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The brain basis of emotion: A meta-analytic review

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Abstract

Researchers have wondered how the brain creates emotions since the early days of psychological science. With a surge of studies in affective neuroscience in recent decades, scientists are poised to answer this question. In this article, we present a meta-analytic summary of the human neuroimaging literature on emotion. We compare the locationist approach (i.e., the hypothesis that discrete emotion categories consistently and specifically correspond to distinct brain regions) with the psychological constructionist approach (i.e., the hypothesis that discrete emotion categories are constructed of more general brain networks not specific to those categories) to better understand the brain basis of emotion. We review both locationist and psychological constructionist hypotheses of brain–emotion correspondence and report meta-analytic findings bearing on these hypotheses. Overall, we found little evidence that discrete emotion categories can be consistently and specifically localized to distinct brain regions. Instead, we found evidence that is consistent with a psychological constructionist approach to the mind: a set of interacting brain regions commonly involved in basic psychological operations of both an emotional and non-emotional

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nature are active during emotion experience and perception across a range of discrete emotion categories.

Keywords

Discrete emotion; emotion; emotion experience; emotion perception; meta-analysis; neuroimaging; psychological construction

1. Introduction

William James framed the question of emotion–brain correspondence when he wrote, "...of two things concerning the emotions, one must be true. Either separate and special centres, affected to them alone, are their brain-seat, or else they correspond to processes occurring in the motor and sensory centres already assigned..." (1890, p. 473). In this article, we statistically summarize the last 15 years of neuroimaging research on emotion in an attempt to determine which of these alternatives is correct. We examine the utility of two different models of emotion that have each existed since the beginning of psychology.

2. A locationist account of the brain basis of emotion

A *locationist* account of emotion assumes that the category *emotion* and individual categories such as *anger*, *disgust*, *fear*, *happiness*, *sadness* (and perhaps a few others) are respected by the body and brain (see Barrett 2006a for a discussion). The guiding hypothesis of this natural kind model (Barrett 2006a) or modal model (Barrett et al. 2007d) of emotion is that different emotion categories refer to states with endowed motivational characteristics that drive cognition and behavior. It is assumed that these states are biologically basic and inherited, and cannot be broken down into more basic psychological components (Izard, in press; Ekman & Cordaro, in press; Panksepp & Watt, in press). Despite these common assumptions, there is variability in how different researchers define emotions as natural kinds. Some theorists emphasize the universal characteristics of emotion categories, suggesting that each emotion category (e.g., *anger*) refers to a "family" of states that share a distinctive universal signal (e.g., facial behavior), physiology, antecedent events, subjective experience, and accompanying thoughts and memories (e.g., Ekman & Cordano, in press). In this view, emotions can be shaped by culture and learning, but all humans possess the capacity to experience and perceive the same core set of emotion categories. Other theorists take a developmental approach and argue that all infants are born with a set of "first order emotions" that are evolutionarily given reactions (including feelings, motivations and behaviors) to specific stimuli (e.g., Izard, in press). First order emotions form the core of the more elaborate "emotion schemas" that develop with age and learning and consist of complex combinations of emotions, cognitions, and behaviors. Still other theorists emphasize the evolutionary aspect of emotion categories, and argue that emotions are specific behavioral adaptations that are shared with other mammalian species and passed down through phylogeny (e.g., Panksepp 1998; 2007; Panksepp & Watt, in press). Some models taking an "appraisal" approach to emotion also draw on natural kind assumptions about emotions (cf. Barrett 2006a) by hypothesizing that dedicated cognitive mechanisms automatically make meaning of a stimulus and trigger the corresponding discrete emotion (e.g., Roseman 1984; Scherer et al. 2003). Relatively little work from an appraisal perspective has investigated the brain basis of emotion (see Sander et al. 2003; 2007). Therefore, we do not discuss appraisal models further in this article.

All natural kind models share the assumption that different emotion categories have their roots in distinct mechanisms in the brain and body. The mechanisms underlying discrete emotion categories have been discussed as residing within particular gross anatomical locations (e.g., Calder 2003; Ekman 1999) or as networks (e.g., Izard, in press; Panksepp 1998) in the brain. These models constitute a locationist account of emotion because they hypothesize that all mental states belonging to the same emotion category (e.g., *fear*) are produced by activity that is consistently and specifically associated with an architecturally defined brain locale (see sections 5.1–5.4)[1] or anatomically defined networks of locales that are inherited and shared with other mammalian species (Panksepp 1998; Panksepp & Watt, in press). Not all natural kind models are locationist, however; for example, some models propose that each discrete emotion is triggered by an inherited mechanism (e.g., an "affect program;" Ekman & Cordaro, in press; Tomkins 1962, 1963) that does not necessarily correspond to a particular brain locale but rather to a specific pattern of autonomic nervous system activity. Much of the contemporary research on emotion makes locationist assumptions and in this article we focus on the models that hypothesize single brain regions to be consistently and specifically associated with different emotion categories because they represent the most frequent hypothesis that has been tested in the cognitive neuroscience literature. We discuss specific predictions of the locationist approach in section 5, Testing Hypotheses of Brain–Emotion Correspondence (also see Fig. 1).

3. A psychological constructionist account of the brain basis of emotion

A *psychological constructionist* account of emotion assumes that emotions are psychological events that emerge out of more basic psychological operations that are not specific to emotion. In this view, mental categories such as *anger*, *sadness*, *and fear* are not respected by the brain (nor are *emotion, perception*, or *cognition*, for that matter; Barrett 2009a; Duncan & Barrett 2007; Pessoa 2008). A psychological constructionist approach to emotion is as old as the locationist approach, at least in its nascent form (e.g., Wundt, James and other early psychologists were psychological constructionists; see Gendron & Barrett 2009). Our contemporary psychological constructionist approach shares much in common with cognitive neuroscience approaches arguing that basic psychological operations are common across diverse task domains (Cole & Schneider 2007; Dosenbach et al. 2006; Smith et al. 2009; van Snellenberg & Wager 2009; Wager et al. 2005; Wager & Smith 2003). As in the neural context hypothesis, it assumes that the psychological function of individual brain regions is determined, in part, by the network of brain regions it is firing with (McIntosh 2004). It is also consistent with recent evidence that large-scale networks

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[1] These hypotheses have been inspired, in large part, by behavioral neuroscience research in non-human animals that has carefully mapped the circuitry for behavioral adaptations that occur in response to specific environmental challenges (e.g., freezing, attack, vocalizations). One variant of a locationist view focuses on the circuitry for behavioral adaptations such as freezing, escaping, aggressing, etc. (e.g., LeDoux 2007; Panksepp 1998), and assume that one behavioral adaptation is at the core of each discrete emotion category. This one-to-one correspondence between a behavioral adaptation and a discrete emotion category has been challenged on the basis of existing research showing that mammals such as rats display a variety of behaviors based on what is most effective in a given context, however (for discussion, Barrett 2009a; Barrett et al. 2007a).

intrinsic to the brain interact to produce psychological events (Seeley et al. 2007; Smith et al. 2009; Spreng et al. 2009; see Deco et al. 2011 for a review). In philosophy of mind, it is consistent with both a token identity and a supervenience approach to mind–brain correspondence (Barrett, in press) and the mental mechanisms approach (Bechtel 2008). We discuss the psychological constructionist view in somewhat more detail because it is unfamiliar to many readers.

In our psychological constructionist model, called the "conceptual act model," emotions emerge when people make meaning out of sensory input from the body and from the world using knowledge of prior experiences. Emotions are "situated conceptualizations" (cf. Barsalou 2003) because the emerging meaning is tailored to the immediate environment and prepares the person to respond to sensory input in a way that is tailored to the situation (Barrett 2006b). "Conceptual acts" could also be called "perceptual acts" because they are thought to emerge in consciousness just as visual and auditory percepts do when sensory input is automatically and effortlessly made meaningful using knowledge from prior experience. The idea is that the brain makes an initial prediction about the meaning of the sensory array in context (Bar 2007), and the error between this initial top-down prediction and the sensory activity is quickly minimized (Friston 2010) to produce a unified conscious field.

In psychological construction, all mental states, whether they are experienced as an instance of a discrete emotion category or not, are realized by more basic psychological operations or "ingredients" of the mind. The goal of psychology is to identify these psychological operations as "psychological primitives," or the most basic psychological descriptions that cannot be further reduced to anything else mental (because at that point they would describe biological mechanisms). These basic psychological operations are not functionally specific to any discrete emotion category, or even to the category *emotion* itself. Instead, they are functionally selective for emotion on certain occasions. Because our own model is relatively new, our current model has not identified the most primitive level of psychological description, and it is not yet possible to definitively claim what the most basic psychological operations of the mind are. What we propose is a set of basic domains of psychological function that are a first approximation in the trajectory of a longer research program to identify psychological primitives. These will no doubt be refined as research proceeds in the coming years.

One operation in all psychological constructionist models of emotion is some form of sensory input from the body, such as raw somatic, visceral, vascular, and motor cues (James 1884), arousal (Duffy 1957; Mandler 1975; 1990; Schachter & Singer 1962), or affect (Harlow & Stagner 1932; Hunt 1941; Wundt 1897/1998; now called core affect; Barrett 2006b; Barrett & Bliss-Moreau 2009; Russell 2003; Russell & Barrett 1999). In our psychological constructionist view, we refer to this basic psychological domain as "core affect." In psychology, the word "affect" is used to mean anything that is emotional. Core affect, on the other hand, is a term used to describe the mental representation of bodily changes that are sometimes experienced as feelings of hedonic pleasure and displeasure with some degree of arousal (Barrett & Bliss-Moreau 2009; Russell 2003; Russell & Barrett 1999). Core affect is realized, in part, by visceral control systems that help organisms deal with motivationally salient stimuli in the environment. A functioning peripheral nervous system is not necessary for a person to experience a core affective state (e.g., Critchley et al. 2001) as long as they have some prior experiences to provide them with central nervous system representations of bodily states. However, in healthy individuals, core affect is usually accompanied by somatovisceral, kinesthetic, proprioceptive, and neurochemical fluctuations that take place within the core of the body and are represented in the brain. Changes in core affect are a homeostatic barometer – the body's way of representing whether objects in the environment are valuable or not in a given context. The concept of core affect shares much in common with the idea that bodily cues constitute a core ingredient in mental life (e.g., the idea that being embodied is essential to consciousness; Craig 2009; Damasio 1999; the idea that feelings are a common currency for valuation of objects in the world; Cabanac 2002). We assume that core affect is not psychologically meaningful unless it is attached to an object; it is made meaningful via a second basic psychological operation, which we describe next.

All psychological constructionist models include a second basic psychological operation by which internal sensory cues or their associated affective feelings are automatically and effortlessly made meaningful (i.e., experienced as related to or caused by an event or object, usually in the external surroundings). Candidates for this second psychological operation include ideas (Wundt 1897), social affiliation (Schachter & Singer 1962), attribution (Russell 2003), or, as we propose in our model, categorization as situated conceptualization (Barrett 2006b). The process of “conceptualization” (and the other operations that support it, such as executive attention) links perceptions of sensory input from the world with input from the body to create a meaningful psychological moment. In our hypothesis, people automatically make meaning of their core affective state by engaging in a situated conceptualization that links it to an object or event. Conceptualization is the process by which stored representations of prior experiences (i.e., memories, knowledge) are used to make meaning out of sensations in the moment (Wilson-Mendenhall et al. 2011). A person can make the situated conceptualization that core affect is a physical symptom (e.g., a racing heart), a simple feeling (e.g., feeling tired or wound up), or an instance of a discrete emotion category (e.g., *anger* vs *fear*). And at other times, core affect is perceived as part of an object itself rather than one's reaction to it. For example, a food is delicious or distasteful, a painting is beautiful or garish, or a person is warm or cold. Because we hypothesize that people make meaning out of their core affective states in context; experiencing them as a part of an emotion, perception, belief, or judgment; a psychological constructionist account does not simply reduce the category of *emotion* to positive or negative affect (as is often claimed in summaries of “dimensional models of emotion;” e.g. Fontaine et al. 2007; Keltner et al. 2003). Conceptualization can be said to produce cognitive appraisals realizing emotion (Barrett et al. 2007c), where such appraisals are descriptions of the features or properties of emotional experience (Clore & Ortony 2008). In many appraisal models, the assumption is that the brain contains a series of specific cognitive appraisal mechanisms (e.g., there is a specific mechanism to appraise the novelty of an object, or whether one's goals are blocked) that when configured into a particular pattern, trigger discrete emotions. In our model, we do not propose any new or unique mental processes that cause emotion; instead, we propose a mechanism (categorization) that has been well documented in the psychological and cognitive neuroscience literature. Categorization (or conceptualization) is a fundamental process in the human brain that functions like a chisel, leading people to attend to certain features in a sensory array and to ignore others. Only some of the wavelengths of light striking our retinas are transformed into seen objects, only some of the changes in air pressure registered in our ears are heard as words or music, and only some bodily changes are experienced as emotion. To categorize something is to render it meaningful. It then becomes possible to make reasonable inferences about that thing, to predict what to do with it, and to communicate our experience of it to others. There are ongoing debates about how categorization works, but the fact that it works is not in question.

In our model, categorization in the form of situated conceptualization is realized in a set of brain regions that reconstitutes prior experiences for use in the present. This set of brain regions has also been called the "episodic memory network" (e.g., Vincent et al. 2006) or the "default network" (e.g., Raichle et al. 2001) and is active when people recall the past (e.g., Buckner & Carroll 2007; Schacter et al. 2007; see McDermott et al. 2009 for a meta-analysis), imagine the future (e.g., Addis et al. 2007; see Hassabis & Maguire 2009; Moulton & Kosslyn 2009; Schacter et al. 2007), make context-sensitive predictions about others' thoughts and feelings (e.g., as in theory of mind; Saxe & Kanwisher 2003; see Mitchell 2009), or make meaning of exteroceptive sensations (e.g., context-sensitive visual perception; Bar et al. 2006; see Bar 2009). In emotion, we hypothesize that this psychological operation makes a prediction about what caused core affective changes within one's own body or what caused the affective cues (e.g., facial actions, body postures, or vocal acoustics) in another person, and this prediction occurs in a context-sensitive way (with the result that core affect in context is categorized as an instance of *anger*, *disgust*, or *fear*; Barrett 2006b; 2009b; e.g., Barrett & Kensinger 2010; Lindquist & Barrett 2008; Wilson-Mendenhall et al., in press). When making meaning out of core affect, conceptualization draws on prior experiences and perceptions of emotion to realize the emotional gestalts that make up part of what Edelman calls "the remembered present" (cf. Edelman 1989; see Barrett et al. 2007c; Barrett 2009b).

