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The role of learning in threat imminence and defensive behaviors

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Life threatening situations as urgent as defending against a predator precludes the use of slow trial and error strategies. Natural selection has led to the evolution of a behavioral system that has three critical elements. (1) When it is activated it limits the behaviors available to the organism to a set of prewired responses that have proven over phylogeny to be effective at defense. (2) A rapid learning system, called Pavlovian fear conditioning, that has the ability to immediately identify threats and promote prewired defensive behaviors. (3) That learning system has the ability to integrate several informational dimensions to determine threat imminence and this allows the organism to match the most effective defensive behavior to the current situation. The adaptive significance of conscious experiential states is also considered.

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Often, we hear that failure is the best teacher. A stochastic sequence of successes and failures allows the environment to select and shape responses [1]. Trial and error learning allows organisms to eventually maximize their benefit to cost ratio, a strategy that would be favored by evolution resulting in neural systems that are capable of such learning. But there are also situations where the cost of a single failure is so absolute that trial and error learning is an evolutionarily unviable option. The most obvious of these is the threat of predation, where the consequence of trying out ineffective responses is likely to mean no future reproductive successes. The central assumption of this essay is that neural systems evolved that allow rapid generation of effective defensive behavior upon an initial experience with a predator. What I wish to consider here are the relative roles of innate programming and learning in the operation of this survival circuit.

Bolles equated fear with activation of a defensive behavior system. From this vantage, one of the essential properties of fear was to constrain the behavioral repertoire of an animal to its species-specific defense reactions (SSDRs [2]). This was a critical juncture in the study of fear as it moved the paradigm from one centered on trial and error learning via fear-reduction reinforcement to the study of defensive behavior. SSDRs are prepackaged biologically programmed responses that could be executed effectively the first time they were called upon. They were based entirely on the phylogenetic history of the species and were minimally shaped by experience [3]. Learning played little role in the form or topography of the behavior.

Learning and the recognition of danger

In order to defend you must recognize danger and then appropriately respond to that danger. Because of the urgency of defense learning plays little role in shaping responses to danger. Equally important is when to respond; for defense to succeed we must be able to recognize threats the first time they are encountered. This has led to the general acceptance of the idea that most fears are innately programmed [4•,5••,6,7]. There are two lines of evidence for the innate recognition hypothesis. The first comes from the clinical literature indicating that phobias are not randomly distributed between stimuli but rather are far more likely for some stimuli (e.g., snakes and spiders) than others (e.g., flowers [8]). The second line of supporting evidence comes from laboratory studies indicating that rats will freeze upon their first exposure to potential predators such as cats [9,10]. While innate recognition of threat would certainly be an advantage, it would also be a fantastic load on the genes to encode all threats in all their variations. I believe that these two lines of evidence for the innate recognition hypothesis are weak and natural selection has favored a very different strategy commonly referred to as Pavlovian fear conditioning. Furthermore, certain features of Pavlovian fear conditioning readily account for the two lines of evidence supporting the innate recognition hypothesis. The genetic space needed for this specialized form of learning is far less than accurately encoding all potential threats. Learning related plasticity should be especially important in species that are confronted by several different predators [11,12] I will briefly examine an

alternative explanation of the nonrandom distribution of phobias and then turn to what I will refer to as the myth of the first time.

Selective association formation

Mineka embarked on a series of studies initially intended to investigate innate fears in primates by examining fear of snakes in rhesus macaques [13••,14]. There were two distinct populations of macaques in the Wisconsin primate facility. Some reacted with remarkably intense fear of both real and toy snakes on the first exposure but others showed no initial fear reaction. Importantly the animals reacting to the snakes were all born in the wild. Lab born monkeys showed no such reaction. She also found that this fear could be rapidly acquired when a young rhesus observed an adult showing fear to a snake. Masataka [15••] also found that wild-born but not lab-born squirrel monkeys had fear of snakes. However, if the lab-reared monkeys had early exposure to a diet containing live insects they showed fear of snakes that was indistinguishable from that of wild-born monkeys. If these primates learned their phobias, might we not expect humans to have such capacity? Learning through such indirect conditioning trials is obviously a less risky strategy than 'face-to-face' learning with a predator and would be expected to be selected for via natural selection [12].

