British Journal of Clinical Psychology (2015)

The British Psychological Society

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Special Issue Paper

Episodic foresight and anxiety: Proximate and ultimate perspectives

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Objective. In this paper, we examine the relationship between episodic foresight and anxiety from an evolutionary perspective, proposing that together they confer an advantage for modifying present moment decision-making and behaviour in the light of potential future threats to fitness.

Methods. We review the body of literature on the role of episodic foresight in anxiety, from both proximate and ultimate perspectives.

Results. We propose that anxious feelings associated with episodic simulation of possible threat-related future events serve to imbue these simulations with motivational currency. Episodic and semantic details of a future threat may be insufficient for motivating its avoidance, but anxiety associated with a simulation can provoke adaptive threat management. As such, we detail how anxiety triggered by a self-generated, threat-related future simulation prepares the individual to manage that threat (in terms of its likelihood and/or consequences) over greater temporal distances than observed in other animals. We then outline how anxiety subtypes may represent specific mechanisms for predicting and managing particular classes of fitness threats.

Conclusions. This approach offers an inroad for understanding the nature of characteristic future thinking patterns in anxiety disorders and serves to illustrate the adaptive function of the mechanism from which clinical anxiety deviates.

Practitioner points

- Episodic foresight can elicit anxiety even when there are no immediate environmental cues of fitness threats.
- Anxiety may be a mechanism by which simulations of future events are imbued with motivational currency, to ensure the management of potential future threats to fitness.
- Subtypes of anxiety disorders may reflect different mechanisms for effectively managing certain potential future threats to fitness.
- Understanding the utility of episodic foresight in anxiety disorders may lead to new insights into diagnosis and treatment.

'. . .A number of our blessings do us harm, for memory brings back the agony of fear while foresight brings it on prematurely. No one confines unhappiness to the present.' Seneca.

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DOI:10.1111/bjc.12080

Anxiety disorders are among the most prevalent and pressing mental health issues today (Baxter, Scott, Vos, & Whiteford, 2013; Grant *et al.*, 2004; Kessler *et al.*, 2005, 2007). Current diagnostic criteria have been challenged based on lack of specificity and large heterogeneity within disorders, and it has been proposed that evolutionary and pathophysiological approaches could provide a more suitable basis for nosology (Insel, 2014; Nesse & Stein, 2012). While the pathophysiological approach focuses on identifying key cognitive and behavioural features and physiological underpinnings that constitute each disorder, the evolutionary approach provides a framework for integrating the various mechanistic traits that characterize each disorder (Cuthbert & Insel, 2013; Nesse *et al.*, 2010).

We begin this paper by considering the adaptive significance of human anxiety. Consistent with an evolutionary perspective, we identify *episodic foresight* as one of its key psychological features. Episodic foresight refers to the mental construction of future scenarios and the organization of current action in the light of such constructions (Suddendorf & Moore, 2011). It is the future-facing component of mental time travel, the ability to revisit or pre-visit past and future episodes (Suddendorf & Corballis, 1997; Tulving, 2005). We proceed to describe patterns of episodic foresight that characterize human anxiety. Next, we consider the phylogenetic origins of the trait. Finally, we describe anxiety disorder subtypes from this evolutionary perspective of episodic foresight.

Anxiety facilitates avoidance of fitness threats

We consider here the possible adaptive benefits of human anxiety from an evolutionary or *ultimate* level of explanation (Tinbergen, 1963). A number of such explanations have been advanced, with the common thread linking these proposals being that anxiety facilitates the detection and avoidance of threats to fitness (Bateson, Brilot & Nettle, 2011; Boyer & Liénard, 2006; Brüne, 2006; Marks & Nesse, 1994; Nesse, 1999; Stein & Nesse, 2011; Szechtmann & Woody, 2004). Although humans are capable of responding appropriately to manifest danger in the absence of anxiety, via emotional action programs such as fear (Feinstein *et al.*, 2013), anxiety enables individuals to take more advanced precautionary measures (Stein & Nesse, 2001; Boyer & Liénard, 2006).

