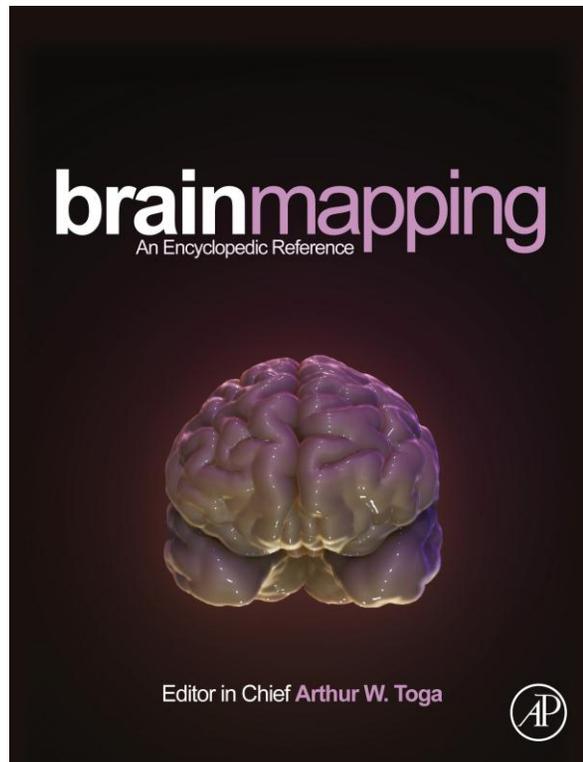


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## Emotional Experience

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### Introduction

People often carve experience into affective or emotional moments (Barrett, 2006; James, 1884). From queasy sensations in the stomach or the flush of the face to the flash of lightening or smell of vomit, these perceptions are often understood as feeling discrete emotions such as 'humiliation,' 'excitement,' or 'disgust' or perhaps more simply as 'pleasant' or 'unpleasant' affective valence. A job for social and affective neuroscientists is to understand how these emotional and affective experiences are constructed from activity in the nervous system (Barrett, 2009; Davidson & Sutton, 1995; Panksepp, 1998). Here, functional neuroimaging methods such as oxygen-15 PET (Mintun, Raichle, Martin, & Herscovitch, 1984) and fMRI (Ogawa, Lee, Kay, & Tank, 1990) have provided an unprecedented ability to measure activity in the entire brain while a person is in the midst of an emotional experience (e.g., Mountz et al., 1989; Reiman, Fusselman, Fox, & Raichle, 1989).

The use of neuroimaging methods is a recent addition for studying emotional experiences. However, integrating biology in the study of human emotion has been of critical interest since the very beginnings of affective science (for a review, see Dalgleish, Dunn, & Mobbs, 2009). In the 1880s, William James suggested that the experience of emotion arises from afferent projections signaling the body state to the brain. This idea was revolutionary. Emotion terms are often used to describe the causes of physiological and behavioral responses (e.g., 'I'm blushing and covering my face because I'm embarrassed'). In contrast, William James proposed that emotional experiences do not cause physiological and behavioral responses; rather, emotional experiences are composed from the perceptions of these responses. James challenged his readers to indicate what an emotional experience was composed of upon taking away all of the visceromotor sensations. His answer was that nothing meaningfully related to emotional experience is left. Although James' evidence was a thought experiment, empirical efforts to determine what constitutes an emotion have been a focus of research ever since (Ellsworth, 1994; Gendron & Barrett, 2009; Lang, 1994).

In this article, we review the neuroscience literature with a focus on neuroimaging studies of human affective and emotional experiences. We begin by describing the landscape of neuroimaging studies to provide the reader with an idea of how neuroimaging studies of affect and emotion are typically conducted. We then describe the main findings pertaining to components of affective and emotional experience and how different experiences may relate to neural activity.