In the Mineka studies the rhesus did not have to see the reaction live; simply viewing another rhesus reacting to a snake on a TV screen was sufficient. This allowed her to employ video editing where the observer could watch a demonstrator that appeared to be reacting to either a snake or a flower. She discovered that while observational conditioning readily occurred to a snake there was little conditioning to flowers [16]. The primate's fear of snakes was not hardwired, however there was a distinct bias in what was learned. This associative bias is an example of a ubiquitous feature of Pavlovian conditioning brought to the fore by Garcia's finding that tastes were readily associated with illness and sounds with shock but little associative learning occurred with the alternative combinations [17]. Selective association formation is not limited to these examples [18•]. Rats more readily associate shock with tones than lights and this is at least in part caused by wiring differences between the sensory system and the amygdala [19,20••]. This selectivity in fear learning easily accounts for the nonrandom distribution of phobias found in the clinical literature. It is important to recognize that the fear learning that occurred in the Mineka studies was found after a single experience; in general, there is significant Pavlovian fear conditioning with a single trial [21].

The myth of the first time

In Pavlovian terminology, an innate fear is the unconditional reaction (UR) to an unconditional stimulus (US). A learned fear is the conditional reaction (CR) to the conditional stimulus (CS). It is important to recognize that the idea that the CR and the UR are similar was rejected some time ago [22,23•]. Fear conditioning in rats with a footshock US is a good example; the jumping and vocalization that characterizes the UR does not get transferred to the CS [24,25]. Rather, the clearest behavioral CR is freezing. While the UR and the CR can be different behaviors, the development of the CR depends on the associative relationship between CS and US. Learning theory outlines a very clear set of comparisons with specific control conditions that allows one to conclude that a CR is in fact a CR dependent on experiencing the CS–US relationship [26,27]. However, there has been little development of the rules for unequivocally concluding that a UR is truly a UR. There is a dearth of control conditions that allows one to say that a response to a stimulus is innate. Just to be clear, what we are talking about is the relationship between US and UR (or CS and CR); the actual topography of both CR and UR is innate. The typical evidence taken as support for the idea that the US–UR relationship is unlearned is that the response is observed the very first time the stimulus is presented. However, this logic is fatally flawed by what I call the *myth of the first time*.

The myth of the first time is that initial reactions to a novel stimulus are necessarily unlearned. Consider a well-studied example, electric shock. On the very first exposure to electric shock rats will freeze and defecate. For many years it was assumed that this meant that these responses were innate URs to shock. This turns out not to be the case; several convergent lines of evidence indicate that they are CRs [21,24,25,28••]. In a single trial, the context and the shock become associated and these responses are elicited by the contextual cues that remain after the shock. The most striking example is what I call the immediate shock deficit [28••]. If the shock is presented as soon as the animal is placed in the box no freezing or defecation occurs after the shock because there has been no opportunity to associate shock and context [21,28••]. Shock does not innately provoke fear it rapidly conditions fear. An analogous situation happens when a rat is exposed to a cat [29]. If the rat is placed into a chamber simultaneously with a cat, freezing is not observed. As with shock, cat presentation must be delayed.

In the above example with electric shock, freezing is conditioned to the context [25,28••]. Similar to the bell and salivation, CS and US are separable stimuli. However, often the CS and US are aspects of the same object [30]. A common example of this is imprinting in birds [31,32]. On the very first exposure to a moving object the visual aspects of the object and its movement become associated. This object then provokes a wide range of behaviors all of which depend on the initial learning experience. The very first exposure to a cat may produce the same sort

Table 1

Predatory imminence continuum and the organization of antipredator behavior in the rat.

