



Review article

Thinking about threats: Memory and prospection in human threat management



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ABSTRACT

Humans have evolved mechanisms for the detection and management of possible threats in order to abate their negative consequences for fitness. Internally generated ('detached') cognition may have evolved in part because of its contributions to this broad function, but important questions remain about its role in threat management. In this article, we therefore present a taxonomy of threat-related internally generated cognition comprising episodic and semantic formats of memory and prospection. We address the proximate mechanisms of each of the capacities in this taxonomy, and discuss their respective contributions to adaptive threat management in humans. For instance, mental time travel empowers people to contemplate and learn from threats experienced long ago, as well as to plan for dangers that might arise in the distant future. However, despite their functional benefits, these thought processes are also central to contemporary anxiety disorders and may be a potent source of distress.

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1. Introduction

Fear keeps pace with hope. Nor does their so moving together surprise me; both belong to a mind in suspense, to a mind in a state of anxiety through looking into the future. Both are mainly due to projecting our thoughts far ahead of us instead of adapting ourselves to the present. Thus it is that foresight, the greatest blessing humanity has been given, is transformed into a curse. Wild animals run from the dangers they actually see, and once they have escaped them worry no more. We however are tormented alike by what is past and what is to come. A number of our blessings do us harm, for memory brings back the agony of fear while foresight brings it on prematurely.

[Seneca 60AD]

Some capacity for defence in the face of immediate danger is perhaps a universal attribute of all animal species. It has long been recognised that humans, like many other animals, have evolved complex suites of physiological and cognitive processes to detect and manage potential threats to fitness (Cannon, 1916; Darwin, 1872). The distinction between immediately perceptible or *manifest* threats, on the one hand, and *potential* threats on the other has since been used to discern defensive responses to threat in terms of temporal proximity (Blanchard, Griebel, Pobbe, & Blanchard, 2011; Boyer & Lienard, 2006; Eilam, Izhar, & Mort, 2011; Woody & Szechtman, 2011). A loosely conceptualised gradient has therefore been drawn between defensive reactions to immediate threats ('fear') and defensive reactions to potential threats ('anxiety'). In both cases, however, an animal may use cues in the environment to assess the presence of threat, and to thereby launch the appropriate response(s). However, detection and preparation for potential threats can extend, at least in humans, beyond a response tethered to perceptible cues in the environment. A capacity for internally generated thinking enables humans to represent potential future threats (prospectively) or reflect on those that they have already experienced (retrospectively), without having to rely on information available in their immediate surroundings (Pearson, Naselaris, Holmes, & Kosslyn, 2015; Schooler et al., 2011; Suddendorf & Corballis, 2007).

In this paper, we present a taxonomy of threat-related internally generated cognition that comprises episodic and semantic formats of memory and prospection, based on an earlier taxonomy presented by Suddendorf and Corballis (2007). For each of the capacities in this taxonomy, we address both proximate mechanisms (in terms of content and phenomenology, cognitive characteristics, development and underlying neurobiology), as well as ultimate questions (in terms of evolutionary heritage and function). As was recognised by early thinkers in ethology (Mayr, 1961; Tinbergen, 1963), there is utility in embedding mechanistic explanations in their proper evolutionary context (Scott-Phillips, Dickins, & West, 2011). Thus, while Seneca in the opening quote regards threat-related memory and prospection as a curse, we propose that despite their costs for wellbeing, these capacities have characteristics that suggest they have been shaped by natural selection as tools in the struggle for survival and reproduction.

2. What are threats?

We here broadly define a threat in evolutionary terms, in line with previous accounts (Gray & McNaughton, 2003; Marks & Nesse, 1994), as any aspect of the environment that could be detrimental to the fitness of the organism. Humans have evolved systems to detect and manage at least certain classes of these threats that have been encountered over many generations in ancestral environments (Beck, Emery, & Greenberg, 1985; Blanchard et al., 2011; Neuberg, Kenrick, & Schaller, 2011; Sherlock, Zietsch, Tybur, & Jern, 2016; Stein & Nesse, 2011; Tooby & Cosmides, 1990). Our forebears were no doubt regularly confronted with many types of potential threats, ranging from the quasi-universal risk of attacks by predators (Barrett, 2005; Hart & Sussman, 2005; Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015) to more subtle risks such as a loss of social status with potentially severe implications for access to cooperative partners, mates, or resources (Bulley, Miloyan, Brilot, Gullo, & Suddendorf, 2016; Gilbert, 2001; Trower, Gilbert, & Sherling, 1990).

It has been suggested that different, albeit somewhat overlapping, processes have evolved in humans for the detection and management of threats in different domains and under different circumstances (Blanchard, Hynd, Minke, Minemoto, & Blanchard, 2001; Harrison, Ahn, & Adolphs, 2015; Marks & Nesse, 1994; Stein & Bouwer, 1997). Detecting a cue of social threat (i.e. to one's status), for example, entails a different set of processes than detecting a cue that a predator is lurking nearby (Sterelny, 2003). For instance, a social threat to status may uniquely require the visual decoding of signs of disapproval on another person's face and interpretation of their intentions. However, there are also shared aspects of threat-detection and response to seemingly disparate threats, such as a state of enhanced vigilance that is useful for many kind of dangers (Brilot, Bateson, Nettle, Whittingham, & Read, 2012; Eilam et al., 2011; Mobbs et al., 2015). Different anxiety responses may therefore represent partially segregated systems for the detection and subsequent management of different classes of threat encountered in past environments, particularly in cases where a generalized response would not sufficiently mitigate the risk (Brilot et al., 2012; Cosmides & Tooby, 1994; McNaughton, 1989; Nesse, 1990; Tooby & Cosmides, 1990).

These different detection and response processes manifest at extreme levels as the various subtypes of anxiety observed in contemporary humans. Social anxiety disorder, for instance, can be conceptualised as the pathological expression of the adaptive social anxiety trait that evolved because it facilitates the navigation of complex social hierarchies (Gilbert, 2001; Stein, 2015; Trower et al., 1990).

A common distinction in the threat-management literature is between immediate or *manifest* threats on the one hand, and *potential* future threats on the other (Boyer & Lienard, 2006; Eilam et al., 2011). It is now widely agreed that animals respond to immediately perceptible manifest threats (i.e. the emergence of a predator from behind a bush) with 'fear' and/or a 'defensive' response (see Adolphs, 2013; LeDoux, 1998). In contrast, when detecting and responding to cues of *potential* (future) threats (i.e. the sound of leaves rustling), an anxiety response is more typical. In both cases, however, cues in the perceptual environment form the basis of these responses.