### Overview of Neuroimaging Studies of Affective and Emotional Experience

In the prototypical neuroimaging study in affective neuroscience, participants are presented with dozens of stimuli that

elicit affective or emotional responses while undergoing PET or fMRI scanning (e.g., Irwin et al., 1996; Lang et al., 1998; Ochsner et al., 2004; Phan et al., 2004; Schneider et al., 1997). Groups of stimuli are intended to induce 'negative,' 'positive,' or 'neutral' affect or emotion categories like 'anger' or 'fear,' and participants are often asked to provide ratings of their affective or emotional experiences. Changes in blood flow in response to neural activity that correlate with the presentation of stimuli in a condition (e.g., negative, positive, and neutral) are then identified using linear regression. Comparisons are then made between different conditions to form 'contrast maps,' which are statistical comparisons between conditions as they relate to neural activity. Stimulus presentation is typically static and visual (~70% of contrast maps across studies), such as presenting pictures of graphic images (e.g., aversive images involving injuries and mutilations or pleasant images involving cute animals, typically from a normed database of affective images (Lang, Bradley, & Cuthbert, 2008; Tottenham et al., 2009)). Other sensory modality-based induction methods are used less frequently (e.g., sound clips ~8%, tastes ~3%, and smells ~3% of contrast maps). Self-generated, or personally relevant, affect or emotion inductions are also used infrequently (e.g., autobiographical memory retrieval ~5% or imagery ~4%). Very few studies have examined an emotional state induced only once but over a prolonged period of time, such as during social rejection (e.g., Eisenberger, Lieberman, & Williams, 2003) or upon social insult leading to an angry state (Denson, Pedersen, Ronquillo, & Nandy, 2009). Most comparisons examine negative states (~58%) or positive states (~24%), with the remaining contrast maps examining affective arousal during both positive and negative states.

Overall, neuroimaging studies of affect and emotion tend to use static, impersonal, visual stimuli to evoke brief or punctuate aversive affective responses. These biases may stem from methodological constraints in neuroimaging and also assumptions underlying various theoretical perspectives. Methodologically, visual presentation of stimuli is simpler given a loud scanning environment and the requirements for building specialized equipment compatible with magnetic environments. Low-frequency drift in fMRI signals prevents the ability to study emotional experiences that last for more than a couple minutes at most. And many trials or time points are obtained to increase statistical power.

Theoretical perspectives about affect and emotion may also lead to biases in the modal characteristics of studies. Some theories, which view emotion as 'basic' biological entities, suggest that some emotions, like 'fear,' 'anger,' and 'disgust,' are composed of 'affect programs' that may have specific neural circuits (Damasio & Carvalho, 2013; Ekman, 1999; Panksepp, 1998). By this view, the 'fear' triggered from one type of visual stimulus (e.g., picture of a spider) may capitalize on much of the same circuitry as the fear triggered by another type of visual stimulus (e.g., fear of heights), a tactile stimulus (e.g., fear of

electrical shock), public speaking anxiety, threatening autobiographical memories or imagined scenarios, or even when seeing another person make a wide-eyed facial expression interpreted as using either visual or nonvisual induction methods, therefore, may be considered not particularly important for studying the basic circuits underlying fear.

Alternatively, other theories referred to broadly as 'constructivist views' (Barrett, 2006; Gendron & Barrett, 2009; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Russell & Barrett, 1999; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011) propose that aspects of a situation that contribute toward categorizing experience into an episodic moment involving 'fear' play a constitutive role in the experience of fear. By this account, the experience of fear that may occur during threat of shock, for example, may not be representative of the fear occurring during public speaking or inferring fearful states of others' facial expressions. Currently, the degree to which affective or emotional experiences are separated into modular neural circuits for each type (e.g., one for fear and one for anger) or whether they distributed across neural circuits that are not specific for each type is hotly debated. From this view, the variations in methods used to induce different emotions are an important part of the emotional experience itself.

### Neural Correlates of Emotional Experience

Large-scale statistical summaries, or meta-analyses, can quantify which brain regions respond most frequently during changes in affect or emotion (Costafreda, Brammer, David, & Fu, 2008; Kober et al., 2008; Lindquist et al., 2012; Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002; Wager et al., 2008). Pooling across hundreds of studies, the meta-analytic map in Figure 1 illustrates that neural activity is frequently observed in several brain regions such as the amygdala, anterior hippocampus, anterior insula, and cingulate gyrus, which contribute to a set of regions often referred to as the limbic system. However, numerous areas outside of the limbic system are also frequently active, including the brain stem nuclei, the thalamus, the ventral striatum, the medial prefrontal cortex, the posterior cingulate cortex, the precuneus, the lateral temporal cortex, and the temporal poles. Such widespread activations raise several questions including why do neuroimaging studies of affective and emotional experience show frequent activity across numerous distinct brain regions and systems, and are some brain areas more critical or important for affective and emotional experiences than others? An overview of neural models of emotional experience may help make sense of the litany of areas shown in Figure 1. While a full review of these theories and their intricacies is beyond the scope of this article, the major brushstrokes are helpful to situate the neuroimaging findings on emotional experience.