Accordingly, a smoke detector serves as a useful analogy for illustrating the ultimate function of anxiety (Nesse, 2001, 2005). The purpose of a smoke detector is to predict the occurrence of fire so that timely action can be taken to prevent a disaster; analogously, it could be said that the ultimate function of anxiety is to predict potential *threats to fitness* so that action can be taken to prevent these threats from eventuating. Clinical manifestations of anxiety can be construed as extremes on a continuum of sensitivity, such that clinically anxious individuals infer threats to fitness more readily than the average individual (Mogg & Bradley, 1998). Although a necessary consequence of this is that anxious individuals with higher anxiety produce a greater number of false alarms (a tendency to detect threat where there is none), the advantage of a more sensitive threat-detection system is that it attenuates the risk of a potentially fatal miss. In other words, the costs associated with different errors in this domain are asymmetric: Avoiding a non-existent (or minor) threat is less costly than failing to detect (or prepare for) a potentially consequential one. Nonetheless, being frequently or permanently in a state of anxiety is also costly because proximate mechanisms of anxiety such as hypertension and the secretion of cortisol and adrenaline can cause tissue damage (e.g., Brüne, 2008).

There is an additional facet to the ultimate explanations outlined above that, to our knowledge, has been largely neglected (but see Boyer & Bergstrom, 2011). Episodic foresight represents an extraordinary evolutionary achievement because it permits anticipatory preparation for maximizing opportunity and avoiding ruin over greater temporal distances than otherwise possible (Suddendorf & Corballis, 2007). Accordingly, the mental construction of threat-related future scenarios in the absence of relevant environmental cues enables one to foresee potential dangers in an extended time frame, spurring one to plan, prepare, and more effectively manage the likelihood and/or consequences of a potential catastrophe. We propose that episodic foresight enables humans to generate, and subsequently manage, inferred threats to fitness, even in the absence of present threat cues. We now turn to the proximate mechanisms by which this function is thought to operate by examining the patterns of foresight and underlying emotional processes found in anxiety.

Foresight biases

Anxious individuals exhibit a pessimism bias, such that they are more likely than asymptomatic individuals to mentally generate negative experiences about the near and far future (Hoerger, Quirk, Chapman, & Duberstein, 2012; MacLeod & Byrne, 1996). Increased generativity of threat-related future events among anxious adults is associated with increased expectation and anticipation of the occurrence of those events, and a tendency to believe that those events will yield negative outcomes (Miranda & Mennin, 2007; Raune, MacLeod, & Holmes, 2005). Anxious individuals also exhibit a pronounced *impact bias* for threat-related events, such that they tend to overestimate the intensity and duration of their affective reactions to these events (Wenze, Gunthert, & German, 2012). In the context of anxiety, the systematic exaggeration of anticipated negative affect is thought to motivate avoidance or appropriate management of the stimulus expected to trigger this negative state. From this perspective, it is perhaps not surprising that the impact bias persists in spite of repeated mispredictions (Meyvis, Ratney, & Levav, 2010), considering the importance of these mispredictions in facilitating management of potential threats. It is important to note that anxiety is not associated with decreased generativity, expectation, or anticipation of positive events, and anxious individuals generally exhibit a comparable impact bias to asymptomatic controls in the positive direction (MacLeod & Byrne, 1996; Martin & Quirk, 2015; Miranda & Mennin, 2007; Wenze *et al.*, 2012).

Phenomenology of mental time travel

In addition to the tendency of anxious individuals to construct threat-related future scenarios, they also tend to reconstruct threat-related past scenarios (Brown *et al.*, 2013; MacLeod, Tata, Kentish, & Jacobsen, 1997). These episodic simulations tend to be overgeneralized, such that they include a higher proportion of semantic relative to episodic details (Brown *et al.*, 2013, 2014). The advantage of this might be that semantic details are more temporally stable than episodic ones (i.e., precise episodic details from the past are less likely to recur than semantic details), and should therefore be more useful for preparing an individual to manage potential threats. The value of the episodic system would then lie in the ability to remember and flexibly imagine anxiety-related experiences, thereby facilitating management of potentially forthcoming threatening situations. Future simulations need not be direct extrapolations of past experiences: By the process of recombination, episodic building blocks from memory can be used to construct a wide array of novel possible threat events (Schacter & Addis, 2007; Schacter, Addis, & Buckner, 2007; Suddendorf & Corballis, 1997, 2007). Episodic simulation can, but does not always necessarily occur deliberately or wilfully; these simulations frequently occur automatically, repetitively, and uncontrollably (Baird, Smallwood, & Schooler, 2011; Segerstrom, Tsao, Alden, & Craske, 2000; Stawarczyk, Cassol, & D'Argembeau, 2013). In general, episodic future simulations may constitute a sequence of thoughts involved in planning the future (Baird *et al.*, 2011; Stawarczyk *et al.*, 2013; Suddendorf & Corballis, 2007). In fact, thoughts related to future events occur frequently in the course of mind-wandering, with associated influences on present mood (Ruby, Smallwood, Engen, & Singer, 2013). For instance, naturally occurring self-generated episodic future thoughts have been shown to attenuate negative affect (measured both subjectively and with objective markers of stress), presumably because they prepare individuals to manage expected future stressors (Engert, Smallwood, & Singer, 2014; Ruby *et al.*, 2013).

