3.3 THE PSYCHOLOGICAL AND NEUROBIOLOGICAL BASES OF DISPOSITIONAL NEGATIVITY

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INTRODUCTION

Here we summarize recent advances in our understanding of the psychological and neurobiological bases of negative emotionality or what we term *dispositional negativity*, one of the most intensely scrutinized dimensions of childhood temperament and adult personality (for more detailed reviews, see Shackman, Kaplan, et al., 2016; Shackman, Tromp, et al., 2016; Shackman, Weinstein, et al., in press). A primary focus of our essay concerns the processes linking enduring individual differences in dispositional negativity to momentary emotional experiences and behaviors.

DISPOSITIONAL NEGATIVITY

Dispositional negativity—the tendency to show increased negative affect—is a fundamental dimension of temperament and personality, subsuming a range of narrower traits (e.g., anxious temperament, behavioral inhibition, harm avoidance, neuroticism, and trait anxiety; Caspi, Roberts, & Shiner, 2005; Soto & John, 2017). Individual differences in dispositional negativity can be conceptualized as an extended family of complex, multi-componential phenotypes that first emerge early in development, persist into adulthood, and reflect a combination of heritable and non-heritable factors (Fox & Kalin, 2014; Soto & John, 2014; Vukasovic & Bratko, 2015). Psychometric measures of dispositional negativity are quite reliable (Pace & Brannick, 2010) and concordance between psychometric measures (Pace & Brannick, 2010) and between self- and informant-reported (e.g., friends, family members, co-workers) dispositional negativity is substantial (e.g., Brunson, Øverup, & Mehta, 2016; Connelly & Ones, 2010; Connolly, Kavanagh, & Viswesvaran, 2007; Mõttus, McCrae, Allik, & Realo, 2014), particularly when multiple informants are employed (McCrae & Costa, 1987). Key features of dispositional negativity are expressed similarly across mammalian species, enabling mechanistic studies (e.g., Oler, Fox, Shackman, & Kalin, 2016). Although the molecular underpinnings of dispositional negativity and its neural substrates remain poorly understood, promising candidates have recently been identified in humans (Alisch et al., 2017; Hill et al., in press; Lo et al., 2017; Luciano et al., 2018; Nagel et al., 2017; Okbay et al., 2016) and monkeys (e.g., Alisch et al., 2014; Fox et al., 2012; Oler et al., 2009; Roseboom et al., 2014). Dispositional negativity is stable, but not immutable, and like other emotional traits continues to develop and change across the lifespan (e.g., Borghuis et al., 2017; Dyson et al., 2015; Graham et al., 2017; Hengartner, 2018; Milojev & Sibley, 2017; Nye, Allemand, Gosling, Potter, & Roberts, 2016; Roberts & DelVecchio, 2000; Roberts, Walton, & Viechtbauer, 2006; Schwaba & Bleidorn, in press; Soto, John, Gosling, & Potter, 2011). Like other personality traits, dispositional negativity is sensitive to experience (Bleidorn, Hopwood, & Lucas, in press), and can be increased by exposure to stress, trauma, and negative life events (Shackman et al., 2016) and decreased by positive experiences (*ibid*), including clinical interventions for anxiety and depression (Roberts et al., 2017). Collectively, these kinds of observations raise the possibility of developing targeted intervention strategies (e.g., Barlow et al., 2017; Bentley et al., 2017; Chronis-Tuscano et al., 2015).

TRAIT-STATE LINKS INFERRED FROM SELF-REPORT AND BEHAVIOR

Increased Stressor Reactivity

Self-report data indicate that individuals with elevated levels of dispositional negativity overreact to a variety of stressors. They report exaggerated negative affect in response to hassles and interpersonal conflict (e.g., Suls & Martin, 2005), aversive laboratory challenges (Matthews, Deary, & Whiteman, 2009), and real-world trauma (Guo, Xue, Shao, Long, & Cao, 2015; Hengartner, van der Linden, Bohleber, & von Wyl, 2017). Likewise, individuals with a more negative disposition are prone to exaggerated behavioral, psychophysiological, and neuroendocrine reactions to potential threat (Shackman et al., 2016). These findings suggest that dispositional negativity represents a diathesis, one which enhances the likelihood, magnitude, or duration of negative affect elicited by stressors.

