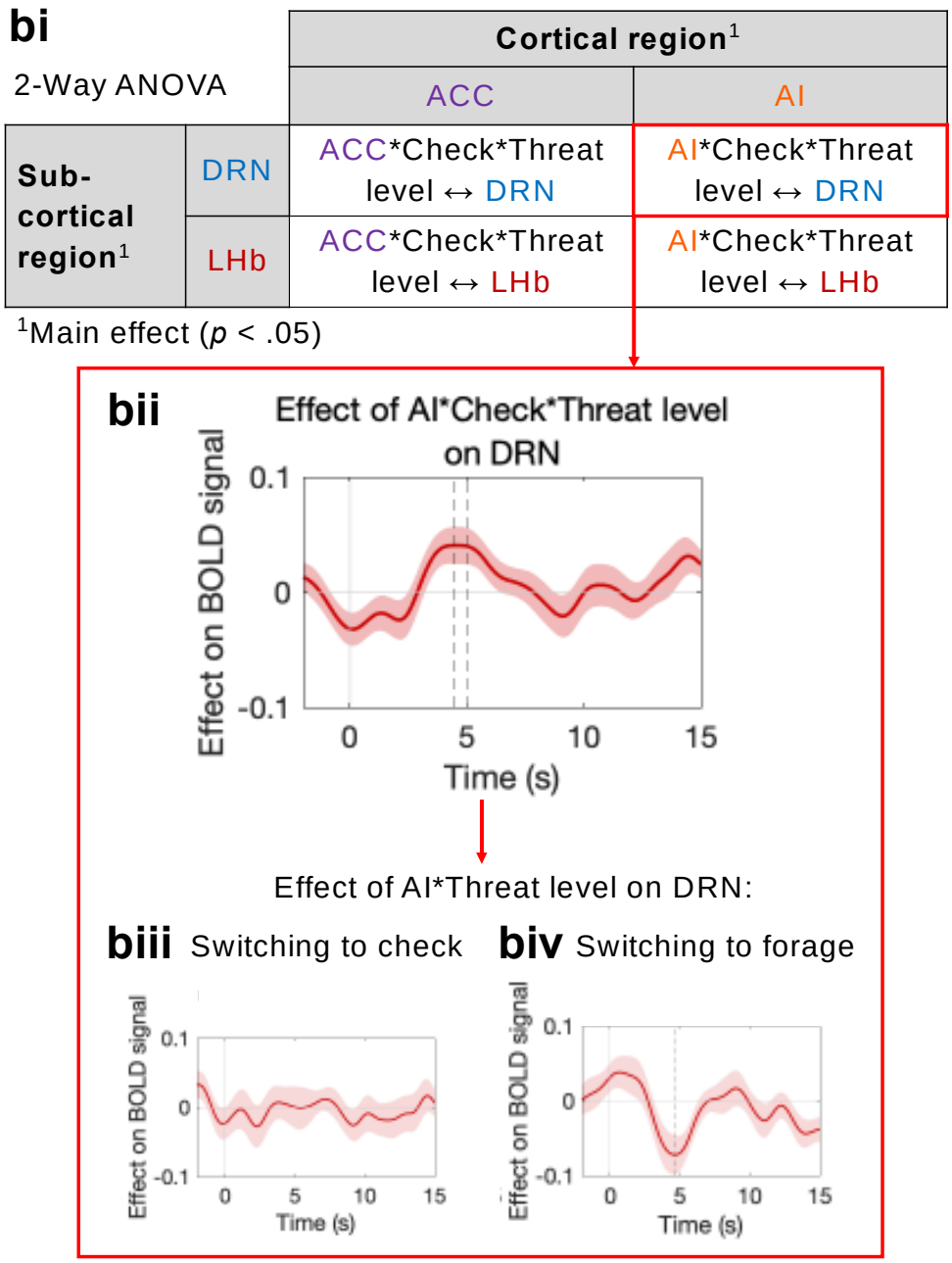


Figure 23. Early relationships between cortical areas ACC and AI and subcortical areas LHb and DRN were modulated as a function of transitioning to checking (A) and as a function of both transitioning to checking and *time pressure* (B). Ai) Two-way ANOVA showed a main effect of cortical region (ACC/AI; $p < 0.01$) and an interaction between cortical and sub-cortical region (LHb/DRN; $p < 0.001$) on the extent to which switching to check moderated functional

connectivity. Average peak values were highest for ACC and LHb activity moderated by checking. Other interactions tested in the ANOVA are plotted in Figure C4A-C. Aii) Functional connectivity between ACC and LHb was significantly moderated by switching to check ($p < 0.01$). ACC activity affected LHb activity differently during switching to checking (Aiii) versus switching to foraging (Aiv). Bi) Two-way ANOVA showed main effects of both cortical ($p < 0.05$) and sub-cortical ($p < 0.01$) ROIs on the extent to which switching to check and threat level (indexed by time pressure) moderated functional connectivity. Average peak values were highest for interactions with AI as the cortical ROI, and for interactions with DRN as the sub-cortical ROI. Other interactions tested in the ANOVA are plotted in Figure C4D-F. Bii) A three-way interaction between AI activity, switching to check, and threat level moderated DRN activity ($p < 0.05$). AI and threat level affected DRN activity differently during switching to check (Biii) versus switching to foraging (Biv). All analyses shown used pre-predator discovery phase data. Significance testing on time course data was performed using a leave-one-out procedure on the group peak signal. Dashed line indicates the average time of peaks across which two-sided Wilcoxon signed rank test was significant. Absence of dashed line indicates non-significance.

Table 9.

PPI Results: Two-Sided Wilcoxon Signed Rank Tests

ROI	Seed ROI	Regressor[2]	*P* value	Z	Mean	SD	Mean peak time[1] (s)	Figure

LHb	ACC	ACC*Check	0.001	3.28	0.05	0.06	-0.88	23Aii
DRN	AI	AI*Threat*Check	0.048	1.98	0.02	0.07	4.49	23Bii
DRN	AI	AI*Threat*Check	0.024	2.25	0.04	0.07	4.98	23Bii
SN	LHb	LHb*Threat*Check (Successful outcome)	0.015	-2.43	-0.10	0.20	8.61	24D
VTA	LHb	LHb*Threat*Check (Successful outcome)	0.003	-2.95	-0.10	0.13	8.71	24E
DRN	LHb	LHb*Threat*Check (Successful outcome)	0.036	-2.10	-0.08	0.19	7.43	24F
LHb	AI	AI*Threat	0.031	2.16	0.04	0.08	2.42	C5
SN	LHb	LHb*Threat*Check	0.031	2.16	0.03	0.06	6.35	24A
VTA	LHb	LHb*Threat*Check	0.033	2.13	0.02	0.06	5.76	24B
DRN	LHb	LHb*Threat*Check	0.042	2.04	0.02	0.05	5.27	24C
Striatum	Precentral gyrus	Precentral gyrus*Reward*Forage	0.048	1.98	0.03	0.06	0.06	C6A
DRN	Precentral gyrus	Precentral gyrus*Reward*Forage	0.029	2.19	0.03	0.07	4.98	C6B
Striatum	ACC	ACC*Reward*Forage	0.045	2.01	0.02	0.05	6.55	C6C
DRN	ACC	ACC*Reward*Forage	0.003	3.01	0.03	0.05	2.03	26Aii

[1]Average time of peaks across which two-sided Wilcoxon signed rank test was significant, relative to button press onset.

[2]'Threat' refers to regressors coded as *time pressure*. 'Check' refers to regressors coded to indicate switching from foraging to checking. 'Forage' refers to regressors coded to indicate switching from checking to foraging.