Humans are additionally capable of representing threats even in the absence of any relevant sensory cues through the mental simulation of past and future scenarios (Boyer & Bergstrom, 2011; Miloyan, Bulley, & Suddendorf, 2016; Mobbs et al., 2015; Perkins, Arnone, Smallwood, & Mobbs, 2015; Suddendorf & Corballis, 2007). Humans are also capable of the abstract, general representation of threat by drawing on semantic knowledge about how the environment used to be, or how it might be in the future (Wu, Szpunar, Godovich, Schacter, & Hofmann, 2015). Together, these capacities afford enormous flexibility in how an individual can respond behaviourally to a variety of potential dangers without being limited to currently incoming perceptual cues. We now turn to a discussion of future-oriented threat-detection and response in humans, by considering the contribution of both episodic and semantic processes.

3. Semantic and episodic processes in internally generated thinking

Traditionally, declarative memory refers to the capacity to process information that can be explicitly recalled, and thus consists of both facts or knowledge about the world – semantic memory – as well as autobiographical details about one's experiences – episodic memory (Martin-Ordas, Atance, & Caza, 2014; Raby & Clayton, 2009; Squire, 1992; Tulving, 1972; Tulving, 1985a; Tulving, 1985b). Semantic memory is therefore generally conceptualised as being 'knowledge-based' and episodic memory as 'event-based'. Tulving (1985b) suggested that while episodic memory was hallmarked by a kind of 'autonoetic' ('self-knowing') consciousness that involved the first-person subjective experience of previously lived events, semantic memory instead was a form of 'noetic' (knowing) consciousness that did not require such mental simulation (see also Szpunar & Tulving, 2011; Wheeler, Stuss, & Tulving, 1997). These memory processes are now considered integral to thinking about or imagining the future (*prospection*), and while they rely on partly dissociable neural systems, their interdependence is essential for episodic 'mental time travel' in both temporal directions (Irish, Addis, Hodges, & Piguet, 2012; Irish & Piguet, 2013; Klooster & Duff, 2015; Martin-Ordas, Atance, & Louw, 2012; Suddendorf & Corballis, 1997; Suddendorf & Corballis, 2007; Szpunar, 2010; Szpunar, Spreng, & Schacter, 2014). However, the contributions of these sub-systems to threat management processes have not, to our knowledge, been discussed.

The distinction between episodic and semantic processes coincides with research on 'representational formats' or 'modes' of thinking that emphasize verbal versus imagery coding schemes (Paivio, 1986; see also Stawarczyk, Cassol, & D'Argembeau, 2013). In memory and *prospection*, semantic knowledge is usually conceptualised as abstracted and primarily verbal-linguistic, whilst episodic knowledge is more commonly conceptualised as an imagery-based thought process involving the projection of the self into mentally constructed scenarios of another time or place (Buckner & Carroll, 2007; Klein, Loftus, & Kihlstrom, 2002; Kosslyn, 1980; Suddendorf & Corballis, 2007). Note, however, that this does not rule out imagery-based representations of semantic facts, or verbal-linguistic representation of episodic events. Some authors have argued that episodic processes should be regarded as a general mental scenario building capacity that encompasses the internal generation of mental imagery relating not only to past and future events, but also fictitious scenarios, theory of mind, dreaming, and more generally creative thought (Addis, Wong, & Schacter, 2007; Domhoff & Fox, 2015; Dong, Collier-Baker, & Suddendorf, 2015; Hassabis & Maguire, 2009; Mullally & Maguire, 2013; Suddendorf, 2013).

From a neural perspective, a number of authors have proposed that these varied imagery-based activities are the product of the *default mode network* of brain regions that includes the medial temporal lobe, midline prefrontal cortex, and cingulate cortex (Buckner, Andrews-Hanna, & Schacter, 2008; Konishi, McLaren, Engen, & Smallwood, 2015; Raichle et al., 2001; Smallwood et al., 2013; Spreng & Grady, 2010). Recent studies also demonstrate a large overlap between the default mode network and the 'semantic knowledge network' (Binder, Desai, Graves, & Conant, 2009), and the results of lesion studies suggest that semantic knowledge plays a critical – if not pivotal – role in episodic cognition (Binder & Desai, 2011; Irish & Piguet, 2013; Irish et al., 2012).

In sum, semantic and episodic processes collectively comprise dissociable but interacting forms of 'internally generated thinking' (Smallwood & Schooler, 2015; Suddendorf & Corballis, 2007; Szpunar et al., 2014). In both cases, these processes entail 'detached' representations that are not entirely contingent upon cues drawn from the immediate perceptual environment, despite the influence these cues might have on resulting content and phenomenology (Craig, 1943; Gärdenfors, 1996). Together, episodic and semantic processes enable the spatiotemporally detached representation of threats in different ways – both in retrospective memory and in prospective cognition (see MacLeod, Tata, Kentish, & Jacobsen, 1997). We will explore how these processes provide diverse mechanistic inroads to the same adaptive challenge of detecting and managing threats

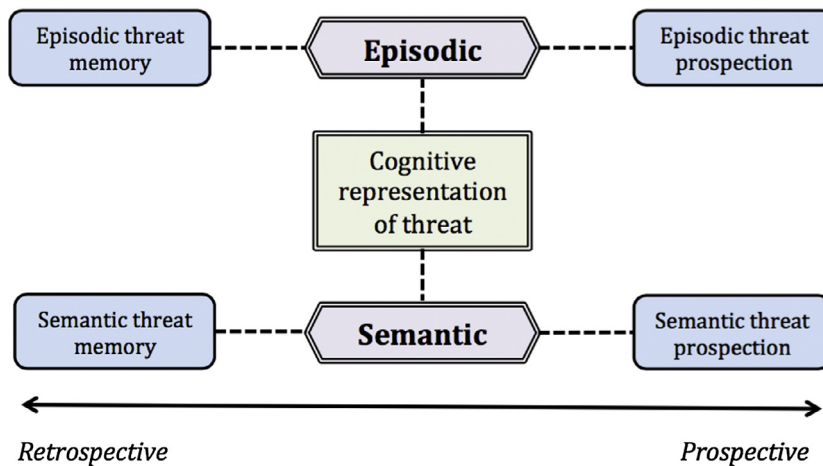


Fig. 1. A taxonomy of threat-related internally generated cognition. Threats can be represented in both episodic and semantic formats, either retrospectively or prospectively. Note that the distinction between episodic and semantic processes is illustrative only, and is not meant to imply unidirectional or independent relationships.

to fitness en route to opportunity. Figure one presents a taxonomy of these four interrelated aspects of threat-related internally generated thinking, each of which we now survey in turn (see Fig. 1).