Increased Negative Affect in the Absence of Immediate Stressors

Individuals with elevated dispositional negativity are also prone to exaggerated negative affect in situations where potential stressors are remote, diffuse, or absent. This kind of pervasive, context-independent negative affect has been described as a tonic or endogenous effect of temperament, given the absence of clear stressors (Gross, Sutton, & Ketelaar, 1998; Watson & Clark, 1984). In the laboratory, dispositionally negative individuals tend to experience more intense negative thoughts and feelings at "baseline" or after viewing emotionally neutral control stimuli (Gross et al., 1998). In daily life, they frequently experience elevated negative affect in comfortable, familiar settings (e.g., Shackman et al., in press). For example, Bolger and Schilling (1991) used statistical decomposition techniques to demonstrate that nearly 60% of heightened negative affect in daily life reflects tonic differences in distress, in settings where there was no clear concurrent source of stress, more than double that attributable to individual differences in stressor reactivity or stressor exposure. These observations indicate that context-independent negative affect is a central feature of dispositional negativity.

Increased Stressor Generation and Exposure

Dispositionally negative individuals often behave in ways that generate hassles and promote social conflict. Increased stressor exposure, in turn, promotes more frequent or intense negative affect. Converging lines of prospective-longitudinal, behavioral-genetic, experience-sampling, and one-shot self-report data collected from tens of thousands of individuals in the U.S. and abroad, some followed for as long as 16 years, demonstrate that individuals with high levels of dispositional negativity report more frequent personal difficulties and conflicts, particularly those of an interpersonal nature (Clarke et al., 2017; Hengartner et al., in press; Leger et al., 2016; Shackman, Tromp, et al., 2016). Other work suggests that dispositionally negative individuals play an instrumental role in evoking interpersonal stress and rejection. Their friends and offspring report increased conflict (Berry, Willingham, & Thayer, 2000; Hutteman et al., 2014), their romantic partners report reduced relationship security (Neyer & Voigt, 2004), and their spouses report reduced relationship satisfaction (Malouff, Thorsteinsson, Schutte, Bhullar, & Rooke, 2010). In the laboratory, randomly assigned social partners judge dispositionally negative individuals to be more moody, uncomfortable, and negative (Creed & Funder, 1998). This negativity begets negativity; random partners often respond with heightened criticism, contempt, and hostility (Creed & Funder, 1998). This evocative effect may reflect dispositionally negative individuals' tendency to express less warmth, be less responsive to social partners, escalate negative affect during conflict, and engage in toxic interpersonal behaviors (e.g., contempt and sarcasm; Clark, Kochanska, & Ready, 2000; Wang, Repetti, & Campos, 2011). Other work shows that interventions targeting these kinds of maladaptive socioemotional behaviors reduce conflict and rejection, indicating a causal role (Snyder & Halford, 2012; Taylor & Alden, 2011). Taken together, these observations provide compelling evidence that dispositionally negative individuals play an active role in shaping their social environment in ways that increase the likelihood of negative affect

THE NEUROBIOLOGY OF DISPOSITIONAL NEGATIVITY

Increased Reactivity to Aversive Laboratory Challenges

Neurobiological research corroborates the link connecting dispositional negativity to heightened stressor reactivity. Imaging studies show that dispositionally negative individuals are prone to increased or prolonged activation in the dorsal amygdala in response to punctate, threat-related cues (Blackford, Avery, Shelton, & Zald, 2009; Calder, Ewbank, & Passamonti, 2011; Fox & Shackman, in press; Schuyler et al., 2012; Sjouwerman, Scharfenort, & Lonsdorf, 2017; Stein, Simmons, Feinstein, & Paulus, 2007; Stout, Shackman, Pedersen, Miskovich, & Larson, 2017).[1] Metabolic activity in the dorsal or central (Ce) nucleus of the amygdala is stable over time and measurement context (i.e., trait-like), heritable, and associated with heightened reactions to potential threat encountered outside the scanner environment (Fox & Kalin, 2014). Moreover, elevated amygdala activity appears to be a shared substrate for different presentations of dispositional negativity (Shackman et al., 2013). Like the dispositional-negativity phenotype, increased amygdala reactivity to acute threat: (a) predicts the development of future internalizing symptoms (Swartz, Knodt, Radtke, & Hariri, 2015), (b) is heightened in mood and anxiety disorders (Etkin & Wager, 2007; Hamilton et al., 2012), (c) is increased by stress and adversity (Dannlowski et al., 2012), and (d) is decreased by cognitive-behavioral and pharmacological treatments for anxiety and depression (Furmark et al., 2002; Paulus, Feinstein, Castillo, Simmons, & Stein, 2005).

