

# The Amygdala Response to Emotional Stimuli: A Comparison of Faces and Scenes

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As a central fear processor of the brain, the amygdala initiates a cascade of critical physiological and behavioral responses. Neuroimaging studies have shown that the human amygdala responds not only to fearful and angry facial expressions but also to fearful and threatening scenes such as attacks, explosions, and mutilations. Given the relative importance of facial expressions in adaptive social behavior, we hypothesized that the human amygdala would exhibit a stronger response to angry and fearful facial expressions in comparison to other fearful and threatening stimuli. Twelve subjects completed two tasks while undergoing fMRI: matching angry or fearful facial expressions, and matching scenes depicting fearful or threatening situations derived from the International Affective Picture System (IAPS). While there was an amygdala response to both facial expressions and IAPS stimuli, direct comparison revealed that the amygdala response to facial expressions was significantly greater than that to IAPS stimuli. Autonomic reactivity, measured by skin conductance responses, was also greater to facial expressions. These results suggest that the human amygdala shows a stronger response to affective facial expressions than to scenes, a bias that should be considered in the design of experimental paradigms interested in probing amygdala function.

## INTRODUCTION

Fear is a strong emotion that is associated with rapid, instinctive responses related to avoiding or preparing for conflict. Perceiving and reacting appropriately to fearful stimuli translates into a direct survival advantage that has been conserved across species (Darwin, 1998). In humans, facial expressions of negative affect are examples of such fearful stimuli. In fact, facial expressions convey such strong emotional

information that merely observing angry or fearful faces elicits strong visceral responses, including increased heart rate and sweating (Ohman and Soares, 1998). Both lesion (Adolphs *et al.*, 1994, 1995; Anderson and Phelps, 2001) and neuroimaging studies (see Davis and Whalen, 2001 for summary) have illustrated that these fearful responses to facial expressions are processed and largely mediated by the amygdala, a subcortical structure with connections to both early sensory processing areas and autonomic reflex centers. Furthermore, amygdala responses to fearful faces have been observed with neuroimaging even in the absence of conscious awareness of their presentation to subjects (Whalen *et al.*, 1998).

In addition to processing fearful and angry facial expressions, the human amygdala exhibits a response to complex pictures of fearful and threatening scenes such as snarling dogs, snakes, explosions and attacks (Davis and Whalen, 2001). Studies of these amygdala responses have largely utilized the International Affective Picture System (IAPS), a data set that has been carefully characterized, in multiple populations, with respect to both valence and arousal (Lang *et al.*, 1997). As with facial expressions, fearful responses to such complex stimuli may confer a strong survival advantage and have been associated with physiological responses such as increased heart rate and sweating (Lang *et al.*, 1998).

While numerous neuroimaging studies have illustrated amygdala responses to both face and non-face stimuli, none to date have examined the strength and specificity of these responses to the different types of fearful stimuli. Here we report the results of an fMRI study to explore the differential response of the amygdala to fearful face and nonface (IAPS) stimuli in a group of normal volunteers. Given the relative importance of facial expressions in human development and adaptive social behavior (Darwin, 1998), we hypothesized that the human amygdala would exhibit a stronger response to angry and fearful facial expressions in comparison to IAPS stimuli.

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## METHODS

### *Subjects*

Twelve healthy subjects (6 males and 6 females, mean age = 28 years) gave written informed consent and participated in the study according to the guidelines of the National Institute of Mental Health Institutional Review Board. Subjects were screened for and cleared of neurological, psychiatric or substance abuse problems, and had no history of other medical problems or medical treatment relevant to cerebral metabolism and blood flow. Eleven subjects were right-handed and one female subject was left-handed (Edinburgh Handedness Inventory).

### *Stimuli*

For facial expressions, 12 different images were used, 6 of each gender and affect (angry or afraid), all derived from a standard set of pictures of facial affect (Ekman and Friesen, 1976). For IAPS stimuli, 12 different images were also used, 6 representing threats of natural origin (i.e., dogs, sharks, snakes, spiders) and 6 threats of artificial origin (i.e., guns, car accidents, plane crashes, explosions). None of the IAPS images contained human faces. The mean ( $\pm$ SEM) valence and arousal on a nine-point scale, where one represents maximum negative and nine maximum positive valence or arousal, for all IAPS stimuli used were  $3.13 \pm 0.20$  and  $6.40 \pm 0.13$ , respectively. Simple geometric shapes (circles, vertical, and horizontal ellipses) were used as control stimuli.

