

Research Article

Affective Flexibility

Evaluative Processing Goals Shape Amygdala Activity

William A. Cunningham,¹ Jay J. Van Bavel,^{1,2} and Ingrid R. Johnsen¹¹The Ohio State University and ²University of Toronto

ABSTRACT—*Although early research implicated the amygdala in automatic processing of negative information, more recent research suggests that it plays a more general role in processing the motivational relevance of various stimuli, suggesting that the relation between valence and amygdala activation may depend on contextual goals. This study provides experimental evidence that the relation between valence and amygdala activity is dynamically modulated by evaluative goals. During functional magnetic resonance imaging, participants evaluated the positive, negative, or overall (positive plus negative) aspects of famous people. When participants were providing overall evaluations, both positive and negative names were associated with amygdala activation. When they were evaluating positivity, positive names were associated with amygdala activity, and when they were evaluating negativity, negative names were associated with amygdala activity. Evidence for a negativity bias was found; modulation was more pronounced for positive than for negative information. These data suggest that the amygdala flexibly processes motivationally relevant evaluative information in accordance with current processing goals, but processes negative information less flexibly than positive information.*

Successfully navigating complex environments requires quick evaluative processes to determine the relative value of stimuli in the context of situational demands. Recent research has begun to illustrate the important cognitive and affective neural processes involved in disambiguating the evaluative connotations of stimuli and preparing the body for action. Convergent evidence across methodologies suggests that the amygdala is particularly relevant for encoding and processing the affective properties of stimuli (Adolphs, Tranel, & Damasio, 1998; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; LeDoux, 2000). Al-

though it is clear that the amygdala plays an important role in evaluation (Cunningham, Raye, & Johnson, 2004), decision making (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005), and social cognition (Adolphs, 2003), the precise operating characteristics of this region remain unclear.

Initial research suggested that the amygdala is specifically involved in detecting threatening stimuli (Isenberg et al., 1999; LeDoux, 2000; Morris et al., 1996), or is more generally engaged in processing negativity (Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002). This valence-specific conceptualization has been called into question by studies showing that positive, like negative, stimuli evoke greater amygdala activity than neutral stimuli (Breiter et al., 2003; Hamann, Ely, Hoffman, & Kilts, 2002). Moreover, studies that have independently manipulated valence and intensity (Anderson et al., 2003; Small et al., 2003), or used statistical methods to separate the contributions of the two (Cunningham, Raye, & Johnson, 2004), have provided evidence that amygdala activity appears to be more associated with processing affective *intensity* than with processing any particular valence. These studies have been critical in reconceptualizing amygdala function from one of threat detection to one of more general vigilance for motivationally relevant stimuli (Anderson & Phelps, 2001; Whalen, 1998).

Although it is clear that the amygdala plays an important role in automatically processing stimuli (Morris, Öhman, & Dolan, 1998; Whalen et al., 1998), other research has shown that it is also influenced by top-down processes, such as self-regulation (Beauregard, Levesque, & Bourgouin, 2001; Cunningham, Johnson, et al., 2004), verbal task demands (Hariri et al., 2002; Lieberman et al., 2007), and attention (Pessoa, Japee, Sturman, & Ungerleider, 2006). For example, research has shown that participants given the goal to “increase” or “decrease” their emotional response can regulate their amygdala activation in response to emotional stimuli (Ochsner et al., 2004).

This research demonstrating the top-down modulation of amygdala activity suggests that a fit between current processing goals and evaluative aspects of stimuli may lead to enhanced amygdala activity—what we call *affective flexibility*. In this

Address correspondence to William Cunningham, The Ohio State University, Psychology Department, 1827 Neil Avenue Mall, Columbus, OH 43210, e-mail: cunningham.417@osu.edu.

context, a *fit* occurs when the valence of a stimulus is consistent with a processing goal. A recent study consistent with this idea found that participants who reported having more promotion-focused goals (sensitivity to gains) showed greater amygdala activation in response to increasingly positive stimuli, whereas participants who reported having more prevention-focused goals (sensitivity to losses) showed greater amygdala activation in response to increasingly negative stimuli (Cunningham, Raye, & Johnson, 2005). It is important to note that these relationships were observed when participants made explicit evaluative (e.g., good/bad) judgments, but not when they made nonevaluative (abstract/concrete) judgments. Similarly, patients with anxiety disorders show heightened amygdala responses to threatening stimuli, compared with control participants (Bishop, Duncan, & Lawrence, 2004). Although these studies were correlational and therefore do not provide causal evidence, they suggest that goals may play a role in shaping the amygdala response to evaluative information.

In the present study, we manipulated processing goals to test the flexibility of amygdala processing. Specifically, during functional magnetic resonance imaging (fMRI), participants were given three different processing goals that involved rating famous people. In the *attitude* condition, participants used a bivalent scale to indicate their overall attitude toward each name. In the other two conditions, participants provided univalent evaluative ratings; they rated only the positive aspects of each name (i.e., “how positive is your response ignoring anything negative?”; scale from *none* to *very good*) in the *positive* condition, and they rated only the negative aspects (scale from *none* to *very bad*) in the *negative* condition. Thus, in the attitude condition, both positive and negative aspects of each name were relevant to the processing goal, whereas in the positive and negative conditions, only positive or only negative aspects of each name, respectively, were relevant. To the extent that the amygdala is engaged in processing aspects of stimuli that fit the current processing goal, stimulus extremity should be associated with activation when overall attitudes are rated (i.e., more extreme positive and negative names were expected to be associated with greater amygdala activation), whereas positive or negative stimuli, respectively, should be associated with enhanced amygdala activation when only positive or only negative aspects of the stimuli are rated (e.g., in the positive condition, names rated as more positive were expected to be associated with greater amygdala activation).