Our model proposes two additional operations that are important to the psychological construction of emotion. We hypothesize that emotion words that anchor emotion categories work hand in hand with conceptualization (Barrett 2006b; Barrett et al. 2007b). Emotion words are essential to our model because we assume that the instances of any emotion category (e.g., *anger*) that are created from affective feelings do not have strong statistical regularities in the real world or firm natural category boundaries (for a discussion of the empirical evidence, see Barrett 2006a; 2009; Barrett et al. 2007a). In our view, emotion categories are abstract categories that are socially constructed (Barrett 2009a). As with all abstract categories, in the absence of strong perceptual statistical regularities within a category, humans use words as the glue that holds the category together (Barsalou & Weimer-Hastings 2005). In fact, even infants routinely use the phonological form of words to make conceptual inferences about novel objects that share little perceptual similarity (Dewar & Xu 2009; Ferry et al. 2010; Xu 2002) and we believe that adults do the same thing. Because words are in part represented via situated simulations of prior experiences (e.g., Simmons et al. 2008), we expect emotion words to work together with conceptualization when perceivers make meaning of core affective states.

Executive attention is the fourth operation that is particular to our psychological constructionist approach (Barrett 2009a; Barrett et al. 2004). Executive attention helps direct the combination of other psychological operations to produce an emotional gestalt. At any point in time, the brain is processing information from the body (core affect), information from outside the body (exteroceptive sensory information), and representations of prior experiences (conceptualizations). For example, many different representations of the past might become active to make meaning out of a core affective state. We hypothesize that executive attention helps determine which representations are utilized to make meaning out of that state, and which are suppressed (c.f. Barrett 2009b; see Barrett et al. 2004, for a discussion). Executive attention can also control which exteroceptive sensory representations are favored for additional processing, or if core affect is consciously represented in awareness. Importantly, executive attention need not be volitional or effortful and can operate well before subjective experience is generated (Barrett et al. 2004). We acknowledge that additional operations are probably important to the construction of emotion and will be incorporated into our model as research accrues.

In the past, most researchers who found brain correlates of emotion merely assumed that their results were consistent with a locationist approach (e.g., the basic emotion approach) because these were the only models to map psychological states to a biological level of analysis in a way that was linked to evolution. Constructionist hypotheses (which where typically social, rather than psychological) were restricted to the psychological level in a manner divorced from evolution. But this is an accident of history. In fact, there are very clear brain hypotheses that develop from a psychological constructionist view (Barrett 2006b), and our psychological constructionist approach is the first that attempts to map basic psychological operations to brain networks that comprise instances of a psychological category such as *emotion*, or to the subordinate categories of *anger*, *sadness, fear, disgust*, and *happiness* (see also Barrett 2006a, b; 2009a, b; Barrett et al. 2007a; 2007c; Kober et al. 2008). Our hypothesized psychological operations, as they currently stand, are associated with assemblies of neurons within distributed networks (rather than a one-to-one mapping of ingredient to network). We hypothesize that these networks combine and constrain one another like ingredients in a recipe, influencing and shaping one another in real time according to the principles of constraint satisfaction (Barrett et al. 2007d). With more research, it will be possible to identify the distributed brain networks that are associated with the most basic psychological operations of the mind.

Together, the functional networks that instantiate basic psychological operations during emotion experiences and perceptions form the “neural reference space for discrete emotion.” According to Gerald Edelman (1989), a “neural reference space” is made up of the neurons that are probabilistically involved in realizing a class of mental events (such as *anger*, or even *emotion*).[2] The functions of distinct brain areas within the neural reference space are best understood within the context of the other brain areas to which they are connected (either anatomically or because of the timing and coordination of neural activity) and in terms of the basic psychological operations they are functionally selective for in a given instance. Unlike a locationist approach, which hypothesizes that a single brain region will be consistently and specifically activated across instances of a single emotion category, a psychological constructionist approach hypothesizes that the same brain areas will be consistently activated across the instances from a range of emotion categories (and although it is beyond the scope of this article, even in non-emotional states), meaning that that brain region is not specific to any emotion category (or even to *emotion* per se). We focus on the brain regions that we believe are hubs in the networks corresponding to basic psychological operations and discuss specific predictions in section 5, Testing Hypotheses of Brain–Emotion Correspondence (also see Fig. 2).

4. Meta-analysis of neuroimaging studies on emotion

In this article, we report a meta-analysis of neuroimaging studies on emotion to assess whether the data are more consistent with a locationist or a psychological constructionist account of emotion. In our meta-analysis, strong evidence for a locationist account would be found if instances of an emotion category (e.g., *fear*) are *consistently* and *specifically* associated with increased activity in a brain region (or a set of regions within an anatomically inspired network) across published neuroimaging studies. *Consistency* refers to the fact that a brain region shows increased activity for every instance of an emotion category (e.g., the amygdala shows increased activity each time a person experiences an instance of the category *fear*). *Specificity* refers to the fact that a given brain region is active for instances of one (and only one) emotion category (e.g., the amygdala does not show increased activity when a person is experiencing an instance of *anger, disgust, happiness*, or *sadness*). Support for a psychological constructionist view, in contrast, would be found if the same brain region(s) were involved in realizing instances of several emotion categories – and, furthermore, if the brain region(s) are more generally important to realizing a basic psychological operation (e.g., core affect, conceptualization, language, or executive attention). From this perspective, we would not expect instances of any emotion category to be specifically related to increased activation in any single brain region or set of regions. A brain region might be functionally selective for a given emotion category in a given instance, however, because it helps realize a more basic operation that contributes to the emergent state.

In 2005, we began our meta-analytic project to probe the brain basis of emotion. We have since published one chapter (Wager et al. 2008) and two papers (Barrett et al. 2007c; Kober et al. 2008) reporting our findings for neuroimaging studies of discrete emotion and affect, between 1990 and 2005. Supporting a psychological constructionist approach to emotion, we found that the neural reference space for emotion and affect could be inductively parsed into six distributed functional groups of brain regions (i.e., regions consistently co-activated across studies) using a series of multidimensional scaling and cluster analyses (Kober et al.

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[2] For example, because the neurons within the amygdala are part of the neural reference space for discrete emotion, we can say with some certainly that the amygdala is likely to have increased activation when a person is experiencing or perceiving any emotion. This does not mean that the amygdala is necessary to each and every instance of emotion or even that it is specific to emotion, however. These ideas distinguish our approach from locationist accounts that assume that neurons within a given brain area (e.g., the amygdala) are consistently and specifically linked to a particular category of mental state (e.g., “fear”).

2008). See Fig. 3. These functional groups can be mapped to the hypothesized psychological operations that we derived from behavioral data (e.g., Barrett 2006).

4.1. Analysis strategy

In the present article, we expanded upon our initial meta-analytic efforts to directly compare the locationist versus the psychological constructionist approach for neuroimaging studies of discrete emotion. A detailed description of our meta-analytic methods and Fig. S1 are included in the supplementary materials (http://www.journals.cambridge.org/bbs2011002). In comparing these hypotheses, we are comparing a hypothesis with very specific empirical requirements (i.e., evidence for consistency and specificity in brain–emotion correspondence) to a hypothesis with more flexible empirical requirements (i.e., evidence of multiple operations across multiple categories). Given the popularity of locationist models of emotion, we made analysis choices that favored a clear and unbiased test of the locationist approach, even though it disadvantaged us in testing the full scope and power of the psychological constructionist approach. After updating our database to include papers from 2006 and 2007, we exclusively sampled studies that focused on discrete emotion experiences or perceptions to increase the likelihood that we would find consistent and specific brain localizations corresponding to these categories, should they exist (see Tables S1 and S2 in supplementary materials for details on the inclusion criteria and database http://www.journals.cambridge.org/bbs2011002). We also conducted a number of statistical analyses with the potential to yield evidence in favor of a locationist account (outlined in the next section).

4.1.1. The neural reference space for discrete emotion—We began by estimating the neural reference space for discrete emotion. This space refers to the brain regions that show a consistent increase in activation for the experience or perception of instances of *anger*, *sadness*, *fear*, *disgust*, and *happiness*. A brain region might appear in this space because its activation consistently increases in studies of one discrete emotion categories but not others, some categories but not others, or all categories of emotion. Alternatively, a brain region could appear in this space even when it does not consistently have increased activation during any discrete emotion category per se, but because it has consistent increases during instances of the entire category *emotion* (e.g., the brain region shows consistent increases in activation in some but not all studies of *anger* experience, *anger* perception, *fear* experience, *fear* perception, and so forth, so that the region is consistently activated across the category *emotion*, but is not specific to any discrete emotion category). Our derived neural reference space for discrete emotion (Fig. 4; Table S3 in supplementary materials, which can be viewed at http://www.journals.cambridge.org/bbs2011002) closely resembles that reported in Kober et al. (2008), even when limiting our analysis to studies of discrete emotion and including papers from 2006–2007. Next, we examined whether any emotion categories were more likely to be associated with increased activity in certain brain areas than in others.

4.1.2. Density analyses—Within the neural reference space, we first searched over the brain for voxels with more consistent activation (within 10 mm) for instances of one emotion category than all others (e.g., for voxels that reached family-wise error-rate corrected significance in the comparison [*fear* perception vs perception of other categories]). This analysis yielded a series of statistical maps reflecting whether each voxel was more frequently activated in studies of each emotion category versus the average of the others, accounting for the different numbers of studies in different categories and the base-rate of background activation across the brain for each emotion category. These analyses are standard for neuroimaging meta-analysis (see Wager et al. 2007) and are described in detail in the supplementary materials. The density analyses speak to whether increases in a brain region are consistently associated with the experience or perception of instances of an emotion category. This provides one kind of information about the consistency and specificity of brain activity for particular emotion categories by considering the activity in each region, for each emotion type, *relative to* background activation levels across the brain.

4.1.3 χ^2 analyses—We next probed the voxels identified in the density analysis further by asking whether there was any *absolute* difference in the proportion of contrasts activating near those voxels (within 10 mm) for each emotion category versus the others. This was accomplished using χ^2 analyses on the contingency table consisting of counts of study contrasts showing activation in or around these voxels versus study contrasts without such activations for the target emotion category versus other categories. This analysis yielded a series of statistical maps reflecting whether each voxel was more frequently activated in studies of each emotion category versus the average of the others, irrespective of activations elsewhere in the brain.

Both density and χ^2analyses speak to whether increased activations in a set of voxels that are consistentlyassociated with the experience or perception of instances of an emotion category are also functionally selective[3] for that emotion category. A region that is functionally selective for instances of an emotion category would show voxels that are significant in both the density analysis and χ^2 analysis. Functional specificity exists if voxels activated selectively for instances of one emotion category also never show increased activity during instances of any other emotion categories. We did not find evidence for functional specificity with respect to any emotion category in our analyses (i.e., every region that was activated for one emotion category was activated for at least one other category). Therefore, our findings only speak to functional selectivity.

4.1.3. Logistic regressions—Finally, in a third set of analyses we used a series of stepwise logistic regressions to ask which emotion categories and experimental methods predicted increased activity in regions of interest. We present the odds ratios for these regressions (in Table S6) or the percent increase in odds that a variable predicted increased activity in a brain area or predicted no increase in a brain area (in Fig. 5) [4]. The logistic regressions speak to both consistency and specificity of increased brain activation.

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[3] Here we use the term "functionally selective" to mean that a brain area can have some preference for certain mental states, even if it is not specific to that mental state. Functional selectivity might occur because a brain area supports a more basic psychological operation that helps to construct a certain mental state (e.g., the amygdala supports detection of salient exteroceptive sensations and is functionally selective for instances of *fear*). Functional selectivity does not refer to specificity, however. A brain area might be functionally selective for one mental state or even one basic psychological operation in one instance and another state or operation in another instance. Functional selectivity is distinct from the concept of "selective influence" (cf. Sternberg 2001), where a brain area being involved in one mental state (e.g., an instance of *fear*) but not another (e.g., an instance of *anger*) is taken as evidence of modularity.

Consistency is observed when any variable significantly predicted increased activity in a given brain area. Specificity is observed when one variable significantly predicted increased activity in a given brain area but all others significantly predicted no increase in activity. If a variable was not a significant predictor, then it is sometimes associated with increased activity, and is sometimes not.

5. Testing hypotheses of brain–emotion correspondence

5.1. The amygdala

According to a locationist hypothesis, the amygdala (Fig. 1, yellow) is either the brain locus of *fear* or is the most important hub in a *fear* circuit. This amygdala-*fear* hypothesis was most clearly popularized by behavioral neuroscience work showing that the amygdala (in particular, the central nucleus) supports the cardiovascular changes that occur when rats freeze or startle in response to tones previously paired with shock (called "fear learning;" LeDoux et al. 1983; 1985; 1990; for reviews see Fanselow & Poulous 2005; Fendt & Fanselow 1999; LeDoux 2007; Öhman 2009; and "fear potentiated startle;" Davis 1992; Hitchcock & Davis 1986; 1987; see Davis et al. 2008; Fendt & Fanselow 1999). Electrical stimulation of the amygdala elicits defensive behavior in rats (e.g., retreat; Maskati & Zbrozyna 1989) and enhances startle to acoustic stimuli (Rosen & Davis 1988). The amygdala-*fear* hypothesis was further strengthened by evidence that humans show increased amygdala activity to neutral tones that have been previously paired with noxious noise blasts (i.e., "fear learning;" LaBar et al. 1998). Individuals with amygdala lesions (LaBar et al. 1995) or atrophy (Bechara et al. 1995) show impaired skin conductance responses during "fear learning" and have difficulty perceiving instances of *fear* in voices (Brierley et al. 2004; Scott et al. 1997, see Adolphs & Tranel 1999; Anderson & Phelps 1998), bodies (Sprengelmeyer et al. 1999; see Atkinson et al. 2007), and startled faces with wide eyes (e.g., Adolphs et al. 1994; 1995; 1999; see Adolphs et al. 2005 and Tsuchiya et al. 2009). An individual with bilateral amygdala lesions failed to report fearful experiences when placed in close contact with snakes, spiders, or when startled (Feinstein et al. in press; see Anderson & Phelps 2002). Finally, the amygdala is implicated in psychopathology involving the experience of anxiety in humans (for a review see Damsa et al. 2009; for a meta-analytic review, see Etkin & Wager 2007).

According to a psychological constructionist view, the amygdala is part of the distributed network that helps to realize core affect (Fig. 2, panel D, bright pink) because it is involved in signaling whether exteroceptive sensory information is motivationally salient (for similar views see Adolphs 2008; 2009; Duncan & Barrett 2007; Pessoa 2010; Pessoa & Adolphs 2010; Sander et al. 2003; Whalen 1998; 2007). The amygdala is most likely to be active when the rest of the brain cannot easily predict what sensations mean, what to do about them, or what value they hold in that context. Salient objects or events influence an organism's body state in a way that can be experienced as core affective feelings (Barrett &

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[4] For example, given that there is an increase in activation in the amygdala, the probability that a person is experiencing fear might be 0.7. The probability that he or she is experiencing another emotion (e.g., anger, disgust, happiness or sadness) is 1 0.7=0.3. The odds ratio = 0.7/0.3=2.33. This means that given increased amygdala activation, the odds are 2.33 to 1 that the person is experiencing fear. In this case, the experience of fear is 113% more likely to predict increased activation in the amygdala than any other emotion state.

