reactions, albeit not on a conceptual level (Condon & Feldman Barrett, 2013). This suggests that accessing the positive core of compassion might require some degree of conditioning and training in order to successfully employ it in daily life.

Several research groups have begun investigating how compassion can be trained through the utilization of meditation techniques adapted from the Buddhist tradition to a secular setting in meditation-naïve participants (e.g., Fredrickson, Cohn, Coffey, Pek, & Finkel, 2008; Jazaieri et al., 2013; Klimecki et al., 2013; Klimecki, Leiberg, Ricard, & Singer, 2014; Mascaro, Rilling, Negi, & Raison, 2013; Weng et al., 2013). In addition to showing that compassion training is possible outside of the strict regimes of Buddhist practice, these results show that such training has a number of beneficial effects. For instance, in our laboratory, we have found that compassion training increased positive affect when participants were exposed to highly distressing videos depicting people suffering, and that this increase was associated with increased activation of a neuronal network involved in affiliation and reward (Klimecki et al., 2013). Underlining the difference between compassion and empathic distress, the activation pattern associated with compassion-training differed markedly from that observed in the same individual after empathy training; the latter leading to an increase in negative affect associated with the well-known empathy for pain network including anterior insula and mid-anterior cingulate cortex (mACC) (Klimecki et al., 2014). Given the similarity of these results to the previously discussed findings on expert practitioners (Engen & Singer, 2015), this suggests that compassion can be trained in a targeted manner. The importance of such training is borne out by studies showing that compassion training is associated with enhanced empathic accuracy (Lutz, Greischar, Perlman, & Davidson, 2009; Mascaro et al., 2013), reduced physiological stress responses (Pace et al., 2009), and overall improved well-being (Fredrickson et al., 2008). Importantly, this type of training has been shown not only to have beneficial effects for the individual, but also to increase prosocial behaviors (Leiberg, Klimecki, & Singer, 2011; Weng et al., 2013).

Overall, these results suggest that compassion can be learned, and that this learning has substantial benefits both for the learner and for society at large. Importantly, it offers a means by which one can volitionally overcome barriers to caring, while at the same time being able to endure and even flourish in the face of the consequences of this caring.

CONCLUSION

Social emotions such as empathy and compassion are a central aspect of our social lives. Through the shared embodiment of emotional states such as in the phenomena of emotion contagion and empathy, we gain access to and communicate core aspects of our emotional experiences. However, many barriers exist to this empathic resonance, including other core social mechanisms such as our tendency to discriminate in-groups from out-groups. Even when we do achieve empathic connection with someone, this can become a source of stress, because, undeniably, sharing affective states with others can be costly. However, as we hope to have shown, we are not incurably bound by our biases, but can actively modulate the occurrence, strength, and type of empathic connection we share with others. We can do this either by engaging in mentalizing processes or by transforming an initial empathic response into a compassionate one, and in so doing, changing our personal and social worlds for the better.

9.7 AFTERWORD

How Are Emotions Embodied in the Social World?

Andrew S. Fox and
Alexander J. Shackman

All of the contributors agree that emotions are profoundly social. At home and at work, social cues, interactions, and relationships dominate the landscape of our emotional lives. The association between the social and the emotional is bidirectional: emotional signals influence the social environment, and shared feelings are critical for understanding and constructively interacting with others. Here, the authors describe socio-emotional interactions from multiple perspectives, ranging from emotional expressions to emotional contagion, from guilt to compassion, and from strategic cooperation to friendship.

Many contributors highlighted evidence that social contexts play an important role in regulating the expression and experience of emotion. Eisenberg and Hernández underscore the importance of emotion display rules—culture-specific norms for when, where, and how emotions can be expressed (cf. Blanchard and Pearson's response

to Question 7; e.g., Ekman, 1972; Safdar et al., 2009). Lemay reminds us that individuals often attempt to deliberately regulate outward signs of emotion, such as anger, in order to preserve or cultivate desired social relationships. He joins with Eisenberg and Hernández in emphasizing that emotions such as guilt, shame, and pride are inherently social, and these "self-conscious" emotions are shaped by our social environment. Lemay goes as far as to provide a general model by which social contexts can influence our emotional state by motivating or interrupting emotional goals. Several authors note that reflexive social appraisals (e.g., perceived closeness, trustworthiness, or group identity) can govern the intensity of emotional experience (Engen and Singer, Fareri and Delgado, Fox, and Parkinson). For example, Parkinson highlights evidence that mothers experience lower levels of disgust in response to diapers soiled by their own baby compared to unrelated babies, and Engen and Singer tell us that sports fans experience lower levels of empathy and show reduced altruism in response to the physical suffering of fans of a rival team. Finally, adopting a developmental perspective, Eisenberg and Hernández remind us that social contexts (e.g., familial and cultural norms, social isolation) can also have profound consequences for emotional development (e.g., McLaughlin, Sheridan, & Lambert, 2014; McLaughlin et al., 2015).