METHOD

Participants

Sixteen right-handed participants (12 females, 4 males; mean age = 22.8 years) provided informed consent and were paid \$50 for completing the study. Two participants were excluded because of head motion greater than 2 mm in any direction, and 2 participants were excluded for knowing less than 75% of the names. Twelve participants remained for analyses.

Procedure

Participants completed eight functional runs, each consisting of three 12-trial blocks. On each trial, participants provided one of three types of evaluative judgments about a famous name. On attitude trials, participants evaluated each name on a 4-point scale from *strongly negative* to *strongly positive*. On negative trials, participants evaluated only negative aspects of the name, using a 4-point scale from *none* to *very bad*. On positive trials, participants evaluated only positive aspects of the name, using a 4-point scale from *none* to *very good*. To help create and maintain evaluative goals, we grouped the trials so that the same evaluative judgment was required for all faces within each block. Each of 96 names (e.g., Adolph Hitler, Paris Hilton, Mother Teresa, George Clooney) was rated once in each condition.

Before each block, a direction screen was presented for 4 s to inform participants of the evaluative judgment required for the following 12 trials. The direction screen was followed by a fixation cross for 4 s. Then, each name appeared for 2 s, during which time participants made a response with a four-button response box placed in their right hand. To allow for the estimation of the event-related hemodynamic signal, we presented a 2-s, 4-s, or 6-s fixation cross after each name; the duration of the cross was pseudorandomly determined. Following fMRI scanning, participants completed a questionnaire on which they rated each of the names on the dimensions of positivity, negativity, and emotionality (i.e., how “emotional” the stimulus made them feel); the scales ranged from 1 (low) to 8 (high). Participants also indicated names they did not know.

fMRI Parameters

All imaging was conducted with a Siemens 3-T scanner. For whole-brain functional coverage, 32 axial slices (slice thickness = 3.5 mm, 0.5-mm skip) were prescribed parallel to the anterior commissure–posterior commissure line. Functional images were acquired using a single-shot gradient echo-planar pulse sequence (echo time = 25 ms, repetition time = 2 s, in-plane resolution = 3.5 × 3.5 mm, matrix size: 64 × 64, field of view = 224 mm).

fMRI Preprocessing and Analysis

Data were prepared for analysis using FSL (University of Oxford, Oxford, United Kingdom) and SPM5 (Wellcome Department of Cognitive Neurology, London, United Kingdom). Data were first corrected for slice-acquisition time, motion, and high-frequency noise using FSL default settings. Data were then transformed to conform to the default EPI Montreal Neurological Institute (MNI) brain interpolated to 3 × 3 × 3 mm and were smoothed using an 8-mm full-width/half-maximum kernel in SPM5. Because we employed a blocked event-related design, a high-pass filter of 160 s was used to retain meaningful signal.

Data were analyzed using the general linear model as implemented in SPM5. In each analysis, a series of regressors was constructed to examine blood-oxygenation-level-dependent

TABLE 1
Descriptive Statistics for Postscan Ratings

| Rating | Mean | SD | Minimum | Maximum | Correlations among ratings | |
|----------------------|------|------|---------|---------|----------------------------|------------|
| | | | | | Positivity | Negativity |
| Measured variables | | | | | | |
| Positivity | 4.07 | 2.10 | 1.00 | 7.92 | | |
| Negativity | 3.61 | 2.32 | 1.00 | 8.00 | -.69 | |
| Emotionality | 3.83 | 1.85 | 1.08 | 7.67 | .18 | .21 |
| Calculated variables | | | | | | |
| Valence (<i>V</i>) | 0.46 | 4.06 | -7.00 | 6.92 | | |
| Ambivalence | 0.75 | 4.05 | -5.17 | 9.17 | | |

Note. The calculated variables are linear transformations of the positivity and negativity ratings.

(BOLD) brain activity for each of the trial types. The BOLD signal was modeled as a function of a canonical hemodynamic response function. For amygdala analyses, an anatomical mask was created, and significant voxels were defined as those exceeding a statistical threshold of $p < .05$ (small-volume corrected, with 10 contiguous voxels). For whole-brain analyses, significant voxels were defined as those exceeding a statistical threshold of $p < .001$ (uncorrected, with 10 contiguous voxels). A statistical threshold of $p < .05$ (uncorrected) was used to explore data from regions of interest extracted from other analyses.

RESULTS

Rather than separating our data according to names rated as more positive than negative and names rated as more negative than positive, we conducted a series of regression analyses in which the continuous postscan ratings were regressed against fMRI data to test for linear and nonlinear trends. The mean ratings for negativity ($M = 3.61$, $SD = 2.32$) and positivity ($M = 4.07$, $SD = 2.10$) were similar, as were the correlations between ratings of positivity and emotionality ($r = .18$) and ratings of negativity and emotionality ($r = .21$; see Table 1).