Bliss-Moreau 2009). They can also cause the amygdala to signal to other parts of the brain to sustain processing so that uncertainty about the stimulus can be resolved (Whalen 2007). As a result, affect can be considered a source of attention in the brain (Barrett & Bar 2009; Duncan & Barrett 2007; Pessoa 2008; 2010; Vuillumier 2005; Vuilleumier & Driver 2007).

From a psychological constructionist point of view, *fear*-inducing stimuli might fall into the class of uncertain and therefore salient stimuli, but the amygdala is not specific to the category *fear*. Consistent with this view, the amygdala is routinely implicated in orienting responses to motivationally relevant stimuli (Holland & Gallagher 1999). Novel stimuli (e.g., Blackford et al. 2010; Breiter et al. 1996; Moriguchi et al. 2010; Schwartz et al. 2003; Weierich et al. 2010; Wilson & Rolls 1993; Wright et al. 2003;.2006; 2008), uncertain stimuli (e.g., Herry et al. 2007), and unusual stimuli (e.g., Blackford et al. 2010) robustly activate the amygdala and produce cardiovascular responses associated with affective changes (Mendes et al. 2007). Amygdala lesions disrupt normal responses to novelty and uncertainty in mammals (e.g. Bliss-Moreau et al. 2010; Burns et al. 1996; Mason et al. 2006; Missilin & Ropartz 1981; Nachman & Ashe 1974; for reviews, see Knight and Grabowecky 1999; Petrides 2007). Individuals with amygdala lesions do not automatically allocate attention to aversive stimuli (Anderson & Phelps 2001) and socially relevant stimuli (Kennedy & Adolphs 2010), as do individuals with intact amygdalae. Amygdala responses habituate rapidly (Breiter et al. 1996; Büchel et al. 1999; Fischer et al. 2003; Whalen et al. 2004; Wright et al. 2001), suggesting that the amygdala is involved in attention to salient stimuli, but calling into question the idea that the amygdala is necessary to *fear* per se (for a similar point, see Adolphs 2008; 2010; Pessoa & Adolphs 2010; Todd & Anderson 2009; Whalen 2007).[5]

The amygdala's role in detecting motivationally salient stimuli would also explain why increased amygdala activity is observed in instances that do not involve the experience of *fear*, such as when stimuli are experienced as subjectively arousing (e.g., Bradley et al. 2001; Weierich et al. 2010), intense (e.g., Bach et al. 2008), emotionally “impactful” (e.g., Ewbank et al. 2009), or valuable (Jenison et al. 2011). Moreover, not all instances of *fear* are accompanied by increased amygdala activity (for a review, see Suvak & Barrett, 2011). For example, some behaviors that rats perform in dangerous contexts are not amygdala-dependent (e.g., avoiding the location of a threat; Vazdarjanova & McGaugh 1998; “defensive treading,” where bedding is kicked in the direction of the threat; Kopchia et al. 1992). In humans, threatening contexts devoid of salient visual stimuli (e.g., preparing to give a speech in front of an audience), actually produce deactivatations in the amygdala

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[5] These findings might explain the amgydala's role in “fear learning” without assuming that the amygdala is specific to fear. In “fear learning,” for example, amygdala activity reflects orienting responses that occur when an organism learns to associate a neutral stimulus with an already salient stimulus. The amygdala contributes to the production of the skin conductance responses (SCRs) (Laine et al. 2009) used to index “fear learning.” Amygdala responses are associated with SCRs that occur immediately following the onset of a conditioned stimulus, suggesting that the amygdala is particularly involved in attention during learning but perhaps not the formation of associations (Cheng et al. 2007; also see Blakeslee 1979 and Spinks et al. 1985 for evidence that SCRs covary with changes in attention). This orienting account would also explain why amygdala activity is observed when animals learn to associate neutral stimuli with rewarding outcomes (e.g., Paton et al. 2006; for a review see Murray 2007), why amygdala activity corresponds to evaluative goals in the presence of both positive and negative stimuli (e.g., Cunningham et al. 2008; Paton et al. 2006), and why stimulation of the amygdala facilitates orienting responses such as startle (Rosen & Davis 1988). Together, these findings make it clear why the amygdala is so ubiquitously involved in mammalian social behavior (i.e., male and female sexual behavior, maternal behavior, aggression; see Newman 1999).

(Wager et al. 2009a; b). Moreover, electrical stimulation to the amygdala produces a range of experiences in humans, calling into question the idea that the amygdala is specifically linked to instances of *fear* (Bancaud et al. 1994; Gloor 1990; Halgren et al. 1978).

Our meta-analytic findings were inconsistent with a locationist hypothesis of amygdala function but were more consistent with the psychological constructionist hypothesis. Our density analyses revealed that as compared to other brain regions, voxels within both amygdalae had more consistent increases in activation during instances of *fear* perception than during the perception of any other emotion category (Table 1). These voxels were not functionally specific for instances of perceiving *fear*, however. An insignificant χ^2 analysis revealed that the voxels with consistent increases in activation during instances of *fear* perception were equally likely to have increased activity during instances of other emotion categories (see Fig. 6 for the proportion of study contrasts in the database for each emotion category that are associated with increased activity in right amygdala; see Fig. S2 for left amygdala). Furthermore, instances of *fear* experience did not show a consistent increase in activation in either amygdala when compared to what would be expected by chance in other regions of the brain. Yet, as compared to other brain regions, voxels within bilateral amygdala had more consistent increases in activation during instances of *disgust* experience than during the experience of other emotion categories (Table 1). A χ^2 analysis revealed that these voxels were functionally selective for of the experience of *disgust*, as there was more likely to be increased activity in those voxels during instances of *disgust experience* than during the experience of *anger*, *fear*, *happiness* or *sadness* (Table 2). Those voxels were not functionally specific to instances of *disgust* experience, however (Fig. 6; Fig. S2). Finally, as compared to other brain regions, a voxel in the left amygdala had more consistent increases in activation during instances of *sadness* perception than during the perception of other emotion categories (Table 1). An insignificant χ^2 analysis revealed that this voxel was not functionally selective for instances of *sadness*, however.

Our logistic regressions confirmed and expanded upon our density and χ^2 findings. There was more likely to be increased activity in the left amygdala when participants were perceiving instances of *fear* or experiencing instances of *disgust* than when perceiving or experiencing any other emotion categories (Fig. 5; Table S6). These findings are consistent with the psychological constructionist hypothesis that the amygdala responds to salient perceptual stimuli because contrasts in our database that assessed the perception of *fear* and experience of *disgust* tended to use visual stimuli that are novel or unfamiliar to participants.[6] Findings for the right amygdala also supported a psychological constructionist view. Increases in activity in the right amygdala were likely when participants were experiencing or perceiving instances of any highly arousing emotion category (i.e., *anger*, *disgust*, *fear*) (Fig. 5; Table S6). There was likely to be no increase in activity in the left amygdala when participants were focusing on their internal state (i.e., when emotion experience was induced via recall of a personal event and mental imagery; Fig. 5; Table S6). This finding replicates

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[6] More than 90% (53/57) of study contrasts assessing *fear* perception in our database used startled faces that are unfamiliar to college students (who are typically participants in neuroimaging studies of healthy samples) (Whalen et al. 2001) and highly arousing (e.g., Russell & Bullock 1986). Approximately 35% (15/43) of study contrasts assessing the experience of *disgust* presented participants with images that were novel (i.e., infrequently experienced in the industrialized world) and highly arousing (i.e., containing contamination, mutilated body parts, maggots, or something similar).

prior meta-analytic evidence (Costafreda et al. 2008) and is consistent with our hypothesis that the amygdala responds preferentially to salient exteroceptive (vs. interoceptive) sensations.

5.2. The anterior insula

Locationist accounts hypothesize that the anterior insula (Fig. 1, green) is the brain basis of *disgust* (e.g., Jabbi et al. 2008; Wicker et al. 2003; see Calder et al. 2001; Calder 2003 for reviews) based on the belief that *disgust* evolved from a primitive food rejection reflex (Rozin et al. 2000) or bodily aversion to disease-threat (e.g., Curtis et al. 2004). Individuals with damage to the anterior insula and basal ganglia have difficulty perceiving instances of *disgust* in facial and vocal caricatures (Adolphs et al. 2003; Calder et al. 2000). They also report experiencing less *disgust* in response to scenarios about body products, envelope violation, and animals that typically evoke disgust in people with intact insulas (Calder et al. 2000). Individuals with neurodegenerative diseases affecting the insula and basal ganglia (such as Huntington's and Parkinson's disease) also show diminished experiences of *disgust* to foul smelling odors (Mitchell et al. 2005) and have difficulty perceiving instances of *disgust* in the faces of others (e.g., Kipps et al. 2007; Sprenglemeyer et al. 1996; 1998; Suzuki et al. 2006; see Calder et al. 2001; Sprengelmeyer 2007 for reviews; although the specificity of these findings remains in question, e.g., Calder et al. 2010; Milders et al. 2003). Patients who received electrical stimulation to the anterior insula reported visceral sensations consistent with (but not specific to) the experience of *disgust* (e.g., sensations in the stomach or throat, smelling or tasting something bad, naseau; Penfield & Faulk 1955).

In a psychological constructionist hypothesis, the anterior insula plays a key role in representing core affective feelings in awareness (Fig. 2, panel D, dark pink). The anterior insula is thought to be involved in the awareness of bodily sensations (Craig 2002) and affective feelings (Craig 2009). Sometimes sensations from the body are experienced as physical symptoms, but more often they are experienced as states that have some hedonic tone and level of arousal. Sometimes those affective feelings are experienced as emotion. To the extent that brain states corresponding to instances of *disgust* represent a stimulus's consequence for the body, then the anterior insula will show increased activation. Indeed, a key ingredient in the mental states labeled “disgust” is likely a representation of how an object will affect the viscera. In support of a psychological constructionist view, anterior insula activation is observed in a number of tasks that involve awareness of body states, but not *disgust* per se. The anterior insula shows increased activation during awareness of body movement (e.g., Tsakiris et al. 2007), gastric distention (e.g., Wang et al. 2008), and orgasm (e.g., Ortigue et al. 2007). Electrical stimulation of the insula produces sensations consistent with the category *disgust*, but it also produces a range of other visceral sensations including feelings of movement, twitching, warmth and tingling in the lips, tongue, teeth, arms, hands, and fingers (Penfield & Faulk 1955). Dorsal anterior insula is also a hub in a large-scale network involved in what has been called a ventral attention system (Corbetta & Shulman 2002, Corbetta et al. 2008) that guides attention allocation and orienting (e.g., Eckert et al. 2009). These findings again point to the idea that body-based sensory signals constitute a source of attention in the brain.

Our meta-analytic findings were inconsistent with the locationist account that the anterior insula is the brain seat of *disgust* but were more consistent with the psychological constructionist account that insula activity is correlated with interoception and the awareness of affective feelings. Our density analyses revealed that as compared to other brain regions, voxels within the right anterior insula had more consistent increases in activation during instances of *disgust* perception than during the perception of any other emotion category (Table 1). Our χ^2 analysis revealed that only four of the voxels identified in the density analysis showed functional selectivity for instances of *disgust* perception (Table 2), however, and increased activity in the right insula was not specific to instances of *disgust* perception (Fig. 6). Our logistic regression findings for the right anterior insula were consistent with the psychological constructionist hypothesis that the insula supports representation of core affective feelings. Increased activity in the right anterior insula was likely when participants were explicitly evaluating their feelings and representing them in awareness (Fig. 5, Table S6). Instances of *disgust* perception might consistently involve increased activation in the insula because people are more likely to simulate visceral states (such as those associated with the gut and food rejection) when perceiving facial behaviors characterized by a wrinkled nose and curled lip (i.e., oral revulsion; Angyal 1941 see Rozin et al. 2008; e.g., von dem Hagen et al. 2009).

As compared to other brain regions, a greater spatial extent of voxels within the left anterior insula had consistent increases in activation during instances of *disgust* experience than during the experience of any other emotion category (Table 1). As compared to other brain regions, two voxels in the left anterior insula also had more consistent increases in activation during instances of *anger* experience than during the experience of any other emotion (Table 1; only one voxel showed functional selectivity, see Table 2). Our logistic regressions replicated this general finding. Increased activity in the left anterior insula was more likely when participants were experiencing an instance of *anger* than when they were experiencing any other emotion category (Fig. 5; Table S6). These findings, along with subsequent findings (see 5.3 The orbitofrontal cortex, 5.6 Anterior temporal lobe and ventrolateral prefrontal cortex, and 5.7 Dorsolateral prefrontal cortex) suggest that instances of *anger* are associated with increased activity in a broad set of areas in the left frontal and temporal lobes.

5.3. The orbitofrontal cortex

Locationist accounts link the orbitofrontal cortex (OFC) to *anger* (Fig. 1, rust), although the OFC is a large structure and has admittedly been linked to many other psychological phenomena. Primary support for the OFC-*anger* hypothesis derives from prior meta-analytic reviews of the neuroimaging literature (Murphy et al. 2003; Vytal & Hamann 2010). Studies using electroencephalography (EEG) also associate instances of *anger* with the prefrontal cortex (PFC).[7] Using EEG, activity in the left PFC is associated with instances of *anger* experience in response to an insult (Harmon-Jones & Sigelman 2001) and with the personality disposition to experience angry feelings (Harmon-Jones & Allen 1998). Other

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[7] EEG findings do not associate instances of *anger* with OFC specifically, probably because EEG does not easily pick up activity in the orbital sector.

evidence for an OFC-*anger* hypothesis is more circumstantial. For example, there is a body of evidence linking the OFC to aggression. It is far from clear that aggression is an unambiguous index of the entire category of *anger*, however. Non-human animals aggress in a number of different contexts (e.g., maternal aggression, sexual aggression, predatory aggression, defensive aggression; Moyer 1968); only some of which are associated with the concept called “anger” in English. Humans do a number of things in *anger*, only some of which constitute aggression. With that caveat, there is certainly evidence linking increased activity in the OFC to aggression. EEG activity in the left PFC is associated with an increased tendency to retaliate toward another person following an insult (by allocating the person a dose of unpleasant hot sauce in a putative taste test; Harmon-Jones & Sigelman 2001). Aggressive behavior in rats is associated with increased activity in the ventral forebrain (including the OFC) (Ferris et al. 2008). Some lesion evidence is consistent with the idea that the OFC produces aggression in monkeys because OFC lesions reduce aggression (toward humans; Butter & Snyder 1972; Kamback 1973; toward other monkeys Raleigh et al. 1979). The majority of lesion studies find that monkeys (e.g., Deets et al. 1970; Machado & Bachevalier 2006; Raleigh et al. 1979) and rats (de Bruin et al. 1983) are more aggressive toward conspecifics following OFC lesions, however. Similarly, electrical stimulation of the lateral OFC (in cats; Siegel et al. 1975) and the medial OFC (in cats, Siegel et al. 1974; and in rats, de Bruin 1990) inhibits, rather than causes, aggressive behavior. Humans with lesions in the ventromedial PFC (which contains the OFC) become frustrated more easily and engage in more verbal (but not physical) aggression than do neurologically intact subjects (Grafman et al. 1996). Psychopathy and antisocial disorder are marked by increased aggression and correspond to structural (e.g., Raine et al. 2000) and functional (e.g., Glenn et al. 2009; Harenski et al. 2009) changes to the medial OFC (Yang & Raine 2009). Fewer studies have linked the lateral OFC to aggressive behavior in humans, but one study found that individuals with borderline personality disorder who have lowered baseline lateral OFC (BA 47) activity are more likely to aggress against others (Goyer et al. 1994).

