Robust Selectivity for Faces in the Human Amygdala in the Absence of Expressions

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Abstract

■ There is a well-established posterior network of cortical regions that plays a central role in face processing and that has been investigated extensively. In contrast, although responsive to faces, the amygdala is not considered a core face-selective region, and its face selectivity has never been a topic of systematic research in human neuroimaging studies. Here, we conducted a large-scale group analysis of fMRI data from 215 participants. We replicated the posterior network observed in prior studies but found equally robust and reliable responses to faces in the amygdala. These responses were detectable in most individual participants, but they were also highly sensitive to the initial statistical threshold and habituated more rapidly than the responses in posterior face-selective regions. A multivariate analysis showed that the pattern of responses to faces across voxels in the amygdala had high reliability over time. Finally, functional connectivity analyses showed stronger coupling between the amygdala and posterior face-selective regions during the perception of faces than during the perception of control visual categories. These findings suggest that the amygdala should be considered a core face-selective region. ■

INTRODUCTION

Of the countless stimuli that populate our visual universe, faces are one of the richest sources of social information. Attentional biases to faces are present early in development. Newborns with virtually no visual experience show robust preferences for faces over other equally complex objects (Pascalis & Kelly, 2009; Farroni et al., 2005; Johnson, 2005). A human face conveys critical information about who a person is (i.e., identity), what social groups they belong to (i.e., race, gender), and what they may be feeling or intending (i.e., emotional expression, gaze direction). People need minimal visual information to identify faces (Grill-Spector & Kanwisher, 2005; Yip & Sinha, 2002), identify their race and gender (Martin & Macrae, 2007; Cloutier, Mason, & Macrae, 2005), recognize their emotional expressions (Esteves & Öhman, 1993), and make a variety of social judgments such as aggressiveness (Bar, Neta, & Linz, 2006) and trustworthiness (Todorov, Pakrashi, & Oosterhof, 2009). This information is extracted rapidly and affects social interactions (Todorov, Mende-Siedlecki, & Dotsch, 2013).

Not surprisingly, faces are one the most studied categories of stimuli in psychology (Calder, Rhodes, Johnson, & Haxby, 2011). In cognitive neuroscience, faces have served as a key tool for understanding the brain, and the neural underpinnings of face perception have been a focal point of ongoing debates about the nature of brain representations of high-level categories (see Haxby et al., 2001, 2011; Kanwisher, 2010; Scherf, Behrmann, Humphreys, & Luna, 2007; Bukach, Gauthier, & Tarr, 2006; Kanwisher & Yovel, 2006). As a result of this research, we know that there is a well-established posterior network of cortical regions contributing to face perception (Freiwald & Tsao, 2012; Haxby & Gobbini, 2012; Kanwisher & Barton, 2012; Nestor, Plaut, & Behrmann, 2011; Said, Haxby, & Todorov, 2011; Turk-Browne, Norman-Haignere, & McCarthy, 2010; Pinsk et al., 2009; Fairhall & Ishai, 2007; Kanwisher & Yovel, 2006; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Haxby, Hoffman, & Gobbini, 2000). These regions include the fusiform face area (FFA; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), the occipital face area (OFA; Gauthier, Skudlarski, Gore, & Anderson, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996), and a region in the posterior STS (pSTS; Allison, Puce, & McCarthy, 2000; Puce et al., 1996), although there is recent evidence that this organization may be more fine-grained with multiple face-selective patches (Freiwald & Tsao, 2012; Weiner & Grill-Spector, 2010, 2012; Rajimehr, Young, & Tootell, 2009). Although the specific functions ascribed to individual regions are still debated, they all show stronger responses to faces than to other categories of stimuli. Hence, these regions have been characterized as face selective.

However, we argue that this view of the neural underpinnings of face perception is limited in scope and misses

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a critical subcortical node, the amygdala. In models of the neural basis of face perception, if the amygdala is mentioned at all, it is accorded a secondary role at best, along with a host of other regions (e.g., Haxby & Gobbini, 2012; Haxby et al., 2000), although there are many studies implicating amygdala in face processing. In fact, meta-analyses of functional neuroimaging studies show that faces are one of the most potent stimuli for eliciting amygdala responses (Costafreda, Brammer, David, & Fu, 2008; Sergerie, Chochol, & Armony, 2008). Yet, the amygdala and its subnuclei have not been characterized as generally face selective and on equal footing with regions like the FFA, OFA, or pSTS.

Here, using functional localizer data from 215 participants, we test the hypothesis that the amygdala shows robust selectivity for faces—selectivity that does not require processing of emotional expressions. Before we describe the methods and findings, we consider reasons why past studies may have failed to characterize the amygdala as face selective and review evidence supporting the role of the amygdala in face processing. On the basis of this review and our findings, we argue the amygdala should be accorded a central role in face processing.

Single-unit Studies on Face Selectivity

In the 1970s, Gross et al. incidentally stumbled upon a hand-selective neuron while trying to characterize the basic visual properties of neurons in inferior temporal (IT) cortex (Gross, Rocha-Miranda, & Bender, 1972). In the same article, they mentioned that for some units "complex colored patterns (e.g., photographs of faces, trees) were more effective than the standard stimuli." The first formal description of face-selective neurons was published in 1981 (Bruce, Desimone, & Gross, 1981; see also Perrett, Rolls, & Caan, 1982). Ten years later, the existence of such neurons was firmly established (Desimone, 1991). Recent studies combining fMRI and single-unit recording in monkeys have found patches in temporal cortex almost entirely populated with face-selective neurons (Tsao, Freiwald, Tootell, & Livingstone, 2006).

In parallel with single-unit recording studies that have identified face-selective neurons in temporal cortex (Desimone, 1991), studies have also identified such neurons in the amygdala (Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007; Kuraoka & Nakamura, 2006; Wilson & Rolls, 1993; Nakamura, Mikami, & Kubota, 1992; Leonard, Rolls, Wilson, & Baylis, 1985; Rolls, 1984; Perrett et al., 1982; for a review, see Rolls, 2000). In fact, as early as 1979, visual neurons in the amygdala responsive to faces were reported (Sanghera, Rolls, & Roper-Hall, 1979). Importantly, a high-resolution fMRI study in monkeys found greater activation in the amygdala to images of monkey faces and bodies than to their scrambled versions (Logothetis, Guggenberger, Peled, & Pauls, 1999). A later high-resolution fMRI study from Hoffman and colleagues observed similar face-selective responses within the amygdala and moreover observed that dissociable aspects of face stimuli activated separate subnuclei within the amygdala (Hoffman, Gothard, Schmid, & Logothetis, 2007).

Findings of face-selective neurons in the monkey amygdala have been generalized to humans in studies of patients undergoing treatment for epilepsy (Rutishauser et al., 2011; Viskontas, Quiroga, & Fried, 2009; Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Kreiman, Koch, & Fried, 2000; Fried, MacDonald, & Wilson, 1997). Consistent with these single-unit studies, a recent study recording intracranial field potentials in the amygdalae of six patients showed stronger gamma-band activity to faces than to houses and scrambled faces (Sato et al., 2012; see also Pourtois, Spinelli, Seeck, & Vuilleumier, 2010). Despite these findings, the amygdala is not considered to contain large populations of face-selective neurons on par with face-selective patches in IT cortex and STS.

Functional Neuroimaging Studies on Face Selectivity

Consistent with the single-unit findings, PET studies of humans in the 1990s found face-sensitive patches of cortex in fusiform and IT regions (Haxby et al., 1993; Sergent, Ohta, & MacDonald, 1992). Similarly, electrophysiological studies recording from the same regions in epileptic patients found negative potentials (N200) evoked by faces (Allison, Ginter, et al., 1994; Allison, McCarthy, Nobre, Puce, & Belger, 1994). Subsequently, fMRI studies pioneered the functional localizer approach (Kanwisher et al., 1997; McCarthy et al., 1997), in which responses to faces were compared with responses for a variety of objects from other visual categories (e.g., houses) to identify face-selective BOLD responses. The first region identified in this approach was the FFA. A recent meta-analysis of face localizer studies showed that the FFA can be reliably identified in individual participants and its location is robust with respect to task demands and control visual categories (Berman et al., 2010). As mentioned above, the OFA and the face-selective pSTS can be consistently identified across most participants as well. These three regions—FFA, OFA, and pSTS—comprise the core system for perceptual analysis of faces (Haxby & Gobbini, 2012; Said et al., 2011; Haxby et al., 2000).

Although fMRI localizer studies and neurophysiological studies have relied on the same approach—presenting participants with stimuli from different categories (e.g., faces, everyday objects, novel objects, etc.) and looking for voxels or neurons that show preference for one or more categories—localizer studies have rarely labeled the amygdala as containing face-selective voxels (cf. Engell & McCarthy, 2013; Rossion, Hanseeuw, & Dricot, 2012). As a result, the face selectivity of the amygdala has never been a topic of systematic research in humans.

We consider three interrelated reasons for this omission in turn: (1) measurement limitations of fMRI, (2) low statistical power, and (3) theoretical biases. First, the

amygdala's small size and location make it difficult to image because of a reduced signal-to-noise ratio relative to cortical regions (Zald, 2003; LaBar, Gitelman, Mesulam, & Parrish, 2001). In fact, because of the generally low signal-to-noise ratio in fMRI, many early studies opted for partial coverage of the brain typically covering only occipital and temporal cortex (e.g., Kanwisher et al., 1997; Puce et al., 1996; Puce, Allison, Gore, & McCarthy, 1995). This is often the case even for new studies that strive to increase the spatial resolution of the measurement in cortical regions (e.g., Weiner & Grill-Spector, 2013).

