Perspective

Rethinking the Emotional Brain

Joseph LeDoux[1,2,*]
[1]Center for Neural Science and Department of Psychology, New York University, New York, NY 10003 USA
[2]Emotional Brain Institute, New York University and Nathan Kline Institute, Orangeburg, NY 10962 USA
*Correspondence: jel1@nyu.edu
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I propose a reconceptualization of key phenomena important in the study of emotion—those phenomena that reflect functions and circuits related to survival, and that are shared by humans and other animals. The approach shifts the focus from questions about whether emotions that humans consciously feel are also present in other animals, and toward questions about the extent to which circuits and corresponding functions that are present in other animals (survival circuits and functions) are also present in humans. Survival circuit functions are not causally related to emotional feelings but obviously contribute to these, at least indirectly. The survival circuit concept integrates ideas about emotion, motivation, reinforcement, and arousal in the effort to understand how organisms survive and thrive by detecting and responding to challenges and opportunities in daily life.

Introduction

Emotion is a major research growth area in neuroscience and psychology today. A search of PubMed citations for the 1960s yields just over 100 papers with the word "emotion" in the title. With each subsequent decade, small increases resulted, until the last decade, when emotion titles grew exponentially—more than 2,000 hits. Emotion has happened.

But what exactly is it that has happened? What is being studied in all these papers on emotion? Actually, the term "emotion" is not well defined in most publications. Perhaps this is not surprising since there is little consensus about what emotion is, and how it differs from other aspects of mind and behavior, in spite of discussion and debate that dates back to the earliest days in modern biology and psychology (e.g., Darwin, 1872; James, 1884; Cannon, 1927, 1931; Duffy, 1934, 1941; Tomkins, 1962; Mandler, 1975; Schachter, 1975; Ekman, 1980, 1984, 1992; Izard, 2007; Frijda, 1986; Russell, 2003;; Ekman and Davidson, 1994; LeDoux, 1996; Panksepp, 1998, 2000, 2005; Rolls, 1999, 2005; Damasio, 1994, 1999; Leventhal and Scherer, 1987; Scherer, 2000; Ortony and Turner, 1990; Öhman, 1986, 2009; Johnson-Laird and Oatley, 1989; Ellsworth, 1994; Zajonc, 1980; Lazarus, 1981, 1991a, 1991b; Barrett, 2006a, 2006b; Barrett et al., 2007; Kagan, 2007; Prinz, 2004; Scarantino, 2009; Griffiths, 2004; Ochsner and Gross, 2005; Lyons, 1980).

One point that many writers on this topic accept is that, while there are unique features of human emotion, at least some aspects of human emotion reflect our ancestral past. This conclusion is the basis of neurobiological approaches to emotion, since animal research is essential for identifying specific circuits and mechanisms in the brain that underlie emotional phenomena.

Progress in understanding emotional phenomena in the brains of laboratory animals has in fact helped elucidate emotional functions in the human brain, including pathological aspects of emotion. But what does this really mean? If we don't have an agreed-upon definition of emotion that allows us to say what emotion is, and how emotion differs from other psychological states, how can we study emotion in animals or humans, and how can we make comparisons between species?

The short answer is that we fake it. Introspections from personal subjective experiences tell us that some mental states have a certain "feeling" associated with them and others do not. Those states that humans associate with feelings are often called emotions. The terms "emotion" and "feeling" are, in fact, often used interchangeably. In English we have words like fear, anger, love, sadness, jealousy, and so on, for these feeling states, and when scientists study emotions in humans they typically use these "feeling words" as guideposts to explore the terrain of emotion.

The wisdom of using common language words that refer to feelings as a means of classifying and studying human emotions has been questioned by a number of authors over the years (e.g., Duffy, 1934, 1941; Mandler, 1975; Russell, 1991, 2003; Barrett, 2006a, 2006b; Kagan, 2007; Griffiths, 1997; Rorty, 1980; Dixon, 2001; Zachar, 2006). Whatever problems might arise from using feeling words to study human emotion, the complications are compounded many fold when such words are applied to other animals. While there are certainly emotional phenomena that are shared by humans and other animals, introspections from human subjective experience are not the best starting point for pursuing these. How, then, should the aspects of emotion relevant to animals and humans alike be pursued?

In answering this question it is important to separate the phenomena of interest from the overarching concept of emotion. One set of such phenomena includes responses that occur when an organism detects and responds to significant events in the course of surviving and/or maintaining well-being—for example, responses that occur when in danger or when in the presence of a potential mate or in the presence of food when hungry or drink when thirsty. These are fundamental phenomena that have always interested animal behavior scientists, and would be of interest even if the terms "emotion" and "feelings" never

existed. The challenge for emotion researchers is to understand the relation of the phenomena to the field of emotion without re-defining them as fundamentally emotional phenomena, and thus infusing the phenomena with confusing implications.

In this Perspective I, therefore, describe a way of conceiving phenomena important to the study of emotion, but with minimal recourse to the terms emotion or feelings. The focus is instead on circuits that instantiate functions that allow organisms to survive and thrive by detecting and responding to challenges and opportunities. Included, at a minimum, are circuits involved in defense, maintenance of energy and nutritional supplies, fluid balance, thermoregulation, and reproduction. These survival circuits and their adaptive functions are conserved to a significant degree in across mammalian species, including humans. While there are species-specific aspects of these functions, there are also core components of these functions that are shared by all mammals.

By focusing on survival functions instantiated in conserved circuits, key phenomena relevant to emotions and feelings are discussed with the natural direction of brain evolution in mind (by asking to what extent are functions and circuits that are present in other mammals also present in humans) rather than by looking backward, and anthropomorphically, into evolutionary history (by asking whether human emotions/feelings have counterparts in other animals).

Emotion, motivation, reinforcement, and arousal are closely related topics and often appear together in proposals about emotion. Focusing on survival functions and circuits allows phenomena related to emotion, motivation, reinforcement, and arousal to be treated as components of a unified process that unfolds when an organism faces a challenge or opportunity.

What follows is *not* an attempt at explaining or defining emotion. Instead, the aim is to offer a framework for thinking about some key phenomena associated with emotion (phenomena related to survival functions) in a way that is not confounded by confusion over what emotion means. Stepping back from the overarching concept of emotion and focusing instead on key phenomena that make emotion an interesting topic may be the best way out of the conceptual stalemate that results from endless debates about what emotion is.

Why Do We Need to Rethink the Relation of Emotion to Survival?

The relation of innate survival functions to emotions is hardly novel, and goes back at least to Darwin (1872). As a result, neuroscientists have long assumed that specific emotional/motivational circuits are innately wired into the brain by evolution, and that these mediate functions that contribute to survival and well-being of the organism (e.g., Cannon, 1929; MacLean, 1949, 1952; Hess, 1954; Stellar, 1954; von Holst and von Saint-Paul, 1962; Flynn, 1967; Olds, 1977; Siegel and Edinger, 1981; Panksepp, 1982, 1998, 2005; Blanchard and Blanchard, 1972; Bolles and Fanselow, 1980; Damasio, 1994, 1999; Berridge, 1999; McNaughton, 1989; Swanson, 2000; Ferris et al., 2008; Choi et al., 2005; Motta et al., 2009; Lin et al., 2011; Öhman, 2009). That certain emotions are wired into the brain is also a major tenet of evolutionary psychology (e.g., Tooby and Cos-

mides, 1990; Pinker, 1997; Nesse, 1990). If many researchers in the field (past and present) believe this, why do we need to bother with another discussion of the topic?

A major controversy in the field of emotion research today is, in fact, about the issue of whether there are innate emotion circuits in the human brain. This debate is centered on the question of whether emotions are "natural kinds," things that exist in nature as opposed to being inventions (constructions) of the human mind (e.g., Panksepp, 2000; Griffiths, 2004; Barrett, 2006a; Izard, 2007; Scarantino, 2009). Much of the discussion is focused the question of whether so-called "basic emotions" are natural kinds. Basic emotions are those that are said to be universally expressed and recognized in people around the world, conserved in our close animal ancestors, and supposedly hard-wired into brain circuits by evolution (Darwin, 1872; Tomkins, 1962; Ekman, 1972, 1980, 1984, 1992, 1999a, 1999b; Izard, 1992, 2007; Damasio, 1994, 1999; Panksepp, 1998, 2000, 2005; Prinz, 2004). Contemporary theories recognize between five and seven of these basic or primary emotions. Ekman's list of six basic emotions is the canonical example (Ekman, 1972) and includes fear, anger, happiness, sadness, disgust, and surprise. This list of putative hard-wired basic emotions in fact serves as the foundation for much research on the neural basis of emotional functions in the human brain—a recent review uncovered 551 studies between 1990 and 2008 that used Ekman's basic emotions faces or variants of these to study functional activity related to emotion in the human brain (see Fusar-Poli et al., 2009).

In spite of being well known and widely applied in research, the basic emotions point of view has been challenged on various grounds (e.g., Averill, 1980; Ortony and Turner, 1990; Russell, 1980, 2003; Barrett, 2006a; Barrett et al., 2007). For one thing, different theories have different numbers of basic emotions, and even different names for similar emotions. In addition, questions have been raised about the methods used to identify basic emotions (e.g., forced choice rather than free labeling of the emotion expressed in a face). Basic emotions theory has also been challenged on the basis of a lack of coherence of the phenomena that constitute individual emotions, and the diversity of states to which a given emotion label can refer. Others argue that emotions, even so-called basic emotions, are psychological/social constructions, things created by the mind when people interact with the physical or social environment, as opposed to biologically determined states. Also relevant is the fact that the main basic emotions theory based on brain research in animals (Panksepp, 1998, 2005) lists emotions that do not match up well with those listed by Ekman or others as human basic emotions.

Of particular relevance here is Barrett's recent challenge to the natural kinds status of basic emotions, and particularly to the idea that the human brain has evolutionarily conserved neural circuits for basic emotions (Barrett, 2006a; Barrett et al., 2007). Her argument is centered on several points: that much of evidence in support of basic emotions in animals is based on older techniques that lack precision (electrical brain stimulation), that basic emotions identified in animals do not map onto the human categories, and that evidence from human imaging studies show that similar brain areas are activated in

response to stimuli associated with different basic emotions. I disagree with Barrett's conclusion that the similarity of functional activation in different emotions is an argument against basic emotions since imaging does not have the resolution necessary to conclude that the similarity of activation in different states means similar neural mechanisms. Yet, I concur with her conclusion that the foundation of support for the idea that basic emotions, as conventionally conceived, have dedicated neural circuits is weak. This does not mean that the mammalian brain lacks innate circuits that mediate fundamental phenomena relevant to emotion. It simply means that emotions, as defined in the context of human basic emotions theory, may not be the best way to conceive of the relevant innate circuits. Enter survival circuits.