### *Experimental Paradigm*

In order to identify amygdala responses to facial expressions and IAPS stimuli, subjects were asked to match one of two simultaneously presented images with an identical target image (Figs. 1A and 1B). As a sensorimotor control task, the subjects were asked to match geometric shapes (Fig. 1C). The fMRI paradigm consisted of nine experimental blocks: two blocks each of matching facial expressions and matching IAPS stimuli interleaved with five control blocks, each lasting 32 s for a total scan length of 4:48 min. Each block began with a brief (2 s) instruction statement: "Match Faces," "Match Pictures," or "Match Forms." Each matching block consisted of six images. For each face block, three images of each gender and target affect (angry or afraid) were presented. For each IAPS block, three images of each threat origin (natural or artificial) were presented. For each control block, six different geometric shapes were presented as targets. All images were presented sequentially, with no interstimulus interval, for a period of 5 s and in a randomized fashion for all conditions. The order of the paradigm was counterbalanced across subjects. During imaging, subjects

responded by pressing one of two buttons with their dominant hand, allowing for the determination of accuracy and reaction time. In order to examine habituation of amygdala responses, each subject was scanned twice in succession using the same paradigm.

### *Physiological Responses*

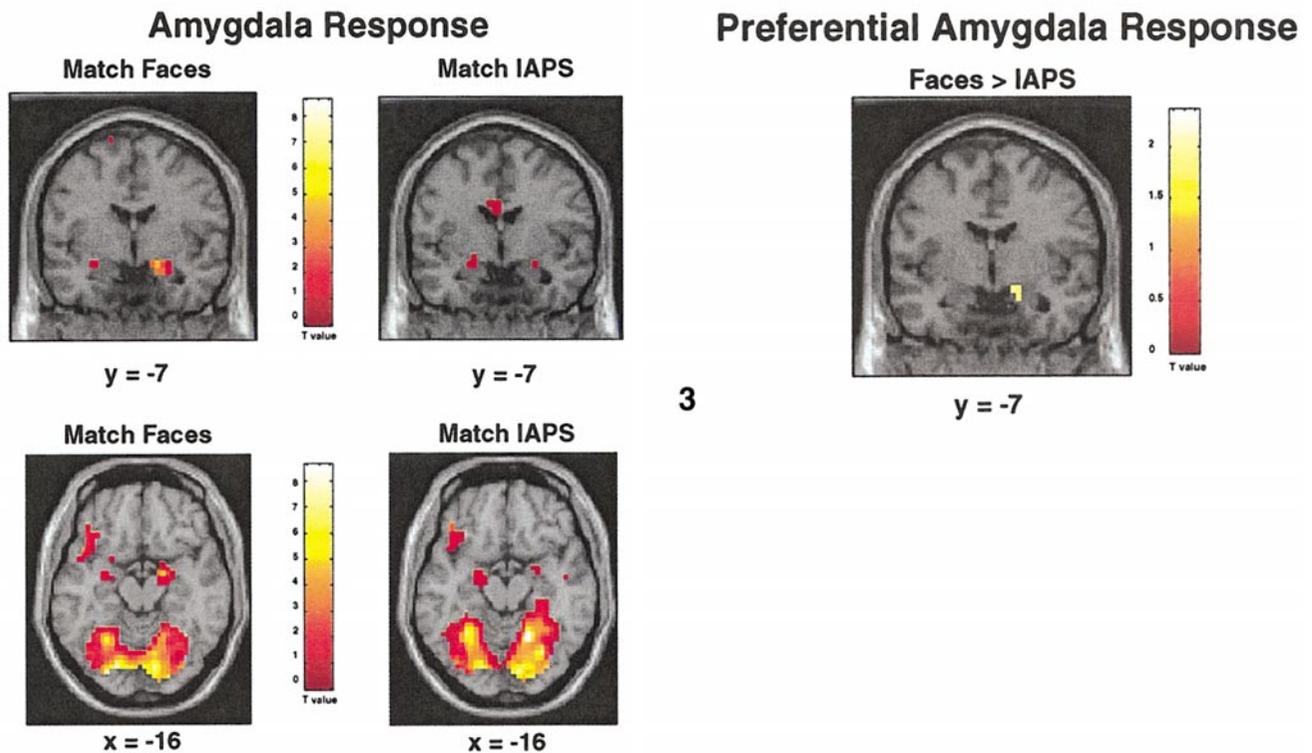
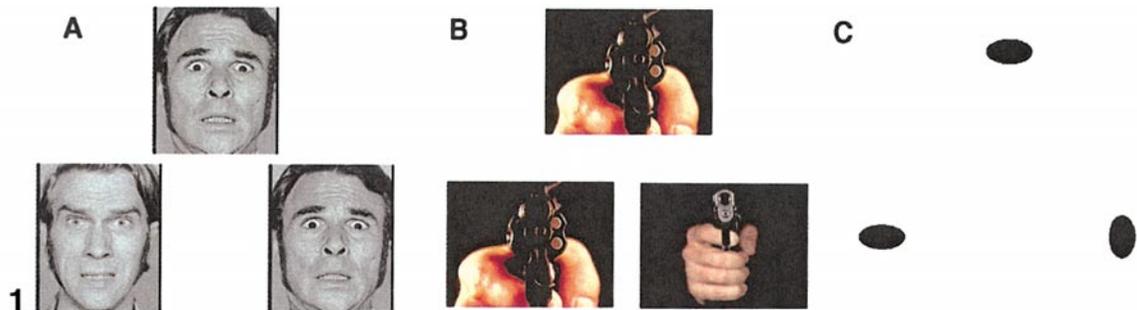
In order to ascertain the relationship between changes in amygdala response and autonomic reactivity, we measured skin conductance response (SCR) during the acquisition of functional scans in all subjects. Due to technical problems, we were unable to obtain data for three (2 males and 1 female) of the 12 subjects. SCR was recorded from the palmar surface of the middle phalanx of the index and middle digits of the left hand using Ag/AgCl electrodes. Digitized (24 bit) signals were acquired using a radio frequency shielded cable, processed through a remote preamplifier and recorded at 20 Hz on a PC (Contact Precision Instruments Inc., Cambridge, MA). Mean percent changes in SCR from adjacent blocks of the sensorimotor control task were determined for both match faces and match IAPS conditions. By calculating task-specific mean percent change in SCR from adjacent control blocks we sought to minimize the influence of signal drift and task-independent phenomenon over the course of the scan.

