

Neural Evidence That Human Emotions Share Core Affective Properties

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Psychological Science
 XX(X) 1–10
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 sagepub.com/journalsPermissions.nav
 DOI: 10.1177/0956797612464242
 pss.sagepub.com


Abstract

Research on the “emotional brain” remains centered around the idea that emotions like fear, happiness, and sadness result from specialized and distinct neural circuitry. Accumulating behavioral and physiological evidence suggests, instead, that emotions are grounded in *core affect*—a person’s fluctuating level of pleasant or unpleasant arousal. A neuroimaging study revealed that participants’ subjective ratings of valence (i.e., pleasure/displeasure) and of arousal evoked by various fear, happiness, and sadness experiences correlated with neural activity in specific brain regions (orbitofrontal cortex and amygdala, respectively). We observed these correlations across diverse instances within each emotion category, as well as across instances from all three categories. Consistent with a psychological construction approach to emotion, the results suggest that neural circuitry realizes more basic processes across discrete emotions. The implicated brain regions regulate the body to deal with the world, producing the affective changes at the core of emotions and many other psychological phenomena.

Keywords

emotions, brain, neuroimaging

Received 5/8/12; Revision accepted 9/18/12

Emotion research focuses predominantly on the idea that a limited number of emotions (e.g., fear, sadness, happiness, anger, disgust) are psychologically and biologically basic (e.g., Ekman, 1999). This view is widespread in psychology, providing inspiration for everything from interventions for psychopathology to popular television shows. Yet recent reviews of accumulating behavioral, psychophysiological, and neural evidence question this theoretical perspective (e.g., Barrett, 2006; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). An emerging alternative view is that diverse human emotions result from the interplay of more basic “ingredients,” namely, domain-general processes that contribute to many psychological phenomena (including discrete emotions; e.g., Barrett, 2009a). One such ingredient in this *psychological construction* approach is *core affect* (Barrett & Bliss-Moreau, 2009), characterized as simple feelings of valence and arousal (Russell, 2003; Wundt, 1897/1998). Here, we present neural evidence that sadness, fear, and happiness experiences share core affective properties.

The hypothesis that emotions are grounded in continuous and fluctuating affective states described as pleasant

or unpleasant, with some level of arousal, is as old as psychological science itself (cf. Wundt, 1897/1998). Recent formulations of this hypothesis refer to these states as *core affect* (Russell, 2003; Russell & Barrett, 1999) because they arise in the core of the body (or representations of change in body state). Core affect is detectable in the face (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000), in the voice (Russell, Bachorowski, & Fernandez-Dols, 2003), in peripheral nervous system activation (Cacioppo et al., 2000), and in reports of subjective experience (Barrett, 2004). The capacity to experience core affect is psychologically universal (Mesquita, 2003; Russell, 1991) and present in infants (M. Lewis, 2000), although many of the sensory patterns that predict pleasure and pain are learned through experience. Physiologists, neuroscientists, and economists alike consider core affect a common mental currency that underlies decision making, choice, and

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action (Cabanac, 2002; Damasio, 1999; Grabenhorst & Rolls, 2011).

Amidst this progress in understanding the nature and functions of core affect, understanding of its exact relation to the experience of emotion remains limited by a key assumption. Studies often confound core affect and emotion by assuming that each emotion category is associated with a specific core affective state: Fear is an unpleasant, high-arousal state; sadness is an unpleasant, mid- to low-arousal state; and happiness is a pleasant, mid- to low-arousal state. Yet the core affective feelings evoked during an emotion depend on the situation (and how the situation is conceptualized): For example, fear can be pleasant and highly arousing when one is rocketing downward in a rollercoaster car, unpleasant and less arousing when one is detecting the first bodily signs of the flu, and so on (Barrett, 2009b; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011).

In this study, we assessed the relationship between each participant's core affective ratings and his or her brain activity *within*, as well as across, the emotion categories of fear, happiness, and sadness. Capitalizing on the normal variability in the emotion experiences of everyday life, for each emotion category we developed familiar scenarios that systematically varied in valence and arousal. Although fear, happiness, and sadness are typically studied as either unpleasant or pleasant (and sometimes as either high or low arousal), we created within each emotion category both unpleasant and pleasant scenarios that varied in arousal. This novel stimulus set included scenarios describing the pleasant fear of thrill seeking, the pleasant sadness of nostalgia, and the unpleasant happiness of unshared success. Thus, we investigated core affect as a dynamic ingredient of emotional experience that varies within an emotion category (e.g., fear can be pleasant or unpleasant and more or less arousing) rather than as a one-to-one description of the category (e.g., fear is unpleasant and highly arousing).

