

Although much remains to be done, we can look upon recent accomplishments in our field and recognize the progress. Strategies for answering questions related to translating basic science insights into improving the experience of human life that were once inconceivable are now quite tractable. Are there ways to selectively enhance learning about rewards but not about threats? Can we reprogram neural circuits by tweaking synaptic strength to provide cures instead of imperfect treatments? The next generation of neuroscience research will be able to provide empirical evidence for answering these questions, old and new.

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Most of the authors highlight the importance of regions classically implicated in emotion, including the periaqueductal gray (PAG), hypothalamus, extended amygdala, ventral striatum, cingulate, insula, and orbitofrontal cortex/ventromedial prefrontal cortex (OFC/vmPFC). Drawing on studies of decorticate animals, Panksepp and Wager place added emphasis on subcortical structures and the brainstem. As Panksepp notes, the “primal emotions of mammals arise subcortically, and hence existed long before humans strode the face of the earth.” Tye seems to come to a similar conclusion. Berridge, Panksepp, Wager, and Tye all adopt variants of the limbic system concept first articulated by Broca, Papez, and Maclean (Broca, 1878; MacLean, 1990; Papez, 1937). Pessoa, in contrast, joins with other theorists (e.g., LeDoux, 1991, 2000) in rejecting the utility of the limbic system, although he does highlight some broader organizing principles: (1) deep regions, those lying closer to the center of the brain (“mesial” or “medial”), are more involved in emotion than superficial territories (“lateral”) and (2) “agranular” (three-layered) and “dysgranular” (four-layered) cortex are more involved than “granular” (six-layered) cortex.

All of the authors seem to agree that emotions cannot be localized to isolated brain regions; that they instead reflect the coordinated interactions of distributed circuits, networks, or systems (see also Adolphs & Adolphs, 2018; Pessoa, 2017; Wager et al., 2015). Wager, for example, emphasizes that activation in particular brain regions, like the amygdala, tends to be much more weakly correlated with emotional experience than patterns of activation that encompass multiple territories (Chang, Gianaros, Manuck, Krishnan, & Wager, 2015; Krishnan et al., 2016). Adolphs reminds us that even in the case of circumscribed lesions, alterations in emotion can reflect changes in downstream regions (Fox & Shackman, in press).

Panksepp and Wager outline the general importance of hierarchical control systems for emotion, with higher levels providing greater complexity and an extended temporal horizon (i.e., beyond the present moment). Wager, in particular, argues that the spinal cord and lower brainstem can trigger reflexive responses to immediate environmental challenges. At the next level of the hierarchy, regions of the upper brainstem and subcortical structures (e.g., PAG, hypothalamus, ventral striatum, extended amygdala, and hippocampus) govern emotions based on a more complex set of appraisals (e.g., threat imminence and certainty),

5.9 AFTERWORD

How Are Emotions Organized in the Brain?

Alexander J. Shackman and
Andrew S. Fox

Is there an emotional brain? Yes and no. All of the authors agree that emotions, like other mental phenomena, critically depend on the brain. As Wager quips, “Of course there are emotion systems [in the brain], because . . . we feel emotions.” The mind necessarily depends on the brain. Yet, as we shall see, there were a number of significant caveats, stipulations, and provisos, with a few authors coming very close to answering “No.”

Adolphs, Berridge, and Panksepp stake out the most affirmative positions. Adolphs, for example, argues that human lesion studies provide clear evidence that specific emotions, such as fear, critically depend on particular parts of the brain, such as the amygdala (Feinstein, Adolphs, Damasio, & Tranel, 2011). He does not address other work indicating that the amygdala is sufficient but not necessary for experiencing feelings of fear or showing signs of panic (Feinstein et al., 2013; Khalsa et al., 2016).

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environmental affordances (e.g., opportunity for escape), and memories (e.g., learned fear and safety). At the highest level, cortical regions regulate these organism–environment interactions and can shape responses in lower-level regions based on more complex contingencies, inferences (e.g., theory of mind), and long-term goals. Fox rejects the notion of strict hierarchical control, arguing that “our brains are not Russian nesting dolls, where we have grown complex cortical controllers for our ‘reptilian brains’” (see also Pessoa, 2017). Drawing on a range of comparative neuroscientific data, he emphasizes the complex, bidirectional nature of interactions between seemingly “lower” (e.g., PAG) and “higher” (e.g., prefrontal cortex) regions, noting that “evolution has resulted in bidirectional connections between the evolutionarily old and new, has altered the molecular composition and regulation of conserved regions, and has inserted evolutionarily old molecules into more recently evolved brain regions.”