2.3.3.1. Habenula interactions with dopaminergic and serotonergic nuclei during re-orienting to threat stimuli. In the previous section we identified a direct route of interaction between cortex (AI) and DRN and a route of interaction between cortex (ACC) and LHb. The LHb is, however, itself an important source of influence over DRN, SN, and VTA (Hikosaka, 2010). When we used similar PPI approaches to examine relationships between LHb and the three other regions we found that, in each case, greater LHb activity was associated with greater activity in the target brain region as a function of both checking and threat level (*time pressure*). This effect was specific to switching to check but found in the interaction patterns of LHb with all three areas: two-way ANOVA showed a main effect of behaviour switching (switching to check vs. switching to forage) for the three-way interaction between LHb, threat level, and action ($F(1, 270) = 4.94$, $p < 0.05$; Table C16), with higher peak values associated with checks. The average time at which peaks were significant for each PPI analysis was 5.79s ± 0.54s after the time-locking event – the initiation of the checking action, suggesting (once the BOLD haemodynamic response is taken into account) that this effect was elicited at the onset of the checking action itself. Significance testing of peak values in separate PPI analyses confirmed functional connectivity with LHb was moderated by switching to check, threat level, and activity in SN ($Z = 2.16$, $p = 0.031$; Fig. 24B), VTA ($Z = 2.13$, $p = 0.033$; Fig. 24C), and DRN ($Z = 2.04$, $p = 0.042$; Fig. 24D).

Several features of the results are notable. First, that LHb and the serotonergic and dopaminergic areas interacted with one another as a function of both *time pressure* and behavioural switching suggests that LHb has access to threat-related activity from some other source such as ACC and/or AI. Indeed, further PPI analysis showed that early phase activity in LHb was moderated by an interaction between AI activity and *time pressure*, regardless of action type ($Z = 2.16$, $p = 0.031$; Table 9; Fig. C5). Second, the interactions between LHb and both dopaminergic and serotonergic areas are less specific than the AI-DRN route linked to behavioural switching in the previous section. Third, of interest is the positive nature of the relationships here; given that LHb is known to inhibit both midbrain dopaminergic and DRN serotonergic neurons, this finding is initially surprising. One possible interpretation is that there is a small but significant risk-related excitation between LHb and DRN, VTA, and SN. Although midbrain dopaminergic neurons largely encode reward prediction errors, some are thought to show an excitation that varies with risk within the context of win/lose uncertainty, during the time between a reward-predicting stimulus and an outcome (Fiorillo et al., 2003; Piantadosi et al., 2021; Schultz, 2010). DRN activity has also been reported to reflect reward variance (Grossman et al., 2022). Both LHb and VTA/SN/DRN activity may be activated by risk as a function of threat level while the participant anticipates the outcome of the check. The positive relationship between LHb and the other areas may reflect projections that also use the excitatory neurotransmitter glutamate; this has been reported in LHb afferents to DRN (Zhao et al., 2015) instead of the overall inhibitory relationship.

2.3.3.2. Sub-Cortical Regions Encode Threat Discovery. In the previous section we were concerned with proactive behaviours to potential threats as participants chose voluntarily

when to initiate checking for predators. Here, by contrast, we focus on the reactive aspect of threat monitoring when participants made a checking response that actually led to the new discovery of the predator. We did this by comparing checks that first led to predator discovery with checks that did not (we refer to this as the check outcome variable). Given that many checks did not lead to predator discovery, these discovery checks seemed to entail surprise and a slowing of the subsequent response (Fig. 21G). Because LHb and some of the regions that it projects to (the dopaminergic midbrain) have been reported to carry signals relating to surprising events, such as reward prediction errors (Bromberg-Martin et al., 2010; Matsumoto & Hikosaka, 2007a) and because there are similar projections from LHb not just to the dopaminergic midbrain but also the DRN (Hikosaka, 2010), we examined interactions between LHb and SN, VTA, and DRN using a PPI approach similar to that reported in the previous section. Now, however, in addition, the interactions were examined as a function of whether or not the check led to the discovery of a predator. We found that interactions within this circuit were sensitive to check outcome: Two-way ANOVA showed a main effect of predator discovery ($F(1, 132) = 23.77$, $p < 0.001$; Fig. 24A, Table C17) on late-phase peak values for the three-way interaction between LHb activity, switching to check, and threat level (*time pressure*) with all three areas (SN, VTA, and DRN). Notably, the average time at which peaks were significant for each PPI analysis was 8.25s ± 0.71s after button press; given the hemodynamic lag in the BOLD signal, this suggests that the three-way interaction effect of ROI activity, switching to check, and threat level on LHb activity was elicited by an event occurring slightly after the action itself such as the outcome – predator discovery or non-discovery that followed.

Significance testing of peak values in separate PPI analyses further revealed that predator discovery was linked with an inhibitory relationship between LHb and each ROI (SN, VTA, and

DRN) that varied by threat level. For these tests we focussed on activity time-locked to the checking action but in a late phase window because BOLD changes could not be expected to occur until after the time of the check outcome. PPI results showed that when a switch to checking resulted in predator discovery, functional connectivity with LHb varied as a function of both switching to check and threat level in SN ($Z = -2.43$, $p = 0.015$; Fig. 24E), VTA ($Z = -2.95$, $p = 0.003$; Fig. 24F), and DRN ($Z = -2.10$, $p = 0.036$; Fig. 24G). In each case greater LHb activity was associated with lower activity in the target brain region. This is consistent with evidence that LHb has an inhibitory effect on midbrain dopamine neurons in the VTA and SN (Brown et al., 2017; Stern et al., 1979; Y. Yang, Wang, et al., 2018) in response to negative-valence and aversive stimuli (Cui et al., 2019; Y. Yang, Wang, et al., 2018), and also plays a role in regulating DRN serotonergic neurons (Zhao et al., 2015). No such relationship was found for any target region when switching to check did not reveal a threat (Fig. 24H-J).

a

2-Way ANOVA		Outcome of switching to check[1]	
		Discovery	No discovery
ROI	SN	SN*Threat level*Disc. ↔ LHb	SN*Threat level*No disc. ↔ LHb
	VTA	VTA*Threat level*Disc. ↔ LHb	VTA*Threat level*No disc. ↔ LHb
	DRN	DRN*Threat level*Disc. ↔ LHb	DRN*Threat level*No disc. ↔ LHb

[1]Main effect ($p < .001$)

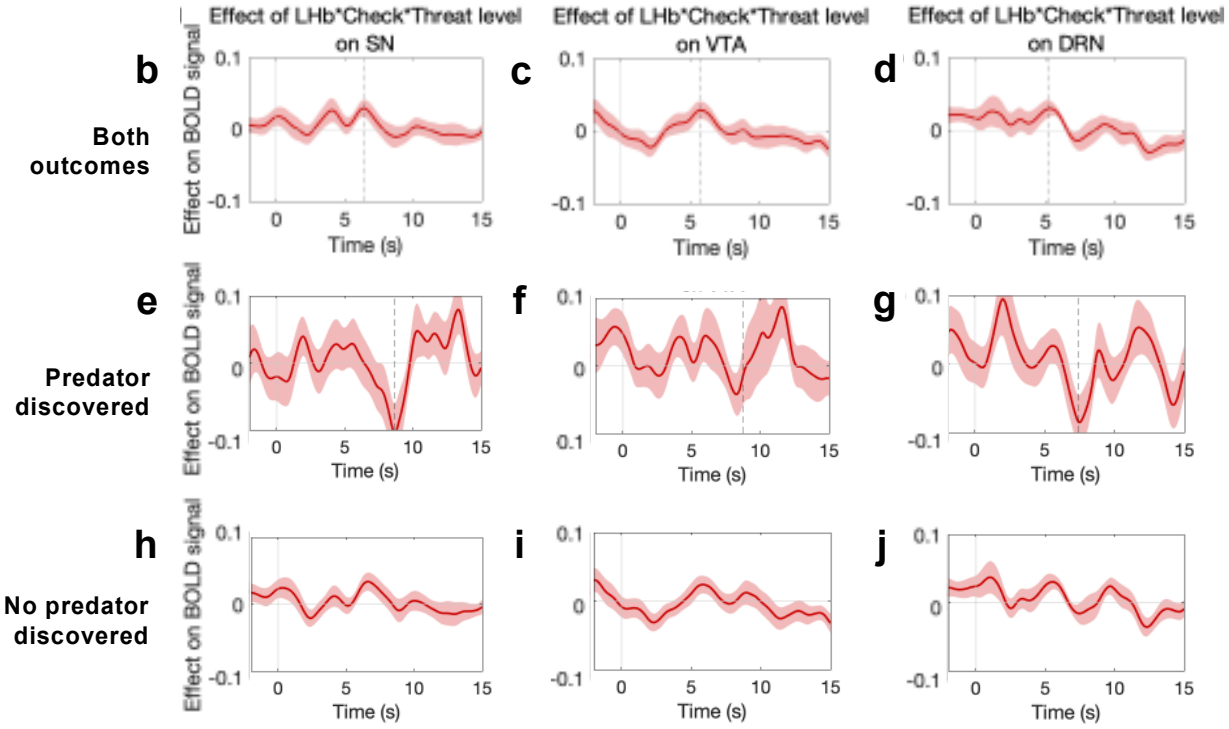


Figure 24. Functional connectivity between LHb and other sub-cortical areas SN, VTA, and DRN were affected by threat level, switching to check, and check outcome. A) Two-way ANOVA showed a main effect of check outcome (discovering a new predator vs. not; $p < 0.001$) on the extent to which switching to check and threat level moderated functional connectivity with LHb. B-J) PPI analyses showing interaction of influence of LHb activity, threat level (as indexed by *time pressure*), and checking on SN (B, E, H), VTA (C, F, I), and DRN (D, G, J). When we looked at all check trials (B, C, D) there was a three-way interaction between LHb activity, threat level, and switching to check on B) SN, D) VTA, and D) DRN activity; as threat