Manipulating core affect within each emotion category, we examined whether the affective feelings evoked by diverse instances of fear, happiness, and sadness are grounded in a common neural system. We first predicted that the varying experience of valence (i.e., participants' ratings of felt pleasure/displeasure) across the fear, happiness, and sadness scenarios would correlate with activity in orbitofrontal cortex (OFC), a region implicated in many studies of reward and value (for reviews, see Grabenhorst & Rolls, 2011; Kringelbach & Rolls, 2004). Critically, we further predicted that this correlation between valence ratings and OFC activity would also be observed within each emotion category, which we could test because we designed the scenarios in each category to evoke emotional experiences varying in hedonic valence. Our second prediction was that the varying

experience of arousal across the fear, happiness, and sadness scenarios would correlate with activity in the amygdala, a region implicated in detecting and coordinating responses to motivationally salient positive and negative events (for reviews, see Costafreda, Brammer, David, & Fu, 2008; Lindquist et al., 2012). We further predicted that this correlation between arousal ratings and amygdala activity would also be observed within each emotion category, which we could test because we designed the scenarios in each category to evoke emotional experiences varying in arousal. As part of a network that represents and regulates the body, OFC and the amygdala, specifically, are uniquely positioned to coordinate bodily responses dynamically as interpretations of the external world unfold (Barrett & Bliss-Moreau, 2009).

Method

Participants

Sixteen right-handed, native English speakers ranging in age from 19 to 30 (8 female, 8 male) received \$100 in compensation. Participants had no history of psychiatric illness and were not taking psychotropic medication.

Neuroimaging design

The functional MRI (fMRI) paradigm was designed to evoke affective feelings through immersion in scenarios depicting real-world fear, happiness, and sadness experiences (Wilson-Mendenhall et al., 2011). Emotion-induction techniques that draw on the imagination are powerful, often producing changes in cognition, experience, behavior, and physiology that rival those produced by real-life manipulations (for a review, see Lench, Flores, & Bench, 2011). Furthermore, the neural overlap observed during imagery and perception suggests that the brain easily emulates how it feels to experience events in the real world (e.g., Kosslyn, Ganis, & Thompson, 2001).

We included two critical trial types in our design to separate neural activity associated with the emotion-induction process from neural activity associated with the affect evoked during the emotion (see Fig. S1a in the Supplemental Material available online). In 144 *complete* trials, participants first immersed themselves in a scenario designed to induce fear, happiness, or sadness (i.e., scenario event) and then focused on and rated the valence or arousal quality of the evoked feeling (i.e., valence or arousal focus event). We instructed participants to focus on their internal feeling state before rating it because empirical evidence shows that attention enhances sensory detection and discrimination (Chun, Golomb, & Turk-Browne, 2011). In 36 *partial* trials, participants immersed themselves in a scenario, but did not focus on

or rate their affective experience. The partial trials, whose occurrence was unpredictable, were critical for mathematically separating neural activity during scenario immersion (which occurred in both complete and partial trials) from neural activity during the subsequent valence or arousal focus event (which occurred only in complete trials; Ollinger, Corbetta, & Shulman, 2001; Ollinger, Shulman, & Corbetta, 2001). Because our hypotheses concerned the core affective feelings evoked during emotions, all brain activations reported here reflect brain activity during the focus events that occurred once an emotion was induced.

In each of the six runs in the neuroimaging experiment, complete and partial trials from six critical conditions were presented. These conditions were created by crossing affective dimension (valence or arousal) with emotion category (fear, happiness, or sadness). To encourage swift immersion and to facilitate focusing on a specific affective dimension of the emotional experience, we blocked trials by affective dimension (i.e., during valence blocks, participants focused on and rated valence, and during arousal blocks, they focused on and rated arousal). One arousal block and one valence block were presented in each run, with block order counterbalanced across runs (see Fig. S1b and the Versions of the Experiment section in the Supplemental Material available online). Within each block, four complete trials per category and one partial trial per category were presented in a pseudorandom order amidst baseline no-sound periods with jittered durations (ranging from 3 to 15 s in increments of 3 s; average baseline period = 6.3 s). Trial sequences were optimized using *optseq2* software (Greve, 2002).