Adolphs, Barrett, Berridge, Panksepp, and Tye make it clear that brain regions large enough to be assessed using conventional imaging techniques, such as fMRI, can contribute to multiple emotional and motivational states, a one-to-many mapping between the brain and mind (see also Pessoa, 2013, 2017; Fox & Shackman, *in press*). Davidson advanced a similar argument in the first edition of this volume (Davidson, 1994). Panksepp notes that the medial forebrain bundle is essential for four of his basic emotion systems (SEEKING, LUST, CARE, and PLAY) and also contributes to FEAR and RAGE. Berridge shows that even diametrically opposed emotions, like desire (i.e., “wanting”) and dread, sometimes rely on shared mechanisms. He also reviews evidence that the precise region involved in either desire or dread can be dynamically switched by the organism’s larger emotional context (e.g., high vs. low levels of stress): “Even in the same individual and in the same hour, both [desire and dread] can be activated together by a brain manipulation, and it is possible to convert one into the other.” Adolphs reminds us that regions like the hypothalamus and PAG show phase transitions, where higher levels of artificial stimulation (which may resemble more imminent or intense challenges *in vivo*) evoke qualitatively different suites of emotional behaviors (e.g., Assareh, Sarrami, Carrive, & McNally, 2016; Lee et al., 2014).

Where does the emotional brain end? Berridge suggests that it is a matter of degree, noting that while “the entire brain does participate in every imaginable psychological function . . . not all

structures participate equally.” Pessoa and Wager go a step further, suggesting that the emotional brain has no borders. As Wager notes, “the space of mechanisms that contribute to emotion is vast. . . . There cannot be ‘an emotional brain’ that is less than the brain in its entirety, because so many processes contribute to the generation of emotional experiences.”²¹ They and Fox suggest that emotion and cognition are deeply interwoven in the fabric of the brain, contrary to conventional ideas about “the emotional brain” as distinct from “the cognitive brain” (see also Pessoa, 2013, 2017; Shackman, Fox, & Seminowicz, 2015). Likewise, Wager and Barrett note that while machine learning techniques have uncovered patterns of brain activity that can reliably distinguish one emotion from another, those multi-voxel patterns encompass regions of the brain typically associated with cognitive, perceptual, motor, and other “non-emotional” functions.

Barrett adopts the most radical position, although it overlaps in many ways with those of Pessoa and especially Wager (see also Engen and Singer’s response to Question 7; Barrett’s response to Question 8; Okon-Singer and colleagues’ response to Question 8; and Barrett, 2017b; Barrett & Satpute, *in press*; Pessoa, 2017). Relying mostly on correlational evidence gleaned from human imaging studies, Barrett emphasizes that particular emotions cannot be localized with any specificity to circumscribed brain regions, circuits, or systems. Far from being a fear center, the amygdala, for example, is non-specifically engaged by a broad spectrum of aversive and appetitive cues (Chase, Eickhoff, Laird, & Hogarth, 2011; Costafreda, Brammer, David, & Fu, 2008; Fusar-Poli et al., 2009; Kuhn & Gallinat, 2011; Namburi, Al-Hasani, Calhoun, Bruchas, & Tye, 2016; Sabatinelli et al., 2011; Sergerie, Chochol, & Armony, 2008; Sescosse, Caldu, Segura, & Dreher, 2013; Tang, Fellows, Small, & Dagher, 2012)—a point also made by Tye. Based on these and other kinds of data, Barrett argues that emotions “cannot be deconstructed and reduced into one system, or a part of a system.” They instead reflect “activity in domain-general, core brain systems that perform more basic psychological functions such as interoception, conceptualization, memory, sensory perception, language, and so on” (but see also Adolphs, 2017). In short, while there may be an emotional brain, none of its constituents are specific to any particular emotion.