A psychological constructionist view hypothesizes that portions of the OFC play a role in core affect as a site that integrates exteroceptive and interoceptive sensory information to guide behavior. Together, sensory information from the world and sensory information from the body guide an organism's response to the environment and allow it to engage in behavior that is well tuned to the context (defined both by the external surroundings and the organism's goals). With the lateral OFC's connections to sensory modalities (e.g., Barbas 1988; Rolls 1999, see Kringelbach & Rolls 2004) and the medial OFC's connections to areas involved in visceral control (e.g., Carmichael & Price 1995; Eblen & Graybiel 1995; Ongür & Price 1998; 2000; Rempel-Clower & Barbas 1998; see Kringelbach & Rolls 2004 for a review), the OFC is anatomically well suited to perform this role. We are not claiming that this is the OFC's specific function, but only that it is a brain region that is important to realizing this function. Consistent with the idea that the OFC unites internal and external sensory information, the lateral OFC and the medial OFC have been linked to associative learning (Rolls et al. 1994; 1996) decision making (e.g., Bechara et al. 1996; 2000; Koenigs et al. 2007) and reversal learning, in which the reward values associated with choice options are reversed and animals must learn the current reward value (Chudasama & Robbins 2003;

Hornak et al. 2004; Rudebeck & Murray 2008). The inability to properly integrate exteroceptive and interoceptive information will result in behavior that is inappropriate to that context, explaining the altered non-aggressive social behavior (e.g., Beer et al. 2003; Eslinger & Damasio 1985; Saver & Damasio 1991; see Damasio et al. 1990) and aggression (Grafman et al. 1996) observed in individuals with OFC damage.

Our meta-analytic findings were inconsistent with the locationist hypothesis that the OFC is the brain seat of *anger*. As compared to voxels within other brain regions, voxels within the OFC did not have more consistent increases during instances of *anger* experience or perception than during any other emotion category. Rather, as compared to voxels within other brain regions, voxels within the left lateral OFC had more consistent increases in activation during instances of *disgust* experience than during the experience of other emotion categories (Table 1). Voxels within the right lateral OFC, as compared to voxels within other brain regions, had more consistent increases in activation during instances of *disgust* perception than during the perception of other emotion categories (Table 1). χ^2 analyses indicated that there was some functional selectivity for instances of *disgust* experience and perception in the voxels in the right and and left lateral OFC that were respectively identified in the density analysis. Activity in the right and left lateral OFC was not specific to instances of *disgust* experience or perception, however (Fig. 6; Fig. S2). Our logistic regressions confirmed that when participants were perceiving an instance of *disgust*, there was more likely to be increased activity in the right lateral OFC than when participants were perceiving instances of any other emotion category (Fig. 5; Table S6).

Our logistic regressions revealed that increased activity in the left lateral OFC was more likely when participants were experiencing instances of *anger* than when they were experiencing instances of any other emotion category (Fig. 5; Table S6). Although in and of itself, this finding provides partial support for the OFC-*anger* hypothesis, our other meta-analytic findings indicate that increased activity in the left hemisphere during instances of *anger* is not restricted to the OFC, or even the prefrontal cortex (see sections 5.2 The anterior insula, 5.6 Anterior temporal lobe and ventrolateral prefrontal cortex and 5.7 Dorsolateral prefrontal cortex). Additionally, our logistic regressions revealed that increased activity in the left and right lateral OFC was likely when participants were experiencing a range of exteroceptive (auditory stimuli, visual pictures) and interoceptive (experience or perception of high-arousal core affect) sensations (Fig. 5; Table S6). This finding is consistent with the psychological constructionist hypothesis that OFC plays a more general role in integrating heteromodal sensations.

5.4. The anterior cingulate cortex

Locationist accounts hypothesize that pregenual anterior cingulate cortex (pACC; BAs 24, 32) and subgenual anterior cingulate cortex (sACC; BA 25) are the brain basis of *sadness* (Fig. 1, blue). The pACC and sACC have known affective function and are thought to instantiate the visceromotor responses observed during classical conditioning, pain, and affective behaviors (Devinksy et al. 1995; Vogt 2005). The ACC-*sadness* hypothesis, similarly to the OFC-*anger* hypothesis, derives support from prior meta-analyses of the neuroimaging literature (e.g., Murphy et al. 2003; Phan et al. 2002). In the behavioral neuroscience literature, pACC has been linked to *sadness* because of its role in producing the vocalizations that infant animals make when separated from their mother (e.g., MacLean & Newman 1988; see Panksepp 1998; 2007); the link between infant vocalizations and unpleasant affect are in question, however (Blumberg & Sokoloff 2001). One study in humans found that pACC lesions (including lesions to dorsomedial prefrontal cortex) produce hypersensitivity and an increased tendency to cry at sad events (Hornak et al. 2003). If the pACC were involved in instantiating instances of *sadness*, then lesions to this structure should abolish the tendency to cry at sad events. These findings are therefore more consistent with the idea that pACC regulates instances of *sadness.* Finally, pACC is implicated in pain, perhaps because it supports the feeling of “suffering” (cf. Vogt 2005). The sACC, on the other hand, has been linked to *sadness* because of its role in depression. Clinical depression is marked by structural and functional changes in sACC (see Gotlib & Hamilton 2008 for a review), although clinical depression involves many symptoms above and beyond the experience of *sadness* (Coyne 1994). Electrical stimulation of the sACC relieves intractable depression by reducing feelings of apathy and anhedonia, normalizing sleep disturbances, and decreasing gross motor impairments (e.g., Mayberg et al. 2005).

Our psychological constructionist hypothesis draws on the neuroscience literature showing that pACC, sACC, and the more dorsal anterior midcingulate cortex (aMCC) (Vogt 1993; Vogt et al. 2003) take part in distinct psychological operations related to realizing core affect. In our view, the pACC and sACC (along with the adjacent posterior medial OFC) are cortical sites for visceral regulation that help to realize a core affective state during motivated action (Devinksy et al. 1995) (Fig. 2, panel B, light pinks). We would therefore predict increased activation in pACC and sACC across a variety of emotional instances. The hypothesized role of sACC in regulating somatovisceral states could explain why sACC is involved in the affective changes that accompany both depression (e.g., Drevets et al. 1992; see Gotlib & Hamilton 2008) and mania (e.g., Fountoulakis et al. 2008), and why electrical stimulation of this region helps to relieve chronic depression (Mayberg, et al. 2005). The aMCC (Fig. 2, panel B, dusty pink) is hypothesized to play a role in executive attention and motor engagement during response selection (Mansouri et al. 2009; Rushworth et al. 2007). In this view, aMCC delivers sources of exteroceptive sensory information (from thalamic projections; Barbas et al. 1991) and internal sensory information (from the insula; Mesulam & Mufson 1982) to direct attention and motor responses (via projections to lateral PFC and the supplementary motor area; e.g., Barbas & Pandya 1989; see Devinsky et al. 1995; Paus 2001 for reviews). These anatomical connections can explain why the aMCC is part of an intrinsic brain network that shows increased activity when stimuli in the environment are personally salient (Seeley et al. 2007). They also explain why the aMCC is responsible for resolving action selection during situations involving conflicting sensory information (e.g., Grindband et al. in press; Milham et al. 2001; Nelson et al. 2003; see Banich 2009; Shackman et al. 2011; van Snellenberg & Wager 2009). By extension, as a visceromotor (i.e., autonomic) control area sACC/pACC might be involved in resolving which sensory inputs influence the body when there are multiple sources of sensory input that can influence an organism's body state.

Our meta-analytic evidence is inconsistent with the locationist account that the ACC is the brain basis of *sadness*, but more consistent with a psychological constructionist hypothesis of ACC function. As compared to voxels within other brain regions, voxels within the sACC, pACC and aMCC did not have more consistent increases when participants were experiencing or perceiving instances of *sadness* than during any other emotion category (Fig. 6). As compared to voxels within other brain regions, a greater spatial extent of voxels within the aMCC had consistent increases in activation during instances of *fear* perception than the perception of any other emotion category (Table 1). The amygdala, which responds to motivationally salient exteroceptive sensory stimuli (see 5.1 The amygdala), projects to this area of aMCC (Vogt & Pandya 1987), so it is possible that increased activity here reflects response preparation to salient stimuli in the environment.

Our logistic regressions revealed that increases in sACC were likely when participants were engaged in cognitive load (Fig. 5; Table S6). Cognitive load typically occurred in studies in which participants were asked to attend to core affective feelings (e.g., focus on their feelings, rate their feelings) or affective stimuli (e.g., focus on an affective stimulus, rate a stimulus' emotional value) and, therefore, it is possible that this finding is indicative of the sACC's role in instantiating core affective feelings. Increased activity in the sACC was marginally ($p < 0.09$) likely when participants were evaluating their feelings, again consistent with this area's role as a visceromotor regulation site. Finally, consistent with a response selection hypothesis of aMCC function, increased activity in the aMCC was likely when participants were engaged in cognitive load (Fig. 5; Table S6).

5.5. Dorsomedial prefrontal cortex, medial temporal lobe, and retrosplenial cortex/posterior cingulate cortex

Our psychological constructionist approach hypothesizes that a range of other brain regions are important to realizing instances of emotion experience and perception, including dorsomedial prefrontal cortex (DMPFC), ventromedial prefrontal cortex (VMPFC), medial temporal lobe (MTL), and retrosplenial cortex/posterior cingulate cortex (PCC) (Fig. 2, panel B, purples), which are associated with the psychological operation of conceptualization. As part of the process of making meaning out of sensory cues, we hypothesize that these brain areas use stored representations of prior experiences to make meaning out of core affective inputs that come from the self or observing others. Locationist views do not hypothesize specific roles for these brain regions in emotion because they are usually considered to have a “cognitive” function, insofar that they support memory (Vincent et al. 2006), object perception (Bar 2009), and theory of mind (Mitchell 2009). In our view, these brain regions should not necessarily be more involved in instances of one category of emotion than another, although we would expect them to be part of the more general neural reference space for discrete emotion.

As we predicted, our meta-analytic results revealed that regions of the conceptualization network such as DMPFC, MTL and retrosplenial cortex (Buckner et al. 2008) were part of the neural reference space for discrete emotion (Fig. 4)[8]. Our findings indicate that the conceptualization network is integral in the experience and perception of discrete emotions, and are consistent with the hypothesis (in Barrett 2006b; 2009a, b) that prior episodic experience helps shape experienced or perceived affect into meaningful instances of *emotion*. Despite general involvement in emotion (Fig. 1; Fig. S3), there was some functional selectivity for instances of certain emotion categories in hubs within the conceptualization network. For instance, across our density analyses and logistic regressions, we found that instances of the experience of *sadness* (Tables 1 & 2) and experience of *happiness* (Table 1) were each associated with relatively greater consistent increases in activation in areas of DMPFC than other emotion categories. Consistent with the role of conceptualization in simulating episodic experience (Schacter et al. 2007), our logistic regressions revealed that increased activity in DMPFC was likely when participants were engaging in emotion inductions involving recall and films (Fig. 5). Increased activity in some clusters of DMPFC was likely when participants were perceiving *emotion* in faces, bodies or voices. This finding is consistent with the psychological constructionist hypothesis that the conceptualization network is brought to bear when affective facial behaviors are perceived as emotional. Other clusters of DMPFC showed an opposite pattern: when participants were perceiving *emotion*, increased activity in DMPFC was not likely (Table S6). Just as perception of others and self-referential thinking involve overlapping yet distinct aspects of DMPFC (Ochsner et al. 2004a), some aspects of DMPFC might be functionally selective for conceptualization during emotion perception whereas others support conceptualization during emotion experience.

Several emotion categories were also associated with consistent increases in activation in the MTL (Tables 1 & 2; see Table S6). Our logistic regressions revealed that, as in the DMPFC, increased activity in the right hippocampus was likely to occur when participants were perceiving an instance *emotion* in a face, body or voice. Increased activity in the left hippocampus, on the other hand, was likely to occur when participants were perceiving instances of *fear* (Table S6). This finding is more likely to be related to the encoding of salient stimuli in memory than simulating prior experiences, as the amygdala also had increased activity during instances of *fear* perception and is known to have functional connectivity with the hippocampus during encoding of salient stimuli (Kensinger & Corkin 2004).

5.6. Anterior temporal lobe and ventrolateral prefrontal cortex

According to a psychological constructionist account, networks supporting language (e.g., Vigneau et al. 2006) should consistently show increased activity during instances of *emotion* experience and perception as linguistically-grounded concepts are brought to bear to make meaning of core affective feelings. In locationist accounts, language is thought to be epiphenomenal to discrete *emotion* (Ekman & Cordano, in press), although recent behavioral studies show that categorical perception of discrete emotion is supported by language (Fugate et al. 2010; Roberson & Davidoff 2000; Roberson et al. 2007).

Consistent with the psychological constructionist view, nodes within networks supporting language were part of the neural reference space for discrete emotion (Fig. 4) In particular,

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[8] mOFC and sACC, which are more generally part of VMPFC, were part of the neural reference space and are reported in separate sections. Aspects of VMPFC that do not include mOFC/sACC were part of the neural reference space, but were not significant at the thresholds we report in this article.

the anterior temporal lobe (ATL) and ventrolateral prefrontal cortex (VLPFC) (Fig. 2, Panels A, B, C, green) had consistent increases in activity across studies of discrete emotion. The ATL supports language as a heteromodal association area involved in the representation of concepts (Lambon Ralph et al. 2009; Pobric et al. 2007; Rogers et al. 2004) and the right ATL has been implicated in the representation of abstract social concepts (e.g., Zahn et al. 2009). Patients with semantic dementia have focal atrophy to the ATL, difficulty utilizing semantic knowledge, and exhibit deficits in emotion perception (Rosen et al. 2004) and empathy (Rankin et al. 2006). Areas of the VLPFC on the other hand, are implicated in semantic processing tasks (e.g., Gitelman et al. 2005), categorization of objects (e.g., Freedman et al. 2001), representation of feature-based information for abstract categories (e.g., Freedman et al. 2002; see Miller et al. 2002), selection amongst competing response representations (e.g., Badre & Wagner 2007; Schnur et al. 2009), and inhibition of responses (Aaron et al. 2004). It is therefore not clear that the VLPFC's role is functionally specific to language, but it is certainly functionally selective for language in certain instances. The VLPFC also helps comprise the ventral frontoparietal network that is thought to be involved in directing attention to salient stimuli in the environment (Corbetta & Shulman 2002; Corbetta et al. 2008), suggesting a more general role for this region in executive attention.