Episodic foresight, decision-making, and delay discounting

It is well known that mental simulations of possible future events are imbued with present-felt affects (Bechara & Damasio, 2005; D'Argembeau & Van der Linden, 2004; Gilbert & Wilson, 2007; Loewenstein, Weber, Hsee, & Welch, 2001). For instance, in anticipating an imminent electric shock, one may mentally simulate the expected pain and dread its onset (Berns *et al.*, 2006). Emotions triggered in the process of episodic simulation of future events can have a profound influence on decision-making and behaviour (Sheldon, McAndrews, & Moscovitch, 2011). Imagining the future during intertemporal choice reduces the rate at which future rewards are discounted (Peters & Büchel, 2010), and can attenuate impulsive behaviour (Daniel, Stanton, & Epstein, 2013). Episodic foresight may enable advanced and adaptive decision-making of this variety by engaging a 'motivational break' (Boyer, 2008); imagining a future event provides present moment feelings, which serve to counter an opposing tendency for immediate gratification. In working towards a temporally distant goal, the pleasant feeling generated when thinking about its completion may be a sufficient reward to spur continued effort in its pursuit in the face of competing present temptations. This serves to facilitate self-control in the face of conflicting temptations and results in maintained striving towards future goals (e.g., adhering to a diet) (Daniel *et al.*, 2013; Suddendorf & Busby, 2005). In the same vein, the feeling of anxiety evoked in the context of an imagined future threat allows the brain to motivate decisions that aim to manage that threat, even in spite of its temporal distance (i.e., future uncertainty and the presence of more immediate concerns, which may require attention).

Humans discount the value of delayed rewards largely because rewards become progressively less certain as they increase in temporal distance (Loewenstein, Read, & Baumeister, 2003). As mentioned, in asymptomatic adults, imagining personally relevant future events can attenuate the rate at which future rewards are discounted (Benoit, Gilbert, & Burgess, 2011; Peters & Büchel, 2010). Further evidence suggests that simply a tendency to engage in task-irrelevant mind-wandering is related to the capacity to delay gratification (Smallwood, Ruby, & Singer, 2013). One reason for this might be that mind-wandering frequently results in episodic future thoughts about personal goals (Baird *et al.*, 2011; Stawarczyk *et al.*, 2013). As such, the individuals can strategically regulate their behaviour in the present moment in the light of explicitly imagined future aims and the emotions these images trigger. Alternatively, it might also be that episodic thoughts, and mind-wandering more generally, serve to counteract a natural tendency to focus on imminent rewards, regardless of whether these thoughts are about the future (Schkade & Kahneman, 1998; Wilson, Wheatley, Meyers, Gilbert, & Axsom, 2000). However, it is important to note that negatively valenced future simulations can lead to intensified delay discounting (Liu, Feng, Chen, & Li, 2013). As discussed, the hallmarks of future thinking in anxiety are increased generativity of threat-related scenarios and pessimistic regard for the phenomenology, likelihood, and impact of negative outcomes (Miloyan, Pachana, & Suddendorf, 2014). This leads to a paradoxical prediction: By frequently engaging in threat-related future thinking, anxious people may be more likely to exhibit myopic decision-making and heightened delay discounting. Repeated simulation of a negatively valenced future event increases the subjective plausibility of that event (Szpunar & Schacter, 2013): In this context, the repeated simulation of a negative event unfolding (e.g., the reward is withheld) could lead to a subjective underestimation of the likelihood of the future reward. In turn, the immediate choice makes sense if the delayed option is not expected to materialize. In line with this prediction, anxiety has been found to be associated with increased discounting of delayed rewards, even if delayed rewards are somewhat more probable and valuable than immediate ones (Luhmann, Ishida, & Hajcak, 2011; Rounds, Beck, & Grant, 2007; Worthy, Byrne, & Fields, 2014).