Second, functional localizer studies typically have limited statistical power to detect face-selective voxels in the amygdala. There is tremendous variation in localizer data from individual brains (Figure 1). Whereas some participants show only a few (and occasionally no) face-selective regions, others show more than a dozen. Typically, a researcher would use a relatively stringent statistical threshold (e.g., $p < .005$) to identify the regions showing reliably stronger activation to faces than control categories. Although this strategy is defensible, it penalizes small subcortical regions. In fact, the number of face-selective neurons rarely exceeds 10% of the recorded neurons in the amygdala (Rutishauser et al., 2011; Viskontas et al., 2009; Quiroga et al., 2005; Kreiman et al., 2000; Fried et al., 1997), suggesting that there would be very few face-selective amygdala voxels (Todorov, 2012). This problem is further compounded by the fact that group analyses of localizer data are not typically performed to avoid cortical misalignment. However, this increases measurement error and reduces statistical power to detect face-selective regions outside the posterior network. The Berman et al. (2010) meta-analysis on face localizer studies included 49 studies that were conducted on healthy adults and reported the coordinates of the FFA and the localization task. As described in Todorov (2012), only nine of these studies reported group analyses. Although only four of these nine studies reported face-selective amygdala activation, a detailed inspection of the studies showed that the remaining five studies were statistically underpowered with small sample sizes and stringent statistical thresholds (for details, see Todorov, 2012). In other cases, researchers would note that they observed amygdala activation in face localizer tasks but would not report the coordinates or inspect further (Berman et al., 2010, p. 69; Jiang, Blanz, & O'Toole, 2009, p. 1085). There are also studies—not included in the Berman et al. meta-analysis—that report group level activation for faces in the amygdala (Ishai, Schmidt, & Boesiger, 2005; Reinders, den Boer, & Büchel, 2005; Blonder et al., 2004).

Finally, in addition to measurement limitations and low statistical power, theoretical biases may have further obstructed the study of the face selectivity of the amygdala. Specifically, studies on category selectivity are often conducted by vision scientists who reasonably focus on visual cortex and have little a priori interest in the amygdala. In contrast, most researchers who focus on the amygdala are interested in affect and emotion and rarely interested in the functions of visual cortex. In fact, fMRI studies on emotion occasionally use paradigms that look like localizer studies—comparing faces with other visual categories (e.g., fearful faces vs. fearful scenes)—but the analysis rarely goes beyond subcortical regions and other putatively affective regions (e.g., Goossens et al., 2009; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002).

The Present Study

To overcome these challenges, we performed group analyses of functional localizer data from 215 human participants. These data were collected as part of 10 studies, using various behavioral tasks and visual control cate-

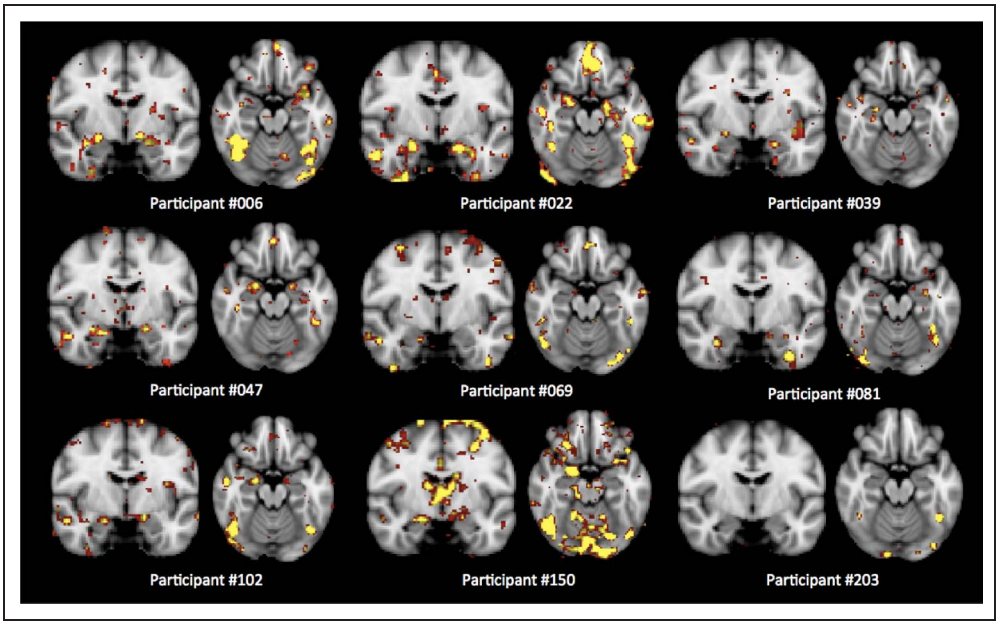

Figure 1. Sample data from nine individual participants in the Faces > Control localizer contrast. Face-selective activity is displayed at two uncorrected one-tailed thresholds for visualization purposes: $p < .05$ (red) and $p < .01$ (yellow). Although the extent and intensity varies across participants, face-selective responses could be observed in the amygdala for almost all participants at the more lenient level of thresholding.

gories. Beyond the posterior network of cortical regions observed in prior studies, we found robust face-selective responses in the amygdala. Because imaging parameters varied across studies and this could affect the results, we performed a conservative conjunction analysis across all studies. This analysis again identified face-selective responses in the amygdala, in addition to the FFA. We validated these findings using the NeuroSynth platform (neurosynth.org), which automatically synthesizes the results of numerous fMRI studies (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

We also found that face-selective responses in the amygdala are detectable in most individual participants, and we explored how this detectability varies as a function of the initial statistical threshold. More stringent thresholds have a larger impact on the amygdala than on the FFA, which we explain in terms of decreased signal-to-fluctuation-noise ratios (SFNRs) in the amygdala compared with posterior cortical regions. To further characterize the face-selective properties of the amygdala, we examine habituation across runs and compare it with other face-selective regions. The amygdala habituates more rapidly than the FFA.

In addition to these standard univariate analyses, we conducted multivariate and connectivity analyses. We found that the pattern of responses across face-selective amygdala voxels has high reliability over time. Examining the covariance of these reliability scores across face-selective regions reveals separable cortical and subcortical face-processing networks. Finally, a psychophysiological interaction analysis shows stronger functional connectivity between the face-selective amygdala and posterior regions during the perception of faces compared with the perception of objects from other visual categories.

METHODS

Participants

A total of 215 participants (85 men, 130 women) were recruited to 10 separate studies conducted at Princeton University. Almost all participants were right-handed, six were left-handed. All participants had normal or corrected-to-normal vision and reported no neurological history. We obtained informed consent for participation using protocols approved by the Institutional Review Board for Human Subjects at Princeton University. Participants were debriefed at study conclusion and compensated $20/hr. Some of the data sets have already been published for other purposes (Turk-Browne, Simon, & Sederberg, 2012; Verosky & Turk-Browne, 2012; Said, Dotsch, & Todorov, 2010).

Stimuli

The 10 studies used a variety of stimuli. All studies included color photographs of faces with neutral expressions and, as control visual object categories, either scenes, chairs, or flowers. Face photographs were obtained from several sources, including the FERET database (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips, Wechsler, Huang, & Rauss, 1998), the NimStim face set (Tottenham et al., 2009), the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Öhman, 1998), and previous literature (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006). Scene stimuli were collected from web resources, including the SUN data set (Xiao, Hays, Ehinger, Oliva, & Torralba, 2010). Chair and flower stimuli were borrowed from a stimulus set used in a previous investigation of visual perception (Downing et al., 2006).

Procedure

The 10 studies also differed in terms of procedure. For the five faces versus scenes studies (n = 77; 45 women), participants were asked to judge whether faces were male or female and whether scenes were indoors or outdoors (judgment tasks). Twelve blocks of stimuli were presented (six face blocks and six scene blocks), each containing 12 images. Each image was presented for 500 msec, separated by an ISI of 1000 msec. Participants had a 1300-msec response window, which began as soon as each image was presented. Each block of images was followed by 12 sec of rest. In four of these studies, participants completed only one localizer run, whereas the fifth study contained two localizer runs. Blocks were presented in alternating order, with a scene block first (n = 33) or a face block first (n = 22) in the four studies with one localizer run, and block order counterbalanced in the one study with two localizer runs (n = 22).

For the four faces versus chairs studies (n = 120; 75 women), participants were asked to judge whether the current face or chair was identical to the one that immediately preceded it (n-back tasks). Sixteen blocks of stimuli were presented (eight face blocks and eight scene blocks), each containing 20 images. Each image was presented for 350 msec, followed by 400 msec of response time window. Four blocks were presented in a row, followed by 15 sec of rest, after which the next set of blocks would begin. Within these smaller sets of blocks, category order was counterbalanced between participants. For half of these participants, the block order for the first block was face–chair–face–chair, whereas the next block's order was chair–face–chair–face. The other half of these participants received the opposite ordering.

For the faces versus flowers study (n = 18; 10 women), participants were asked to judge whether the current face or flower was identical to the one that immediately preceded it. Aside from the control stimulus category, parameters and timing for this study were identical to the faces versus chairs studies.

Imaging Parameters

All participants were scanned on a Siemens 3.0-T Allegra head-dedicated scanner (Siemens, Erlangen, Germany) with a volume head coil at Princeton University. For 138 participants, functional data were acquired with a T2*-weighted EPI sequence and a resolution of 3 × 3 × 4 mm (repetition time [TR] = 2000 msec, echo time [TE] = 30 msec, flip angle = 80°, matrix = 64 × 64, slices = 32). In addition, a high-resolution anatomical image was acquired with a T1-weighted MPRAGE sequence and a resolution of 1 × 1 × 1 mm (TR = 2500 msec, TE = 4.3 msec, flip angle = 8°, matrix = 256 × 256, slices = 160) for registration and normalization.

An additional 77 participants were scanned with different parameters, where functional data were acquired with EPI at a resolution of 3.5 × 3.5 × 5 mm (TR = 1500 msec, TE = 28 msec, flip angle = 64°, matrix = 64 × 64, slices = 26). The same high-resolution MPRAGE image as above was acquired for registration and normalization. In addition, for 55 of these participants, a coplanar T1-weighted FLASH image with a resolution of 0.875 × 0.875 × 5 mm (TR = 400 msec, TE = 4.6 msec, flip angle = 90°, matrix = 256 × 256, slices = 26) was acquired.