As compared to in other brain regions, voxels within the ATL did not have more consistent increases during instances of one emotion category than others (Fig. S3). Our logistic regressions suggested that increased activity in the left ATL was more likely when participants were experiencing an instance of *anger* than any other emotion category, however (Fig. 5; Table S6). Instances of *anger* experience therefore involve areas throughout the left frontal and temporal lobes (see 5.2 The anterior insula, 5.3 The orbitofrontal cortex, and 5.7 Dorsolateral prefrontal cortex). Increased activity in the right ATL, on the other hand, was likely when participants were evaluating a stimulus (i.e., determining the emotional meaning of a face, voice, or picture; Table S6). This finding is consistent with the hypothesis that language is brought to bear when constructing emotional percepts from exteroceptive sensations.

Our density analyses revealed that as compared to voxels within other brain regions, voxels within the right VLPFC had more consistent increases during instances of *disgust* perception than during the perception of any other emotion category; these findings were confirmed with a logistic regression (Table 1; Table S6). χ^2 analyses revealed that a subset of the voxels identified in the density analysis were functionally selective for instances of *disgust* perception (Table 2), although they were not specific to instances of *disgust* (Fig. S3). The most common finding across our logistic regressions linked increases in the left VLPFC to instances in which participants were explicitly paying attention to emotional information (Fig. 5; Table S6). As in other left frontal and temporal areas (see 5.2 The anterior insula, 5.3 The orbitofrontal cortex, 5.6 Anterior temporal lobe and ventrolateral prefrontal cortex),increased activity in the left VLPFC was likely when participants were experiencing or perceiving instances of *anger*.

5.7. Dorsolateral prefrontal cortex

According to a psychological constructionist account, networks supporting executive attention (see Miller & Cohen 2001; Petrides 2005; for a meta-analysis, Wager & Smith 2003) should consistently show increased activity during instances of *emotion* experience and perception because executive attention directs other psychological operations during the construction of emotion. Locationist accounts do not propose specific roles for these networks in emotion, although they might allow that networks supporting executive attention take part in regulation of emotion after it is generated (as in Ochsner et al. 2004b; Urry et al. 2006).[9]

Consistent with our psychological constructionist hypothesis, nodes within networks supporting executive attention were part of the neural reference space for discrete emotion. In particular, the VLPFC and dorsolateral prefrontal cortex (DLPFC) (Fig. 2, Panel A orange and striped green/orange) had consistent increases in activity across studies of discrete emotion. The DLPFC is part of the dorsal frontoparietal network that is thought to be involved in top-down, goal-directed selection for responses (Corbetta & Shulman 2002; Corbetta et al. 2008). Consistent with this functional connectivity, bilateral DLPFC is known to be involved in working memory (e.g., Champod & Petrides 2007; Constantinidis et al. 2002) and in the goal-directed control of attention (e.g., Rainer et al. 1998; see Miller 2000).

We predicted that DLPFC would be part of the neural reference space for emotion (Fig. 4) because these voxels would be active during mental states in which participants attended to emotional feelings or perceptions (i.e., when participants had to hold affective information in mind in order to categorize it). Consistent with this prediction, increased activity in the right DLPFC was likely when participants were explicitly evaluating stimuli (Fig. 5; Table S6). Our density analyses also revealed that as compared to voxels within other brain regions, voxels in the right DLPFC were more likely to have increased activity during instances of *anger* perception than any other emotion categories (Table 1). Our χ^2 analyses indicated that some of these voxels were functionally selective to instances of *anger* perception (Table 2), although they were not specific to perceiving *anger* (Fig. S3).

5.8. The periaqueducal gray

The periaqueducal gray (PAG) is involved in regulating the autonomic substrates that allow for behavioral adaptations such as freezing, fleeing, vocalization, and reproductive behavior (e.g., Carrive et al. 1989; Behbehani 1995; Gregg & Siegel 2001; Kim et al. 1993; Lovick 1992; Mobbs et al. 2007; Van der Horst & Holstege 1998) and also sends projections back to cortical sites involved in the regulation of visceral activations in the body (An et al. 1998; Mantyh 1983). It is believed that certain adaptations are associated with certain emotion categories (e.g., animals freeze in *fear*, aggress in *anger*) but such links are far from empirically clear. Humans (like other mammals) do many things during instances of *anger*, for example. Sometimes humans yell, sometimes they hit, sometimes they remain very still, and sometimes they smile. Even rats do many things within a single emotion category: in the

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[9] In some theoretical treatments of emotion, emotion regulation is thought to be a separate psychological event from emotion generation, with distinctive neural correlates; in a psychological constructionist approach, however, the processes are the same because there is no conceptual distinction between generation and regulation (Gross & Barrett, 2011).

face of a threat, rats can freeze (e.g., LeDoux et al. 1990), flee (Vazdarjanova & McGaugh 1998), or engage in "defensive treading," in which they kick bedding in the direction of a known threat (Reynolds & Berridge 2002; 2003; 2008). In all these instances, PAG activity and the associated autonomic states it produces, are yoked to the action, and not to the emotion category. As a result, a psychological constructionist approach views PAG activity as nonspecifically involved in instances of emotion. A locationist approach has linked the PAG to distinct circuits corresponding to several emotion categories: *rage, fear, joy, distress, love* and *lust* (Panksepp 1998). In a psychological construction approach, the assumption is that a given dedicated circuit for a specific behavioral adaptation (e.g., withdrawal) will be active across a range of emotion categories (e.g., a person can withdraw in instances of both *fear* and *anger*), and different dedicated circuits within the PAG (e.g., fight, flight) will be active within instances of a single emotion category depending upon which behavioral adaptation is more relevant for the immediate context.

Testing any hypothesis about the specificity of a subcortical region such as the PAG is practically impossible, given the spatial and temporal limitations of brain imaging. Still, it is instructive to note that the PAG was consistently activated within the neural reference space for discrete emotion (even though subjects were lying still and not engaging in any overt physical action; see Fig. S4). Moreover, we did not find evidence of functional specificity for the PAG in our meta-analysis. It is possible that given the resolution problems, different circuits within the PAG were specifically active for discrete emotions. That said, it is also entirely plausible from the behavioral data that humans, like animals, perform a range of actions within a single category, and perform the same action at times across categories (even if it does not match our stereotypes of *emotion*–action links). In this meta-analysis, increased activity in the PAG did not correspond to any emotion category more than to another (although instances of the experience of *sadness* were associated with consistent increases in activation in one voxel within ventral PAG; Tables 1 & 2). The logistic regressions demonstrated that increased activity in the PAG was likely when participants were experiencing or perceiving an instance of any high-arousal emotion category (Table S6). Consistent with this finding, activity in a separate cluster of PAG was likely when participants were experiencing instances of *fear* (Table S6). In a previous meta-analysis, we found that the PAG was most likely to have increased activity during unpleasant emotions (Wager et al. 2008). As all high-arousal emotion categories in our database were unpleasant (e.g., *fear, anger, disgust*), our present findings are consistent with Wager et al. (2008). Future research should probe whether the PAG preferentially shows increased activity during unpleasant states, highly aroused states, or during states that are both unpleasant and highly aroused.

5.9. Visual cortex

From our psychological construction approach, we would not be surprised to observe voxels within visual cortex (or any sensory modality) to show increased activation during emotion. In its most basic form, our hypothesis is that emotion emerges as a situated conceptualization of internal sensations from the body and external sensations from the world to create a unified conscious experience of the self in context. In fact, regions of visual cortex were some of the most frequent to appear in our meta-analytic findings (replicating several recent meta-analyses; e.g., Fusar-Poli et al. 2009 Kober et al. 2008; Vytal & Hamann, 2010). It is beyond the scope of this article to discuss these findings in detail, but we found that instances of *fear* experience, *anger* perception, and *disgust* experience were consistently associated with increased activity in regions of visual cortex ranging from V2 to visual association cortex (Tables 1 & 2). Our logistic regressions revealed that activation in visual cortex was not merely a by-product of the methods used. Although increased activity in visual cortex was likely when visual methods were used (e.g., pictures, faces, studies of perception; see Table S6), it was also likely in studies of unpleasant, high-arousal emotions (e.g., *fear, disgust*, unpleasant emotions more generally; Table S6). Together, these findings indicate that experiences or perceptions of unpleasant emotion categories are realized by brain states that include increased activity in visual cortex. See Gendron et al. (in preparation) for a discussion.

6. Conclusion

Over a century ago, William James wrote, “A science of the relations of mind and brain must show how the elementary ingredients of the former correspond to the elementary functions of the latter,” (p. 28, 1890). James believed that *emotions, thoughts*, and *memories* are categories derived from commonsense with instances that do not require special brain centers. With respect to *emotion*, he wrote, “sensational, associational, and motor elements are all that [the brain] need contain” to produce the variety of mental states that correspond to our commonsense categories for emotion (cf., p. 473, James 1890/1998). James’ view foreshadowed modern psychological constructionist models of the mind and the findings of our meta-analytic review, which are largely in agreement with this approach. Our findings are consistent with the idea that emotion categories are not natural kinds that are respected by the brain. The fact that some of the regions we report also appear in meta-analyses of other task domains (e.g., action simulation and perception, Grezes & Decety 2001; autobiographical memory, Svoboda et al. 2006; decision making, Krain et al. 2006; executive control, Owen et al. 2005; Wager & Smith 2003; Wager et al. 2004; language, Vigneau et al. 2006; self-referential processing, Northoff 2006) means that these regions are not specific to *emotion* per se, and are also involved in constituting other cognitive and perceptual events (for a discussion of domain general networks, see Dosenbach et al. 2006; Nelson et al. 2010; Spreng et al. 2009; van Snellenberg & Wager 2009). Such findings show that even categories such as *emotion, cognition*, and *perception* are not respected by the brain (Barrett 2009a; Duncan & Barrett 2007; Pessoa 2008).

In keeping with James’ predictions, our meta-analytic review did not find strong evidence for a locationist hypothesis of brain–emotion correspondence (see Table 3 for a summary of findings). In all instances in which a brain region showed consistent increases in activation during instances of a discrete emotion category (e.g., the amygdala in instances of *fear* perception), this increase was not specific to that category, failing to support a key locationist assumption. Some brain regions showed functional selectivity for instances of certain emotion categories; these findings perhaps point to differences in the contents of mental states (e.g., instances of *anger* experience often involve approach motivation, instances of *disgust* perception often involve simulation of bodily activation, and instances of *fear* perception often involve detection of unusual and hence salient stimuli).

Our meta-analytic findings were relatively more consistent with the psychological operations that we have considered ingredients of emotion here and in other articles (e.g., Barrett 2006b; 2009; Barrett et al. 2007a; Kober et al. 2008; Lindquist & Barrett 2008; Wager et al. 2008). In Kober et al. (2008), we hinted at the existence of basic psychological operations in the psychological construction of emotion. In other theoretical discussions (Barrett 2009) we explicitly hypothesized the need for mid-level scientific categories that describe the most basic psychological ingredients of the mind by referencing both biology and folk psychology when explaining how mental states like emotion experiences and perceptions arise (for a similar view, see Cacioppo et al. 2008). This article is the first to investigate the extent to which brain regions associated with basic psychological domains show consistent increases in activation in neuroimaging studies of discrete emotion categories, despite a range of methodological variables. Of course, more work needs to be done to hone and refine our conceptions of the operations that are most psychologically primitive and map them to networks in the brain, but this is a start.

Most notably, we observed consistent increases in activation in the brain regions implicated in conceptualization (simulation of prior episodic experiences), language (representation and retrieval of semantic concepts), and executive attention (volitional attention and working memory), suggesting that these more “cognitive” functions play a routine role in constructing experiences and perceptions of emotion. For example, increased activation in the DMPFC was observed when participants perceived instances of *emotion* on others’ faces. Increased activation in the ATL was observed when participants focused on emotional stimuli. Increased activity in the VLPFC occurred when participants focused on the affective content of feelings or perceived instances of *emotion* on another person's face. Increased activity in the DLPFC occurred when participants evaluated the emotional content of a stimulus. One interpretation of these findings is that they are merely the result of the types of psychological tasks participants are asked to perform in the scanner during neuroimaging studies of emotion (e.g., recall, labeling, response selection), and that because of the limits of neuroimaging, these influences cannot be separated from an emotion itself. Yet, all data in our meta-analysis were derived from emotion versus neutral contrasts, meaning that, regardless of the task at hand, activation in these brain areas was greater when participants were experiencing or perceiving an emotion category than when they were experiencing or perceiving in a neutral control state. Activity in these brain regions is therefore integral to producing instances of *emotion*.

Our findings suggested the need to refine and add additional psychological operations to our model. Just as executive attention has been parsed into a set of distinguishable networks (e.g., Corbetta & Shulman 2002; Corbetta et al. 2008; Dosenbach et al. 2007; Seeley et al. 2007), we might further refine core affect into a set of smaller networks that correspond to even more basic mechanisms. For example, we might find separable networks corresponding to approach versus avoidance-related states. Our findings hint that brain regions in the left PFC might be candidates for a network involved in approach motivation because regions in the left lateral PFC (including the anterior and mid-insula, VLPFC, DLPFC and OFC) were consistently observed during instances of the experience of *anger*. This hypothesis is consistent with a large body of EEG evidence associating the left PFC with the experience of instances of *anger* (Harmon-Jones & Allen 1997; Harmon-Jones & Sigelman 2001) and approach motivation more generally (Amodio, et al. 2008; Fox 1991; Sutton & Davidson 1997). Future meta-analytic investigations should investigate the degree to which the left PFC and subcortical regions supporting incentive salience (e.g., ventral tegmentum, amygdala, and aspects of the nucleus accumbens and ventral pallidum; see Berridge & Robinson 2003) comprise a network for approach-related affect within the operation of core affect. We might also add ingredients for processing exteroceptive sensory sensations to our theoretical framework since visual cortex was one of the most frequently activated brain regions in our meta-analysis of discrete emotions. Exteroceptive sensory sensations are also important components of other types of mental states (e.g., perception, memory, judgments).