This line of reasoning might also shed light on some inconsistent results regarding decision-making patterns in anxiety. Three studies (two with clinically anxious individuals and one with trait-anxious individuals) found that anxiety is associated with a preference for 'low risk, low reward' (i.e., risk avoidant) options in sequential decision-making tasks (Giorgetta *et al.*, 2012; Maner *et al.*, 2007; Schmitt, Brinkley, & Newman, 1999). However, three other studies conducted with trait-anxious individuals identified the opposite pattern, namely a preference for 'high risk, high reward' options (De Visser *et al.*, 2010; Haegler *et al.*, 2010; Miu, Heilman, & Houser, 2008). It might be that clinically anxious individuals are avoidant of the possibility of large losses, whereas more moderately trait-anxious individuals could either be avoidant of the possibility of large losses or of the possibility of surrendering large immediate rewards. In this sense, the tendency to make 'risky' decisions in these tasks is not necessarily inconsistent with trait anxiety. However, there are some notable differences between these studies that could account for the observed pattern of results. First, half of these studies used the Iowa Gambling Task (De Visser *et al.*, 2010; Miu *et al.*, 2008; Schmitt *et al.*, 1999), whereas the other half did not. Second, there were noticeable differences in average trait anxiety scores across samples, suggesting that these groups were not directly comparable. More detailed studies are needed to examine the conditions that give rise to impulsive and risk-avoidant decision-making strategies in anxious individuals, and how this might vary as a function of engaging in episodic future thought.

The anxious self

Anxious individuals tend to remember, generate, predict, anticipate, and overestimate the affective impact of personally relevant threat-related future events (Anderson, Goldin, Kurita, & Gross, 2008; Butler & Mathews, 1987; D'Argembeau, Van der Linden, d'Acremont, & Mayers, 2006; Hoerger *et al.*, 2012; Martin & Quirk, 2015; Miloyan *et al.*, 2014; Mogg, Mathews, & Weinman, 1987; Nesse & Klaas, 1994; Reidy & Richards, 1997). Self-reflection has been proposed to represent a key model for conceptualizing and classifying psychiatric disorders, whereby anxiety would be associated with an increased tendency to focus on one's own feelings and thoughts (Philippi & Koenigs, 2014). In fact, there is considerable overlap between the neurocognitive systems involved in anxiety, in self-reflection, and in ascribing value to future thoughts (Buckner, Andrews-Hanna, & Schacter, 2008; D'Argembeau, 2013; D'Argembeau, Xue, Lu, Van der Linden, & Bechara, 2008; Damasio, 2003; Philippi, Duff, Denburg, Tranel, & Rudrauf, 2011). For instance, bilateral damage to the ventromedial prefrontal cortex (vmPFC) has been found to impair self-referential processing and decision-making, and to abolish post-traumatic stress disorder (PTSD), suggesting that these processes are strongly interlinked at a cognitive and neuroanatomical level (Bechara, Damasio, Tranel, & Damasio, 1997; Koenigs *et al.*, 2008; Philippi *et al.*, 2011). Additionally, vmPFC damage is associated with impaired physiological anticipation of aversive stimuli (Motzkin, Philippi, Wolf, Baskaya, & Koenigs, 2014). Taken together, these findings suggest that the mental image of an emotionally competent expected threat triggers a cascade of neural and physiological reactions that constitute the feeling of anxiety. This feeling of anxiety serves to signal the biological significance of the expected threat, and can drive one to take appropriate action in an attempt to avoid its potentially deleterious consequences (Damasio & Carvalho, 2013). As such, mental time travel enables one to envisage, prepare for, and respond to temporally distant threats.

Some further evolutionary considerations

Here, we consider the phylogenetic history of anxiety, from a complementary ultimate level of explanation to the one provided above (Tinbergen, 1963). Human anxiety is associated with a pessimistically biased interpretation of ambiguous stimuli (Eysenck, Mogg, May, Richards, & Mathews, 1991). Similarly, recent studies have demonstrated state-dependent pessimistic interpretation biases in a variety of non-human animals, ranging from honeybees to rhesus macaques (Bateson, Desire, Gartside & Wright, 2011; Bethell, Holmes, MacLarnon, & Semple, 2012; Brilot & Bateson, 2012). For instance, one study in rats demonstrated that an increase in anxiety (achieved by enhancing ambient light, putatively an anxiety-inducing manipulation for the nocturnal laboratory rat) led to more pessimistically biased judgement of ambiguous stimuli (Burman, Parker, Paul, & Mendl, 2009). Specifically, rats were trained to associate one maze location with reward and another with punishment. After learning this association (gauged by faster running towards the rewarded location), rats were tested on the speed at which they ran towards ambiguous locations (spatially interspersed between the rewarded and punished). Rats that underwent the anxiety induction approached the ambiguous spatial locations significantly slower. This study demonstrates that an immediate change in emotional state can lead to pessimistically biased judgement, and bilateral inactivation of the amygdala in rats has been found to suppress such a pessimistic interpretation bias (Choi & Kim, 2010).

