biases have been identified in investigations of children's anxiety and can be found or induced in non-anxious children as well (Bell-Dolan, 1995; Hadwin et al., 1997; Muris et al., 2000a; 2000b; 2008). In instances of social interaction, such temperamental biases lead to the decreased positive engagement with social peers indicative of reduced social competence (Degnan et al., 2014; Walker et al., 2013).

Our data lay a foundation for future research to more directly examine how individual differences in automatic and controlled processes predict social understanding and behavior. Indeed, several studies already show clear links between assessments of children's temperament and their theory of mind (Wellman et al. 2011, Lane et al., 2012, Suway et al., 2012).

The notion that temperament is an important factor in children's social information processing and social competence is in line with a model already proposed by Lemerise and Arsenio (2000). They argue that the child's biological predisposition in "emotionality and emotion regulation" affects information-processing and decision-making in challenging social situations. Their model—an amendment to Crick and Dodge's (1994) model of social information processing (which outlines how children encode and interpret social cues to form peer evaluations and behavioral responses)—argues that temperamental differences are critical in understanding children's social behavior. We have argued that temperament is a powerful source of variability in social behavior and social understanding, given its constituents of individual differences in reactivity and regulation that are subsumed by neural systems evolved to deal with social approach and withdrawal. Thus, a particularly intriguing question concerns how emotions or moods could also account for heterogeneity in the emergence of social behavior and understanding. Given the argument that classically viewed emotions and moods may not be linked to particular neural systems (LeDoux, 2012; 2014), what mechanisms might support causal or predictive links between emotion and social development?

Existing research demonstrates connections between aspects of emotion-processing and social understanding and behavior (Eisenberg et al., 1995; Shultz et al., 2010; Trentacosta & Fine, 2010). But the neural and physiological mechanisms by which early emotion-processing relates to later social understanding, and critically, how it relates to temperament as we have defined it here, are unclear. Future longitudinal research examining behavioral, neural, and physiological correlates of emotion-processing in infancy and how these processes relate to (a) emerging social cognition, and (b) measurable temperamental reactivity and regulation, can shed light on these important questions.

SUMMARY

In this chapter, we have argued for an approach to temperament that separates it from classic views of emotion and mood. Our view is that, while temperament may include downstream differences in emotions and mood, identification and measurement of discrete emotions are not the fundamental core of temperament. Rather, as illustrated by investigations of the temperament of behavioral inhibition, temperament consists of individual differences in reactivity and regulation which are outcomes of neurobiological systems evolved to subserve approach and withdrawal—outcomes characterized by responses and neural correlates that are measurable in humans and non-human animals in ways that do not necessitate identification or assessment of discrete emotions. Critically, temperament, as defined in this way, plays a key role in the heterogeneity evident in an organism's understanding of and engagement in its social environment. Open questions include the mechanisms by which emotions or moods could also account for heterogeneity in the emergence of social understanding and behavior.

2.5 AFTERWORD

How are Emotions, Mood, and Temperament Related?

Alexander J. Shackman,
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All the contributors to this section seem to agree that emotions, mood, and temperament form a temporal continuum. Emotions and moods are transient, episodic states, but emotions are especially fleeting, lasting as little as a few seconds; whereas moods can endure for hours, even days. At the far end of this continuum, temperament and personality represent stable, trait-like tendencies or biases that slowly evolve over the course of months and years. The distinction between "brief" emotions and "sustained" moods is fuzzy and descriptive. In contrast with the first edition of *The Nature of Emotion*, none of the authors explicitly addresses the possibility of sustained emotions in the presence of longer-lasting challenges (e.g., exploring a novel, potentially dangerous environment; an extended fight with one's spouse).

Several authors describe other features that distinguish emotion from mood. Naragon-Gainey argues that they differ in their characteristic intensity, specificity, expression, and consequences:

- Emotions are intense, whereas moods tend to be milder
- Emotions are elicited by specific, overt challenges in the external environment, whereas moods are precipitated by internal, homeostatic changes (e.g., fatigue, hunger) or diffuse challenges (e.g., contexts associated with stress, potential danger, or conflict).

Naragon-Gainey and Bowman and Fox emphasize that moods represent a persistent affective background on which emotions are superimposed. All three note that moods can bias attention, memory, and choice (see Question 8) and can lower the threshold or increase the intensity of congruent emotions (e.g., anger when feeling irritable, or fear when feeling anxious).