Imaging Analyses

Data were analyzed using FSL 4.1 and FMRIB software libraries (Analysis Group, FMRIB, Oxford, UK). The first several EPI volumes from each run were discarded to allow T1 equilibrium (the exact number varied by study from 3 to 6 volumes). Data were corrected for slice acquisition time and head motion, high-passed filtered with a period cutoff of 128 sec, spatial smoothing with a 4-mm FWHM Gaussian kernel. Functional runs were registered to the high-resolution anatomical scan and subsequently normalized into Montreal Neurological Institute (MNI) space. A coplanar anatomical scan was used as an intermediate step when available.

In the first level of analysis, each localizer run was fit with a general linear model (GLM) composed of boxcar regressors convolved with a canonical hemodynamic response function representing face and control blocks. The Face > Control contrast was calculated for each localizer run by subtracting the corresponding parameter estimates. When two localizer runs were available for a participant, a second-level fixed-effects GLM was used to combine these contrast maps from each run.

Finally, we performed a third-level group analysis across the localizer data of all 215 participants. Contrast maps that remained in participant space (participants with only one localizer run) were first registered into standard space. We then combined across all 215 data sets using a mixed-effects GLM (FLAME1 in FSL). Given our unusually large sample size, we sought to threshold the resulting statistical maps as stringently as possible. Consequently, we applied the strictest correction procedure in FSL, voxel-based Gaussian random field theory maximum height thresholding (corrected familywise $p < .05$, one-tailed). This thresholding technique is analogous to, but slightly less conservative than, the Bonferroni correction. To ensure that the Face versus Control contrast reflected the modulation of a positive response, the corrected statistical map was masked by another map of all voxels that showed above-baseline responses to either Face or Control blocks.

Amygdala ROI Definition

We sought to ensure that all responses associated with the amygdala were extracted from a region that reflected a canonical definition of the amygdala size and location in the medial-temporal lobe. To accomplish this, we intersected the face-selective ROIs in right and left amygdala observed in our full group analyses with anatomically defined right and left amygdala ROIs, using the Harvard-Oxford Atlas. The areas of overlap in right and left amygdala were isolated, defined as new "trimmed" ROIs, and used in all subsequent ROI-based analyses (Figure 2). We performed the same process of intersection and definition to create additional "trimmed" amygdala ROIs for the reliability analyses, which were based on the group analysis restricted to multirun participants.

SFNR Analysis

We also tested whether the amygdala suffers from a weak signal-to-noise ratio compared with posterior cortical areas, which would reduce sensitivity for detecting face-selective responses. Because face selectivity is defined as the difference in mean BOLD activity for face versus control conditions in a voxel, the most relevant noise term is the variance of the activity over time within voxel. Thus, we calculated the voxelwise SFNR for all runs from each individual participant: $\text{SFNR} = \sqrt{[(\text{temporal mean})^2/(\text{temporal variance})]}$ (Friedman & Glover, 2006; Glover & Lai, 1998). We then extracted SFNR from anatomically defined ROIs by averaging over voxels in right and left amygdala, as well as in fusiform cortex (for purposes of comparison), then averaged across runs for multirun participants. Comparisons of SFNR between ROIs were performed across all 215 participants using *t* tests.

Habituation Analyses

To assess the habituation of responses in each face-selective region, we restricted our analyses to the 119 participants who completed two localizer runs. We first ran a group analysis on only the first run of data from these participants (corrected for multiple comparisons as described above), yielding a set of face-selective functional ROIs. We assessed the mean response in each ROI

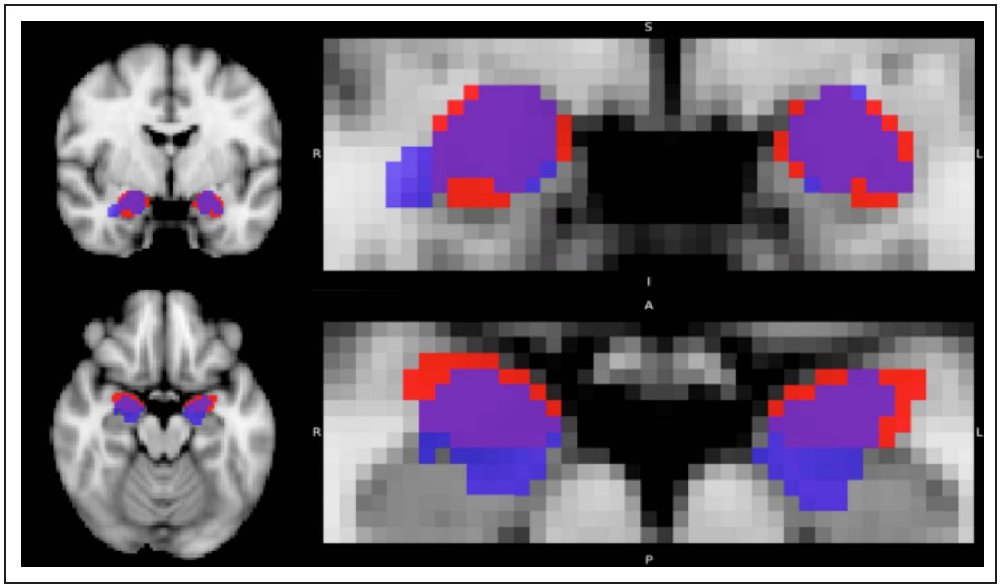

Figure 2. Definition of amygdala ROIs. All ROI-based analyses in amygdala were conducted using a region defined as the intersection (purple) of functionally defined amygdala ROIs from the full group analysis (blue) and anatomically defined amygdala ROIs taken from the Harvard-Oxford Atlas (red).

during both the first and second run and performed a series of t tests to test for significant habituation across the two runs.

Psychophysiological Interaction Analyses

As an assay of functional connectivity, we performed a series of psychophysiological interaction (PPI; Friston et al., 1997) analyses on each face-selective ROI. Specifically, we sought to identify which regions showed enhanced functional connectivity with each other during the presentation of faces, relative to the presentation of control stimuli.

Before our analyses, we extracted the full average time course across each ROI, for each participant. Next, in the first level of analysis, we ran a GLM analysis that included three regressors: (a) a psychological regressor, coding when faces and controls were presented during the task, convolved with a canonical hemodynamic response function; (b) a physiological regressor, the average time course across a given seed ROI; and (c) the interaction (product) between the psychological and physiological regressors. When two localizer runs were available for a participant, a second-level fixed-effects GLM was used to combine the resulting maps from each run.

Finally, we performed a third-level group analysis across the PPI data of all 215 participants. The setup for this full group analysis was identical to the setup of the full Faces > Controls group analysis discussed previously. As this analysis was more exploratory than the full localizer contrast, we examined these data at several levels of thresholding: (a) uncorrected $p < .01$ ($z = 2.3$), (b) corrected $p < .05$ using cluster-mass correction (cluster forming threshold, $z = 2.3$), and (c) corrected $p < .05$ using voxel-based correction. Using these three thresholds allows us to convey the robustness of the results.

Reliability Analyses

Finally, to assess the reliability of responses for each face-selective region, we again limited our analysis to the 119 participants who completed two localizer runs. Having identified a set of functional ROIs displaying face-selective responses across these multirun participants, we then used these ROIs to extract the patterns of BOLD responses across voxels for the first and second run of each participant.

The reliability of face selectivity for a given ROI and participant was calculated as the Pearson correlation between these patterns. To the extent that the pattern of activation in an ROI is category specific, this correlation should be positive. The resulting correlation coefficients were Fisher-transformed and tested for whether they were greater than zero with one-sample t tests (one-tailed). Paired t tests (one-tailed) were used to assess whether these correlations were also greater than the reliability scores extracted from control regions in bilateral primary auditory cortex (A1), which were defined anatomically using the Harvard-Oxford Atlas. These control ROIs were chosen because they are unlikely to be involved in face processing and thus provide an empirical baseline for various analyses.

To assess functional relationships between regions, we tested for significant correlations between reliability scores in each possible pairing of ROIs. To the extent that two regions are functionally related, high reliability in one region for a given participant might predict high reliability in the other region for that participant, and we

should observe a positive correlation between reliability scores across participants. Specifically, we computed correlations of reliability scores of each participant between every possible pairing of ROIs, including control ROIs, for comparison. Finally, we submitted these reliability scores to a PCA. Extraction of components was followed by a Varimax rotation with Kaiser normalization. Only the first two components displayed eigenvalues greater than 1, and as such, only these components were included in the rotation.

RESULTS

Identifying Face-selective ROIs

Our full analysis (n = 215) revealed face-selective BOLD responses (Faces > Control, corrected $p < .05$) in posterior brain regions, including bilateral FFA, right STS, and right OFA. Importantly, we found several additional regions not typically observed in single-participant localizer analyses, including bilateral amygdala, right dorsolateral pFC (dlPFC), and superior colliculus (SC), as well as smaller activations in anterior temporal lobe, precentral gyrus, and hippocampus (Figure 3A–C; see Table 1 for specific coordinates). A conjunction analysis, in which the minimum statistic across the behavioral tasks of the component studies was assigned to each voxel, showed that the face selectivity of bilateral FFA, bilateral amygdala, and right pSTS were robust with respect to task constraints (Table 2).

To assess differential responses between tasks, we performed separate group analyses within task type. Within n-back tasks, we observed face-selective responses in SC, dlPFC, ACC, and bilateral anterior insula that were not observed in participants in judgment tasks. Conversely, within judgment tasks, we observed face-selective responses in anterior temporal lobe that were not observed in participants in n-back tasks.