Even in humans, bilateral damage to the amygdala bars anticipation and appropriate management of potential threats in the external environment (Feinstein, Adolphs, Damasio, & Tranel, 2011). In this sense, the behaviour of non-human animals is compatible with anxiety in response to immediate (e.g., Burman *et al.*, 2009) and environmentally consistent (e.g., Harding, Paul, & Mendl, 2004) threat-related stimuli, allowing them to adaptively manage perceived imminent and/or potential sources of threat in their surrounds. Moreover, the neuroanatomical underpinnings of anxiety-related behavioural patterns appear to be phylogenetically conserved. Interestingly, even organisms lacking a central nervous system (e.g., amoebae) have the capacity to exhibit analogues to anxious responses by anticipating and avoiding aversive stimuli (Saigusa, Tero, Nakagaki, & Kuramoto, 2008).

With the emergence of mental time travel, humans acquired the capacity to exhibit anxious responses in a wider variety of situations and for more extended time frames. This may constitute a critical divide between human and non-human animals: Whereas many organisms are capable of responding to imminent or potential threats (through fear or anxiety, respectively), only humans have heretofore demonstrated an additional capacity to trigger and sustain anxiety in response to self-generated episodic mental simulations (Suddendorf & Corballis, 2007; but see also Cheke & Clayton, 2010; Corballis, 2013a,b; Suddendorf, 2013a; Redshaw, 2014). The ability to steer present behaviour away from possible disaster that as of yet has no analogue in the immediate environment confers a self-evident benefit (Suddendorf & Corballis, 1997). Alongside the enhanced ability for delayed gratification endowed by episodic foresight, this capacity engenders a powerhouse of behavioural flexibility that enables humans to pursue temporally distant future goals while attempting to avoid catastrophe (though of course we often fail to predict the future accurately). Indeed, as previously mentioned, anxiety is not associated with decreased expectation of positive events, suggesting that anxiety promotes the management of risk in the process of goal pursuit.

As discussed, the emergence of mental time travel would have capacitated humans to *self-generate* anxiety through threat-related episodic foresight (and, in the light of this, adaptively modulate behaviour). These capacities might have evolved sometime after the line leading to modern humans split from the line leading to chimpanzees. The first material evidence of episodic foresight can be found as recently as c. 1.7 million years ago when the first bifacial hand axes appear to have been crafted and carried for use in the future. Once one can flexibly imagine potential future scenarios, one may be confronted with a host of new possibilities and facts to worry about, including the most unwelcome of all insights: The inevitability of one's own ultimate demise. While episodic foresight gives us tremendous opportunities to prepare for and shape the future, it also confronts us with future realities we cannot do anything about (e.g., Suddendorf, 2013a,b). And because we are not clairvoyants, many of our anticipations turn out to be wrong, sometimes leading to anxieties about the very fact that the future is uncertain (Dugas, Gagnon, Ladouceur, & Freeston, 1998). Next, we will examine the role of episodic foresight in types of anxiety disorders and their potential evolutionary functions.

Anxiety disorder subtypes

Despite extensive commonalities across the anxiety disorders, differences between subtypes might enable more effective detection and management of different types of potential fitness threats (Tooby & Cosmides, 1990). In this section, we will summarize, for each sub-type, potential fitness threats that may be dealt with and the proximate mechanisms that may manage those particular fitness threats. Of course, not every type of anxiety needs to be an adaption to specific threats, but in the light of a mental time travel perspective, there are plausible potential functions worth considering.

