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Neuroscientific Perspectives of Emotion

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Edited by Rafael Calvo, Sidney K. D'Mello, Jonathan Gratch, and Arvid Kappas

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[–] Abstract and Keywords

This chapter is from the forthcoming *The Oxford Handbook of Affective Computing* edited by Rafael Calvo, Sidney K. D'Mello, Jonathan Gratch, and Arvid Kappas. Emotion is often defined as a multicomponent response to a significant stimulus characterized by brain and body arousal and a subjective feeling state, eliciting a tendency toward motivated action. This chapter reviews the neuroscience of emotion, especially highlighting a psychological constructionist approach that considers certain events to result from the interplay of basic neurophysiological operations not specific to emotion. The authors adopt an embodied cognition perspective, highlighting the importance of the whole body—not just the brain—to better understand the biological basis of emotion and drawing on influential theories, including Polyvagal Theory and the Somatic Marker Hypothesis, which emphasize the importance of bidirectional communication between viscera and brain, and the impact of visceral responses on subjective feeling state and decision making, respectively. Embodied cognition has important implications for understanding emotion, and the authors emphasize the need for further research that draws on affective computing principles and focuses on objective measures of body and brain to further elucidate the specificity of different emotional states.

Keywords: Basic emotions, natural kinds, psychological constructionism, emotion specificity, embodied cognition, psychophysiology, neuroimaging

Introduction

Bidirectional projections underpin emotional experience, such that the brain impacts on the body via visceral efferent pathways and the body impacts on the brain through afferent feedback. Take, for example, the case of laughter yoga, an activity that involves groups of people getting together to ... laugh! Initially, the experience is awkward and forced, but very soon—with the help of yogic breathing techniques and physical movement—the forced laughter becomes spontaneous and contagious. Laughter is not unique to our species: Jaak Panksepp's work on rodent tickling indicates that 50-kHz chirping (laughter?) may be an evolutionary antecedent of human joy (Panksepp, 2005; Panksepp & Burgdorf, 2000; 2003). This research, along with that of others (Wild, Rodden, Grodd, & Ruch, 2003), suggests that laughter may depend on two partially independent neuronal pathways: an "involuntary," emotionally driven subcortical system and a cortical network that supports the human capacity for verbal joking. Laughter is an excellent example of the impact of the body on emotion experience, highlighting that laughter is possible without humor or cognitive thought. Although autonomic activation normally colors our subjective experience, in some cases, it is able to actually drive the emotions we experience.

Psychological research indicates that voluntary contraction of facial muscles contributes to emotional experience (Strack, Martin, & Stepper, 1988). Participants who hold a pencil with their lips, forcing their face to prevent or inhibit a smile, rate cartoons as less amusing than participants who hold a pencil in their teeth, mimicking a smile. Similarly, participants trained to produce typical emotional expressions muscle by muscle report subjective emotional experience and display specific physiological changes (Levenson, Ekman, & Friesen, 1990). More

recent studies on botulinum toxin (or “botox”) have shown that injection to the glabellar region—the space between the eyebrows and above the nose—to inhibit the activity of the corrugator and procerus muscles reduces the experience of fear and sadness in healthy females (Lewis & Bowler, 2009). Another study (Wollmer et al., 2012) on patients with major depressive disorder has even reported that glabellar botulinum toxin treatment is associated with a 47% reduction in depression severity over a 6-week treatment period (relative to only 9.2% in placebo-treated participants). These surprising findings are supported by current influential neuroscientific theories of emotion (Damasio, 1994; Porges, 1995; 2011; Reimann & Bechara, 2010; Thayer & Lane, 2000; 2009) that explicitly incorporate brain–body interactions into formal models.

Here, we emphasize the importance of an “embodied cognition” perspective in order to better understand the biological basis for emotion. Emotion is often defined as a multicomponent response to a significant stimulus characterized by brain and bodily arousal and a subjective feeling state that elicits a tendency toward motivated action. Note however, that there may be instances of emotion in which significant stimulus (cf., emotions without obvious causes), subjective feeling state (cf., unconscious emotions), and motivated action (cf., sadness) are not necessary. In this review, we first describe the role of several key brain regions in regards to emotion processing. These include the prefrontal cortex (PFC; involved in emotional experience and its regulation), amygdala (stimulus salience and motivational significance), anterior cingulate (selection of stimuli for further processing), and insula (feelings and consciousness). We then describe a major intellectual stalemate that has arisen with respect to understanding how different emotions arise. This is the debate over whether the basic emotions are “natural kinds” versus a product of “psychological construction.” We suggest that one of the reasons for the difficulty in resolving this debate is the tendency to draw conclusions from different theoretical standpoints and experimental approaches. For example, recent efforts to understand human emotion may be characterized by a neurocentric approach arising from the wide use of functional magnetic resonance imaging (fMRI). This technique, however, has its limitations in regards to advancing our knowledge of emotion. Critically, it is often not clear whether emotional experiences are being evoked by the weak emotional stimuli that are often used in the scanner. Furthermore, fMRI studies require participants to remain in a supine body position during emotion elicitation, yet research has revealed that such a position reduces emotional responses (e.g., asymmetric frontal cortical activity as well as amygdala activity measured with other techniques) to appetitive emotional stimuli (Harmon-Jones, Gable, & Price, 2011; Price, Dieckman, & Harmon-Jones, 2012). (Readers interested in further details on neuroscientific approaches to affect detection are referred to Chapter 17).

Despite the many challenges to determining emotional specificity and correctly detecting the specificity of emotions—interested readers are referred to excellent reviews by Calvo & D’Mello, 2010, and Fairclough, 2009—we conclude this review by highlighting the need for future research that produce stronger manipulations of affective experiences, draws on affective computing principles, and employs multiple physiological and behavioral response systems under different conditions. We suggest that a multimodal approach to affective neuroscience may help to resolve the debate over whether the brain and body produce emotions as “natural kinds” or as “psychological constructions.”

The Emotional Brain

Specific brain regions including the PFC, amygdala, anterior cingulate, and insula play a major role in the neurobiological basis of emotion. These regions and their interconnectivity are briefly described here.