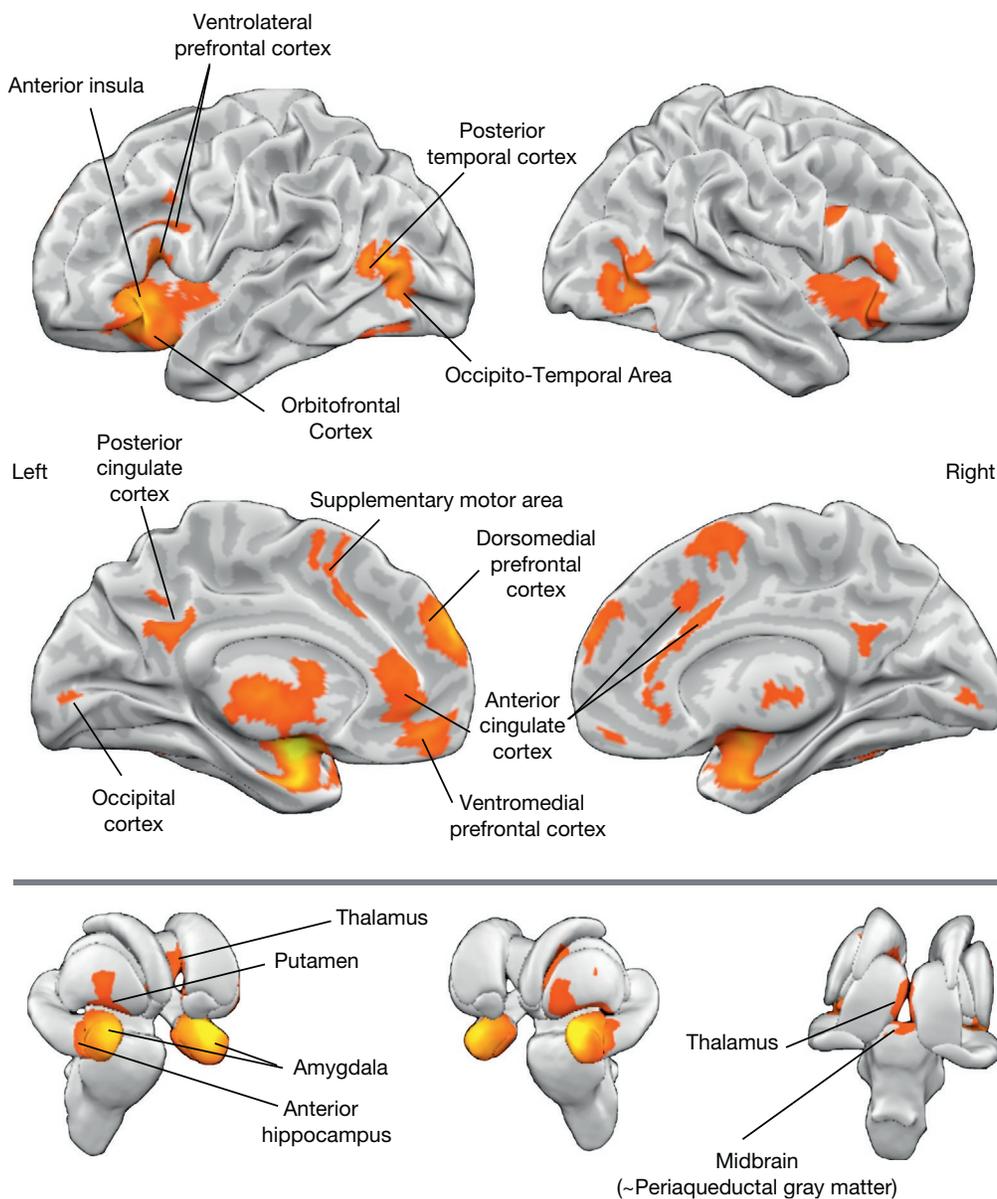
### Neural Models of Emotional Experience