The past five years have witnessed dramatic advances in our understanding of the neural bases of emotion, many driven by enhanced spatial and



temporal resolution afforded by new optogenetic and chemogenetic techniques (Calhoun & Tye, 2015; Fox & Shackman, *in press*; Janak & Tye, 2015; Namburi et al., 2016; Tovote, Fadok, & Luthi, 2015). Adolphs opens his essay by emphasizing just how little we actually know about the brain bases of emotion. Wager ends his essay on a similar note. In part, this perspective reflects a growing awareness—prompted by the kinds of work described in Tye’s essay—that key regions of the emotional brain, like the amygdala and nucleus accumbens, are divisible into distinct sub-regions (e.g., shell and core of the accumbens); that these sub-regions are massively interconnected within one another and other, more distal regions; and that each sub-region contains intermingled or interdigitated populations of neurons with distinct, even opposing functional properties (see Adolphs, Berridge, and Pessoa, as well as Fadok et al., 2017; Gungor & Paré, 2016; Namburi et al., 2016; Pearson, Watson, & Platt, 2014; Shackman & Fox, 2016; Xiu et al., 2014). As a consequence, research that relies on conventional lesion, pharmacological, or brain imaging approaches will generally reflect a mixture of cells or signals. As Adolphs notes, addressing this barrier will require a new generation of emotion research based on systems biology that employs techniques with cellular resolution. Fox, too, emphasizes the importance of a cellular and molecular understanding of emotion, and he reminds us that understanding the relevance of that more granular knowledge for

human emotions will require the development of more integrative, cross-species models.

Several contributors highlight some of the other challenges of deciphering the emotional brain. Adolphs, Barrett, and Wager remind us that emotions are complex states—involving weakly correlated changes in experience, peripheral physiology, action tendencies, and cognition (Shackman et al., 2013). Adolphs cautions us not to over-interpret animal studies that rely on a single behavioral index of emotion (e.g., freezing as an index of fear), reminiscent of classic suggestions in the human psychophysiological literature (Bradley & Lang, 2000). Wager, like Barrett, stresses that it will be impossible to discover a singular “brain representation for an emotion *per se*, because an emotion is not a single process.” He also warns us that lay people (and even scientists, in unguarded moments) use emotional words in inconsistent ways, making it particularly difficult to identify the circuits underlying the subjective experience of emotion (see also Block, 1995; Ekman & Cordaro, 2011; Kagan, 2010a, b, 2016a, 2016b, *in press*; Levenson, 2011; Poldrack & Yarkoni, 2016; Schaafsma, Pfaff, Spunt, & Adolphs, 2015; Shackman & Fox, 2016). Finally, Adolphs highlights the value of using more formal functional, architectural, and computational criteria for understanding how different emotions are organized in the brain (Adolphs, 2017; Anderson & Adolphs, 2014; Adolphs & Anderson, 2018).

SECOND EDITION

THE NATURE OF EMOTION

Fundamental Questions

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NOTES

INTRODUCTION

1. For example, the International Society of Research on Emotion (ISRE); Society for Affective Science (SAS); and Social & Affective Neuroscience Society (SANS).

2. *Cognition and Emotion; Cognitive, Affective, & Behavioral Neuroscience; Emotion; Emotion Review; IEEE Transactions on Affective Computing; Motivation and Emotion; and Social Cognitive and Affective Neuroscience.*

CHAPTER 1.1

1. All the transcriptions of James's words are drawn from Volume II of *The Principles of Psychology*, in the Dover Edition, 1950. Italicized passages are as published by James.

CHAPTER 1.5

1. Davidson, D., personal communication, April 16, 1978.
2. Personal communication, November 1, 2014.

CHAPTER 1.9

1. Ekman and Davidson made a similar point in the first edition of this volume: "Is there a sine qua non for emotion? The answer at this time must be No. The investigator must use multiple methods to study emotion, including, wherever possible, measures of behavior, subjective experience, and physiology" (p. 414).

CHAPTER 3.3

1. Anatomically, the amygdala is poised to assemble a broad spectrum of emotional reactions via projections to the brain regions that proximally mediate many of the behavioral (e.g., passive and active avoidance), peripheral physiological (e.g., cardiovascular and neuroendocrine activity), and cognitive (e.g., vigilance) features of momentary negative affect (Shackman et al., 2016; Fox & Shackman, in press).