### *Image Acquisition*

Each subject was scanned using a GE Signa 3T scanner with a real-time functional imaging upgrade (Milwaukee, WI). An automated shim procedure was applied to minimize possible magnetic field inhomogeneities. Functional image planes were prescribed using a T2-weighted sagittal scout. Functional images were acquired with a gradient echo EPI sequence, and covered 24 axial slices (4 mm thick, 1 mm gap) that began at the cerebral vertex and encompassed the entire cerebrum and the majority of the cerebellum (TR/TE = 2000/28 ms, FOV = 24 cm, matrix =  $64 \times 64$ ). All scanning parameters were selected to optimize the quality of the BOLD signal while maintaining a sufficient number of slices to acquire whole-brain data. Before the collection of fMRI data for each subject we acquired a reference EPI scan that we visually inspected for artifacts (e.g., ghosting) as well as good signal across the entire volume of acquisition, including the medial temporal lobes. The fMRI data from all 12 subjects included in this study were cleared of such problems.

### *Data Analysis*

Whole-brain image analysis was completed using SPM99 (Friston *et al.*, 1995). For each scan, images for each subject were realigned to the first volume in the



**FIG. 1.** Experimental paradigm. Subjects performed three tasks while undergoing fMRI. In order to identify amygdala responses to facial expressions (A) and IAPS stimuli (B), subjects were asked to match one of two simultaneously presented images with an identical target image. As a control task, the subjects were asked to match geometric shapes; six different shapes were presented as targets (C).

**FIG. 2.** Statistical parametric maps illustrating BOLD responses in the amygdala during matching of facial expressions and IAPS stimuli. See Table 1 for complete Talairach coordinates and values ( $P < 0.05$ , uncorrected).