To examine the relation between postscan attitude ratings and amygdala activity, we computed valence (V) scores from the postscan ratings of each name by subtracting each participant's negativity rating from his or her positivity rating; higher scores represented more positive overall evaluations. BOLD activity for each participant and each trial was then predicted as a function of V and V^2 (the quadratic term). Because V was zero-centered, V^2 represented the extremity of the ratings of positivity or negativity (i.e., highly negative and highly positive stimuli would both receive a high score). Rated emotionality was used as a covariate to ensure that the effect of valence could not be attributed to generalized emotionality. Because values of V close to zero could reflect either no valence or a mix of positivity and negativity, we included an index of ambivalence (having both positive and

negative responses; Thompson, Zanna, & Griffin, 1995) as a covariate.¹ Unknown names were modeled using separate regressors, so the reported analyses are based on known names (91% on average). To test for differences between experimental conditions, we modeled each of these parameters separately for each condition.

Affective Flexibility in the Amygdala

Analyses of amygdala activation were conducted using an anatomical mask generated in MRIcro (Rorden & Brett, 2000). Results were consistent with recent research linking stimulus intensity to amygdala activity; an overall effect of extremity (V^2) was found bilaterally—right amygdala: $t(11) = 5.76$, $p < .0001$, $p_{\text{rep}} > .99$; left amygdala: $t(11) = 5.31$, $p < .0001$, $p_{\text{rep}} > .99$ (see Fig. 1, top panel). This effect was not moderated by experimental condition, $F(2, 22) = 0.70$, $p = .51$, $p_{\text{rep}} = .50$, and was significant in each condition ($ps < .05$, $p_{\text{rep}} > .88$). There was no main effect of valence on amygdala activity, $t(11) = 0.11$, $p = .91$, $p_{\text{rep}} = .17$.

To examine whether amygdala activity was flexibly related to stimulus aspects that fit the current processing goal, we analyzed the valence-by-condition interaction. The results were consistent with the idea of affective flexibility; the effect of valence on amygdala activity differed across experimental conditions—right amygdala: $F(2, 22) = 11.07$, $p < .001$, $p_{\text{rep}} = .99$; left amygdala: $F(2, 22) = 9.44$, $p < .001$, $p_{\text{rep}} = .99$ (see Fig. 1, bottom panel). To be conservative in identifying regions of the amygdala engaged in processing the motivational relevance of stimuli, we decomposed these effects by extracting the overlapping significant voxels from the preceding analyses of the effects of valence and extremity.

¹Ambivalence was computed for each stimulus for each participant using standard equations. These equations take into consideration both the conflict between positive and negative information (C , the minimum of the two ratings for a given stimulus) and the strength of the dominant response (D , the maximum of the two ratings). Because C contributes more to ambivalence than D and is in the opposite direction, ambivalence was computed as $3C - D$ (see Thompson et al., 1995).

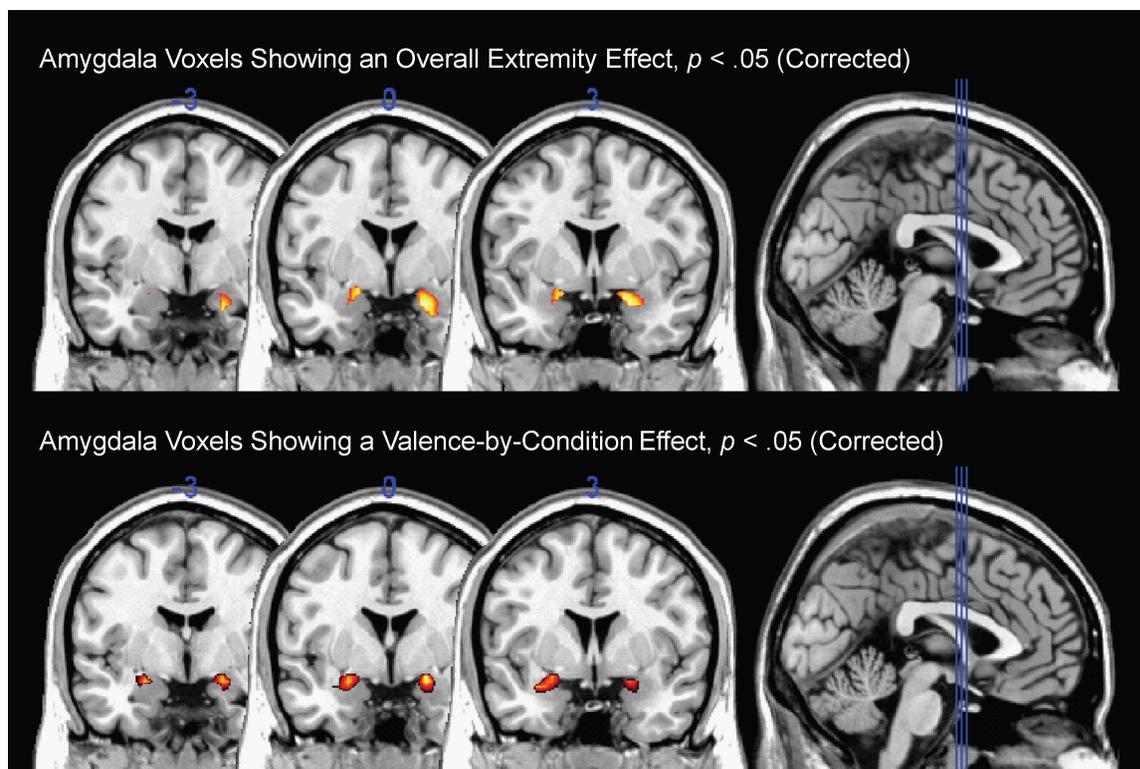


Fig. 1. Significant activations in the amygdala region of interest. The planes from which these coronal maps were taken are shown in the illustrations on the right. The maps on the top show areas exhibiting a significant overall effect of stimulus extremity (V^2), and the maps on the bottom show areas exhibiting a significant interaction of valence and condition.