The hypothesis that emotional experiences arise from afferent projections signaling the body state to the brain, which is

attributed to James, has served as a major inspiration for several neural models of emotional experience. We review four contemporary neural models to provide the reader with a sense of the guiding theoretical dimensions. First, one influential model proposed by Bud Craig highlights the insular cortex as being critical for emotional experience based on the observation that the insula is among the primary cortical targets of neurons that project from the bodily milieu to the brain (i.e., neurons relaying interoceptive information; Craig, 2002, 2009). Based on tract-tracing studies in monkeys and functional neuroimaging studies in humans, Craig proposed that the insula has a posterior to anterior processing gradient in which primary interoceptive inputs projecting to the posterior insula become integrated with exteroceptive sensory inputs and hedonic cues (stemming in part from the nucleus accumbens and orbitofrontal cortex) projecting to the mid-insula, which become integrated with motivational, social, and cognitive factors (stemming from the anterior cingulate cortex, ventromedial prefrontal cortex, and dorsolateral prefrontal cortex) projecting to the anterior insula. These inputs may represent contextual information including goals to help make meaning of otherwise diffuse bodily signals into a coherent emotional experience. Consistent with Craig's view, the anterior insula is among the most frequently active areas during emotional or affective experiences.

In a second influential model, Damasio and Carvalho have proposed a more structurally distributed neural model of emotional experience than Craig. Specifically, they propose that regions of the brain that carry a somatotopic representation of information from the body are particularly important for the neural substrates of 'feeling' (Damasio & Carvalho, 2013). This model defines 'feelings' as consciously perceived inputs from the body (i.e. experience) and 'emotions' as motor action patterns, rather than mental states per se,) for which presumably awareness is not necessarily required. Hence, we focus on the model's perspective on feelings as it may relate more closely with the experience of affect or emotion as discussed in this article. Areas showing some degree of somatotopic organization include the brain stem nuclei, thalamic nuclei, posterior insula, and somatosensory areas. Figure 1 shows that portions of the brain stem and thalamus are often engaged during affective experiences. However, these relatively small regions (e.g., in the brainstem) are difficult to study because standard neuroimaging methods are unable to localize activity on such a small spatial scale. Despite Damasio et al.'s emphasis on the posterior insula and somatosensory cortices in feelings, these areas are not as reliably active during inductions of affective experience. Importantly, the absence of activation in these cortical areas suggests that they are not drawn upon more strongly during an affective experience relative to more neutral experiences, but this does not necessarily mean that they are unimportant for affective experiences.

A third approach to neural models of emotional experience stems from the concept of the triune brain (Maclean, 1990), as inspired by Papez (1937) and first developed by Maclean (1952). The triune brain model divides the brain into three parts: the reptilian complex, which includes the basal ganglia and brain stem, among other structures; the limbic system, which includes the amygdala, hippocampus, and cingulate gyrus, among other structures; and the neocortex. The triune



**Figure 1** A meta-analysis of neural regions frequently engaged during emotional experience. A multilevel kernel density analysis map was calculated to analytically summarize activations occurring across 373 contrast maps from neuroimaging experiments that targeted emotional experience inductions (see Kober et al., 2008 for methodology details). The map updates results first reported by Wager et al. (2008) to include studies conducted through 2011. Results are corrected for multiple comparisons across the whole brain (family-wise error rate corrected cluster threshold,  $p < 0.05$ ; uncorrected voxel threshold,  $p < 0.001$ ). Descriptive labels are provided for cortical locations in the left hemisphere and on the right hemisphere only for selected areas.

brain and closely related models tend to place affect and emotion in the reptilian complex or limbic system (Panksepp, 1998, 2011), whereas the neocortex, and particularly the prefrontal cortex, has been ascribed with the role of higher-order thinking, reasoning, and cognitive control. The specialization of the limbic system for affect or emotion has been criticized based on observations that several limbic areas of the brain, including the hippocampus and amygdala, are also involved in 'cognitive' functions such as learning and memory (Ledoux, 1991). Nonetheless, models similar to the triune brain concept have been generative as an organizational framework in the neuroscience of emotion and emotion regulation.