Location	Home/nest	Foraging ground	Prey and predator in contact
Predatory module	Search	Procurement	Consumption
Antipredator module	Pre-encounter	Post-encounter	Circa-strike
Examples of defensive behavior primarily based on rodents	Stretched approach, nocturnal feeding	Freezing, Thigmotaxis	Protean escape attempts from predator, vocalization, biting, thrashing
Emotional experience	Anxiety	Fear	Panic

of object learning that is found in imprinting. In this case the object learning results in the many features of a cat becoming integrated and this associative learning endows the cat with the ability to produce a fear CR. This interpretation fits very well with the finding that hippocampal lesions, which impair the integration of multiple features into a unitary whole [33], reduces freezing to cats just as it does to contexts [34,35].

A remarkably creative series of studies conducted by Kim provides direct evidence that this mechanism operates effectively [36••,37]. To study more naturalistic defensive behavior, he built a motorized lego robot that could surge at a foraging rat. On the very first exposure to 'robogator' the rat engaged in a suite of defensive behaviors. Clearly, there is no way that natural selection could have favored innate recognition of this predator. Rather, the rat had to immediately learn this predator and respond accordingly. But if this mechanism can protect against robogator, certainly it would be effective against natural threats.

In conclusion, I believe that evolution handled the problem of recognizing danger by selecting for a specialized fear learning circuit. Such a circuit would require far less genetic coding than recognition of all individual dangers. Furthermore, already evolved synaptic plasticity mechanisms could be co-opted by this circuit further saving genetic space.

Selection of species specific defense reactions

While fear profoundly constricts the behavioral repertoire to SSDRs, for the most part mammalian species have several SSDRs. This immediately raises the question of how does the animal match the SSDR to the situation. Several early proposals were found wanting [38•]. One view that accurately predicts defensive behavioral topography while providing insight into anxiety disorders is predatory imminence theory [39••,40•,41,42]. This theory suggested that SSDRs were organized along a continuum that corresponded to the proximity to fatal contact with the predator [39••]. Prior analyses of foraging had also looked at the organization of predatory behavior along a continuum of search, procurement and consumption [43]. Therefore, it makes sense that antipredator behavior is

organized along a similar sequence because different SSDRs would be successful against search, procurement, and consummatory strategies. Predatory imminence theory envisioned the prey's behavior consisting of independent modules phylogenetically designed to thwart search, procurement and consumption (see Table 1).

Learning and predatory imminence

Actual physical distance is one factor in determining the prey's assessment of where it stands on the predatory imminence continuum. But there are other factors just as important as this spatial dimension. For example, one aspect of pre-encounter defense is the modification of meal patterns if the feeding ground is a place of high risk [44]. Predators forage near sources of water because prey must travel there to exploit this resource. The distance from nest to water may be fixed but what is important is the probability that a predator will be present. Feeding and drinking patterns change as the probability of predation in the foraging area increases [39••,44]. The size/effectiveness of the predator is also a factor; gazelle allow hyenas to approach more closely than cheetahs before fleeing [45]. Predatory encounters during foraging can even entrain the circadian rhythm of feeding [46]. Thus, spatial distance, probability, timing and identity of the predator are all elements of predatory imminence.

Given that the determination of predatory imminence is multifaceted these factors must be integrated with each other [39••]. The properties of Pavlovian conditioning make it an ideal process for the necessary integration. Spatial distance and the time a predator needs to close that distance are part and parcel of the same construct. Pavlovian conditioning is one way the brain represents such timing information [47]. Spatial factors influence Pavlovian learning in another way; stimuli coming from similar locations are more readily associated [48]. The probability of stimulus occurrence is also an essential factor in the strength of conditioning because conditioning requires an integration or comparison between the probability of an outcome in both the presence and absence of the CS [49]. Finally, the first studies using revaluation techniques such as devaluation and inflation demonstrated that Pavlovian conditioning encodes the identity of the outcome [50,51]. Thus while (instrumental) learning plays little role in shaping the topography of

defensive behavior, Pavlovian learning may be at the core of selecting which innately programmed response is selected under a set of stimulus conditions [52].