Work in animals shows that the amygdala causally contributes to negative affect elicited by threat (e.g., Oler et al., 2016; Kalin et al., 2016). This is consistent with observations made in humans with naturally occurring amygdala damage. For example, Patient SM, who has near-complete bilateral destruction of the amygdala, shows a profound lack of fear and anxiety when exposed to frightening movies, haunted houses, tarantulas, and snakes, and consistently endorses low levels of dispositional negativity on standard self-report measures (Feinstein, Adolphs, Damasio, & Tranel, 2011). These data suggest that dispositionally negative individuals' heightened reactivity to threat and other kinds of stressors in the external environment reflects larger or longer-lasting responses in a distributed neural circuit centered on the amygdala.[2]

Trait-like Individual Differences in Stressor Reactivity Are Discernible at Rest

Although most human neurobiological research has focused on reactivity to acute threat-related cues—faces, images, and so on—stable individual differences in threat-reactivity can also be discerned in the brain's spontaneous or "resting" activity. For example, monkeys with elevated amygdala activity at "baseline" (e.g., in their home cage) show increased freezing and elevated levels of the stress-sensitive hormone cortisol when threat is encountered in other contexts (Fox et al., 2008). Likewise, humans with higher levels of dispositional negativity show increased amygdala activity at rest (Canli et al., 2006; Kaczkurkin et al., 2016). These observations suggest that variation in the basal activity of the amygdala and other regions of the brain (e.g., dorsolateral prefrontal cortex[3]) represent a diathesis for heightened negative affect in response to trait-relevant challenges.

Altered Resting Activity—Traits or States, Tonic or Reactive Differences?

The data reviewed in the prior section would seem to suggest that reactive features of temperament are embodied in the ongoing activity of the brain. Yet it remains unclear whether alterations in "resting" activity reflect trait-like differences in momentary affect, fleeting states elicited by the novelty or stress of the experimental context, or some combination of the two. After all, most neurophysiological assays are intrusive and can elicit substantial negative affect (e.g., Törnqvist, Månsson, Larsson, & Hallström, 2006). More sophisticated psychometric analyses will be required to determine the relative contribution of traits and states to "resting-state" measures of brain function (cf. Coan, Allen, & McKnight, 2006).

"Tonic" Negative Affect May Reflect Heightened Reactivity to Diffuse Threat

Self-report data show that dispositionally negative individuals experience heightened negative affect in the absence of clear-cut stressors. Although this could reflect a direct or endogenous effect of dispositional negativity on mood, a wealth of biological evidence suggests that it partially reflects a reaction to stressors that are uncertain, temporally remote (i.e., occurred in the past or may occur in the future), or psychologically diffuse (e.g., a novel or mildly aversive experimental context) (Grupe & Nitschke, 2013). For example, individuals with extreme dispositional negativity show elevated defensive responses (e.g., startle) and experience elevated negative affect during periods of safety embedded within instructed fear paradigms (i.e., safety cues or the inter-cue interval); that is, in the periods before and after the randomized presentation of learned threat cues (Barker, Reeb-Sutherland, & Fox, 2014). Conversely, anxiety-reducing drugs selectively dampen sustained negative affect elicited by uncertain threat, while mostly sparing phasic reactions to cues signaling clear and immediate danger (Bradford, Shapiro, & Curtin, 2013). These findings suggest that apparently endogenous increases in negative affect, as described in the self-report literature, probably reflect heightened sensitivity to distal, uncertain stressors, rather than a fixed or "tonic" consequence of dispositional negativity.