level increased, and when participants switched to checking, then higher LHb activity was associated with higher activity in SN, VTA, and DRN. Subsequent analyses looked at checks separately as a function of whether they revealed a predator for the first time (E, F, G) or did not reveal a predator (H, I, J). When a switch to checking revealed a new predator, there was an additional, slightly later, negative three-way interaction between LHb activity, threat level, and switching to check in SN, VTA, and DRN. The timing of positive interaction highlighted in panels B-D suggests that it is linked to the checking action itself while the later timing of the negative interaction on predator discovery in panels E-G suggests that it is linked to the discovery of the predator rather than the initiation of the checking action. Significance testing on time course data was performed using a leave-one-out procedure on the group peak signal. Dashed line indicates the average time of peaks across which two-sided Wilcoxon signed rank test was significant.

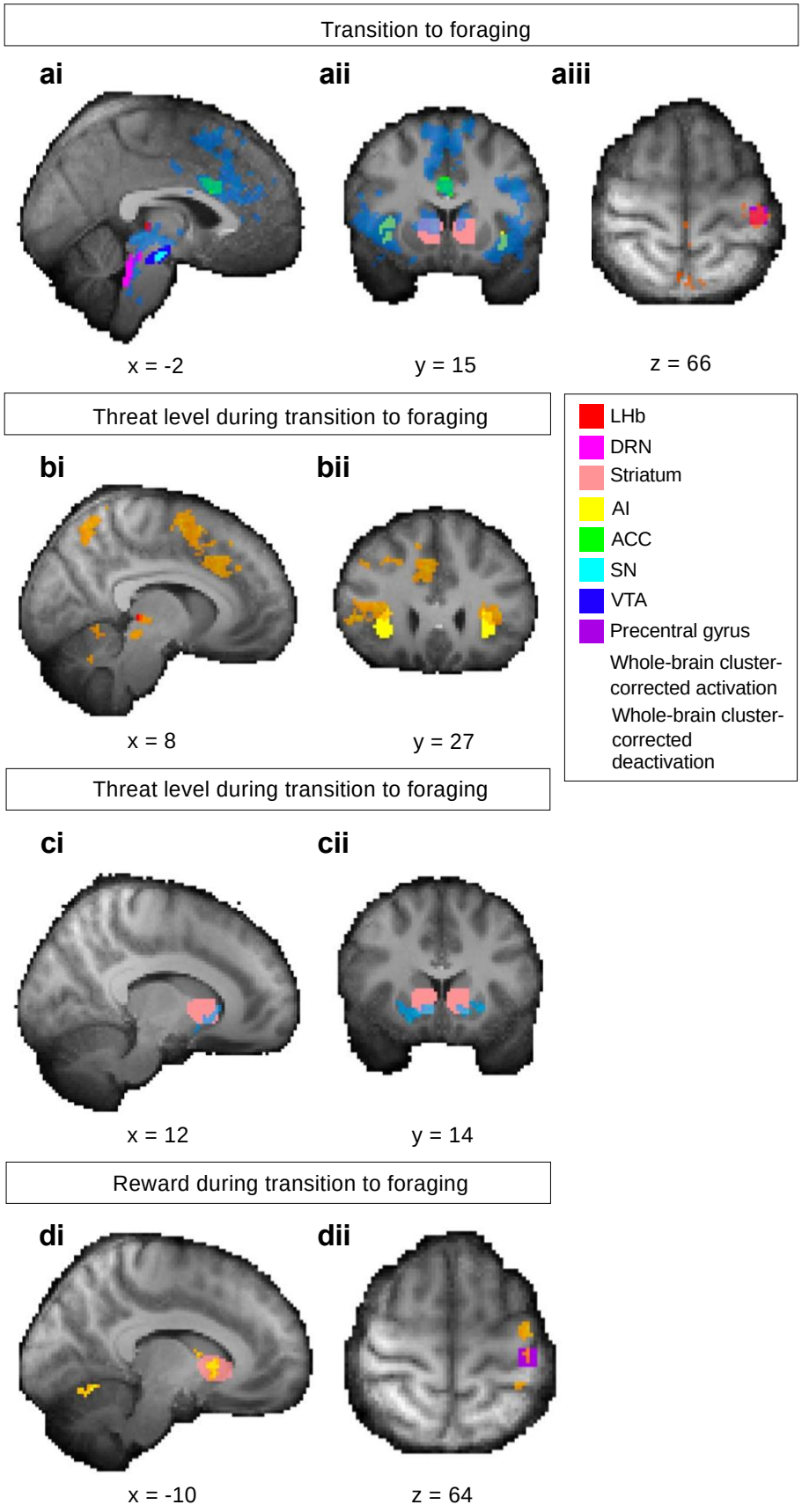
4.4.4. A Distributed Neural Network for the Monitoring of Reward and the Transition to Foraging

So far, we have focused on proactive transitioning from foraging to checking as a function of the potential for threat – *time pressure* – and as function of reactive detection of threat when the predator was discovered. In a final set of analyses we looked for evidence of a complementary neural circuit mediating behavioural transition in the opposite direction – from checking to foraging. When looking at the transition to foraging, we also considered reward level because transitioning from checking to foraging was promoted by higher reward levels (Fig. 21D).

First, we noted that the network of areas that was linked to threat and checking exhibited no reward related activity and, as previously noted, was less active during transitions to foraging

as opposed to checking (Fig. 22C, D). This is striking given that the actions participants made to forage or to check were very similar finger movements. The difference in the goal of the action—foraging or checking—rather than the manner of achieving the action meant that the distributed pattern of activity across the brain was profoundly different.

However, it was possible to find reward-related activity when participants were transitioning to foraging. It was especially prominent in the left striatum just dorsal to nucleus accumbens. The activity was notable on either side of the white matter in the internal capsule and the cross bridges spanning the white matter. Activity here was linked with parametric variation in *reward* during transitioning to foraging in the pre-threat discovery phase (Fig. 25; see Table 8). Another region of reward-related activity was also identified in the precentral gyrus in premotor cortex adjacent to motor cortex. Additionally, increases in activity related to the transition to foraging per se were also apparent in adjacent areas. One region was in the central sulcus and included motor cortex while the other was in the striatum close to the reward-related activation. Some reward-related activity was also identified in the ACC during transitions to foraging. Visualization (Fig. 25E,F) of reward-related activity during switches to foraging and to checking revealed that this area had a positive reward signal in the precentral gyrus during transitions to foraging that was greater than in transitions to checking. In addition, both striatum and precentral gyrus encoded reward during switching to foraging (Fig. 25E) to a greater extent than during switching to checking (Fig. 25F).