As illustrated in Figure 1, regions at all three levels of the 'triune brain' are often active during affective and emotional experiences, suggesting that affective experience is not supported by only one or two levels of the triune brain. One potential explanation that may account for the neuroimaging data is to distinguish between primary and secondary forms of consciousness (Lieberman, Gaunt, Gilbert, & Trope, 2002; Panksepp, 2005; Satpute & Lieberman, 2006). Here, primary consciousness refers to the specific sensory or perceptual contents associated with the presence of affect or emotion. Secondary consciousness refers to the ability to reflect on this content, for instance, by describing it with words. By this

account, the meaningful content of an affective experience falls in the domain of primary awareness and maps onto structures in the limbic system and/or reptilian complex. Activation in neocortical structures is then explained as functions underlying the ability to reflect on this content. Another potential explanation for activation in neocortex during affective experience is that it reflects regulation that may occur without being instructed to regulate (i.e., implicitly) or as an incidental 'side effect' of other psychological activities that may co-occur with the presence of an affect-inducing stimulus, such as retrieving semantic labels for an affective or emotional state (Berkman & Lieberman, 2009; Lieberman et al., 2007).

Finally, a fourth a neural model of emotional experience comes from a theoretical approach proposing that affective and emotional experiences emerge from a family of basic processes, many of which may be shared with other categories of experience that are not considered 'emotions' by folk psychological terms (e.g., 'memories' and 'pain'). This view stems in part from empirical work showing that measurements of peripheral physiological activity only loosely distinguish different categories of emotional or affective experiences (see reviews by Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Quigley & Barrett, 2014). Thus, peripheral feedback provides an important but incomplete account of emotional experience (Schachter & Singer, 1962). Contemporary theories have pointed to categorization or conceptualization as a second basic process that constitutes emotional experience (e.g., Fehr & Russell, 1984). Conceptualization involves processes that draw experience into a mental-state category of 'anger' or 'happiness,' etc. (Barrett, 2006). These processes are considered to be domain general or apply similarly to emotion categories as they do for nonemotion categories (Barsalou, 2008; Wilson-Mendenhall et al., 2011).

In one instantiation of this kind of theoretical approach, Barrett and colleagues hypothesized that emotional experiences arise from two main circuits (Barrett, Mesquita, Ochsner, & Gross, 2007; although other networks are also likely to be involved; Barrett & Satpute, 2013). One circuit is involved in representations of pleasant or unpleasant affect grounded in the body and is supported by brain regions associated with mediating autonomic and visceromotor responses, including the lateral orbitofrontal cortex, the anterior insula, the amygdala, the medial orbitofrontal cortex/ventromedial prefrontal cortex, the subgenual cingulate, and the brain stem nuclei. The second circuit supports conceptualization, which refers to a process that binds together information from diverse sources including the external world, the internal body, and memories into an episodic moment that involves an attribution of mental state in self or other. The conceptualization circuit is believed to include the dorsal portions of medial prefrontal and anterior cingulate cortices and associated regions comprising the default-mode network (see Barrett & Satpute, 2013; Barrett, Mesquita, Ochsner, & Gross, 2007; Roy, Shohamy, & Wager, 2012). These regions are also frequently drawn upon during retrieving and attributing mental states, suggesting that emotional experience draws on processes shared with forming mental-state attributions (Barrett, Mesquita, Ochsner, & Gross, 2007; Ochsner et al., 2004; Satpute, Shu, Weber, Roy, & Ochsner, 2012).

The model that best accounts for the available evidence is currently a matter of debate. Against this background, the

meta-analytic map provided in Figure 1 has two limitations. The first limitation, which is common for all functional neuroimaging studies, is that findings are correlations of functional activity during the presence of hypothetical psychological processes. Consequently, activity in a given region does not mean the region is necessary for emotional experience, and the absence of activation does not mean that it is unnecessary. Thus, interpretation of imaging data improves greatly when considered in the context of several other sources of brain data such as lesion studies in humans and animals and manipulations of neural activity (e.g., using transcranial magnetic stimulation). The second limitation is that meta-analysis requires ignoring the intricacies that motivate each individual experiment, some of which are better tailored to address questions of theoretical relevance.