Predatory imminence, conscious experience and survival

I view the three major modes of defense, pre-encounter, post-encounter and circa-strike as corresponding to the experiential states of anxiety, fear and panic, respectively [42]. By contrast, LeDoux [53,54] has argued that the 'survival circuits' that mediate defensive behavior are not causally related to subjective emotional experience. From LeDoux's perspective fear arises from orthogonal circuitry that supports consciousness. No one would deny that these emotional states are powerful and resource demanding. Evolutionary biology suggests that investing energy in anything that does not, in some way, promote survival would be selected against. From this perspective there are two possible views of emotional states. One is that they are epiphenomenal artifacts of brain function that impose little cost and little benefit. The other is that they were selected for because, despite their cost, they provide some phylogenetic advantage. The latter view is consistent with the idea that the experience of intense emotion is resource demanding; but what are the benefits of these states? To answer this question, one first has to consider the adaptive function of consciousness. Pierson and Trout [55•] have put forth the view that consciousness evolved for the volitional control of movement. They further argue that volitional movement provides the conscious organism with 'the flexibility to non-deterministically yet non-randomly' support action. Insight into the function of conscious emotional experience can be gained by understanding how the behaviors called for in each stage of defense interact with volitional actions.

Because pre-encounter defense is the furthest defensive mode from consumption by the predator this mode is more permissive of flexibility. Mobbs et al. [12] point out that this level of predatory imminence 'allows animals to prepare for, and flexibly attend to, potential danger' and thereby derive flexible solutions. As an example, we have found that one aspect of pre-encounter defense is a reconfiguring of meal patterns that reduces exposure to danger while maintaining caloric intake [44]. This flexibility is consistent with the involvement of prefrontal cortex in pre-encounter defense [56]. Anxiety plays a critical role in pre-encounter defense as it draws heightened attention to the potential dangers that may exist allowing the prey to maximize the effectiveness of pre-encounter responses that reduce the probability of encounters.

Quite the opposite is true during post-encounter defense. At this highly vulnerable stage preprogrammed defensive responses must occur, and we see that flexible trial and error based behaviors are lost [2,3]. At this point fear overwhelms consciousness and volition so that SSDRs reel off unabatedly [57••]. A critical component of the circa-strike behaviors that occur surrounding the point of contact with the predator are ballistic protean escape behaviors [40•,57••]. Panic may help drive the necessary randomness of such behavior, in part by suppressing, necessarily nonrandom, volitional action. Similarly, during suffocation, the accompanying panic suppresses the slow conscious deliberation needed for volitional behavior favoring the necessary violent thrashing needed to attain immediate respiratory freedom. Thus, in complete contrast with the perspective of LeDoux [53,54], I view conscious experience as an integral and critical component of survival circuits.

Conclusion

Survival in the face of predation often requires brain mechanisms that instantaneously select effective defensive responses. Trial and error learning cannot be accommodated into such a system. Here I try to shake the idea that Pavlovian fear conditioning is a laboratory model. Rather, it is the natural mechanism that allows the best preprogrammed defensive responses to occur instantaneously under conditions of new and old threats. The conscious experiences that accompany behavior under threat provide integral support for survival-related activity.

Conflict of interest statement

Nothing declared.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Skinner BF: **Selection by consequences**. *Science* 1981, **213**:501-504.

2. Bolles RC: **Species-specific defense reactions and avoidance learning**. *Psychol Rev* 1970, **77**:32-48.

3. Bolles RC: *Theories of Motivation*. edn 2. Harper & Row; 1975.

4. Garcia R: **Neurobiology of fear and specific phobias**. *Learn*
•   *Mem* 2017, **24**:462-471.
Provides a review of the development of phobias from the traditional perspective that the origin of phobias has both innate and learned sources.

5. Souchet J, Aubret F: **Revisiting the fear of snakes in children:**
•• **the role of aposematic signaling**. *Sci Rep* 2016, **6**:37619.
Analyzes fear of snakes in children and makes the argument that it is not snakes *per se* that are prone to fear. Rather, it is triangular shapes that have an association with danger such as sharp objects, teeth, and snake heads. Thus, there may be a common element that supports the development of fear.