Table 1. Regions Showing Face-selective BOLD Responses (Faces > Control) across All Participants (n = 215)

Region	*Hemi*	*# Voxels*	*x*	*y*	*z*	*z Value*
Amygdala	R	281	20	−6	−20	12.9
Amygdala	L	241	−20	−8	−18	11.8
Fusiform gyrus	R	415	48	−52	−24	10
pSTS	R	213	52	−42	6	8.07
Fusiform gyrus	L	90	−44	−50	−24	7.95
dlPFC	R	336	52	18	20	6.59
SC	–	21	2	−32	−8	5.91
Anterior temporal lobe	R	2	38	−2	−44	5.05
Hippocampus	R	11	30	0	−40	4.91
Precentral gyrus	R	9	52	0	44	4.88
OFA	R	5	42	−82	−12	4.83
Hippocampus	R	1	34	−20	−14	4.54

Group results thresholded using FSL's conservative voxel-based procedure (corrected for multiple comparisons, $p < .05$). Coordinates refer to the peak voxel in MNI space. For each cluster, we report its hemisphere (Hemi), size in voxels (# Voxels), and z value at the peak voxel.

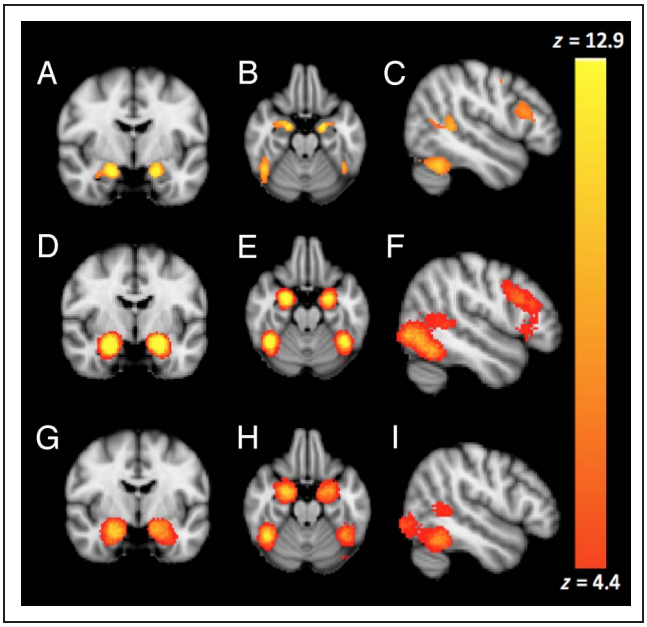

Figure 3. Full group analysis and NeuroSynth "replication." (A–C) Hot colors denote greater BOLD responses to face vs. control stimuli (n = 215, $p < .05$, corrected): bilateral amygdala, bilateral FFA, right pSTS, right dlPFC, and right FFA. For validation, we report data obtained from NeuroSynth, a tool for automatically synthesizing the results of multiple neuroimaging studies. (D–F) Results of a forward inference analysis on the same slices, showing activation across the NeuroSynth database for the term "face." These maps indicate the consistency of activation for the term. (G–I) Results of a reverse inference analysis on the same slices. These maps indicate the relative selectivity of activation for the term (see Yarkoni et al., 2011, for details).

Table 2. Regions from Conjunction Analysis of Face Selectivity, Showing Independent Significance ($p < .05$ Corrected) in Both the n-back Task (n = 138) and Discrimination Task (n = 77)

Region	*Hemi*	*# Voxels*	*x*	*y*	*z*	*z Value*
Amygdala	L	129	−18	−10	−18	7.87
Amygdala	R	128	22	−8	−18	7.87
Fusiform gyrus	R	95	48	−52	−24	6.92
pSTS	R	46	50	−42	8	5.51
Fusiform gyrus	L	6	−42	−50	−24	5.13
pSTS	R	1	58	−58	8	4.57

Coordinates refer to the peak voxel in MNI space. For each cluster, we report its hemisphere (Hemi), size in voxels (# Voxels), and the minimum z value across the two tasks at the peak voxel.

In the overall analysis, we observed clusters of 281 and 241 voxels in the vicinity of right and left amygdala, respectively, showing stronger responses to faces than to control stimuli. As shown in Figure 2, these functionally defined ROIs largely overlapped with an anatomically defined mask of the amygdala. For all subsequent analyses, we use only those functionally defined voxels that intersected with the anatomical amygdala mask.

External Validation

We capitalized on the framework of NeuroSynth (neurosynth.org)—a tool for automatically synthesizing the results of multiple neuroimaging studies (Yarkoni et al., 2011)—to test whether activation in the amygdala is associated with face processing. Relying on a library of 4393 fMRI studies, the platform creates interactive statistical brain maps for specific terms (over 2000) that are frequently mentioned in neuroimaging articles. The platform performs two types of calculations, referred to as forward inference and reverse inference. The forward inference maps show the likelihood of activation in a region given the term. For the term "face," the strongest activations were centered in bilateral amygdalae and bilateral FFA (see Figure 3D–F). Almost all of the regions detected in our group analysis were also found in this automated analysis, including bilateral FFA, bilateral amygdala, right pSTS, and right dlPFC.

The reverse inference maps show the likelihood that a term is used in a study given the presence of activation. Thus, whereas the forward inference maps indicate the consistency of activation for a specific term, the reverse inference maps indicate the relative selectivity of activation for the term. As in the case of the forward inference maps, the strongest activations in the reverse inference maps were observed in bilateral amygdalae and FFA (see Figure 3G–I). At the same time, many of the activations in other regions (e.g., dlPFC) were no longer present in the reverse inference maps, indicating that their activation is non-specific for faces. Importantly, all of the regions identified in our conjunction analysis (see Table 2) were also observed in the reverse inference maps.

Face Selectivity in Individual Participants

To assess whether face selectivity in the amygdala is detectable in individual participants, we tabulated how many individuals displayed face-selective responses in right and left amygdala-defined as any voxels showing Face > Control within the left and right anatomical masks of the amygdala (Table 3). We performed this calculation at three different uncorrected statistical thresholds ($p < .05$, $p < .01$, and $p < .001$) to test how the stringency of the statistical threshold affects the likelihood of detecting face-selective amygdala voxels in individual brains (our motivation for this is that such information may prove useful to researchers in future studies). For purposes of comparison, we also tabulated face-selective responses in the more established nodes of the face processing network (right and left FFA, right pSTS, and right OFA) as well as additional regions that emerged in our full group analysis (right dlPFC and SC).

Table 3. Tabulation of Individual Participant Responses

		A. % of Participants Presenting Activation in ROI			*B. Average % of ROI Activated*			*C. Average Maximum z Value*		
ROI	*Hemi*	*<.05*	*<.01*	*<.001*	*<.05*	*<.01*	*<.001*	*<.05*	*<.01*	*<.001*
Amygdala	R	86.5	63.3	41.9	23.3	10.9	4.6	3.37	3.83	4.32
Amygdala	L	84.2	59.5	34.4	18.8	8.2	3.2	3.09	3.58	4.18
FFA	R	99.1	96.3	93.0	34.8	25.6	17.8	7.11	7.26	7.44
FFA	L	92.1	82.3	72.6	34.7	25.0	17.2	5.43	5.83	6.28
pSTS	R	92.1	80.0	63.7	20.7	10.3	4.8	4.01	4.33	4.77
dlPFC	R	78.6	59.5	34.9	15.8	7.7	3.2	3.21	3.63	4.27
SC	–	32.1	17.2	6.5	10.8	4.8	1.5	2.56	3.11	3.92
OFA	R	54.0	42.8	32.1	37.1	26.2	17.2	3.86	4.36	4.90
Primary auditory cortex	R	56.3	25.6	7.4	4.5	1.3	0.2	2.50	2.92	3.54
Primary auditory cortex	L	56.7	28.4	7.4	5.0	1.0	0.1	2.42	3.00	3.85

(A) Percentage of participants who displayed any face-selective voxels. (B) Extent of ROI activation, as measured by the number of face-selective voxels divided by the total number of voxels in the ROI. (Participants with subthreshold activity were coded as "0.") (C) Average peak activity (z score) in participants presenting face-selective responses. For each metric, we present the data at three levels of thresholding ($p < .05$, $p < .01$, and $p < .001$). (Participants with subthreshold activity were coded as "0.") Data from control ROIs in right and left A1 are included for comparison.

As shown in Table 3A, face-selective amygdala activity was more strongly affected by increases in statistical threshold than face-selective activity in FFA. For example, although a large majority of participants displayed face-selective responses in the amygdala at a lenient threshold of $p < .05$ (right: 86.5%, left: 84.2%), these responses were substantially impacted by more stringent levels of thresholding (at $p < .01$, right: 63.3%, left 59.5%; and $p < .001$, right: 41.9%, left 34.4%). In contrast, the percentage of participants showing face-selective FFA responses decreased minimally at greater thresholds, especially right FFA ($p < .05$: 99.1%, $p < .01$: 96.2%, $p < .001$: 92.9%). This pattern was reflected in a significant interaction between ROI (amygdala or FFA) and threshold ($p = .05$, $p = .01$, or $p = .001$), separately for both right ($F(2, 428) = 61.31$, $p < .001$, $\eta_p^2 = .22$) and left ROIs ($F(2, 428) = 31.08$, $p < .001$, $\eta_p^2 = .13$).

This sensitivity to threshold may partly explain why the amygdala is rarely a target of investigation in functional localizer studies, relative to the more stable FFA. Nonetheless, a greater percentage of participants displayed face-selective responses in the amygdala compared with right A1 ($p < .05$: 56.3%, $p < .01$: 25.6%, $p < .001$: 7.4%) and left A1 ($p < .05$: 56.7%, $p < .01$: 28.4%, $p < .001$: 7.4%). These levels for A1 were significantly lower than those for the amygdala in both right and left hemispheres (one-tailed t tests at each threshold, all ps $< .001$).