Transition to foraging
ai
aii
aiii
x = -2
y = 15
z = 66
Threat level during transition to foraging
bi
bii
x = 8
y = 27
Threat level during transition to foraging
ci
cii
x = 12
y = 14
Reward during transition to foraging
di
dii
x = -10
z = 64
LHb
DRN
Striatum
AI
ACC
SN
VTA
Precentral gyrus
Whole-brain cluster-corrected activation
Whole-brain cluster-corrected deactivation

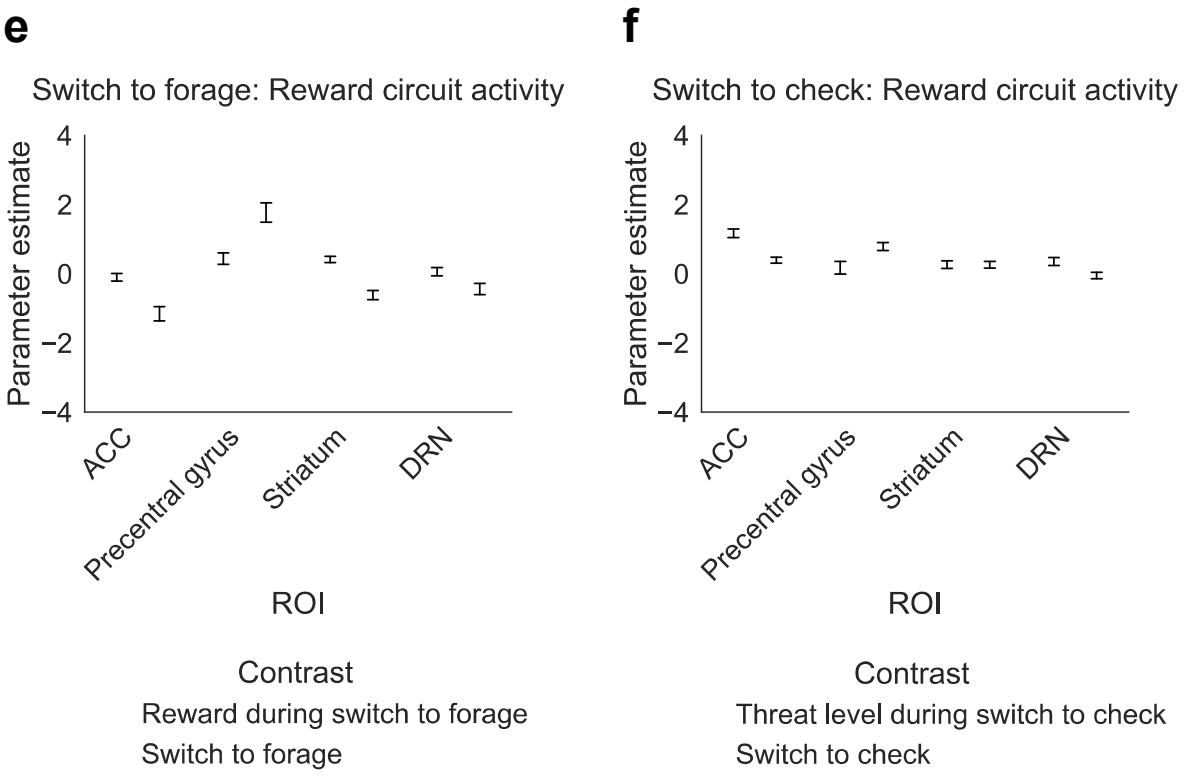


Figure 25. **Activity related to transitions to foraging, threat level, and reward.** A) Whole-brain analysis revealed activity in LHb, DRN, striatum, AI, ACC, SN, VTA, and precentral gyrus was correlated with transitioning to forage; there was less activity in the majority of these areas, LHb (Ai), DRN (Ai), striatum (Aii), AI (Aii), ACC (Ai, Aii), SN (Ai), VTA (Ai), when transitioning to foraging as opposed to checking although there was an increase in precentral gyrus (Aiii). B-C) Even at the moment of switching to foraging, whole-brain analysis showed activity in LHb (Bi) and AI (Bii) continued to be positively correlated with *time pressure*. There was also a significant relationship between *time pressure* and activity at the moment of switching to foraging in the striatum (Ci, Cii) but whole-brain analysis showed that the effect was negative. D) Activity in striatum (Di) and precentral gyrus (Dii) was correlated with reward level during transitioning to foraging. Whole-brain cluster-based correction, $Z > 3.1$, $p < 0.0001$. Legend

indicates color-coding of whole-brain cluster corrected activations, deactivations, and ROI masks. E-F) Parameter estimates (mean and standard error) associated with reward and during switches for foraging and the transition to foraging itself. E) There was a positive reward signal in the precentral gyrus during transitions to foraging that was greater than in transitions to checking. Some of the same areas exhibited activation associated with switching to check and threat level (F). Full ROI statistics from whole-brain analysis reported in Table C9. Significance testing on time course data was performed using a leave-one-out procedure on the group peak signal. Dashed line indicates the average time of peaks across which two-sided Wilcoxon signed rank test was significant.

4.4.5. Interactions Across the Distributed Network for Reward Monitoring and Transition to Foraging

Our analysis focused on one cortical area identified as relevant to reward-related activity in this task—the precentral gyrus—and the sub-cortical area—the striatal area in which a similar pattern was identified. Given their apparent central role in switching to checking, we also examined activity in ACC and DRN. PPI analysis partitioned into early and late windows showed a three-way interaction between precentral gyrus activity, reward, and switching to forage that modulated striatal activity ($Z = 1.98$, $p = 0.048$; Fig. C6A), occurring around the same time as the button press and thus likely elicited by preparation for the transition to foraging. The same interaction was related to DRN activity later in the peak search window ($Z = 2.19$, $p = 0.029$; Fig. C6B). Similarly, there was a three-way interaction between ACC activity, reward, and switching to forage that mediated striatal activity ($Z = 2.01$, $p = 0.045$; Fig. C6C) and DRN activity ($Z = 3.01$, $p = 0.003$; Fig. 26Aii). All interactions reflected a positive relationship

between the cortical ROI and target sub-cortical ROI that was stronger when switching to forage: a three-way ANOVA testing the effects of cortical ROI, sub-cortical ROI, and action type (switching to check vs. switching to forage) on the interactions depicted in Figures 26Aii and C6 found a main effect of behaviour transition—checking-to-foraging or foraging-to-checking—on peak values ($F(1, 361) = 43.07$, $p < 0.001$; Table C18) such that switching to forage was associated with higher peak values on average (post-hoc Tukey HSD test, p adj. < 0.001, 95% CI = [0.02, 0.05]; Table C19). There was also a significant interaction between sub-cortical ROI (DRN or striatum) and behaviour transition type ($F(1, 361) = 5.71$, $p = 0.017$; Table C18), with the highest peaks associated with the DRN during switching to forage. Further analysis of the ACC-DRN interaction during transitions to foraging or to checking revealed the origin of the three-way interaction; the interaction between ACC and DRN remained at a fairly constant level during the transition to foraging (Fig. 26Aiv) but they were suppressed as a function of reward levels during the transition to checking (Fig. 26Aiii).