Mechanistic work in rodents and monkeys suggests that sustained levels of heightened negative affect reflect the central extended amygdala, an anatomical concept encompassing the Ce and neighboring bed nucleus of the stria terminalis (BST) (Fox, Oler, Tromp, et al., 2015; Shackman & Fox, 2016; Fox & Shackman, in press). Consistent with this view, imaging studies show that dispositionally negative monkeys and humans are marked by heightened activity in the extended amygdala during periods of diffuse or uncertain threat (Fox et al., 2008; Shackman, Fox, et al., 2017;

Somerville, Whalen, & Kelley, 2010). Furthermore, variation in BST activation and functional connectivity predict negative affect, freezing, skin conductance, and cortisol elicited by uncertain danger (Shackman & Fox, 2016). Although this activity is often described as a "sustained" response to uncertain threat, it has also been found using much briefer challenges (<10 seconds; Brinkmann et al., 2018; Choi, Padmala, & Pessoa, 2012; Grupe, Oathes, & Nitschke, 2013; Klumpers et al., 2015; Mobbs et al., 2010; Pedersen et al., 2017), consistent with the spillover effects found in fear-potentiated startle studies. Collectively, this work indicates that a circuit[4] centered on the extended amygdala is a key substrate for the kinds of context-independent negative affect that characterize individuals with heightened levels of dispositional negativity (Shackman & Fox, 2016).[5]

Pervasive Negative Affect May Reflect Stress-Induced Sensitization

Self-report data indicate that individuals with a more negative disposition tend to carry negative affect from stressful to less stressful contexts (Shackman, Tromp, et al., 2016; Suls & Martin, 2005). Imaging work suggests that the amygdala could contribute to this spillover of negative mood via a process of stress-induced sensitization. Indeed, there is evidence that brief exposure to acute stressors leads to sustained increases in amygdala activity (Cousijn et al., 2010) and amplifies amygdala reactivity to threat (van Marle, Hermans, Qin, & Fernandez, 2009). Acute stressors can produce even longer-lasting changes—on the order of minutes to hours—in the functional connectivity of the amygdala (Vaisvaser et al., 2013; van Marle, Hermans, Qin, & Fernandez, 2010). Furthermore, these neural spillover effects are exaggerated among individuals with a more negative disposition (Everaerd, Klumpers, van Wingen, Tendolkar, & Fernandez, 2015). Sensitization of the amygdala following exposure to stress could promote negative affect either directly, by enhancing reactions to mild threat (Grillon & Charney, 2011), or indirectly, by increasing the likelihood that attention will be allocated to threat-related information (Gamer, Schmitz, Tittgemeyer, & Schilbach, 2013; MacLeod & Clarke, 2015).

Increased Stressor Generation and Exposure May Reflect Differences in the Way Social Cues Are Processed

Self-report data indicate that individuals with a more negative disposition are prone to behave in ways that evoke stress. Although the neurobiological mechanisms underlying this recursive Temperament—Environment—Affect relationship remain poorly understood, it is known that damage to the amygdala is associated with heightened, even pathological levels of social approach and trust (Adolphs, 2010; Feinstein, Adolphs, Damasio, & Tranel, 2011; Feinstein, Adolphs, & Tranel, 2016). Conversely, imaging studies in neurologically intact adults indicate that amygdala activation is associated with increased suspicion and is sensitive to betrayal during economic bargaining games (Bhatt, Lohrenz, Camerer, & Montague, 2012). These observations raise the possibility that differences in social-appraisal processes mediated by the amygdala contribute, at least in a distal way, to dispositionally negative individuals' tendency to experience relationship insecurity, express less warmth and reciprocity, engage in active and passive forms of avoidance, and evoke negative reactions from social partners.

AN INTEGRATIVE PERSPECTIVE

Recent years have witnessed the emergence of powerful tools for assaying emotion and brain function and new insights into the psychological and neurobiological bases of dispositional negativity.

First, there is clear evidence that dispositionally negative individuals respond more strongly to explicit stressors and aversive challenges. Variation in threat-reactivity reflects stable individual differences in the sensitivity and functional connectivity of a number of brain regions, including the amygdala. These differences manifest as heightened activation in response to punctate challenges, but they are also evident in the spontaneous, ongoing activity of the brain. At present, it remains unclear whether temperament-related variation in resting-state activity and connectivity reflects tonic differences in neurophysiology, momentary states precipitated by diffuse threat, or some combination of the two.