Analysis of these voxels revealed a significant relation between valence and amygdala activity in the positive condition ($M = 0.05$), $t(11) = 2.06$, $p < .05$, $p_{\text{rep}} = .91$, and the negative condition ($M = -0.06$), $t(11) = -2.36$, $p < .05$, $p_{\text{rep}} = .93$, but not in the attitude condition ($M = 0.01$), $t(11) = 0.09$, $p = .46$, $p_{\text{rep}} = .53$. The effect of valence was reversed for the positive and negative conditions; in each case, the most amygdala activity was found for stimulus aspects that fit the current processing goal.

This pattern implicates the amygdala in tracking the fit between processing goals and evaluative aspects of stimuli within the environment. To further elucidate these effects, we used the beta weights generated for V and V^2 in the previous analysis to estimate expected amygdala activity at each level of valence for each experimental condition (see Fig. 2). Results for the attitude condition replicated previous work: Amygdala activity increased for both increasingly positive and increasingly negative names. Although there was evidence of affective flexibility for both the positive and the negative conditions, the pattern of data suggested a *negativity bias* (Cacioppo & Berntson, 1994), in which negative information was weighted more heavily than positive information.² Specifically, in the negative condition,

²The measures in Table 1 indicate that it is unlikely that reported effects can be attributed to differences in extremity of the stimuli. Further, we analyzed the data using simultaneous regression analysis with ratings as continuous variables, and this approach also makes it unlikely for the significant results obtained to be due to differences in extremity.

greater activity was found for increasingly negative names, and almost no activity was found for positive names. In contrast, in the positive condition, activity was found for both positive and negative names (though the activity in response to negative names was less than in the negative and attitude conditions).³

Separating Positive and Negative Aspects

Recent models of evaluation suggest that the processing of valence can be subdivided into the processing of positivity and negativity (Cacioppo & Berntson, 1994). The previous analysis suggests that affective flexibility may be asymmetric, such that the effect of the fit between valence and processing goal on amygdala activity is more pronounced for positive than for negative information. To provide a more direct test of this possibility, we analyzed the data by estimating separate parameters for positive and negative aspects of each name. Specifically, we modeled BOLD activity as a function of postscan positivity ratings, postscan negativity ratings, the positivity-by-negativity

³Although we report direct evidence for this asymmetry in the next section, initial evidence for a negativity bias can be found by comparing predicted activity in the positive and negative conditions with predicted activity in the attitude condition. Whereas the difference between the predicted activity in response to positive stimuli in the negative condition and in the attitude condition was significant, $t(11) = 2.27$, $p < .05$, $p_{\text{rep}} = .88$, there was no difference between predicted activity in response to negative stimuli in the positive condition and in the attitude condition, $t(11) = 0.79$, $p = .45$, $p_{\text{rep}} = .54$.

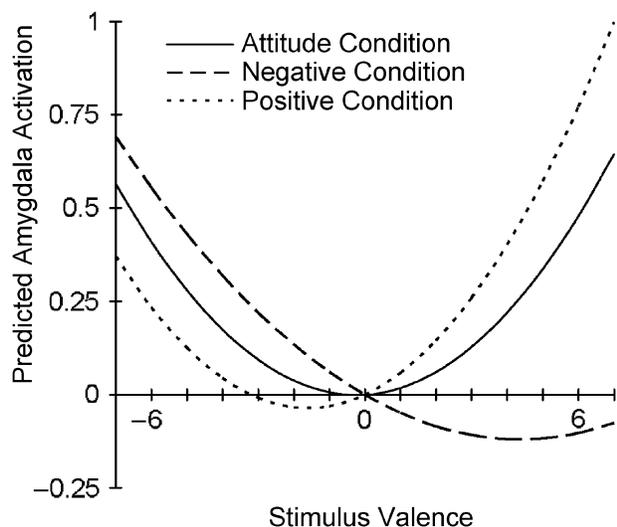


Fig. 2. Predicted bilateral amygdala activity as a function of stimulus valence and condition. Bilateral amygdala activity is plotted as the score predicted from the postscan valence (V) and quadratic valence (V^2) beta terms as determined by ratings in each of the three conditions.

interaction, and emotionality. For the regression analyses, the positivity and negativity ratings were centered to allow for a meaningful interaction term. To extract voxels for the second-level analysis, we generated from the previous analyses a mask that contained the significant voxels for both the extremity and the fit effects. By analyzing only these voxels, we were able to make direct comparisons between the two sets of analyses.