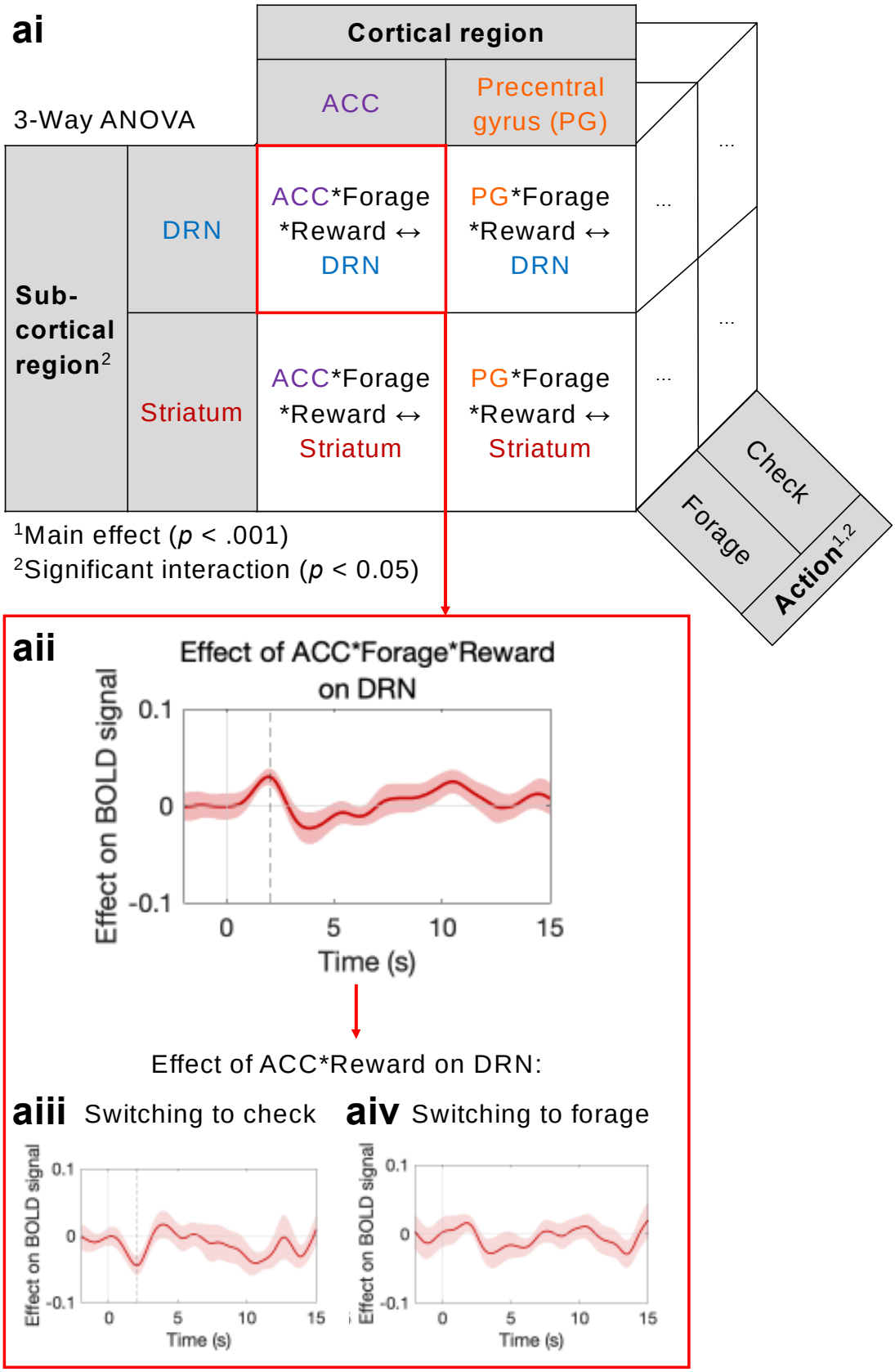

ai
Cortical region
ACC
Precentral gyrus (PG)
3-Way ANOVA
Sub-cortical region[2]
DRN
Striatum
ACC*Forage *Reward ↔ DRN
PG*Forage *Reward ↔ DRN
ACC*Forage *Reward ↔ Striatum
PG*Forage *Reward ↔ Striatum
Check
Forage
Action[1,2]
[1]Main effect (p < .001)
[2]Significant interaction (p < 0.05)
aii
Effect of ACC*Forage*Reward on DRN
Effect on BOLD signal
Time (s)
Effect of ACC*Reward on DRN:
aiii Switching to check
aiv Switching to forage

Figure 26. Relationships between cortical areas precentral gyrus and ACC and subcortical areas striatum and DRN were affected by reward level, subcortical ROI, and behavioural transition type (switching to check vs. forage). Ai) Three-way ANOVA showed a main effect of action transition type (switching to check vs. switching to forage) ($p < 0.001$) and an interaction between action and subcortical region (striatum/DRN; $p < 0.05$) on the extent to which behavioural transition and reward moderated functional connectivity, with the highest peak values associated with DRN and switching to forage. Other interactions tested in the ANOVA are plotted in Figure C6. Aii) A three-way interaction between ACC activity, reward, and switching to forage modulated DRN activity ($p < 0.01$). The interaction between ACC and reward affected DRN activity differently during switching to check (Aiii) versus switching to forage (Aiv).

4.5. Discussion

Life in naturalistic environments requires the balancing between reward pursuit and threat monitoring. While progress has been made in understanding mechanisms underlying reward- and threat-guided behaviour independently, decisions to switch between the two behavioural modes are not well understood. In addition to the fundamental importance of such decisions, individual variation in how they are taken is related to individual variation in clinical anxiety scores (see Chapter 3 of this thesis). In the present experimental paradigm, participants were allowed to freely manage their time and to decide themselves when to switch between foraging for rewards and checking for approaching predators. Our analysis focused on transition points where participants changed their behaviour in order to capture mechanisms leading up to and facilitating a shift in behavioural motivation. We also focused a large part of our analysis on behaviour that occurred before a participant had discovered a predator in the environment (the

'pre-threat discovery phase'), because during this phase checks constituted a much higher proportion of participants' actions—which allowed us to examine transitions between extended checking and foraging sequences.

First, we demonstrated that participants considered contextual factors such as reward and the prospect of an approaching predator (*time pressure*) when selecting actions. Participants were more likely to check for predators when an approaching predator was likely, and more likely to forage when available reward was high. We also analysed inter-response times (IRTs) to gain insight into how contextual factors affected the time needed to select and execute actions. IRTs were hastened by high rewards and slowed by threat. In addition, IRTs were slowed by transitioning from foraging to checking (Fig. 21E, F) and slowed after discovering a new predator as a function of greater predator speed (Fig. 21G)—indicating that re-orienting to vigilance and processing a new threat encounter may require particularly effortful processing.

Next we used ultra-high field imaging to examine neural activity associated with these behavioural transitions. We focused on a group of *a priori* selected cortical and subcortical structures known to be involved in phenomena such as harm avoidance, anxiety and depression: a circuit including the lateral habenula nucleus (LHb), dorsal raphe nucleus (DRN), ventral tegmental area (VTA), substantia nigra pars compacta (SN), and striatum, as well as cortical structures anterior cingulate cortex (ACC), anterior insula (AI), and precentral gyrus. The first two are known to monosynaptically interconnect with both the LHb and DRN while precentral gyrus has a well-established role in the selection and initiation of action (Passingham, 1993; Shenoy et al., 2013; Wise et al., 1997). In examining activity in these areas and relationships between these structures with a series of psychophysiological interaction (PPI) analyses, we discovered two distinct, distributed neural networks: one underlying the monitoring of threat and

switching from foraging to vigilance, and another tracking reward and switching from vigilance to foraging.

With whole-brain analysis we confirmed that variation in threat level when participants switched from foraging to checking was associated with increases in activity across LHb, DRN, VTA, SN, ACC, and AI, while the action of a check switch itself was linked with significant activation in ACC and LHb—suggesting the presence of a distributed circuit spanning both cortical and subcortical structures integral to tracking and orienting behaviour toward threat. We proceeded to extract BOLD signal from these areas and demonstrated several functional relationships within this circuit. First we showed evidence of functional relationships encoding threat anticipation and vigilance planning between several cortical and subcortical ROIs. Consistent with evidence of positive functional connectivity between AI and DRN (Beliveau et al., 2015) and that both have been found to respond to aversive events such as losses (Johnston et al., 2015), we found that the functional connectivity between AI and DRN was mediated by both threat level and switching to check (Fig. 23Bii). We also showed that the functional relationship between ACC and LHb was moderated by switching to check (Fig. 23Ai)—notably peaking immediately prior to the button press. The early timing of each of these relationships—peaking less than 5s after a switch to forage button press—indicates that the functional relationships described here play a role in encoding threat anticipation and planning a transition to vigilance. While preparing to switch to vigilance was encoded by each pairing (AI-DRN, ACC-LHb), threat anticipation (i.e., encoding of expected threat level) was specific to the AI-DRN relationship.

Next we showed evidence of functional relationships encoding threat level and vigilance among sub-cortical regions that were sensitive to check outcomes. With analyses of extracted

BOLD signal from SN, VTA, DRN, and LHb we showed that functional connectivity between LHb and each other region was mediated by threat level and switching to vigilance *after* action commission—and that this was sensitive to check outcome (i.e., whether the check revealed a new threat or not). When a new threat was discovered, a strong inverse relationship between LHb and each region was observed as a function of threat level and vigilance (Fig. 24E-G); this was absent when no threat was detected (Fig. 24H-J). These findings indicate that selected sub-cortical regions are critical for encoding threat response; further, they show that while LHb does not appear to encode threat level in anticipation of action selection alongside cortical regions in this case (Fig. 23E, F), it does encode threat level in response to threat encounters alongside other sub-cortical regions.