4. Prospection and preparation

The mental representation of future threats has long been a central focus of cognitive models of anxiety (Beck et al., 1985; MacLeod & Byrne, 1996). Findings of recent studies suggest that in fact most internally generated thinking that naturally arises during daily life is future-oriented, and often emotionally charged, implying that such thinking routinely engenders a form of adaptive goal identification and planning that necessarily involves the identification of potential threats as well as opportunities (Baird, Smallwood, & Schooler, 2011; Barsics, Van der Linden, & D'Argembeau, 2015; D'Argembeau, Renaud, & Van Der Linden, 2011; Finnbogad & Berntsen, 2011; Finnbogadóttir & Berntsen, 2013; Poerio, Totterdell, & Miles, 2013; Song & Wang, 2012). In lay usage, the word 'worry' often denotes the mental representation of negative future possibilities, and a large body of research now underscores the centrality of prospective representations to threat-management and anxiety disorders (Borkovec & Inz, 1990; Borkovec & Ray, 1998; Finnbogad & Berntsen, 2011; Hirsch & Mathews, 2012; Szabó & Lovibond, 2002).

'Worry' has been defined in the clinical literature as the predominantly abstracted, verbal representation of future threats (Borkovec & Ray, 1998). It has been conceptualised as relying primarily on semantic, rather than episodic, processes (Behar, DiMarco, Hekler, Mohlman, & Staples, 2009; Borkovec & Lyonfields, 1993; Borkovec & Ray, 1998; Freeston, Dugas, & Ladouceur, 1996; Stöber, 1998; Stöber, Tepperwien, & Staak, 2000). Although threats can, and often are, represented with both semantic and episodic processes, each may contribute to threat detection and management in somewhat different ways (see Table 1). We therefore distinguish the notion of *semantic threat prospection*, which is characterised mostly by verbal and abstracted representations of threat (commonly called 'worry' in clinical psychology) from *episodic threat prospection*, which is characterised mostly by vivid and narrative mental simulations of possible threat events. Although much research has been conducted on semantic threat prospection, probably because this is the type of thought process most often associated with clinical anxiety, (especially GAD; Hirsch, Hayes, Mathews, Perman, & Borkovec, 2012), only more recently has episodic threat prospection become the focus of intense research interest (e.g. Finnbogad & Berntsen, 2011; Jing, Madore, & Schacter, 2016; Miloyan, Pachana, & Suddendorf, 2014; Wu et al., 2015). We now discuss episodic and semantic threat prospection in turn.

4.1. Episodic threat prospection

Episodic threat prospection involves the simulation of future threat-related mental scenarios. More specifically, an individual can create narratives involving possible future threat events (detection) by projecting the self into the future, as well as generate strategies, plans and intentions to deal with those threats (management). For example, a person who wishes to embark upon a journey in a freezing tundra climate may envisage the biting pain of the cold weather, and imagine multiple potential problematic situations that could arise in order to assemble the most appropriate equipment to bring along. This is an ability that relies on a suite of interacting component processes including some capacity for meta-representation and the nesting of imagined scenarios (Redshaw, 2014; Suddendorf, 2013), and occurs frequently both voluntarily and involuntarily

Table 1

Characteristics of four interrelated threat representation processes.

Internally generated thought process		Characteristics
Prospection	Episodic threat prospection	<ul style="list-style-type: none"> • Concrete, specific and flexible • Primarily imagery based representation • Emotionally salient • Enables affective forecasting • Motivates the avoidance or management of future threat events • Enables flexible (collaborative) planning and goal-setting
	Semantic threat prospection	<ul style="list-style-type: none"> • Abstract and generalised • Primarily verbal-linguistic representation • Provides a bank of knowledge about potential future threats • May facilitate attention to environmental threats
Memory	Episodic threat memory	<ul style="list-style-type: none"> • Concrete, specific and flexible • Primarily imagery based representation • Emotionally salient • Facilitates learning through revisiting of past experiences • Can involve counterfactual simulations of how a threat could have been managed differently
	Semantic threat memory	<ul style="list-style-type: none"> • Abstract and generalised • Primarily verbal-linguistic representation • Provides a bank of knowledge about threats in the environment • Individually learned or culturally transmitted • Enables the rapid retrieval of relevant information during threat-representation

(i.e. without wilful effort) in everyday life (Berntsen & Jacobsen, 2008; Busby Grant & Walsh, 2016; Finnbogad & Berntsen, 2011).

In the brain, episodic simulations of future scenarios are tied to neural activity across a distributed network of default mode regions and conceptual knowledge hubs, centrally subserved by hippocampal activity (Addis et al., 2007; Binder & Desai, 2011). Associated neural activity in prefrontal valuation and emotion processing areas is involved in encoding the biological value of imagined stimuli (Andrews-Hanna, 2012; Benoit, Szpunar, & Schacter, 2014; Hakimi & Hare, 2015). Mentally simulated objects or events can thereby evoke an affective response ‘as if’ the stimulus were being directly perceived (Hesslow, 2002; Pearson et al., 2015), and can subsequently influence decision-making and behaviour over long timescales (Ainslie, 2007; Boyer, 2008; Bulley, Henry, & Suddendorf, 2016; Damasio, 1989; Damasio, 1996; Gilbert & Wilson, 2007; Meyer & Damasio, 2009; Miloyan, Bulley et al., 2016). In practice, this also means that valuation signals from diverse brain regions, including the amygdala (see Seymour & Dolan, 2008), may interact with decision-making networks to modify current action via emotionally salient imagined future threat events. It is in this way that people can predict how they will feel in response to future events, and act in light of these predictions (Gilbert & Wilson, 2007; Rachman, 1994; Suddendorf & Busby, 2005; Wilson & Gilbert, 2003; Wilson & Gilbert, 2005).