Results were consistent with the idea of affective flexibility. There was a significant interaction between scanning condition (positive or negative) and stimulus valence (postscan ratings of positivity or negativity), $F(1, 11) = 9.67, p < .01, p_{\text{rep}} = .95$ (see Fig. 3). More positively rated names were associated with more amygdala activity in the positive condition and less amygdala activity in the negative condition. Further, more negatively rated names were associated with greater amygdala activity in the negative condition, but were unrelated to amygdala activity in the positive condition. The graph in Figure 3 further illustrates the heightened amygdala activity in response to positive stimuli in the positive condition and the offset of the extremity effect (V^2) in the negative condition. In other words, the effects illustrated in Figure 3 can be understood as modulations of the extremity effect, in which positivity and negativity are both associated with increased amygdala activity. When there was a fit between stimulus valence and task, the extremity effect was enhanced (i.e., positive beta weights). However, when there was a mismatch, the extremity effect was not altered for negative stimuli in the positive condition, but was significantly reduced for positive stimuli in the negative condition (i.e., negative beta weight). Indeed, the latter reduction was sufficient to completely eliminate the extremity effect, as Figure 2 shows. Figure 3, like Figure 2, shows evidence of a negativity bias. The beta weights for negativity ratings suggest that although it is possible to in-

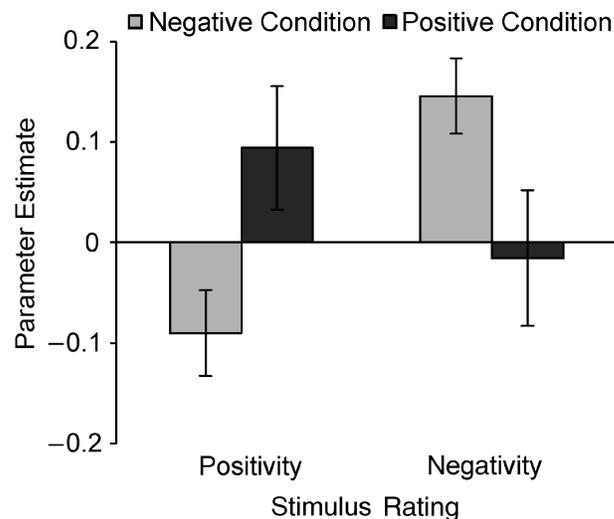


Fig. 3. Beta weights associated with bilateral amygdala activity as a function of independent postscan ratings of positivity and negativity, graphed separately for the positive and negative conditions during scanning.

crease the processing of negative information, it may be more difficult to *decrease* the processing of negative information—even when the information is unrelated to current goals.

Affective Flexibility in Other Brain Regions

Whole-brain analyses were conducted to identify other regions showing affective flexibility in the form of enhanced activity when there was a fit between valence and goals. For these analyses, we defined significant regions of activity as those in which the regression parameter estimates were larger for fit associations (e.g., relation between stimulus positivity and activity in the positive condition) than nonfit associations (e.g., relation between stimulus negativity and activity in the positive condition). In addition to identifying the amygdala, this analysis identified several other regions previously implicated in emotional or reward processing, such as right and left insula (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Barrett & Wager, in press), $t(11) = 4.16, p < .001, p_{\text{rep}} = .99$, and $t(11) = 4.29, p < .001, p_{\text{rep}} = .99$, respectively, and left nucleus accumbens (Knutson, Adams, Fong, & Hommer, 2001), $t(11) = 3.73, p < .001, p_{\text{rep}} = .99$. These results suggest that a widespread network of brain regions is involved in processing motivational relevance.

Prefrontal Contributions to Affective Flexibility

We expected that not only regions typically associated with affective processing, but also regions associated with executive function and emotion regulation might be involved in guiding affective flexibility. Having to selectively process a subset of information to determine the affective connotations of a stimulus may require deliberate attention and selective processing.

Evidence for this would be found if regions associated with executive function either had greater overall activity in the positive and negative conditions than in the attitude condition or were shown to have greater connectivity with the amygdala in the positive and negative conditions than in the attitude condition. In addition, executive function may play a particularly active role when participants' processing goal is to attend to either positive or negative aspects of stimuli and both positive and negative information are present (ambivalence). In these cases, the presence of goal-relevant information would activate additional processing, and relevant information would need to be foregrounded from goal-irrelevant (and in this case conflicting) information to make an appropriate judgment.

Whole-brain analyses of the main effect of condition and the ambivalence-by-condition interaction provided evidence for both hypotheses. Right dorsolateral prefrontal cortex (PFC) differentiated conditions in the main-effects analysis, showing greater activation in the positive and negative conditions than in the attitude condition, $t(11) = 3.02, p < .01, p_{\text{rep}} = .96$ (MNI coordinates: 42, 33, 42), although this effect was significant at a slightly more lenient threshold than used in the other analyses. This finding was bolstered by an independent components analysis that we used to examine connectivity (Calhoun, Adali, Pearlson, & Pekar, 2001). Of the 25 components extracted, 2 contained both amygdala and prefrontal correlations. The first suggested a network that also included both medial areas of orbitofrontal cortex, $t(11) = 5.92, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: -3, 27, -24), and right lateral areas of orbitofrontal cortex, $t(11) = 4.25, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: 39, 39, -12), as well as a large area of right rostralateral PFC, $t(11) = 3.68, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: 24, 69, 12). The second network included right orbitofrontal cortex, $t(11) = 4.61, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: 45, 57, -9); left orbitofrontal cortex, $t(11) = 7.17, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: -36, 54, -12); and anterior cingulate, $t(11) = 4.35, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: 12, 24, 27). We conducted a test of differences in connectivity by regressing the time courses of these 2 components from the expected hemodynamic signals from the three conditions. These analyses indicated that both components were significantly more present in the positive and negative conditions than in the attitude condition—first component: $t(11) = 2.29, p < .05, p_{\text{rep}} = .88$; second component: $t(11) = 3.47, p < .001, p_{\text{rep}} = .99$.