6.1. Alternate interpretations

Of course, there are alternate explanations for why we did not find strong evidence in support of a locationist framework. First, it is possible that neuroimaging is not well suited to yield evidence for functional specialization for emotion in the brain because of its spatial limitations. It therefore remains possible that scientists might find functional specialization for emotion at a more refined level of spatial analysis (e.g., at the level of smaller circuits or even cortical columns of neurons). Whereas this always remains a possibility, it is important to note that even the most highly specialized brain regions (e.g., primary visual cortex) contain neurons that participate in different neural assemblies associated with different functions (e.g., Basole et al. 2003). This makes strong locationist interpretations of brain function unlikely when such interpretations attempt to find specificity for psychological categories (particularly at the level of the cortical column). Instead, the idea of neural re-use (e.g., Anderson 2010) is consistent with the psychological constructionist model of brain–emotion correspondence. Neuroimaging also has temporal limitations. It takes a few seconds for a BOLD response to materialize and we do not know whether emotions are episodes that extend over many seconds or more instantaneous states that fire and resolve within that time frame. It is possible that scientists might find functional specialization for emotion at a more refined level of temporal analysis (e.g., using single cell recording), although such evidence has yet to be revealed. Moreover, we find it unlikely that neuroimaging and single cell recordings are measuring totally different phenomena. More likely, they are methods that complement one another (e.g., Horowitz 2005).

Second, it remains a possibility that we failed to locate a specific brain basis for discrete emotion categories because emotion categories are represented as anatomical *networks* of brain regions. Some researchers hypothesize that “resting state” analyses[10] of the brain's function, which reveal the intrinsic anatomical networks that chronically support the brain's fundamental processes, are influenced by anatomical connections (Deco, Jirsa & McIntosh 2011). If emotion categories were supported by anatomically given, inherited networks, then there should be intrinsic networks that correspond to the brain regions active during the experience or perception of instances of *anger, sadness, fear*, and other emotion categories.

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[10] “Resting state” or “default” networks are evidenced as correlations between low-frequency signals in fMRI data that are recorded when there is no external stimulus or task. These networks are thought to be intrinsic in the human brain. For a review of intrinsic networks and their function, see Deco, Jirsa and McIntosh (2011).

To date, however, no such intrinsic networks have been identified in broad inductive studies of such brain organization (e.g., Smith et al. 2009). Instead, the intrinsic networks that have thus far been identified bear resemblance to the psychological domains that are hypothesized by a psychological constructionist view (see functional groups in Kober et al. 2008). For example, the “default network” that is active when a person is not probed by an external stimulus in fMRI experiments (Buckner & Vincent 2007; Raichle et al. 2001) is not only important to constructing representations of the past and the future, but also for constructing representations of emotion experience and perception in the moment. Portions of the intrinsic networks for “personal salience” (e.g., Seeley et al. 2007) and “executive control” (e.g., Corbetta & Shulman 2002; Seeley et al. 2007) appear anatomically similar to brain regions that we observed within our meta-analyses as well.

Of course, there is evidence for more limited brain circuits that correspond to specific behavioral adaptations in mammals. There is well-documented evidence for the anatomical circuitry underlying specific actions such as vocalizations (Jürgens 2009), maternal behavior (e.g., pup retrieval, grooming, nest building, and nursing; Numan 2007), freezing (Fanselow & Poulos 2005), startle (Davis et al. 2008; Lang et al. 2000), attack (Blanchard & Blanchard 2003) and appetitive behavior (Berridge & Kringelbach 2008; Shultz 2006), just to name a few. In our view, these are just another set of basic operations and are not, in and of themselves, evidence that there is distinct anatomical circuitry for complex psychological categories such as *sadness, love, fear*, *anger*, or *greed* (each of which could contain instances of a range of behaviors) (Barrett et al. 2007a). Animals produce actions in a way to maximize their outcome in a specific context. Therefore, many different behaviors can be associated with a given discrete emotion category; there is variety in the behaviors and the autonomics that populate any given emotion category. Sometimes, to make their findings more accessible, researchers will equate a specific behavior and its circuitry (e.g., freezing in the face of an uncertain danger) with an emotion category (e.g., *fear*). The problem with this logic is that it limits the definition of a complex psychological category to one or two behaviors. If *fear* is defined by freezing then is *fear* not occurring at times when a rat flees, attacks, kicks bedding at a predator, or avoids an unknown corner of a maze? Or when humans avoid a dark alley, bungee jump, remember the events of September 11th, lock the door at night, or password-protect their bank accounts? As each of these actions is associated with a different neural network, which one is the *fear* network? If they are all fear networks, then what is the scientific value of the category *fear* for explaining behavior?

If discrete emotion categories are not associated with a specific brain locale, or even an anatomically inspired network that can be inherited, it is still possible that a pattern classification analysis on our meta-analytic database might reveal that each emotion category is represented by a specific combination of brain regions that co-activate together in time as a functional unit. We did not test this hypothesis, although we are in the process of developing these techniques for our software package. To the extent that such patterns are widely distributed across the brain, however (as opposed to being organized anatomically as inheritable units), such functionally defined networks for emotion categories (i.e., networks that only combine in a given context to produce a given type of mental state) would be consistent with a psychological constructionist (as opposed to a locationist) view.

It is possible that we failed to find evidence for the brain basis of discrete emotions because the methods employed in neuroimaging studies (or the laboratory for that matter) do not reliably elicit the type of discrete emotion experiences observed in the real world. After all, many scientists believe that emotions involve action (or action tendencies), and during scanning experiments participants must lie very still. Although this always remains a possibility, we do not believe it is a serious concern. First of all, even when participants are asked to lie still in a scanner, we still routinely observe increases in PAG activity in emotion. The PAG is necessary for motivated action patterns in animals, therefore these findings argue against the criticism that emotions invoked in the scanner are superficial. Even studies in which people are asked to imagine an emotional scenario probably create real experiences (as anyone knows who has become immersed in a mental reverie).

Finally, and perhaps most importantly, our observation that common brain activations exist across emotion categories is echoed in the pattern of findings for other (non-brain) measures of emotion. Since the beginning of psychology, researchers have questioned the idea that discrete emotion categories are each associated with a single, diagnostic pattern of response in the brain and body (e.g., Duffy 1934; Hunt 1941; James 1884; for a review of such theories, see Gendron & Barrett 2009). More recently, a number of empirical reviews (Barrett 2006a; Barrett 2007a; Mauss & Robinson 2009; Ortony & Turner 1990; Russell 2003) have highlighted the disconfirming evidence: Different discrete emotion categories are not distinguished by distinct patterns of peripheral physiology (Cacioppo et al. 2000; Mauss & Robinson 2009), facial muscle movements (Cacioppo et al. 2000; Russell, Bachorowski & Fernandez-Dols 2003), vocal acoustics (Bachorowski & Owren 1995; Barrett 2006a; Russell, Bachorowski & Fernandez-Dols 2003) or by subcortical circuits in the mammalian brain (Barrett 2006a; Barrett et al. 2007a). The present meta-analytic review adds to this literature by demonstrating that emotion categories do not map to discrete brain locales in the human brain either. Instead, evidence from our meta-analysis, as well as studies of emotion that use psychophysiological measures, objective measures of the face and voice, and subjective experience of emotion, all point to the idea that emotions emerge from a set of more basic operations (cf. Barrett 2006b). As neuroscientific methodologies progress, it will become increasingly important for scientists to formulate a viable conceptual framework for mapping emotions to the brain. Our findings suggest that a psychological constructionist approach might offer just such a framework. Locationist views might be deeply entrenched in common sense, which makes the corresponding scientific models particularly compelling, but they do not match the scientific evidence in any measurement domain for emotion.

6.2. Future directions in the search for the brain basis of emotion

Despite the field's emphasis on locationist views (that inspired many of the experiments used in our meta-analysis), we found that the bulk of the empirical evidence is more consistent with the hypothesis that emotions emerge from the interplay of more basic psychological operations. We hypothesize that these operations and their corresponding neural networks influence and constrain one another to produce a variety of brain states that correspond to a variety of emotional states. To fully explore the power of a psychological constructionist approach in future research, researchers might combine traditional neuroimaging techniques with methods that make more network-based assumptions about brain function (e.g., Multivoxel Pattern Analysis; Haxby et al. 2001; Multivariate Partial Least Squares Analysis; McIntosh et al. 1996; see Schienle & Schafer 2009 for additional analysis approaches). Researchers might also utilize resting state analysis to identify functional networks that are intrinsic to the brain and compare those to the task-related assemblies of brain areas found across neuroimaging experiments (e.g., Smith et al. 2009). Finally, researchers must employ studies that capture and model the variability inherent in the collection of instances that form an emotion category such as *anger*, *disgust*, or *fear* (e.g., Wilson-Mendenhall et al., in press). Most studies in our database utilize stimuli and induction techniques that invoke the most typical – and even caricatured – instances of an emotion category. Yet, daily experience tells us that there is great variability in the instances of *anger*, *disgust*, *fear*, *happiness* and *sadness* that we experience, and research bears this out. For example, an instance of *disgust* that occurs when watching others eat repulsive food involves a different brain state than an instance of *disgust* that occurs when watching surgical operations (Harrison et al. 2010). Brain states that occur during instances of *fear* and *anger* are best described by an interaction between the content of the experience (e.g., whether the state is labeled *fear* vs. *anger*) and the context in which it occurred (e.g., a physical vs. social context) (Wilson-Mendenhall et al. in press).

7. Unifying the Mind

A psychological constructionist approach is not only a viable approach for understanding the brain basis of emotion, but it might also offer a new psychological ontology for a neuroscientific approach to understanding the mind. If a psychological constructionist approach to the mind is correct, then some of psychology's time-honored folk distinctions become phenomenological distinctions. This has implications for understanding a range of psychological phenomena, including decision making, attention, visual perception, mental illness, and perhaps even consciousness more generally. Indeed, similar efforts are emerging in other psychological domains (Fuster 2006; Poldrack et al. 2009; Price & Friston 2005; Warnick et al. 2010). According to a psychological constructionist view of the mind, *emotion* does not influence *cognition* during decision making as one pool ball exerts influence on another. Instead the view suggests that core affect, conceptualization, and executive attention (and perhaps other psychological operations) cooperate to realize a behavioral outcome. If this is the case, then we might not assume that *emotion* and *cognition* battle it out in the brain when a person makes the moral decision to sacrifice one life to save many (e.g., Greene et al. 2004), or that consumer decisions are predicated on competing affective and rational representations (e.g., Knutson et al. 2007). Instead, we might assume that affect and executive attention are merely different sources of attention in the brain rather than processes that differ in kind (Barrett 2009b; Vuilleumier & Driver 2007). Feeling and seeing might not be as distinct as typically assumed (Barrett & Bar 2009; Duncan & Barrett 2007). Even conceptions about “internal” versus “external” processing begin to break down when we take into account the fact that “internal” ingredients such as affect and conceptualization shape the very way in which exteroceptive sensory input is realized as perceptions by the brain (Bar 2009; Barrett & Bar 2009). A psychological constructionist framework of the mind therefore begins to break down the most steadfast assumptions of our commonsense categories. In so doing, it charts a different but exciting path forward for the science of the mind.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Definitions

Natural kind approach	A theoretical framework for understanding the ontology of emotions. The natural kinds approach assumes that emotion categories such as *anger*, *sadness*, and *fear* map on to biological categories that are given by the brain and body, and cannot be reduced to more basic psychological parts.
Locationist approach	Many national kind models of emotion conform to a locationist approach in which discrete emotion categories (e.g., *anger*) are assumed to be consistently and specifically localized to discrete brain locales or anatomical networks.
Psychological constructionist approach	A theoretical framework for understanding the ontology of emotions. The psychological constructionist approach assumes that emotion categories such as *anger*, *sadness*, and *fear* are common sense categories whose instances emerge from the combination of more basic psychological operations that are the common ingredients of all mental states.
Core affect	The mental representation of bodily sensations that are sometimes (but not always) experienced as feelings of hedonic pleasure and displeasure with some degree of arousal. Core affect is what allows an organism know if something in the environment has motivational salience (i.e., is good for it, bad for it, approachable, or avoidable). Barring organic abnormality, core affect is accompanied by somatovisceral, kinesthetic, proprioceptive, and neurochemical fluctuations that take place within the core of body and feed back to be represented in the brain.

Conceptualization	The process by which sensations from the body or external world are made meaningful in a given context using representations of prior experience. Conceptualization occurs in a situated fashion (as in “situated conceptualization;” see Barslou et al., in press), drawing on the representations of prior experience that are activated by the present physical and psychological situation.
Executive attention	The process by which some representations are selectively enhanced and others are suppressed. This is also known as “endogenous,” “controlled,” or “goal-based” attention and can be exerted both volitionally and without the conscious experience of volition. Executive attention can shape the activity in other processes such as core affect, conceptualization, or language use. In the case of emotion, executive attention foregrounds certain core affective feelings and exteroceptive sensory sensations in a moment, and guides which situated conceptualizations are brought to bear to make meaning out of those sensations in the given context.
Emotion words	The set of words that ground the abstract categories that humans experience and communicate about. In the case of abstract categories such as emotions, words are “essence placeholders” that help cohere feelings, behaviors, and facial expressions together as instances of a meaningful category.
Neural reference space	The set of neurons that are probabilistically involved in realizing a class of mental events (such as *anger*, or even *emotion*).
Functional selectivity	This occurs when a set of neurons show a consistent increase in activation for one mental state (e.g., *anger, disgust, emotion*) or basic psychological operation (e.g., categorization, core affect) more so than for others in a given instant. The neurons are not specific to any mental state, although they might be more frequently activated in some than in others. Functional selectivity might occur because a brain region supports a more basic psychological operation that helps to construct a certain mental state (e.g., the amygdala supports detection of salient exteroceptive sensations and is functionally selective for perceptions of *fear*). A brain area might be functionally selective for one mental state or even one basic psychological operation in one instance, and for another state or operation in another instance (e.g., ventromedial prefrontal cortex helps to realize both core affect and conceptualization).