The Prefrontal Cortex

The PFC is the most anterior part of the frontal lobes and is generally considered to play a primary role in higher order cognitive activity, judgment, and planning. However, contemporary neuroscientific views of emotion highlight a role of the PFC in emotional experience, motivation, and its regulation. The PFC is comprised of a number of discrete regions, including the orbitofrontal, dorsomedial, ventromedial, dorsolateral, and ventrolateral cortices, all of which may play specific roles in the generation of emotional processes. The orbitofrontal cortex integrates exteroceptive and interoceptive sensory information to guide behavior and plays a role in core affect, a psychological primitive that relates to the mental representation of bodily changes experienced as pleasure or displeasure with some degree of arousal (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). The dorsomedial and ventromedial prefrontal cortices play a role in realizing instances of emotion perception and experience by

drawing on stored representations of prior experiences to make meaning of core affect. The dorsolateral PFC is involved in top-down, goal-directed selection of responses and plays a key role in executive function critical for directing other psychological operations involved in the generation of emotion. The ventrolateral PFC is implicated in selecting among competing response representations, response inhibition, and directing attention to salient stimuli in the environment (Lindquist et al., 2012).

Experimental research conducted in the 1950s and 1960s involving suppression of prefrontal cortical activity by injecting Amytal—a barbiturate derivative—into an internal carotid artery demonstrated a role of hemispheric asymmetry in emotion (Alema, Rosadini, & Rossi, 1961; Perria, Rosadini, & Rossi, 1961; Rossi & Rosadini, 1967; Terzian & Cecotto, 1959). Amytal injections in the left side—releasing the right hemisphere from contralateral inhibitory influences of the left—produced depression, whereas injections in the right side—releasing the left hemisphere—produced euphoria (see Harmon-Jones, Gable, & Peterson, 2010, for review). Research using the electroencephalogram (EEG) is consistent with these findings, demonstrating a role for the left PFC in positive affect and well-being and implicating right PFC in emotional vulnerability and affective disturbance, suggesting that activity in the left hemisphere region may provide a neurobiological marker of resilience (Begley & Davidson, 2012). Findings from normative and clinically depressed and anxious samples indicate that relative left-sided activation is decreased or that right-sided activation is increased in affective disturbance (Kemp, Griffiths et al., 2010a; Mathersul, Williams, Hopkinson, & Kemp, 2008; see also Kemp & Felmingham, 2008). Transcranial magnetic stimulation (TMS)—a technique applied to the scalp to either depolarize or hyperpolarize local neurons of the brain up to a depth of 2 cm—is an alternative nonpharmacological treatment for depression (Slotema, Blom, Hoek, & Sommer, 2010). Low-frequency (inhibitory) right-sided repetitive TMS (rTMS) or high-frequency (excitatory) left-sided rTMS is applied to the dorsolateral PFC of depressed patients to shift hemispheric asymmetry and ameliorate depressive symptoms. Other work (Harmon-Jones et al., 2010), however, demonstrates a role for left PFC in the emotion of anger—a basic emotion characterized by negative valence and approach-related motivation—highlighting a role for PFC in approach and withdrawal motivation, rather than positive and negative valence per se. Consistent with these electrophysiological findings, a meta-analysis of neuroimaging studies reported that the left ventrolateral PFC displays increased activity when participants perceive or experience instances of anger (Lindquist et al., 2012).

The Amygdala

The amygdala is an almond-shaped cluster of nuclei located in the anterior medial temporal lobe. Animal research has highlighted a central role for the amygdala in negative emotions such as fear and anxiety (Ledoux, 1998), and neuroimaging studies have confirmed its role in these emotions in humans (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, 2002). Amygdala activation is also observed in response to a variety of emotional states and stimuli including fear, disgust, sadness, anger, happiness, humor, sexually explicit images, and social emotions (Costafreda, Brammer, David, & Fu, 2008; Sergerie, Chochol, & Armony, 2008). A recent meta-analysis (Lindquist et al., 2012) concluded that the amygdala is part of a distributed network involved in core affect rather than fear per se and that it responds preferentially to salient exteroceptive sensations that are motivationally significant. Findings from several published meta-analyses of neuroimaging studies focusing on amygdala function in humans (Costafreda et al., 2008; Lindquist et al., 2012; Murphy et al., 2003; Phan, 2002; Sergerie et al., 2008; Vytal & Hamann, 2010) highlight a general role for the amygdala in processing stimulus salience, motivational significance, and arousal.

Although researchers (Costafreda et al., 2008) have emphasized that amygdala activation is more likely to respond to fear and disgust emotions, this may be due to the often weak evocative stimuli using in neuroimaging studies. Notably, a number of studies have examined amygdala activation during the experience of positive emotion, such as sexual arousal, and have produced findings highlighting an important distinction between motivated versus consummatory behavior. One study involving presentation of sexually explicit stimuli (Hamann, Herman, Nolan, & Wallen, 2004) reported strong activation in amygdala (and hypothalamus) and that this difference was greater in males than in females. The authors interpreted these gender differences in light of greater motivation in men to seek out and interact with such stimuli. An earlier positron emission tomography (PET) study (Holstege et al., 2003) on the brain activation during human male ejaculation reported decreases in amygdala activation. Together, these findings indicate that increased activity is associated with viewing appetitive sexual stimuli associated with approach-related motivation, whereas consummatory sexual behavior (or quiescence) is associated with

decreased activity, reflecting conservation of amygdala function (Hamann et al., 2004).

Anterior Cingulate

The anterior cingulate cortex (ACC) forms a collar around the corpus callosum and is a key substrate for conscious emotion experience. The most ventral portion of this structure—known as the subgenual cingulate (sACC; Brodmann's area or BA 25)—is a localized target in deep brain stimulation studies of patients with “treatment resistant” depression. Acute stimulation of this region (up to 9 V at each of the eight electrode contacts; four per hemisphere) is associated with a variety of psychological experiences including “sudden calmness or lightness,” “disappearance of the void,” “sense of heightened awareness,” “increased interest,” and “connectedness.” Although the rostral ventral region of ACC—including sACC and pregenual ACC (pACC; BAs 24,32)—was initially singled out as the ACC subregion involved in emotional processing (Bush, Luu, & Posner, 2000), a more recent review of the literature (Etkin, Egner, & Kalisch, 2011) focusing on fear conditioning and extinction in particular has characterized the caudal dorsal region as playing an important role in the appraisal and expression of emotion and the ventral rostral region in the regulation of regions such as the amygdala. It was noted (Etkin et al., 2011) that activity within dorsal ACC (and medial PFC [mPFC]) are observed during classical (Pavlovian) fear conditioning and instructed fear-based tasks and that this activity is positively correlated with sympathetic nervous system activity but negatively with ventral ACC (and mPFC regions). By contrast, recall of extinction 24 hours after conditioning—a process that is less confounded by residual expression of fear responses—yields activity in ventral ACC (and mPFC), thus providing support for the proposal that these regions are a neural correlate of fear inhibition that occurs during extinction (Etkin et al., 2011). Extending on this, a recent meta-analysis of functional neuroimaging studies (Lindquist et al., 2012) characterizes the sACC and pACC (Bas 24,32) (as well as adjacent posterior medial orbitofrontal cortex) as key sites for visceral regulation that helps to resolve which sensory input is selected for processing. By contrast, the more dorsal anterior midcingulate cortex is implicated in executive attention and motor engagement during response selection through connections to lateral PFC and the supplementary motor area.

