

Bird, 2016). In an important early demonstration, Critchley and his colleagues (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004) demonstrated the important role of the insula in interoceptive awareness. More recently, Chong and colleagues demonstrated that participants with higher levels of interoceptive accuracy, as assessed with a heartbeat detection task, had greater resting state connectivity with the insula sector of the salience network (Chong, Ng, Lee, & Zhou, 2016). Interestingly other recent work suggests that interoceptive accuracy is part of a more general form of meta-awareness (Chua & Bliss-Moreau, 2016), and this invites the possibility that individual differences in meta-awareness (including the awareness of internal bodily states as well as memories and other types of mental content) may play an important role in modulating emotional responses.

## CONCLUSIONS AND FUTURE DIRECTIONS

This brief essay highlights some of the dimensions along which individuals vary in responding to emotional challenges. Of particular importance are variations in the time course of emotional responding. We still lack basic information on whether faster recovery in response to negative stimuli is correlated with prolonged responding to positive incentives. The fact that at least some of the neural correlates of affective chronometry in response to negative versus positive stimuli is different suggests that this is not a single unitary dimension.

A related issue concerns the valence dimension itself. While this issue is not specific to the question of what are bases for lasting individual differences in emotion, nevertheless, the issue of how to frame the valence dimension is critical. While there is certainly a valence dimension, the most appropriate and accurate anchors for this dimension remain unresolved. Indeed, other cultures have framed the valence dimension in ways that are fundamentally different from how we typically describe it in Western psychology (Ekman, Davidson, Ricard, & Wallace, 2005).

Of particular importance for the application of these concepts to those who suffer from emotional disorders, we critically need further study of the plasticity of these systems and strategies for altering the underlying neural circuitry, particularly with non-invasive behavioral methods. I have referred to this possibility as “neurally inspired behavioral interventions.” Are there specific ways in which we can train these circuits to, for example, improve resilience or positive outlook? We can use temporal parameters of neural and behavioral

responding to examine proximal mechanisms that may be modulated by such training (e.g., Heller et al., 2015). Such training may be useful in treating depressive symptoms, as we have found that depressed patients display atypically brief responses in the ventral striatum to positive incentives and fail to sustain activation in this region. This abbreviated neural response is correlated with low levels of positive affect (Heller et al., 2009).

In conclusion, what is of utmost importance is the incorporation of individual differences in regulatory processes in our conceptions of individual differences in emotional responding. The negative and positive valence systems in the Research Domain Criteria (RDoC) (Insel et al., 2010) would benefit from an explicit incorporation of regulatory processes so that a more complete understanding of the mechanisms and bases for individual differences in emotional responding can be developed.

## 3.5 AFTERWORD

### *What are the Dimensions and Bases for Lasting Individual Differences in Emotion?*

Alexander J. Shackman and  
Andrew S. Fox

Humans and other animals show enduring individual differences in a range of positive and negative emotions (Boissy, 1995; Gosling, 2008). These emotional traits lie at the core of childhood temperament and adult personality (Caspi, Roberts, & Shiner, 2005; Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Goldsmith, 1994; Goldsmith et al., 1987; Gray & McNaughton, 2000; Shiner et al., 2012; Shiner & DeYoung, 2013), and there is compelling evidence that they exert a profound influence on health, wealth, and well-being across the lifespan (Lahey, 2009; Moffitt, Poulton, & Caspi, 2013; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007; Shackman, Kaplan, et al., 2016; Shackman, Tromp, et al., 2016). In Question 2, we asked our contributors to address the distinction between *emotions* and *temperament*. Here, we focused on a closely related question: *How are emotional traits structured, and what mechanisms underlie them?*