Moreover, we extracted the peak z value across voxels in each ROI for each participant and calculated the group average across all participants. (For participants

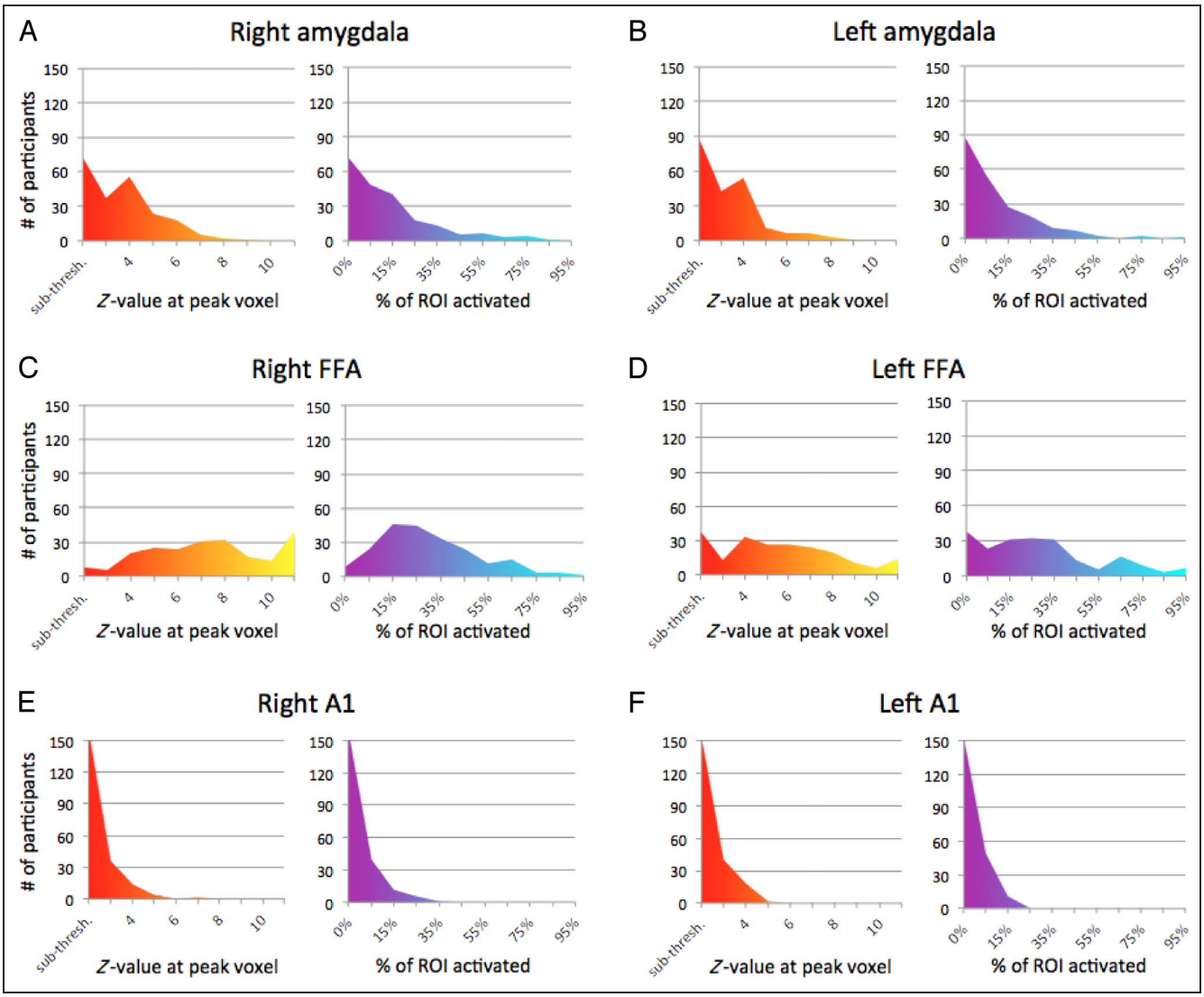

Figure 4. Intensity and extent of face-selective responses in individual participants. For each ROI, histograms across all 215 participants of peak and proportion activation. Data were thresholded at uncorrected $p < .01$ (one-tailed). Peak activation graphs (red-to-yellow gradients in left panels) reflect the distribution of the maximum z value within each ROI for each participant, with participants showing only subthreshold activity represented by the bin at the far left of the x axis. Proportion activation graphs (purple-to-cyan gradients in right panels) reflect the percent of voxels in each ROI that showed above threshold face-selective activation. Although face-selective responses in right and left amygdala (A, B) were not as intense or extensive as those observed in right and left FFA (C, D), they were considerably more intense and extensive than the responses observed in the control regions defined anatomically in right and left A1 (E, F).

with subthreshold activity, the peak z value was entered as "0.") Face-selective activations in right ($p < .05$: $z = 2.98$, $p < .01$: $z = 2.54$, $p < .001$: $z = 1.98$) and left amygdala ($p < .05$: $z = 2.59$, $p < .01$: $z = 2.08$, $p < .001$: $z = 1.43$) were more intense than those observed in right ($p < .05$: $z = 1.36$, $p < .01$: $z = 0.77$, $p < .001$: $z = 0.29$) and left A1 ($p < .05$: $z = 1.42$, $p < .01$: $z = 0.83$, $p < .001$: $z = 0.26$). Activations in A1 were significantly less intense than those in the amygdala in both right and left hemispheres (one-tailed t tests at each threshold, all ps $< .001$).

Finally, we calculated the proportion of voxels active in each ROI compared with the total voxels present in that ROI. (Once again, when calculating group averages, participants with subthreshold activity were assigned a "0.") Face-selective activations in right ($p < .05$: 23.3%, $p < .01$: 10.9%, $p < .001$: 4.6%) and left amygdala ($p < .05$: 18.8%, $p < .01$: 8.2%, $p < .001$: 3.2%) was more widespread than those observed in right ($p < .05$: 4.5%, $p < .01$: 1.3%, $p < .001$: 0.2%) and left A1 ($p < .05$: 5.0%, $p < .01$: 1.0%, $p < .001$: 0.1%). Activations in A1 were significantly less extensive than those in the amygdala in both right and left hemispheres (one-tailed t tests at each threshold, all ps $< .001$).

We display comparisons between bilateral amygdala, bilateral FFA, and bilateral A1 at the intermediate threshold of $p < .01$ in Figure 4 (activation intensity is presented in red-to-yellow gradients, whereas activation extent is presented in purple-to-cyan gradients). For the full details of average intensity and extent in each ROI and at each threshold, see Table 3 (sections B and C, respectively).

The greater consequence of statistical thresholding for the amygdala than other regions may be because of lower SFNR in this region. To test this possibility, we compared average SFNR extracted from anatomically defined ROIs in right and left amygdala and fusiform cortex. Paired t tests (two-tailed) suggested that, across our sample, average SFNR was much greater in fusiform cortex ($M = 149.95$, $SD = 31.74$) than either right ($M = 121.26$, $SD = 32.16$; $t(214) = 19.94$, $p < .001$) or left amygdala ($M = 121.82$, $SD = 30.71$; $t(214) = 18.80$, $p < .001$). SFNR did not differ between right and left amygdala ($t(214) = 0.49$, $p = .627$).

Habituation of Face-selective Responses across Runs

A meta-analysis of neuroimaging studies on the amygdala shows that the right amygdala rapidly habituates to repeated stimuli (Sergerie et al., 2008). We tested for the habituation of face-selective responses across runs (i.e., decreases in responses to face stimuli compared with control stimuli from Runs 1 to 2 in multirun participants) across the seven face-selective ROIs (see Table 4 for means). Right and left amygdala showed significant habituation from Run 1 to Run 2, as did SC, whereas right dlPFC displayed only marginally significant habituation. Right and left FFA did not display significant habituation of face-selective responses, nor did right pSTS. The fact that we defined these regions as face-selective using only the first run might have biased us to find habituation in the second run (simply because of regression to the mean). However, given that certain regions did not habituate, including the most strongly responsive ones, the robust habituation observed in the amygdala is unlikely to reflect a statistical artifact.

PPI Analysis

Our chief interest in the PPI analyses was identifying regions that showed enhanced connectivity while faces were presented, compared with when control stimuli were presented. The right amygdala seed displayed face-specific connectivity with bilateral fusiform, as well as right dlPFC and a large portion of primary visual cortex (cluster-based correction, $p < .05$; Figure 5A). At more lenient thresholds (uncorrected, $p < .01$, $z = 2.3$), right

Table 4. Habituation of Responses in Face-selective ROIs in Multirun Participants

ROI	*Hemi*	*Run 1, Mean Percent Signal Change*	*Run 2, Mean Percent Signal Change*	*t Statistic*
Amygdala	R	.079 (.078)	.054 (.080)	2.99***
Amgydala	L	.077 (.080)	.054 (.070)	2.90***
SC	–	.044 (.068)	.025 (.084)	2.19**
dlPFC	R	.050 (.085)	.034 (.098)	1.69*
pSTS	R	.054 (.097)	.045 (.098)	0.94
FFA	L	.110 (.169)	.103 (.158)	0.55
FFA	R	.134 (.167)	.121 (.177)	0.49

*$p < .10$.