Materials

During training sessions and during the scan session, participants listened to scenarios designed to induce fear, sadness, and happiness (see Table 1 for examples and the Appendix in the Supplemental Material for the complete stimulus set). The full, paragraph-long form of each scenario provided a richly detailed and affectively compelling description of an event inducing fear, sadness, or happiness, to guide vivid immersion during training sessions. A corresponding shortened, core form of each scenario served to minimize presentation time in the scanner so that the number of trials necessary for a powerful design could be implemented. In both forms, the scenarios included an explicit categorization of the emotional state as fear, sadness, or happiness, to avoid ambiguity.

To vary the core affective properties as much as possible within each emotion category, we developed scenarios to evoke typical valence (i.e., unpleasant fear, pleasant happiness, and unpleasant sadness) and atypical valence (i.e., pleasant fear, unpleasant happiness, and

pleasant sadness; see Table 1). The atypical scenarios described familiar experiences, such as the pleasant fear involved in zooming downward on a rollercoaster or encountering a secret crush, the pleasant sadness involved in inspiring others through one's own loss or unwinding after sacrificing the evening to work, and the unpleasant happiness involved in confronting a surly colleague or being unable to share good news. Ratings collected during the training sessions validated that the emotions induced by the typical and atypical scenarios were familiar and relatively easy to imagine from a first-person perspective (Fig. S2 in the Supplemental Material). Variation in arousal was similarly introduced through the nature of the events and through vivid descriptions of actions and physiological reactions. (See the Scenarios section in the Supplemental Material for details on the construction and selection of scenarios.)

Procedure

The experiment consisted of two training sessions and an fMRI scan session. The first training session occurred 24 to 48 hr before the second training session, which occurred just prior to the scan session (Fig. S1c). The training sessions were designed to give participants practice vividly imagining the full versions of the scenarios they would hear later during practice trials and in the scanner, when they would reinstate the rich imagery of each full scenario upon hearing the core version, and focus on and rate the valence or arousal quality of the feeling state induced by the scenario. During the first training session, participants listened to the full versions of the scenarios, immersing themselves with eyes closed, and rated their personal familiarity with each induced emotion. After a short break, they listened to the core versions of the same scenarios, reinstating imagined details from the full versions, and then rated the internal, external, and thought imagery they experienced (which further encouraged immersion in the imagined scenarios).

When participants returned to the lab 24 to 48 hr later, they began the second training session by listening to and vividly imagining each full scenario again. For each scenario, they provided one rating of how much they experienced "being there," immersed in the feeling of fear, happiness, or sadness described in the scenario. Having participants imagine the full versions in the second training session ensured that participants were reacquainted with the details of the scenarios just prior to hearing the core versions during the scan session.

During the second part of this training session, participants practiced the task that they would perform in the scanner, using scenarios that were not included in the critical scans. The trial structures were as follows. During the 15-s complete trials, participants first listened to the core version of a scenario that lasted no longer than 8 s.

Table 1. Examples of the Fear, Happiness, and Sadness Scenarios

Valence	High arousal	Low arousal
Pleasant	<p><i>You are sitting stiffly in a rollercoaster car, creeping up one click at a time. You reach the peak of the hill and are suddenly whizzing downwards. Your heart is pounding and your stomach drops as crisp air blasts your face. You delight in the uncontrollable rush dipping and swirling high above the ground. You feel an invigorating fear.</i></p> <p><i>You are performing a challenging piano solo, your fingers working the keys. You finish the piece and receive thunderous applause as you rise. You bend at the waist into a deep bow and sense your heart thumping rapidly. Glowing with satisfaction, you continue to feed off the crowd's energy. You feel a proud happiness.</i></p> <p><i>You are running in a charity race, your first time covering this long a distance. You see the finish line and remember your aunt's lost battle with cancer. Covered in sweat and heart pumping, you pick up your pace. The cheerful chanting ahead instills an overwhelming sense of courage. You feel a beneficial sadness.</i></p>	<p><i>You are sipping punch at a school reunion, scanning the growing crowd. You notice your high school crush from across the room returning your gaze. Your crush looks away and you smile to yourself in the private moment. A soft amusement begins to arise as your mind becomes lost in a familiar fantasy. You feel a lovely fear.</i></p> <p><i>You are lounging on a cushy floor pillow, opening a new magazine. You glance up as your puppy trots over and wiggles into your lap. As her small body relaxes, you sense both your hearts beating evenly. Tenderly petting her soft fur cultivates a lovely sense of ease. You feel an affectionate happiness.</i></p> <p><i>You are inching under the sheets, slowly getting settled at the late hour. You long for a good night's sleep after spending all your waking hours working. You sense your stiff neck relax as you rest your head on a pillow. You curl up and let go of the day, finally a moment of lovely calm. You feel a peaceful sadness.</i></p>
Unpleasant	<p><i>You are walking to your car alone, the city parking deck dimly lit. You bear an explosive bang and see a man running with a pointed gun. You quickly drop behind a car and attempt to control your shallow breathing. You try to dismiss the horrendous vision of what will happen if he finds you. You feel a perilous fear.</i></p> <p><i>You are walking down the hall, trying to get to a meeting on time. You run into a difficult colleague and end a tense exchange with a biting remark. Your stomach tightens the moment the last sarcastic jab escapes your lips. The cutting retort echoes poisonously in your head as your colleague sulks away. You feel a disturbing happiness.</i></p> <p><i>You are walking into a friend's house, dropping by to return a movie. You witness your significant other in an intimate embrace with your friend. Your stomach is nauseated, the shocking infidelity settling into your body. Your mind is spinning trying to understand the terrible betrayal of trust. You feel a devastating sadness.</i></p>	<p><i>You are sitting down after lunch out, your desktop reappearing at your touch. You notice a pressing e-mail from your boss that you forgot to address. Taking a deep breath, you lengthen your spine in an attempt to reenergize. You slowly re-read the message with the burden of responding quickly. You feel an inconvenient fear.</i></p> <p><i>You are rocking in your favorite chair, gently flipping your cell phone open and closed. You want to share a recent promotion with your brother who is unavailable overseas. Wishing you could call him, you close your eyes and release a held breath. You continue fiddling with your phone, a tender solitude clouding your mind. You feel a lonely happiness.</i></p> <p><i>You are sitting at the table, spooning a heap of food on your plate. You taste the casserole made from a new recipe and are disappointed. Setting down your fork momentarily, you hear your stomach quietly rumbling. You look at your plate and avoid taking another bite of disagreeable blandness. You feel a dissatisfied sadness.</i></p>