In addition, the condition-by-ambivalence interaction indicated that several regions were more associated with ambivalence in the positive and negative conditions than in the attitude condition. These regions included several areas associated with executive function and the foregrounding or backgrounding of information (Cunningham & Zelazo, 2007; Miller, 2000), such as ventrolateral PFC, $t(11) = 5.14, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: -36, 27, -18), and rostralateral PFC,

$t(11) = 4.75, p < .001, p_{\text{rep}} = .99$ (MNI coordinates: 24, 66, 18). The activations in lateral PFC suggest that additional processing was required for ambivalent stimuli. A regression analysis (repeated within subjects) revealed that more ambivalent names were associated with longer in-scanner reaction times ($\beta = .15, p < .001, p_{\text{rep}} > .99$). Taken together, these results suggest that a simple goal state was likely insufficient for processing ambivalence in the positive and negative conditions, and that lateral PFC regions were recruited to resolve the conflict in rendering an evaluation, perhaps by foregrounding relevant aspects of stimuli over irrelevant aspects.

Results of the region-of-interest and whole-brain analyses are summarized in Table 2.

DISCUSSION

The present study demonstrates a new degree of processing flexibility within the human amygdala. These data suggest that the amygdala may play a relatively flexible role in evaluation, processing stimulus aspects in accordance with current goals and motivations. Specifically, activity in the amygdala tracked the fit between experimentally manipulated evaluative goals and the valence of target stimuli. The amygdala was most active when participants evaluated (a) positive stimuli in the positive condition, (b) negative stimuli in the negative condition, and (c) both positive and negative stimuli in the attitude condition. Although the “default” mode of amygdala activation may be to process affective intensity or extremity (positive or negative information could be equally important)—which serves an important vigilance function (Davis & Whalen, 2001)—these data suggest that the amygdala, in concert with other neural components of evaluative processing, may track and process the fit between stimuli and situational demands.

Although these data provide an important demonstration of affective flexibility in the amygdala, it is important to consider the asymmetry in evaluative processing. Whereas the amygdala was relatively unresponsive to positive names in the negative condition (Fig. 2 shows a nearly flat line of amygdala activity for such names), some residual activation in the amygdala was observed for negative names in the positive condition. Further evidence of this negativity bias (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001) was obtained from the analysis in which we separated the independent positive and negative ratings of each stimulus. Whereas the processing of positive information was associated with increased amygdala activity in the positive condition and decreased amygdala activity in the negative condition (offsetting the extremity effect), processing negative information only increased amygdala activity in the negative condition. Compared with positive information, negative information may not have been as easily inhibited when it was task irrelevant. These results suggest an important constraint on the affective flexibility of the amygdala.

TABLE 2
Areas Exhibiting Significant Blood-Oxygen-Level-Dependent (BOLD) Activation

| Area | BA | Hemisphere | <i>t</i> or <i>F</i> statistic | MNI coordinates | | | No. of voxels |
|--|-------|------------|-----------------------------------|-----------------|----------|----------|---------------|
| | | | | <i>x</i> | <i>y</i> | <i>z</i> | |
| Areas associated with valence extremity (collapsing across conditions): region-of-interest analysis | | | | | | | |
| Amygdala | — | Right | 5.76 | 21 | 0 | −21 | 34 |
| Amygdala | — | Left | 5.31 | −18 | 6 | −15 | 15 |
| Areas associated with valence extremity (collapsing across conditions): whole-brain analysis | | | | | | | |
| Amygdala | — | Right | 5.76 | 21 | 0 | −21 | 32 |
| Amygdala | — | Left | 5.31 | −18 | 6 | −15 | 15 |
| Anterior cingulate | 32 | Left | 6.90 | −3 | 42 | 9 | 90 |
| Parahippocampal gyrus | 20/30 | Left | 7.62 | −30 | −27 | −21 | 56 |
| Middle temporal gyrus | 20 | Left | 6.67 | −63 | −18 | −24 | 45 |
| Inferior temporal gyrus | 37 | Left | 7.40 | −51 | −57 | −18 | 117 |
| Inferior parietal gyrus | 40 | Left | 9.60 | −60 | −45 | 45 | 165 |
| Areas associated with a significant valence-by-condition effect (affective fit): region-of-interest analysis | | | | | | | |
| Amygdala | — | Right | 11.07 | 21 | 0 | −12 | 26 |
| Amygdala | — | Left | 9.44 | −24 | −3 | −15 | 40 |
| Areas associated with a significant valence-by-condition effect (affective fit): whole-brain analysis | | | | | | | |
| Amygdala | — | Right | 4.46 | 21 | 0 | −12 | 13 |
| Amygdala | — | Left | 4.29 | −24 | 0 | −15 | 28 |
| Insula | 48 | Right | 4.16 | 45 | 0 | 6 | 16 |
| Insula | 48 | Left | 4.78 | −42 | 0 | 9 | 36 |
| Precentral gyrus | 6 | Left | 4.59 | −36 | −12 | 60 | 40 |
| Precentral gyrus | 6 | Right | 4.38 | 27 | −12 | 66 | 16 |
| Supramarginal gyrus | 48 | Right | 4.57 | 63 | −21 | 27 | 26 |
| Areas exhibiting greater activity in the positive and negative conditions than in the attitude condition: whole-brain analysis | | | | | | | |
| Lateral orbital frontal cortex (VLPFC) | 47 | Right | 5.14 | −36 | 27 | −18 | 34 |
| Superior frontal gyrus (RLPFC) | 10 | Left | 4.75 | 24 | 66 | 18 | 49 |
| Superior frontal gyrus | 8 | Left | 5.88 | 3 | 30 | 63 | 167 |
| Middle frontal gyrus | 9 | Right | 4.74 | −39 | 27 | 48 | 10 |
| Angular gyrus | 48 | Left | 4.86 | 51 | −42 | 30 | 64 |
| Angular gyrus | 39 | Right | 4.18 | −60 | −54 | 36 | 43 |
| Inferior occipital gyrus | 19 | Left | 5.15 | 45 | −72 | −15 | 40 |
| Calcarine fissure | 17 | — | 3.83 | 0 | −72 | 12 | 11 |