Just as the social environment can influence emotions, emotions can alter social interactions (Eisenberg and Hernández, Fareri and Delgado, Lemay, and Parkinson; see also Shackman et al., 2016). The expression of anger, for example, tends to promote avoidance and conflict. In contrast, positive expressions (e.g., a smiling baby, laughter) encourage social approach, engagement, and bonding. As Fox and Fareri and Delgado note, such stimuli are highly motivating to observers and engage the same neural circuits recruited by other rewards, including food and money. Engen and Singer, Fareri and Delgado, and Parkinson all highlight evidence that this reward-relevant circuitry is also sensitive to reward delivered to others. For example, seeing another person receive a reward can activate one's own reward circuitry, and, potentially, impart positive affect. Fareri and Delgado argue that this vicarious reward information provides the information that is required to develop predictions about how people will act (i.e., social priors), which explains unique variance in reward-related neural activity (i.e. ventral striatal Blood Oxygen Level Dependent [BOLD] response). Fareri and Delgado go on to suggest this social-value signal contributes to the development and maintenance of social relationships. Parkinson picks up this argument by emphasizing how humans develop uniquely intense affiliative bonds with people who are neither kin nor mates—our friends.

Several contributors emphasize the importance of feelings for motivating social behavior. Parkinson argues that feelings of loneliness motivate individuals to seek out new social connections and to evaluate potential partners more favorably. Engen and Singer, Fareri and Delgado, and Parkinson tell us that feelings of empathy and, even more so, compassion can motivate prosocial behavior, facilitate social understanding, and strengthen social cohesion. Eisenberg and Hernández, Fox, and Parkinson point out that the reverse is also true and emphasize the importance of social forms of emotion regulation, noting that the presence of friends, family members, and other forms of social support reduces distress (Shackman et al., in press). Fox and Engen and Singer go on to suggest that deliberate mental training, such as cultivating feelings of compassion, can motivate feelings of kindness and prosocial actions.

As Engen and Singer, Fareri and Delgado, and Fox note, the deep connection between the social and the emotional is evident in the high degree of overlap between the social and emotional brain. In addition to the role for social-valuation signals outlined here, Fareri and Delgado and Fox emphasize the amygdala's role in basic social processes, such as perception, trust, and proximity aversion. Engen and Singer highlight evidence that perception and action often engage overlapping substrates, and that some of the same neural systems that underlie emotion processing seem to enable emotion perception and empathy for others. In fact, many of these same systems are those that are thought to change with explicit prosocial training.

Finally, many of the contributors agree that, once elicited, moods and emotions can leapfrog from person-to-person via empathic distress and facial mimicry and spread across larger groups via emotional contagion (Eisenberg and Hernández, Engen and Singer, Fox, and Parkinson; see also Hatfield, Cacioppo, & Rapson, 1993). Fox takes this argument the furthest, arguing that implicit social communication of emotion (see Question 14) can form the basis for unconscious emotional

transmission and group-affect. As Parkinson suggests, "better understanding how our emotional responses to the world around us are shaped by details of our social relationships, as well as by our relative positions in the social networks in which we are each embedded, comprises an important direction for future research."

ACKNOWLEDGMENTS

This work was supported by the National Institutes of Health (DA040717, MH107444), the University of California, Davis, and the California National Primate Research Center, CA, and the University of Maryland, College Park, MD. Authors declare no conflicts of interest.

SECOND EDITION

THE NATURE OF EMOTION

Fundamental Questions

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OXFORD
UNIVERSITY PRESS

OXFORD
UNIVERSITY PRESS

Oxford University Press is a department of the University of Oxford. It furthers the University's objective of excellence in research, scholarship, and education by publishing worldwide. Oxford is a registered trade mark of Oxford University Press in the UK and certain other countries.

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America.

First Edition published in 1994
Second Edition published in 2018

Library of Congress Cataloging-in-Publication Data
To Come
ISBN 978–0–19–061257–3

1 3 5 7 9 8 6 4 2

Printed by Sheridan Books, Inc., United States of America

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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