Note: Italics signify the core forms of the scenarios, which were presented during the scan session. Each scenario referred explicitly to the emotion induced, as indicated by the words in boldface.

A sequence of three beeps (1 s) following each scenario indicated that immersion in the emotional experience should continue as participants centered on the valence or arousal quality of the feeling (depending on the block), maintaining focus for 3 s. Finally, the sound of a cowbell (1 s) cued participants to rate their introspective sense of valence or arousal within the next 2 s, using the

appropriate scale. During the 9-s partial trials, participants also listened to the core version of a scenario (again, no more than 8 s in duration); a 1-s "whoosh" sound following the scenario signified the end of the trial. During baseline rest periods, participants cleared their mind during the 3- to 15-s period of no sound as they waited to hear the next scenario begin.

Participants were informed that one block of valence trials and one block of arousal trials would occur in each imaging run (with the cue word “valence” or “arousal” indicating the start of each block) and that they should immerse themselves fully, with their eyes closed, as they listened to the scenarios. After receiving these instructions, participants completed several practice complete trials and then several practice partial trials with their eyes closed. During the complete trials, participants used E-Prime (Psychology Software Tools, Pittsburgh, PA) button boxes to make their valence and arousal ratings. At this point, they had received much practice using button boxes to make ratings on the 5-point valence scale (*very unpleasant, somewhat unpleasant, neutral, somewhat pleasant, very pleasant*) and the 5-point arousal scale (*low, medium-low, medium, medium-high, high*) with their eyes closed (see the Training Procedure section in the Supplemental Material for more details on all training procedures). Participants then practiced several short arousal and valence blocks in which the complete and partial trials were intermixed with baseline periods, much as they would be in the critical scans.

Following training, participants completed the scan session. Once a participant was situated comfortably in the scanner, an initial anatomical scan was collected. The participant was then briefly reminded of the task and of the valence and arousal scales. When the participant was ready, the experimenter initiated the first functional task run and then continued with the next five runs, pausing for short breaks between runs. During complete trials, participants responded using button boxes designed for high-magnetic-field environments. A second anatomical scan was collected last. Total time spent in the scanner was a little over an hour.

Imaging and analysis

Images were collected at the Emory Biomedical Imaging Technology Center on a 3-T Siemens Trio scanner and preprocessed using standard methods in AFNI (Cox, 1996; see the Image Acquisition and Preprocessing section in the Supplemental Material for details). Two critical regression analyses were performed on each participant's preprocessed data; in these analyses, canonical gamma functions were convolved with boxcar functions reflecting event duration to model the hemodynamic response. In the first analysis, the onset times were specified for five conditions: cues beginning the blocks, scenario events during valence blocks, scenario events during arousal blocks, focus events during valence blocks, and focus events during arousal blocks. Scenario events corresponded to the 9 s during which participants immersed themselves in a scenario and heard the brief auditory cue that followed; both complete and partial trials included

scenario events. Modeling the scenario events from the complete and partial trials in each type of block as a single condition allowed for the mathematical separation of the scenario events from the focus events during complete trials. The focus events included the 6 s during which participants focused on and rated the valence or arousal quality of the evoked feeling.