Survival Circuits

It has long been known that the body is a highly integrated system consisting of multiple subsystems that work in concert to sustain life both on a moment to moment to basis and over long time scales (Bernard, 1878–1879; Cannon, 1929; Lashley, 1938; Morgan, 1943; Stellar, 1954; Selye, 1955; McEwen, 2009; Damasio, 1994, 1999; Pfaff, 1999; Schulkin, 2003). A major function of the brain is to coordinate the activity of these various body systems. An important category of life-sustaining brain functions are those that are achieved through behavioral interactions with the environment. As noted, these survival circuits include, at a minimum, circuits involved in defense, maintenance of energy and nutritional supplies, fluid balance, thermoregulation, and reproduction.

Survival circuits have their ultimate origins in primordial mechanisms that were present in early life forms. This is suggested by the fact that extant single-cell organisms, such as bacteria, have the capacity to retract from harmful chemicals and to accept chemicals that have nutritional value (Macnab and Koshland, 1972). With the evolution of multicellular, and multisystem, eukaryotic organisms (Metazoa, or what we usually call animals), fundamental survival capacities increase in complexity and sophistication, in large part due to the presence of specialized sensory receptors and motor effectors, and a central nervous system that can coordinate bodily functions and interactions with the environment (Shepherd, 1988).

The brains of vertebrate organisms vary in size and complexity. Yet, in spite of these differences, there is a highly conserved organizational plan that is characteristic of all vertebrate brains (Nauta and Karten, 1970; Northcutt and Kaas, 1995; Swanson, 2002; Butler and Hodos, 2005; Striedter, 2005). This conservation is most often discussed in terms of central sensory and motor systems. However, sensory motor systems do not exist in isolation, and in fact evolved to negotiate interactions with the environment for the purpose of sustaining life—for example, by maintaining energy and fluid supplies, regulating body temperature, defending against harm, and enabling reproduction.

The survival circuits listed do not align well with human basic emotions. However, my goal is not to align survival circuits with basic emotion categories. It is instead to break free from basic emotion categories based on human emotional feelings (introspectively labeled subjective states) and instead let conserved circuits do the heavy lifting. For example, there is no anger/aggression circuit in the present scheme. This might at first seem like a striking omission. However, it is important to note that aggression is not a unitary state with a single neural representation (Moyer, 1976; Chi and Flynn, 1971; Siegel and Edinger, 1981). Distinct forms of aggression (conspecific, defensive, and predatory aggression) might be more effectively segregated by the context in which the aggression occurs: defense circuitry (aggression in an attempt to protect one's self from harm); reproductive circuitry (aggression related to competition for mates); feeding circuitry (predatory aggression toward prey species). Similarly, a joy/pleasure/happiness kind of circuit is not listed and might seem like a fatal flaw. However, behaviors used to index joy/pleasure/happiness are instead treated products of specific circuits involved in energy and nutrition, fluid balance, procreation, thermoregulation, etc. By focusing on the subjective state, joy/pleasure/happiness, emotion theories tend to gloss over the underlying details of emotional processing for the sake of converging on a single word that symbolizes diverse underlying states mediated by different kinds of circuits.

Each survival circuit may itself need to be refined. For example, it is unlikely that there is a single unified defense or reproductive circuit. The range of functions studied needs to be expanded to more effectively characterize these. Some variations on defense are described below, but still other refinements may be needed.

Another key difference between the survival circuit and basic emotions approaches is this. Basic emotion circuits are meant as an explanation of the feelings for which each circuit is said to be responsible. Survival circuits are not posited to have any direct relation (causal role) in feelings. They indirectly influence feelings, as described later, but their function is to negotiate behavioral interactions in situations in which challenges and opportunities exist, not to create feelings.

Survival circuits help organisms survive and thrive by organizing brain functions. When activated, specific kinds of responses rise in priority, other activities are inhibited, the brain and body are aroused, attention is focused on relevant environmental and internal stimuli, motivational systems are engaged, learning occurs, and memories are formed (e.g., Morgan, 1943; Hebb, 1949; Bindra, 1969; Gallistel, 1980; Scherer, 1984, 2000; Maturana and Varela, 1987; LeDoux, 2002).

In sum, survival circuits are sensory-motor integrative devices that serve specific adaptive purposes. They are tuned to detect information relevant to particular kinds of environmental challenges and opportunities, and they use this information to control behavioral responses and internal physiological adjustment that help bring closure to the situation. All complex animals (invertebrates and vertebrates) have survival circuits. Core components of these circuits are highly conserved in vertebrates. I focus on vertebrates, especially mammals in this article, but consider the relation of invertebrate to vertebrate survival functions toward the end.

Nature and Nurture in Survival Circuits

Survival circuits detect key trigger stimuli on the basis of innate programming or past experience. By innate programming I mean genetically specified synaptic arrangements that are

established in early development. Innate evaluative networks make possible species-wide stimulus-response connections that allow organisms to respond to specific stimulus patterns in tried and true ways (i.e., with hard-wired/innate reactions) that have been honed by natural selection.

By experience I mean conditions under which associations are formed between novel stimuli and biologically innately significant events, typically innate triggers. These experience-dependent associations allow meaningless stimuli that occur in conjunction with significant events to acquire the ability to activate the innate response patterns that are genetically wired to innate trigger stimuli. The fact that the response patterns are innately wired and initially expressed involuntarily does not mean that they are completely inflexible. Not only can they be coupled to novel stimuli through experience and learning, they can be regulated in terms of their time course and intensity, and perhaps in other ways.

Innate and experience-based evaluative mechanisms are, as noted, circuit-specific. Thus, defense, nutritional, reproductive, thermoregulatory and other survival systems are wired to detect unique innate triggers. By entering into associations with biologically significant stimuli, novel sensory events become learned triggers that activate survival circuits. We will consider innate and learned survival circuit triggers in the context of defense next. In the field of emotion, these are described as unconditioned and conditioned fear stimuli.

Defense as an Example

The evidence for conservation across mammals of mechanisms underlying survival functions such as defense (e.g., LeDoux, 1996, 2012; Phelps and LeDoux, 2005; Motta et al., 2009; Choi et al., 2005; Kalin et al., 2004; Amaral, 2003; Antoniadis et al., 2007), reproduction (e.g., Pfaff, 1999; Oomura et al., 1988; Blaustein, 2008), thermoregulation (Nakamura and Morrison, 2007), fluid balance (Johnson, 2007; Fitzsimons, 1979), and energy/nutritional regulation (Elmquist et al., 2005; Morton et al., 2006; Saper et al., 2002) is strong. Space does not permit a detailed discussion of these circuits and their functions. Defense circuits in mammals will be used as an initial illustration.

Defense against harm is a fundamental requirement of life. As noted above, even single-cell organisms can detect and respond to harmful environmental stimuli. In complex organisms (invertebrates and vertebrates), threat detection involves processing of innate and learned threats by the nervous system via transmission of information about the threat through sensory systems to specialized defense circuits.

Unconditioned threat stimuli are species-specific. The most common threat triggers are stimuli that signal other animals (predators and potentially harmful conspecifics), and these will obviously be different for different species. Examples of innately wired stimuli for rodents include predator odors (e.g., Motta et al., 2009; Pagani and Rosen, 2009; Blanchard et al., 1990), as well as high-frequency predator warning sounds emitted by conspecifics (e.g., Litvin et al., 2007; Choi and Brown, 2003), high-intensity auditory stimuli (e.g., Bordi and LeDoux, 1992), and bright open spaces (Thompson and LeDoux, 1974; Gray, 1987; Walker and Davis, 2002). In primates, the sight of snakes and spiders has an innate propensity to trigger defense (Amaral, 2003; Öhman, 1986; Mineka and Öhman, 2002). In spite of being genetically specified, innate stimulus processing is nevertheless subject to epigenetic modulation by various factors inside and outside the organism during development, and throughout life (Bendesky and Bargmann, 2011; Monsey et al., 2011; McEwen et al, 2012; Brown and Hariri, 2006; Casey et al., 2011; Zhang et al., 2004). Indeed, some aspects of defense stimulus processing in primates, including humans, involves preferential rapid learning to certain classes of innately "prepared" stimuli (Seligman, 1971; Öhman, 1986; Mineka and Öhman, 2002). Fearful and aggressive faces of conspecifics are also a potent innate defense trigger in humans and other primates (Adolphs, 2008; Davis et al., 2011).

Recent studies have revealed in some detail the circuits that allow rodents to respond to unconditioned threats, especially odors that signal predators or potentially dangerous conspecifics (Dielenberg et al., 2001; Canteras, 2002; Petrovich et al., 2001; Markham et al., 2004; Blanchard et al., 2003; Motta et al., 2009; Choi et al., 2005; Vyas et al., 2007; Pagani and Rosen, 2009) (Figure 1). The odors are detected by the vomeronasal olfactory system and sent to the medial amygdala (MEA), which connects with the ventromedial hypothalamus (VMH). Outputs of the latter reach the premammillary nucleus (PMH) of the hypothalamus, which connects with dorsal periaqueductal gray (PAGd). But not all unconditioned threats are signaled by odors. Unconditioned threats processed by other (nonolfactory) modalities involve sensory transmission to the lateral amygdala (LA) and from there to the accessory basal amygdala (ABA), which connects with the VMH-PM-PAGv circuitry (Motta et al., 2009). Different subnuclei of the MEA, PMH, and PAGd are involved in processing conspecific and predatory threats. In the case of both olfactory and nonolfactory unconditioned threat signals, the PAGd and its outputs to motor control areas direct the expression of behavioral responses that help promote successful resolution of the threatening event. The PAG is also involved in detection of internal physiological signals that trigger defensive behavior (Schimitel et al., 2012).

