

Research Article

Bottom-Up and Top-Down Processes in Emotion Generation

Common and Distinct Neural Mechanisms

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ABSTRACT—Emotions are generally thought to arise through the interaction of bottom-up and top-down processes. However, prior work has not delineated their relative contributions. In a sample of 20 females, we used functional magnetic resonance imaging to compare the neural correlates of negative emotions generated by the bottom-up perception of aversive images and by the top-down interpretation of neutral images as aversive. We found that (a) both types of responses activated the amygdala, although bottom-up responses did so more strongly; (b) bottom-up responses activated systems for attending to and encoding perceptual and affective stimulus properties, whereas top-down responses activated prefrontal regions that represent high-level cognitive interpretations; and (c) self-reported affect correlated with activity in the amygdala during bottom-up responding and with activity in the medial prefrontal cortex during top-down responding. These findings provide a neural foundation for emotion theories that posit multiple kinds of appraisal processes and help to clarify mechanisms underlying clinically relevant forms of emotion dysregulation.

How do emotions arise? Do they arise via low-level processes that provide quick, bottom-up affective analyses of stimuli? Or do they arise via high-level, top-down cognitive appraisal processes that draw upon stored knowledge? This has long been one of the most contentious issues in the field (Lazarus, 1982; Zajonc, 1984), and these opposing viewpoints have only gradually yielded to a synthetic perspective holding that both types

of processes are important for emotion generation (Scherer, Schorr, & Johnstone, 2001).

BOTTOM-UP AND TOP-DOWN PROCESSES IN EMOTION GENERATION

Despite the long history of interest in this issue, direct evidence of separable bottom-up and top-down processes in emotion generation is remarkably scarce. In part, this is because behavioral studies that have been the coin of the realm for much of the field's history measure only the inputs to and outputs of emotion-generation processes and, as a consequence, cannot specify which particular processes were involved in generating a given emotion.

Researchers in other areas have dealt with this type of problem by using neuroscience methods to clarify the mechanisms underlying processes of interest (Kosslyn, 1994). Although neuroscience methods have a similar potential in the domain of emotion, to date neuroscientists have focused primarily on the bottom-up processes involved in simple forms of affective perception, learning, and memory (LeDoux, 2000; Phelps, 2006). In so doing, they have successfully identified brain systems—such as the amygdala—involved in the learning and bottom-up triggering of emotion in various species. But they have paid less attention to cognitive processes involved in top-down emotion generation (Wager, Barrett, et al., 2008). Although neuroimaging studies have begun to examine top-down processes, they have not been designed to distinguish the relative contributions of bottom-up and top-down processes to a given emotional response (e.g., Phelps et al., 2001; Teasdale et al., 1999).

THE PRESENT STUDY

The goal of the present study was to use functional magnetic resonance imaging (fMRI) to determine whether common or

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distinct neural systems are involved in generating a negative emotional response via bottom-up versus via top-down processing. To achieve this goal, we examined responses (a) on trials with normatively aversive images (bottom-up trials) and (b) on novel trials in which participants cognitively interpreted neutral images as aversive (top-down trials). Visual images were chosen as stimuli because of their well-characterized affective properties (Lang, Greenwald, Bradley, & Hamm, 1993). These two types of trials were designed to depend primarily on bottom-up and top-down processing, respectively, although we recognized that it is not possible to make a task condition completely process pure (Jacoby, Toth, & Yonelinas, 1993). Our aim was to capitalize on the power of functional imaging to dissociate the mechanisms underlying each type of emotion processing in a way not possible using behavioral methods alone (Kosslyn, 1994). Using this approach, we sought to test three hypotheses about the neural mechanisms involved in each type of emotion-generative processing.

First, we hypothesized that both bottom-up and top-down generation might depend on regions like the amygdala, which are involved in learning about and triggering responses to emotionally salient stimuli (LeDoux, 2000; Phelps, 2006). Second, we hypothesized that the two types of generation might take different routes to their common influence on affective learning systems. On the one hand, if bottom-up generation entails encoding the affective value of stimulus features, then viewing aversive images should activate the amygdala in concert with posterior cortical regions implicated in attending to and encoding visual features (Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Whalen et al., 2004). On the other hand, if top-down generation relies on high-level processes that elaborate the emotional meaning of stimuli and experiences, then it should differ from its bottom-up counterpart in its dependence on prefrontal regions implicated in cognitive control (Ochsner & Gross, 2005). In particular, we expected medial prefrontal cortex (mPFC) to play a key role because of its connections with subcortical regions implicated in emotional responding and its association with attention to and reasoning about emotion (Lane & McRae, 2004; Ochsner, Knierim, et al., 2004; Ongur, Ferry, & Price, 2003; Wager, Barrett, et al., 2008). Third, we expected that if the amygdala and mPFC are critical for generating emotion from the bottom up and from the top down, respectively, then activity in each region might be correlated with the magnitude of affective response only on the corresponding type of trial.¹ Finding such condition-specific correlations would both confirm the roles that these regions play in each pathway to emotion and clarify which neural systems are most closely linked to self-reported experience.