Note. In the region-of-interest analyses (small-volume-corrected $p < .05$) and whole-brain analyses ($p < .001$), identified regions had to meet a threshold of activity in 10 or more contiguous voxels. Regions are identified by Brodmann's areas (BA) and Montreal Neurological Institute (MNI) coordinates (x , y , z). RLPFC = rostralateral prefrontal cortex; VLPFC = ventrolateral prefrontal cortex.

In addition, the current study provides insights into the processes of emotional regulation. Although there were differences in PFC activation and connectivity with the amygdala between conditions, there was a stronger interaction between ambivalence and condition, which suggests that the shifts in affective processing (Ochsner & Gross, 2007) may result from PFC-mediated processes. PFC regions may maintain the goal and trigger processes when stimuli are too complex (ambivalent) for the current processing goal (i.e., in the positive and negative conditions). For ambivalent stimuli, the recruitment of additional PFC-mediated control processes may have been necessary to foreground relevant valenced information so that an appropriate evaluation could be rendered (Aron, Robbins, & Poldrack, 2004).

One possible interpretation of these data is that the amygdala itself filters information on the basis of motivational significance. An alternative possibility is that top-down attentional processes foreground motivationally relevant information, which is then processed by the amygdala (Anderson et al., 2003; Pessoa et al., 2006). It is likely that such processes came into play in our task, as word meaning needs to be extracted prior to affective processing, and different memories may contribute to different evaluations. Thus, the observed modulation may have come from the inputs to the amygdala, rather than from differences in processing within the amygdala proper. According to this account, processing was not changed; rather, the afferents were altered.

It is becoming increasingly clear that evaluation is remarkably complex and dependent on the integration of existing stimulus-based attitudes with current goals, motivations, and contextual demands (Cunningham & Zelazo, 2007; Ferguson & Bargh, 2004). Although amygdala processing has been shown to occur rapidly and unconsciously, these data add to the growing evidence that goals may modulate amygdala activation to generate contextually appropriate and nuanced evaluations (Kim et al., 2004). Although complex neural networks play an important role in rendering an evaluation, we suggest that flexibility may be a core operating characteristic of specific components within these networks. Specifically, the amygdala may respond flexibly to the valence and extremity of stimuli in a goal-congruent fashion, but process negativity in a less flexible fashion than positivity. This combination of flexible and fixed processing may allow humans to solve new and old evaluative problems while successfully navigating complex environments.

Acknowledgments—The authors thank Ken Fujita, Steve Most, Sharon David, Mike Edwards, and members of the Social Cognitive and Affective Neuroscience Lab for helpful comments on this manuscript. This work was supported by grants from the Natural Sciences and Engineering Research Council and the Social Sciences and Humanities Research Council.