Biologically insignificant stimuli acquire status as threat signals results when they occur in conjunction with biologically significant threats. This is called Pavlovian defense conditioning, more commonly known as fear conditioning. Thus, a meaningless conditioned stimulus (CS) acquires threat status after occurring in conjunction with an aversive unconditioned stimulus (US). Most studies of Pavlovian defense conditioning involve the use of electric shock as the biologically significant US, though other modalities have been used as well. Typically, auditory, visual, or olfactory stimuli as the insignificant CS. While a strong US can induce learning to most kinds of sensory stimuli, associability is not completely promiscuous—for example, taste stimuli associate more readily with gastric discomfort than with electric shock (Garcia et al., 1968). Once the association is formed, the CS itself has the ability to elicit innate defense responses.

The neural circuit by which a CS (auditory, visual, olfactory) elicits innate defense responses, such as freezing behavior, involves transmission of sensory inputs to the LA, intra-amygdala connections (direct and indirect) linking the LA with the central nucleus of the amygdala (CEA), and connections from
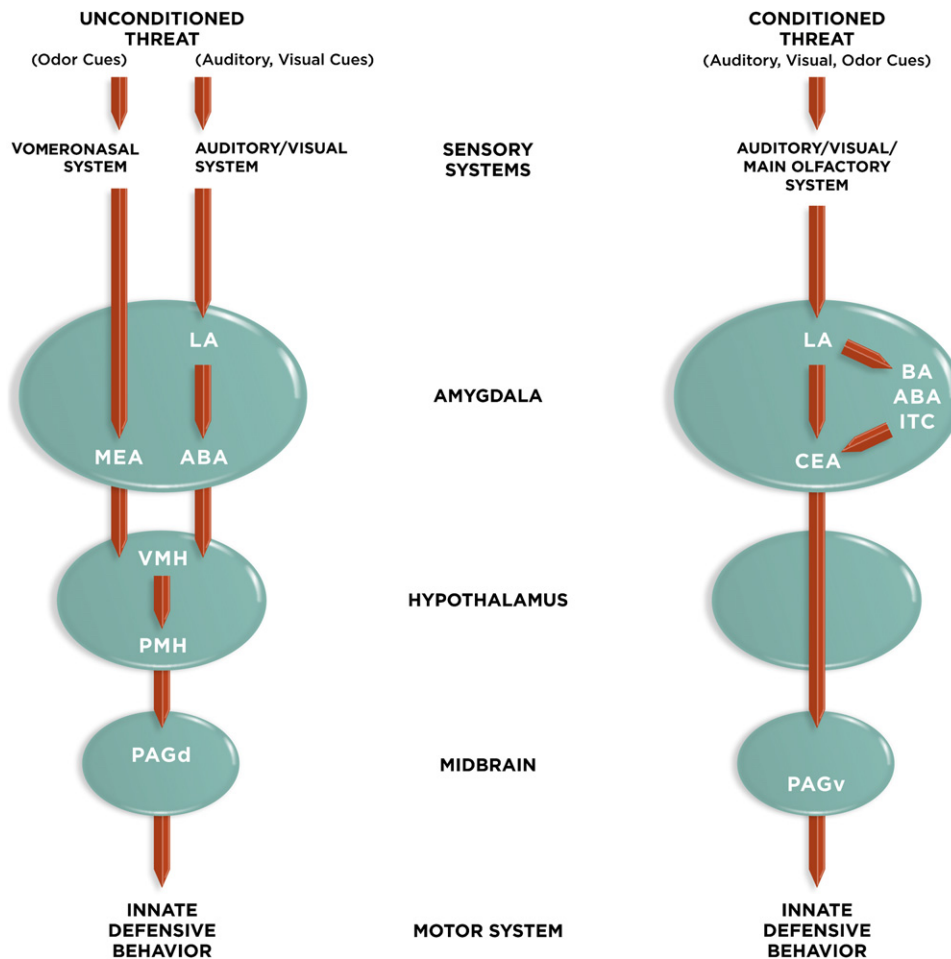
Figure 1. Circuits Underlying Defense Reactions Elicited by Unconditioned (Unlearned) and Conditioned (Learned) Threats
Abbreviations: ABA, accessory basal amygdala; BA, basal amygdala; CEA, central amygdala; LA, lateral amygdala; LH, lateral hypothalamus; MEA, medial amygdala; NAcc, nucleus accumbens; VMH, ventromedial hypothalamus; PAGd, dorsal periaqueductal gray region; PAGv, venral periaqueductal gray region; PMH, premammilary nucleus of the hypothalamus.

the medial CEA (CEm) to the ventrolateral PAG (PAGvl) (Johansen et al., 2011; LeDoux, 2000; Maren, 2001; Fanselow and Poulos, 2005; Davis et al., 1997; Rosenkranz and Grace, 2002; Cousens and Otto, 1998; Paré et al., 2004; Maren and Quirk, 2004; Quirk and Mueller, 2008; Haubensak et al., 2010). The indirect connections between LA and CEA include the basal (BA), AB, and intercalated (ITC) nuclei (Pitkänen et al., 1997; Paré et al., 2004). As with unconditioned threats, PAG outputs to motor control regions direct behavioral responses to the threat. While damage to the PAGvl disrupts defensive freezing behavior, lesions of the PAGdl enhance freezing (De Oca et al., 1998), suggesting interactions between these regions. Whether the CEA and PAG might also be linked via the VMH or other hypothalamic nuclei has not been carefully explored.

While most studies have focused on freezing, this behavior mainly occurs in confined spaces where escape is not possible (Fanselow, 1994; Blanchard et al., 1990; de Oca et al., 2007; Canteras et al., 2010). Little work has been done on the neural basis of defense responses other than freezing that are elicited by a conditioned cues (but see de Oca and Fanselow, 2004).

An important goal for future work is to examine the relation of circuits involved in innate and learned behavior. Electric shock simulates tissue damage produced by predator-induced wounds. However, it is difficult to trace the unconditioned stimulus pathways with this kind of stimulus. Recent studies exploring interactions between circuits processing olfactory conditioned and unconditioned stimuli is an important new direction (Pavesi et al., 2011).

Another form of Pavlovian defense conditioning involves the association between a taste CS and a nausea-inducing US. The circuits underlying so called conditioned taste aversion also involve regions of the amygdala, such as CEA and the basoloateral complex (which includes the LA, BA, and ABA nuclei), as well as areas of taste cortex (Lamprecht and Dudai, 2000). However, the exact contribution of amygdala areas to learning and performance of the learned avoidance response is less clear than for the standard defense conditioning paradigms described above.

While much of the work on threat processing has been conducted in rodents, many of the findings apply to other species.

For example, the amygdala nuclei involved in responding to conditioned threats in rodents appear to function similarly in rabbits (Kapp et al., 1992) and nonhuman primates (Kalin et al., 2001, 2004; Antoniadis et al., 2007). Evidence also exists for homologous amygdala circuitry in reptiles (Martínez-García et al., 2002; Davies et al., 2002; Bruce and Neary, 1995) and birds (Cohen, 1974). In addition, functional imaging and lesion results from humans (e.g., Phelps, 2006; Damasio, 1994, 1999; LaBar and Cabeza, 2006; Whalen and Phelps, 2009; Büchel and Dolan, 2000; Mobbs et al., 2009; Schiller and Delgado, 2010) show that the amygdala plays a key role in defense conditioning, and thus suggest that, at least to a first approximation, similar circuits are involved in humans as in other mammals. However, the level of detail that has been achieved in humans pales in comparison to the animal work. Methods available for studying humans are, and are likely to continue to be, limited to levels of anatomical resolution that obscure circuit details.

Because animal research is thus essential for relating detailed structure to function in the brain, it is extremely important that the phenomena of interest be conceptualized in a way that is most conducive to understanding the relation of findings from animal research to the human condition. Survival circuits provide such a conceptualization.

Interactions between Survival Circuit Functions

Survival circuits interact to meet challenges and opportunities. Indeed, survival functions are closely intertwined (e.g., Saper, 2006). In the presence of a threat to survival or well-being, the brain's resources are monopolized by the task of coping with the threat. Other activities, such as eating, drinking, and sex, are actively suppressed (Gray, 1987; Lima and Dill, 1990; Blanchard et al., 1990; Fanselow, 1994; Choi et al., 2005). However, increased behavioral activity of any kind (fighting, fleeing, foraging for food or drink, sexual intercourse) expends energy, depleting metabolic resources. At some point, the need to replenish energy rises in priority and overrides defensive vigilance, which might otherwise keep the animal close to home. Foraging for food or liquids often requires exposure to threats and a balance has to be struck between seeking the needed resources and staying put. Metabolic activity during any active behavior (whether fighting, feeding, foraging, fornicating) produces heat that has to be counteracted by lowering body temperature. Thermoregulation is controlled directly by homeostatic alterations that include increased sweating or panting, and by various behavioral means, such as altering fluid intake or seeking shelter. We cannot consider all possible interactions between survival circuits here. Thus, interactions between the energy/nutritional regulation system and the defense system will be discussed in some detail for illustrative purposes.

Across mammalian species, circuits involving the arcuate, ventromeidal, dorsomedial, and lateral hypothalamus, and regulated by leptin, ghrelin, glucose, and insulin, control feeding in relation to energy and nutritional demands (Elmquist et al., 2005; Morton et al., 2006; Saper et al., 2002; Saper, 2006). In satisfying nutritional/energy demands, behavioral responses are guided by the sensory properties of potential food sources and by cues associated with food. For example, auditory or visual cues that occur in connection with food items can modulate the energy/nutritional circuitry (e.g., Petrovich, 2011). Specifically, areas of the amygdala (LA, BA, ABA) process these learned cues associated with food and relay them to the LH. Such cues, if sufficiently potent, can stimulate eating in animals that are sated.

Feeding does not occur in a vacuum. As noted above, when threat levels rise, feeding is suppressed (Gray, 1987; Lima and Dill, 1990; Blanchard et al., 1990; Fanselow, 1994). For example, a tone previously paired with shock inhibits feeding (Petrovich, 2011) and food-motivated instrumental behavior (e.g., Cardinal et al., 2002). Connections from the basolateral amygdala to the LH facilitate feeding by a CS associated with food, while the suppression of feeding by an aversive CS involves outputs of the CEA. The exact target remains to be determined but CEA connects with LH both directly and indirectly (Petrovich et al., 1996; Pitkänen et al., 1997). While threat processing normally trumps feeding, at some point the risk of encountering harm is balanced against the risk of starvation. A similar case can be made for the suppression of other behaviors by threat processing. For example, medial amygdala areas that process threat related odors suppress reproduction via connections to VHM reproductive circuits (Choi et al., 2005).