**FIG. 3.** Statistical parametric map illustrating a significantly greater BOLD response in the right amygdala to facial expressions in comparison to IAPS stimuli. See Table 1 for complete Talairach coordinates and values ( $P < 0.05$ , uncorrected).

time series to correct for head motion. Data sets were then selected for their high quality (scan stability) as demonstrated by small ( $< 2$  mm) motion correction (Mattay *et al.*, 1996). Based on this criterion, data from all 12 subjects were included in subsequent analyses. Realigned images were spatially normalized into a standard stereotactic space (Montreal Neurological Institute template) using a 12 parameter affine model. These normalized images were then smoothed to minimize noise and residual differences in gyral anatomy with a Gaussian filter, set at 8 mm full-width at half-

maximum, producing an effective spatial resolution of  $12.3 \times 12.6 \times 12.1$  mm. Voxel-wise signal intensities were ratio normalized to the whole-brain global mean.

These preprocessed data sets were analyzed using second-level random effects models that account for both scan-to-scan and subject-to-subject variability. This approach allows for a more critical and stringent exploration of BOLD responses than traditional fixed effects models that only account for scan-to-scan variability. For each subject and scan, predetermined condition effects at each voxel were calculated using a  $t$

**TABLE 1**  
Significant BOLD fMRI Responses in the Amygdala for All Comparisons

	Talairach coordinates (x, y, z)	Cluster size	Z score	P value <sup>a</sup>
<b>Main effects of task</b>				
Match Faces vs. Control				
L. amygdala	-28, -6, -16	3	1.88	0.03
R. amygdala	20, -4, -16	19	3.64	0.001
Match IAPS vs. Control				
L. amygdala	-18, -10, -16	9	2.23	0.013
R. amygdala	24, 0, -16	3	1.94	0.026
<b>Direct comparisons</b>				
Match Faces > Match IAPS				
R. amygdala	16, -4, -16	3	1.87	0.03
Match IAPS > Match Faces				
No significant differences				
<b>Habituation of response</b>				
Match Faces (Scan 1 > Scan 2)				
R. amygdala	20, -4, -16	2	2.11	0.017
Match IAPS (Scan 1 > Scan 2)				
L. amygdala	-18, -10, -12	4	1.97	0.024

Note. Coordinates represent voxels in the amygdala with the most significant magnitude and spatial extent.

<sup>a</sup> All reported statistical values are derived from a second-level random effects analysis using an uncorrected threshold of  $P < 0.05$ . A fixed effects analysis of the imaging data using a statistical threshold of  $P < 0.05$ , corrected for multiple comparisons, revealed identical patterns of amygdala responses to faces and scenes.

statistic, producing a statistical image for each contrast: (1) match faces > control and (2) match IAPS > control. These individual contrast images were then used to determine task-specific regional responses using one-sample (main effects of task) and paired  $t$  tests (direct comparisons). Habituation effects were explored using paired  $t$  tests between contrast images derived from the first and second scans. Because of our strong *a priori* hypothesis and utilization of rigorous statistical methods that account for both scan-to-scan and subject-to-subject variability, we chose to explore the differential response of the amygdala using an uncorrected statistical threshold of  $P < 0.05$ .

Behavioral and physiological data were analyzed using repeated-measures ANOVA and post-hoc comparisons using Fisher's Paired Least Significant Difference test.

## RESULTS

### BOLD fMRI Responses

Table 1 provides a summary of significant BOLD amygdala responses for main effects of task, direct task comparisons and response habituation. In comparison to the control condition, there was a strong bilateral amygdala response to both facial expressions and IAPS stimuli (Fig. 2). With facial expressions, the response of the right amygdala was larger than that of the left. An opposite pattern (left > right) was observed with IAPS stimuli. Direct comparison of the two tasks revealed that the response of the right amygdala was significantly greater to facial expressions than to IAPS stimuli (Fig. 3). There was no difference in the response of

the left amygdala between tasks. Comparison of the amygdala response over successive scans revealed significant habituation of the right amygdala response to facial expressions and of the left amygdala response to IAPS stimuli. There were no significant gender differences in the response of the amygdala during either task or over successive scans.

In addition to the response of the amygdala, both tasks were associated with BOLD responses in face and object processing areas, namely the bilateral posterior fusiform and parahippocampal gyri. Direct comparisons revealed that these responses were significantly greater for IAPS stimuli. Matching IAPS stimuli was also associated with a response in the anterior cingulate cortex (ACC). Both facial expressions and IAPS stimuli were associated with a bilateral response in the ventral prefrontal cortex (PFC). Direct comparisons revealed that the responses of the ACC as well as the PFC were significantly larger for IAPS stimuli.