## THE NATURE OF EMOTIONAL TRAITS

All of the authors seem to agree that emotional traits constitute stable, but not immutable, biases

in the likelihood of experiencing and expressing particular emotions. For Shackman et al., they represent diatheses that serve to increase the likelihood, magnitude, or duration of emotional responses in the presence of a trait-relevant challenge (e.g., threat for fear). Shiner stakes out a similar position, while Davidson underscores the importance of finer-grained response parameters, including variation in the time-to-peak and return-to-baseline (“recovery”). Shiner, Kagan, and Shackman et al. suggest that emotional traits first emerge in infancy but continue to evolve for many years as a consequence of learning, experience, and changes in biology (i.e., as more slowly developing biological systems mature and come on-line). While acknowledging that the correspondence between emotional traits in childhood and adulthood is imperfect, Shiner and Kagan emphasize significant continuity across the lifespan, with Shiner noting that early emotional tendencies become more complex across development and can influence the development of related cognitive styles (e.g., hopelessness, worry, self-esteem).

Shiner and Davidson tell us that emotional traits encompass individual differences in emotion regulation as well as reactivity (see Question 7). Building on work by Rothbart and her colleagues (Rothbart, 1994, 2011), Shiner argues that trait-like differences in attention, inhibition, and other aspects of *Effortful Control* play a key role in governing emotional responses, while Davidson suggests that deficits in these regulatory processes can contribute to the development of psychopathology (see also Stanton, Rozek, Stasik, Ellickson-Larew, & Watson, 2016).

### THE STRUCTURE OF EMOTIONAL TRAITS

Shiner and Shackman et al. agree that emotional traits are structured hierarchically, with broader traits, like *Negative Emotionality/Neuroticism*, subsuming narrower facets (e.g., fear, anger, sadness). Shiner provides the most comprehensive description of how emotional traits are structured. Drawing on decades of factor-analytic work, she highlights the utility of a five-factor (“Big 5”) model encompassing the traits of *Positive Emotionality/Extraversion*, *Negative Emotionality/Neuroticism*, *Effortful Control/Conscientiousness*, *Agreeableness*, and *Openness* (Caspi et al., 2005). *Agreeableness* includes tendencies to be considerate, kind, generous, compliant, and, especially later in development, empathic. *Openness* encompasses tendencies to be curious, artistic, and interested in intellectual matters and aesthetics. While acknowledging that

*Agreeableness* and *Openness* lack clear counterparts in the temperament literature, Shiner argues that all five dimensions reflect early-emerging emotional tendencies. Kagan focuses on evidence that infants can be classified into those with a “high-reactive” or a “low-reactive” temperament (Fox et al., 2005; Kagan, 1997). He seems to suggest that these temperaments are sculpted by experience to form the emotional core (“anima”) of *Negative Emotionality/Neuroticism* and *Positive Emotionality/Extraversion*, respectively. Shackman et al. narrowly focus their response on aspects of *Negative Emotionality/Neuroticism* (“Dispositional Negativity”). Davidson largely eschews traditional, factor-analytically derived dimensions, instead focusing on traits derived from several decades of psychophysiological and imaging research, mostly by his own group (e.g., *Resilience*, *Positive Outlook*, *Sensitivity to Context*, and *Interoceptive Accuracy*) (Davidson & Begley, 2012). Although much less is known about these novel traits, they have the virtue of being derived directly from measures of the nervous system, rather than from preexisting nosologies or the covariance structure of external indicators, such as introspective ratings or behavior (Davidson, 2001).

## THE BASES OF EMOTIONAL TRAITS

### Genetic and Experiential

Shiner, Kagan, and Shackman et al. seem to agree that emotional traits reflect the dynamic interaction of genetic and experiential mechanisms. Kagan notes that culture and exposure to early adversity (e.g., poverty, exposure to violence) can have a lasting impact on emotional reactivity and mood. Shackman et al. tell us that *Negative Emotionality/Neuroticism* is increased by stress and decreased by treatments for anxiety and depression. Davidson highlights evidence that exposure to marital stress is associated with a less persistent emotional response to positive stimuli.

### Psychological and Neurobiological Processes

Focusing on *Negative Emotionality/Neuroticism*, Shackman et al. offer the most detailed description of the psychological and neurobiological processes underlying an emotional trait. First, they highlight evidence that individuals with a more negative disposition tend to respond more strongly to aversive challenges and that this reflects trait-like variation in the activity and connectivity of a network of brain regions centered on the amygdala.