Insula

The insula is located at the base of the lateral (Sylvian) fissure and plays a role in the experiential and expressive aspects of internally generated emotion. Early work highlighted a role for the insula cortex in gustatory function. Studies conducted in the 1950s demonstrated that electrically stimulating this region in conscious human patients produced nausea, the experience of smelling or tasting something bad, and unpleasant tastes or sensations (Penfield & Faulk, 1955). Consistent with these findings, one of the first meta-analyses of human neuroimaging studies (Murphy et al., 2003) reported that the insula was the most consistently activated brain region (along with the globus pallidus) for the emotion of disgust. This study reported insula activity in more than 70% of neuroimaging studies on disgust, whereas activity in this region was only observed in 40% of the studies on other discrete emotions. A more recent meta-analysis (Lindquist et al., 2012) indicated that the left anterior insula displays consistent increases in activation during instances of both disgust and anger, whereas the right anterior insula displays more consistent increases in activation during disgust, although activity in this region was not specific to this emotion.

The view of the insula's role in emotion has now expanded to a more general role for the awareness of bodily sensations, affective feeling, and consciousness (see Craig, 2009, for review). Work by Bud Craig and colleagues (Craig, 2002; 2003) indicates that ascending pathways originating from lamina I neurons in the spinal cord carry information about the physiological status of the body to the thalamus via the lateral spinothalamic tract. Thalamic nuclei then project to the mid/posterior dorsal insula, which then projects to the anterior insula. These pathways provide a neurophysiological basis for interoception (the physiological condition of the body) (Craig, 2002). The homeostatic afferent input received from the body is first represented in the dorsal insula—the primary sensory cortex of interoception—and this information is then re-represented in the anterior insula, providing a substrate for conscious awareness of the changes in internal physiological states and emotional feelings (Craig, 2002; 2003; 2009). The emotion of disgust involves a mental representation of how an object will affect the body (Lindquist et al., 2012), thus providing a potential explanation for neuroimaging findings that highlight a role for insula in this emotion.

The Great Emotion Debate

The fierce, ongoing debate over whether the emotions are discrete, innate human mental states has been likened to the Hundred Years' War between England and France (Lindquist, Siegel, Quigley, & Barrett, 2013). On the one hand, emotions may be considered as fundamental processes in the brain that exist across species (and human cultures); a phenomenon that is discovered, not created, by the human mind. In this regard, the basic emotions are characterized as “natural kinds,” hardwired into the brain and associated with distinctive patterns of neural activation (Panksepp & Watt, 2011; Vytal & Hamann, 2010). On the other hand, those who favor a psychological constructionist approach (Barrett, 2006; 2012; Lindquist et al., 2012) argue that emotions are themselves constructed from activation relating to more basic building blocks, such as core dimensions like valence (positive vs. negative affect) and arousal (deactivation to activation). Ledoux (2012) recently observed that although neuroscientific research on emotion has increased exponentially over the past decade, “emotion” remains ill-defined and that this situation has led to an intellectual stalemate. One of the problems here is that the terms “emotion” and “feeling” are used interchangeably, and this has led to the use of common language “feeling” words such as fear, anger, love, and sadness to guide the scientific study of emotion, rather than focusing on specific phenomena of interest (such as the detection of and response to significant events) (LeDoux, 2012). Another explanation for different competing theories is that researchers have often tackled the same question from different theoretical standpoints and experimental approaches. In this regard, Panksepp (2011) distinguishes between behavioral neuroscientists who study “instinctual” primary processes that provide the foundation for understanding the biological basis of emotion versus cognitive psychologists who study the higher levels of emotion along with their associated “regulatory nuances.”

Research on facial expressions—particularly the universally recognizable expressions of emotion—has been central to the ongoing debate about the nature of emotion. In the 1960s, Paul Ekman traveled to Papua New Guinea and conducted experiments on the isolated Fore tribesman who, at that time, had had little or no contact with the outside world. The ability of these tribesmen to reliably recognize certain facial expressions led to the proposal that there are certain “basic” emotions. These included fear, anger, disgust, surprise, happiness, and sadness; all of which are universally recognized, innate, and not reliant on social construction (Ekman, Sorenson, & Friesen, 1969). This work highlights that negative emotions are easily revealed in facial expressions of emotion. Research on vocalizations, however (Sauter & Scott, 2007), has revealed five putative positive emotions, including achievement/triumph, amusement, contentment, sensual pleasure, and relief. More recently, Ekman has expanded the basic emotions to include amusement, contempt, contentment, embarrassment, excitement, guilt, pride, relief, satisfaction, sensory pleasure, and shame (Ekman, 2012), emotions not associated with specific facial expressions. Ekman's work has led to extensive neuroscientific research on the neurobiology of emotion perception, and this research is being conducted more than 40 years after his findings were first reported.