The fact that the amygdala contributes to appetitive states (e.g., Rolls, 1999, 2005; Everitt et al., 1999, 2003; Gallagher and Holland, 1994; Holland and Gallagher, 2004; Cardinal et al., 2002; Baxter and Murray, 2002; Moscarello et al., 2009) as well as defense (see above) does not mean that the amygdala processes food and threat related cues in the same way. Similarly, the fact that both appetitive and aversive stimuli activate the amgydala in fMRI studies (e.g., Canli et al., 2002; Hamann et al., 2002; Lane et al., 1999) does not mean that these stimuli are processed the same by the amygdala. Recent unit recording studies in primates show that appetitive and aversive signals are processed by distinct neuronal populations of cells in the lateral/basal amygdala (Paton et al., 2006; Belova et al., 2007; Belova et al., 2008; Morrison and Salzman, 2010; Ono and Nishijo, 1992; Rolls, 1992, 1999, 2005). Molecular imaging techniques with cellular resolution show that similarities in activation at the level of brain areas obscures differences at the microcircuit level (Lin et al., 2011).

Circuit Functions versus Behavioral Responses

Because different groups of mammals faced different selective pressures, the behavioral responses controlled by conserved survival circuits can differ. As ethologists have long noted, many survival-related behaviors are expressed in species-specific ways (e.g., Tinbergen, 1951; Lorenz, 1981; Manning, 1967).

Consider escape from a threat. We've seen evidence for conserved defense circuits across mammals and even across vertebrates, but behavioral responses controlled by these circuits can differ dramatically. For example, while most mammals flee on all fours, some use only two legs (humans), others escape by flying (bats), and still others by swimming (whales, seals, and walrus). Similarly, sexual and feeding behavior, while largely conserved at the neural system level, is also expressed behaviorally in diverse ways within mammals. For example, although androgen activity in the hypothalamus

is important in all male mammals, the semen delivery process varies in males, in part because of different approaches required given the configuration of the male and female body (e.g., Pfaff, 1999). This is perhaps most dramatically illustrated by the lordosis posture of female rats. The male cannot insert his penis into the vaginal cavity of a female unless she arches her back to adopt this posture, which is regulated by the binding of estrogen during the fertile phase of her cycle (Pfaff, 1999; Blaustein, 2008). Further, some mammals use their snouts when eating and others their paws/hands, but the core circuits described above nevertheless regulate the various homeostatic and behavioral functions required to regulate energy and nutritional supplies.

Thus, the responses used by survival circuits to achieve survival goals can be species-specific even though the circuit is largely species-general (obviously, there must be some differences in circuitry, at least in terms of motor output circuitry for different kinds of behaviors, but the core circuit is conserved). By focusing on the evolved function of a circuit (defense, reproduction, energy and nutrition maintenance, fluid balance, thermoregulation), rather than on the actual responses controlled by the circuit, a species-independent set of criteria emerge for defining brain systems that detect significant events and control responses that help meet the challenges and opportunities posed by those events.

Information Processing by Survival Circuits: Computation of Stimulus Significance

A key component of a survival circuits is a mechanism for computing circuit-specific stimulus information. A defense circuit needs to be activated by stimuli related to predators, potentially harmful conspecifcs, and other potential sources of harm, and not be triggered by potential mates or food items. The goal of such computational networks is to determine whether circuit-specific triggers are present in the current situation, and, if a trigger is detected, to initiate hard-wired (innate) responses that are appropriate to the computed evaluation. Such responses are automatically released (in the ethological sense—see Tinbergen, 1951; Lorenz, 1981; Manning, 1967) by trigger stimuli.

The nature of behavioral responses released by survival circuit triggers should be briefly discussed. Activation of a survival circuit elicits behavioral responses on the spot in some cases (e.g., in the presence of defense triggers) but in other cases unless the goal object (sexual partner, food, drink) is immediately present, the more general effect is the alteration of information processing throughout the brain in such a way as to mobilize resources for bringing the organism into proximity with suitable goal objects and thus dealing with the opportunity or challenge signaled by the trigger. We will consider a number of different consequences of survival circuit activation below. Here, we focus on information processing related to trigger detection.

Above we briefly noted the species-specific nature of innate trigger stimuli. While the original idea of the ethologists focused on complex Gestalt configural stimuli and pattern recognition, simpler features are now emphasized. Thus, a rat can recognize a predator (cat, fox) by specific chemical constituents of predator odors (Wallace and Rosen, 2000; Vyas et al., 2007; Dielenberg et al., 2001; Markham et al., 2004; Blanchard et al., 2003) and does not have to recognize the predator as a complex

perceptual pattern. Moreover, humans can recognize certain emotions by the eyes alone and do not need to process the face as a whole (e.g., Whalen et al., 2004), and evidence exists that this can be handled subcortically (Liddell et al., 2005; Morris et al., 1999; Tamietto et al., 2009; Luo et al., 2007). These findings are consistent with the notion that that relatively simple sensory processing by subcortical areas can provide the requisite inputs to structures such as the amygdala, bypassing or short-circuiting cortical areas (LeDoux, 1996). In contrast to innate trigger stimuli, learned triggers are less restricted by species characteristics. Thus, many (though not all, as noted above) stimuli can be associated with harm and become a trigger of defense circuits later.

In the field of emotion, the term *automatic appraisal* is sometimes used when discussing how significant stimuli elicit so-called emotional responses automatically (without deliberate control), and is contrasted with *cognitive* or *reflective appraisal*, where processing that is deliberate, controlled and often conscious, determines stimulus meaning and predisposes actions (e.g., Arnold, 1960; Bowlby, 1969; Frijda, 1986; Lazarus, 1991a, 1991b; Leventhal and Scherer, 1987; Lazarus and Folkman, 1984; Smith and Ellsworth, 1985; Scherer, 1988; Scherer et al., 2001; Sander et al., 2005; Jarymowicz, 2009).

The stimulus significance evaluations by survival circuits are obviously more in line with automatic, unconscious appraisal mechanisms. However, while stimulus evaluations by survival circuits is clearly an example of automatic appraisal, one should not be too quick to assume that what psychologists refer to as automatic appraisals in humans is identical to survival circuit processing. The latter probably refers to a narrower set of phenomena than the former, at least in humans, if not other species, though the range of phenomena in question clearly overlap.

Multiple Roles of Innate and Learned Stimuli

So far we've seen that unconditioned and conditioned emotional stimuli can be thought of in other terms, as unconditioned and conditioned survival circuit triggers. In addition, though, they can also be described as incentives—stimuli that motivate instrumental behavior. The same stimuli additionally function as reinforcers—stimuli that strengthen the probability that an instrumental response will be learned and later performed. Motivation and reinforcement are obviously closely aligned with the topic of emotion, though these are often studied separately today. Let's look more closely at how closely intertwined these processes are to one another (Figure 2).

Consider a tone that is paired with food. This is a typical method used to study positive emotional states in animals. The tone in other words is an appetitive Pavlovian CS that elicits innate approach behavior. However, it is also a survival circuit trigger, as it can stimulate eating, even in satiated rats, by activating hypothalamic circuits involved in energy management (Petrovich, 2011). The same CS will also function as a conditioned incentive that can modulate instrumental behaviors (in contrast to the ability of a CS to elicit Pavlovian innate (unconditioned approach) behaviors. Thus, a CS associated with food will facilitate performance of an instrumental response that is also maintained by food (e.g., bar-pressing for food) (Corbit and Balleine, 2005; Cardinal et al., 2002; Balleine and Killcross,
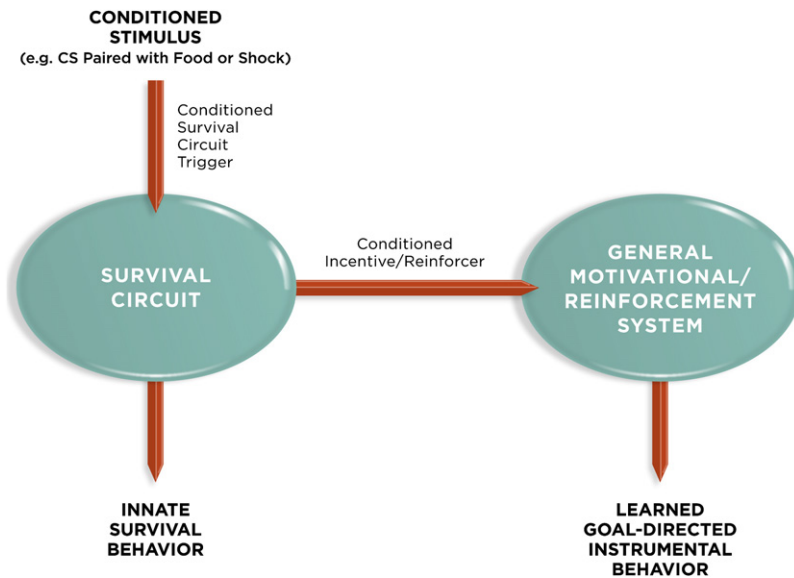
Figure 2. Multiple Roles for a Conditioned Stimulus

A CS functions as a survival circuit trigger (by activating a specific survival circuit related to the US that was used during conditioning), and as a conditioned incentive and a conditioned reinforcer (by way of connections from the survival circuit to motivational and reinforcement systems). Other routes by which a CS might influence motivational and reinforcement circuitry are not shown.

"emotional." These are innate or learned stimuli that activate survival circuits and trigger the expression of the innate responses controlled by these circuits, that modulate the performance of learned (previously reinforced) instrumental behaviors, and that lead to the reinforcement of new instrumental behaviors (Table 1).

Motivation in the Survival Circuit Scheme

Emotion and motivation were traditionally treated as separate topics. Emotion was viewed as a reaction (e.g., a fearful, angry, disgusted, joyful, or sad emotional reaction) to some environmental situation, and motivation as a drive from within (e.g., hunger, thirst, or sexual drive) (e.g., Hull, 1943; Stellar, 1954). In the late 1960s, the emergence of the concept of incentives helped bring these together (Bindra, 1969; Trowill et al., 1969). Bindra (1969), for example, argued that emotion, like motivation, is influenced by internal factors (e.g., hormones) and motivation, like emotion, is impacted by external stimuli (incentives).