¹We assume that networks are crucial for each type of responding, with different regions—such as the amygdala or mPFC—being the most important rate-limiting steps for different types of responding.

METHOD

Participants

In compliance with the human-subjects regulations of Stanford University, 20 female participants (mean age = 20.3 years) were paid \$60 for voluntary completion of this study. Only women were studied to reduce variability introduced by potential gender differences in emotional responding (Wager, Phan, Liberzon, & Taylor, 2003).

Behavioral Paradigm

In a session 3 to 4 days prior to scanning, participants received training in how to perform the task using a separate set of images matched to those used in the scanner (for procedural details, see Ochsner, Ray, et al., 2004). During the task, participants viewed both neutral and normatively aversive images selected from the International Affective Picture System (Lang et al., 1993); negative image sets were matched for valence and arousal and counterbalanced across instruction types. There were two main types of trials. On top-down negative trials, participants were instructed to think about the actions, persons, and outcomes depicted in neutral images (e.g., an unmade bed) in ways that made them feel negative (e.g., the couple who had just slept there were killed in a car accident). On bottom-up negative trials, participants were instructed to simply view images and let themselves respond naturally.² A third trial type, bottom-up neutral trials, provided a common baseline that differed from top-down negative trials only in instruction type and from bottom-up negative trials only in stimulus type (see Fig. 1). In the scanner, 27 images were shown for each of these three trial types (11 images different from those shown in the scanner were shown during practice). Comparisons between top-down negative and bottom-up neutral trials were used to reveal the effects of top-down emotion generation, and comparisons between bottom-up-negative and bottom-up-neutral trials were used to reveal the effects of bottom-up emotion generation.

In addition to these three key trial types, there were three other trial types focusing on top-down appraisals that concerned not emotion generation, but rather the up- or down-regulation of responses to aversive or neutral images. Contrasts involving these trial types have been reported elsewhere (Ochsner, Ray, et al., 2004).

Each trial began with an initial 2-s instruction word presented in the center of the screen. The word “INCREASE” cued participants to increase negative emotion on top-down trials. The word “LOOK” cued participants to look at and respond naturally to images on bottom-up trials. Participants followed this instruction during the subsequent 10-s presentation of an aversive or neutral image. They then had 4 s to rate the current strength of their negative affect on a scale consisting of a horizontal rectangular bar (with scalar markings underneath: 0 = *weak*,

²In prior work, this type of instruction has resulted in bottom-up emotional responses to stimuli with relatively little deliberate engagement of top-down control processes (see, e.g., the work reviewed in Ochsner & Gross, 2008).

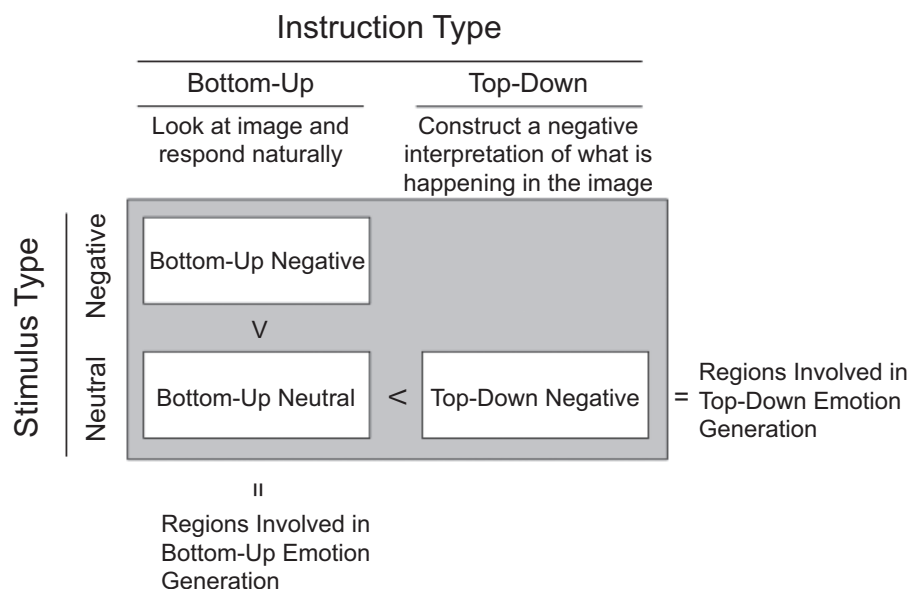


Fig. 1. Schematic illustration of the design of the experimental task, which employed two types of stimulus images and two types of instructions. The task was designed so that bottom-up neutral trials provided a baseline that differed from bottom-up negative trials only in the affective nature of the stimulus and from top-down negative trials only in the instruction. Comparisons of the two emotion-generation trial types with the baseline bottom-up neutral trials may therefore identify brain regions involved in either bottom-up or top-down emotional responding. This logic is illustrated in the diagram using mathematical operators. The “bottom-up negative > bottom-up neutral” contrast yields activation in regions involved in bottom-up emotion generation, whereas the “top-down negative > bottom-up neutral” contrast yields activation in regions involved in top-down emotion generation.

7 = *strong*) that grew from left to right to provide a continuously graded index of the subjective experience of emotion. A key press was made when the bar’s size indicated the strength of negative affect on the associated scale. The word “RELAX” appeared during the 4-s intertrial intervals.