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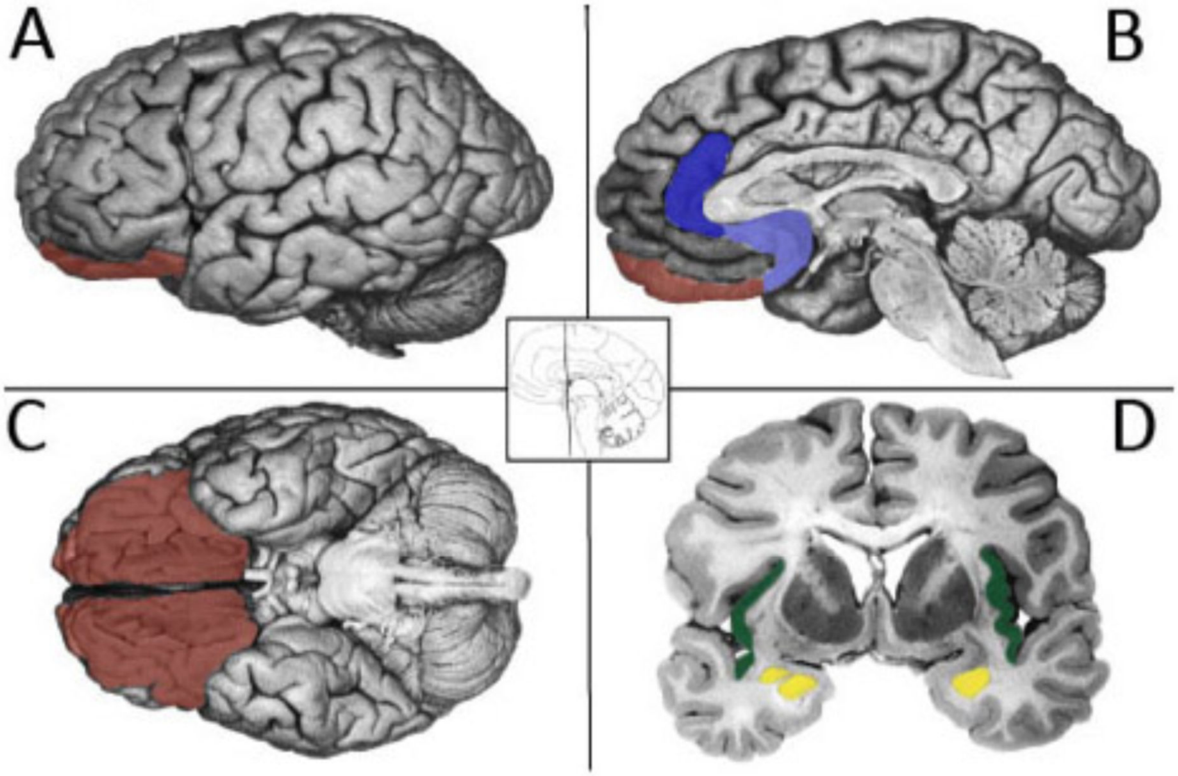

Figure 1. Locationist Hypotheses of Brain–Emotion Correspondence

A: Lateral view. B: Sagital view at the midline. C: Ventral view. D: Coronal view.

Brain regions hypothesized to be associated with emotion categories are depicted. Here we depict the most popular locationist hypotheses, although other locationist hypotheses of brain–emotion correspondence exist (e.g., Panksepp, 1998).

Fear: amygdala (yellow); *Disgust:* insula (green); *Anger:* OFC (rust); *Sadness:* ACC (blue)

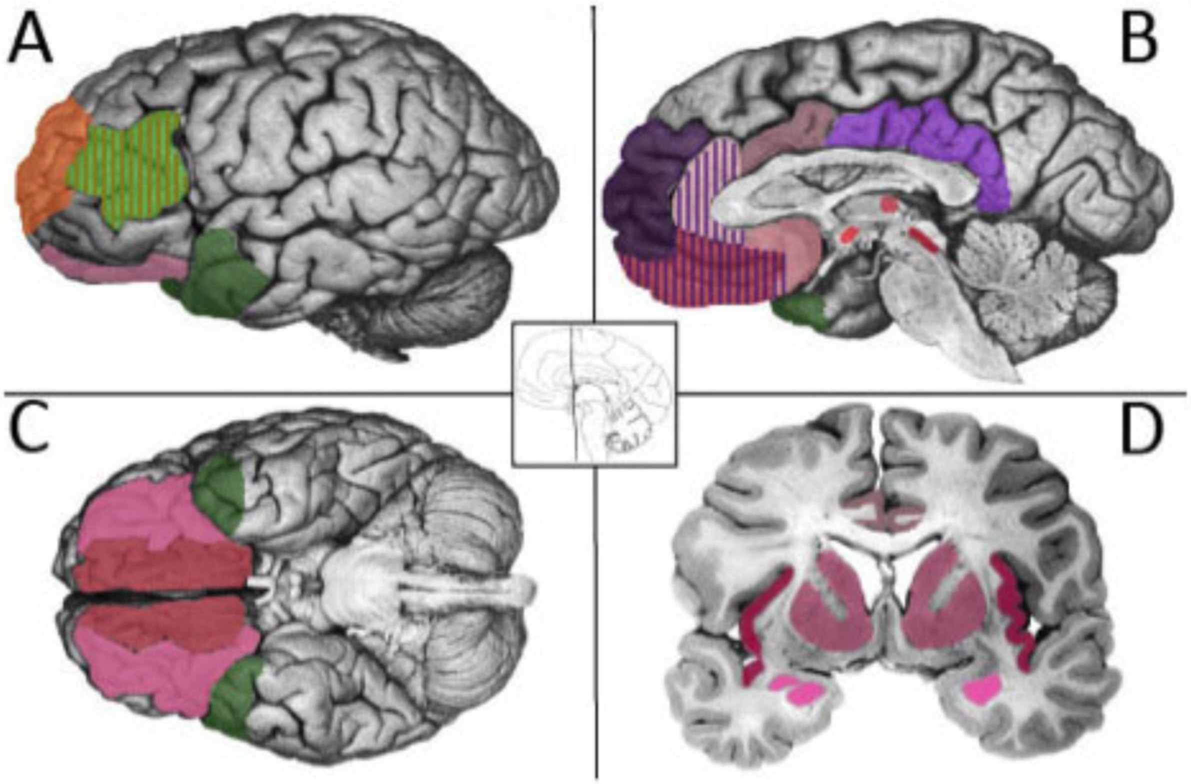

Figure 2. Psychological Constructionist Hypotheses of Brain–Emotion Correspondence

A: Lateral view. B: Sagital view at the midline. C: Ventral view. D: Coronal view. Brain regions hypothesized to be associated with psychological operations are depicted. In some cases, we present only the key brain regions within networks that have been empirically linked to our hypothesized psychological operations. In instances where the whole brain network is not depicted, we point readers to relevant literature. *Core Affect* (pink): amygdala, insula, mOFC (Bas 10m, 11m, 13a, b, 14r, c), lOFC (BAs 47, 12, 13l, m, 11l), ACC (Bas, 32, 24, 25), thalamus, hypothalamus, bed nucleus of the stria terminalis, basal forebrain, PAG. *Conceptualization* (purple): VMPFC (Bas 11, 25, 32, 34), DMPFC (BAs 9, 10p), medial temporal lobe* (hippocampus, entorhinal cortex, parahippocampal cortex), posterior cingulate cortex/retrosplenial area (BA 23, 31). *Language* (green): VLPFC (Bas 44, 45, 46), anterior temporal lobe (BA 38); for additional regions see Vigneau et al. (2006). *Executive Attention* (orange): DLPFC (BAs 9, 10, 46), VLPFC (BAs 44, 45, 46); for additional regions see Corbetta & Shulman, (2002); Dosenbach et al. (2006); Wager et al. (2004). (*this structure is not visible in this view of the brain).

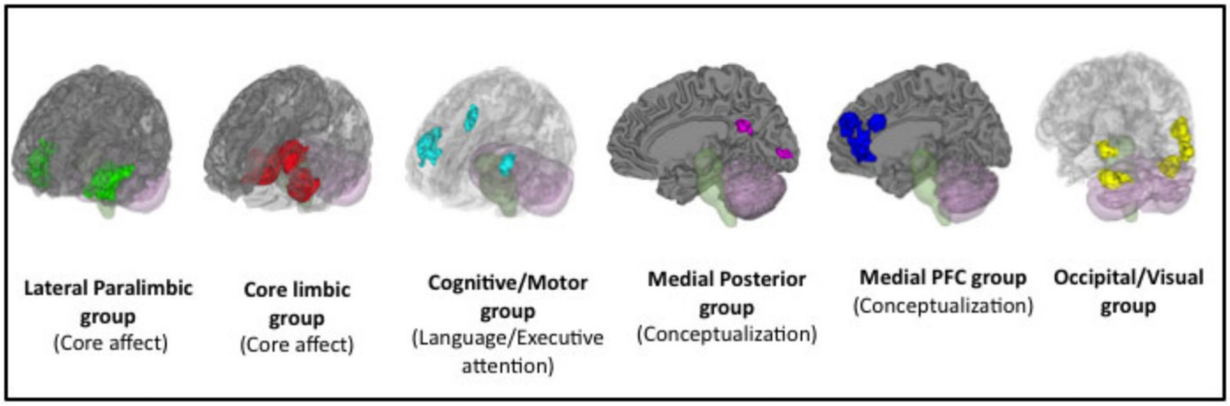

Figure 3. Kober et al.'s (2008) Functional Clusters

Kober et al.'s (2008) six functional clusters are consistent with the ingredients hypothesized by our psychological constructionist model. The brain areas making up the “core limbic group” and “lateral paralimbic group” are part of the network that helps to constitute core affect. Aspects of the “medial posterior group” and “medial PFC group” are part of the network involved with conceptualization. Areas in the “cognitive/motor control group” are consistent with the networks supporting language and executive attention. In addition, an “occipital/visual group” was also identified as part of the neural reference space for emotion. Visual cortex has connectivity with areas involved in core affect (e.g., amygdala, orbitofrontal cortex) Amaral & Price, 1982; Barrett & Bar, 2009; Pessoa & Adolphs, 2010), and there is growing evidence that a person's core affective state modulates activity in primary visual cortex (Damaraju et al, 2009). Core affect even shapes aspects of visual perception ranging from contrast sensitivity (Phelps et al. 2006) to visual awareness (Anderson et al. submitted).

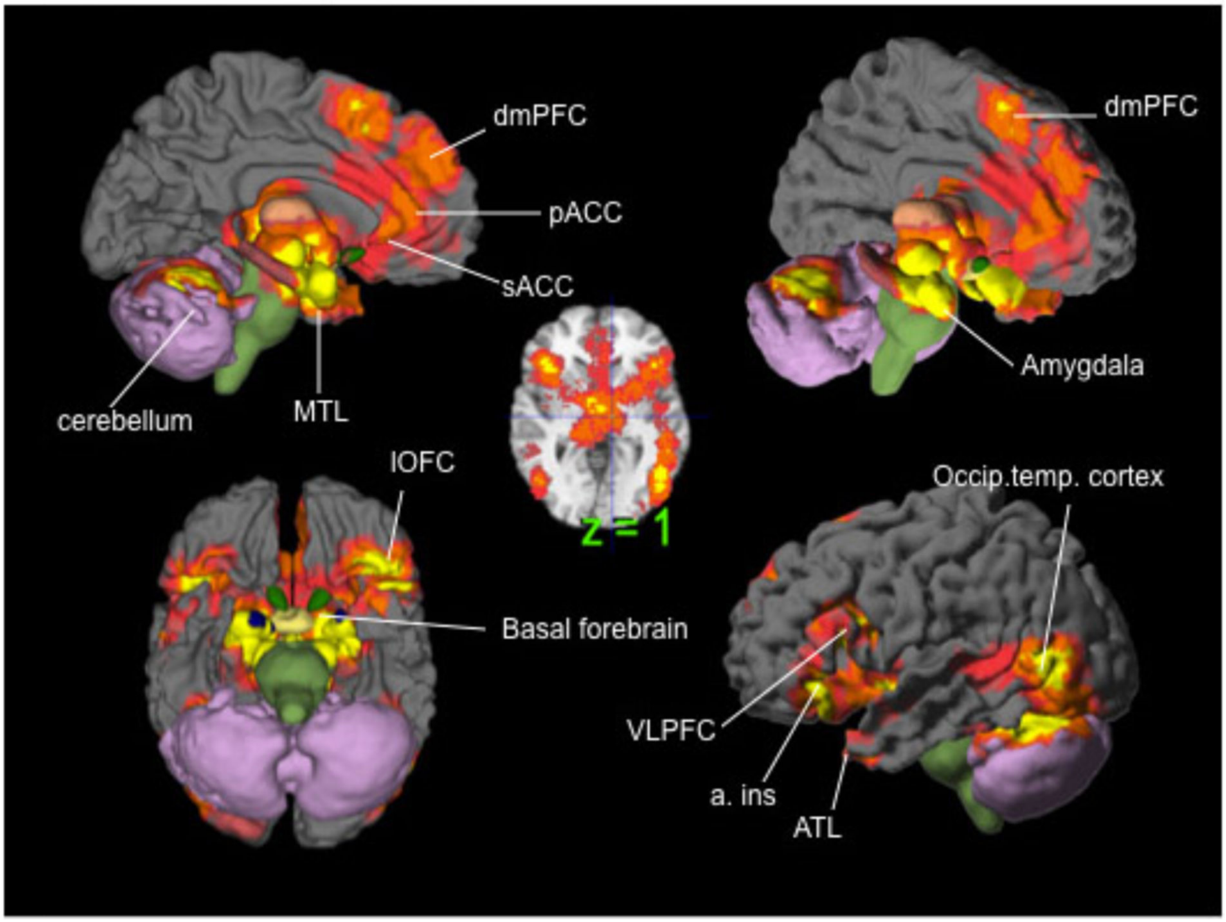

Figure 4. The Neural Reference Space for Discrete Emotion

The neural reference space (phrase coined by Edelman, 1989) is the set of brain regions consistently activated across all studies assessing the experience or perception of *anger, disgust, fear, happiness and sadness* (i.e. the superordinate category *emotion*). Brain regions in yellow exceeded the height threshold ($p < 05$) and regions in orange exceeded the most stringent extent-based threshold ($p < 001$). Regions in pink and magenta correspond to lesser extent-based thresholds and are not discussed in this article. Cortex is grey, the brainstem and nucleus accumbens are green, the amygdala is blue and the cerebellum is purple.