Motivation, as assessed behaviorally, involves approach toward desired outcomes and avoidance of undesired outcomes (Tolman, 1932; McClelland et al., 1953; Schneirla 1959, Elliot and Church, 1997; Cofer, 1972; Cofer and Appley, 1964; Miller, 1944; Trowill et al., 1969; Bindra, 1969; Davidson, 1993; Gray, 1982; Lang et al., 1990; Berridge, 2004; Cardinal et al., 2002; Balleine and Dickinson, 1998; Holland and Gallagher, 2004; Gallagher and Holland, 1994; Everitt and Robbins, 2005). So-called approach/avoidance motivation often occurs in two stages: an anticipatory/exploratory/search for goal objects and the performance and consummatory responses (innate responses controlled by surival circuits) once goal objects are in reach (Sherrington, 1906; Tinbergen, 1951; Cardinal et al., 2002; Berridge, 1999, 2007).

The anticipatory/exploratory/search phase is guided by incentives (Bindra, 1968; Trowill et al., 1969; Balleine and Dickinson, 1998; Cardinal et al., 2002; Johnson et al., 2009; Petrovich et al., 2002; Berridge, 1999, 2007, 2004; Rolls, 1999, 2005; Glimcher, 2003). Incentives, as noted, are essentially innate or conditioned emotional stimuli; in other words, stimuli with the potential to activate survival circuits.

One of the key discoveries that led to the rise of incentive views was that stimuli that lacked the ability to satisfy needs and reduce drives (for example, the nonnutritive sugar substitute saccharin) were nevertheless motivating (Sheffield and Roby, 1950; Cofer, 1972). A major consequence was that the connection between motivation and specific functional circuits

2006). This is called Pavlovain-to-instrumental transfer since the value of the Pavlovian CS is transferred to (alters performance of) the instrumental response. The degree of transfer depends in part on the similarity of the US in the Pavlovian and instrumental tasks. A tone CS can also be used to reinforce the learning of a new instrumental response (e.g., Holland and Rescorla, 1975). Thus, a hungry rat will learn to press a bar simply to receive the tone CS. In this case the tone is considered a reinforcer, a second-order or conditioned reinforcer (a first order or primary reinforcer would be something like food itself rather than a stimulus associated with food).

Similar relations hold for a tone paired with an aversive US, footshock. The tone CS elicits innate freezing behavior (see above) and is thus often described as a conditioned emotional stimulus (conditioned fear stimulus in this case). And just as an appetitive CS enhances bar pressing for food, and aversive CS suppresses food-maintained bar pressing (Estes and Skinner, 1941; Hammond, 1970; Cardinal et al., 2002; Balleine and Killcross, 2006). However, an aversive CS will also facilitate performance of an aversively motivated behavior (Hammond, 1970; Lázaro-Muñoz et al., 2010). Further, just as rats will learn to perform new instrumental responses for the sole reward of receiving an appetitive CS, they will also learn new instrumental responses that are rewarded by the elimination of an aversive CS (e.g., Cain and LeDoux, 2007).

Although we've focused on multiple roles of CSs a similar argument can be made for USs. These are simply stimuli that innately activate survival circuits, promote the performance of consummatory responses (food is eaten, sex is consummated) in their presence, or support Pavlovian associative conditioning or instrumental conditioning.

If we choose, we can thus describe a variety of the effects of so-called "emotional" stimuli without the use of the adjective

Table 1. Multiple Roles for So-Called "Emotional" Stimuli

1. Survival Circuit Trigger Stimulus	Activates a specific survival circuit
Innate (Unconditioned) trigger	Elicits innate responses to stimuli without the need for prior exposure to the stimulus and mobilizes other brain resources to deal with the opportunity or challenge presented by the innate trigger
Learned (Conditioned) trigger	Potentially elicits innate responses to stimuli after being associated (via Pavlovian conditioning) with an innate trigger; more generally, mobilizes brain resources to deal with the challenge or opportunity signaled by the learned trigger
2. Incentive	Modulates instrumental goal-directed behavior to help meet the opportunity or challenge signaled by the stimulus that is triggering activation of a specific survival circuit
Innate (unconditioned or primary) incentive	Increases approach toward or avoidance of the stimulus in an effort to resolve the challenge or opportunity present
Learned (conditioned or secondary) incentive	Invigorates and guides behavior toward situations where the challenge or opportunity present can be resolved
3. Reinforcer	Supports the learning of Pavlovian or instrumental associations
Innate (unconditioned or primary) reinforce	Induces the formation of associations with neutral stimuli that occur in its presence (through Pavlovian conditioning) and to the formation of associations with responses that lead to the presentation (appetitive stimuli) or removal (aversive stimuli) of the stimulus (through instrumental conditioning)
Learned (conditioned or second-order) reinforce	Induces formation of associations with other stimuli (through Pavlovian second-order conditioning) or with goal directed responses (through second-order instrumental conditioning)

(what we are calling survival circuits) began to be deemphasized. Motivation became a somewhat generic process by which behavior was invigorated and guided toward goals by incentives.

The nucleus accumbens emerged as a key focal point of this general motivational system (Graybiel, 1976; Mogenson et al., 1980; Balleine and Killcross, 1994; Killcross and Robbins, 1993; Everitt et al., 1999; Cardinal et al., 2002; Ikemoto and Panksepp, 1999; Parkinson et al., 1999; Koob, 2009; Sesack and Grace, 2010; Berridge, 2007, 2009; Berridge and Robinson, 1998; Hyman et al., 2006; Nestler, 2004; Kelley, 2004). Behavioral invigoration or energization was said to be a function of dopamine release in the accumbens and incentive processing by the accumbens was thought to guide behavior toward goals. Other areas involved in incentive motivation, such as the obrbito-frontal cortex, are not considered here (see Rolls, 1999, 2005).

A key question is whether motivation is a generic process or whether motivationally specific processing by survival circuits might be significant as well. While there may indeed be generic aspects of motivation (e.g., behavioral invigoration), evidence also supports motivationally specific information processing as well. At the behavioral level, bar pressing for food by a hungry obtain food is facilitated by a conditioned incentive that signals food, is facilitated less by one that signals water and is inhibited by one that signals shock (Corbit and Balleine, 2005; Hammond, 1970), indicating that motivation is tied to specific survival functions. Lateral hypothalamic circuits that control energy maintenance through feeding modulate nucleus accumbens activity (Sears et al., 2010). The accumbens, once thought to be mainly involved in processing appetitive stimuli, is now know to contribute to the processing of aversive incentives as well (Salamone, 1994; Schoenbaum and Setlow, 2003; Roitman et al., 2005; Reynolds and Berridge, 2008). Within the

accumbens information processing segregated along motivational lines—aversive and appetitive stimuli are processed separately at the cellular and molecular level (Roitman et al., 2005, 2008). While most work is at the level of appetitive versus aversive states, it would be important to determine whether incentives related to different appetitive survival circuits (e.g., incentives related to food versus sex) are processed separately.

Once incentives have guided the organism to goal objects, innate consummatory responses, which are specific to the particular survival circuit and function, are initiated. Their termination essentially ends the survival (emotional) episode—food is eaten, liquid is drunk, sex is consummated, safety is reached.

Before leaving the topic of motivation of instrumental goal-directed behavior it is important to mention that such behaviors, when repeatedly performed in recurring situations, can become habitual and divorced from the actual attainment of the goal. In such cases of stimulus-response habit formation, the neural control switches from the ventral to the dorsal striatum (Everitt and Robbins, 2005; Wickens et al., 2007; Packard and Knowlton, 2002).

Reinforcement and Survival Circuits

Reinforcement and motivation are closely related. Things that motivate are often reinforcing, and vice versa. Like motivation, reinforcement was once linked to drive states (Hull, 1943), but drifted toward generic mechanisms over the years. The discovery that behavior could be reinforced by electrical stimulation of brain areas (Olds and Milner, 1954), and findings that electrical reinforcement could summate with different natural reinforcers (Coons and White, 1977; Conover and Shizgal, 1994), were compatible with a generic mechanism of reinforcement. Similarly, that addictive drugs and natural or electrical reinforcers interact (Wise, 2006) is also consistent with a generic

mechanism. Further, influential mathematical models of reinforcement (e.g., Rescorla and Wagner, 1972; Sutton and Barto, 1987) explained learning with singular learning rules. The modern paradigmatic example of a generic reinforcement mechanism is the role of dopamine in the striatum as a reward prediction error signal (Schultz, 1997).

Nevertheless, there have from time to time been calls for linking reinforcement more directly to specific neurobiological systems. For example, Glickman and Schiff (1967) proposed that reinforcement is a facilitation of activity in neural systems that mediate species-specific consummatory acts. In other words, they proposed a link between reinforcement and motivationally-specific survival circuits. It is therefore of great interest that recent work on the role of dopamine as a reward prediction error signal is beginning to recognize the importance of specific motivational states in modulating the effects of dopamine as a reward prediction error signal (Schultz, 2006; Glimcher, 2011).

The expression of reinforcement as a change in the probability that an instrumental response will be performed may well occur via a generic system in which the reinforcer strengthens the response (e.g., via contributions of dopamine in the striatum to reward prediction errors). But, in addition, survival circuit-specific motivational information is likely to contribute at a fundamental level, providing the stimulus with the motivational value that allows it to ultimately engage the more generic mechanisms that strengthen instrumental responses and that motivate their performance.

Reinforcement principles have been used by some authors to classify emotional states (e.g., Gray, 1982; Rolls, 1999, 2005; Cardinal et al., 2002; Hammond, 1970; Mowrer, 1960). In these models various emotions defined in terms of the presentation or removal of reinforcers. Mowrer (1960), for example, proposed a theory in which fear, hope, relief, and disappointment were explained in these terms. Later authors have attempted to account for more conventional emotions (fear, sadness, anger, pleasure, etc) as products of the presentation or removal of reinforcement. This approach suffers from some of the same problems as basic emotions theory in that it focuses on common language words related to human feelings as the way to identify emotion mechanisms in the brain. Perhaps reinforcement, like motivation, might be fruitfully linked to emotional phenomena through the survival circuit conception.

Survival Circuits and Arousal
Survival circuits are engaged in situations in which challenges and/or opportunities exist, in other words what we commonly call emotional or motivated situations. So far we have focused on two major consequence of survival circuit activation. One is the elicitation of specific kinds of hard-wired behavioral reactions. The second is an increase in the probability that instrumental goal-directed actions relevant to the opportunity or challenge will be learned (reinforced) and performed (motivated)—or, if the situation has been experienced by the individual repeatedly in the past, stimulus-response habits may substitute for incentive guided instrumental goal-directed action.