2. Although these findings highlight the contributions of the amygdala to trait-like differences in threat reactivity, it is by no means the only relevant region. Mechanistic and imaging work highlights the important contributions of a distributed circuit encompassing the anterior hippocampus, anterior insula/orbitofrontal cortex, and periaqueductal gray (PAG) (Fox & Kalin, 2014; Fox, Oler, Shackman, et al., 2015; Fox, Oler, Tromp, Fudge, & Kalin, 2015; Fox et al., 2010; Fox, Shelton, Oakes, Davidson, & Kalin, 2008; Kalin, Shelton, & Davidson, 2007; Oler et al., 2010; Shackman et al., 2013). Like the amygdala, activity in each of these regions predicts trait-like individual differences in stressor reactivity.

3. Relations between temperament and resting-state brain activity are not limited to the amygdala—dispositionally negative monkeys, children, and adults also show greater resting-state activity in the electroencephalogram (EEG) over the right compared to the left prefrontal cortex (PFC) (Oler et al., 2016; Wacker, Chavanon, & Stemmler, 2010). Like the negative phenotype, individual differences in resting prefrontal EEG asymmetry emerge early in life and are relatively stable over time, reliable, heritable, and predictive of the intensity of emotional reactions to aversive stimuli (Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Smit, Posthuma, Boomsma, & De Geus, 2007; Towers & Allen, 2009; Wheeler, Davidson, & Tomarken, 1993). Like the dispositional-negativity phenotype, resting prefrontal EEG asymmetry: (a) prospectively predicts the first onset of mood disorders (Nusslock et al., 2011), (b) is exaggerated in patients with anxiety and mood disorders (Thibodeau, Jorgensen, & Kim, 2006; Nusslock et al., 2018), and is normalized by anxiolytic drugs (Oler et al., 2016). Furthermore, direct neurofeedback manipulations of prefrontal EEG attenuate negative affect elicited by subsequent exposure to aversive stimuli (Allen, Harmon-Jones, & Cavender, 2001). With the pharmacological evidence, this suggests that the neural mechanisms responsible for generating this electrophysiological marker causally

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contribute to trait-like individual differences in threat reactivity. Recent efforts to pinpoint the source of the scalp-recorded EEG asymmetry have highlighted the importance of the dorsolateral prefrontal cortex (dlPFC; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009), consistent with this region's well-established role in regulating momentary affect (Buhle et al., 2014).

4. Individual differences in BST activity may reflect altered communication with the orbitofrontal cortex (OFC). Large-scale imaging studies in monkeys ($n = 592$) demonstrate that threat-related metabolic activity in the OFC is heritable and predictive of trait-like differences in dispositional negativity (Fox, Oler, Shackman, et al., 2015). Moreover, selective OFC lesions are associated with decreased passive avoidance of uncertain threat and reduced BST activity in monkeys (Fox et al., 2010; Kalin et al., 2007), paralleling the consequences of naturally occurring OFC insults for BST activity in humans (Motzkin et al., 2015).

5. Deficient filtering of threat-related information from fronto-parietal working memory circuits, leading to elevated rumination over the past and increased worry about the future, may also contribute to context-independent negative affect (Stout, Shackman, Johnson, & Larson, 2014; Stout, Shackman, & Larson, 2013; Stout, Shackman, Pedersen, Miskovich, & Larson, 2017).

CHAPTER 5.3

1. Our friend and colleague, Dr. Jaak Panssepp (June 5, 1943–April 18, 2017), passed away just before this volume was published.

CHAPTER 5.9

1. This position is reminiscent of Lazarus' suggestion that "Emotion and cognition are each so complex and their mechanisms are spread so widely over the central and peripheral nervous system that, in my opinion, it is difficult to argue convincingly for separate systems as though there were a special brain organ for each" (Lazarus, 1991, p. 357).

CHAPTER 6.3

1. Note that in this essay I will not discuss the first portion of Wakefield's definition related to cultural factors. Those interested are referred to (Lutz & White, 1986; Markus & Kitayama, 1991)

CHAPTER 7.4

1. President George W. Bush, war, 2001 Remarks to State Department Employees. URL: <http://www.sourcwatch.org/index.php?title=Evildoers>.
2. <http://www.businessinsider.com/ted-cruz-defunding-obamacare-nazi-germany-filibuster-2013-9>.
3. Thanks to Ben Converse for this formalization.