**$p < .05$.

***$p < .01$.

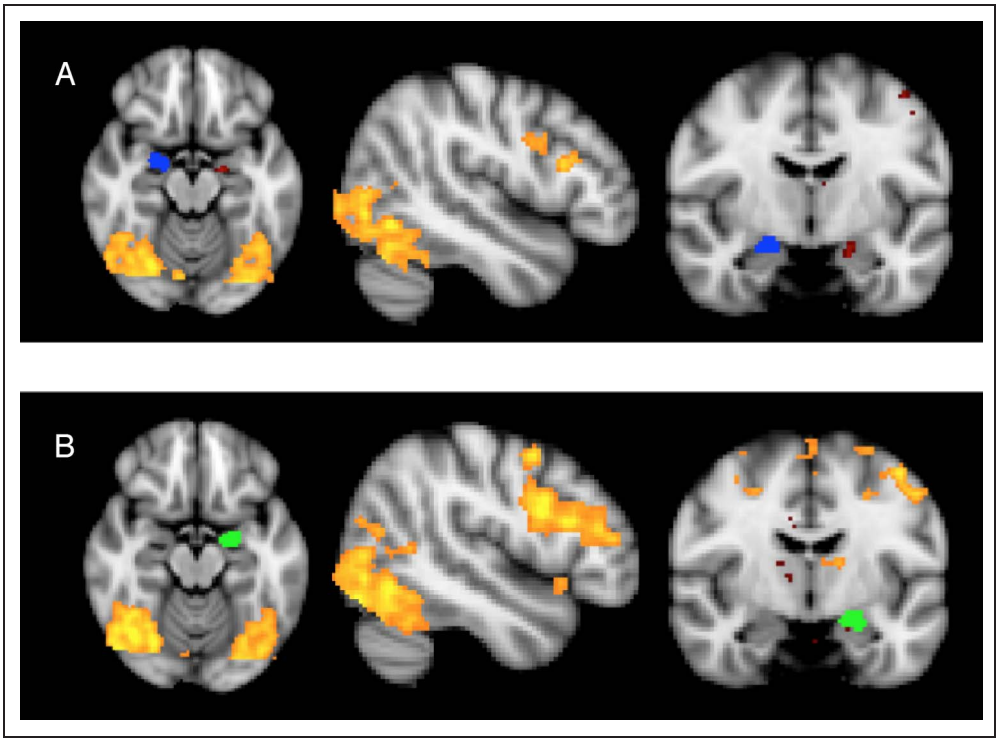

Figure 5. PPI analyses for amygdala seeds. We observed a network of regions that showed enhanced connectivity with (A) right amygdala (seed in blue) and (B) left amygdala (seed in green). Yellow-orange indicates regions that withstood cluster correction ($p < .05$); red indicates regions surpassing the initial cluster-forming threshold ($p < .01$) but uncorrected for cluster mass. Bilateral FFA, broader visual cortex, and right dlPFC showed stronger connectivity with both seeds during the presentation of faces, compared with controls. (Additional regions detailed in Table 5.)

amygdala displayed a similar relationship with left amygdala, ACC, and left dlPFC. Meanwhile, the left amygdala seed displayed face-specific connectivity with bilateral fusiform, primary visual cortex, bilateral dlPFC (extending ventrally into frontal operculum bilaterally), superior parietal lobule, and ACC (Figure 5B). At a lower threshold, left amygdala also displayed face-specific connectivity with right amygdala. PPI results for the additional face-selective ROIs are reported in Table 5.

Multivariate Reliability of Face-selective Responses

Because half of the participants ($n = 119$) completed multiple runs of a face localizer task, we tested whether the pattern of face-selective BOLD responses across voxels in a given ROI was reliable over time. Such reliability would further validate the existence of robust face selectivity. A group analysis restricted to the first run of functional localizer data from multirun participants yielded seven face-selective ROIs: bilateral FFA, bilateral amygdala, right dlPFC, right pSTS, and SC (see Table 6 for specific coordinates). As an index of reliability, we computed the Pearson correlation between the Face > Control pattern of parameter estimates from all voxels for this first run and a second run to which ROI selection was blind. We repeated this procedure for each of the ROIs and participants.

In all seven ROIs, the average pattern correlation between the first and second runs was significantly greater than zero in one-sample t test of Fisher-transformed correlations: right amygdala, $t(118) = 8.11$, $p < .001$; left amygdala, $t(118) = 6.47$, $p < .001$; right FFA, $t(118) = 22.65$, $p < .001$; left FFA, $t(118) = 22.97$, $p < .001$; right dlPFC, $t(118) = 7.37$, $p < .001$; right pSTS, $t(118) = 8.12$, $p < .001$; and SC, $t(118) = 3.82$, $p < .001$ (Figure 6).

As a comparison, reliability in the face-selective ROIs was significantly stronger than in the corresponding (ipsilateral) A1 control ROI in paired t tests of Fisher-transformed correlations (one-tailed): right amygdala, $t(118) = 4.51$, $p < .001$; left amygdala, $t(118) = 3.53$, $p = .001$; right FFA, $t(118) = 13.85$, $p < .001$; left FFA, $t(118) = 15.29$, $p < .001$; right dlPFC, $t(118) = 4.65$, $p < .001$; right pSTS, $t(118) = 4.92$, $p < .001$; and SC, $t(118) = 2.28$, $p = .024$).

Principal Components Analysis of Reliability Scores

We explored whether the reliability of multivoxel patterns in face-selective ROIs covary in systematic ways. To the extent that two regions are functionally related, high reliability in one region for a given participant might predict high reliability in the other region for that participant, resulting in a positive correlation between reliability scores across participants. These scores in right FFA and right amygdala were most highly intercorrelated with those of other ROIs (Figure 7; see Table 7 for a full table of correlations). Reliability in right FFA correlated with reliability in left FFA ($r = .55$, $p < .001$), right amygdala ($r = .32$, $p < .001$), right dlPFC ($r = .19$, $p = .036$), and right pSTS ($r = .19$, $p = .044$), whereas reliability in right amygdala correlated with left amygdala ($r = .45$, $p < .001$), right FFA ($r = .32$, $p < .001$), left FFA ($r = .23$,

Table 5. Regions Showing Enhanced Connectivity with Face-selective ROIs (Faces > Control), across All Participants (n = 215)

Region	*Hemi*	*# Voxels*	*x*	*y*	*z*	*z Value*
Right Amygdala Seed						
Primary visual cortex/fusiform gyrus	R	4126	34	−84	6	5.01
Primary visual cortex/fusiform gyrus	L	2335	−42	−66	−8	4.84
dlPFC	R	409	46	18	18	3.92
Amygdala	L	15	−20	−8	−16	2.69[a]
Left Amygdala Seed						
Primary visual cortex/fusiform gyrus	R	5514	36	−84	6	5.65
Primary visual cortex/fusiform gyrus	L	3076	−40	−64	−10	4.86
dlPFC/frontal operculum/anterior insula	R	2179	48	8	24	4.88
dlPFC	L	857	−44	−8	56	4.19
ACC	–	808	4	10	54	4.40
Intraparietal sulcus	L	590	−36	−46	36	4.02
Frontal operculum/anterior insula	L	149	−34	20	0	3.30
Cerebellum	–	112	−32	−36	−34	3.32
Thalamus	L	94	−14	−6	12	3.39
Amygdala	R	8	28	2	−24	2.72[a]
Right FFA Seed						
Bilateral primary visual cortex/bilateral fusiform gyrus	–	4270	−14	−100	2	6.96
Left FFA Seed						
Primary visual cortex/fusiform gyrus	R	3100	36	−88	6	5.70
Primary visual cortex/fusiform gyrus	L	2606	−20	−96	8	6.30
Right pSTS Seed						
Primary visual cortex/fusiform gyrus	R	5188	32	−82	2	6.35
Primary visual cortex/fusiform gyrus	L	4384	−28	−92	6	6.03
dlPFC/frontal operculum/anterior insula	R	738	−34	26	0	4.20
Right dlPFC Seed						
Bilateral primary visual cortex/bilateral fusiform gyrus	–	7994	34	−82	2	5.91
Intraparietal sulcus	L	127	−28	−50	46	3.48
Amygdala	L	120	−20	−2	−22	3.87
ACC	–	85	−6	10	52	3.44

Group results thresholded using FSL's cluster-based procedure (corrected for multiple comparisons, $p < .05$). Coordinates refer to the peak voxel in MNI space. For each cluster, we report its hemisphere (Hemi), size in voxels (# Voxels), and z value at the peak voxel.

[a]Indicates regions surpassing the initial cluster-forming threshold ($p < .01$) but uncorrected for cluster mass.

$p = .013$), right pSTS ($r = .21, p = .024$), and SC ($r = .22$, $p = .015$). Reliability in all face-selective ROIs was uncorrelated with reliability in A1 control ROIs, except for SC and right A1 ($r = .19, p = .044$).

Submitting these zero-order correlations to a PCA suggested two distinct sources of variance. Whereas the cortical regions of right and left FFA and right dlPFC loaded highly on the first PC, the three subcortical regions (right

Table 6. Regions Showing Face-selective BOLD Responses (Faces > Control, $p < .05$ Corrected) across Multirun Participants ($n = 119$)

Region	*Hemi*	*# Voxels*	*x*	*y*	*z*	*z Value*
Amygdala	R	200	20	−6	−20	10.10
Fusiform gyrus	R	191	48	−52	−26	7.46
Amygdala	R	185	−18	−8	−20	8.96
SC	–	48	0	−34	−6	6.48
Fusiform gyrus	L	31	−44	−50	−24	6.14
dlPFC	L	82	52	16	22	5.82
STS	R	50	52	−42	6	5.82
dlPFC	R	5	40	24	20	4.78
dlPFC	R	3	52	6	20	4.67
dlPFC	R	1	48	6	22	4.56

Group results thresholded using FSL's conservative voxel-based procedure (corrected for multiple comparisons, $p < .05$). Coordinates refer to the peak voxel in MNI space. For each cluster, we report its hemisphere (Hemi), size in voxels (# Voxels), and z value at the peak voxel.

and left amygdala, SC) loaded highly on the second PC. The right pSTS loaded weakly on both PCs. These first two components accounted for approximately 50% of the total variance (see Table 8 for full details).