Indeed, there is now a growing literature indicating that mental imagery-based thought processes elicit greater emotional reactions than verbal representations (Holmes & Mathews, 2005; Ji, Heyes, MacLeod, & Holmes, 2016; Pearson et al., 2015). A simple introspective exercise illustrates this point: vividly imagining crashing your car on the way home from work is more unpleasant than merely stating the fact that you might be in such an accident. For this reason, episodic (to a greater extent than semantic) threat prospection enables the individual to flexibly anticipate the emotional costs (i.e. negative biological value) as well as the likelihood of various possible dangers, thereby flexibly modulating decision-making and behaviour in light of anticipated future possibilities (Bulley, Henry et al., 2016). It is worth noting that even a highly unlikely danger can be expected to exert large selective pressure on mechanisms for representing possible threats if it is associated with an extremely high cost such as death (Woody & Szechtman, 2011).

It has been argued that because episodic simulations of costly future threat events are often emotionally charged (D’Argembeau et al., 2011), they play an important motivational role in avoiding or abating potential dangers (Boyer & Bergstrom, 2011; Miloyan, Bulley et al., 2016). Once an individual has derived information about the negative value of an anticipated event, this then determines their motivation to act upon that simulation (Miloyan & Suddendorf, 2015). Episodic threat prospection therefore interfaces directly with older, emotional regulatory mechanisms for the avoidance of threat – e.g. those found in a ‘core self’ common to mammalian species (Northoff & Panksepp, 2008) – and can spur the engagement of avoidance or preparatory behaviours involved in preventing or overcoming future dangers. Nonetheless, these emotionally charged simulations can also feed back to negatively impact mood and may therefore be costly to wellbeing in some circumstances despite their clear adaptive functions (Perkins et al., 2015; Poerio et al., 2013; Ruby, Smallwood, Engen, & Singer, 2013; Stawarczyk, Majerus, & D’Argembeau, 2013). Indeed, recent evidence suggests that the capacity to suppress anticipatory simulations of fearful events may be important in regulating anxiety about the future (Benoit, Davies, Anderson, & Schiller, 2016).

Once capable of simulating future situations and threats, and remembering these thoughts sufficiently to compare them with what subsequently occurred, one can begin to abstract more general rules about potential threats that may lurk in the

future. This allows humans to worry about what might be even without vividly simulating concrete future scenarios. We now turn to a discussion of this ‘semantic’ threat prospection process.

4.2. Semantic threat prospection

As mentioned, most previous studies of future threat representation have focused on semantic threat prospection, which comprises generalized and abstract chains of thoughts about possible future negative outcomes, and is primarily verbal and generally sparse in mental imagery (Borkovec & Inz, 1990; Borkovec, Robinson, Pruzinsky, & DePree, 1983; Stöber & Borkovec, 2002a). The ability to represent a possible future threat on the basis of generalized semantic knowledge about the nature of the world (e.g. “cold weather requires warm clothes”, “tigers may attack” or “climate change may cause floods”) does not require the generation of mental simulations about these possibilities (Klein, Loftus et al., 2002). This is future thinking in semantic terms because it is the projection forward of abstract factual knowledge about the world that represents how things might be in the future (Atance & O’Neill, 2001).

Indeed, Gray and McNaughton (2003) argue that anxiety has become much more substantial (and pathological) in humans because of the emergence of a verbal representational capacity (Gray & McNaughton, 2003). For example, one of the characteristic features of some anxiety disorders is so-called ‘meta-worry’. This comprises verbal-linguistic/conceptual worries about worrying itself, such as “if I keep worrying I am going to give myself a heart attack” or “my worrying is getting out of control” (Wells, 1995; Wells, 2005). This meta-worry is associated with a large degree of attendant suffering, and is unlikely to represent a targeted adaptive response to environmental threats (Kennair, 2007). Instead, this thought-process may be made possible in humans by the joint operation of open-ended recursive language and metacognition, alongside a degree of self-awareness (Corballis & Suddendorf, 2007; Hauser, Chomsky, & Fitch, 2002; Thielsch, Andor, & Ehring, 2015). Meta-worry may therefore be the by-product of these complex human abilities, interacting together along with physiological systems responsible for regulating anxiety (see Kennair, 2003; Kennair, 2007).

With this said, a capacity to represent past and future threats semantically may provide a number of adaptive benefits when not expressed as ‘worrying about worrying’. For instance, semantic threat prospection enables the generation of a storehouse of information about what may be threatening in the future environment, the rapid retrieval of this knowledge when appropriate, and the co-operative sharing of this information with conspecifics. Generally, semantic knowledge about the world is organized into conceptual categories on the basis of shared essential properties between informational elements. This includes criteria such as stimulus features, temporal relationships, and affective information (Barsalou, 1999; Evans, 2006). When worrying about spatiotemporally detached threats, the individual can thereby rapidly access relevant pieces of information (about the threat, its cause, or how to manage it, e.g. what tools would be appropriate) on the basis of a present environmental circumstance or an internally generated thought during planning (Doré, Ort, Braverman, & Ochsner, 2015; Klein, Robertson, & Delton, 2011).

However, it is important to note that semantic worry frequency has not been found to improve problem-solving ability *per se*, and may in some cases instead interfere (Davey, 1994; Dugas, Letarte, Rhéaume, Freeston, & Ladouceur, 1995; Ladouceur, Blais, Freeston, & Dugas, 1998), suggesting that its function may be more to do with alerting the individual to the presence of potential threats and related information, rather than solving them. Solving these threats may be a task better reserved for the planning made possible by episodic threat prospection. Indeed, there is now a body of evidence suggesting that verbal worrying can facilitate attention to threat (Oathes, Squillante, Ray, & Nitschke, 2010; Williams, Mathews, & Hirsch, 2014), but that it is hardly ever ‘solution-focussed’ which is what would be expected of a cognitive process whose function is to generate response strategies for threat encounters (see Kennair, 2014). These findings nonetheless suggest that functional threat detection can be facilitated without a full episodic simulation of a future threat possibility.