Each participant's valence ratings were specified trial by trial in the valence-focus blocks, using the following numerical codes: 1 = *very unpleasant*, 2 = *somewhat unpleasant*, 3 = *neutral*, 4 = *somewhat pleasant*, 5 = *very pleasant*. Similarly, each participant's arousal ratings were specified trial by trial in the arousal-focus blocks, using the following numerical codes: 1 = *low*, 2 = *medium-low*, 3 = *medium*, 4 = *medium-high*, 5 = *high*. Any missing rating was replaced with the participant's mean rating (1% of trials on average). For the focus conditions, both the onset times for the focus events and the corresponding ratings were entered into the regression analysis using the amplitude modulation option in AFNI. This option specified two regressors for each focus condition; these regressors were used to detect (a) voxels in which activity was correlated with the ratings (a parametric regressor) and (b) voxels in which activity was constant for the condition and was not correlated with the ratings.

Next, each participant's betas produced from the parametric regressors for the two focus conditions (i.e., betas indicating the strength of the correlations with the valence and with the arousal ratings) were entered into random-effects group analyses. In this analysis, the critical statistic for each condition was a *t* test indicating if the mean across subjects differed significantly from zero (zero indicating no correlation between brain activity and the ratings). To test our regional hypotheses, we computed the group analysis within anatomical masks of OFC and of the amygdala (Eickhoff et al., 2005). A voxel-wise threshold of $p < .005$ was used in conjunction with an extent threshold that produced a corrected threshold of $p < .05$ within each mask (12 voxels for medial OFC, 9 voxels for lateral OFC, 3 voxels for amygdala).

Any significant cluster identified in the first analysis was used to mask a second analysis, which analyzed the emotion categories separately. The critical difference from the first analysis was that the scenario and focus events were divided into three conditions—for the emotion categories of fear, happiness, and sadness. Otherwise the second analysis was exactly the same as the first. Table S1 in the Supplemental Material provides descriptive statistics for the valence and arousal ratings for each emotion category. Participants' betas produced from the parametric regressors for the six focus conditions (i.e., fear-valence, happiness-valence, sadness-valence, fear-arousal, happiness-arousal, sadness-arousal) were then

entered into a random-effects group analysis following the same procedure as in the first analysis. At the group level, voxel-wise t statistics representing significant correlations with valence and arousal ratings for the three categories ($p < .05$) were entered into a conjunction analysis. The conjunction was computed only within clusters identified in the first analysis to determine if these voxels were significantly correlated with valence or arousal in each emotion category. This key analysis allowed us to examine whether each voxel that correlated with valence or arousal in the first analysis, which was conducted across categories, was correlated with valence or arousal in one or more emotion categories when each category was modeled separately.

Results

Valence

We predicted, and found, that neural activity in OFC correlated with ratings of subjective valence both across and within the three emotion categories. Activity in medial OFC correlated significantly with valence ratings when we collapsed the data across all fear, happiness, and sadness scenarios ($p < .005$; peak: $x = -2$, $y = 38$, $z = -13$; 24 voxels).¹ Illustrated in Figure 1a, activity in this medial OFC cluster increased as the unpleasantness that participants experienced decreased and as the pleasantness they experienced increased (i.e., activity was positively correlated with the bipolar valence scale, in which higher ratings indicated more pleasantness).

Remarkably, this correlation held within each emotion category when the three emotion categories were modeled independently ($p < .05$ for each category). Within the medial OFC cluster identified from the correlation across categories, the activity in 92% of the voxels showed a significant correlation with the valence ratings of at least one emotion category, and the activity in 50% of the voxels correlated with valence ratings in more than one emotion category (Fig. 1b). Taken together, these results show that as activity changes in medial OFC, so does the subjective experience of valence (i.e., pleasure/displeasure) during all three emotions. Because this result was observed independently within three emotion categories, our findings suggest that valence is a basic property of human emotional experience.