Second, individuals with elevated dispositional negativity often show heightened negative affect in contexts where stressors are diffuse, remote, or absent. Neurobiological research suggests that this reflects alterations in a neural circuit centered on the extended amygdala. Other work indicates that enduring stress-induced changes in amygdala reactivity and functional connectivity may contribute to the spillover of negative affect across contexts.

Third, individuals with a more negative disposition tend to act in ways that evoke stress, increasing the likelihood of negative affect. Although the neurobiological mechanisms underlying stressor generation have received scant attention, the existing evidentiary record highlights the potential importance of circuitry encompassing the amygdala.

Of these three pathways, the tendency to experience sustained levels of heightened negative affect in response to diffuse, uncertain, or remote threat appears to be most central to dispositional negativity. The vast majority of negative affect experienced by dispositionally negative individuals in daily life is indiscriminate and cannot be attributed to clear and present stressors (Bolger & Schilling, 1991; Watson & Clark, 1984). In the laboratory, heightened negative affect in safe contexts is generally more sensitive to differences in dispositional negativity and pathological anxiety than that elicited by overt threat (Davis, Walker, Miles, & Grillon, 2010; Duits et al., 2015) and prospectively predicts the first onset of anxiety disorders (Craske et al., 2012).

This pervasive, context-insensitive emotional bias probably reinforces other maladaptive components of the negative phenotype (e.g., avoidance and hypervigilance) and may promote the expression of maladaptive interpersonal behaviors that increase the likelihood of conflict, alienation, and rejection.

CONCLUSION

Individual differences in dispositional negativity can have profound consequences for health, wealth, and happiness (Shackman et al., 2016). The work that we have reviewed provides an integrative framework for understanding the cascade of psychological and biological processes that bind dispositional negativity to momentary emotional states, to emotional disorders, and to a range of other adverse outcomes.

3.4 REACTIVITY, RECOVERY, REGULATION

The Three R's of Emotional Responding

Richard J. Davidson

One of the most striking and salient characteristics of emotion in humans is the remarkable individual variation in how different people respond to emotional incentives and challenges. Some of these variations across individuals appear to be stable and influence major life outcomes—mental and physical health, well-being, decision-making, and even longevity (Davidson & Begley, 2012). In this brief essay, I will consider the dimensions and bases of individual differences in emotion and suggest important new directions for future research in this area.

REACTIVITY, REGULATION, RECOVERY—THE THREE R'S OF EMOTIONAL RESPONDING

In response to an emotional incentive or challenge, a cascade of partially orthogonal processes is activated, some of which serve to generate an emotion in response to a challenge, and other processes that serve to modulate the emotional response. In most cases, these processes at least partially overlap in time, and they include both implicit and explicit processes. On this view, reactivity and regulation show temporal overlap and thus make it difficult to disentangle the contributions from each of these processes. Nevertheless, it is reasonable to assume that there are individual differences in both reactivity and regulation that contribute to stable differences in emotional responding.

Recovery can be viewed as a specific form of emotion regulation. It refers to the return to baseline of responses that were activated or perturbed by an emotional stimulus. Recovery can be automatic or voluntary, or somewhere in between. The suggestion that recovery can fall in between automatic and voluntary suggests that this is a dimensional continuum and not a binary outcome. In addition, it is likely that both automatic and voluntary processes contribute to many instances of recovery in the wild, where voluntary strategies can be used to supplement those that are automatically activated.

AFFECTIVE CHRONOMETRY

The discussion of the three R's of emotional responding immediately invites a consideration of affective chronometry, which broadly connotes the time course of emotional responding (Davidson, 1998). There are individual differences in the peak of an emotional response, in the rise-time to peak, and in the recovery. The latter two parameters are temporal characteristics that shape affective chronometry. For example, individuals who recover slowly from negative challenges, as reflected in greater amygdala signal during a recovery period, report increased neuroticism (Schuyler et al., 2012). Faster recovery

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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

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 "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

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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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

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 "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

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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