CHAPTER 8.1

1. The terms "threat-related" or "threat-relevant" encompass a broad range of stimuli, including clear and immediate dangers (e.g., cues paired with shock), novel situations or individuals, uncertain or diffuse dangers (e.g., darkness), aversive stimuli (e.g., unpleasant images or films), and angry and fearful facial expressions. Angry faces signal a direct threat to the observer and prompt the mobilization of defensive responses, as indexed by potentiation of the startle reflex (Dunning et al., 2010; Hess, Sabourin, & Kleck, 2007; Springer et al., 2007), facilitation of avoidance-related movements (Marsh, Ambady, & Kleck, 2005), and increased fear ratings (Dimberg, 1988). In contrast, fearful faces signal the presence, but not the source of potential threat, and promote heightened vigilance in the absence of defensive mobilization. That is, static images of fearful faces do not amplify the startle reflex (Grillon & Charney, 2011; Springer et al., 2007) or autonomic measures (Dunsmoor, Mitroff, & LaBar, 2009). But they can increase subjective feelings of anxiety (Blairy, Herrera, & Hess, 1999) and are perceived as more threatening and arousing than neutral or happy faces (Grillon & Charney, 2011; Wieser & Keil, 2014).

CHAPTER 10.1

1. It is worth noting that Darwin (1872) stated that these opposing forms sometimes may not serve any function.

2. Calculated by using 20 facial action coding units, bilaterally where applicable, each of which may contract independently at five different levels of intensity.

3. An immediate physical utility distinguishes itself from the more distant social utility. Expression forms selected for social utility could also be considered "evolutionary" and functionally "egocentric." However, purely symbolic associated forms for social utility need not have any physical consequences.

CHAPTER 12.4

1. Surprise may also be considered to contain the fundamental property of unexpectedness that characterizes fear.

CHAPTER 12.5

1. Such as 2-alternative forced choice (2AFC) stimulus identification procedures: In 2AFC, the participant is asked to indicate a particular property of the stimulus in trials of "invisible" stimulus presentation (even if they claim they did not see the stimulus and thus are guessing)—for example, observers may report on whether a face was upright or upside down; or whether a facial expression was happy vs. fearful. This is in contrast with methods relying on subjective reports, such as when a participant is asked to

say “yes” or “no” to whether they saw a face. Different individuals have different response biases (e.g., different propensities to indicate that a stimulus is present given a particular sensory experience). Therefore, subjective measures may be confounded by response biases and are typically regarded as less conservative than 2AFC procedures (Wiens, 2006).

2. Note that the magnitude of amygdalar activation does not appear to be reliably modulated by conscious access to an emotional stimulus (Costafreda, Brammer, David, & Fu, 2008).

3. Replications cited include those of investigators adopting important procedural variations, such as alterations in the specific awareness manipulation method (including the original backward masking method, as well as interocular suppression and crowding), and the type of neutral target to be rated (originally a Chinese ideograph, and now, in several studies, a neutral face).

4. Note that awareness may not be required when cognitive control is not triggered implicitly but rather *explicitly* (Kunde et al., 2012), such as in the case of slowing down following a stop signal (van Gaal, Lamme, Fahrenfort, & Ridderinkhof, 2011), or switching a task set following a cue (Lau & Passingham, 2007).

5. Indeed, symptoms of degenerative disease to the LPFC are obvious if the patient has a job requiring mental flexibility and decision making, but not if s/he has a routinized job or lifestyle (Knight & D’Esposito, 2003).

CHAPTER 13.2

1. Here we use the term *emotion* as a catch-all. There are, of course, many affective states, which range from mood, to arousal, to true emotions. There is every reason to believe that all of these influence rationality and preferences in some way. We use the expression “emotion” in this brief essay as an exemplar for understanding how affective states in general influence decision-making.

2. Of course, if humans do become intransitive in some emotional states, then we need to be more creative in trying to understand the structure of their behavior. Under conditions in which a decision-maker is intransitive, a simple study of preferences will prove unsupportable mathematically. The economist David Laibson’s famous dual-process beta-delta model (Laibson, 1997) is one example of a structural model for dealing meaningfully with intransitive behavior.