The pattern of LHb activity identified here contributes to an emerging understanding of its functional role. We found that LHb interacted with a higher-level cortical area (ACC) as well as other sub-cortical areas, SN, VTA, and DRN, that are important nuclei from which the ascending dopaminergic and serotonergic neuromodulatory systems originate) to encode decisions about orienting toward threat. This is consistent with evidence that LHb uses information passed from cortical regions—encoding both rewarding and aversive attributes of external stimuli—to control decisions about whether and when to act through its largely inhibitory connections with serotonergic and dopaminergic neuromodulatory systems (Boulos et al., 2017; Khalighinejad et al., 2021). Our results further emphasize that LHb plays a role not just in deciding whether to act but also in choosing the nature of the action—in this case, choosing vigilance over foraging. We also highlight that LHb activity extends to threat response, consistent with a potential role for LHb in facilitating expression of defensive behaviours in response to stress and fear (Benarroch, 2015; Namboodiri et al., 2016).

Whole-brain analysis further confirmed that variation in reward level when participants switched from checking to foraging was associated with increased activity in striatum and precentral gyrus, suggesting the presence of a distributed neural network involving in tracking available rewards and switching from vigilance to foraging. Extracted BOLD signal from these regions demonstrated functional relationships encoding reward levels and switching to foraging alongside ACC and DRN. We showed that striatal and DRN activity were both mediated by a three-way interaction between reward level, switching to foraging, and activity in precentral gyrus (Fig. 26A, B) as well as ACC activity (Fig. 26C, 26Di).

Of particular interest is the relevance of the DRN across many of our analyses: it encoded available reward, threat level, and transitions from foraging to vigilance and vice versa. One influential idea has been that DRN encodes a prediction error signal in response to aversive stimuli that might complement one for tracking rewards in dopaminergic nuclei (Daw et al., 2002; Dayan & Huys, 2009; Schweimer & Ungless, 2010). More recent research, however, has suggested that while DRN activity may indeed reflect aversive events it also reflects appetitive ones (J. Y. Cohen et al., 2015; Grossman et al., 2022; Iigaya et al., 2018; Khalighinejad et al., 2022; Lottem et al., 2018; Matias et al., 2017). Nevertheless, the induction of activity in DRN does not appear to be rewarding in a simple way but instead, it leads to changes in the choices animals make as a function of both costs and benefits; for example, after DRN stimulation, mice become more likely to wait through a delay to obtain a reward (Fonseca et al., 2015; Iigaya et al., 2018; Lottem et al., 2018; K. Miyazaki et al., 2011, 2012, 2018, 2020; K. W. Miyazaki et al., 2011, 2012, 2014). The current results suggest that this is because DRN is not simply concerned with the regulation of patience or motor inhibition when deciding how long to wait for a reward but, instead, that it has a more general role in regulating the impact that aversive and appetitive

prospects have on behaviour. In the current study, this is linked to the maintenance of reward-driven behaviour, foraging, even in the presence of potential aversive events and, *vice versa*, attention to potential aversive events – checking – despite the presence of rewards, and alteration between these two behaviours.

5. General Discussion

Flexibly switching between reward- and threat-oriented behaviours is critical for survival and ubiquitous across species. Although likely evolutionarily ancient, it is also common in modern human decision-making. Its importance in everyday human behaviour could make it a useful target in the study of mental health. Indeed, many symptoms of psychiatric disorders involve changes in appetitive or threat-oriented behaviours, including anxiety, fear, apathy, and anhedonia. The experiments presented in this thesis sought to understand switching between foraging and vigilance, including its fundamental mechanisms, its relationship to emotions and symptoms of psychopathology, and its neural correlates. This was carried out in three parts. First, an ecological task and cognitive model demonstrated that people track reward- and threat-related aspects of the environment—including latent variables—in order to switch behavioural modes. Second, a large-scale online study demonstrated a role for emotion in decision-making and linked symptoms of psychopathology to distinct behavioural patterns. Third, an ultra-high field fMRI study revealed networks of interconnected brain regions involved in tracking reward and threat and switching behaviours. Results contribute to a mechanistic understanding of task switching between foraging and vigilance and demonstrate the application of ecological, transdiagnostic approaches to understanding cognition in health and disease.

5.1. A Computational Account of Switching Between Foraging and Vigilance

Laboratory tasks paired with computational modelling have detailed many cognitive processes relevant to flexibly switching between reward- and threat-oriented behaviour, including information sampling, task-switching, vigilance, and foraging. Each behaviour is sensitive to both observed and latent variables. When choosing what information to sample, people consider

the perceived instrumental, emotional, and cognitive value of the information (Sharot & Sunstein, 2020). When choosing when to sample information, people weigh in factors such as uncertainty level and time horizon (Section 1.1.1). In task switching, the need to suppress the previous task results in switch costs that are sensitive to task priming and working memory load (Section 1.1.2). Vigilance and defensive behaviour are guided by threat proximity, which constrains the complexity of computation that can be carried out (Section 1.1.3), and when foraging, decision-makers track the reward statistics of their environment (Section 1.1.4). Through validating our computational model with simulation and analysing participant behaviour from online and fMRI datasets, experiments in this thesis found evidence that many of these factors affected performance and were used to guide decision-making.

5.1.1. Reward

Behavioural measures of choice and reaction time showed that participants considered the amount of reward available when allocating their time toward foraging versus vigilance. As expected, participants were less likely to check for predators when presented with a high reward, and higher rewards were linked with faster inter-response times (IRTs) (Fig. 21D, E, G, H). The link between high rewards and faster IRTs may reflect that the task design used in this thesis frames foraging as the ‘default’ action. Specifically, foraging was the only action for which the outcome was displayed on the screen in advance (participants could watch the level of available reward increase and decrease at all times), and foraging was always profitable, so predicting the outcome of foraging required no additional processing. Evidence that foraging was associated with reduced processing was shown in the Chapter 4 reaction time analysis: repeated foraging actions had the fastest IRTs of all behavioural sequences, faster even than repeated checking

actions (Fig. 21E, F). Therefore an optimal strategy is to default to repeatedly foraging until the utility of an alternative action reaches a certain threshold. High rewards may have led to faster IRTs because participants who adopted this strategy were already primed to forage and could quickly compute the benefit of the action. An interesting follow-up experiment might investigate the effect of adding uncertainty to the reward value: for example, hidden reward values that must be inferred based on experience (as threat level was inferred). Some behavioural dimensions related to psychopathology are sensitive to uncertainty in both reward and threat domains, such as intolerance of uncertainty (IU) (Gorka et al., 2016). It may be valuable to explore how tracking uncertainty across multiple domains affects behavioural transitions in health and disease.

5.1.2. Threat Level

Participants also calculated latent variables related to threat level and weighed them in their decision-making. Unlike reward level, threat presence and proximity were hidden from participants during action deliberation and had to be inferred based on task experience to decide when to check and hide. This appeared to require greater cognitive resources: an index of threat level was positively associated with longer IRTs, suggesting more effortful processing (Fig. 21E, H). In each computational model, participants used two types of threat level estimates. One was based on task knowledge, a mental model of how the task works (modelled as *predator probability* in the pre-discovery phase and *proximity* in the post-discovery phase; see Section 2.3.6). Another was computed based on experience and updated after sampling information about threat (i.e., after a check; modelled as *time pressure* in the pre-discovery phase and *time since last check* in the post-discovery phase; see Section 2.3.6). Their influence on task behaviour can be interpreted in two (compatible) ways. First, the use of both variables is consistent with

Fanselow and Lester's (1988) threat imminence continuum model, which proposed that threat proximity is a key factor guiding vigilance and defensive behaviours and mapped these behaviours onto varying levels of threat proximity. Even though the number of possible states and actions in this task is more constrained than in their continuum model, we still saw the effects of threat proximity in many behavioural and neural measures, indicating that participants were indeed tracking and adapting their behaviour based on estimates of threat proximity. Were we to expand on the number of states and actions possible in this task, we would likely observe a similar mapping of behaviours to proximity (e.g., strategizing when threat is distant, active defence when threat is imminent). Second, the use of threat estimates based on both updated experience and immutable task knowledge suggests that people use a combination of effortful prediction and cached, habitual values to improve performance while reducing computation. There is evidence that decision-makers compensate for cognitive constraints such as proximal threat by switching between or integrating complex models (e.g. model-based RL, optimal policy models) with computationally faster and simpler models (e.g. model-free RL, heuristics) (Keramati et al., 2016; Mobbs et al., 2020). Although the task used in these experiments obviated the need for learning models such RL, we still observed the use of both effortful prediction (updating threat level assessments based on checking outcomes) and a heuristic (knowledge of the average time until predator appearance), each of which might be sufficient alone but together suggest that participants engaged in balancing a need for response accuracy and computational efficiency. An interesting follow-up study might investigate factors that affect this trade-off in an ecological paradigm and how this is affected by symptoms of psychopathology such as anxiety.