A third consequence of survival circuit activation is "generalized arousal" (Moruzzi and Magoun, 1949; Lindsley, 1951;

Schober et al., 2011; Lang, 1994; Pfaff et al., 2008). As originally conceived, generalized arousal was a function of the brainstem reticular activating system (Moruzzi and Magoun, 1949; Lindsley, 1951). Later, the undifferentiated reticular activating system concept gave way to the notion that distinct populations of chemically specific neurons that underlie sleep-wake cycles and the degree of arousal, attention, and vigilance while awake (Jouvet, 1969, 1999; Steriade, 1995, 2004; Jacobs et al., 1990; Jones, 2003; Aston-Jones, 2005; Monti and Jantos, 2008; Sarter et al., 2005; Arnsten and Li, 2005; Robbins, 2005; Nieuwenhuys, 1985; Nishino, 2011). Specifically, neurons that synthesize and release biogenic amines (norepinephrine, dopamine, serotoinin, or acetylcholine) and peptides (e.g., orexins) are believed to make significant contributions to brain arousal. While these transmitters are released in widespread areas of the brain, their effects are especially profound on neurons that are actively engaged in information processing (Aston-Jones et al., 1991; Foote et al., 1983, 1991; Aston-Jones and Bloom, 1981). That is, they modulate rather than initiate neural activity, regulating neuronal excitability and neurotransmission (Schildkraut and Kety, 1967; Hasselmo, 1995; Lopez and Brown, 1992). Also contributing to generalized arousal are peripheral systems that release hormones into the circulation (e.g., cortisol released from the adrenal cortex, adrenergic hormones, epinephrine and norepinephrine, from the adrenal medulla; and others) (Axelrod and Reisine, 1984; McEwen, 2009; Sapolsky et al., 1986). Cortisol crosses the blood brain barrier and binds to receptors in a variety of areas, while adrenergic hormones affect the CNS indirectly (McGaugh, 2000). The modulatory effects of central modulators are relatively rapid, whereas the effects of peripheral hormones are considerably slower, allowing the prolongation of the survival state for extended periods of time.

Generalized arousal has played a key role in a number of theories of emotion over the years (e.g., Duffy, 1941; Lindsley, 1951; Schachter and Singer, 1962; Schachter, 1975; Schildkraut and Kety, 1967; Mandler, 1975; Lang, 1994; Robbins, 1997) and is also important in contemporary dimensional theories of emotion (Russell, 1980, 2003; Russell and Barrett, 1999) and some neural models of emotion (e.g., Davis and Whalen, 2001; Gallagher and Holland, 1994; Kapp et al., 1994; Lang and Davis, 2006). However, it is important to ask how generalized arousal is triggered in emotional situations, and how the arousal, once present, affects further processing. Again, the defense circuit is useful for illustrative purposes.

The detection of a threat by defense circuits of the amygdala leads to the activation of central neuromodulatory and peripheral hormonal systems (see Gray, 1993; LeDoux, 1992, 1995; Davis, 1992; Rodrigues et al., 2009). Thus, central amygdala outputs target dendritic areas of norpeiphrine, dopamine, serotonin, and acetylcholine containing neurons and cause these to release their chemical products in widespread brain areas (e.g., Reyes et al., 2011; Gray, 1993; Weinberger, 1995; Kapp et al., 1994). Central amygdala outputs also target neurons that activate the sympathetic division of the autonomic nervous system, which releases adrenergic hormones from the adrenal medulla, and the hypothalamic-pituitary-adrenal axis, which releases cortisol from the adrenal cortex (Gray, 1993; Talarovicova et al., 2007; Loewy, 1991; Reis and LeDoux, 1987). Threats thus not only elicit
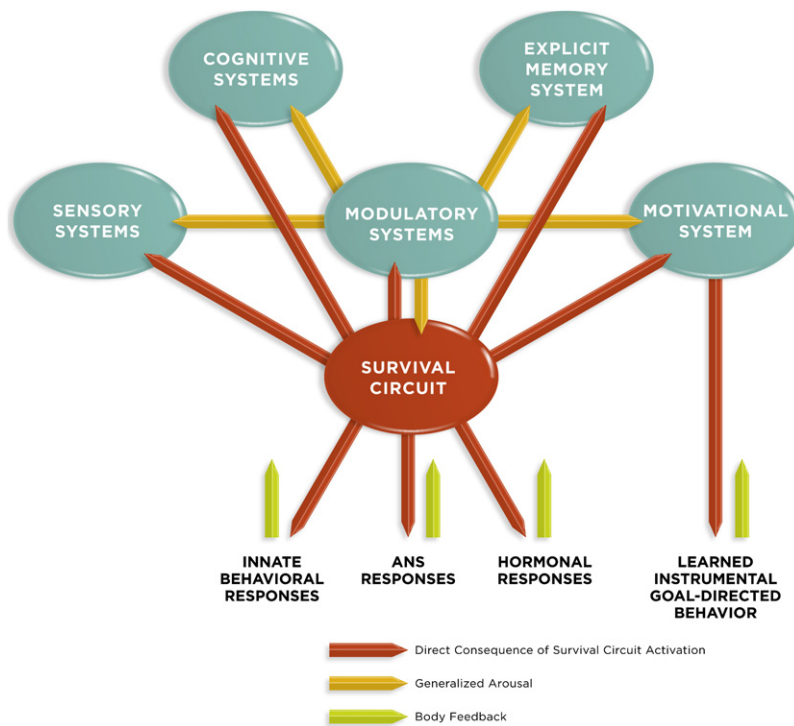
Figure 3. Consequences of Survival Circuit Activation
When a survival circuit trigger activates a survival circuit, a number of consequences follow. (1) Innate behavioral responses are potentially activated, as well as autonomic nervous system (ANS) responses and hormonal responses. These each generate feedback to the brain. (2) Neuromodulator systems are activated and begin to regulate excitability and neurotransmission throughout the brain. (3) Goal-directed instrumental behavior is initiated by the motivation system. (4) Sensory, cognitive, and explicit memory systems are also affected, leading to enhanced attention to relevant stimuli and the formation of new explicit memories (memories formed by the hippocampus and related cortical areas) and implicit memories (memories formed within the survival circuit).

Global Organismic States

Survival circuit activation leads to the triggering of arousal responses in the CNS and to the potential expression of innate behaviors (depending on the circumstances), as well as expression of autonomic nervous system and hormonal responses in the body. Behavioral, autonomic, and endocrine responses feedback to the brain and also contribute to arousal. In addition, motivational systems are activated, potentially leading to goal-directed behaviors (Figure 3). The overall result of survival circuit-specific activity, motivational activity, and generalized arousal is the establishment of a state in which brain resources are coordinated and monopolized for the purpose of enhancing the organism's ability to cope with a challenge and/or benefit from opportunities. The organism becomes especially attentive to and sensitive to stimuli relevant to the survival function, memories relevant to the survival function are retrieved, and previously learned instrumental responses relevant to the survival function are potentiated. New learning occurs and new explicit memories (via the hippocampus and related cortical areas) and implicit memories (memories stored in the survival circuit) are formed. Such states will be referred to here as global organismic states. The fact that these states are global does not mean that they completely lack specificity. They include survival circuit-specific components, as well as general motivational components that control instrumental behavior and components that control nonspecific or generalized arousal within the brain and body.

specific defense responses but also initiate generalized arousal in the brain and body. Body feedback has played an important role in emotion theory for more than a century (James, 1884; Lange, 1885/1922; Schachter and Singer, 1962; Tomkins, 1962; Adelmann and Zajonc, 1989; Buck, 1980; Damasio, 1994, 1999).

One consequence of this pattern of connectivity is that central and peripheral arousal signals facilitate processing in the survival circuit that triggered the activation of arousal. This establishes a loop in which continued activation of the survival circuit by external stimuli produces continued activation of the modulator release, which in turn facilitates the ability of external stimuli to continue to drive the survival circuit. Indeed, modulators facilitate activity in sensory processing areas (e.g., Hurley et al., 2004), which should enhance attention to external stimuli present during survival circuit activation. Modulators also facilitate processing areas involved in retrieving forming, and storing memories (McGaugh, 2003; Roozendaal et al., 2009). All of these effects are recapitulated in motivational circuits once the initial reaction begins to give way to goal-directed instrumental actions. For example, dopamine contributes to the invigoration or activation of behavior during the exploratory search phase of a motivated state (Berridge 2004; Berridge and Robinson, 1998; Robbins and Everitt, 2007). Norepinephrine, serotoin, acetylcholine, orexins and other modulators also contribute. While arousal is often discussed in terms of generic (generalized) mechanisms, the possibility that some aspects of arousal might be survival circuit specific should also be explored (Pfaff et al., 2008; Schober et al., 2011).

The notion that emotional and motivated states have profound effects on the brain, recruiting widespread areas into the service of the immediate situation, monopolizing and/or synchronizing brain resources, has been proposed previously (Gallistel, 1980; Maturana and Varela, 1987; Scherer, 2000; LeDoux, 2002, 2008). Particularly relevant is the "central motive state" hypothesis (Morgan, 1943; Hebb, 1949; Bindra, 1969). Yet, the exact nature of global organismic states is poorly understood. In part this is likely attributable to the lack of techniques for assessing neural activity across widespread areas of the brain at a sufficiently detailed level of resolution. Measurement of BOLD activity in the brains of humans or animals with fMRI allows whole brain analysis of functional activity, but lacks

spatial resolution at the level of cells and circuits. Use of molecular markers, such as the expression of immediate early gene activity, in relation to behavior holds promise. Particularly important would be the development of techniques that could provide widespread simultaneous assessment of changes in body physiology and brain activation and related to survival circuit processing, general-purpose motivational processing, and generalized arousal.

Transcending Neuroanatomical Homology: Survival throughout the Animal World

Invertebrates do not have the same conserved circuits that vertebrates have. However, they face many of the same problems of survival that vertebrates do: they must defend against danger, satisfy energy and nutritional needs, maintain fluid balance and body temperature, and reproduce. As in vertebrates, specific circuits are associated with such functions, though different invertebrates have different nervous systems and different circuits.