Over time, people may come to rely more on semantic representations rather than episodic ones, as the latter can become superfluous once an environmental regularity has been established through learning. One reason for this shift is that the use of semantic representations to solve problems may be less costly (e.g. temporally or in terms of computational efficiency) than episodic ones (Klein, Cosmides, Tooby, & Chance, 2002). Episodic processes, however, remain important in that they allow representation of the particularities, rather than regularities, of past and potential future events (Suddendorf & Corballis, 2007). Indeed, episodic threat prospection may, in turn, draw upon semantic knowledge about a threat in the process of creating complex narratives about its possible specific manifestation or how to manage it if and when it happens (Cheng, Werning, & Suddendorf, 2016).

Interestingly, semantic threat prospection may additionally serve a ‘self-protective’ role in coping with unpleasant anxiety evoked by episodic processes. Borkovec and Inz (1990) and others have suggested that worry (in the semantic threat prospection sense) is thereby a type of avoidance coping for dealing with the unpleasant generation of mental imagery (Borkovec, Alcaine, & Behar, 2004; Borkovec & Lyonfields, 1993; Borkovec et al., 1983; McGowan et al., 2016; Stöber, 1998; Stöber & Borkovec, 2002b; Stöber et al., 2000). More specifically, because mental imagery is often more emotionally salient than verbal representations, people may strategically engage in semantic threat prospection in order to suppress the negative emotions that would otherwise be triggered by mental imagery. A full discussion of this proposition is beyond the scope of this article (but see Behar et al., 2009; Behar et al., 2012; Borkovec et al., 2004; Eysenck & Van Berkum, 1992; Finnogad & Berntsen, 2011; Ottaviani et al., 2014).

5. Retrospective memory and threats

If I step aside on seeing a rattlesnake, from considering how dangerous an animal he is, the mental materials which constitute my prudential reflection are images more or less vivid of the movement of his head, of a sudden pain in my leg, of a state of terror, a swelling of the limb, a chill, delirium, unconsciousness, etc., and the ruin of my hopes. But all these images are constructed out of my past experiences. They are reproductions of what I have felt or witnessed. They are, in short, remote sensations.

[(James, 1890)]

Prospective cognition is, by definition, geared towards future possibilities. However, as James (1890) argued, such thoughts are “reproductions” of a sort – they are built out of elements from memory (Suddendorf & Corballis, 2007; Szpunar & McDermott, 2008). Indeed, prospective cognition is generated from the ingredients accrued through lived experience – regardless of whether this knowledge is semantic or episodic, suggesting that memory is in essence forward-facing inasmuch as it empowers an organism to prepare for the future (Baumeister et al., 2016; Ingvar, 1985; Klein, 2013; Klein, Robertson, & Delton, 2010; Seligman, Railton, Baumeister, & Sripada, 2013; Suddendorf & Corballis, 1997; Suddendorf & Henry, 2013).

The ability to generate novel expectations about future events relies in part on the recursive nesting of the information accrued through past experience (Hassabis & Maguire, 2009; Spreng, Mar, & Kim, 2009; Suddendorf & Corballis, 1997; Suddendorf & Corballis, 2007), and similar processes underlie the reconstruction of past episodes (Busby & Suddendorf, 2005; Schacter & Addis, 2007). The important role of mnemonic representations has previously been alluded to in cognitive accounts of future threat representation by authors since James (1890). For instance, Eysenck (1992) wrote: “Worry is triggered by a threat. . . the threat may be in the form of an environmental stimulus or it may be in the form of activated information in long-term memory” (Eysenck, 1992, p. 116). Thus, semantic and episodic memories provide the ‘raw material’ from which prospective thoughts are constructed. However, mentally revisiting previously experienced threat events in memory may also serve a range of other preparatory functions (Boyer, 2009), for instance by enabling a decision-maker to consider what went wrong in the past, and why – with implications for how to behave differently next time in the event of a reoccurrence. Indeed, recent experimental work by Nairne and colleagues suggest that memory systems are adapted to prioritise information of fitness-relevance – including a range of threats (Nairne & Pandeirada, 2008a; Nairne & Pandeirada, 2008b; Nairne, Pandeirada, Gregory, & Van Arsdall, 2009; Nairne, Pandeirada, & Thompson, 2008; Vanarsdall, Nairne, Pandeirada, & Cogdill, 2014). We now turn to a discussion of the ways in which a capacity for episodic and semantic memory broadly might facilitate future threat management moving forwards.

5.1. Episodic threat memory

The episodic recollection of previously encountered threats can enable the individual to re-play the past, learn from the consequences of their actions, and to entertain how alternative histories may have unfolded had they acted differently. Anxious individuals consistently exhibit a bias for threat-related information during the retrieval of episodic memories (for review see Zlomuzica et al., 2014). For example, individuals with social anxiety disorder tend to recall threatening social situations from the perspective of another rather than from their own perspective (Wells, Clark, & Ahmad, 1998). Socially anxious individuals also show enhanced recall, specificity and emotionality of social threat-related autobiographical memories (Krans, de Bree, & Bryant, 2014; Morgan, 2010; Wenzel & Cochran, 2006). Collectively, these results suggest a tendency amongst socially anxious people to reflect on social situations in a manner conducive to learning (i.e. by vividly imagining their own performance), motivated by the potential improvements to performance that this might enable. Indeed, a number of studies have found that higher specificity (more episodic details) in autobiographical memory retrieval generally is associated with better problem-solving capacities (Brown, Dorfman, Marmar, & Bryant, 2012; Vander Morris, Sheldon, Winocur, & Moscovitch, 2013). Such findings suggest that vivid episodic recollection may confer their beneficial effects by enhancing interpretation and learning from previous encounters.

Episodic memories are not facsimile images of past events, and their reconstructive nature leaves them prone to biases and errors (Damasio, 2010; Schacter, 2001; Schacter & Addis, 2007; Wilson & Gilbert, 2003). Indeed, as mentioned, the adaptive significance of memory may be largely attributed to its role in preparing individuals for the future, rather than accuracy in past recall *per se* (Suddendorf & Henry, 2013). However, the reconstructive nature of memory not only enables informational elements to be combined to construct novel future events, but also to construct novel *counterfactual simulations* of alternative histories using if-then conditionals (Barbey, Krueger, Grafman, & Bar, 2011; Roese, 1997; Schacter, Benoit, De Brigard, & Szpunar, 2015). For example, in remembering an anxiety-provoking social blunder, one could imagine having used an alternative turn of phrase that might have evoked warm laughter rather than uncomfortable silence. Recent neuroimaging evidence suggests that such counterfactual simulations engage the common core network involved in other episodic processes including episodic memory and foresight (Schacter et al., 2015).

