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Emotion, motivation and function

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Biological approaches to emotion require that adaptive function is an organizing principle in defining the emotion. The emotion of fear is taken as the complete behavioral, physiological and experiential components of a system that evolved for antipredator defense. In part, fear is a motivation that selects and drives overt defensive action. But the emotion also contains the autonomic changes supporting these behaviors and the conscious experience that accompanies danger. Fear has the ability to overwhelm consciousness so that that nothing but phylogenetically selected action occurs. By filling consciousness fear prevents flexible behaviors and that is one reason why anxiety disorders can be so debilitating. Anxiety, fear and panic are states within the emotion that correspond to different levels of threat.

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Introduction

I have long advocated that the emotion of fear should be conceptualized as the brain and behavioral systems that evolved to protect organisms from external threats with the main source of selection being predators [1•]. Here I will first relate this view to various ways that emotions have been conceptualized generally and to show how this approach addresses problems inherent in the study of emotions. I conclude with an overview of the rich network of defensive behaviors that characterize the mammalian emotion associated with fear.

Why do we have emotions? Why do humans, and other animals, experience fear [2••]? If fear is a real biological process the answer to the 'why' question is the same answer given to virtually everything that exists in biology. Emotion serves some function that provides a selective advantage. It should be recognized that in higher animals what contacts selection pressure, the thing that is selected for, is behavior. Reproduction, energy intake and defense are behaviors that make direct contact with the consequences of selection pressure. Selection cares more about the ends (behavior) and less about the underlying mechanisms. If emotion is a real biological entity it exists in the service of behavior and must be tied to specific classes of behavior. Following this idea the emotion of fear is the complete brain, body and behavioral system that supports defense. In this article I make a distinction between fear as an emotional system and the state of fear. The emotional system of fear refers to the entire complex of brain mechanisms, bodily changes, subjective experience and suite of behaviors that serve defense. Within that emotion, the state of fear is a particular component of the suite that occurs at a particular level of danger. Anxiety and panic are two other component states that are part of the emotion [3••]. Initially this piece concentrates on the emotional system. How the state of fear fits into the broader system is developed in the final section.

Emotion versus motivation

The terms emotion and motivation are inextricably linked. For example, incentive motivation theory was intended to explain the drive behind behavior and also the emotions of hope, fear, disappointment and relief [4•,5,6]. A convenient way to use this terminology is that fear as a motivator selects a particular set of behaviors from the response repertoire and provides the drive or force behind the behavior. Motivation is one component of the emotion but emotion is a broader term. It includes motivation but also the subconscious physiological processes that support the overt behaviors as well as the subjective conscious experience that accompanies the emotion. The emotion exists even if a single component is eliminated. When lesions of the lateral hypothalamus eliminate hypertension in response to threatening stimuli fear is still present [7]. And while patients that suffer hippocampal damage after a trauma are unable to remember the traumatic experience they still develop all the symptoms of post-traumatic stress disorder (PTSD) [8,9,10•].

Dimensional versus categorical theories of emotion

There are two distinct classes of theories of emotion, categorical and dimensional. The categorical approach views each emotion as an independent discrete entity

[11•,12]. A categorical view would say that fear and joy are independent functional entities. For example, Ekman has argued that fear is its own distinct universal state that differs from other aversive emotions such as anger and disgust [12]. One danger of such a view is that it can lead to a proliferation of individual emotions, unless some rules are taken to limit what is conceived of as an emotion. This sort of condition led to the demise of instinct theory where theorists continually proposed additional instincts for particular behaviors [13••,14].

Dimensional approaches provide for much greater parsimony by proposing that there are a limited number of continuous dimensions that emotional experiences fall on. The most simple of these comes from incentive motivation theory that proposes a single hedonic dimension anchored at one end by aversiveness and the other by pleasurableness (appetitive) [5,15•]. Within this view stimuli that predict danger and stimuli that predict the absence of pleasant events such as food are emotionally equivalent; they move the organism toward the aversive end of the continuum. Likewise stimuli that predict the absence of danger and those that predict food are equivalent shifting emotion and corresponding behaviors toward the appetitive end [5]. Virtually all dimensional theories rely on a hedonic continuum but additional orthogonal dimensions are added to capture a greater range of experiences [16•]. Something capturing intensity is a common addition, such as Schlosberg's proposal of a dimension corresponding to 'level of activation' [16•]. As long as the number of dimensions is limited the theory maintains some level of parsimony because seemingly different states are collapsed into a single place on the continuum becoming more-or-less equivalent.