Whereas some theories postulate that qualitatively different systems support positive and negative evaluation (e.g., Cacioppo, Gardner, & Berntson, 1997), other theories emphasize that multiple sources of value information must be compared and integrated for action selection (e.g., Barrett & Bliss-Moreau, 2009; Cabanac, 2002). To determine if medial OFC activity was driven by positive affect, negative affect, or both, we recoded the ratings to reflect unipolar scales, one weighted for pleasant

intensity (2 = very pleasant, 1 = somewhat pleasant, 0 = neutral, somewhat unpleasant, or very unpleasant) and the other weighted for unpleasant intensity (2 = very unpleasant, 1 = somewhat unpleasant, 0 = neutral, somewhat pleasant, or very pleasant). For both unipolar codings, correlations in medial OFC were observed, and these correlations were in the same direction as found using the original bipolar coding; activity increased as participants experienced more pleasantness (i.e., positive correlation with the pleasant-intensity scale; $p < .005$; peak: $x = -2$, $y = 44$, $z = -4$; 36 voxels) and less unpleasantness (i.e., negative correlation with the unpleasant-intensity scale; $p < .005$, peak: $x = -2$, $y = 32$, $z = -16$; 19 voxels).

As illustrated in Figure 1c, however, differences emerged in the spatial location of the correlations within medial OFC: Ratings reflecting the weighting of pleasantness correlated with activity in the superior aspect of medial OFC, whereas ratings reflecting the weighting of unpleasantness correlated with activity in the inferior aspect of medial OFC. Figure 1c also illustrates that the cluster in which the original bipolar ratings correlated with neural activity overlapped centrally with the clusters in which the unipolar ratings correlated with neural activity. Animal work has revealed somewhat similar valence gradients in subcortical structures tightly coupled with action (e.g., bivalent rostrocaudal gradients in the nucleus accumbens shell; Reynolds & Berridge, 2002). To our knowledge, this is the first time such an inferior-superior cortical gradient for affective valence has been identified in humans.

Arousal

We predicted, and found, that neural activity in the amygdala correlated with subjective arousal ratings both across and within the three emotion categories. Activity in left amygdala correlated significantly with arousal ratings when we collapsed the data across all fear, sadness, and happiness scenarios ($p < .005$; peak: $x = -23$, $y = -2$, $z = -10$; 6 voxels).² Illustrated in Figure 2a, activity in this amygdala cluster increased as subjective arousal experiences became more intense.

This correlation held within the sadness and happiness categories (but not within fear) when each category was modeled independently ($p < .05$ for each category; Fig. 2b). Although the arousal ratings varied substantially within each category (see Table S1), the arousal ratings for scenarios inducing fear varied less than the arousal ratings for scenarios inducing happiness or sadness (Levene's test, $p < .05$), with fear scenarios rated more arousing on average ($M = 4.13$) than happiness scenarios ($M = 3.40$) or sadness scenarios ($M = 3.38$). We addressed this restriction of range within the fear category by conducting a follow-up analysis that split each category into

