



The ethological deconstruction of fear(s)

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The natural world presents a myriad of dangers that can threaten an organism's survival. This diversity of threats is matched by a set of universal and species specific defensive behaviors which are often subsumed under the emotions of fear and anxiety. A major issue in the field of affective science, however, is that these emotions are often conflated and scientists fail to reflect the ecological conditions that gave rise to them. I attempt to clarify these semantic issues by describing the link between ethologically defined defensive strategies and fear. This in turn, provides a clearer differentiation between fears, the contexts that evoke them and how they are organized within defensive survival circuits.

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Current Opinion in Behavioral Sciences 2018, **24**:32–37

This review comes from a themed issue on **Survival circuits**

Edited by **Dean Mobbs** and **Joe LeDoux**

<https://doi.org/10.1016/j.cobeha.2018.02.008>

2352-1546/© 2018 Published by Elsevier Ltd.

Introduction

Charles Lyell's *Principles of Geology* [1], which proposed the theory that the Earth's surface was shaped by slow incremental changes, was a key inspiration for Darwin's 'On the Origin of Species' [2]. Analogous to Lyell's geological theory, the idea that complex nervous systems emerged from simpler organisms via similar incremental processes fit with both Darwin's and Lamarck's theories that the inheritance of phenotypes are the direct result of the changes in the organism's ecology. Reaching across the modern scientific disciplines of paleobiology, ethology and neuroscience, there is agreement that when one views the human brain through the lens of evolution, our brains have gone through the same gradual processes, and in turn, that we possess some of the same phyletic neural structures and innate reactions that our mammalian cousins use to survive. It has also become clear, however, that the human neural circuits are unique. This uniqueness comes from our highly expanded cortex, which includes a plastic

machinery that allows us to probe near and distant futures [3], to consciously experience emotions (i.e. feelings) [4] and cognitively regulate them [5]. The current consensus is that older neural structures combine with newer ones to form a highly complex circuitry that has evolved to maximize fitness by reacting to, and anticipating, predatory, social and homeostatic threats [6**].

While few scientists dispute that animal and human brains have evolved similar circuits to combat a variety of ecological threats, there is controversy. At the forefront of this debate is LeDoux's 'Survival Circuits Theory' [7] which states that affective scientists should rethink the notion that emotions, such as fear, are similar between humans and other animals. LeDoux proposes that 'fear' is a cognitive process associated with higher order 'feelings' of terror or horror. Thus, fear comes about via conscious experiences and emerges from brain structures involved in what LeDoux calls general networks of cognition [4]. This is differentiated from defensive survival circuits, which are involved the first line of defense against predators and result in innate defensive reactions. Defensive survival circuits contribute to cognitive fear, but do not constitute fear. Thus, given the conscious and subjective nature of fear, only defensive survival circuits can be studied in other animals. This distinction has vigorously been debated [8], yet this debate opens up a new opportunity for affective scientists to reconsider how to define and investigate fear.

In this article, I argue that to successfully map human and animal defensive survival circuits, researchers should first investigate the ecological conditions that evoke them. This approach also provides clearer definitions of fear and anxiety, which are often used interchangeably, conflated and not tied to a well-defined set of natural conditions. In turn, describing the ecological conditions that map onto different level of predation, we find that different patterns emerge in behavior, computations, strategies, psychological states that have distinct and overlapping defensive survival circuits. This is not a new concept. Theorist such as Jeffery Gray have proposed that a central question when studying fear is 'what are the conditions that give rise to fear' [9] (pp. 8). Behavioral ecologists and the like, have also considered these conditions, most prominently captured in Fanselow and Lester's 'Threat Imminence Continuum' [10] and Lima and Dill's 'Predator-Prey Interaction' model [11]. By investigating how animals evade and combat threats across a variety of natural contexts allows researchers to elucidate survival strategies and how these are modulated by other survival behaviors such as mating, sustenance and protection of progeny

[12,13*]. Understanding these strategies allows one to create better computational models and consequently create a better understanding of the defensive survival circuits that have evolved within and across species. Therefore, to understand fear, and potentially other emotions, one must first consider the evolutionary and ecological conditions that give rise to them.