5.2. A Mechanistic Understanding of Emotions, Traits, and Decision-Making

This thesis has examined not just foundations of switching between foraging and vigilance but also how the underlying mechanisms were affected by emotions and individual traits linked with symptoms of psychiatric disease. In a large online sample, participants rated their stress and excitement between task blocks and completed validated psychiatric questionnaires with subscales representing distinct behavioural dimensions (e.g., compulsivity, apathy). Data were analysed with techniques inspired by the emerging field of computational psychiatry, a framework for using computational methods to understand and improve mental health. Importantly, this framework focuses on behavioural dimensions that exist on a spectrum from health to disease and cut across traditional diagnostic profiles (Cuthbert, 2014; Dalgleish et al., 2020; Mitelman, 2019; Stephan et al., 2016). Results suggest that emotions play both reactive and regulatory roles in decision-making, and that specific psychiatric symptoms are linked to specific behavioural patterns that emerge in the semi-naturalistic scenario of the task. Further, the present work speaks to the utility of ecological paradigms and the transdiagnostic approach in studying symptoms of poor mental health.

5.2.1. Mood is Both Reactive and Homeostatic

Results from Chapter 3 are consistent with emotion being reactive. In other words, subjective mood ratings reported by the participants varied as a function of features of the task environment that affected task difficulty, such as predator speed. This is consistent with a longstanding view that emotion constitutes a response to situational factors. One such theory, appraisal theory, proposes that emotional response arises from an individual's interpretation of circumstances as either helping or hindering their personal goals (Ortony et al., 2022; Roseman, 1991).

Increasingly, however, emotion is considered not just reactive but also adaptive, having a complex, bidirectional relationship with decision-making. Recent computational accounts of decision-making have proposed ways in which emotional reactions can help adapt behaviour to changing circumstances: for instance, emotions may improve computational efficiency by focusing decision-making on behaviours relevant to one's personal goals, thereby narrowing the number of future outcomes to compute (Huys & Renz, 2017). Additional results from Chapter 3 support the role of emotion in behavioural adaptation. Mood ratings and task behaviour demonstrated homeostatic interactions; in other words, mood and behaviour served to regulate one another. In one instance, we observed a complex interplay among stress ratings, foraging, and efficient checking, suggesting bidirectional relationships between stress and behaviour. One interpretation is that these homeostatic relationships help to manage moods and encourage decisions that are appropriate for the current circumstances. This would align with evidence that people tend to make choices that maximise positive emotions and minimise negative ones (the hedonic principle; see Kron et al., 2014; Taquet et al., 2016; Tice et al., 2001; Wegener & Petty, 1994), and with clinical reports that the inability to use emotions in decision-making (resulting from, for example, vmPFC damage) is associated with disadvantageous choices across personal, financial, and moral domains (Naqvi et al., 2006).

Aside from providing insight about the role of emotion in decision-making, these results also highlight the usefulness of collecting mood self-report data throughout an ecological task. Because emotion is deeply interwoven with everyday decision-making processes, a mechanistic account of choice—especially one that aims to understand symptoms of mood disorders—must consider its influence. More work incorporating emotional states into computational models of

behaviour is needed to improve our understanding of how mood changes, and is changed by, decisions in naturalistic contexts.

5.2.2. Clinical Symptoms Manifest as Unique Behavioural Patterns

Evidence presented in Chapter 3 also contributes to an understanding of mechanisms associated with disordered vigilant and appetitive behaviour. Psychiatric questionnaire data collected in the large online sample was broken down into subscales that represented distinct behavioural dimensions characteristic of multiple psychiatric disorders (e.g., compulsive checking, apathy). Results showed that these dimensions were associated with unique behavioural profiles—strategies and responses characteristic of individuals scoring highly on that subscale. For example, within the symptom domain of fear and anxiety, participants tended toward increased or decreased vigilance depending on whether they scored highly on the OCI-R checking subscale (increased) or the trait-somatic anxiety subscale (decreased). Within the symptom domain of appetitive behaviour, participants tended toward decision inertia if scoring highly on behavioural apathy and toward lack of engagement/excitement if scoring highly on anhedonia. Each of these findings advances understanding of the relevant psychiatric symptom (and by extension, psychiatric disorders associated with that symptom) by revealing specific computational idiosyncracies associated with it and characterizing how these manifest in a naturalistic decision-making scenario.

Importantly, understanding mechanisms linked with psychiatric disease such as these may lead to improved diagnostic criteria. Currently, psychiatric diagnosis is still based primarily on behavioural observations and self-report data. However, the accuracy of introspection is disputed: although in some cases people's self-reported experiences can be linked with their

objective behaviour (Scholl et al., 2022), other studies suggest that people have very little access to their own higher order cognitive processes, or are able to self-report accurately only under certain circumstances (Johansson et al., 2005; Nisbett & Wilson, 1977). People do not always remember correctly what they have done, are unaware or misled about the true causes of their actions, and are vulnerable to personal and cultural biases (e.g., telling the interviewer what they might want to hear). Objective behavioural measures that are exhibited in ecological contexts and associated with a mental disorder might one day be translated into alternative criteria for diagnosis. For instance, apathy is currently assessed via clinical interviews or validated questionnaires (e.g. the Apathy Motivation Index, or AMI; (Ang et al., 2017) that require patients to self-report their everyday life experiences. As an alternative—or complementary—approach, a criterion could be based on evidence such as findings presented in Chapter 3 and in Scholl et al. (2022) that apathy is linked with decision inertia. This could potentially provide a way to quantify the degree to which an individual's decision-making is characteristic of apathy in naturalistic contexts. Further, it is hoped that detailed computational accounts of mental disorder will eventually lead to the development of new treatments to improve mental health. Cognitive Bias Modification (CBM), for example, is a behavioural treatment based on evidence that anxiety is linked with attentional and interpretive cognitive biases. Further work is needed to fully understand mechanisms underlying psychiatric symptoms such as anxiety and translate this knowledge into clinical insight.

5.2.3. Support for Ecological, Transdiagnostic, and Online Methods

Experiments presented in this thesis support the use of ecological tasks, the transdiagnostic approach, and online data collection in studying symptoms of poor mental health. First, results

from Chapter 3 show that an ecological paradigm can be successful in eliciting behaviour characteristic of psychiatric symptoms. Although decision-making impairments are easily reported and observed in many psychiatric patients, conventional laboratory-based tasks have often failed to detect such impairments and have contributed little to a mechanistic understanding of psychiatric disorders so far. Proponents of the ecological approach in cognitive neuroscience speculate that this is because conventional laboratory tasks—often involving trials at predetermined intervals with unnatural stimuli—do not reflect decisions made in everyday life; and further, that the source of impairment in psychiatric disorder is atypical computation in neural networks that have evolutionarily adapted to respond to highly contextualised environments. Thus, psychiatric symptoms are thought not to manifest fully in tasks that do not probe everyday decision-making mechanisms (Hitchcock et al., 2022; J. M. Pearson et al., 2014; Scholl & Klein-Flügge, 2018). Results from Chapter 3 add to the growing number of studies have successfully elicited behaviour predictive of psychiatric measures in a laboratory context using an ecological paradigm that mimics natural animal behaviour.