6. Silva BA, Gross CT, Gräff J: **The neural circuits of innate fear: detection, integration, action, and memorization**. *Learn Mem* 2016, **23**:544-555.

7. Polák J, Sedláčková K, Nácar D, Landová E, Frynta D: **Fear the serpent: a psychometric study of snake phobia**. *Psychiatry Res* 2016, **242**:163-168.

8. Agras S, Sylvester D, Oliveau D: **The epidemiology of common fears and phobias**. *Compr Psychiatry* 1969, **10**:151-156.

9. Lester LS, Fanselow MS: **Exposure to a cat produces opioid analgesia in rats**. *Behav Neurosci* 1984, **99**:756-759.

10. Blanchard DC, Blanchard RJ: **Innate and conditioned reactions to threat in rats with amygdaloid lesions**. *J Comp Physiol Psychol* 1972, **81**:281-290.

11. Ferrari MCO, Gonzalo A, Messier F, Chivers DP: **Generalization of learned predator recognition: an experimental test and framework for future studies**. *Proc R Soc B* 2007, **274**:1853-1859.

12. Mobbs D, Hagan CC, Dalgleish T, Silston B, Prevost C: **The ecology of human fear: survival optimization and the nervous system**. *Frontiers Neurosci* 2015, **9** 55 (1–22).

13. Cook M, Mineka S: **Observational conditioning of fear to fear-**
•• **relevant versus fear-irrelevant stimuli in rhesus monkeys**. *J Abnorm Psychol* 1989, **98**:448-459.
This is one paper in a series by Mineka that provides evidence that snake fear in primates is an example of observational fear conditioning but that the conditioning is biased toward certain types of stimuli (e.g., snakes over flowers).

14. Mineka S, Davidson M, Cook M, Keir R: **Observational conditioning of snake fear in rhesus monkeys**. *J Abnorm Psychol* 1984, **93**:355-372.

15. Masataka N: **Effects of experience with live insects on the**
•• **development of fear of snakes in squirrel monkeys, *Saimiri sciureus***. *Anim Behav* 1993, **46**:741-746.
Besides showing that snake fear in primates is learned rather than innate, it is also a demonstration that the outcome of a learning experience is often neither obvious or intuitive. Here eating live insects leads to development of a snake fear.

16. Cook M, Mineka S: **Selective associations in the observational conditioning of fear in rhesus monkeys**. *J Exp Psychol Anim Behav Process* 1990, **16**:372-389.

17. Garcia J, Koelling RA: **Relation of cue to consequence in avoidance learning**. *Psychon Sci* 1996, **4**:123-124.

18. LoLordo VM: **Selective associations**. In *Mechanisms of Animal*
• *Learning and Motivation: Memorial Volume to Jerzy Konorski*. Edited by Dickinson A, Boakes RA. Erlbaum; 1979:367-398.
Excellent review of selective associations in Pavlovian conditioning and how to test for them.

19. Sigmundi RA, Bouton ME, Bolles RC: **Conditioned freezing in the rat as a function of shock intensity and CS modality**. *Bull Psychon Soci* 1980, **15**:254-256.

20. Newton J, Ellsworth C, Miyakawa T, Tonegawa S, Sur M:
•• **Acceleration of visually cued conditioned fear through the auditory pathway**. *Nat Neurosci* 2004, **7**:968-973.
These authors rewire a neonatal mouse's visual system into auditory circuits. When adults, these mice show conditioning to a normally poor visual CS more like that to a more effective auditory stimulus. This is a rare example of showing a potential mechanism of selective associations.

21. Fanselow MS: **Factors governing one trial contextual conditioning**. *Anim Learn Behav* 1990, **18**:264-270.

22. Fanselow MS, Wassum KM: **The origins and organization of vertebrate pavlovian conditioning**. In *Perspectives in Biology: Learning and Memory*. Edited by Kandel ER, Dudai Y, Mayford MR. Cold Spring Harbor; 2015:83-109.