Kagan and Davidson stake out broadly similar positions. Second, Shackman et al. make it clear that *Negative Emotionality/Neuroticism* is more than just hyper-reactivity, noting that individuals with a more negative disposition are prone to heightened negative affect in contexts where stressors are uncertain, temporally remote (i.e., occurred in the past or may occur in the future), or psychologically diffuse (e.g., a novel experimental context). In fact, they review evidence that the vast majority of negative affect experienced in daily life is indiscriminate and cannot be attributed to clear-and-present challenges. They hypothesize that this contextually inappropriate negative affect partially reflects alterations in the function of the central extended amygdala, an anatomical macrostructure encompassing the central nucleus of the amygdala and neighboring bed nucleus of the stria terminalis. They also highlight the possibility of that stress-induced sensitization of this circuitry contributes to the spillover of negative affect across sequential contexts. Davidson outlines a broadly similar position, which he calls *Sensitivity to Context*, but focuses on work suggesting that contextually inappropriate negative affect reflects alteration in hippocampal function. Finally, Shackman et al. remind us that dispositionally negative individuals are often their own worst enemies, and that they tend to behave in ways that increase the likelihood of stress, ultimately leading to more frequent, intense, or persistent negative affect. While acknowledging that the neurobiology of “stress generation” remains ill-understood, they speculate that differences in social appraisal processes mediated by the amygdala could contribute, at least in a distal way, to negative individuals’ tendency to experience relationship insecurity, express less warmth and reciprocity, engage in avoidance, and evoke negative reactions from social partners.

Davidson was the only author to focus on the biological bases of *Positive Emotionality/Extraversion*. Building on other recent work (Berridge & Kringelbach, 2015; Greer, Trujillo, Glover, & Knutson, 2014; Kringelbach & Berridge, 2012; Wu, Samanez-Larkin, Katovich, & Knutson, 2014), he highlights new evidence that individuals marked by longer-lasting striatal activity in the scanner environment tend to experience more

persistent positive affect in their daily lives, as indexed using ecological momentary assessment techniques.

### MOVING BEYOND CONVENTIONAL EMOTIONAL TRAITS

Shiner and Kagan emphasize that we will need to move beyond conventional traits if we are to fully understand lasting individual differences in mood and emotion. Shiner emphasizes the role of personal narratives: the stories that individuals tell themselves and others as a way of making sense of their identities. Kagan tells us that people often identify with their demographic group (e.g., social class, race) or with other individuals (e.g., parents, grandparents) in ways that can promote recurrent feelings of pride, shame, guilt, or anger.

### CONCLUSIONS

In the first edition of this volume, Ekman and Davidson challenged several leading theorists (Jeffrey Gray, Richard Lazarus, Mary Rothbart, and Davidson himself) to address the nature and origins of individual differences in emotion. Their responses, which drew on what was at the time cutting-edge research (e.g., gross lesions in rodents, low-density electroencephalography recordings in humans), highlight the tremendous advances that have been made in the past two decades, especially as concerns the biological bases of emotional traits. Rothbart’s prescient essay, which focused on the broad dimensions of *Positive Emotionality*, *Negative Emotionality*, and *Effortful Control*, reminds us that powerful new tools are not, in themselves, sufficient, to rewrite theory. Nevertheless, existing theories of emotional traits are mostly superficial and descriptive (Epstein, 1994; Funder, 1994). Developing a deep understanding of emotional traits will require a greater integration of work in humans and animal models, a greater emphasis on mechanistic approaches (e.g., neurofeedback, pharmacological interventions), and a willingness to develop and refine new traits based on observable differences in brain structure and function (Fox & Shackman, in press; Shackman & Fox, 2016; Shackman, Tromp, et al., 2016). Doing so promises crucial new opportunities for constructive intervention.

SECOND EDITION

THE NATURE OF EMOTION

*Fundamental Questions*

EDITED BY

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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 Pansepp (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.sourcewatch.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 "ego-centric." 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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