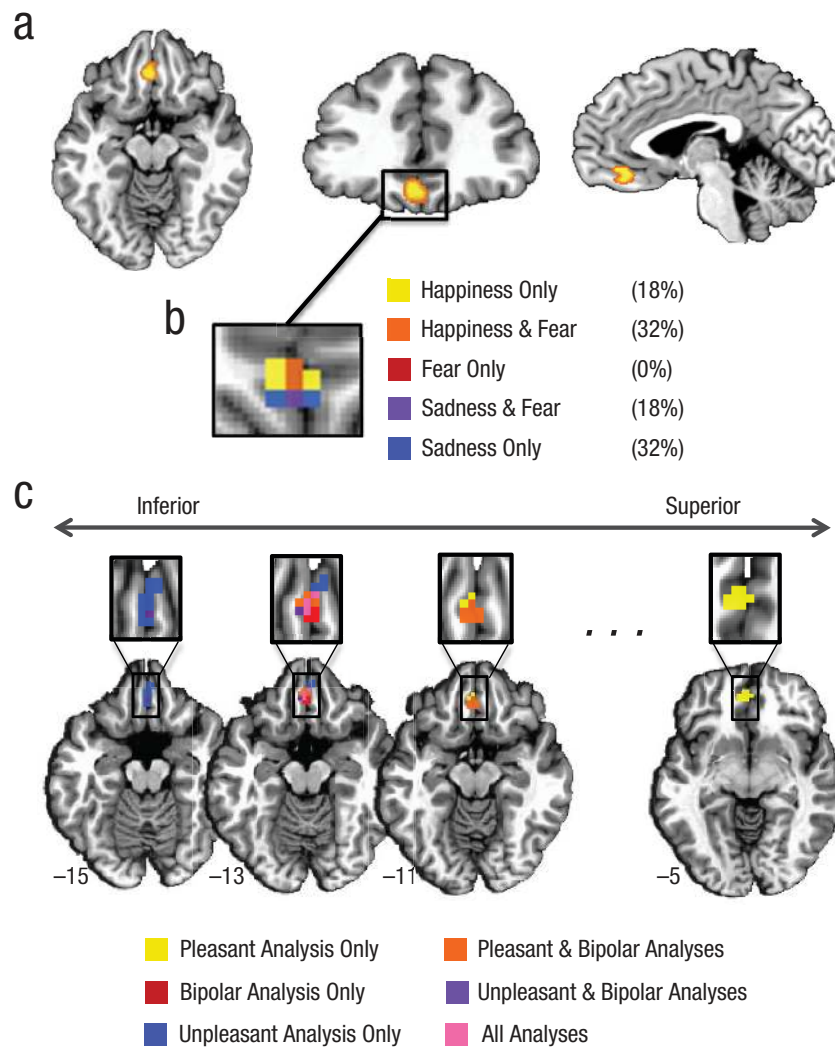


Fig. 1. Valence results in orbitofrontal cortex (OFC). The images in (a) show the location of the medial OFC cluster in which activity correlated positively with the bipolar valence ratings across the three emotion categories; from left to right, axial ($z = -11$), coronal ($y = 34$), and sagittal ($x = -2$) views are shown. The enlarged section (b) shows the within-category results (i.e., voxels in which activity correlated with valence ratings within each emotion category). The percentages indicate the percentage of voxels in which activity correlated with valence ratings across the entire three-dimensional cluster (not just the slice displayed). The images in (c) show the results of a conjunction analysis of the three medial OFC clusters observed in the unipolar-focused and bipolar valence analyses (across categories); from left to right, these axial slices are arranged from inferior to superior. The ellipsis signifies that the results for axial slices between -11 and -5 look very similar to the results shown for the slice at -11 .

(relatively) high- and low-arousal conditions (see the Supplemental Material for details). As Figure 2c illustrates, left amygdala activity was significantly greater in the high- than in the low-arousal condition for fear, as well as for the other emotion categories ($p < .05$). Taken together, these analyses show that as activity changes in left amygdala, so does the subjective experience of arousal during all three emotions. Because this result was observed independently within three emotion categories,

our findings suggest that arousal is a basic property of human emotional experience.

Discussion

Our results support the century-old scientific hypothesis that core affect is a common building block of emotion experience, showing that subjective ratings of core affect correlate with brain activity both within and across