Generalized anxiety disorder

Worry, defined as a sequence of thoughts aimed at avoiding or minimizing the possibility/impact of negative outcomes (even if those outcomes lie outside of the control of the worrier), is the hallmark feature of generalized anxiety disorder (GAD) (Borkovec, Robinson, Pruzinsky, & DePree, 1983; Szabó & Lovibond, 2002). These thoughts are centred on negative or undesired consequences, and often occur automatically and uncontrollably (Borkovec, Ray, & Stöber, 1998; Hallion, Ruscio, & Jha, 2014). By disrupting cognitive processes and taxing the working memory system in the course of episodic simulation of future events, worry serves to alarm, prompt, and prepare the individual to deal with a likely, costly, and/or expected threat (Hallion *et al.*, 2014; Tallis & Eysenck, 1994). Worry can also be classified as a meta-cognitive process, such that the worrying individual constantly monitors the relationship between her present state and reality (Wells, 1995). In doing so, she attempts to adjust her worry based on ongoing expectations about the occurrence of a potential threat. Worry tends to have a more verbal rather than visual manifestation, and individuals with GAD report less concrete descriptions of major worries relative to control participants (Leigh & Hirsch, 2011; Stöber & Borkovec, 2002; Williams, Mathews, & Hirsch, 2014). Given that the future is inherently uncertain, highly concretized worries may be a less efficient solution for enabling management of unexpected contingencies when they do arise, insofar as the occurrence of a threatening event may differ substantially from one's expectations. As such, the advantage of having broader and more abstract worries (at least to begin with) is that these may, on average, tend to facilitate more flexible problem-focused coping mechanisms by spurring ongoing vigilance to cues that could more accurately forebode the appearance of potential threats.

Higher GAD morbidity is associated with greater physiological hyperarousal associated with worry, reflecting the preparedness of the individual to manage the expected threat (Ruscio & Borkovec, 2004). Thoughts about negative future outcomes unaccompanied by physiological arousal might be inadequate for spurring the individual to manage the potential threat in a timely fashion (Bechara *et al.*, 1997). Viewed in this light, worry fundamentally depends on the capacity for episodic foresight, for imbuing these simulations with feeling, and reflects an ongoing effort to foresee and manage threat in the process of goal striving. Importantly, as noted in the section on foresight biases, the capacity for generating, expecting, and anticipating positive events in clinical anxiety is spared, suggesting that worry may facilitate the avoidance or management of threats en route to opportunity. This tendency might also confer social benefits. For instance, the worrying individual could be valuable to others by foreseeing and detecting threats to their collective pursuit of an opportunity.

Post-traumatic stress disorder

While neurobiological and psychological approaches may provide an account for the mechanisms that leave some individuals vulnerable to PTSD, evolutionary approaches may provide explanations as to why these individuals exhibit a particularly pronounced and persistent adverse reaction to catastrophic events. In the context of mental time travel, PTSD is associated with a tendency to generate highly generalized simulations of the past and future, which are concentrated with semantic relative to episodic details, and typically involve content associated with the initial source of trauma (Brown *et al.*, 2013, 2014). The generalized nature of future simulations and the high prevalence of semantic details suggest that PTSD is a biological response that puts the afflicted individual in an extended state of preparedness for subsequent catastrophe (Cantor, 2009). PTSD symptoms are highly associated with the context or setting in which the traumatic episode took place (Ehlers & Clark, 2000; McNally, 2003). Environmental cues would have been strong predictors of recurrent threat in ancestral environments, where adverse reactions to traumatic events evolved in the first place (Tooby & Cosmides, 1990). In this sense, PTSD may reflect an extreme manifestation of this evolved mechanism.

Lesion studies suggest that the amygdala and vmPFC play critical roles, such that lesions to these sectors reduce the likelihood of developing PTSD (Koenigs & Grafman, 2009; Koenigs *et al.*, 2008). As previously mentioned, vmPFC damage is associated with impaired self-referential processing and physiological anticipation of aversive stimuli, suggesting that the cognitive and physiological expectation of harm to oneself is a central feature of PTSD. Indeed, individuals with PTSD tend to engage in pessimistic expectation of future events related to the source of their traumatic experience (Ehlers & Clark, 2000). Recent neurobiological work on memory reconsolidation suggests that interrupting reconsolidation by inhibiting protein synthesis may lead to profound changes in the way traumatic events are recalled (Nader, Hardt, & Lanius, 2013), with potential subsequent effects on how future events are anticipated. If memory reconsolidation for a traumatic event is interrupted, its episodic and thusly affective components may also be diminished in future-oriented episodic thinking. Recent evidence suggests that disrupting reconsolidation after fear learning in humans can reduce anxious anticipation of an imagined threat event (Soeter & Kindt, 2012).

