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Review

Threat detection: Behavioral practices in animals and humans

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ABSTRACT

In contrast to a perceptible threat that releases freezing, fleeing and fighting, abstract potential threat elicits anxiety and vigilance. The prevalent view is that the larger the animal groups the lower the individual vigilance. Vigilance is a reflection of anxiety, and here we show that anxiety is contagious in grouped social animals. In humans, anxiety frequently results in rituals that confer a sense of controllability and thereby a means to cope with anxiety. Accordingly, in mental disorders with sustained anxiety, rituals predominate the behavior and consequently reduce functionality. Finally, the adaptive value of precautionary behavior, including rituals, lies in providing individuals with the opportunity to practice defensive means safely, and thus to prepare for the eventuality of real danger. Accordingly, the prevalence of anxiety in human and animal behavior accords with the "better safe than sorry" principle.

Contents

1. Prolog

Both humans and other animals display emotions of fear and anxiety. While fear is the response to a perceptible threat such as fire or an attacking predator, anxiety is the response to an abstract danger, such as the potential risk of severe earthquake, or smelling the olfactory signals of a predator, signals that may attest its possible presence in the vicinity (Ohman, 2000). Ever since the seminal study of Darwin (Darwin, 1872), fear and anxiety have been considered as homologous in animals and humans (see Dalgleish, 2004 for a review on the history of the research on emotions). Implicit in Darwin's notion was the idea that fear and anxiety are essential for survival since they trigger vestigial defense responses. In the face of perceptible threat, the defensive behavioral response is generalized into three forms: freezing, fleeing or fighting (Eilam, 2005). Freezing is exercised in order to fade from the enemy's attention; fleeing is aimed at increasing the distance from the danger; while fighting back is intended to dissuade the enemy (Blanchard, 1997; Blanchard et al., 1991; Blanchard and Blanchard, 1989). In each case, an obvious end to the conflict occurs when the opponents can no longer detect one another. From that point onward, post-traumatic anxiety may arise but not fear, since the danger is now obscure. Anxiety, however, is not always or necessarily post-traumatic since humans and animals may perceive a certain situation as risky, and consequently display risk assessment in order to avoid the danger or be prepared in advance for a potentially negative event (Barlow, 2000; Herwig et al., 2007; Blanchard et al., 2011). It is noteworthy that, unlike fear, in anxiety there is no external termination signal that may alleviate it. In other words, an animal that is anxious about the possibility of a nearby predator, might then come face to face with a predator, which will convert the anxiety into a real and

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perceptible danger that produces a fear response. Alternatively, the anxious animal might not encounter a predator, and the question is then one of when it will calm down and become less anxious. Relief from a state of anxiety is subjective and thus varies among individuals. It is based on the individual's risk assessment, which involves gathering information regarding the threat in order to produce an optimal response (Blanchard et al., 1991, 2011). Both fear and anxiety can be experienced by individuals or by large communities. For example, seeing a snake or being concerned with contamination or contracting a serious illness may be a threat to individuals, whereas war, terror, earthquake, or a tsunami may simultaneously affect entire nations or communities (Lowe and Fothergill, 2003; Tierney et al., 2001). This raises the question of the social impact of an anxious society on individuals; or, in other words, what is the difference between being exposed to a threat individually or as a group? Finally, while the aforementioned threats are external, other threats may stem from internal reasons such as conflicting motives and desires in normal behavior, or obsessive illusionary images of death and horrific events in anxiety disorders. In this survey, we discuss precautionary behavior in animals and humans under either real, abstract or illusionary threat. We mainly focus on two themes: (i) precautionary behavior in groups or solitary individuals (humans or animals) that have experienced a real life-threat and (ii) behavior in a pathologic state of sustained anxiety in obsessive-compulsive behavior. In both cases, precautionary behavior is manifested in excess due to a salient evolutionary shaping force: the real life-threat of predation in the former situation or a strong biological–psychological impact of sustained illusionary threat in the latter pathological situation. Common to both situations is the uncontrollability and unpredictability of the threat, and we therefore suggest that a salient characteristic of precaution in humans is that of ritual-like behavior, which is executed according to explicit rules and thereby confers a sense of controllability and predictability.