I believe that it is the use of a single hedonic continuum that undermines dimensional theories. Incentive motivation theories equate fear and pain, suggesting that fear is nothing more than the conditionable component of pain [17,18]. A stimulus like shock is an unconditional pain stimulus that moves emotional expression toward the negative hedonic end. Stimuli associated with pain become fear stimuli because they acquire this ability. Pleasurable events like food and water are similarly collapsed. However, I have argued that fear and pain are categorically different. Fear and pain serve different biological functions, defense on one hand, recuperation on the other [1•]. They promote completely different behaviors and fear-induced analgesia allows fear to powerfully inhibit pain [19]. It is illogical to think that fear and pain are aspects of a single emotion when they are mutually incompatible. Similarly, thirst and hunger have an antagonistic role to each other [13••,20]. One could try and pull fear and pain apart by adding multiple dimensions but that comes at the cost of exactly the parsimony that makes dimensional theories attractive.

My position on fear clearly seats it within the categorical view. However, to maintain a healthy degree of parsimony successful categorical theories must impose constraints or rules in defining categories. Therefore, I have advocated a quadral requirement for defining an emotion [21]. One must specify: *Evolutionary or phylogenetic function*; thwarting predation in the case of fear. *Antecedent conditions* that activate the emotion; signals for threat promote fear. *Consequent conditions* are the measureable behaviors that occur when the emotion is activated and serve to fulfill the function, defense in the case of fear. *Circuitry*: the brain must have a definable circuit that mediates between the antecedent and consequent conditions.

The subjective emotional state of fear: primary or indicative?

When we are threatened we become keenly aware of our fear; it dominates our consciousness. The power of fear to dominate consciousness must come from the biological importance of defense. One failure to defend means no future reproduction, while a single failure to mate has far less long-term consequences for reproductive success. When we are afraid we must concentrate on defense; we do not have the luxury of thinking about anything else. Indeed, we need to put aside any feelings of hunger and pain as well. But what is the role of the conscious subjective experience of fear from this functional perspective? One possible function is that by dominating consciousness fear can readily suppress systems supporting voluntary behavior allowing rapid and automatic execution of phylogenetically programmed defensive behaviors. Thus the conscious experience of fear is an indicator of the activation of an emotion that is far richer than simply what we are aware of. Like freezing and hypertension the subjective report of fear is one of the consequent conditions of this emotion. Strong fear must fill consciousness to preclude anything but defense.

When I say fear is functional I mean function in the ultimate phylogenetic sense and not in the proximal ontogenetic sense. Fear motivation limits the behavioral repertoire to responses that have a phylogenetic history of defending members of the species [22•]. These behaviors occur even if at the particular moment they are deleterious. This suppressive effect of the conscious experience of fear helps explain this loss of behavioral flexibility. In the laboratory rat this manifests as the well-known failure for rats to learn arbitrary responses to avoid shock, even if they are perfectly capable of making those responses to obtain food [22•]. Indeed, modern studies of instrumental avoidance typically incorporate fear reduction procedures such as extinction, large numbers of trials with mild shock to promote habituation and/or discard the most fearful animals, which is often a substantial portion [23•,24,25]. Indeed, damaging the circuits responsible for fear often facilitate performance of instrumental avoidance [26].

This loss of flexibility is also a key contributor to anxiety disorders. Clinical fears are defined by their lack of rationality. You cannot tell a combat veteran to lose his or her PTSD simply by pointing out that they are no longer in a combat situation. And the suppression of behavioral flexibility blocks avenues toward proximally adaptive behavior, similar to the frightened rats inability to press a lever to avoid shock [22•].

Some other approaches to emotion take the subjective state that is communicated by verbal report as a primary; fear is the subjective state, nothing more and nothing less [27,28]. For LeDoux the subjective report of fear is taken as a primary that exists in its on right, it exists independently of unconscious (e.g. subcortical) processes [29••]. Indeed, according to this rather extreme model nonverbal indicators often used to assess emotion such as behavior and physiological arousal are taken as irrelevant and misleading because fear is only the conscious subjective experience [27,29••]. Such views fail to capture the richness of fear and they fail to explain why fear can be a clinical problem. Nor do they explain why such a powerful process evolved. Instead I take the subjective state and its reporting as indicative of a more complex internal process. A process that is largely subcortical and involuntary but also strongly influences our consciousness. Interestingly, Freud recognized that the conscious experience of emotion was the tip of the iceberg that emerged from powerful unconscious processes [30]. For him unconscious processes could directly drive behavior such that an individual may be unaware of the actual causes of behavior. If nothing else I agree with Freud that equating fear with subjectively reportable experience makes for a simplistically barren and often inaccurate view of emotion.