A number of the features of counterfactual simulations suggest they are well tuned to serve an adaptive function (Byrne, 2007; Epstude & Roese, 2008). For example, counterfactual simulations most commonly occur after negative outcomes (Roese, Sanna, & Galinsky, 2005) and are often centrally focussed on aspects of controllability – things that the individual perceives ‘could have been done differently’ (Byrne, 2002; Girotto, Legrenzi, & Rizzo, 1991). Counterfactual simulations relating to negative events are tied closely to the emotion of regret. And, despite being unpleasant, regret may be adaptive

insofar as it enables one to avoid repeating past mistakes with a view towards the future (Hoerl & McCormack, 2015; Saffrey, Summerville, & Roese, 2008). For instance, in a recent experiment children who experienced regret about a simple decision were more likely to change their choice when given the same decision again (O'Connor, McCormack, & Feeney, 2014).

Thus, counterfactual simulations may play a key role in learning from past encounters alongside episodic memory because they allow people to determine alternative courses of action that might have better handled a perceived stressor (Byrne, 2002). Support for this view comes from the fact that counterfactual thinking appears to improve subsequent performance in various tasks (Morris & Moore, 2000; Roese, 1994; Van Hoec et al., 2012). Increased counterfactual thinking has also been associated with some specific anxiety disorders (e.g. Kocovski, Endler, Rector, & Flett, 2005; Prokopčáková & Ruiselová, 2008) suggesting that retrospective counterfactuals may be an important aspect of threat-related internally generated thinking. Taken together, the above evidence supports the idea that threat-related counterfactuals that use episodic memory processes may facilitate future threat preparation and management, and therefore may have an important evolutionary function in this domain.

5.2. Semantic threat memory

Semantic memory often represents factual knowledge about the general environment, but can also refer to one's own self or life (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012). For instance, one might *know* that the scar on one's arm was caused by a bite from a dog during childhood, but this does not necessitate a full mental simulation of the event every time one recalls this fact. Although episodic memory impairments may lead to impairments in semantic recall (Klooster & Duff, 2015), semantic memory is unique in that it provides a lingering knowledge of past threats in abstracted terms.

This abstracted semantic knowledge can be learned via personal experience (as per the dog bite example above), but may also be socially transmitted. This means people can learn vicariously from others about threats in their environment, and these facts can incorporate valuation information (Boyer & Parren, 2015). For instance, one can learn which particular stimuli and categories of stimuli are threatening, like the food items that are poisonous or the weather changes that signal a storm. A sign by a river that reads: "beware of crocodiles", for instance, can thus effectively impart factual knowledge about an environmental threat. Thus, while semantic threat memories are useful individually, humans can also collectively pool together factual information about dangers in their environment, as well as the most appropriate responses to these threats. Of course, this possibility does not arise unless humans are motivated to seek out information of this nature and to share it with one-another (Suddendorf, 2013). Indeed, cooperative sharing of information of all kinds (including future plans) would have been a boon to early hominins. With this said, there is little of more relevance to fitness than information about which aspects of the environment are harmful. Among other benefits afforded by cooperation and information-sharing, access to a collective repository of threat knowledge may therefore have provided a critical adaptive advantage to willingly cooperative early humans attempting to navigate dangerous and unpredictable environments.

In the clinical domain, there is a tendency towards the overgeneralization or semanticisation of memories in some anxiety disorders, particularly those precipitated by traumatic events (Brown et al., 2013). A number of theorists have suggested that these changes reflect a motivated avoidance of traumatic memories that might instigate emotional distress during retrieval, such that individuals will avoid recalling specific threat-related episodic memories and instead opt to report general categories of events (for reviews see Moore & Zoellner, 2007; Williams et al., 2007; Zlomuzica et al., 2014). The phenomenon of overgeneral memory in anxiety-related psychopathology serves to further underscore the heterogeneity of memory processes in the anxiety disorders. For instance, overgeneral memory is not typically observed in other anxiety disorders, including social anxiety disorder, generalised anxiety disorder, or specific phobia, which are in some cases in fact associated with an intensification of some elements of episodic recall (for review see Zlomuzica et al., 2014).

The generality of memories (and foresight) in trauma-related anxiety disorders such as PTSD may represent an ancient and efficient solution for predicting future threats on the basis of cues that were associated with previous environmental stressors. Evolutionary accounts of PTSD recognise that hyperactivity in the amygdala and other neural structures involved in inferring the presence of threats in the environment are sensitized through learning after experiences of great distress and danger (Diamond & Zoladz, 2015). While a specific episode of experienced trauma is unlikely to repeat in exactly the same way, broader and more abstract semantic knowledge about threats drawn from these events can be useful for general preparation (Miloyan, Bulley et al., 2016). Semantic knowledge derived from the traumatic event informs the individual about what is threatening (and should be avoided), thereby providing a mechanism for guiding appropriate action without necessitating a fully-fledged mental simulation of future possibilities. However, evidence that over-general memories occur in other disorders such as depression or anorexia means it may be premature to infer an adaptive role for this process in threat-management specifically, and future research will be required to determine if this shift in memory content reflects a similar underlying process in each instantiation of psychopathology.

Semantic knowledge is not only a crucial 'ingredient' in the construction of mental scenarios, but it may also guide and facilitate the construction of episodic cognition (see Klein, Cosmides et al., 2002). Indeed, it has been suggested that semantic memory underpins episodic processing in both memory and prospection (Binder & Desai, 2011; Irish & Piguet, 2013; Irish et al., 2012), and that semantic knowledge may be integrated into the scenario building process as a crucial aspect of subsequently imagined possibilities (Cheng et al., 2016). Next we turn to the retrieval processes underlying the generation of internally generated thinking in threat-management systems, and the adaptive behavioural responses facilitated by the components of the taxonomy.

6. Retrieval processes and adaptive responses

A large body of research suggests that an anxious affective state precipitates the biased retrieval of threat-related information from memory, inducing a tendency to construct threat-related mental scenarios (e.g. Richards & French, 1992). The reconstructive memory model of episodic future thinking in anxiety (Miloyan, Pachana et al., 2014) suggests that the biased retrieval of information from memory in the process of imagining future events therefore shapes the affective and phenomenological characteristics of those imagined events. Thus, because anxiety has been associated with a suite of threat-related biases in memory retrieval, an anxious mood may cause threat-related episodic foresight (see also Miloyan, Pachana, & Suddendorf, 2016).