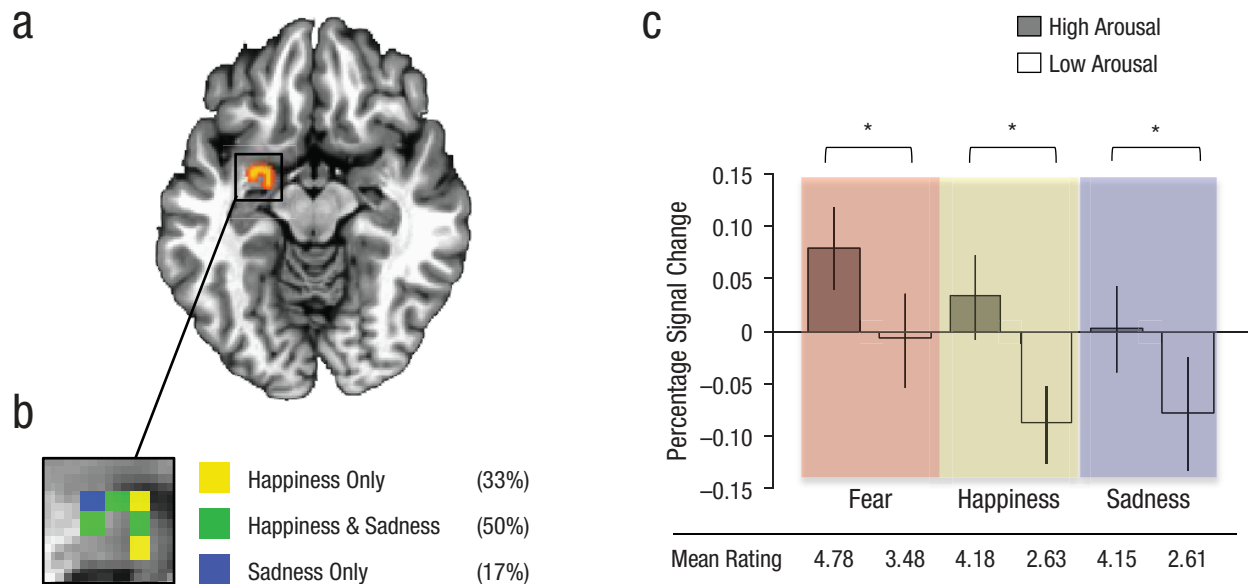


Fig. 2. Arousal results in the amygdala. The image in (a) shows the location of the left amygdala cluster in which activity correlated positively with arousal ratings across the three emotion categories ($z = -10$). The enlarged section (b) shows the within-category results (i.e., voxels in which activity correlated with arousal ratings within each emotion category). The percentages indicate the percentage of voxels in which activity correlated with arousal ratings across the entire three-dimensional cluster (not just the slice displayed). The graph (c) shows mean betas (percentage signal change) for the high- and low-arousal conditions of each emotion category. Asterisks indicate a significant difference between conditions ($p < .05$). Error bars represent standard errors of the mean. The mean arousal ratings for the high- and low-arousal conditions of each emotion category are provided below the graph.

emotion categories. The valence (pleasure or displeasure) and arousal that participants experienced during varied instances of fear, sadness, and happiness correlated with neural activity in medial OFC and left amygdala, respectively. These brain regions are highly connected structures that have continual access to information about the state of the body and the state of the world, and are thereby able to influence the body to do what is necessary to deal with the world (Barrett & Bliss-Moreau, 2009). Integrating external sensory information with internal homeostatic and interoceptive information, in the context of prior experience, is vital not only for safely navigating the physical and social environment, but also for creating richly textured subjective experiences.

Our results are also consistent with the idea that core affect is a basic ingredient of many psychological phenomena, as the affect experienced during discrete emotions in our study shares neural correlates with the affect experienced during simple sensations. Investigations of the affect-inducing properties of taste, smell, touch, and temperature have revealed activity in OFC and amygdala, among other connected regions, that varies with the valence and intensity of sensory stimuli (for reviews, see Kringelbach & Rolls, 2004; Rolls, 2010). To date, the findings of studies examining the valence and arousal properties of more complex stimuli, such as faces (Gerber et al., 2008), scenes (Anders, Eippert, Weiskopf, & Veit, 2008;

Anders, Lotze, Erb, Grodd, & Birbaumer, 2004), sounds (Anders et al., 2008), and words or phrases (Colibazzi et al., 2010; P. A. Lewis, Critchley, Rotshtein, & Dolan, 2007; Posner et al., 2009), have been less consistent. Because our experiment addressed several methodological challenges (by using rich scenarios to induce familiar emotion experiences, collecting on-line ratings to avoid memory confounds, and measuring brain activity once the emotion was induced), it is significant that this study produced results consistent with studies of sensory affect. It will be important for future work to examine if these effects can be replicated for other emotion categories and in larger samples.

The findings presented here support a theoretical approach that contrasts with studying the discreteness of five or so emotions: studying the fundamental neural processes that underlie a wide variety of emotions (Barrett, 2009a). We propose that this psychological construction view, which is consistent with a number of emerging scientific models of emotion (e.g., Clore & Ortony, 2008; Coan, 2010; Cunningham & Zelazo, 2007), has much to contribute to psychological science.

Acknowledgments

Lisa Feldman Barrett and Lawrence W. Barsalou are joint senior authors of this article. We thank Lynne Nygaard for her assistance and guidance in recording the scenarios. We thank Yesenia Mares, Sarah Brown, Robert Smith, and the Emory

Biomedical Imaging Technology Center for assistance with data collection. Finally, we thank Lynne Nygaard, Stephan Hamann, and Kim Wallen for their comments on an earlier version of this manuscript.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

Preparation of this manuscript was supported by National Institute of Health Director's Pioneer Award DPI OD003312 to Lisa Feldman Barrett at Northeastern University, with a subcontract to Lawrence W. Barsalou at Emory University.

Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

Notes

1. Whole-brain analyses revealed that no other cluster showed a significant correlation with the valence ratings ($p < .05$ corrected at a voxel-wise threshold of $p < .005$ and cluster threshold of 36 voxels).

2. Whole-brain analyses revealed two additional clusters in visual cortex that exhibited positive correlations with participants' arousal ratings ($p < .05$ corrected at a voxel-wise threshold of $p < .005$ and cluster threshold of 36 voxels; see Table S2 in the Supplemental Material). The amygdala is strongly connected with visual cortex (Amaral, Behnia, & Kelly, 2003), which may explain the heightened activity there.

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