In addition, the finding that specific dimensions of disordered cognition can be linked with task-based behavioural profiles highlights the importance of the transdiagnostic approach. Participants in the Chapter 3 study completed psychiatric questionnaires that contained subscales representing distinct dimensions of the phenomena being measured. For example, the Apathy Motivation Index (AMI) measured three subtypes that reflect individual differences in apathy: behavioural, social, and emotional, each associated with different comorbidities and symptoms (Ang et al., 2017). Analysis of behavioural and emotional AMI subscales in that experiment revealed that a set of behaviours including reduced vigilance and increased foraging were associated with behavioural apathy but not emotional apathy. The distinction between the two

subtypes emphasises the heterogeneity of decision-making mechanisms affected by apathy, a symptom that features in many psychiatric and neurological conditions. Thus, transdiagnostic research is important for characterising behavioural dimensions that cut across traditional diagnostic profiles. Complex symptoms such as apathy, and collections of symptoms that constitute disease, cannot be fully understood without such an approach.

One criticism of the transdiagnostic approach contests whether knowledge about sub-clinical levels of psychiatric symptoms is useful for making inferences about clinically significant conditions. The study presented in Chapter 3, for instance, did not screen participants based on psychiatric scores, so its results describe behavioural patterns associated with clinical measures ranging in severity from sub-clinical to above diagnostic threshold. It is still debated whether such studies might lead to effective diagnostic tools. A future study might explore this topic by investigating whether behavioural patterns linked with wide-ranging clinical scores in Chapter 3 replicate in sample of participants with exclusively clinically significant scores. Thus, the findings presented here might provide useful reference points for future work.

Finally, results from Chapter 3 of this thesis demonstrate that such effects can be detected even when data is collected online. Online research has received increasing attention despite its challenges. On one hand, large, remote, rapidly collected datasets are extremely valuable for behavioural psychiatric research: great statistical power is required to reliably distinguish between comorbid but heterogenous symptoms, and psychiatric symptoms are best observed in the context of an individual's everyday environment. On the other hand, the validity of data from unobserved, anonymous participants is disputed, and results do not always replicate. Here rigorous data quality checks excluded participants who did not submit consistent, timely, and sufficiently high performing responses, and a test-retest strategy replicated many findings. As a

result, we confirmed a number of hypotheses that align with clinical literature on the relevant psychiatric symptoms. Overall, results support the use of online data collection paired with a test-retest strategy as a valid and rewarding approach for future studies.

5.3. Neural Substrate of Switching Between Foraging and Vigilance

A unique aspect of the current thesis is that it used the same task in a clinically relevant online study as well as a neuroimaging study in healthy adults. Together, these experiments can help narrow the gaps between cognitive science, psychiatry, and neuroscience by exploring both the clinical relevance and neural substrate of ecological task-switching mechanisms. Results from the fMRI study described in Chapter 4 provided insight into the implementation of such mechanisms by mapping how several brain areas work together to encode threat level, reward level, and the decision to switch behavioural modes.

5.3.1. Key Brain Areas Engage Both Reward- and Threat-Related Networks

Our fMRI analysis focused on behavioural transition points and revealed two distinct, distributed neural networks facilitating these transitions: in one, functional connectivity between regions was associated with the monitoring of threat and switching to vigilance; in the other, functional connectivity encoded reward levels and switching to foraging. The threat-related network involved the lateral habenula (LHb), dorsal raphe nucleus (DRN), ventral tegmental area (VTA), substantia nigra (SN), anterior cingulate cortex (ACC), and anterior insula (AI), while the reward-related network included the ACC, DRN, precentral gyrus, and striatum (see Chapter 4 for an in-depth discussion of each area's role). Notably, the networks overlap. Brain areas involved in both reward- and threat-oriented behaviour are of interest because they likely play

an important role in flexibly switching between the two. Cortical areas ACC and AI as well as the subcortical DRN stand out in this regard. ACC encoded switching to check with LHb (Fig. 23Aii and encoded both switching to forage and reward level with DRN (Fig. 26Aii), demonstrating a critical role for the ACC in communicating with subcortical regions to coordinate and initiate action selection. DRN activity was relevant across many analyses, variously encoding reward, threat level, and both types of behavioural transitions. Its relationship to both rewarding and aversive stimuli suggests a nuanced role in regulating the effects of environmental motivators on behaviour, building on evidence that the DRN may encode aversive prediction errors as well as reward signals (J. Y. Cohen, 2015; Daw et al., 2002; Dayan & Huys, 2009; Grossman et al., 2022; Iigaya et al., 2018; Khalighinejad et al., 2022; Lottem et al., 2018; Schweimer & Ungless, 2010). Although not included in the reward network presented in Chapter 4, the AI was influential in both networks as well: it encoded threat level and switching to check with DRN (Fig. 23Bii), and its activity was linked with threat level during both behavioural transitions. These findings suggest that AI may mediate the impact of perceived threat on decisions, consistent with evidence of AI involvement in both emotional processing and cognitive control. Together, Chapter 4 results map the process of transitioning between foraging and vigilance and the encoding of relevant motivating factors across two distributed neural networks. Areas relevant to both networks are of particular interest for their role in integrating information across domains to inform action selection, and may present targets of interest for clinical research.

5.4. Limitations

It is important to note limitations of the current body of work. First, the novel task used in Chapters 2-4 has strengths and weaknesses as an ecological paradigm. Participants were able to choose both the timing and nature of their actions, which is more akin to real-life decision-making than many laboratory tasks in the existing literature. In addition, the presence of virtual predatory threat with varying proximity and speed was designed to be comparable to circumstances encountered by animals in nature. However, our ability to observe decisions to track rewards and attend to foraging was compromised by the fact that available rewards were constantly displayed (instead of being hidden until investigated, like the predators). Further, while the online study format provided easy access to large sample sizes and therefore statistical power, button presses are an unnatural way to engage with vigilance, threats, foraging, and escape; technology such as virtual reality (VR) would create a more realistic experience for participants. Future studies may benefit from altering the task to hide both threats and rewards, and from pursuing technologies that allow participants to respond physically as they would in a real-life scenario.

Second, none of the studies presented here involved manipulations that would enable us to make causal claims. For example, in Chapter 3, we note associations between certain patterns of behavior and clinical subscales that replicate above a pre-specified level of significance. However, we cannot infer that any clinical conditions or task behaviors are causes of one another, or rule out the possibility that the observed behaviors are also characteristic of other clinical symptoms aside from those tested. We can only demonstrate associations that occurred within the scope of our experimental paradigm. Similarly, in Chapter 4 we found associations between model variables (e.g. threat level during switching to vigilance) and the activity of brain areas of interest. However, our results do not provide evidence that these brain

areas are essential to the computations of interest or demonstrate their functional role. To make such assertions, a follow-up study involving a causal manipulation such as drug administration or transcranial magnetic stimulation would be needed.

5.5. Ongoing and Future Work

The task design used in all three experimental chapters of this thesis has already been carried forward into planned and ongoing collaborative studies. It is worth noting several of these studies to demonstrate the broad utility of this naturalistic paradigm. One study is a double-blind placebo-controlled study of the effects of the drug losartan on threat and reward processing in which this task is included as part of a battery. Another study is hoping to build on our results linking aspects of this task with threat processing in the habenula by using this task to investigate behavioural effects of ketamine infusion. A third collaboration, encouraged by our findings linking ACC activity with task behaviours such as switching to vigilance, has included this task in a study examining the effect of cingulotomy on decision-making in a cohort of NHS patients. A fourth group of collaborators are using this task to study risky decision-making in adolescents. Finally, discussions with potential collaborators have raised the possibility of including this task in a study of borderline disorder to examine naturalistic emotion regulation. The naturalistic, unconstrained design of this task, together with behavioural, clinical, and neural findings presented here, might prove a useful to a variety of current and future investigations.

5.6. Summary

In summary, this thesis has presented several experiments exploring the cognitive mechanisms, clinical relevance, and neural substrate of a natural behaviour that is critical to survival: flexibly

switching between foraging and vigilance. Human participants were shown to use observed information (reward level) as well as latent variables (expectation of threat level) to make decisions about transitioning between behaviours. In addition, adopting an ecological, transdiagnostic approach with online data collection proved a useful strategy: Results demonstrated a homeostatic relationship between mood and behaviour, and dimensions of clinical symptoms were identified by unique behavioural patterns. Finally, fMRI analysis revealed separate threat- and reward-related networks featuring several brain areas active in tracking information across multiple domains and coordinating action transitions. It is hoped that the experiments presented in this thesis may support future work that bridges the gap between cognitive science, psychiatry, and neuroscience.

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