MRI Data Acquisition and Analysis

A 3-T GE Signa LX Horizon Echospeed scanner collected twenty-five 4-mm axial slices (1-mm gap) using a T2*-sensitive gradient echo spiral-in/out pulse sequence (echo time = 30 ms, repetition time = 2,000 ms, odd-even interleave, 60° flip angle, 24-cm field of view, 64 × 64 data-acquisition matrix). T2-weighted scans were acquired for anatomical localization using the functional slice prescription (echo time = 85 ms, repetition time = 2,000 ms). Analysis followed established protocols using SPM2 (Ochsner, Ray, et al., 2004); preprocessing (slice-time and motion correction, coregistration, normalization, and reslicing to 2-mm × 2-mm × 2-mm voxels) was followed by a general linear model analysis that modeled the instruction and rating periods as events and the image and relaxation periods as boxcars convolved with the canonical hemodynamic response function for each participant; for group random-effects analyses, the threshold was $p < .001$ uncorrected, with a minimum cluster size (k) of 50 voxels. These parameters corresponded to an overall alpha level of $p < .05$ corrected for multiple comparisons, as calculated by the Monte Carlo simulation method im-

plemented in AFNI, which takes into account both family-wise error and extent thresholds (e.g., Ochsner, Knierim, et al., 2004). Given our a priori interest in the difficult-to-image amygdala, in whole-brain analyses we dropped the threshold to $p = .05$ to identify active voxels within a structural region of interest defined by the amygdala coordinates in the Wake Forest University School of Medicine PickAtlas (<http://fmri.wfubmc.edu/cms/software#PickAtlas>). BrainVoyager QX (Brain Innovation, <http://www.brainvoyager.com/>) was used for display and for correlational analyses relating changes in brain activity to changes in self-reported affect.

To identify the neural bases of each type of emotion generation, we first contrasted activity on bottom-up negative versus bottom-up neutral trials (the *bottom-up emotion-generation contrast*) and on top-down negative versus bottom-up neutral trials (the *top-down emotion-generation contrast*). Common neural bases were identified using a conjunction analysis. Distinct neural bases were identified by directly comparing activity in the bottom-up and top-down emotion-generation contrasts within a mask comprising the regions active in either contrast. This restricted the search for regions more active during each type of emotion generation to regions known to be active during at least one type of generation. For all activated regions, parameter estimates were extracted and compared in planned pair-wise t tests ($p < .05$) to confirm the status of those regions as common or distinct.

RESULTS

Manipulation Check

To confirm that negative emotions were generated on both bottom-up negative and top-down negative trials, we used planned t tests to compare self-reported affect on the three trial types. These tests confirmed that relative to bottom-up neutral trials ($M = 3.58$, $SE = 0.14$), both bottom-up negative trials ($M = 5.89$, $SE = 0.22$), $t(19) = 11.68$, $p < .001$, and top-down negative trials ($M = 5.24$, $SE = 0.24$), $t(19) = 8.26$, $p < .001$, elicited more negative affect; bottom-up negative trials elicited the most negative affect of all, $t(19) = 4.43$, $p < .001$, for the comparison with top-down negative trials. The relation between self-reported emotion and brain activity is considered later in the Results and Discussion sections.

Common Neural Bases for Bottom-Up and Top-Down Emotion Processing

A conjunction analysis revealed one region commonly involved in both types of emotion processing—the left amygdala (Table 1,

Figs. 2a and 2b). This region included almost all the voxels active during top-down negative trials and was of a priori interest given the amygdala's known role in emotion. Although left amygdala activity was observed in both cases, activity was greater overall during bottom-up emotion generation. Activation time courses extracted from this cluster's peak voxel showed activity on both top-down and bottom-up negative trials (Fig. 2c). Planned comparisons on extracted parameter estimates confirmed that this subregion of the amygdala showed significant ($p < .05$) and equivalent ($p > .5$) activity on top-down and bottom-up negative trials, whereas comparisons for non-overlapping regions in both the right and left amygdala confirmed that they were active only during bottom-up negative trials ($p < .05$).

Distinct Neural Bases for Bottom-Up and Top-Down Emotion Generation

Regions distinctly involved in bottom-up emotion generation included bilateral amygdala, occipitotemporal cortex, and right

TABLE 1

Regions of Activation Identified in the Direct Comparison of Trial Types and in the Conjunction Analysis