In contrast to the work by Paul Ekman on human facial expressions, Jaak Panksepp has explored emotions through electrical stimulation of discrete subcortical brain structures in the rat. This approach has important methodological advantages over human neuroimaging in that localized electrical stimulation of the brain provides causal evidence for the role of certain subcortical regions in affective experience. Panksepp has employed a different experimental approach to that of Ekman, and his work has led to the identification of a different set of “basic” emotions (Panksepp, 2011) including seeking, rage, fear, lust, care, panic/grief, and play, which he labels as emotional instinctual behaviors. Panksepp employs special nomenclature—full capitalizations of common emotional words (e.g., RAGE, FEAR, etc.)—to distinguish these primary-process emotions as identified using electrical stimulation of discrete subcortical neural loci from their vernacular use in language. Although (some of) these behaviors are not typically thought of as emotions (i.e. SEEKING, CARE, and PLAY), Panksepp argues that these basic emotions provide “tools for living” that make up the “building blocks” for the higher emotions (Panksepp & Watt, 2011). Interestingly, and in contrast to Ekman, he specifically argues that disgust is not a basic emotion; rather, he categorizes disgust, like hunger, as a sensory and homeostatic affect. Panksepp argues that the higher emotional feelings experienced by humans are based on primitive emotional feelings emerging from the “ancient reaches of the mammalian brain, influencing the higher cognitive apparatus” (Panksepp, 2007). On the basis of findings obtained during electrical stimulation, Panksepp (2007) highlights the mesencephalon (or midbrain of the brainstem)—especially the periaqueductal gray—extending through the diencephalon (including the thalamus and hypothalamus) to the orbitofrontal cortex and then to the medial (anterior cingulate, medial frontal cortices) and lateral forebrain areas (including the temporal lobes and insula) as critical regions.

Although different experimental approaches have led to different conclusions over what the specific basic emotions may be, researchers have also drawn entirely different conclusions using the same technique in humans (Lindquist et al., 2012; Vytal & Hamann, 2010). An early meta-analysis of 106 neuroimaging studies using PET or fMRI found evidence for distinctive patterns of activity relating to the basic emotions (Murphy et al., 2003). Fear was associated with activation in the amygdala, disgust with activation in the insula and globus pallidus, and anger with activation in the lateral orbitofrontal cortex. Importantly, these regions are also associated with respective processing deficits when damaged. Extending on these findings, a more recent meta-analysis including 30 new studies also obtained results consistent with basic emotion theory (Vytal & Hamann, 2010). The authors reported that fear, happiness, sadness, anger, and disgust all elicited consistent, characteristic, and discriminable patterns of regional brain activity (Vytal & Hamann, 2010), albeit with somewhat different conclusions to the earlier meta-analysis by Murphy and colleagues. Fear was associated with greater activation in the amygdala and insula, happiness with activation in rostral ACC and right superior temporal gyrus, sadness in middle frontal gyrus and subgenual ACC, anger in inferior frontal gyrus (IFG) and parahippocampal gyrus, and disgust in IFG and anterior insula. It is worth noting here that facial emotion stimuli are the most frequently used stimuli in studies of human emotion and that it is important to distinguish between emotion perception (as is assessed most often in studies using facial emotion) and emotion experience. However, the authors of this meta-analytic study (Vytal & Hamann, 2010) noted that—although preliminary—their results provided evidence to suggest that findings are not unique to studies of facial emotion stimuli.

In direct contrast to these prior studies (Murphy et al., 2003; Vytal & Hamann, 2010), another meta-analysis (Lindquist et al., 2012) on 234 PET or fMRI studies reported that discrete emotion categories are neither consistently nor specifically localized to distinct brain areas. Instead, these authors concluded that their findings provide support for a psychological constructionist model of emotion in which emotions emerge from a more basic set of psychological operations that are not specific to emotion. This model has a number of features; these include core affect underpinned by processing in a host of regions including the amygdala, insula, medial orbitofrontal cortex (mOFC), lateral orbitofrontal cortex (lOFC), ACC, thalamus, hypothalamus, bed nucleus of the stria terminalis, basal forebrain, and the periaqueductal gray. The authors clearly distinguish core affect from the more general term, *affect*, which is often used to mean anything emotional. Although the authors highlight the dimensional constructs of valence and arousal, other dimensional constructs—such as approach and withdrawal (Davidson & Irwin, 1999)—have been proposed. Approach and withdrawal motivations are considered to be fundamental motivational states on which emotional reactions are based and may actually provide a superior explanation for the way some brain regions process emotional stimuli (Barrett & Wager, 2006; Harmon-Jones, 2003).

Systematic reviews using meta-analytic statistical procedures generally provide a more objective review of the literature, allow for generalizations to be made on a body of literature, and avoid low study power. One of the problems associated with individual neuroimaging studies on emotion in humans is the multiple comparisons problem, making it more likely to identify an effect when there is none (otherwise known as a type 1 error). A case in point is a recent fMRI study using a “social perspective-taking task” in a postmortem Atlantic salmon (Bennett & Miller, 2010; Bennett, Baird, Miller, & Wolford, 2011). When statistical analysis did not correct for multiple comparisons, this study observed evidence of activity in the tiny dead salmon’s brain. Although farcical, this study has a serious message: that inadequate control for type 1 error risks drawing conclusions on the basis of random noise, in part highlighting an important role for meta-analysis (Radua & Mataix-Cols, 2012). However, the observation that different meta-analyses have led to contradictory findings and entirely opposite conclusions on a body of literature could leave one feeling rather perplexed. Surely, meta-analyses should aid in resolving the many reported inconsistencies rather than making them more explicit and further contributing to contradictory findings!

There are actually a number of explanations to this conundrum and a number of considerations to bear in mind when reviewing the neuroimaging literature. Hamann (2012) suggests that rather than presenting these different proposals as competing theories, an alternative hybrid view could combine the key advantages of both. A major limitation of the work by Lindquist and colleagues (2012) is the focus on single brain regions rather than on networks of two or more regions. Hamann (2012) argues that once the neural correlates of basic emotions are identified—which could relate to brain connectivity rather than discrete brain regions—these correlates could then be encompassed within the psychological constructionist framework as part of core affect. Indeed, recent preliminary work (Tettamanti et al., 2012) has reported that whereas functional integration of visual cortex and

amygdala underpins the processing of all emotions (elicited using video clips), distinct pathways of neural coupling were identified (in females) for the emotions of fear, disgust, and happiness. The authors noted that these emotions were associated with cortical networks involved in the processing of sensorimotor (for fear), somatosensory (for disgust), and cognitive aspects (happiness) of basic emotions. We now review various influential neuroscientific models relating to the neural circuitry of emotion.