2. Behavior in the face of a real life-threat: an automated response but with a grain of discernment

> "Some have been thought brave because they were too afraid to run away" (English proverb)

Upon encountering a perceptible life-threat, humans and animals need to respond appropriately, since a split-second decision can make a life or death difference. This split-second decision usually represents an adaptive defense response, which takes the form of freezing, fleeing or fighting back (Blanchard, 1997; Blanchard et al., 1991; Blanchard and Blanchard, 1989) – three basic and general defense responses that span the animal kingdom (Eilam, 2005). Before undertaking any of the three responses, however, some discernment is necessary and even within each response there is a certain hiatus for such consideration (Blanchard et al., 2011). An example of the flexibility obtaining within each defense is that of four different patterns of freezing that were revealed in the behavior of rats, with each pattern associated with a different contextual threat (Brandão et al., 2008). An additional example is that of vervet monkeys (*Cercopithecus aethiops*) that emit alarm calls that vary according to the presence of a terrestrial or an aerial predator (Seyfarth and Cheney, 1980, 1986). Domestic chickens (*Gallus gallus*) too produce alarm calls that may be differentiated along the same lines (Collias, 1987; Evans et al., 1993), and woodmice (*Apodemous mystacinus*) either freeze or leap when exposed to stoats (*Mustela ermina*) (Erlinge et al., 1974) but scamper away when exposed to other predators (Bolles, 1970; King, 1985). See Neuroscience and Biobehavioral Reviews, Vol. 21(6) for several reviews on the different perspectives of defensive behavior.

Making a judgment about the appropriate response before reacting is individual and subjective, giving rise to variation. Such variation has an important adaptive value in preventing the predator from predicting the defense response of the prey, despite the latter's limited defense repertoire. Accordingly, despite resorting only to freezing or fleeing responses, voles display a wide range of variety to owl attack within these responses: some freeze, others flee, while yet others switch several times or alternate frequently between freezing and fleeing (Edut and Eilam, 2004, 2003). These various combinations face the owl with a random rather than predictable response of an individual vole. Such random patterns have been termed 'protean behavior', named after Proteus, a sea god in Greek mythology, who could change his shape at will in order to confuse others. In the same vein, while individual cockroaches displayed some regularity in the direction of escape routes, the accumulation of the individual directions of a population of cockroaches adds up to a set of variable (random) escape routes. Accordingly, it was suggested that by utilizing multimodal escape options, cockroaches demonstrate an unpredictable defense response (Domenici et al., 2008). It should be noted that the above examples of voles and cockroaches illustrate that although the defense response of specific individuals is relatively fix, it varies among individuals and thus confronts the opponent with an unpredictable defense reaction. An unpredictable response also emerged within the same defense response of fleeing in spiny mice (*Acomy cahirinus*) when attacked by an owl. Some of these mice waited for the last moment in their attempt to escape whereas other fled as soon as they noticed the attacking owl (Ilany and Eilam, 2008). This behavior illustrates again the pre-response individual discernment, since implicit in executing a last moment escape is the ability to discern when is the last moment. Moreover, a decision to escape involves other judgments such as in which direction to escape: away from the predator in order to increase the distance from it, or toward it in order to kinematically impede its attack (Fishman, 1999; Hochachka, 2004; Shifferman and Eilam, 2004). Discerning the trajectory of escape is also important, with movement along a straight path being more efficient when escaping a slow or distant predator, whereas a zigzag path is advantageous when escaping a nearby or fast predator (Furuichi, 2002). Variation in precautions and risk avoidance were also correlate with age (Boyer and Bergstrom, 2011; Lienard, 2010). All in all, the above examples demonstrate that precaution behavior varies, and even the seemingly split-second response to a perceptible life-threat involves the discernment of various factors. This requires fast and flexible control mechanisms that able to adjust to the circumstances in order to provide an optimal defense response.

3. Anxiety and precaution: defense response without an identifiable triggering threat

> "He who was bitten by a snake avoids tall grass" (a Chinese proverb)

So far we have discussed the response to perceptible life-threat. Humans and other animals, however, are also capable of risk assessment, followed by precautionary measures undertaken in order to avoid the potential danger (Blanchard et al., 2011). Risk assessment (Blanchard et al., 1991) involves gathering information regarding a potential threat in order to produce an optimal response. In animal behavior this is manifested as vigilance, which is alertness or readiness to detect events that could be of serious concern to the animal and its companions (Immelmann and Beer, 1989). A very familiar form of vigilance is that of a bird ceasing to peck for seeds or insects in order to scan the environment. It was demonstrated that this scanning is specifically aimed at detecting approaching predators (Bednekoff and Lima, 1998). Sequences of vigilance consist in