

Afterword: *How are emotions organized in the brain?*

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

Adolphs, Berridge, and Panksepp stake out the most affirmative positions. Adolphs, for example, argues that human lesion studies provide clear evidence that specific emotions, such as fear, critically depend on particular parts of the brain, such as the amygdala (Feinstein, Adolphs, Damasio, & Tranel, 2011). He does not directly address evidence suggesting that the amygdala is not necessary for feelings of fear and panic, at least when they are elicited by interoceptive challenges (i.e., breathing CO₂-enriched air; Adolphs, 2017; Feinstein et al., 2013). Most of the authors highlight the importance of regions classically implicated in emotion, including the periaqueductal gray (PAG), hypothalamus, extended amygdala, ventral striatum, cingulate, insula, and orbitofrontal cortex/ventromedial prefrontal cortex (OFC/vmPFC). Drawing on studies of decorticate animals, Panksepp and Wager place added emphasis on subcortical structures and the brainstem. As Panksepp notes, the “primal emotions of mammals arise subcortically, and hence existed long before humans strode the face of the earth.” Tye seems to come to a similar conclusion. Berridge, Panksepp, Wager, and Tye all adopt variants of the limbic system concept first articulated by Broca, Papez, and Maclean (Broca, 1878; MacLean, 1990; Papez, 1937). Pessoa, in contrast, joins with other theorists (LeDoux, 1991, 2000) in rejecting the utility of the limbic system. He does highlight some broader organizing principles: (1) Deep regions, those lying closer to the center of the brain (‘mesial’ or ‘medial’), are more involved in emotion than superficial territories (‘lateral’) and (2) ‘Agranular’ (three-layered) and ‘dysgranular’ cortex (four-layered) are more involved than ‘granular’ cortex (six-layered).

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

Panksepp and Wager outline the general importance of hierarchical control systems for emotion, with higher levels providing greater complexity and an extended temporal horizon (i.e., beyond the present moment). Wager, in particular, argues that the spinal cord and lower brainstem can trigger reflexive responses to immediate environmental challenges. At the next level of the hierarchy, regions of the upper brainstem and subcortical structures (e.g., PAG, hypothalamus, ventral striatum, extended amygdala, and hippocampus) govern emotions based on a more complex set of appraisals (e.g., threat imminence and certainty), environmental affordances (e.g., opportunity for escape), and memories (e.g., learned fear and safety). At the highest level, cortical regions regulate these organism-environment interactions and can shape responses in lower-level regions based on more complex contingencies, inferences (e.g., theory of mind), and long-term goals. Fox stakes out a superficially similar position, but rejects the notion of strict hierarchical control, arguing that “our brains are not Russian nesting dolls, where we have grown complex cortical controllers for our ‘reptilian brains’” (see also Pessoa, 2017). Drawing on a range of comparative neuroscientific data, he emphasizes the complex, bidirectional nature of interactions between seemingly ‘lower’ (e.g., PAG) and ‘higher’ (e.g., prefrontal cortex) regions, noting that “evolution has resulted in bidirectional connections between the evolutionarily old and new, has altered the

molecular composition and regulation of conserved regions, and has inserted evolutionarily old molecules into more recently evolved brain regions.”

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

Where does the emotional brain end? Berridge suggests that it is a matter of degree, noting that while “the entire brain does participate in every imaginable psychological function...not all structures participate equally.” Pessoa and Wager go a step further, suggesting that the emotional brain has no borders. As Wager notes, “the space of mechanisms that contribute to emotion is vast...There cannot be ‘an emotional brain’ that is less than the brain in its entirety, because so many processes contribute to the

generation of emotional experiences.¹ They and Fox suggest that emotion and cognition are deeply interwoven in the fabric of the brain, contrary to conventional ideas about ‘the emotional brain’ as distinct from ‘the cognitive brain’ (see also Pessoa, 2013, 2017; Shackman, Fox, & Seminowicz, 2015). Likewise, Wager and Barrett note that although machine learning techniques have uncovered patterns of brain activity that can reliably distinguish one emotion from another, those multi-voxel patterns encompass regions of the brain typically associated with cognitive, perceptual, motor, and other ‘non-emotional’ functions.

Barrett adopts the most radical position, although it overlaps in many ways with those of Pessoa and especially Wager (see also Engen and Singer’s response to Question 7; Barrett’s response to Question 8; Okon-Singer and colleagues’ response to Question 8; and Barrett, 2017; Barrett, *in press*; Pessoa, 2017). Relying mostly on correlational evidence gleaned from human imaging studies, she emphasizes that particular emotions cannot be localized with any specificity to circumscribed brain regions, circuits, or systems. Far from being a fear center, the amygdala, for example, is nonspecifically engaged by a broad spectrum of aversive and appetitive cues (Chase, Eickhoff, Laird, & Hogarth, 2011; Costafreda, Brammer, David, & Fu, 2008; Fusar-Poli et al., 2009; Kuhn & Gallinat, 2011; Namburi, Al-Hasani, Calhoon, Bruchas, & Tye, 2016; Sabatinelli et al., 2011; Sergerie, Chochol, & Armony, 2008; Sescousse, Caldu, Segura, & Dreher, 2013; Tang, Fellows, Small, & Dagher, 2012)—a point also made by Tye. Based on these and other kinds of data, Barrett argues that emotions “cannot be deconstructed and reduced into one system, or a part of a system.” They instead reflect “activity in domain-general, core brain systems that perform more basic psychological functions such as interoception, conceptualization, memory, sensory perception, language, and so on” (but see also Adolphs, 2017, his Figure 1). In short, while there may be an emotional brain, none of its constituents are specific to any particular emotion.

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).

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

Several contributors highlight some of the other challenges of deciphering the emotional brain. Adolphs, Barrett, and Wager remind us that emotions are complex states—involving weakly correlated changes in experience, peripheral physiology, action tendencies, and cognition (Shackman et al., 2013). Adolphs cautions us not to over-interpret animal studies that rely on a single behavioral index of emotion (e.g., freezing as an index of fear), reminiscent of classic suggestions in the human psychophysiological literature (Bradley & Lang, 2000). Wager, like Barrett, stresses that it will be impossible to discover a singular “brain representation for an emotion *per se*, because an emotion is not a single process.” He also

warns us that lay people (and even scientists, in unguarded moments) use emotional words in inconsistent ways, making it particularly difficult to identify the circuits underlying the subjective experience of emotion (see also Block, 1995; Kagan, 2016a, 2016b, *in press*; Poldrack & Yarkoni, 2016; Schaafsma, Pfaff, Spunt, & Adolphs, 2015; Shackman & Fox, 2016). Finally, Adolphs highlights the value of using more formal functional, architectural, and computational criteria for understanding how different emotions are organized in the brain (Adolphs, 2017; Anderson & Adolphs, 2014).

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