The fact that invertebrate nervous systems are diverse and differ from the canonical vertebrate nervous system does not mean the invertebrates are irrelevant to understanding survival functions (and thus so-called emotional behavior) in vertebrates. Much progress is being made in understanding innate behaviors related to survival functions such as defense, reproduction and arousal in invertebrates such as *Drosophila* (Wang et al., 2011; Lebestky et al., 2009; Dickson, 2008) and *C. elegans* (McGrath et al., 2009; Pirri and Alkema, 2012; Garrity et al., 2010; Bendesky et al. 2011). In these creatures, as in mammals and other vertebrates, G protein-coupled receptors and their regulators play key roles in modulating neuronal excitability and synaptic strength, and in setting the threshold for behavioral responses to incentives associated with specific motivational/emotional states (Bendesky and Bargmann, 2011). Biogenic amines and their G protein-coupled receptors also play a key role in arousal and behavioral decision making in *Drosophila* (Lebestky et al., 2009) and *C. elegans* (Bendesky et al., 2011) as in vertebrates (see above), and genetic mechanisms underlying survival-based learning in invertebrates. For example, such as in *Aplysia californica* many of the neurotransmitters (e.g., glutamate), neuromodulators (e.g., serotonin, dopamine), intracellular signals (e.g., protein kinase A, map kinase), transcription factors (e.g., cyclic AMP response element binding protein) involved in defense conditioning *Aplysia* (e.g., Hawkins et al., 2006; Kandel, 2001; Carew and Sutton, 2001; Glanzman, 2010; Mozzachiodi and Byrne, 2010) have been implicated in defense conditioning in the mammalian amygdala (see Johansen et al., 2011). Further, studies in *Drosophila* have implicated some of the same intracellular signals and transcription factors in defense-based learning (Dudai, 1988; Yovell et al., 1992; Yin and Tully, 1996; Margulies et al., 2005).

Similarities at the cellular and molecular level, and presumably at the level of genes that encode these processes, across diverse groups of animals is impressive evidence for conserved principles of organization underlying survival functions. However, an important question is whether there might be more fundamental circuit principles that are instantiated at the microcircuit level in nervous systems that are superficially distinct. If

so, the key to understanding the relation of survival functions across invertebrates and vertebrates is likely to involve conserved principles of organization at the microcircuit level rather similarity of anatomical structures or molecules (David Anderson, personal communication). Very interesting examples are emerging from studies of olfactory processing, for which analogies in behaviorally relevant peripheral odor-encoding and central representation occur using similar organizational principles in anatomically distinct (nonhomologous) structures in *Drosophila* and rodents (see Bargmann, 2006; Sosulski et al., 2011; Wang et al., 2011).

Survival functions instantiated in specific neural circuits likely reflect conserved neural principles. We should at least be amenable to the possibility that defense, reproduction, and other survival functions in humans, may be related to survival functions in invertebrates. This notion is not likely to be surprising to card carrying comparative neurobiologist, but might meet more resistance from researchers who study humans since survival functions account for some fundamental emotional functions in humans, and in humans emotions are often equated with or closely tied to feelings. But the thrust of what has been said here is that survival functions should not be treated as qualitatively differently in humans and other mammals, in mammals and other vertebrates, in vertebrates and invertebrates. As noted earlier, a case can even be made that solutions to fundamental problems of survival are in the final analysis derived from solutions to these problems present primordial single-cell organisms.

Survival Circuits and Human Feelings: What Is An Emotional State?

When the term "emotional state" is used, the user typically has the notion of "feeling" in mind. This article is an attempt to redefine the nature of such states, at least the components of such states that are shared across mammalian species (and likely across vertebrates, and to some extent in invertebrates as well). Nevertheless, the history of emotion research and theory is for the most part the history of trying to understand what feelings are and how they come about. It is thus important to comment on the nature of feelings and their relation to survival circuits.

One might be tempted to conclude that global organismic states, or at least the central representation of such sates, constitute neural correlates of feelings. Global organismic states make major contributions to conscious feelings but the two are not the same. Global organismic states are part of the raw material from which certain classes of feelings are constructed (those feelings associated with survival circuit activation). But they could, and likely do, exist, independent of feelings, at least in relation to what humans call feelings. My proposal is that these kinds of feelings (those associated with survival circuit activation) occur in humans when consciousness (1) detects that a survival circuit is active or witnesses the existence of a global organismic state initiated by the activation of a survival circuit in the presence of particular kind of challenge or opportunity and (2) appraises and labels this state. These are not the only kinds of feelings that can occur in humans. Other kinds include feelings associated with higher-order or social emotions (guilt,

shame, envy, pride) or sensory feelings (a pleasant touch or an annoying itch).

What about other animals? To the extent that nonhuman organisms have consciousness and cognition, capacities that allow the observation, appraisal, and categorization of survival circuit activity or global organismic states, they can have feelings when survival circuit activity or global organismic states occur. To the extent that the mechanisms of consciousness and cognition differ in different animals (with humans included as an animal), and to the extent that the mechanisms underlying survival circuit or global organismic states themselves differ, feelings will be different. This leaves open the possibility that conscious feelings can be present in other mammals, other vertebrates, or even in invertebrates. But rather than engaging in idle speculation about this, criteria can be offered that can help address the question. Specifically, if we can understand what underlies conscious feelings in humans, we can then search for whether those mechanisms are present, and to what extent they are present, in other animals.

This, you probably noticed, is a different approach from the one advocated earlier for survival circuits. We now ask whether processes in humans are present in other animals. But just as the survival circuit question should be asked about whether mechanisms in other animals are present in humans, the question of whether mechanisms shown to be present in humans are present in other animals seems only addressable in the other direction. We can never know whether another animal has conscious emotional feelings, but we might be able to determine whether the mechanisms that make of consciousness and feelings possible in humans also present in other animals.

The fact is that the brain mechanisms that underlie conscious emotional feelings in humans are still poorly understood. However, this should not stand in the way of understanding survival functions and the states that occur in the brain when the circuits mediating survival functions are activated. There is much work to be done even if we don't have viable solutions to the problems of conscious feelings.

Research on feelings is complicated because feelings cannot be measured directly. We rely on the outward expression of emotional responses, or on verbal declarations by the person experiencing the feeling, as ways of assessing what that person is feeling. This is true both when scientists do research on emotions, and when people judge emotions in their social interactions with one another.

When not wearing a scientific hat, most of us apply introspectively based concepts to other animals. When a deer freezes to the sound of a shotgun we say it is afraid, and when a kitten purrs or a dog wags its tail, we say it is happy. In other words, we use words that refer to human subjective feelings to describe our interpretation of what is going on in the animal's mind when it acts in way that has some similarity to the way we act when we have those feelings. Some authors also claim that similarity of behavior is strongly suggestive of similarity at the level of subjective experience (Panksepp, 1998, 2005) or more generally that humans know what an animal feels from observing its behavior (Bekoff, 2007; Masson and McCarthy, 1996). But it's hard to justify anthropomorphic speculation in science. Panksepp has

attempted this (Panksepp, 1982; 1998, 2000; 2005), but few scientists are convinced that this is the way to go, as there is no way to objectively verify what another organism experiences.

So what's the difference, if any, between attributing feelings to other people and to other animals? There is a strong rationalization for assuming all humans have subjective mental states, such as feelings, that are similar in kind. In the absence of genetic mutations of the nervous system or acquired brain damage, each human possesses the same basic kind of brain, a brain with the same basic neural systems, as every other human. As a result we expect that other people have the same kinds of basic brain functions, and corresponding mental capacities, that we have, and we can assume with some confidence that other people experience the same kinds of feelings we do when we they behave the way we behave when we have those feelings (unless they are being intentionally deceitful). We can therefore fairly comfortably apply our introspections about our own feelings to the mental states of other people on the basis of their behavior.

We should not, however, be so comfortable in talking about the mental states of other species because their brains differ from ours. A key question, of course, is whether their brains differ from ours in ways that matter. In other words, do the brain areas responsible for states of consciousness, such as feelings, differ in humans and other animals?

There is considerable support for the idea that states of consciousness are made possible, at least in part, through the representation of experience in a cognitive workspace involving neocortical areas, especially prefrontal and parietal cortical areas (Crick and Koch, 1990, 2004, Dehaene and Changeux, 2004, Baars, 2005; Frith and Dolan, 1996; Frith et al., 1999; Frith, 2008; Shallice, 1988; Shallice et al., 2008). To the extent that feelings are states of consciousness about emotional situations, they should be represented in these cognitive workspace circuits (LeDoux, 1996, 2002, 2008). The idea proposed here is that conscious feelings result when global organismic states are represented in the cognitive workspace. The basic ingredients of the global organismic state would include information about the stimulus and other aspects of the social and physical environment, the survival circuit the stimulus activates, CNS arousal initiated by the survival circuit, feedback from survival responses that are expressed in the body, and long-term memories (episodic and semantic) about the stimulus and about the resulting state (Figure 4). Thus, in the presence of a survival circuit trigger (a.k.a. an emotional stimulus), the various ingredients would be integrated, and the resulting state categorized by matching the state with long-term memory stores. When this occurs, a conscious feeling of the global organismic state begins to exist. Such a state, having been categorized on the basis of memories of similar states, could be dimensional in nature (just based on arousal and valence) or could take on specific qualities (could be more like what one felt when previously in danger than when frustrated or when enjoying a tasty meal). Labeling of the state with emotion words adds additional specificity to the experience, creating specific feelings (fear, pleasure, disgust, etc).