23. Rescorla RA: **Pavlovian conditioning: it's not what you think it**
• **is**. *Am Psychol* 1988, **43**:151-160.
I often tell colleagues and students that they have an archaic inacurate understanding of what Pavlovian conditioning is (as do most introductory psychology textbooks). This paper does a succinct job of correcting several of these misconceptions.

24. Fanselow MS: **The post-shock activity burst**. *Anim Learn Behav* 1982, **10**:448-454.

25. Fanselow MS: **Conditional and unconditional components of post-shock freezing in rats**. *Pavlov J Biol Sci* 1980, **15**:177-182.

26. Rescorla RA: **Pavlovian conditioning and its proper control procedures**. *Psychol Rev* 1967, **74**:71-80.

27. Rescorla RA, Furrow DR: **Stimulus similarity as a determinant of Pavlovian conditioning**. *J Exp Psychol Anim Behav Process* 1977, **3**:203-215.

28. Fanselow MS: **Associative vs. topographical accounts of the**
•• **immediate shock freezing deficit in rats: implications for the response selection rules governing species specific defensive reactions**. *Learn Moti* 1989, **17**:16-39.
Provides a powerful demonstration in fear conditioning that the fear behaviors (freezing and defecation) are not produced by shock but are instead conditional responses. Destroys the notion that seeing a response after the first presentation of a stimulus indicates that the stimulus innately produces the reaction.

29. Blanchard RJ, Fukunaga KK, Blanchard DC: **Environmental control of defensive reactions to a cat**. *Bull Psychon Soci* 1976, **8**:179-181.

30. Domjan M: **Pavlovian conditioning: a functional perspective**. *Annu Rev Psychol* 2005, **56**:179-206.

31. Lorenz K: *Here I Am — Where Are You? — A Lifetime's Study of the Uncannily Human Behaviour of the Greylag Goose*. Harper Collins; 1992.

32. Bolhuis JJ, de Vos GJ, Kruijt JP: **Filial imprinting and associative learning**. *Q J Exp Psychol B* 1990, **42**:313-329.

33. Fanselow MS: **Contextual fear, gestalt memories, and the hippocampus**. *Behav Brain Res* 2000, **110**:73-81.

34. Blanchard RJ, Blanchard DC: **Effects of hippocampal lesions on the rat's reaction to a cat**. *J Comp Physiol Psychol* 1972, **8**:77-82.

35. Kim JJ, Fanselow MS: **Modality-specific retrograde amnesia of fear following hippocampal lesions**. *Science* 1992, **256**:675-677.

36. Kim EJ, Park M, Kong MS, Park SG, Cho J, Kim JJ: **Alterations of**
•• **hippocampal place cells in foraging rats facing a "predatory" threat**. *Curr Biol* 2015, **25**:1362-1367.
One in a series of studies showing the organization of defensive behaviors to a robotic predator. Since the artificial predator moves it reveals how predator movement and distance are determines of defensive behavioral topography.

37. Choi JS, Kim JJ: **Amygdala regulates risk of predation in rats foraging in a dynamic fear environment**. *Proc Natl Acad Sci USA* 2010, **107**:21773-21777.

38. Fanselow MS: **Species-specific defense reactions: retrospect**
• **and prospect**. In *Learning, Motivation, and Cognition: The Functional Behaviorism of Robert C. Bolles*. Edited by Bouton ME, Fanselow MS. American Psychological Association; 1997:321-341.
Species specific defense reaction theory is often presented as it was in Bolles' 1970 Psychological Review paper. However, this was really an initial transitional form of the theory that has undergone significant revision. This chapter describes the development of theory that occurred after the original Psychological Review paper.

39. Fanselow MS, Lester LS: **A functional behavioristic approach to**
•• **aversively motivated behavior: predatory imminence as a determinant of the topography of defensive behavior**. In *Evolution and Learning*. Edited by Bolles RC, Beecher MD. Erlbaum; 1988:185-211.
As the first presentation of the idea that threat imminence is a determinant of defensive action this paper is critical to the ideas developed in this volume.