Obsessive-compulsive disorder

Obsessive-compulsive disorder (OCD) involves chronic, automatic, repetitive, and unpleasant thoughts, followed by ritualized behaviours aimed at avoiding or managing perceived threats. Common obsessions include contamination, infection, harm to others, or social ostracism (Boyer & Liénard, 2006). Episodic foresight has previously been implicated to play a critical role in OCD, such that obsessional thoughts are components of an 'involuntary risk scenario generating system' (Abed & de Pauw, 1999). Some experimental support has emerged in favour of this hypothesis. Whereas asymptomatic individuals exhibit a discrepancy between episodic simulation of past (real) and future (imagined) scenarios, such that experienced events are imbued with more episodic details, individuals with OCD symptoms have been found to exhibit similar simulations of real and imagined events, suggesting that these individuals find it more difficult to distinguish imagination from reality (Zermatten, Van der Linden, D'Argembeau, & Ceschi, 2008).

Obsessive-compulsive disorder can also be viewed as a meta-representational defect, such that there is a dysfunction in the system that adjusts ritualized behaviours based on the expectation of harm (Brüne, 2006). Ritualized behaviours can be seen to represent precautionary behavioural reactions to inferred fitness threats (Boyer & Liénard, 2006; Marks & Nesse, 1994). The tendency of individuals with OCD to overengage in ritualized behaviours might be due to the repetitive nature of obsessions regarding threatening scenarios. Repeated simulation of these scenarios makes their occurrence seem more plausible (Szpunar & Schacter, 2013), leading in turn to the excessive performance of a ritualized precautionary behaviour (Woody & Szechtman, 2011). An obsessive-compulsive disposition might also confer social benefits. For instance, compulsive checkers bear a high sense of responsibility for social others, threat-related cognitive processes have been found to be pronounced in the context of social responsibility, and a sense of responsibility to avoid harm to others could reduce the likelihood of being ostracized (Boyer & Liénard, 2006; Radomsky, Rachman, & Hammond, 2001; Salkovskis *et al.*, 2000). The tendency to generate and manage potential threats to others', as well as our own, fitness could effectively serve to signal cooperation.

Social anxiety disorder

Social anxiety disorder (SAD) is characterized by apprehension towards interpersonal situations. Despite a general desire for interpersonal relations, these individuals endure social situations with severe discomfort due to a fear of criticism, rejection, or humiliation. Relative to asymptomatic controls, socially anxious individuals have been found to exhibit a greater positive impact bias for a Valentine's Day date, suggesting that these individuals are driven to cultivate safe interpersonal relations (Martin & Quirk, 2015). Similar to GAD, SAD involves worry about potential (social) threats; however, unlike GAD, SAD appears to be accentuated by visual imagery rather than inner speech (Brozovich & Heimberg, 2013). Socially anxious individuals remember social events with a higher degree of self-referential detail, and tend to remember these events more from an observer's point of view (rather than a personal one), relative to asymptomatic controls (D'Argembeau *et al.*, 2006). Higher degrees of social anxiety are associated with a self-referential learning bias for negative versus positive information, and SAD is associated with increased vmPFC activation in response to second relative to first person perspectives on social situations (Blair *et al.*, 2011; Button, Browning, Munafò, & Lewis, 2012).

In contrast to those with SAD, vmPFC patients are impaired in triggering emotional responses to socially salient stimuli and these individuals also tend to judge malicious intentions as being morally permissible (Damasio, Tranel, & Damasio, 1990; Young *et al.*, 2010). Taken together, these findings suggest hyperactive theory of mind meta-representation for socially salient stimuli in social anxiety. This manifests primarily in two ways when thinking about the future: (1) as a concern for how a social other could interpret and/or respond to a personal action ('What will s/he think if I do/say X?'); and (2) as an attempt to avoid or cope with the potentially self-threatening behaviour of a social other ('What will I do if s/he says/does Y?'). The afflicted individual attempts to adjust present behaviour based on the expectation of social threat, frequently well in advance of social encounters.