The repeated internal generation of threat-related thoughts may also exacerbate an anxious affective state by increasing the subjective plausibility of those events (Brown et al., 2016; Raune, Macleod, & Holmes, 2005; Wu et al., 2015), further biasing the retrieval of threat-related content from semantic and episodic memory. However, the selective retrieval of threat-related content from memory during internally generated thinking may not be solely restricted to instances of current negative affect, and in fact there exists a wide bias in attention and retrieval for threat-related information generally (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Nesse, 2005). Revonsuo (2000) has argued that dreaming serves the adaptive function of preparing the individual to manage upcoming dangers by the recurrent simulation of various possible threats (see also Valli & Revonsuo, 2006; Valli et al., 2005; Zadra, Desjardins, & Marcotte, 2006). Threats, in this hypothesis, are therefore overrepresented (retrieved selectively) in dreams because this facilitates the ultimate goal of detecting and managing future dangers when and if they arise.

The aforementioned retrieval tendencies can come to be associated with significant distress. For a recent review on the mental health and wellbeing implications of semantic and episodic memory and prospection, see MacLeod (2016). Nonetheless, these processes may be considered adaptive inasmuch as they facilitate effective preparation for future threats (Klein et al., 2010; Suddendorf & Corballis, 2007). Representing past or future threats, whether based on semantic or episodic processes, may lead people to engage in a wide variety of adaptive behaviours they might otherwise forego. For instance, humans may acquire relevant resources, create tools or weapons (Hallos, 2005), selectively foster useful alliances (Boyer, Firat, & van Leeuwen, 2015), or practice new skills (Suddendorf, Brinums, & Imuta, 2015) in anticipation of future threats or upon recalling past ones. Episodic processes, for instance, enable people to collaboratively share stories and plans for the management of potential danger, such as the collective production of hypothetical battle strategies if another group were to attack (Suddendorf, 2013). Humans may also differentially allocate behavioural and decision-making effort in the present moment as a function of anticipated threats, for instance in the context of intertemporal decision-making where anticipated future threats might encourage a greater preference for (more certain) immediate rewards (Bulley, Henry et al., 2016). None of these behavioural strategies would emerge without the capacity to represent future dangers that would otherwise cause harm – or those that have already done so in the past.

Evolutionary theories about cognitive processes often hypothesize adaptation to particular environmental problems faced in ancestral environments (Barkow, Cosmides, & Tooby, 1995). However, this approach faces a challenge in that many useful capacities cannot readily be conceptualised as modules with one circumscribed function. For example, a capacity for operant conditioning is an immensely useful tool for an organism insofar as it enables flexible responses to both potential rewards and punishments. We cannot know which environmental pressures brought it first to existence, and indeed the capacity has a collection of implementations. Likewise, memory and prospection may represent domain-general utilities that provide adaptive benefits for many environmental challenges, not limited to threats (Suddendorf & Corballis, 2007). In turn, these abilities are also immensely useful for dealing with problems they could not possibly have evolved to solve (e.g. planning for an asteroid collision), which must instead be considered helpful current implementations of the evolved capacities (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Thus, the evolutionary argument we make here does not depend on the claim that memory and prospection are uniquely adapted for dealing with threats. It is plausible, however, that certain threats produced particularly potent pressures in forging these capacities.

Consider the following observations. A global shift to a cooler climate occurred some 2.5 million years ago, and much of southern and eastern Africa became more open and sparsely wooded, exposing our ancestors to greater danger from predators. Indeed, unlike our ape relatives and earlier hominins who were adapted to live in the trees, our ancestors at that stage had to adapt to the very different environmental challenges of savannah life. Faced with many species of sabre-toothed cats, hyenas and other predators (see Hart & Sussman, 2005), and in the absence of both sufficient speed and strength to deal with this, selection pressure would have been strong on avoiding these threats and effectively dealing with them when confronted. One strategy would have been cooperative defence, for instance in the form of throwing stones and hence hurting predators before they came within striking distance. This in turn would have selected for preparation, and the carrying of projectiles (Suddendorf, 2013).

The earliest evidence for foresight is that of stone tools that appear to have been transported for repeated use. Reconstruction of knapping routines (using refit data) suggests that at least by the Middle Pleistocene hominins produced stone tools in one site to use them later at another (e.g., Hallos, 2005). Savannah-dwelling bipedal hominins may have relied increasingly on throwing stones at predators (Calvin, 1982), and eventually to bring down prey. Carrying rocks for use as missiles at some

future point may have been vital, and a capacity to plan for this might have been under strong selection pressure (see [Suddendorf & Corballis, 2007](#)). One possibility, then, is that extensive foresight evolved first in the context of cooperative defence from savannah predators.

Although we think this is a plausible account, it is, of course, speculation. Many other pressures may have contributed to the evolution of human foresight and threat management. For instance, increasing cooperation itself harbours numerous powerful threats ([Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012](#)). Failing to detect cheaters, negative appraisal from a social dominant and attacks from other organised groups, are just some of the many threats borne of human hypersociality ([Cosmides & Tooby, 1992](#); [Richerson & Boyd, 2005](#)). Some of these threats may have been pivotal in driving the evolution of a new kind of cognitive representational system, one flexible enough to represent the minds of conspecifics as well as their past – and possible future – behaviours ([Sterelny, 2003](#)). Accordingly, the threats posed by other humans in early social groups potentially shaped and fine-tuned the evolution of complex cognitive capacities to enable the mapping of the social world and subsequent prediction of conspecific action ([Nesse, 2009](#); [Sznycer et al., 2016](#); [Trower & Gilbert, 1989](#)). Suffice it to say that plausibility should not be mistaken as proof. We suspect that many factors dynamically interacted in forging these modern capacities.

7. Further directions and remaining questions

We offer a number of proposals for future research in this area based on each of [Tinbergen's four questions \(1963\)](#) for comprehensively addressing the nature of a trait (see also [Mayr, 1961](#)). In so doing, we hope to encourage cross-disciplinary consideration of both proximate and ultimate explanations for internally generated cognition more broadly, considering an important goal of the life sciences should be to integrate these levels of analysis to provide a comprehensive account of a phenomenon (see [Scott-Phillips et al., 2011](#)). In some cases the answer to the following questions would provide direct empirical support for, or falsification of, the ideas presented in this paper.