Dorsolateral prefrontal cortex, a key component of the cognitive workspace, is lacking in most other mammals, and is less developed in nonhuman primates than in humans (Reep, 1984; Braak, 1980; Preuss, 1995; Wise, 2008). In humans, granular
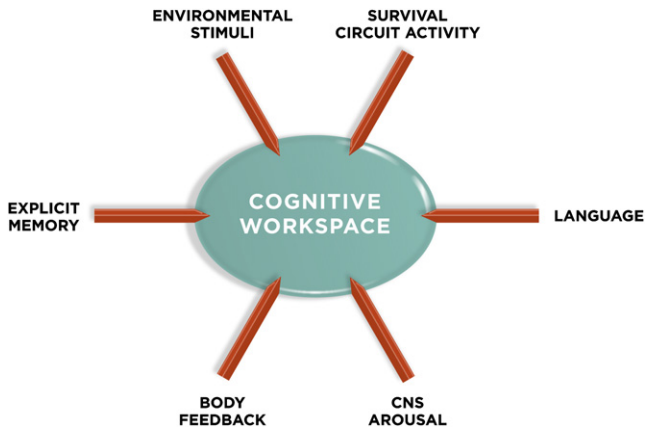
Figure 4. Ingredients of Feelings in a Cognitive Workspace
An emotional feeling is hypothesized to be a representation of a global organismic state initiated by an external stimulus. The representation includes sensory information about the stimulus and the social and physical context, information about the survival circuit that is active, information about CNS arousal, body feedback information, and mnemonic information about the stimulus situation and the state itself. When such a global organismic state is categorized and labeled a conscious feeling of a certain type (e.g. a feeling of fear, pleasure, disgust, etc) results. To the extent that any of these components differ in human and nonhuman species, the nature of the resulting state would differ as well.

prefrontal cortex also has unique cellular features (Semendeferi et al., 2011). Given that feelings are a category of conscious experience, the usual mechanisms of conscious experience should be at work when we have emotional experiences (Le-Doux, 1996, 2002, 2008). And given that some of the neural mechanisms involved in conscious representations may be different in humans and other animals, we should be cautious in assuming that the subjectively experienced phenomena that humans label as feelings are experienced by other animals when they engage in behaviors that have some similarity to human emotional behavior. In short, if the circuits that give rise to conscious representations are different in two species, we cannot use behavioral similarity to argue for similarity of conscious feelings functionally. These observations add neurobiological substance to the point famously argued by the philosopher Thomas Nagel. He proposed that only a bat can experience the world like a bat, and only a human can experience the world like a human (Nagel, 1974). We should resist the inclination to apply our introspections to other species.

Also, given that humans are the only organisms with natural language, and language allows a unique mode of information processing in the human brain, we need to be very cautious when we make assumptions about nonhuman behavior regarding processes that language affects. While the idea that language affects thought and conscious experience (Whorf, 1956) was out of favor for a while, it has reemerged as an important principle in recent times (Lakoff, 1987; Lucy, 1997). One way that language is important is that it allows the semantic categorization of experience, including emotional experience. For example, there are more than 30 words in English for gradations of fear (fear, panic, anxiety, worry, trepidation, consternation, etc.) (Marks, 1987). The human brain may be able to categorize

emotional states in broad strokes without language but it is unlikely that specific emotions (fear, anger, sadness, joy) could come about without words. Accordingly, lacking language and emotion words, an animal brain cannot partition emotional experience in this way. In short, the language of emotion likely contributes to the experiences one has in emotional situations (Schachter, 1975; Johnson-Laird and Oatley, 1989; Scherer, 1984; Reisenzein, 1995). Indeed, different cultures and their languages express emotions differently (Kitayama and Markus, 1994; Wierzbicka, 1994; Averill, 1980). The dimensional theory of emotion views emotion words as markers in a multidimensional semantic space of feelings (Russell, 1980; Russell and Barrett, 1999). The dimensional theory is incompatible with a basic emotions view, since the latter argues that feelings associated with basic emotions are due to hard-wired circuits, but is compatible with the survival circuit view, which posits indirect and nonobligatory, as opposed to casual, links between survival circuits and feelings.

But the impact of language goes far beyond simple semantics and labeling. We use syntactic processes to evaluate the logical truth of propositional statements. While not all human thought involves propositional statements and logic, syntactic processing provides the human brain and mind with unique features and advantages. Through syntax, the human mind can simulate who will do what to whom in a social situation instantaneously rather than having to learn by trial and error.

So what then might a bat or a rat experience without the kind of cerebral hardware that is characteristic of the human brain? Some have proposed that in addition to full blown feelings that humans talk about, more basic, less differentiated feelings (crude states of positive or negative valence, or maybe even somewhat finer categories based on memory of feelings from the past in similar situations) may exist in other animals. Such states have been called core affects (Panksepp, 1998, 2005; Damasio. 1994, 1999; Barrett et al., 2007; Russell, 2003). While we cannot ask other animals about their feelings, studies of humans can begin to unravel how such states are experienced. Similarity of the structure of these circuits in animals might then provide insight into their function in other animals (Panksepp, 1998, 2005), provided that we do a good job of clarifying the function of the circuits in question (see survival circuit discussion above).

Consciousness and feelings are topics that are best studied in humans. Research on the neural basis of feelings in humans is in its infancy (Panksepp, 1998; 2005; Damasio, 2003; Damasio et al., 2000; Ochsner et al., 2002; Barrett et al., 2007; Rudrauf et al., 2009; Critchley et al., 2004; Pollatos et al., 2007). We will never know what an animal feels. But if we can find neural correlates of conscious feelings in humans (and distinguish them from correlates of unconscious emotional computations in survival circuits), and show that similar correlates exists in homologous brain regions in animals, then some basis for *speculating* about animal feelings and their nature would exist. While such speculations would be empirically based, they would nevertheless remain speculations.

Future Directions of Research
There are many topics that need further exploration in the study of emotional phenomena in the brain. The following list is meant

to point out a few of the many examples and is not meant to be exhaustive.

1. The circuits underlying defense in rodents is fairly well characterized and provides a good starting point for further advancement. An important first step is elucidation of the exact relation between innate and learned defense circuits. Paradigms should be devised that directly compare circuits that are activated by innate and learned cues of the same sensory modality and that elicit similar behavioral defense responses (freezing, escape, attack, etc). Comparisons should proceed in stepwise fashion within a species, with variation in the stimulus and response modalities (though mundane, systematic studies are important).

2. More information is also needed regarding the manner in which external stimuli function as defense triggers, incentives, and reinforcers within defense circuits. Tasks should be developed that can be readily applied across species, but at the same time easily tailored to species-specific factors. Further exploration of whether there are different circuits for defense in different contexts would also be useful.

3. How do innate and learned stimuli trigger, motivate and reinforce behaviors in nondefense survival circuits? What are the evaluative mechanisms that process such stimuli within specific survival circuits (e.g., energy/nutrition, fluid balance, reproduction, etc)? While incentives and reinforcers have been studied extensively in the context of generic appetitive processes, also of interest is the relation of such stimuli to the specific survival circuit on which they depend.

4. Can survival circuits be further differentiated? For example, to what extent do different forms of defense utilize different circuits? Beyond classifications based on the sensory modality that detects threats and whether the threat is learned or unlearned, are there different circuits for threats related to conspecifics, predators, ingested substances, territory, etc. Similar questions arises for each survival circuit category.

5. When a given brain area is involved in multiple survival functions, an effort should be made to determine the extent to which underlying cellular mechanisms might make distinct contributions. For example, the LA and BA and nucleus accumbens have been implicated in defensive and appetitive behaviors. As noted above, single unit recordings suggest some independence of responses to aversive and appetitive stimuli in these areas. However, questions remain. Do amygdala or accumbens cells simply encode positive and negative valence or are they tied to more specific survival functions? This is readily explored by examining cellular responses to incentive stimuli related different forms of appetitive motivation. For example, do the cells that respond to incentives related to food, drink and reproduction overlap or are they survival-function specific? Single unit recordings are often restricted to one or a small number of brain areas. New molecular imaging

techniques are beginning to allow such differences to be explored at the cellular level across the whole brain. A recent study by Lin et al. (2011) showing distinct populations of cells in the ventromedial hypothalamus that contribute to mating and intruder attack is a prime example. Genetic tools can also be used to provide more detailed information about connectivity, including connectivity at the level of brain areas but also between specific cell types. Such approaches have begun to be used but systematic studies are needed.

6. It is generally assumed that circuits underlying defense, energy, fluid balance, reproduction, thermoregulation, and other survival functions interact, but this has been not been studied to any significant degree. This is a particularly important topic that is best pursued by methods that allow evaluation of concurrent activity in the multiple brain areas, such as fMRI in humans and fMRI and molecular imaging in animals. Studies comparing activity patterns across the whole brain in response processing signals related to various survival circuit functions could provide very important information, especially if animal and human projects use related behavioral paradigms. If homologies are found at the level of brain areas between humans and other mammals, molecular imaging can be used in animal studies to search for unique microcircuits that differentiate between functions and the cellular and synaptic level.

7. Techniques are needed to assess physiological activity at the cellular level across the whole brain and throughout the body (global organismic states) in the presence of biological significant stimuli (triggers of survival circuit activity or motivating incentives,) and during the performance of innate or learned survival responses as well as goal directed responses. It will be especially useful to develop analytic tools that will be able to separate contributions that are survival circuit specific from more general purpose mechanisms, such as nonspecific arousal, and generic aspects of reinforcement and instrumental behavior control.

8. More comparative work is needed to elucidate similarities and differences in survival functions and circuits between various groups of vertebrates. Particularly pressing are studies of non-mammalian vertebrates.

9. What is the relation of survival functions in invertebrates to vertebrates? Are there conserved molecules or genes, or conserved computational principles, that underlie anatomically distinct kinds of circuits but that perform similar survival functions in vertebrates and invertebrates?

10. Explorations of the mechanisms underlying conscious emotional feelings in humans should be pursued more vigorously, including full-blown conscious feelings (feelings of fear, joy, sadness, shame, embarrassment) and coarser conditions (pleasant or unpleasant feelings). This information is important because feelings are such a defining feature of human mental life. But in addition with such information it will then be possible to ask if the required mechanisms of a given kind of conscious

state are present in other animals. Even if the mechanisms are present, the results would not allow the conclusion that other animals have feelings that are homologous with human feelings. However, such a result would at least provide a basis for saying whether there is a physical possibility for such states in other animals.

Conclusion

The survival circuit concept provides a conceptualization of an important set of phenomena that are often studied under the rubric of emotion—those phenomena that reflect circuits and functions that are conserved across mammals. Included are circuits responsible for defense, energy/nutrition management, fluid balance, thermoregulation, and procreation, among others. With this approach, key phenomena relevant to the topic of emotion can be accounted for without assuming that the phenomena in question are fundamentally the same or even similar to the phenomena people refer to when they use emotion words to characterize subjective emotional feelings (like feeling afraid, angry, or sad). This approach shifts the focus away from questions about whether emotions that humans consciously experience (feel) are also present in other mammals, and toward questions about the extent to which circuits and corresponding functions that are relevant to the field of emotion and that are present in other mammals are also present in humans. And by reassembling ideas about emotion, motivation, reinforcement, and arousal in the context of survival circuits, hypotheses emerge about how organisms negotiate behavioral interactions with the environment in process of dealing with challenges and opportunities in daily life.

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