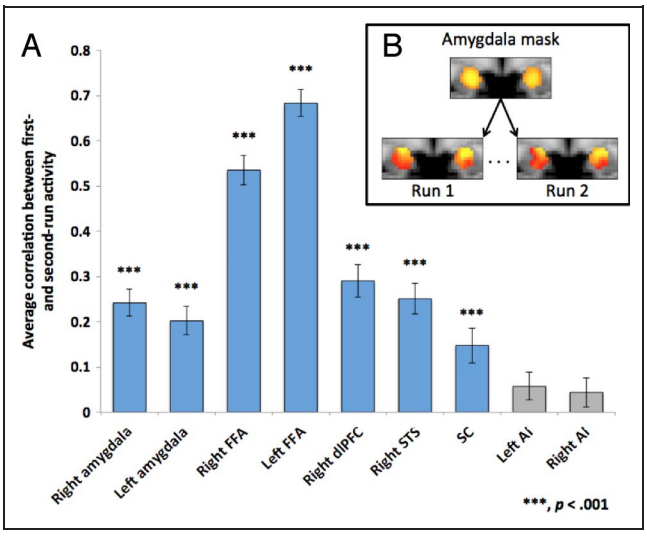

Figure 6. Multivoxel reliability of face-selective responses. (A) Blue bars represent correlations between voxel values in first-run and second-run activity within face-selective ROIs identified from the group analysis of the first run of multirun participants ($n = 119$). Gray bars represent the correlations for anatomically defined control ROIs in bilateral A1. Within-participant correlations were Fisher-transformed and then compared against zero and the ipsilateral control ROI (all comparisons significant, $ps < .05$). The mean correlation across participants is plotted for each ROI. Error bars reflect ±1 *SEM*. (B) Example amygdala ROIs from which first- and second-run activity were extracted on a voxel-by-voxel basis and correlated.

DISCUSSION

By capitalizing on the statistical power afforded by the large sample size, we were able to show that the bilateral human amygdala displays robust face-selective responses, comparable with the expected face-selective responses observed in the FFA and pSTS. These results are consistent with several recent meta-analyses that highlight the amygdala's role in the social evaluation of faces (Mende-Siedlecki, Said, & Todorov, 2012; Bzdok et al., 2011), as well as emotional processing in the context of faces (Costafreda et al., 2008; Sergerie et al., 2008). Importantly, we validated our results using the NeuroSynth platform, which is relatively immune to prior theoretical biases (Yarkoni et al., 2011). Moreover, while working on this manuscript, we became aware of two other large-scale group analyses of brain regions involved in face processing, which also indicated that the amygdala is face-selective (Engell & McCarthy, 2013; Rossion et al., 2012).

In addition to the group analyses, we conducted analyses at the level of the individual participants. As shown in Table 3 and Figure 4, it is possible to identify face-selective amygdala voxels in most participants. However, the detectability of face-selective voxels was affected by the initial statistical threshold to a larger extent in the amygdala than in the FFA. For instance, at an uncorrected threshold of $p < .001$, 41.9% of participants showed face-selective activity within the amygdala, compared with the 92.9% of participants in FFA. In other words, the probability of observing face-selective responses at this threshold and with the same amount of data is 2.2 times lower in the amygdala than FFA. We provided evidence that this may be due, at least in part, to lower SFNR in

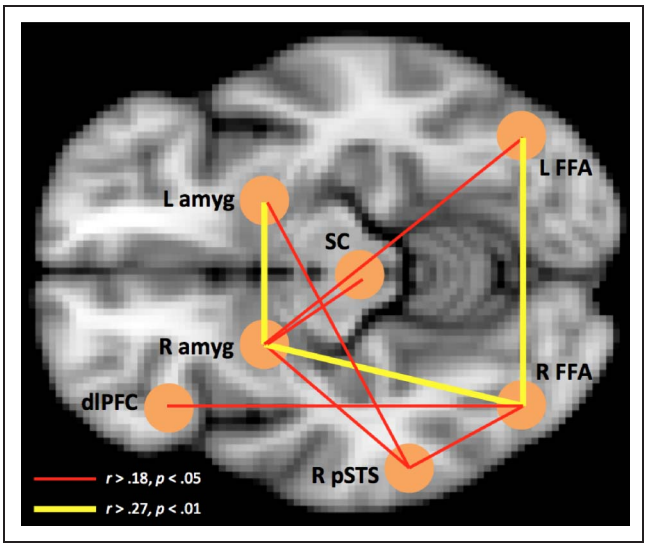

Figure 7. Relationship of reliability scores across face-selective ROIs. Pairwise correlations of first- and second-run reliability scores across ROIs. Significant correlations are plotted on a standard brain. Right amygdala and right fusiform were key nodes, each strongly correlated with many of the remaining ROIs.

Table 7. Reliability Correlations between Face-selective ROIs

	Right Amygdala	*Left Amygdala*	*Right FFA*	*Left FFA*	*Right dlPFC*	*Right pSTS*	*SC*
Right amygdala	–	.446****	.317****	.226**	.036	.207**	.222**
Left amygdala		–	.149	.195**	.109	.209**	.179*
Right FFA			–	.550****	.192**	.185**	.044
Left FFA				–	.178*	.125	.047
Right dlPFC					–	.122	−.024
Right pSTS						–	.019
SC							–

*$p < .10$.

**$p < .05$.

***$p < .01$.

****$p < .001$.

the amygdala compared with posterior regions like the fusiform cortex. Investigators interested in exploring the face-selective properties of the amygdala should thus consider using more lenient statistical thresholds (and validating the results with other methods, such as MVPA or connectivity). We also found that the amygdala response to faces habituated more rapidly than the FFA response. In localizer studies that average responses across multiple runs, this could disproportionately impact the amygdala. At the same time, it is advisable to use multiple runs, as this allows for MVPA of the reliability of face-selective responses.

Table 8. Loadings of First/Second Run Reliability Scores in Face-selective ROIs onto the First Two Principal Components ($n = 119$) Extracted from a Principal Components Analysis with Varimax Rotation

ROI	*Hemi*	*Component 1*	*Component 2*
FFA	R	.792***	.185*
FFA	L	.773***	.151
dlPFC	R	.545***	−.098
pSTS	R	.317***	.317***
Amygdala	R	.235*	.759***
Amgydala	L	.157	.730***
SC	–	−.206	.628***
Explained variance		31.19%	17.59%

Factor loadings indicate the correlation of each ROI's reliability score with each principal component.

*$p < .05$.

**$p < .01$.

***$p < .001$.

Connectivity Analysis

The PPI analyses showed that both the right and left amygdala seeds displayed face-specific connectivity with bilateral fusiform gyri, as well as right dlPFC and a large portion of visual cortex (Figure 5). These results dovetail with animal work on anatomical connections between amygdala and IT cortex, as well as striate and extrastriate cortex (Amaral, Behniea, & Kelly, 2003; Amaral, Price, Pitkänen, & Carmichael, 1992). Moreover, these results are consistent with human diffusion tensor imaging work, suggesting strong connectivity between amygdala and early visual areas via direct, long-range projections (Avidan, Hadj-Bouziane, Liu, Ungerleider, & Behrmann, 2013; Gschwind, Pourtois, Schwartz, van de Ville, & Vuilleumier, 2012; Pugliese et al., 2009; Catani, Jones, Donato, & Ffytche, 2003). They are also consistent with dynamic causal modeling work observing increased coupling between amygdala and FFA in response to emotional faces (Fairhall & Ishai, 2007). Taken in context, the PPI results further strengthen the hypothesis that the amygdala is a core region in the face processing system.

Reliability Analysis (MVPA)

Not only did the amygdala show stronger responses to faces than to objects from other visual categories, but also these responses were reliable over time, as indicated by significant multivoxel correlations between first-run and second-run amygdala activity. These correlations were significantly stronger than those in anatomically defined control regions. In fact, given the disadvantageous signal-to-noise ratio encountered when imaging subcortical structures, the correlations between first-run and second-run activity in bilateral amygdala are likely somewhat conservative estimates of reliability.

We observed several other nontraditional regions displaying face-selective responses as well, including SC and

right dlPFC. The latter finding is consistent with a recent study showing face-selective responses in lateral pFC, primarily driven by the presence of eyes (Chan & Downing, 2011; see also Engell & Haxby, 2007). However, these regions did not survive the conjunction analysis across task type and were not observed in the reverse inference statistical maps. Given the dlPFC's role in working memory (Wagner, Maril, Bjork, & Schacter, 2001; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Cohen et al., 1997) and the SC's contributions to visual attention (Sparks, 2002; Desimone & Duncan, 1995; Sprague, 1991; Posner & Peterson, 1990; Lee, Rohrer, & Sparks, 1988), the activity in these regions may be reflective of particular aspects of the stimuli or task that are not specific to faces, but still different from the control categories. Ultimately, we remain agnostic as to whether these other obtained regions are truly face selective as well, because the amygdala is the focus of the current work.

The results of the PCA are suggestive of separate cortical and subcortical streams of face processing, with the right fusiform and right amygdala serving as primary nodes, respectively. However, as these results are ultimately correlational, this dissociation is speculative at present, although thematically consistent with prior research (Garrido, Barnes, Sahani, & Dolan, 2012; de Gelder, van Honk, & Tamietto, 2011; Santos, Mier, Kirsch, & Meyer-Lindenberg, 2011; Williams et al., 2006). Future work should explore this possibility more explicitly. Nevertheless, the robustness and reliability of the face-selective amygdala response that we observed suggests that the amygdala may play a central role in face processing as part of an extended network outside posterior visual areas (Todorov, 2012; Said et al., 2011; Fairhall & Ishai, 2007; Haxby et al., 2000), providing some of the first evidence that subcortical regions can be specialized for high-level cognitive processes.