The “Emotional” Circuitry

Regional brain interconnectivity, rather than the activity in specific regions per se, is critical to further understanding the brain basis of emotion. An early model of brain connectivity relating to emotion experience and the cortical control of emotion was proposed by Papez in 1937 a specific circuit of neural structures lying on the medial wall of the brain. These structures included the hypothalamus, anterior thalamus, cingulate, and hippocampus. Two emotional pathways were proposed, including the “stream of thinking” (involving the cingulate cortex) and the “stream of feeling” (hypothalamus). Extending on earlier work by Papez and others, LeDoux (1998) highlighted an important role of the amygdala, proposing two pathways associated with the processing of emotional stimuli, the “low road” (thalamo-amygdala) and “high road” (thalamo-cortico-amygdala). The “low road” or direct pathway reflects a preconscious emotional processing route that is fast acting and allows for rapid responsiveness and survival. This pathway transmits sensory messages from the thalamus to the lateral nucleus of the amygdala, which then elicits the fear response. Information from other areas, including the hippocampus, hypothalamus, and cortex, is integrated in the basal and accessory basal nuclei of the amygdala. The signal is then transmitted to the central nucleus of the amygdala (amygdaloid output nuclei), which projects to anatomical targets that elicit a variety of responses characteristic of the fear response (e.g., tachycardia, increased sweating, panting, startle response, facial expressions of fear, and corticosteroid release). By contrast, the “high road” or indirect pathway facilitates conscious and cognitive “emotional processing” that is slow acting and allows for situational assessment. Overprocessing of stimuli by the subcortical emotional processing pathway and ineffective cortical regulation has provided useful insights to understanding affective disturbance displayed by various psychiatric disorders, including posttraumatic stress disorder and panic disorder. Although this theory has been tremendously influential, it has also been criticized for ignoring the “royal road” (Panksepp & Watt, 2011)—involving the central amygdala, ventrolateral hypothalamus and periaqueductal gray (located around the cerebral aqueduct within the tegmentum of the midbrain)—which governs instinctual actions such as freezing and flight that help animals avoid danger.

This low- versus high-road distinction has also been called into question (Pessoa & Adolphs, 2010) with respect to the processing of affective visual stimuli in humans. The work by LeDoux and others is based on rodent studies that identified the subcortical pathway using auditory fear conditioning paradigms. Fear conditioning is a behavioral paradigm in which the relationship between an environmental stimulus and aversive event is learned (Maren, 2001). The assumption that this same subcortical route exists for visual information processing in humans was questioned (Pessoa & Adolphs, 2010) on the basis of findings indicating that visual processing of emotional stimuli in the subcortical pathway is no faster than in the cortical pathway. For instance, visual response latencies in some frontal sites including the frontal eye fields may be as short as 40–70 ms, highlighting that subcortical visual processing is not discernably faster than cortical processing (Pessoa & Adolphs, 2010). These findings led to the proposal of a “multiple-waves” model (Pessoa & Adolphs, 2010) that highlights that the amygdala and the pulvinar nucleus of the thalamus coordinate the function of cortical networks during evaluation of biological significance in humans. According to this view, the amygdala is part of a core brain circuit that aggregates and distributes information, whereas the pulvinar—which does not exist in the brains of rodents or other small mammals—acts as an important control site for attentional mechanisms.

Brain–Body Interaction and Embodied Cognition

Here, we consider emotion as an embodied cognition, the idea that the body plays a crucial role in emotion, motivation, and cognition (see Price, Peterson, & Harmon-Jones, 2011, for review). Although regional brain connectivity is a necessary development in neuroscientific understanding of the emotions (discussed in the preceding section), current influential neuroscientific theories of emotion (Damasio, 1994; Porges, 1995; 2011; Reimann & Bechara, 2010; Thayer & Lane, 2000; 2009) incorporate brain–body interactions into formal models.

These include the neurovisceral integration model (Thayer & Lane, 2000; 2009; Thayer, Hansen, Saus-Rose, & Johnsen, 2009), the polyvagal theory (Porges, 1995; 2001; 2003; 2007; 2009; 2011), the somatic marker hypothesis (Damasio, 1994; Reimann & Bechara, 2010), and the homeostatic model for awareness (Craig, 2002; 2003; 2005). These complementary models provide mechanisms for better understanding the impact of interventions such as exercise, yoga, and meditation and how they might impact on emotion and mood.

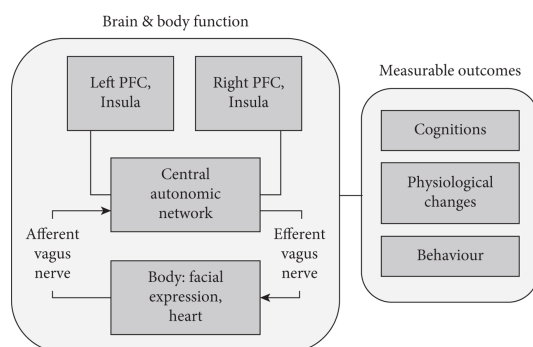
The neurovisceral integration model (Thayer & Lane, 2000; 2009; Thayer et al., 2009) describes a network of brain structures including the PFC, cingulate cortex, insula, amygdala, and brainstem regions in the control of visceral response to stimuli. This *central autonomic network* (CAN) is responsible for the inhibition of medullary cardioacceleratory circuits, for controlling psychophysiological resources during emotion, for goal-directed behavior, and for flexibility to environmental change. The primary output of the CAN is heart rate variability (HRV), mediated primarily by parasympathetic nervous system innervation—vagal inhibition—of the heart. Increased HRV—reflecting increased parasympathetic nervous system function—is associated with trait positive emotionality (Geisler, Vennewald, Kubiak, & Weber, 2010; Oveis et al., 2009). By contrast, decreased HRV—reflecting decreased parasympathetic nervous system function—is associated with depression and anxiety (Kemp, Quintana, Felmingham, Matthews, & Jelinek, 2012a; Kemp, Quintana, Gray, Felmingham, Brown, & Gatt, 2010b). Polyvagal theory (Porges, 2011) is consistent with the neurovisceral integration model, but further emphasizes vagal afferent feedback from the viscera and internal milieu to the nucleus of solitary tract (NST) and cortex, allowing for subsequent regulation of initial emotional responses. This theory also distinguishes between the myelinated and unmyelinated vagus nerves (hence “polyvagal”), such that the myelinated vagus underpins changes in HRV and approach-related behaviors including social engagement, whereas the phylogenetically older unmyelinated vagus—in combination with the sympathetic nervous system—supports the organism during dangerous or life-threatening events. According to this model, social engagement is associated with cortical inhibition of amygdala; activation of the vagus nerve—increasing vagal tone—and connected cranial nerves then allow socially engaging facial expressions to be elicited, leading to positive interactions with the environment. The NST receives vagal afferent feedback from the viscera and internal milieu, and this information is then directed to cortical structures responsible for the top-down regulation of emotion. Increased activation of the vagus nerve—indexed by increased HRV—therefore provides a psychophysiological framework compatible for social engagement facilitating positive emotion. By contrast, social withdrawal is associated with perception of threat underpinned by increased amygdala activity and vagal withdrawal—decreasing vagal tone—triggering fight-or-flight responses leading to negative social interactions with the environment. Again, information relating to the status of the viscera and internal milieu are fed back to the nucleus of solitary tract and the cortex, allowing for subsequent regulation of the emotion response. Decreased activation of the vagus nerve—indexed by decreased HRV—therefore provides the framework compatible for fight-or-flight responses facilitating negative emotion.