The fuzzy semantics and measurement of fear

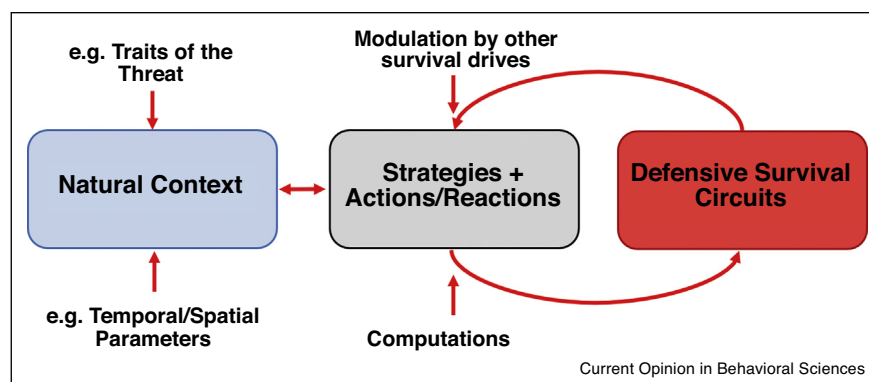
Stanley Rachman has stated that ‘although the word fear is used without difficulty in everyday language . . . problems arise when it is used as a scientific term’ [14] (pp. 11). LeDoux [15**] stays close to the common usage of the term by suggesting that: ‘fear’ can be described as ‘the feeling that invades your conscious mind when you are in danger’ (pp. 303). Given that fear is a conscious operation, it is common for affective scientists to directly probe a subject’s fear state by recording their subjective appraisal or state of mind. However, this has been problematic as Rachman points out that ‘subjective reports of fear also tend to be of limited value in assessing the intensity of the experience because of the difficulties involved in translating phrases such as ‘extremely frightened’, ‘terrified’ and ‘slightly anxious’ into a quantitative scale with stable properties’ [14] (pp. 12). This criticism along with the inability to probe ‘fear as a feelings’ in animals, has led others to consider other measures of fear. For example, Mower [16], Bolles [17] and Fanselow [10] have operationalized fear as a reactive response to danger characterized by, for example, freezing or fleeing, and do not consider the subjective cognitive baggage that accompanies such behaviors. This makes sense when studying rodents, however, as LeDoux [7] points out, fear responses are species specific despite the fact that the circuitry may be species general and defensive behaviors may only reflect the motivation state of the organism.

To make matters confusing, fear and anxiety are often conflated. For example, Rosen and Schulkin [18] define normal fear as ‘both the adaptive fear and anxiety state’ and further state that fear is a response to a ‘potentially dangerous event’. This conflation and confusion between fear states is important to address, because until there is consensus on semantics as well as the conditions by which to evoke and measure fear, we can never have consensus on the neural circuits associated fear and anxiety, and we will ultimately fail when trying to understand how these are disrupted in patients suffering from affective psychopathology [19]. How do we remedy this? One approach is to reverse engineer the problem and disassemble fear states by the variety of ecological contexts that they evolved for (Figure 1). As I will discuss, this approach allows one to create unambiguous definitions and experimental paradigms.

Fear and anxiety in the natural world

Julian Huxley [20], and later Niko Tinbergen [21], proposed that one must consider the ultimate function of behavior or ‘why’ behaviors relate to survival of the species. While adaptationist accounts, which propose that evolutionary acts as an optimizing agent, have been criticized [22], they do provide a conjectural window into the ecological conditions that drive survival behaviors. As Stephens and Krebs [23] point out: ‘asking what a machine is for helps the engineer understand how it works.’ Further, adaptationist accounts become testable questions when behaviors are examined in the ecological niche of the species and how these behaviors relate to survival (e.g. how Galapagos finches’ beaks relate to feeding behavior). O’Keefe and Nadel [24] suggest that one should examine the natural world before experimentation. Likewise, to understand fear, one must first consider the natural conditions by which survival behaviors are elicited (Figure 1).

Figure 1



A simple flow model showing the links between the natural world, including the traits, spatial and temporal properties of the threat and the cognitive/behavioral strategies and computations that have evolved for successful escape and avoidance of danger. Finally, these strategies are embedded in defensive survival circuits.

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