### Behavior and Physiology

While there was no significant difference in mean accuracy between conditions ( $F(1,22) = 1.00$ ,  $P = 0.33$ ), the mean reaction time for IAPS stimuli was significantly slower than for faces ( $F(1,22) = 8.72$ ,  $P < 0.01$ ). Mean accuracy ( $\pm$ SEM) for faces and IAPS were  $100.0 \pm 0.0\%$  and  $99.3 \pm 0.7\%$ , respectively. Mean reaction time ( $\pm$ SEM) for faces and IAPS were  $1472.8 \pm 67.5$  ms and  $1737.6 \pm 58.9$  ms, respectively. While the values reported are from the first scanning session only, a similar performance pattern was observed dur-

ing the second session. There were no gender differences in performance for either task.

There was no main effect of task on mean percent change in SCR ( $F(7,64) = 1.53, P < 0.17$ ). Nevertheless, SCR increased significantly from the sensorimotor control task (mean percent change  $\pm$  SEM) during facial expression matching ( $2.50 \pm 1.3\%$ ,  $P = 0.02$ ) but not during IAPS stimuli matching ( $0.07 \pm 1.0\%$ ,  $P = 0.95$ ). Furthermore, direct comparisons revealed that the mean percent change in SCR was significantly greater for facial expressions in comparison to IAPS ( $P = 0.02$ ). Post-hoc comparisons also revealed significant habituation of this response over successive scans for faces (difference between first and second scans =  $-0.22 \pm 0.9\%$ ,  $P = 0.01$ ) but not for IAPS ( $0.25 \pm 0.8\%$ ,  $P = 0.86$ ). Again, there were no gender differences in mean percent change in SCR for either task.

## DISCUSSION

Our results suggest that the human amygdala exhibits a stronger BOLD fMRI response to fearful and threatening facial expressions in comparison to non-face IAPS stimuli, and that this difference extends to the physiological fear response, as reflected by larger autonomic (skin conductance) changes to facial expressions. Furthermore, the results suggest a differential laterality of the amygdala response to these stimulus sets with a relatively larger right amygdala response to facial expressions and relatively larger left amygdala response to IAPS stimuli.

### *Laterality of the Amygdala Response*

While there was a significant BOLD response in both the right and left amygdala to facial expressions, the magnitude of the right amygdala response was larger than that of the left, and it was the response of the right amygdala alone that habituated over successive scans. In addition, the significantly larger response to facial expressions in comparison to IAPS stimuli was in the right and not the left amygdala. In contrast, the amygdala response to IAPS stimuli was larger in the left than the right hemisphere, and it was this left amygdala response alone that habituated over successive scans.

At a functional level, the stimulus-specific laterality of these responses may reflect the inherent nature and value of these stimulus types. The right biased response to faces is consistent with studies implicating right hemisphere brain regions in general and the right amygdala in specific for processing facial expressions, especially those of negative affect (Adolphs *et al.*, 2001). Furthermore, our group has found that dextro-amphetamine, a nonspecific monoaminergic agonist and anxiogenic, selectively potentiates the response of only the right amygdala during the perceptual processing of angry and fearful faces, suggesting that this

structure may be especially critical in processing the emotional content of stimuli (Hariri *et al.*, 2002).

The opposite relative laterality to scenes may reflect the more cognitive nature of processing these stimuli in comparison to facial expressions. Many fearful and threatening IAPS stimuli, such as aimed guns and car accidents, do not represent objects of intrinsic biological importance, such as facial expressions (Darwin, 1998). Our fearful responses to these nonface stimuli are likely learned through experience and social transmission and thus, may be derived from, if not dependent on, responses in left hemisphere brain regions subserving cognitive operations such as language. A left lateralized amygdala response is consistent with several recent neuroimaging studies using IAPS stimuli (Lane *et al.*, 1997; Taylor *et al.*, 1998; Paradiso *et al.*, 1999). In addition, both neuroimaging (Phelps *et al.*, 2001) and human lesion (Anderson and Phelps, 2001; Funayama *et al.*, 2001) studies have implicated the left amygdala in the processing and appreciation of cognitive representations of fear such as fearful words.