The vagus nerve, which has been termed the single most important nerve in the body (Tracey, 2007), not only supports the capacity for social engagement (Porges, 2011) and mental well-being (reviewed in Kemp & Quintana, 2013), but also plays an important role in longer term physical health (reviewed in Kemp & Quintana, 2013). The vagus nerve plays an important regulatory role over a variety of allostatic systems including inflammatory processes, glucose regulation, and hypothalamic-pituitary-adrenal (HPA) function (Thayer, Yamamoto, & Brosschot, 2010). A proper functioning vagus nerve helps to contain acute inflammation and prevent the spread of inflammation to the bloodstream. Intriguingly, increased HRV is not only associated with various indices of psychological well-being including, cheerfulness and calmness (Geisler et al., 2010), trait positive emotionality (Oveis et al., 2009), motivation for social engagement (Porges, 2011), and psychological flexibility (Kashdan & Rottenberg, 2010), but it also appears to be fundamental for resilience and long-term health (Kashdan & Rottenberg, 2010). These observations are also consistent with research findings on the association between positive psychological well-being and cardiovascular health, highlighting a key role for attributes such as mindfulness, optimism, and gratitude in reducing the risk of cardiovascular disease (Boehm & Kubzansky, 2012; DuBois et al., 2012). By contrast, chronic decreases in vagal inhibition—indexed by reductions in HRV—will lead to premature aging, cardiovascular disease, and mortality (Thayer, Yamamoto, & Brosschot, 2010). The process by which vagal activity regulates these allostatic systems relates to the “inflammatory reflex” (Pavlov & Tracey, 2012; Tracey, 2002; 2007): the afferent (sensory) vagus nerve detects cytokines and pathogen-derived products, whereas the efferent (motor) vagus nerve regulates and controls their release.

In addition to parasympathetic (vagal) afferent feedback, afferents from sympathetic and somatic nerves further

contribute to interoception and the homeostatic emotions involving distinct sensations such as pain, temperature and itch in particular (Craig, 2002; 2003; 2005). Although the presence of parasympathetic afferent feedback has long been recognized, the functional anatomy of the lamina I spinothalamocortical system has only been elucidated more recently. This system conveys signals from small-diameter primary afferents that represent the physiological condition of the entire body (the “material me”). It first projects to the spinal cord and brainstem and then generates a direct thalamocortical representation of the state of the body involving the insula and ACC. Consistent with electrophysiological work highlighting a role for prefrontal cortical structures in approach and withdrawal motivation (Harmon-Jones, Gable, & Peterson, 2010), Craig’s homeostatic model for awareness (Craig, 2002; 2005; 2009) links approach (appetitive) behaviors, parasympathetic activity, and affiliative emotions to activity in the left anterior insula and ACC and withdrawal (aversive) behaviors, sympathetic activity, and arousal to activity in the right anterior insula and ACC. Stimulation of left insula cortex produces parasympathetic effects including heart rate slowing and blood pressure suppression, whereas stimulation of right insula produces sympathetic effects including tachycardia and pressor response (increased blood pressure) (Oppenheimer, Gelb, Girvin, & Hachinski, 1992). Research, for example, indicates that although left anterior insula (and ACC) are strongly activated during parasympathetic or enrichment emotions such as romantic love and maternal attachment (Bartels & Zeki, 2004; Leibenluft, Gobbini, Harrison, & Haxby, 2004), right-sided activity is observed during aroused or sympathetic emotions elicited through experimental challenge (see Craig, 2005, for review). We note, however, that directly linking positive emotions to parasympathetic activity and negative emotions to sympathetic activity is somewhat problematic on the basis of findings from psychophysiological research. For instance, emotion images containing threat, violent death, and erotica elicit the strongest emotional arousal and the largest skin conductance responses, thus highlighting a role for sympathetic activation in both defensive and appetitive responses (Bradley, Codispoti, Cuthbert, & Lang, 2001). These findings were argued to reflect a motivational system that is engaged and ready for action.

Finally, the somatic marker hypothesis highlights a key role for the ventromedial PFC in translating the sensory properties of external stimuli into “somatic markers” that reflect their biological relevance and guide subsequent decision-making (Damasio, 1994; Reimann & Bechara, 2010). Based on a body of research inspired by Phineas Gage—a nineteenth-century railroad worker who survived an accident involving serious damage to the prefrontal cortices—patients with damage to the ventromedial PFC display major difficulties in decision making that may have negative consequences, such as poor judgment and financial loss, despite having normal intellect (Reimann & Bechara, 2010). According to this model, the ventromedial PFC indexes changes in heart rate, blood pressure, gut motility, and glandular secretion, which then contribute to decision making and affective experience (Reimann & Bechara, 2010). Visceral responses contribute to the subjective feeling state, which subsequently “marks” potential choices of future behavior as advantageous or disadvantageous.



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Figure 1 . Model of brain and body function with regards to emotion processing highlighting role of hemispheric asymmetry (Davidson, Harmon-Jones), the central autonomic network (Thayer), and inhibition of sympathetic nervous system contribution to the heart (Thayer, Porges, Kemp) via the efferent vagus nerve and afferent feedback. The role of brain and body in emotion is bidirectional, and visceral afferent feedback to the brain makes an important contribution to emotion experience and subsequent social behavior (i.e., “embodied cognition”). Also highlighted are broad categories of measures needed to distinguish between “natural kinds” and “psychological construction” (Lindquist, Barrett).