Panic disorder

It has been proposed that panic evolved to facilitate escape from dangerous situations and that a panic attack may come about through a misinterpretation of one's own bodily sensations (Clark, 1986; Nesse, 1987; Rosmarin, Bourque, Antony, & McCabe, 2009). From this perspective, panic disorder (PD) appears to be outside the purview of a mental time travel approach to anxiety disorders, insofar as it involves immediate responses to facilitate escape from (perceived) imminent or manifest threats. However, it has been proposed that PD could be appropriately characterized as a 'fear of fear', such that afflicted individuals are anxious about the possibility of experiencing subsequent panic attacks (McNally, 1990). This is entirely consistent with a mental time travel perspective of anxiety disorders, and some support for this notion comes from studies with patients with PD that identified a memory bias for a wide range of anxiety- and panic-related stimuli (as well as threat-related stimuli associated with panic attacks) (For review, see Ziomuzica *et al.*, 2014).

Individuals with PD may come to ruminate on the locations and contexts where a panic attack has occurred in the past, and are therefore inclined to avoid these locations and contexts in the future in spite of a lack of immediate danger or cues to danger. Agoraphobia represents a pronounced example of this. Once again, a tendency to avoid situations previously associated with a panic response (i.e., mortal danger) is likely to have been adaptive in the context of ancestral environments. There are no studies we know of that have investigated patterns of episodic foresight in patients with PD; however, we would hypothesize a similar pattern of findings to those observed in GAD and PTSD (i.e., generalized future simulations). We would also expect within-group differences whereby agoraphobics would generate more generalized simulations relative to those with PD alone. Additionally, it has been proposed that PD could arise from prediction errors about one's expected body state in the future (Paulus & Stein, 2006). This raises the intriguing possibility that PD involves pessimistic predictions specifically about one's own physiological responses to threat-related future events.

Specific phobia

Specific phobia involves chronic fear and avoidance of specific objects or situations. Specific phobias are most commonly classified as fear of animals or the natural environment (Curtis, Magee, Eaton, Wittchen, & Kessler, 1998). From an evolutionary perspective, these could largely be considered stimuli that were consistently associated with danger over many generations (Mallan, Lipp, & Cochrane, 2013; Mineka & Ohman, 2002). A phobic tendency promotes the acquisition of experientially based threat-related associations, and phobias are not easily amenable to cognitive control (Ohman & Mineka, 2001). As mentioned, the vast majority of humans are capable of exhibiting an appropriate fear response in the face of manifest danger, and in this sense, individuals with specific phobia are no different. In asymptomatic individuals, a fear response is typically transient – It dissipates sometime after the stimulus has been appropriately managed. We posit that, in humans, a capacity for mental time travel plays a key role in the chronicity of specific phobia: Specific phobia involves persistent and, if necessary, planned avoidance of threatening stimuli that were reliably associated with danger in ancestral environments and/or with aversive experience in one's lifetime. While a non-human animal may acquire a chronic fear of a particular stimulus through repeated aversive experiences, a phobic human may generate consistent and intrusive thoughts about their phobic stimulus even when it is temporally and spatially distant. Though there is some support for an enhanced recall bias for threatening stimuli in specific phobia (Rusted & Dighton, 1991; Watts & Coyle, 1993; but see Watts & Dalgleish, 1991; Thorpe & Salkovskis, 2000), episodic foresight patterns have not been investigated. Like GAD and PTSD, we expect threat-related future simulations to be concentrated with semantic relative to episodic details.

Conclusion

Mental time travel allows human beings to mentally simulate possible future events and guide behaviour in their light (Suddendorf & Corballis, 1997). An anxiety response is characterized by physiological and cognitive changes that prepare one for action in the face of potential threat (Stein & Nesse, 2001). By imbuing fitness-threat related future simulations with this emotional valence in the present, episodic foresight provides motivational salience for the management of future threats to fitness long before they may eventuate. As such, the feeling of anxiety triggered in response to self-generated threat-related future scenarios is the conductor by which current action is orchestrated to avoid disaster. This is consistent with, and complementary to, previous work linking the capacity for mental time travel to enhanced strategic future-minded decision-making and behaviour (Boyer, 2008). Through this lens, specific manifestations of anxiety may represent targeted and fine-tuned proximate responses to a number of different fitness threats, each with the ultimate goal of reducing possible threats to fitness before they eventuate and/or their potential consequential impact. Clinical anxiety may represent extremes on a continuum of response sensitivity for engaging these mechanisms (Mogg & Bradley, 1998). Episodic foresight is a critical feature of anxiety in humans, underlying much of the chronicity observed in those with clinical disorders. A deeper understanding of the role of future thinking in anxiety, including its evolutionary heritage, may lead to new insights into diagnosis and treatment.

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Received 24 October 2014; revised version received 21 January 2015