Region of activation	Peak coordinates			No. of voxels	BU $t(19)$	TD $t(19)$	Diff $t(19)$
	x	y	z				
Bottom-up activation > top-down activation							
Inferior frontal gyrus	45	27	19	376	4.21****	-2.49*	8.85*****
Inferior parietal lobule	37	-55	49	294	3.69***	-5.55*****	7.76*****
Middle occipital gyrus	37	-83	-3	3,006	10.86*****	0.10	11.46*****
Middle occipital gyrus	-45	-87	-3	2,019	6.68*****	-0.94	9.46*****
Amygdala	-23	-3	-17	89	6.01*****	0.38	6.21*****
Amygdala	23	-5	-15	155	6.96*****	-2.34*	7.07*****
Top-down activation > bottom-up activation							
Superior and medial frontal gyri, dorsal cingulate	-7	3	67	1,555	-0.64	6.17*****	8.48*****
Middle frontal gyrus	-45	5	53	736	-2.52*	7.36*****	9.09*****
Middle frontal gyrus	-25	27	49	25	-2.14*	3.62***	4.77*****
Inferior frontal gyrus	-47	33	-3	222	-0.59	4.64*****	6.94*****
Inferior frontal gyrus	-59	17	15	144	0.06	5.95*****	6.67*****
Superior temporal gyrus	-57	-59	23	282	-1.31	4.75*****	6.99*****
Middle temporal gyrus	-63	-15	-15	82	-1.36	3.65***	6.30*****
Middle temporal gyrus	-53	-71	27	20	-0.70	4.43****	4.94*****
Middle temporal gyrus	-49	-39	-3	13	-2.26*	3.85***	4.46*****
Middle temporal gyrus	59	-35	-5	15	-1.55	3.68***	4.54*****
Posterior temporal cortex	29	-67	-41	244	-0.42	3.62***	5.51*****
Posterior temporal cortex	31	-87	-43	17	-1.90*	3.70***	4.91*****
Putamen	-19	5	1	104	-0.56	4.28****	4.68*****
Putamen	21	9	15	8	0.63	4.28****	4.23*****
Conjunction of bottom-up and top-down emotion generation							
Amygdala	-17	-9	-11	68	4.45*****	2.43*	—
Amygdala	-21	5	-27	44	3.19**	3.14**	—

Note. BU t and TD t are values from t tests comparing bottom-up negative and top-down negative trials, respectively, with bottom-up neutral trials. Diff t is the t value for the direct comparison of bottom-up negative and top-down negative trials. Voxel size is 8 mm^3 . The amygdala regions in the conjunction analysis were of a priori interest and were identified at a whole-brain threshold of $p < .05$.

* $p < .05$. ** $p < .005$. *** $p < .001$. **** $p < .0005$. ***** $p < .0001$.