40. Bouton ME, Mineka S, Barlow DH: **A modern learning theory**
• **perspective on the etiology of panic disorder**. *Psychol Rev* 2001, **108**:4-32.
First application of predatory imminence theory to anxiety disorders.

41. Davies CD, Craske MG: **Psychophysiological responses to unpredictable threat: effects of cue and temporal unpredictability**. *Emotion* 2015, **15**:195-200.

42. Perusini JN, Fanselow MS: **Neurobehavioral perspectives on the distinction between fear and anxiety**. *Learn Mem* 2015, **22**:417-425.

43. Collier G, Hirsch E, Hamlin PH: **The ecological determinants of reinforcement in the rat**. *Physiol Behav* 1972, **9**:705-716.

44. Fanselow MS, Lester LS, Helmstetter FJ: **Changes in feeding and foraging patterns as an antipredator defensive strategy: a laboratory simulation using aversive stimulation in a closed economy**. *J Exp Anal Behav* 1988, **50**:361-374.

45. Walther FR: **Flight behaviour and avoidance of predators in Thomson's Gazelle (Gazella Thomsoni Guenther 1884)**. *Behaviour* 1969, **34**:184-220.

46. Pellman BA, Kim E, Reilly M, Kashima J, Motch O, de la Iglesia HO, Kim JJ: **Time-specific fear acts as a non-photic entraining stimulus of circadian rhythms in rats**. *Sci Rep* 2015, **15**:14916.

47. Blaisdell AP, Denniston JC, Miller RR: **Temporal encoding as a determinant of overshadowing**. *J Exp Psychol Animl Behav Process* 1998, **24**:72-83.

48. Testa TJ: **Effects of similarity of location and temporal intensity pattern of conditioned and unconditioned stimuli on the acquisition of conditioned suppression in rats**. *J Exp Psychol Anim Behav Process* 1975, **1**:114-121.

49. Rescorla RA: **Probability of shock in the presence and absence of CS in fear conditioning**. *J Comp Physiol Psychol* 1968, **66**:1-5.

50. Rescorla RA: **Effect of inflation of the unconditioned stimulus value following conditioning**. *J Comp Physiol Psychol* 1974, **86**:101-106.

51. Rescorla RA: **Effects of US habituation following conditioning**. *J Comp Physiol Psychol* 1973, **82**:137-143.

52. Fanselow MS: **The adaptive function of conditioned defensive behavior: an ecological approach to Pavlovian stimulus substitution theory**. In *Ethoexperimental Approaches to the Study of Behavior. NATO ASI Series D*, vol 48. Edited by Blanchard RJ, Brain PF, Blanchard DC, Parmigiani S . Kluver Academic Publishers; 1989:151-166.

53. LeDoux J: **Rethinking the emotional brain**. *Neuron* 2012, **73**:653-676.

54. LeDoux JE, Brown R: **A higher-order theory of emotional consciousness**. *Proc Natl Acad Sci USA* 2017, **114**:E2016-E2025.

55. Pierson LM, Trout M: **What is consciousness for?** *New Ideas*
• *Psychol* 2017, **47**:62-71.
Insight into psychological processes can often be had when one considers their functional significance, although this alone is not sufficient to define a psychological construct (see [57••]). This paper carefully develops ideas about the evolution of consciousness and its adaptive function.

56. Mobbs D, Petrovic P, Marchant JL, Hassabis D, Weiskopf N, Seymour B, Dolan RJ, Frith CD: **When fear is near: threat imminence elicits prefrontal-periaqueductal gray shifts in humans**. *Science* 2007, **317**:1079-1083.

57. Fanselow MS: **Emotion, motivation and function**. *Curr Opin*
•• *Behav Sci* 2017, **19**:105-109.
This is a companion piece to the current article and specifies four essential components for defining emotional and motivational states.