The Role of the Amygdala in Face Processing

Here we showed that there are face-selective voxels in the amygdala, at least according to standard criteria for defining face-selective regions in the brain. The next generation of questions should be about the computational role of the amygdala in face processing. Our findings suggest that the conventional view—that the main function of the amygdala in this context is processing emotional expressions—is incomplete at best and inaccurate at worst. All of the faces that were used in the face localizer studies here were emotionally neutral. Hence, emotional expressions are not a necessary condition to observe amygdala activation to faces. It is worth noting, however, that although the faces were neutral based on a standard definition, the neutrality of any given face can vary between individuals (Somerville, Kim, Johnstone, Alexander, & Whalen, 2004). Moreover, even objectively neutral faces may engage the amygdala because they provide a scaffolding for previously encountered facial expressions (Whalen, Davis, Oler, Kim, Kim, & Neta, 2009).

Regardless, our results add to the growing evidence from neuroimaging studies that amygdala activation does not depend on emotional expressions per se. First, although early fMRI studies focused on the role of the amygdala in processing of fearful expressions (e.g., Whalen et al., 1998; Morris et al., 1996), many later studies observed amygdala responses not only to fearful but also to other emotional expressions, including positive expressions (e.g., Sergerie et al., 2008; Pessoa, Japee, Sturman, & Ungerleider, 2006; Winston, O'Doherty, & Dolan, 2003; Yang et al., 2002). Second, meta-analyses of face evaluation studies that typically use emotionally neutral faces show that the amygdala is one of the most consistently activated regions (Bzdok, Laird, Zilles, Fox, & Eickhoff, in press; Mende-Siedlecki et al., in press). Third, several studies have reported nonlinear amygdala activation, with stronger responses to both negatively valenced (i.e., untrustworthy-looking or unattractive) and positively valenced faces (i.e., trustworthy-looking or attractive) than to neutral faces at the middle of the continuum (Todorov, Said, Oosterhof, & Engell, 2011; Said et al., 2010; Said, Baron, & Todorov, 2009; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). Fourth, amygdala responses have been observed to bizarre faces (faces with inverted features; Rotshtein, Malach, Hadar, Graif, & Hendler, 2001) and to novel faces (Kosaka et al., 2003; Schwartz et al., 2003). These findings suggest a broader role of the amygdala in face processing.

A promising approach is to use computational models of face representation to probe the role of the amygdala in face processing. One of the best empirically supported models is the norm-based model, according to which faces are represented as vectors in a multidimensional face space centered on the average face (Rhodes & Leopold, 2012; Rhodes & Jeffery, 2006; Tsao & Freiwald, 2006; Leopold, Rhodes, Müller, & Jeffery, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001). Versions of these models have been successful in characterizing the social perception of faces (Todorov & Oosterhof, 2011; Walker & Vetter, 2009; Oosterhof & Todorov, 2008). In these models, the distance from the average face is a critical variable. This distance maps onto the psychological dimension of typicality, with more distant faces perceived as less typical. Interestingly, both single-unit recording and fMRI studies have shown increased responses in face-selective regions as a function of the distance from the average face (Leopold, Bondar, & Giese, 2006; Loffler, Yourganov, Wilkinson, & Wilson, 2005; but see Davidenko, Remus, & Grill-Spector, 2011).

Several studies have used faces generated by computational models of social judgments to test how neural responses change as a function of the face variation along the respective model (Todorov et al., 2011; Said et al., 2010). All of these studies have observed U-shaped responses in bilateral amygdala and fusiform gyri as the faces become more extreme with respect to the average

face (see Said et al., 2011). In these studies, the two extremes typically correspond to positive (e.g., trustworthy looking) and negative (e.g., untrustworthy looking) faces. Hence, one interpretation is that the amygdala tracks the affective salience of faces. However, two recent studies suggest that it may track even more general face properties (Mattavelli, Andrews, Asghar, Towler, & Young, 2012; Said et al., 2010). Specifically, these studies tested whether the amygdala and posterior face-selective regions respond to the distance from the average face per se (i.e., face typicality), rather than to the positivity and negativity of faces. Both studies found that the amygdala and FFA tracked typicality, with stronger responses to atypical than typical faces, and that these responses were not modulated by valence.

These findings help to account for both linear and nonlinear responses to faces in the amygdala (Todorov et al., 2013), as well as stronger responses to bizarre faces (Rotshtein et al., 2001), novel faces (Kosaka et al., 2003; Schwartz et al., 2003), and emotional expressions (Whalen et al., 2009). Moreover, the typicality hypothesis provides a computationally parsimonious framework for the development of face evaluation. The perception of typicality is shaped over time through the statistical learning of facial attributes, whereby more frequently seen faces shape what is perceived as "typical." By definition, faces appearing atypical will be encountered less frequently and are therefore a greater source of uncertainty, compared with typical faces. For example, although the amygdala is typically thought of as responding to fearful faces because they signal an imminent threat (Adolphs, 2008; Whalen, 1998), some behavioral work suggests that this result can just as easily be explained by a relatively low frequency of real-world experience with fearful faces (Somerville & Whalen, 2006).

The amygdala is an excellent candidate for monitoring this kind of stimulus—rare and unpredictable, bearing motivational significance for an individual—given its reciprocal connections with IT cortex and back-projections to striate and extrastriate cortex (Amaral et al., 1992, 2003). This proposal is consistent with animal work demonstrating the role of the amygdala in the regulation of attention (Davis & Whalen, 2001; Gallagher, 2000; Holland & Gallagher, 1999). Specifically, the amygdala has an excitatory influence on sensory neurons in cortical regions via pathways connecting the amygdala and the nucleus basalis of Meynert (located in the substantia innominata) and subsequent cholinergic projections from the nucleus basalis of Meynert to the cortex (Whalen, 1998; Kapp, Whalen, Supple, & Pascoe, 1992). Within this framework, amygdala responses can ultimately serve to facilitate responses of neurons in sensory regions (for instance, visual cortex). Along the same lines, Vuilleumier (2005) later argued that the amygdala regulates attention in a bottom–up fashion: Unexpected and unpredictable stimuli can elicit responses in amygdala, which subsequently, may act to bias attention toward those stimuli. In the context of face evaluation and perception, the role of the amygdala may be to regulate attention toward atypical faces.

Subsequent to face processing in posterior regions (e.g., the FFA), atypical and/or unexpected faces could drive amygdala activity, potentially further augmenting responses in posterior regions to these faces via feedback projections. Not only is this account in line with recent conceptualizations of the amygdala with respect to vigilance (Whalen, 2007) and the detection of salient or motivationally relevant stimuli (Adolphs, 2010; Sander, Grafman, & Zalla, 2003), but it is also in line with a myriad of more specific findings across a host of domains, including vision (Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005), olfaction (Anderson et al., 2003), gustation (Small et al., 2003), and audition (Bach et al., 2008; Herry et al., 2007). We acknowledge the speculative nature of this framework at this juncture. However, the present research opens the door to a host of more specific questions about the computational role of the amygdala in face processing.

Caveats and Future Directions

Although this study offers substantial evidence that the amygdala possesses face-selective properties, many open questions remain. First and foremost, it is important to note that the amygdala is composed of at least 13 individual subnuclei, each of which has distinct functionality and connectivity (Freese & Amaral, 2005, 2006, 2009; Aggleton, 2000). Moreover, in the context of face processing, research has demonstrated that separate subnuclei are involved in processing dissociable aspects of face stimuli (Hoffman et al., 2007). Because of spatial resolution constraints, it is difficult to precisely identify which subnuclei might be displaying face-selective responses across our group analysis. Indeed, the amygdala ROI observed in that analysis encompasses almost the entire amygdala. That said, we note that the peak area of activity within the amygdala includes portions of the central, medial, and basal nuclei of the amygdala. Future work should attempt to pinpoint the precise locus of face-selective responses within the amygdala potentially through the use of diffusion tensor imaging (Bach, Behrens, Garrido, Weiskop, & Dolan, 2011; Saygin, Osher, Augustinack, Fischl, & Gabrieli, 2011; see also Bzdok et al., in press, for a meta-analytic method of parcellating the human amygdala).

Along the same lines, it will be important to address what differentiates face-selective regions in the amygdala from other regions in the brain with face-selective properties, such as FFA and pSTS. Similar patterns of face selectivity could reflect vastly different underlying neuronal selectivity. For example, in the primate literature, face-selective neurons in the amygdala have been found intermingled with neurons that do not show selectivity for faces (Fried et al., 1997; Nakamura et al., 1992; Sanghera et al., 1979), whereas face-selective regions in posterior regions are, by and large, entirely composed

of face-selective neurons (e.g., the middle face patch in Tsao et al., 2006).

One criticism of studies that focus on face selectivity is that, even if a region displays robust responses to faces compared with control stimuli, there may always be some untested stimulus class that evokes even stronger responses in that region than faces. Beyond this general critique, this study also does not identify the specific function of the amygdala in face processing. Face-selective amygdala responses may reflect visual properties of faces per se, differences in attention provoked by faces, the social meaning inherent in faces, or some combination of these possibilities. It is also important to stress that the current study in no way suggests that the amygdala's duties are limited to the domain of faces. Rather, we have provided evidence that the amygdala responds preferentially to faces over other categories and thus has relative selectivity for faces during object perception.

We established face selectivity using the same criteria that are applied when examining posterior cortical areas. By generalizing across 10 separate studies, we have taken a first step toward showing that responses in the amygdala to faces occur irrespective of control category, imaging parameters, and task constraints. Additional research is needed to clarify the precise nature and anatomical location of face-specific computations within the amygdala.

Conclusions

The present research adds to a growing compendium of evidence reframing the role of the amygdala in social perception (Todorov, 2012; Adolphs, 2010; Cunningham, Van Bavel, & Johnsen, 2008; Sander et al., 2003). These accounts cast the amygdala as a "relevance detector," a means of directing attention based on motivational or contextual significance. The robust amygdala response to faces observed in this large-scale group analysis is consistent with this account—faces are powerful social stimuli to which we, as social animals, must be attentive. Moreover, our findings suggest that the human amygdala contains populations of neurons specialized for processing one of the most relevant social stimuli—the faces of conspecifics.

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