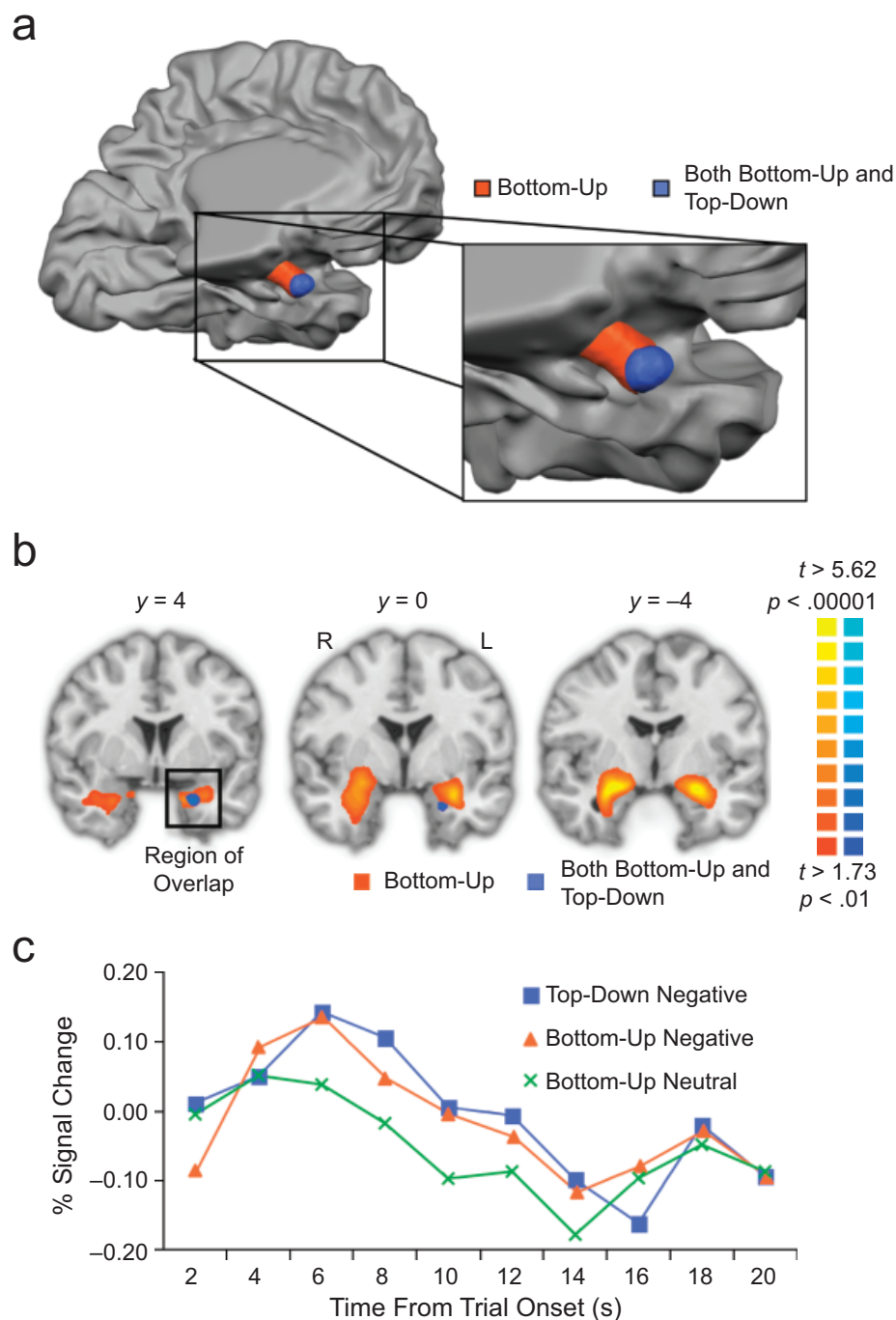


Fig. 2. Amygdala activation during bottom-up and top-down emotional processing: (a) three-dimensional medial view (and blowup) and (b) axial views of left amygdala voxels activated during only bottom-up or both bottom-up and top-down emotional responding and (c) blood-oxygenation-level-dependent (BOLD) response in overlapping voxels as a function of time in the three trial types. R = right; L = left.

parietal cortex and lateral PFC. Regions distinctly involved in top-down emotion generation included left ventral and dorsal lateral PFC, bilateral dorsal medial prefrontal and anterior cingulate cortex (in one cluster spanning Brodmann's areas 8, 9, and 24), and bilateral temporal cortex and putamen (Table 1, Fig. 3).

Relationship Between Brain Activity and Magnitude of Affective Response

If the amygdala and mPFC are the key structures for bottom-up and top-down emotion generation, respectively, then their activity should predict the magnitude of affective response, indexed here by self-reported negative affect. To address this

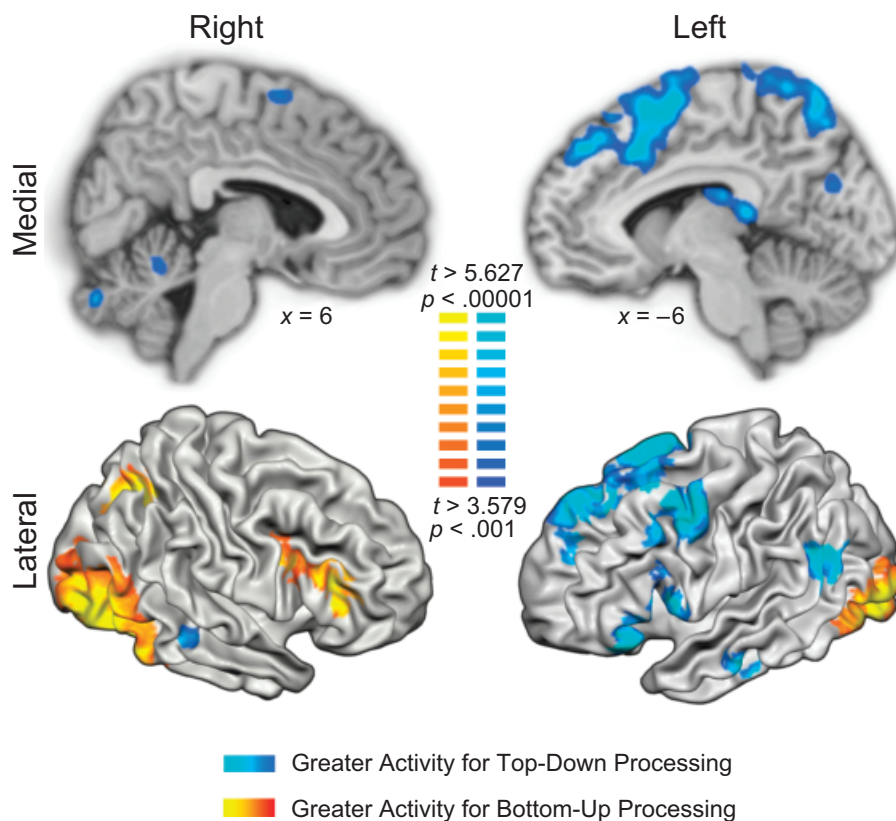


Fig. 3. Medial (top) and lateral (bottom) views of brain regions active during either bottom-up or top-down emotion generation. See Figure 2 for regions where common activation was found.

hypothesis, we used BrainVoyager to search for voxels whose activity was correlated with increases in negative affect on each negative trial type in comparison with bottom-up neutral trials. The mask was created at a more liberal threshold of $p = .05$ both because regions correlated with behavior often are not identical to those showing main effects and to avoid false negative findings. We then determined whether each region was correlated with affect more strongly ($p < .05$) for one type of emotion generation than for the other, using the method for comparing dependent correlations. Results showed that self-reported negative affect was more strongly correlated with activity in the bilateral dorsal/sublenticular extended amygdala during bottom-up emotional responding and with activity in the dorsal mPFC during top-down emotional responding (Table 2, Fig. 4).