### Neuroimaging Findings and Neuropsychological Case Reports

Data from neuropsychological studies can help designate whether a region is likely to be necessary for emotional experience. Perhaps, contrary to what one might expect, case studies suggest that the amygdala and the anterior insula are not necessary for the experience of emotion (Anderson & Phelps, 2002; Damasio & Carvalho, 2013; Feinstein, 2013; Feinstein et al., 2013) cf. (Calder, Keane, Manes, Antoun, & Young, 2000). Damage to these regions may change the degree to which stimuli have an impact upon affective feeling (e.g., lessens their impact), but individuals nonetheless carve their experiences into their affective or emotional qualities. Alternatively, damage to the medial prefrontal cortex appears to reduce emotion-related behavioral expressions that involve self-awareness (Beer, Heerey, Keltner, Scabini, & Knight, 2003; Beer, John, Scabini, & Knight, 2006; Camille et al., 2004; Hornak et al., 2003; Sturm, Rosen, Allison, Miller, & Levenson, 2006). This area is considered to be part of a larger network of regions including the temporoparietal junction and posterior cingulate cortex, which as a network may play an important role in conceptualizing experience by integrating across diverse sources of information (autonomic, situational/contextual, mnemonic, linguistic/semantic, etc.; Barrett & Satpute, 2013; Roy et al., 2012). In general however, the handful of case reports suggest that damage to specific brain areas may not produce profound impairments in affective or emotional experiences. Correspondingly, a more distributed architecture of emotional experience may be called for.

Indeed, a recent imaging study suggests that an affective experience may be better understood as an emergent property from the combination of multiple functionally dissociable brain systems (Satpute, Shu, Weber, Roy, & Ochsner, 2012). One system, associated with orienting attentional awareness upon affective feeling, involves the dorsomedial prefrontal cortex and temporoparietal junction (among other areas; also see Gusnard, Akbudak, Shulman, & Raichle, 2001; Lane, Fink, Chau, & Dolan, 1997). These regions are also engaged when making judgments about another person's emotional experience (Denny, Kober, Wager, & Ochsner, 2012; Ochsner et al., 2004) and more broadly in several domains including language use and semantic retrieval (Binder, Desai, Graves, &

Conant, 2009), autobiographical memory (Svoboda, Mckinnon, & Levine, 2006), and self-generated thought (Andrews-Hanna, Smallwood, & Spreng, 2014). A second system, associated with bringing semantic categories online (e.g., affect labels like 'good' or 'bad' or emotion labels like 'fear' or 'anger') during an affective experience, involves the ventrolateral prefrontal cortex. Activations in similar portions of the ventrolateral prefrontal cortex are also observed during labeling facial expression stimuli in emotion perception (Lieberman et al., 2007), when using thought to evaluate a stimulus so as to increase or decrease its affective potency (i.e., 'reappraisal'; Buhle et al., 2013), in social and semantic retrieval (Badre & Wagner, 2007; Satpute, Badre, & Ochsner, 2013), and in category learning (Passingham, Toni, & Rushworth, 2000). And a third system, which tracks with the intensity of a pleasant or unpleasant affective experience, includes the amygdala and anterior insula (Phan et al., 2002; Wager et al., 2008). Taken together, the findings support a distributed neural architecture for constructing experiences of emotion (Barrett & Satpute, 2013).

### Categories of Emotional Experiences

So far, this article has focussed on affective and emotional experiences as a category relative to neutral categories. However, a brain basis of emotional experience must also account for the diversity of emotional experiences that people experience. What distinguishes 'fear' from 'anger' or 'happiness' from mere 'pleasantness'? Neuroscience models vary widely in how they account for different categories of emotional experience (Lane & Nadel, 2002). These models can be broadly organized into those proposing relatively modular and reductionist architectures (e.g., Panksepp, 2011) to those proposing highly distributed neural architectures (Barrett et al., 2007; Wilson-Mendenhall et al., 2011). Models in the former class tend to ground the diversity of emotions into a handful of 'basic' emotion categories (e.g., anger, fear, disgust, and happiness) that are homologous across species and that differ from 'non-basic' emotion categories in which social and/or cognitive processes play an independent role (e.g., shame, guilt, and pride). Neural models stemming from this perspective have proposed that dedicated and specific neural circuits underlie different basic emotions (e.g., Panksepp, 2011).

Early on, several imaging studies were considered to support modular neural architectures of emotion. For example, studies found greater amygdala activity when processing stimuli with fear-related content (e.g., fearful facial expressions or fear-inducing stimuli) and greater insula activity when processing stimuli with disgust content (Murphy et al., 2003; Phan et al., 2002; Phillips et al., 2004, 1997). However, as studies in affective neuroscience accumulated, insula activity was also shown to correlate with several other emotions including sadness, anger, and fear, as was activity in the amygdala and other brain regions initially associated with individual emotions (e.g., Schienle et al., 2002; meta-analysis by Lindquist et al., 2012).