A simplified model of emotion processing is presented in Figure 1, drawing on current state of the literature and major theories described earlier. The model highlights the role of hemispheric effects in emotion experience (Craig, 2005; Davidson & Irwin, 1999; Harmon-Jones, 2003), the regulatory role of the central autonomic network (Thayer

& Lane, 2009; Thayer et al., 2009), and vagal nerve inhibition over sympathetic nervous system contribution to the heart (Huston & Tracey, 2010; Pavlov & Tracey, 2012; Thayer et al., 2009). An adequately functioning vagal nerve will serve to facilitate positive emotions and social engagement (Porges, 2011), whereas a poorly functioning vagal nerve will lead to negative emotion and, over the longer term, mood and anxiety disorders (Kemp et al., 2012a; Kemp, Quintana, Gray, Felmingham, Brown, & Gatt, 2010b) and poor physical health (Thayer & Brosschot, 2005; Thayer & Lane, 2007; Thayer et al., 2010). The model further highlights an important role of vagal afferent feedback, which makes an important contribution to emotion experience and subsequent social behavior (i.e., “embodied cognition”). Also highlighted are the many observable outcome measures needed to help move affective neuroscience beyond the current debate over whether the brain and body respects the “natural kind” versus the “psychological constructionist” view of emotion (see also Lindquist et al., 2013, for recent commentary on this debate).

Specificity of the Emotions

There is significant interest (and debate) over the ability to discriminate the emotions using a variety of affect detection methods. Although the basic emotions are characterized by specific facial expressions (Ekman & Friesen, 1975), a single set of facial actions can become different emotional expressions in different contexts (Barrett, 2012). For example, the same face posing the same facial actions appears to become a different facial expression when paired with the words “surprise,” “fear,” and “anger” (Barrett, 2012). Despite the many challenges to correctly detecting specific emotions—interested readers are referred to reviews by Calvo and D’Mello (2010) and Fairclough (2009)—we are confident that the reliability and validity of detection will be improved in research that draws on affective computing principles, focuses on multiple objective measures of emotion (see Figure 2), and utilizes stronger manipulations of emotion. Studies on emotion specificity have employed a variety of detection measures ranging from facial expressions to psychophysiological measures and neuroimaging. We now provide a brief review of this literature.

Unlike the disagreement over the neural specificity of different emotions (Lindquist et al., 2012; Vytal & Hamann, 2010) discussed earlier, recent reviews of autonomic nervous system (ANS) activity (Harrison, Kreibig, & Critchley, 2013; Kreibig, 2010) highlight considerable specificity in the presentation of emotion. However, it is important to note that these specific patterns are often only revealed by inspection of data from a broad range of autonomic measures, a key point with regards to emotion detection more generally. This specificity of discrete emotions may be understood in the context of the *component model of somatovisceral response organization* (Stemmler, Heldmann, Pauls, & Scherer, 2001). According to this model, state-driven psychophysiological responses are associated with three components. The first relates to demands by processes not in the service of emotions (e.g., ongoing motor activity); the second relates to the effects of organismic, behavioral, and mental demands determined by a certain context (e.g., motivation to approach vs. withdraw); the third relates to the “emotion signature proper,” characterized by emotion-specific responses. This model therefore allows for considerable overlap of activity associated with emotion responses but also emotion specificity. Emotion-specific features of fear, anger, disgust, sadness, and happiness detected using a variety of techniques are now briefly reviewed.

The emotion of fear is characterized by eyebrows raised and drawn together, wide-open eyes, tense lowered eyelids, and stretched lips (Ekman & Friesen, 1975). It is associated with activation within frontoparietal brain regions (Tettamanti et al., 2012) and a broad pattern of sympathetic activation (Harrison et al., 2013; Kreibig, 2010), allowing for the preparation of adaptive motor responses. Autonomic nervous system function reflects a general activation response and vagal withdrawal (reduced HRV), but may be distinguishable from anger (associated with harassment or personalized recall) by reduction in peripheral vascular resistance (Harrison et al., 2013; Kreibig, 2010), a measure of resistance to flow that must be overcome to push blood through the circulatory system. Fear is also associated with more numerous skin conductance responses and larger electromyographic corrugator activity than is anger (Stemmler et al., 2001), a finding that was interpreted in line with the adrenaline hypothesis of fear (Funkenstein, 1955). By contrast, the emotion of anger is characterized by lowered eyebrows drawn together, tensed lowered eyelids and pressed lips. A body of literature highlights a role for left frontal PFC in approach-related emotions including positive affect (Begley & Davidson, 2012), as well as the emotion of anger (Harmon-Jones et al., 2010). By contrast, the right PFC is implicated in withdrawal-related behaviors (such as fear), although the EEG literature in this regard has been contradictory (Wacker, Chavanon, Leue, & Stemmler, 2008). Contradictory findings highlight the need for better manipulations of affective experience. It is also important to note

that anger may elicit either an anger-mirroring or a reciprocating fear response (Harrison et al., 2013), and that psychophysiological responses will be dependent on the response elicited.

The physiological differentiation between fear and anger in humans has been a topic of great interest for decades (see, e.g., Ax, 1953). Walter Cannon (1929) introduced the concept of the “fight-or-flight” response arguing for similar underlying visceral patterns in the two responses. By contrast, Magda Arnold (1950) highlighted a key role for the sympathetic branch of the ANS in fear and a role for both the sympathetic and parasympathetic branches in anger. Although an interesting proposal in light of an important role of parasympathetic activity in approach-related motivation (Kemp et al., 2012b; Porges, 2011)—an important characteristic of anger—research findings have generally reported no change in HRV (e.g., Rainville, Bechara, Naqvi, & Damasio, 2006), a psychophysiological variable primarily driven by the parasympathetic nervous system. Critically, research has highlighted the importance of context and individual differences in order to understand emotion-specific responses and their discriminability (e.g., Stemmler et al., 2001). For instance, whereas fear is generally associated with an active coping response reflected in sympathetic activation, such as increases in heart rate, imminence of threat may shift responses toward more of an immobilization response and sympathetic inhibition (heart rate decreases). These differential responses to fear-inducing stimuli may be understood in the context of polyvagal theory (Porges, 2011), which distinguishes between immobilization and mobilization responses. Although immobilization is the most phylogenetically primitive behavioral response to threat involving the unmyelinated vagus nerve (associated with fear-related bradycardia), mobilization involves the sympathetic nervous system, which prepares the organism for flight or fight.