Despite the above evidence supporting a differential functional role for the left and right amygdala during the processing of different types of emotional stimuli, the laterality findings of the current study may simply reflect methodological phenomenon. In a recent fMRI study, LaBar *et al.* explored the contribution of the signal-to-noise ratio (SNR) to the BOLD response patterns of the amygdala during a picture-encoding task (LaBar *et al.*, 2001). They found that in single subjects asymmetries in the BOLD response pattern of the amygdala mirrored asymmetries in BOLD sensitivity or SNR maps. Thus, they concluded that the presence or absence of significant responses in the amygdala might be related to sufficient or insufficient SNR in these regions.

While such methodological factors do not explain the observed stimulus-specific differential laterality of the amygdala response we describe, they may contribute to the discrepancies between our current right amygdala biased response to facial expressions and previously reported left amygdala biased responses (Phillips *et al.*, 1998, 2001; Killgore *et al.*, 2000). The specific experimental task, paradigm design, and imaging parameters may also contribute to these reported laterality differences. For example, in an fMRI conditioning paradigm Morris *et al.* reported a right amygdala response during masked (unconscious) presentations of angry faces and a left amygdala response during unmasked (conscious) presentations (Morris *et al.*, 1998). These and other differences make it difficult to compare laterality findings across studies.

### *Differential Amygdala Response*

Direct comparisons of the amygdala response to facial expressions and IAPS stimuli revealed a significantly greater right amygdala response to facial ex-

pressions. From a theoretical perspective, our results are consistent with the critical importance of facial expressions to our emotional and social behavior, and may reflect the influence of selective pressures and adaptation to stimuli essential for our survival. Conspicuous likely represent the most persistent threat to our survival (e.g., anger over competition for limited resources) and provide the most useful appraisals of our immediate environment (e.g., fear of a common predator). Thus, facial expressions may represent more consistent and honest indicators of danger than IAPS stimuli and provoke a relatively larger amygdala response. This interpretation is supported by behavioral studies that have illustrated a preferential detection of and attention to a threatening face in a crowd of faces (Hansen and Hansen, 1988; Ohman *et al.*, 2001). Moreover, neurons sensitive to both faces and facial expressions in comparison to inanimate objects have been identified in the human amygdala (Fried *et al.*, 1997).

From an experimental perspective, our results may be surprising given the relative simplicity of angry and fearful facial expressions in comparison to more complex images depicting such seemingly terrible things as snarling dogs, venomous snakes, explosions, guns and car accidents. However, this relative difference in complexity and also similarity of face relative to nonface IAPS stimuli may drive the preferential response of the amygdala. Perceptually, facial expressions represent a relatively homogeneous set of stimuli that are of intrinsic biological importance to all individuals. In contrast, IAPS stimuli are perceptually more complex, far less homogeneous, and, generally, not of intrinsic biological value to all individuals. These differences not only make it difficult to balance the intensity of these stimulus types but also may lead to higher levels of arousal to faces in comparison to IAPS stimuli. Thus, one may expect a more consistent amygdala response to facial expressions across all stimulus presentations and this response consistency may be reflected as a greater overall response in comparison to IAPS stimuli. Unfortunately, our blocked design does not allow us to identify the amygdala response to individual face or IAPS stimuli and limits our ability to effectively explore the influence of these factors. Future studies utilizing an event-related approach or a more homogeneous set of nonface stimuli (i.e., all snakes or all accident scenes) will allow us to address these possibilities.

In addition, the increased complexity and variability of IAPS stimuli may have required more cognitive processing that in turn may have influenced the response of the amygdala. Such increased cognitive load is suggested by the longer reaction times as well as the relatively stronger left amygdala, PFC and ACC responses to IAPS stimuli. Hariri *et al.* have demonstrated that cognitive evaluation of emotional stimuli in comparison to perceptual evaluation is associated with an increase in the response of the PFC, and a

corresponding decrease in the response of the amygdala (Hariri *et al.*, 2000).

Notwithstanding the inherent limitations of the blocked design employed, our results indicate that fearful and threatening facial expressions are more effective at engaging a strong and consistent amygdala response than nonface IAPS stimuli. This response preference may reflect the intrinsic importance and usefulness of facial expressions in directing our behavior and regulating our social interactions. Or, it may only reflect the relative complexity and homogeneity of these stimulus types. Regardless, investigators interested in using noninvasive neuroimaging techniques, such as fMRI, to explore the response and behavior of the human amygdala should consider these differences in the design of future experimental paradigms.

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