One possible recourse for modular views of brain function is that neuroimaging studies lack the requisite temporal or spatial resolution to identify discrete circuits for emotion

categories. For instance, circuits related to defensive behaviors have been identified in nonhuman animals. Excitation directed at different portions of the periaqueductal gray region in the brain stem elicits stereotyped 'fight'- or 'flight'-style behaviors, with corresponding physiological profiles (e.g., heart rate acceleration/deceleration, vasoconstriction/dilation, and opiate- or non-opiate-mediated analgesic responses) even upon severing connections between the brain stem with the neocortex and limbic system (Bandler & Shipley, 1994). These subcortical circuits have been proposed to serve as modules that underlie the primary emotional experience of emotions such as 'fear' and 'rage' (Panksepp, 2011). Several neuroimaging studies in humans have also observed activity in the vicinity of the periaqueductal gray during threat, emotion, and pain (e.g., Kober et al., 2008; Mobbs et al., 2007; Tracey et al., 2002). But due to poor spatial resolution, whether functional activity during specific emotional experiences is independently localized to discrete brain stem circuits in humans remains unclear. Recently developed high-field strength imaging techniques, which provide sufficient resolution to isolate activity to subregions of the periaqueductal gray (Satpute et al., 2013), may be able to test this hypothesis more directly.

In contrast to the modular perspective for neural representations of emotion categories, distributed processing models propose that individual emotional experiences are constructed from activity occurring across several brain regions, none of which are dedicated to specific categories of emotions (e.g., Wilson-Mendenhall et al., 2011). In one recently developed model (Barrett & Satpute, 2013; Lindquist & Barrett, 2012; Wilson-Mendenhall et al., 2011), individual episodes from the emotion category 'anger,' for example, likely have some elements in common with other episodes of anger. However, these elements may not be present for all episodes of anger, and they may also be shared with emotional experiences that are not considered anger (Wilson-Mendenhall, Barrett, & Barsalou, 2013). These elements may also be shared with experiences that are not necessarily classified as emotions or affective experiences, too (Barrett & Satpute, 2013; Satpute, Shu, Weber, Roy, & Ochsner, 2012). In this sense, there is no 'essence' of anger or discrete modular circuits that uniquely distinguishes episodes of anger from episodes of other emotions. The diversity of experiences within an emotion category and across emotion categories is instead generated from various mixtures of processes that are not specific to particular emotions (Lindquist & Barrett, 2012).

Importantly, distributed models do not state that there is no structure for different emotional experiences (Barrett, 2012). In contrast, they suggest that identifying this structure requires sampling from a population of situationally embedded instances for each individual. Variability in activity across these instances can then be modeled for each individual to examine how he or she carves their experiences into emotion categories. To date, no neuroimaging studies in affective neuroscience have implemented this kind of individual-tailored or 'idiographic' (In contrast to an idiographic approach, 'nomothetic' approaches in affective neuroscience make the assumption that all else being equal, each individual accesses the same psychological processes during a task manipulation and that these psychological processes are organized in the same way in the brain.) approach to address the aforementioned questions,

in part because doing so can be costly and computationally intensive. Instead, most experiments tend to induce the occurrence of an emotional experience using the same kinds of stimuli (e.g., fearful facial expressions) rather than sampling from a population of situationally embedded episodes for each category of emotional experience.

Still, distributed models have inspired studies that induce a variety of discrete emotional episodes using scenarios and situations based on real-world experiences. In the scenario immersion method, for example, participants immerse in imagined emotional episodes as they listen to detailed, imagery-evoking audio scripts with their eyes closed (Wilson-Mendenhall, Barrett, & Barsalou, 2013). Evidence of increased neural activity across primary sensory cortices (e.g., visual and motor cortices) and across limbic regions involved in the multisensory integration that influences what is salient and remembered (e.g., amygdala and hippocampus), along with participants' high self-reported immersion ratings, suggests that this scenario immersion procedure produces vivid, engaging experiences. Such induction methods, which are strikingly different from viewing a decontextualized facial expression, are useful for examining the rich situations that characterize emotional experiences. It was recently demonstrated, for example, that the distributed neural patterns that underlie fear experiences during social evaluation versus physical danger situations differ, with the distinct distributed patterns composed of neural circuitry shared across the two situations and neural circuitry unique to each situation (Wilson-Mendenhall et al., 2011). Further, the shared neural circuitry involved in fear experiences across the two situations (e.g., medial prefrontal cortex) was also involved in anger experiences and in experiences of planning (instead of emoting), suggesting that this neural circuitry is not specific to fear. This and other recent works emphasize the importance of examining the wide variety of situated emotions that people experience in everyday life.