DISCUSSION

Contemporary emotion theory holds that bottom-up and top-down processes are important to emotion generation. However, behavioral research has failed to differentiate their contributions, and the majority of neuroscience work has addressed only bottom-up processing. The goal of this study was to probe bottom-up and top-down processes in emotion generation using fMRI measures that could help disambiguate the common and unique mechanisms of these processes. To achieve this goal, we

compared brain activation during the simple bottom-up perception of aversive images with brain activation during the top-down interpretation of otherwise neutral images as aversive. Three key findings were obtained.

First, we found that the left amygdala showed overlapping activity during the two types of emotional processing. This region has been implicated in affective learning (LeDoux, 2000), which suggests that bottom-up and top-down emotional responses may share a dependence on systems that mediate learning about the affective properties of stimuli. The fact that bottom-up responses drove both amygdalae but top-down responses modulated only the left amygdala fits with prior studies (Glascher & Adolphs, 2003; Ochsner & Gross, 2008; Phelps et al., 2001) suggesting that the left amygdala may be more susceptible than the right amygdala to influence by top-down inputs during emotion and anxiety.

Second, we found that distinct cortical networks were involved in each type of emotion generation. On the one hand, bottom-up emotion generation activated the amygdala and occipital cortex, which have been implicated in detecting affectively arousing stimuli and modulating their encoding into memory (LeDoux, 2000; Phelps, 2006; Sabatinelli et al., 2005), as well as right prefrontal and parietal regions implicated in attentional vigilance and individual differences in negative affective style (Davidson, 2000; Posner & Petersen, 1990). On

TABLE 2
Regions Whose Activation Correlated With Increases in Self-Reported Negative Affect During Bottom-Up or Top-Down Emotion Generation

Region of activation	Peak coordinates			No. of voxels	Bottom-up r	Top-down r
	x	y	z			
Bottom-up emotion generation						
Amygdala (dorsal)	33	-3	-5	188	.75****	.41
Amygdala (dorsal)	-29	-1	-11	68	.71****	.23
Top-down emotion generation						
Dorsal medial prefrontal cortex	-1	49	29	138	-.02	.64**

Note. Correlations are for the peak voxel. Voxel size is 8 mm³.
 ** $p < .005$. **** $p < .0005$.

the other hand, top-down emotion generation activated left prefrontal, cingulate, and temporal regions implicated in working memory and the retrieval of information from semantic memory (Badre & Wagner, 2007), as well as the left amygdala and a dorsal mPFC region involved in making attributions about mental—and especially emotional—states (Lane & McRae,

2004; Ochsner, Knierim, et al., 2004). Working together, these systems may support cognitive appraisals that generate emotions from the top down.

Third, we found that activity in the dorsal portions of amygdala tracked with the magnitude of self-reported experience only during bottom-up responding, whereas activity in dorsal mPFC tracked