The emotion of disgust is characterized by a raised upper lip, wrinkled nose bridge and raised cheeks (Ekman & Friesen, 1975). Interestingly, research indicates that gustatory distaste elicited by unpleasant tastes, core disgust elicited by photographs of contaminants, and moral disgust elicited by unfair treatment in an economic game all evoke activation of the levator labii muscle of the face, which raises the upper lip and wrinkles the nose. Disgust is also associated with activity in somatosensory brain regions and reductions in cardiac output reflecting protective responses (Harrison et al., 2013; Tettamanti et al., 2012). Differential skin conductance responses may depend on whether the emotion is elicited by “core-disgust” inducing stimuli (e.g., pictures of dirty toilets, foul smells) or body-boundary violating stimuli (e.g., mutilation scenes, images of injection) (Harrison et al., 2013). For example, whereas “core-disgust” is associated with unchanged or decreased skin conductance (Harrison et al., 2013; Kreibig, 2010), body-boundary violating disgust is associated with increased skin conductance (Bradley et al., 2001).

The emotion of sadness is characterized by raised inner eyebrows and lowered lip corners (Ekman & Friesen, 1975) contributing to facial features like the “omega melancholicum” and Veraguth’s folds (Greden, Genero, & Price, 1985). It is associated with increased blood flow in ventral regions, including subgenual cingulate and anterior insula, and decreases in neocortical regions, including dorsolateral prefrontal and inferior parietal cortices (Mayberg et al., 1999). Autonomic nervous system responses may be either activated or deactivated (Harrison et al., 2013), which may depend on whether sadness is associated with crying. Crying-related sadness is associated with increased heart rate—but no change in HRV—and increased skin conductance (Gross, Frederickson, & Levenson, 1994), whereas noncrying sadness is associated with a reduction in heart rate, reduced skin conductance, reduced HRV, and increased respiration (Gross et al., 1994; Rottenberg, Wilhelm, Gross, & Gotlib, 2003). We have observed robust reductions in HRV in patients with major depressive disorder (Kemp et al., 2010b), and these findings have implications for long-term well-being and physical health of patients (see Kemp & Quintana, in press, for review).

The emotion of happiness is characterized by tensed lowered eyelids, raised cheeks and raised lip corners (Ekman & Friesen, 1975). Reliable expressions of positive emotion—the Duchenne smile—involve contraction of the orbicularis oculi muscles at the corner of the eyes. By contrast, forced smiles only involve contraction of the zygomaticus major, the muscle that raises the corner of the mouth. Interestingly, the intensity of smiling in photographs when a young adult has been found to predict longevity (Abel & Kruger, 2010): longevity ranged from 72.9 years for individuals with no smiles, 75.0 years for those with partial smiles, to 79.9 years for those with Duchenne smiles. With respects to brain function, happiness is associated with activation in medial prefrontal and temporoparietal cortices, which may reflect the cognitive aspects associated with understanding positive social interactions (Tettamanti et al., 2012). A body of work further highlights a role for the left PFC in positive affect (Engels et al., 2007; Urry et al., 2004; see also Begley & Davidson, 2012) consistent with brain-based models of

approach related motivation (Harmon-Jones, Gable, & Peterson, 2010).

Like the negative emotions, happiness is associated with cardiac activation secondary to vagal withdrawal (Harrison et al., 2013) but may be distinguishable from the negative emotions by peripheral vasodilation (Harrison et al., 2013; dilation of blood vessels leading to lower blood pressure). Whereas vagal withdrawal during the experience of happiness may be somewhat unexpected, it is important to distinguish between happiness as an emotion—a relatively transient event—and positive mood, a relatively longer lasting emotional state. Unlike the emotion of happiness, positive mood is associated with increased HRV (Geisler et al., 2010; Oveis et al., 2009). It is also important to distinguish among the positive emotions. A review of the studies on ANS function, for example, indicates that whereas happiness is associated with decreased HRV, amusement and joy are associated with increases (Kreibig, 2010).

Conclusion

Here, we reviewed the affective neuroscience of emotion focusing on the basic emotions including fear, anger, disgust, happiness, and sadness and the contrasting approach of psychological constructionism. Although there is considerable debate over whether the brain and body “respect” the basic emotion categories, studies have generally focused on single measures and have reported limited success in discriminating the basic emotions (but see Rainville et al., 2006; Tettamanti et al., 2012). We suggest that this debate may soon be resolved in future research that draws on affective computing principles and focuses on a broad range of objective information from the brain and body (e.g., facial expressions, brain electrical activity, sweat response, heart rate, and respiration), as well as better manipulations of affective experiences. The extent to which consistent and specific changes are observable in various physiological systems for emotion inductions across contexts within and between individuals will help to resolve this “hundred-year emotion war” (Lindquist et al., 2013). With developments in technology, more sophisticated modeling, and increasing knowledge about the neuroanatomical and physiological correlates of emotion, the future is bright for a better understanding of the neuroscientific basis of emotion in humans.

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“Emotion” definition for glossary: Emotion is often defined as a multicomponent response to a significant stimulus characterized by brain and bodily arousal and a subjective feeling state that elicits a tendency toward motivated action. Note however, that there may be instances of emotion in which significant stimulus (cf., emotions without obvious causes), subjective feeling state (cf., unconscious emotions) and motivated action (cf., sadness) are not necessary.

“Approach and withdrawal motivation” definition for glossary: Approach and withdrawal motivations are fundamental motivational states on which emotional reactions are based. The approach system controls appetitive and other goal directed behaviors, while the withdrawal system facilitates behavior that removes the individual from sources of aversive stimulation. The left prefrontal cortex plays a key role in approach motivation (including positive affect, social engagement and anger) while the right prefrontal cortex (e.g., fear) plays a key role in withdrawal.

“Natural kinds” definition for glossary: fundamental processes in the brain that exists across species and human cultures; a phenomenon that is discovered, not created by the human mind. In this regard the basic emotions are characterized as “natural kinds,” hardwired into the brain and associated with distinctive patterns of neural activation. Note that different conceptualizations of the basic emotions have been proposed (e.g., Ekman versus Panksepp).

“Psychological constructionism” definition for glossary: this view considers emotions as a construct resulting from more basic building blocks such as core dimensions like approach-withdrawal or valence-arousal. The debate over whether emotions are “natural kinds” versus a “psychological construction” has been likened to the “Hundred Years” War between England and France (see Lindquist, Siegel, Quigley & Barrett, 2013).

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