REFERENCES

- Adolphs, R. (2003). Is the human amygdala specialized for processing social information? In P. Shinnick-Gallagher, A. Pitkanen, A. Shekhar, & L. Cahill (Eds.), *The amygdala in brain function: Basic and clinical approaches* (Annals of the New York Academy of Sciences Vol. 985, pp. 326–340). New York: New York Academy of Sciences.
- Adolphs, R., Tranel, D., & Damasio, A.R. (1998). The human amygdala in social judgment. *Nature*, *393*, 470–474.
- Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G., et al. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, *6*, 196–202.
- Anderson, A.K., & Phelps, E.A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Aron, A.R., Robbins, T.W., & Poldrack, R.A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*, 170–177.
- Barrett, L.F., & Wager, T.D. (in press). The structure of emotion: Evidence from neuroimaging studies. *Current Directions in Psychological Science*.
- Baumeister, R.F., Bratslavsky, E., Finkenauer, C., & Vohs, K.D. (2001). Bad is stronger than good. *Review of General Psychology*, *5*, 323–370.
- Beauregard, M., Levesque, J., & Bourgouin, P. (2001). Neural correlates of the conscious self-regulation of emotion. *Journal of Neuroscience*, *21*, 1–6.
- Bishop, S.J., Duncan, J., & Lawrence, A.D. (2004). State anxiety modulation of the amygdala response to unattended threat-related stimuli. *Journal of Neuroscience*, *24*, 10364–10368.
- Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., et al. (2003). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, *17*, 875–887.
- Cacioppo, J.T., & Berntson, G.G. (1994). Relationship between attitudes and evaluative space: A critical review with emphasis on the separability of positive and negative substrates. *Psychological Bulletin*, *115*, 401–423.
- Calhoun, V.D., Adali, T., Pearlson, G.D., & Pekar, J.J. (2001). A method for making group inferences from functional MRI data using independent component analysis. *Human Brain Mapping*, *14*, 140–151.
- Canli, T., Zhao, Z., Brewer, J., Gabrieli, J.D.E., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *Journal of Neuroscience*, *20*, 1–5.
- Critchley, H.D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R.J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*, 189–195.
- Cunningham, W.A., Johnson, M.K., Gatenby, J.C., Gore, J.C., & Banaji, M.R. (2003). Neural components of social evaluation. *Journal of Personality and Social Psychology*, *85*, 639–649.
- Cunningham, W.A., Johnson, M.K., Raye, C.L., Gatenby, J.C., Gore, J.C., & Banaji, M.R. (2004). Separable neural components in the processing of Black and White faces. *Psychological Science*, *15*, 806–813.
- Cunningham, W.A., Raye, C.L., & Johnson, M.K. (2004). Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *Journal of Cognitive Neuroscience*, *16*, 1717–1729.
- Cunningham, W.A., Raye, C.L., & Johnson, M.K. (2005). Neural correlates of evaluation associated with promotion and prevention regulatory focus. *Cognitive, Affective, and Behavioral Neuroscience*, *5*, 202–211.
- Cunningham, W.A., & Zelazo, P.D. (2007). Attitudes and evaluations: A social cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *11*, 97–104.
- Davis, M., & Whalen, P.J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry*, *6*, 13–34.
- Ferguson, M.J., & Bargh, J.A. (2004). Liking is for doing: The effects of goal pursuit on automatic evaluation. *Journal of Personality and Social Psychology*, *87*, 557–572.
- Hamann, S.B., Ely, T.D., Hoffman, J.M., & Kilts, C.D. (2002). Ecstasy and agony: Activation of the human amygdala in positive and negative emotion. *Psychological Science*, *13*, 135–141.
- Hariri, A.R., Tessitore, A., Mattay, V.S., Fera, F., & Weinberger, D.R. (2002). The amygdala response to emotional stimuli: A comparison of faces and scenes. *NeuroImage*, *17*, 317–323.
- Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., & Camerer, C.F. (2005). Neural systems responding to degrees of uncertainty in human decision-making. *Science*, *310*, 1680–1683.
- Izenberg, N., Silbersweig, D., Engelien, A., Emmerich, S., Malavade, K., Beattie, B., et al. (1999). Linguistic threat activates the human amygdala. *Proceedings of the National Academy of Sciences, USA*, *96*, 10456–10459.
- Kim, H., Somerville, L.H., Johnstone, T., Polis, S., Alexander, A.L., Shin, L.M., & Whalen, P.J. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience*, *16*, 1730–1745.
- Knutson, B., Adams, C.M., Fong, G.W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience*, *21*, 1–5.

- LeDoux, J.E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, 23, 155–184.
- Lieberman, M.D., Eisenberger, N.I., Crockett, M.J., Tom, S.M., Pfeifer, J.H., & Way, B.M. (2007). Putting feelings into words: Affect labeling disrupts amygdala activity to affective stimuli. *Psychological Science*, 18, 421–428.
- Miller, E.K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience*, 1, 59–65.
- Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., & Dolan, R.J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383, 812–815.
- Morris, J.S., Öhman, A., & Dolan, R.J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393, 467–470.
- Ochsner, K.N., & Gross, J.J. (2007). The neural architecture of emotion regulation. In J.J. Gross & R. Buck (Eds.), *The handbook of emotion regulation* (pp. 87–109). New York: Guilford Press.
- Ochsner, K.N., Ray, R.D., Cooper, J.C., Robertson, E.R., Gabrieli, J.D.E., & Gross, J.J. (2004). For better or for worse: Neural systems supporting the cognitive down- and up-regulation of negative emotion. *NeuroImage*, 23, 483–499.
- Pessoa, L., Japee, S., Sturman, D., & Ungerleider, L.G. (2006). Target visibility and visual awareness modulate amygdala responses to fearful faces. *Cerebral Cortex*, 16, 366–375.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioral Neurology*, 12, 191–200.
- Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, 39, 701–711.
- Thompson, M.M., Zanna, M.P., & Griffin, D.W. (1995). Let's not be indifferent about (attitudinal) ambivalence. In R.E. Petty & J.A. Krosnick (Eds.), *Attitude strength: Antecedents and consequences* (pp. 361–386). Mahwah, NJ: Erlbaum.
- Whalen, P.J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, 7, 177–188.
- Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., & Jenike, M.A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, 18, 411–418.

(RECEIVED 3/29/07; REVISION ACCEPTED 7/22/07)