The organization of defense

There are already several reviews that describe the organization of defense in detail [31••,32,33]. Below is a brief summary illustrating a quadral definition of fear. The emotion of fear serves the purpose of antipredator defense and the organization of defense is tightly tied to the organization of predation. Predators need to go through a sequence of stages before prey can be consumed. First they choose where and when to forage and then have to find prey. Once found prey must be captured. In order to thwart a predator, antipredator behavior goes through a corresponding sequence of stages called modes [21,34].

Each mode is characterized by its functional relationship with predation, the antecedent stimuli that call forth the mode, the specific defensive behavioral consequents that serve the antipredator function and the circuitry that supports the coordination of antecedent stimuli and behavioral consequences [21]. The schema is summarized in Table 1. Since defensive behaviors are species typical, the behaviors in the table are most directly related to the rat. I also believe that there is a discriminable internal state that corresponds to each mode and these states correspond to anxiety, fear and panic [3••]. The state of fear describes the intermediate mode where a predator has been detected but contact is not immediate. Clinically, this framework has been applied as an aid to understanding anxiety disorders and has driven the National Institute of Mental Health's Response Domain Criteria (RDoC) for negative affect [3••,36•,37•,38].

Predatory imminence. The trauma that precipitates PTSD in a patient is very rarely experience with a predator. Similarly, the lab rat that advanced this theory of defense more likely experienced electric footshock than a predator. *In vivo* threats are highly variable but they still need to be contended with quickly. In the face of a novel threat the brain must immediately tap into the defensive system it has built over countless generations. The rat never evolved a specific system for shock so it responds to stimuli associated with shock exactly how it does to a cat in its vicinity [39]. The rat will also respond defensively to a plastic robot (Robogator) that has never existed in its phylogenetic history [40,41]. We refer to the construct that all these stimuli map onto as predatory imminence [31••]. The term derives from the idea that defensive modes vary with the distance of the predator but this

Table 1

The organization of defense

	Pre-Encounter	Post-Encounter	Circa-Strike
Function	Reduce the likelihood of encountering a predator	Decrease the likelihood of detection and attack	Survive direct contact with a predator
State	Anxiety	Fear	Panic
Antecedent stimuli	Past experiences with predation or threats	Detection of a predator or imminent threat	A striking predator is making or is about to make physical contact
Consequent behaviors	Stretched approach, alterations in meal patterns (less frequent larger meals [35]), retreat to nest	Freezing	Audible vocalizations (scream), vigorous escape attempts
Neural circuit includes:	Prefrontal cortex, ventral hippocampus	Amygdala, bed nuclei of the stria terminalis, ventral periaqueductal gray	Dorsal periaqueductal gray with sensory inputs from the superior colliculus

distance is not only physical it is psychological. The speed or size of the predator or the probability of an encounter can influence imminence as much as spatial distance [31••]. Changing the probability of shock in an environment can alter the mode of defense [32].

Learning and memory. Learning plays a fundamental role in determining predatory imminence. Fear conditioning is extremely rapid (single trial) and immediately impacts behavior [42]. A rat begins to freeze at shock termination but this response relies solely on the building of an association between the shock and context [43]. The rat faced with robogator instantly learns a new threat and immediately shows a defensive response to that threat [40,41]. Learning is a natural integrator; it is influenced by how events are distributed in time and space [44,45]. In this way learning can place the animal on a particular point in the predatory imminence continuum thereby selecting the most functional mode at any particular point in time. Thus learning and conditioning are intrinsic to effective defense.

Conclusion

This essay starts with the premise that if emotion exists it must have arisen through natural selection and serves some adaptive function. Further, since behavior is the interface between natural selection and genes, emotion arose to drive and support behavior. The behaviors relevant to fear are those that defend against environmental dangers. Defense is organized in discrete stages corresponding to the psychological proximity of danger. Fear is an intermediate stage. More imminent threats produce panic, while less imminent threats produce anxiety.

Emotions consist of motivators that select specific responses (e.g. freezing), subconscious physiological responses that support behavior (e.g. altered respiration), and conscious experience. Emotion is better understood in terms of function than hedonics because there are multiple independent aversive motivations and multiple independent pleasurable emotions. Ideally emotions have a quadral definition specifying function, antecedents, consequents and circuitry. The debilitating nature of anxiety disorders derives from fear's promotion of phylogenetically successful behavior over proximally or ontogenetically beneficial behavior.

Conflict of interest statement

Dr. Fanselow is a founding board member of Neurovation, Inc., which is developing diagnostic and treatment tools for Post-Trumatic Stress Disorder.

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