### Summary and Future Directions

Affective neuroscience represents one of the largest domains of study in the neuroimaging literature, with several hundreds of studies conducted to date. In this article, we presented some of the main findings in the brain mapping literature on affective and emotional experience, including: (i) During affective and emotional experiences, neural activity is not restricted to only the amygdala, the limbic system, or a handful of few circumscribed structures, but instead, activity correlates with numerous brain areas extending across all levels of the neural hierarchy; (ii) episodes from different categories of emotional experiences activate many of the same brain areas, and specific circuits for specific emotions have not been identified with neuroimaging data (even though probabilistic patterns may be present); and (iii) there has been considerable interest in developing more precise theoretical formulations for relating affective and emotional experiences with neural activity, but which theory best suits the future of affective neuroscience is currently a matter of vigorous debate.

Many current directions in the field carry a great deal of promise for surpassing previous limitations and uncovering how the brain gives rise to affective and emotional experiences.

For example, brain stem nuclei are known to be crucially important in affective neuroscience and may play a pivotal role in adjudicating between various theoretical models. However, they have received only modest attention due to poor spatial resolution. Emerging use of high-field strength magnets has considerably increased the signal to noise ratio (Wiggins et al., 2006), allowing for submillimeter resolution of activity in the brain stem nuclei during affective experience including in subregions of the periaqueductal gray (Satpute et al., 2013). Alternative mathematical approaches for relating brain activity with psychological processes have also expanded the scope of the field (Kriegeskorte, Goebel, & Bandettini, 2006). Using machine learning techniques, a recent study observed that distributed patterns of neural activity were capable of predicting the presence of specific emotional states (e.g., an episode of anger, sadness, and fear) with a mean rank accuracy of 84% (chance was 50%). In combination with extant meta-analyses, such work suggests that information about emotional experiences may be present in distributed patterns of neural activity even though specific and discrete circuits may not underlie each various episodes from the same emotion category. Finally, a growing body of work is also highlighting the importance of temporal dynamics in the unfolding of emotion on both psychological (e.g., Cunningham, Dunfield, & Stillman, 2013) and neural levels (e.g., Raz et al., 2012; Touroutoglou, Hollenbeck, Dickerson, & Feldman Barrett, 2012). Such dynamics may be essential for uncovering relationships between individual differences in emotional experiences and underlying neural activity (e.g., Heller et al., 2009; Moriguchi et al., 2011).

A potential outcome of this work is to provide a mechanistic, biologically grounded understanding of how psychological measures of emotional experiences contribute to physical measures of health and illness. By peering into the brain during affective and emotional experiences, neuroimaging research provides evidence for the necessary mind/brain mapping that links emotional experiences with neural activity and, from there, identifies the physical pathways relating neural activity with biological measures of health and illness. Developing precise models for how emotional experiences relate with neural activity is perhaps the penultimate challenge toward this goal.

**See also:** **INTRODUCTION TO ACQUISITION METHODS:** Temporal Resolution and Spatial Resolution of fMRI; **INTRODUCTION TO ANATOMY AND PHYSIOLOGY:** Amygdala; Insular Cortex; Somatosensory Cortex; The Brain Stem; **INTRODUCTION TO CLINICAL BRAIN MAPPING:** Depression; Emotion and Stress; Imaging Studies of Anxiety Disorders; **INTRODUCTION TO COGNITIVE NEUROSCIENCE:** Reward Processing; Value Representation; **INTRODUCTION TO METHODS AND MODELING:** BrainMap Database as a Resource for Computational Modeling; Meta-Analyses in Functional Neuroimaging; The General Linear Model; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE:** Emotion Perception and Elicitation; How the Brain Feels the Hurt of Heartbreak: Examining the Neurobiological Overlap Between Social and Physical Pain; Mentalizing; The Amygdala and Social Perception; **INTRODUCTION TO SYSTEMS:** Autonomic Control; Emotion; Large-Scale Functional Brain Organization; Reward; Salience Network; Taste, Flavor, and Appetite; The Mesolimbic Dopamine Pathway and Romantic Love.

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