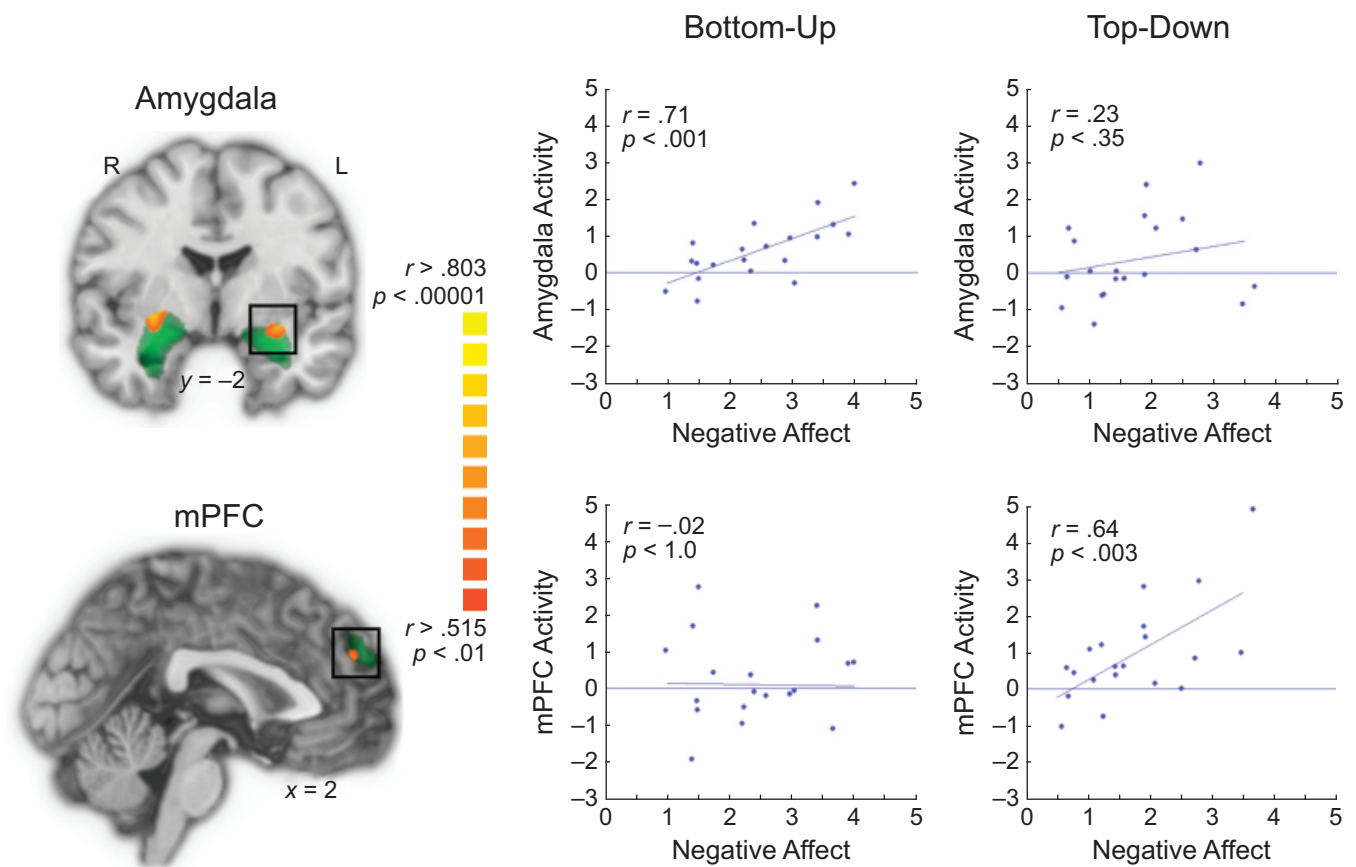


Fig. 4. Correlations between self-reported negative affect and brain activity during bottom-up and top-down emotion generation. Green regions illustrate the clusters (from the main-effect analysis, $p < .05$) within which the correlated regions (shown in hot colors) were found. For bottom-up processing, negative affect was calculated as the increase in self-reported negative emotion on bottom-up negative relative to bottom-up neutral trials. For top-down processing, negative affect was calculated as the increase in self-reported negative emotion on top-down negative relative to bottom-up neutral trials. mPFC = medial prefrontal cortex; R = right; L = left.

with self-reported experience only during top-down responding. Although prior studies have shown experience-activity correlations in these regions (Abercrombie et al., 1998; Ochsner, Ray, et al., 2004; Phan et al., 2003), those studies were not designed to determine whether bottom-up or top-down processes were responsible. In humans, the dorsal amygdala has been implicated in perceiving and orienting to arousing and potentially anxiety-provoking stimuli (Davis & Shi, 1999; Liberzon, Phan, Decker, & Taylor, 2003; Whalen et al., 2004), functions that may be critical for the stimulus-triggered emotional responses studied on our bottom-up negative trials. By contrast, the dorsal mPFC correlation during top-down responding highlights the role of this region as an integrator of cognitive and affective inputs that can exert control over autonomic centers and modulate emotional experience as a function of the cognitive meaning ascribed to a stimulus in a given task (Lane & McRae, 2004; Ochsner, Knierim, et al., 2004). The fact that self-reported emotion correlated with activity in discrete regions need not mean those are the only regions involved in affective experience, however, or that those regions represent the contents of awareness. Indeed, in the context of the networks identified in the group contrasts, these correlations likely reflect the specific rate-limiting processes within the larger network that are most strongly related to individual variability in experience.

One potential caveat concerns the finding that self-reports of negative affect were slightly greater for bottom-up than for top-down negative trials, which raises the possibility that the activations observed here reflect only differences in strength of affect. If this were true, then one would expect that activity would have been greater for bottom-up than for top-down negative trials, but not the reverse, and—most critically—that activity would have correlated with increases in self-reported emotion in the same regions for both trial types, with the correlation being strongest for bottom-up negative trials. Neither of these patterns was found: As described earlier, activity was greater on top-down negative trials than on bottom-up negative trials in many theoretically predicted regions (Fig. 3), and affect was correlated with activity on top-down negative trials in a region different from where activity and affect were correlated on bottom-up negative trials (Fig. 4). Thus, we take the imaging data to reflect the generation of slightly different quantities of negative emotion by qualitatively different processes (i.e., low-level perceptual vs. high-level cognitive processes).

Another caveat concerns our inclusion of only female participants, which raises the question as to whether our results generalize to men. Studies of cognitive emotion regulation have reported either no gender differences (Wager, Davidson, et al., 2008) or greater prefrontal and lesser amygdala modulation among women than among men (McRae, Ochsner, Mauss, Gabrieli, & Gross, 2008). Those studies suggest that the cognitive emotion-generation effects we observed likely generalize to men, although the genders may differ in the extent to which they recruit top-down processes. This will be an important issue to address in future research.

Implications for Emotion Theory and Research

Taken together, our findings have three implications for emotion theory and research. The first concerns the question that motivated this study: How do emotions arise? The present data provide strong evidence for separate, but related, bottom-up and top-down mechanisms that depend on links between the amygdala and either perceptual representations that are accessed from the bottom up or high-level cognitive representations of stimulus meaning that are accessed from the top down. Intriguingly, both types of emotion generation activated prefrontal cortex. Whereas left PFC activity during top-down generation is consistent with increased semantic processing, right PFC activity during bottom-up generation may relate to attention shifting. For example, the mere perception of an emotional stimulus could trigger a parietal-lobe-mediated attentional shift to its affective attributes, which in turn might recruit prefrontal mechanisms to further direct attention to the stimulus, possibly enhancing occipital and amygdala activity as a result (cf. Wright et al., 2008). The common recruitment of PFC highlights that top-down and bottom-up processes may be coactive in many circumstances, and that any task may only partially disentangle them.