Naragon-Gainey provides the most detailed account of features that distinguish emotion from mood. She notes that emotions are characterized by a relatively intense, but "loosely coupled characteristic multimodal expression (e.g., physiological response, cognitions, behaviors, facial expressions)" (see also Reisenzein, Studtmann, & Horstmann, 2013), whereas moods manifest in more subtle expressions, such as posture or muscle tension. From a functional perspective, she suggests that emotions and moods provide different kinds of information: "emotions primarily give information about our current environment, and moods primarily give information about our internal resources available to respond to current or potential demands." In other contexts, some theorists have emphasized that moods can also provide information about the statistical regularities in the external world—anxious mood may reflect exposure to an environment where threat is more probable or more difficult to accurately predict, whereas an irritable mood may indicate the absence of food (Nettle & Bateson, 2012).

While all of the authors agree that mood and temperament involve emotional states, there are striking differences in their perspectives on the precise nature of this arrangement. Naragon-Gainey suggests that the three constructs are linked by their basis in emotional experience and feelings, which gives rise to similar dimensional structures (e.g., positive and negative affect). For her, temperament reflects stable individual differences in the propensity to experience particular feelings and to engage in related thoughts and actions. Kagan, and Blackford and Zald seem to hold a similar view. Bowman and Fox adopt the most radical position. Drawing on the work of LeDoux (LeDoux, 2012; 2014; 2015), they argue that temperament cannot be reduced to particular emotions or moods (e.g., fear or anxiety); that while there may be downstream consequences for emotions and mood, feelings do *not* form the core of temperament; and that the neural systems that underlie differences in temperament (e.g., circuits centered on the amygdala) are *not* specific to discrete emotions. Instead, Bowman and Fox view temperament as reflecting, at least in part, neurobiological systems sensitive to threat, reward, and other phylogenetically ancient, motivationally significant challenges. It remains to be seen whether this perspective has substantive implications for research aimed at understanding the biological bases of emotions, mood, or temperament.

Many of the authors emphasize the importance of regulatory processes. Naragon-Gainey highlights ways in which these processes can alter the intensity of momentary emotions and help transform fleeting emotions into sustained moods (e.g., via a failure to regulate, or maladaptive rumination on the past). She also indicates that characteristic individual differences in emotion regulation also contribute to temperament. Bowman and Fox review the importance of regulatory processes to temperament, but emphasize the importance of automatic (e.g., attentional biases) and controlled (e.g., conflict monitoring) cognitive processes that are not specific to the regulation of emotion or mood. Along broadly similar lines, Blackford and Zald make the case that temperament reflects variations in the function of at least two kinds of neural circuits, some involved in triggering or orchestrating emotional states (e.g., amygdala), and others involved in the adaptive control of emotion and cognition (e.g., orbitofrontal cortex, dorsolateral prefrontal cortex, and anterior cingulate; for related perspectives, see Questions 7 and 8).

Several authors highlight the challenges of dissecting emotions and mood from temperament. Blackford and Zald remind us that emotions and temperament are often defined in ways that are circular—temperament causes emotions, emotions cause temperament—making it difficult to parse the two in the brain or other measurable systems (e.g., verbal report). Naragon-Gainey reminds us that assessments of emotional traits, like temperament and personality, are invariably contaminated by momentary fluctuations in mood and emotion. Conversely, assessments of emotions and mood are influenced in important ways by trait-like individual differences in temperament. While not addressed directly by the contributors, this problem is not specific to verbal report, and there is ample evidence that it influences biological measures as well (Gee et al., 2015; Hagemann, Hewig, Seifert, Naumann, & Bartussek, 2005; Tomarken, 1995). As Naragon-Gainey notes, a key challenge for the field is to adopt statistical tools that can quantify the relative contributions of state and trait variance.

Finally, echoing other commentators (Adolphs, 2017a and b; Block, 1995; Bradley & Lang, 2007), Kagan cautions that isolated measures of emotions—whether verbal, behavioral, or biological—often fail to detect emotions when they are present and can reflect multiple emotional or even non-emotional processes (i.e., can suffer from insufficient sensitivity and specificity). Instead, he argues that a multivariate approach will be most helpful for understanding the mechanisms underlying emotions, mood, and temperament (for related views, see Lang & Bradley's and Adolphs's response to Question 1, and Kagan, in press).

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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