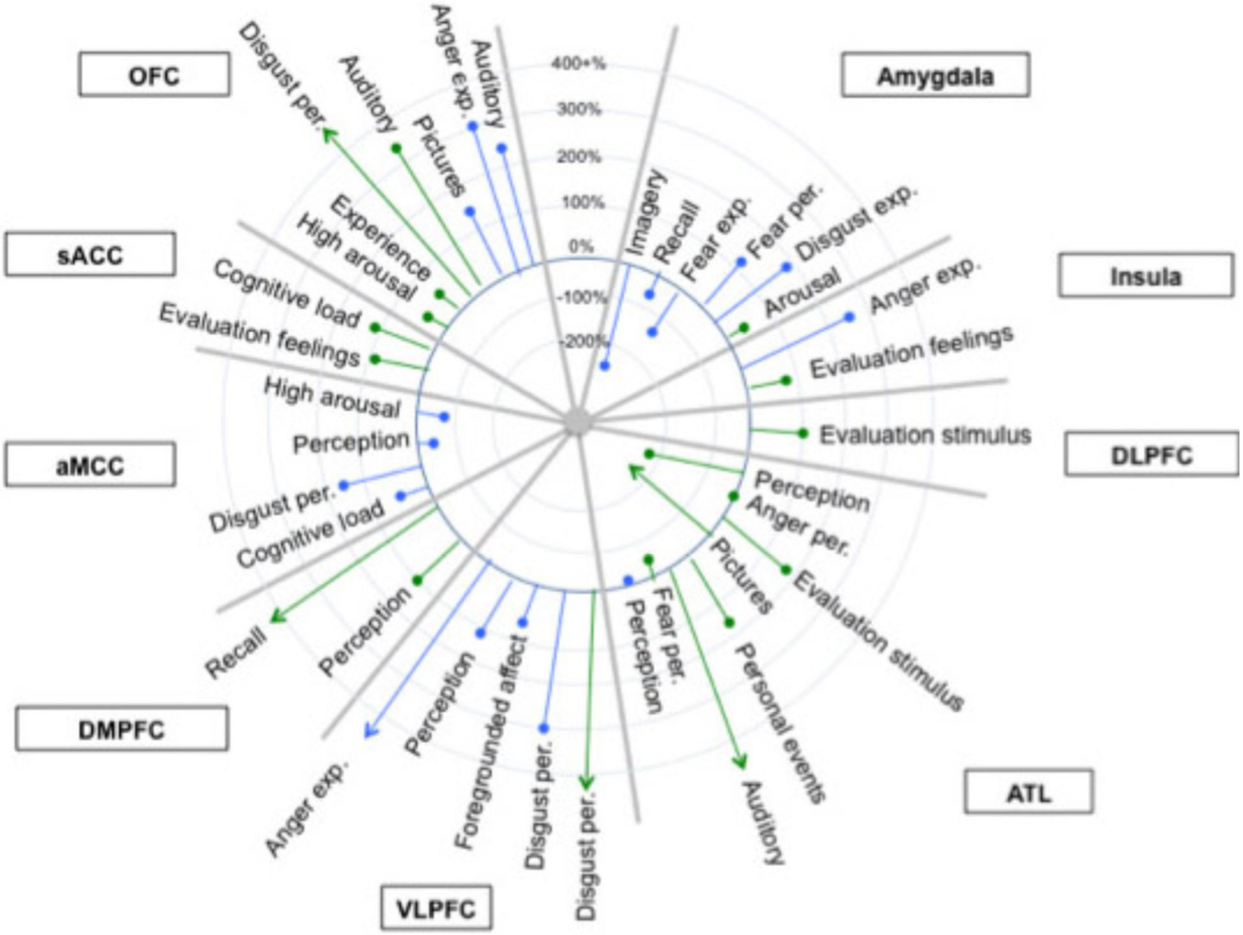

Figure 5. Logistic Regression Findings

Selected results from the logistic regressions are presented (for additional findings, see Table S6 in supplemenatary materials). Circles with positive values represent a 100% increase in the odds that a variable predicted an increase in activity in that brain area. Circles with negative values represent a 100% increase in the odds that a variable predicted there would not be an increase in activity in that brain area. **Legend:** Blue lines: left hemisphere; Green lines: right hemisphere. Arrowheads: % change in odds is greater than values represented in this figure. **Abbreviations:** OFC: orbitofrontal cortex; DLPFC: dorsolateral prefrontal cortex; ATL: anterior temporal lobe; VLPFC: ventrolateral prefrontal cortex; DMPFC: dorsomedial prefrontal cortex; aMCC: anterior mid-cingulate cortex; sAAC: subgenual ACC.

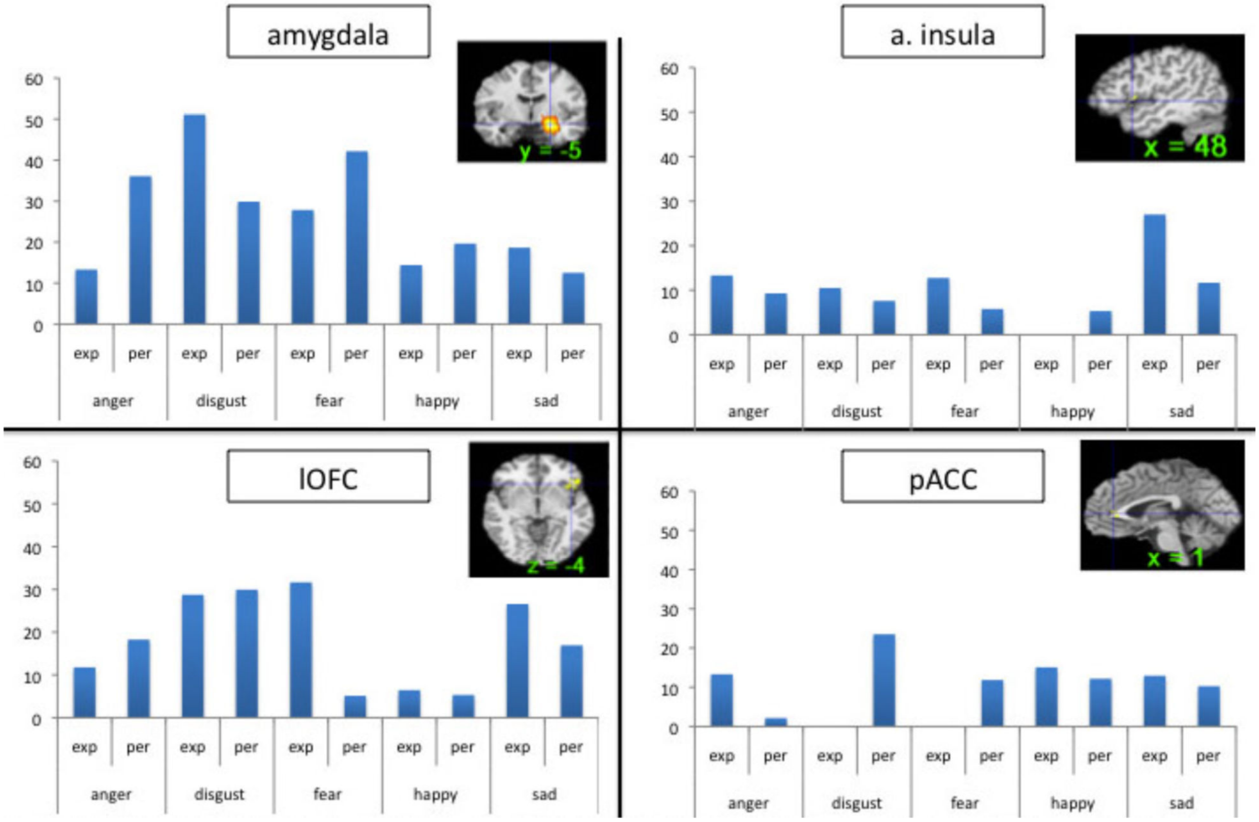

Figure 6. Proportion of Study Contrasts with Increased Activation in Four Key Brain Areas

The y-axes plot the proportion of study contrasts in our database that had increased activation within 10 mm of that brain area. The *x*-axes denote the contrast type separated by experience (exp) and perception (per). All brain regions depicted are in the right hemisphere. See Figure S2 and S3 in supplementary materials for additional regions.

Table 1

Brain Regions with a Consistent Increase in Activity Associated with the Experience or Perception of Discrete Emotion Categories in Density Analyses

Region	BA	Threshold	Contrast	Coordinates (MNI)			Volume (voxels)
				x	y	z	
Amygdala-Fear Hypothesis							
L. Amygdala		*Height*	Disgust experience	–32	–2	–20	2
				–20	–4	–22	124
			Fear perception	–30	–2	–24	1
				–24	–2	–12	360
			Sad perception	–30	–4	–20	1
R. Amygdala		*Height*	Disgust experience	26	0	–22	121
			Fear perception	24	–4	–12	250
Insula-Disgust Hypothesis							
L. a. insula		*Height*	Anger experience	–42	22	–2	2
		Extent	Disgust perception	–26	22	–12	252
R. a. insula/R. lOFC		*Height*	Disgust perception	38	20	4	37
OFC-Anger Hypothesis							
L. lOFC	11	*Height*	Disgust experience	–30	36	–18	167
ACC-Sadness Hypothesis							
aMCC	24	*Extent*	Fear perception	–2	16	22	196
Conceptualization							
L. dorsal entorhinal	34	*Height*	Disgust experience	–16	2	–16	1
				–18	0	–14	1
		Height	Sad experience	–24	2	–12	19
L. hippocampus		*Height*	Sad perception	–28	–10	–20	1
R. dorsal entorhinal	34	*Height*	Anger perception	18	–12	–16	27
		Height	Fear perception	14	–6	–12	1
DMPFC	9	*Extent*	Happy experience	–2	44	20	324
		Height	Sad experience	2	50	38	1
Executive control							
R. VLPFC	44	*Height*	Disgust perception	46	18	10	71
L. VLPFC	9	*Height*	Anger perception	–52	12	24	27
R. DLPFC	9	*Height*	Anger perception	54	22	28	130
Exteroceptive Sensory Processing							
R. parastriate	18	*Height*	Anger perception	52	–76	–2	2
				48	–76	0	1
				42	–86	2	3
		Height	Fear experience	8	–96	4	10
L. peristriate	19	*Extent*	Anger perception	–48	–80	–8	197

Region	**BA**	**Threshold**	**Contrast**	**Coordinates (MNI)**			**Volume (voxels)**
				x	**y**	**z**	
L. occipitotemporal	37	*Height*	Disgust experience	–44	–58	–12	7
		Extent	Anger perception	–44	–54	–20	232
				–50	–62	6	254
R. occipitotemporal	37	*Height*	Anger perception	44	–56	–24	1
				40	–56	–20	1
				40	–54	–14	7
L. middle temporal	21	*Height*	Fear experience	–52	–70	8	72
		Extent	Sad perception	–66	–48	8	323
R. middle temporal	21		Sad experience	52	–10	–16	2
Uncus		*Height*	Fear perception	–30	4	–22	5
Other							
R. SMA	6	*Height*	Anger perception	44	–2	56	1
R. putamen		*Height*	Sad experience	26	4	–4	1
				28	8	–2	3
				22	4	–2	1
PAG		*Height*	Sad experience	0	–38	–10	1

Table 2

Brain Regions with a Consistent Increase in Activity Associated with the Experience or Perception of Discrete Emotion Categories in χ^2 Analyses

Region	BA	Contrast	Coordinates (MNI)			Volume (voxels)
			x	y	z	
Amygdala-Fear Hypothesis						
L. Amygdala		Disgust experience	–20	–6	–24	50
			–32	–2	–20	2
R. Amygdala		Disgust experience	26	2	–20	59
Insula-Disgust Hypothesis						
L. a. insula		Anger experience	–44	20	–2	1
R. a. insula		Disgust perception	42	14	4	4
			34	20	6	3
			36	18	2	1
OFC-Anger Hypothesis						
L. lOFC	11	Disgust experience	–30	36	–18	167
R. lOFC	47	Disgust perception	38	22	0	8
Other regions in the neural reference space						
Conceptualization						
L. entorhinal cortex	34	Disgust experience	–26	–6	–20	1
		Sad experience	–24	2	–12	10
R. entorhinal cortex	34	Anger perception	16	–10	–16	23
DMPFC	9	Sad experience	2	50	38	1
Executive attention						
L. VLPFC	9	Anger perception	–52	14	24	27
R. VLPFC	44	Disgust perception	46	20	10	66
R. DLPFC	9	Anger perception	54	22	28	130
Exteroceptive Sensory Processing						
R. parastriate	18	Anger perception	52	–76	–2	2
			48	–76	0	1
			42	–86	2	3
		Fear experience	8	–96	4	10
L. occipitotemporal	37	Disgust experience	–46	–58	–14	1
			–42	–58	–10	1
R. occipitotemporal	37	Fear experience	48	–72	2	127
		Anger perception	44	–56	–24	1
			38	–52	–14	6
L. middle temporal	21	Fear experience	–52	–70	8	72
R. middle temporal	21	Sad experience	52	–10	–16	2
Other						

Region	BA	Contrast	Coordinates (MNI)			Volume (voxels)
			x	y	z	
R. SMA	6	Anger perception	44	–2	56	1
R. putamen		Sad experience	26	4	–4	1
			28	8	–2	3
			22	4	–2	1
PAG		Sad experience	0	–38	–10	1

Table 3

Summary of Brain Regions Showing Consistent Increases in Activation During Mental States and Methodological Manipulations

	Variable	Area
Mode	*Experience of emotion*	**R. lOFC**
	Perception of emotion	**DMPFC/dACC**
		R. hippocampus
		L. VLPFC
		R. peristriate
		R. occipitotemporal
Affect	*High arousal emotions*	**R. amygdala**
		R. lOFC
		PAG
	Unpleasant emotions	**L. peristriate**
Emotion	*Anger experience*	**L a. ins.***
		L. a. ins.
		L. lOFC
		L. VLPFC
		L. ATL
	Anger perception	**L. VLFPC***
		R. entorhinal cortex
		R. DLPFC
		R. parastriate
		R. occipitotemporal
		R. supplementary motor area
	Disgust experience	**L. amygdala***
		R. amygdala
		L. entorhinal cortex
		R. lOFC
		L. occipitotemporal*
	Disgust perception	**R. lOFC***
		R. a. ins
		aMCC
		L. VLPFC
		R. VLPFC*
		R. peristriate
		R. occipitotemporal
	Fear experience	**PAG**
		R. peristriate
		R. parastriate
		R. occipitotemporal*
		L. middle temporal

	Variable	Area
	Fear perception	**L. amygdala**
		L. entorhinal cortex
		R. entorhinal cortex
		L. hippocampus
		R. middle temporal
	Happiness experience	**L. peristriate**
	Sadness experience	L. entorhinal cortex
		DMPFC
		R. middle temporal
		R. putamen
		PAG
Method Types	*Recall*	**pACC**
		DMPFC/aMCC
	Auditory	**R. lOFC**
		R. VLPFC
		R. ATL
	Imagery	**R. occipitotemporal**
		R. middle temporal
	Visual	**R. peristriate**
		L. occipitotemporal
Stimuli	*Pictures*	**L. lOFC**
		R. peristriate
		R. occipitotemporal
	Faces	**L. VLPFC**
	Films	**DMPFC/aMCC**
		L. peristriate
		R. occipitotemporal
		R. middle temporal
Other Psychological Variables	*Evaluation of feelings*	**R. a. ins**
		sACC
	Evaluation of stimulus	**R. ATL**
		R. DLPFC
		PAG
		L. peristriate
		L. occipitotemporal
	Foregrounded affect	**L. VLPFC**
		L. peristriate
	Cognitive load	**sACC**
		aMCC

Mental states include states related to experiencing versus *perceiving discrete emotions, the experience and perception of affect, the experience or perception of individual discrete emotion categories, and mental states related to method types, stimulus types and other psychological variables. Brain regions consistently associated with mental states in the* χ^2 *analyses and logistic regressions are listed. Mental state-brain associations* *observed in the χ^2 analyses are printed in regular font. Logistic regression findings are in bold face font. Mental state-brain region associations observed in both types of analyses are marked with an asterisk (*).*