That being said, the present method provides a starting point for distinguishing the contributions of bottom-up and top-down processes to experience, and such work could help clarify the meaning of commonly observed prefrontal activity in studies of emotion (Wager, Barrett, et al., 2008) and other mixed findings from prior research. For example, it has been reported that amygdala lesions do not affect retrospective reports of global mood (Anderson & Phelps, 2002) even though they do disrupt preferences for, and judgments of arousal elicited by, visual stimuli (Adolphs, Russell, & Tranel, 1999; Adolphs & Tranel, 1999). It is possible that global reports of mood given at the end of a day depend on the retrieval of stored knowledge and top-down mPFC mechanisms to a greater extent than they depend on more transient stimulus-driven emotional responses that may be more associated with the amygdala (Barrett et al., 2007).

The second implication of our findings concerns how best to study emotion mechanisms. One method would be to follow the logic of neuroscience studies that use stimuli with intrinsic pleasant and unpleasant properties (e.g., shock), or stimuli that have social signal value but do not elicit strong emotional responses (e.g., faces), in learning, memory, and perception paradigms that depend strongly on bottom-up processes humans share with nonhuman primates and rodents. Such work implicitly treats emotions as if they are properties of stimuli, like shape, size, or color, rather than products of contextually sensitive appraisals that can involve top-down processes humans may not share with nonhuman species. The present imaging study joins prior behavioral work to suggest that a bottom-up account of emotion tells only half of the story: Emotions may be generated by top-down processes as well, and it is important to understand the type or combination of processes from which any given response arose. An important goal for future research will be to continue

differentiating the contributions of bottom-up and top-down processes to emotion, given that both kinds of processing likely contribute to emotion in many, if not all, situations.

The third implication concerns the relationship between emotion generation and emotion regulation. The finding that top-down (i.e., cognitively constructed) negative emotion involves prefrontal-amygdala interactions converges with research showing that similar neural dynamics support cognitive reappraisal (reviewed in Ochsner & Gross, 2005, 2008), as well as the effects of expectancies on pain and emotion (Wager, 2005). This similarity suggests that a core neural dynamic may underlie the use of high-level cognition to initiate an emotional response, as shown here, and to modify or stop an emotional response, as shown in prior work. The reliance on similar neural circuitry implies that the line separating emotion generation and emotion regulation cannot be defined in simple anatomical terms. That is, there may not be brain centers uniquely dedicated to emotion generation or emotion regulation per se. Instead, various brain systems may perform computations involved in both, depending on the behavioral context. Thus, which term one uses may depend more on the functional analysis of the situation than on the neural systems involved.

Implications for Developmental, Social, and Clinical Psychology

The view that emotions may arise via different combinations of bottom-up and top-down processes has implications for at least three additional areas of psychological research. The first is developmental research, which has shown prefrontal maturation through the teen years that often is taken to reflect increasing control over emotional impulses as an individual enters adulthood (Bunge & Wright, 2007). The present data suggest that prefrontal development may enable not just emotion regulation, but also the top-down generation of emotions with increasing cognitive complexity.

This work also speaks to the role of affective responses in various social-cognitive phenomena. One salient example concerns the study of attitudes, which have a strong evaluative component. Our findings suggest that not all attitudes are created equal, and that attitudes could be classified in terms of the bottom-up or top-down processes from which they arose. This suggestion fits with research showing that implicit and explicit attitudes depend on some of the same systems associated here with bottom-up and top-down emotion (Cunningham & Zelazo, 2007).

Finally, these data suggest new ways in which bottom-up and top-down processes may play a role in clinical disorders. One possibility is that optimal treatment regimens for dysfunctional emotions might differ depending on whether those emotions were generated primarily by bottom-up or top-down processes. Bottom-up abnormalities might be most amenable to change via behavioral reinforcement methods that reshape response tendencies over time (Quirk & Beer, 2006), whereas top-down abnormalities may be best addressed using cognitive methods

that restructure one's consciously accessible appraisals (Ochsner & Gross, 2005). Future translational work could examine this idea in disorders such as phobia and panic, in which bottom-up reactions (as opposed to top-down interpretations of physical sensations) generate problematic negative emotions.

Conclusions and Future Directions

The present study dovetails with the old observation (Hebb & Thompson, 1954, cited in Washburn, 1963) that "emotional susceptibility increases with intellectual capacity" (p. 328). Our data suggest that humans are emotional in part *because* of their intellectual—that is, cognitive—capabilities. More broadly, the finding of separable bottom-up and top-down routes for generation of negative emotion provides a neural foundation for emotion theories positing multiple kinds of appraisal processes, some of which are bottom-up and triggered reflexively, and some of which are top-down and highly cognitive (Scherer et al., 2001). This study suggests new directions for future work, including research on how bottom-up and top-down processes contribute to positive as well as negative emotions, and also on the roles these processes play in development, social cognition, and psychopathology.

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