7.1. Phylogeny

Humans may be unique in their capacity to imagine past and future threat narratives without immediately perceptible cues ([Miloyan, Bulley et al., 2016](#)). This does not mean that other animals may not be capable of representing threats with some kind of memory trace or mental imagery ([Barsalou, 1999](#); [Cheng et al., 2016](#); [Gärdenfors, 1996](#); [Osvath & Gärdenfors, 2005](#)), but with the caveat that only humans may *know* that they are remembering or imagining that threat ([Redshaw, 2014](#)). With a better understanding of whether, and if so which, other species share some of these capacities, their evolution can be reconstructed ([Suddendorf, 2013](#)). Indeed, the capacities and limits of non-human animal memory and prospection are the focus of on-going debate ([Cheke & Clayton, 2010](#); [Osvath & Martin-Ordas, 2014](#); [Raby & Clayton, 2009](#); [Redshaw & Bulley, in press](#); [Scarf, Smith, & Stuart, 2014](#); [Suddendorf & Corballis, 2010](#); [Thom & Clayton, 2016](#)). However, while most previous research has focussed on how non-human animals remember or plan for rewards, to date very little research has examined animal performance in similar tasks when subjects must remember or prepare for threats. This is important because threats to reproductive fitness likely played a critical role in the evolution of predictive cognitive processes more generally ([Mobbs et al., 2015](#)), and, as we have suggested here, it is possible that preparation for threats may have been a potent selective pressure in the evolution of complex memory and prospection. There are obvious ethical roadblocks, however, that may explain why this has gone understudied.

7.2. Adaptive significance

Anxiety disorders can be conceptualised as extreme values at the high tail end of a distribution of the adaptive underlying trait. The other extreme, lack of anxiety, generally goes unreported because it is not usually associated with distress but may nonetheless be maladaptive because it prevents adequate precautionary behaviour in the face of danger ([Marks & Nesse, 1994](#)). This generates questions about what an 'adaptive' or 'functional' range of threat-related internally-generated thinking might be ([Perkins et al., 2015](#)). An evolutionary perspective on threat-related internally-generated thinking cannot consider these processes entirely maladaptive despite the costs they entail ([Brüne, 2006](#), [Brüne, 2008](#); [Del Giudice, 2014](#)). In this regard, [Nesse \(2001\)](#) notes that: "If a drug were found that abolished all anxiety for all time it could be as harmful as a drug that induced anxiety of crippling degree". These questions will undoubtedly have a different answer depending on whether they are posed about the environments in which the trait evolved, or in contemporary societies¹ ([Bateson & Laland, 2013](#)). One avenue into the 'current utility' question might be to look for associations between scores on a modified threat-related autobiographical memory/prospection interview (see [Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002](#)) and real world mortality and reproductive outcomes. For instance, might the imagery vividness with which people can foresee prospective threats be associated with reduced accident-related mortality?

¹ Note that a separate, non-evolutionary question along these lines can also be posed about human wellbeing rather than reproductive success.

7.3. Proximate mechanisms

As a threat becomes physically closer in space, the processing of defensive reactions in neural circuitry undergoes a shift from more frontal regions (e.g. ventromedial prefrontal cortex) to more midbrain and brainstem regions (e.g. periaqueductal gray) (Mobbs et al., 2009; Mobbs, Petrovic, Marchant, Hassabis, & Weiskopf, 2007). It remains to be seen if there is a temporal threat proximity analogue to this process, and if so whether it is subserved by similar neural structures. In fact, the spatial proximity studies could be construed in temporal terms, though no work to our knowledge has attempted to tease these apart (see also Trope & Liberman, 2010). This is relevant because, as we have outlined in this paper, different cognitive and neural processes are involved in inferring a threat *without* directly perceptible cues compared to when these cues are available in the immediate environment.

7.4. Development

Approaches drawn from developmental or lifespan psychology may prove informative given that large changes are observed in anxiety symptomology and processes through childhood and the adult lifespan, often in different ways depending on the anxiety subtype (Miloyan & Bulley, 2016; Miloyan, Bulley, Pachana, & Byrne, 2014; Miloyan, Byrne, & Pachana, 2014; Waters et al., 2008). There is also solid theoretical rationale based in behavioural ecology about how anxiety (and hence threat-related internally generated thinking) will change based on developmental stages in childhood, as well as some evidence to corroborate these predictions (for review see Boyer & Bergstrom, 2011; Marks & Nesse, 1994). While there is an increasing appreciation of the developmental milestones underpinning episodic processes in children (for reviews see Martin-Ordas et al., 2014; Suddendorf & Redshaw, 2013), little is known about age-related changes to the internally generated representation of threat across the lifespan despite some recent attempts to address this phenomenon in the context of clinical anxiety in older adulthood (for review see Miloyan, Pachana et al., 2016). For example, because older adults consistently generate fewer episodic relative to semantic details when remembering the past or imagining the future, the nature of their cognitive threat representations should shift towards semantic processing, and thereby account for some of the characteristic worry patterns observed in this age group (Miloyan & Bulley, 2016).

8. Concluding remarks

A capacity for internally generated cognition in humans enables the spatiotemporally detached representation of threats, thereby extending the functionality of threat-detection and threat-management farther into the future. We have presented a taxonomy of this threat-related internally generated cognition comprising memory and prospection in both semantic and episodic formats. Each of the processes in this taxonomy may contribute to the same adaptive end-goal of threat-management, but via different proximate mechanisms. Phylogenetically novel cognitive capacities such as mental time travel may be responsible for the rapid, efficient and complex manner in which humans can detect and respond to potential threats lurking even in the distant future. However, because this means threat detection can be engaged even without immediate cues of danger, these capacities may also account to a large degree for the protracted and deleterious nature of anxiety disorders in contemporary humans. Nonetheless, a species capable of both abstracted and narrative mental representations of threats, past and future, attains a powerful advantage in managing potential dangers moving forward. Internally generated thinking about threats, not restrained solely to cues in the external environment, opens wider the temporal window between the present moment and future dangers, affording valuable time for avoidance or preparation.

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