3. GARP stands for the “Generalized Axiom of Revealed Preference,” developed by Hendrik Houthakker as a mathematical specification for what is probably the most common definition of full transitivity. For a more detailed explanation of this approach to transitivity, see Chapter 3, pp. 52–70, in Glimcher, 2010.

4. For simplicity, we completely neglect here the fact that apples and oranges, when bundled together in groups, may cause nonlinear utility interactions. This is a hugely important point taught to first-year economics students and called “substitution.” In the references to which we point, this is developed in some detail. But in order to convey the most basic concepts, we neglect it here.

5. For an economist, this is an important distinction because significant differences in the shape of the preference function in the gain and loss domain can imply a specific form of intransitivity, an important point, which we again neglect for simplicity.

6. As pointed out first by Kahneman and Tversky (1979), people in some situations behave according to distorted rather than objectively given probabilities, which we can capture by replacing p in the DEU equation with a probability weighting function $w(p)$.

CHAPTER 15

1. Naturally, emotion researchers must remain mindful of measurement reliability in choosing between different within- vs. between-subjects designs (cf. Bradford, Starr, Shackman, & Curtin, 2015; Cannon, Cao, Mathalon, Gee, & NAPLS Consortium, 2018; Fox et al., 2012; Hedge, Powell, & Sumner, *in press*; Herting, Gautam, Chen, Mezher, & Vetter, *in press*).

2. From a clinical perspective, categorical approaches to diagnosing emotional disorders pose several critical barriers to discovering the nature and origins of psychopathology: rampant co-morbidity, low symptom specificity (e.g., insomnia), marked symptom heterogeneity, and poor reliability (Chmielewski, Clark, Bagby, & Watson, 2015; Clark, Cuthbert, Lewis-Fernandez, Narrow, & Reed, 2017; Fried, 2015, 2017; Fried & Nesse, 2015; Galatzer-Levy & Bryant, 2013; Goldstein-Piekarski, Williams, & Humphreys, 2016; Hasin et al., 2015; Kessler, Chiu, Demler, & Walters, 2005; Kotov et al., 2017; Krueger et al., *in press*; Olbert, Gala, & Tupler, 2014; Regier et al., 2013; Watson & Stasik, 2014). Addressing these problems requires a different kind of approach—one focused on narrower sets of transdiagnostic symptoms (e.g., anxiety, anhedonia)—as with the Hierarchical Taxonomy of Psychopathology (HiTOP) and Research Domain Criteria (RDoC) approaches (Clark et al., 2017; Kotov et al., 2017; Krueger et al., *in press*; Zald & Lahey, 2017). This ‘symptoms-not-syndromes’ dimensional approach (Fried, 2015) would also more naturally align with animal models (Fox & Kalin, 2014; Fox & Shackman, *in press*; Oler, Fox, Shackman, & Kalin, 2016). There is compelling evidence that traditional categorical approaches to diagnosing emotional disorders present several significant barriers to understanding the underlying mechanisms, including substantial

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symptom heterogeneity, frequent co-morbidity, and low inter-rater reliability (i.e., uncertain ‘ground truth’) (Fried, 2017; Galatzer-Levy & Bryant, 2013; Hasin et al., 2015; Regier et al., 2013). The adoption of narrower dimensional phenotypes is likely to provide useful (Kotov et al., 2017; Krueger et al., in press).

3. Aggression can be split on functional and neurobiological grounds into systems involved in defensive, offensive (predatory), and conspecific aggression, with the latter including maternal aggression and resource competition (food, mates, and territory/shelter) (Adams, 2006; Berkowitz,

1993; Nelson & Trainor, 2007). Naturally, researchers must remain mindful of measurement reliability in choosing between different experimental designs (e.g., within- vs. between-subjects); e.g., Bradford, Starr, Shackman, & Curtin, 2015; Cannon et al., 2018; Hedge, Powell, & Sumner, in press; Herting et al., in press; Larson et al., 2000; Shackman et al., 2017).

4. See also <https://www.nimh.nih.gov/research-priorities/rdoc/constructs/potential-threat-anxiety.shtml>; <https://www.nimh.nih.gov/research-priorities/rdoc/negative-valence-systems-workshop-proceedings.shtml>.

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