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Face-selective regions differ in their ability to classify facial expressions

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ABSTRACT

Recognition of facial expressions is crucial for effective social interactions. Yet, the extent to which the various face-selective regions in the human brain classify different facial expressions remains unclear. We used functional magnetic resonance imaging (fMRI) and support vector machine pattern classification analysis to determine how well face-selective brain regions are able to decode different categories of facial expression. Subjects participated in a slow event-related fMRI experiment in which they were shown 32 face pictures, portraying four different expressions: neutral, fearful, angry, and happy and belonging to eight different identities. Our results showed that only the amygdala and the posterior superior temporal sulcus (STS) were able to accurately discriminate between these expressions, albeit in different ways: the amygdala discriminated fearful faces from non-fearful faces, whereas STS discriminated neutral from emotional (fearful, angry and happy) faces. In contrast to these findings on the classification of emotional expression, only the fusiform face area (FFA) and anterior inferior temporal cortex (aIT) could discriminate among the various facial identities. Further, the amygdala and STS were better than FFA and aIT at classifying expression, while FFA and aIT were better than the amygdala and STS at classifying identity. Taken together, our findings indicate that the decoding of facial emotion and facial identity occurs in different neural substrates: the amygdala and STS for the former and FFA and aIT for the latter.

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Introduction

Facial expressions convey a wealth of social information. The ability to discriminate between expressions is critical for effective social interaction and communication. Although it is apparent that humans discriminate different facial expressions automatically and effortlessly, the underlying neural computations for this ability remain unclear.

Researchers have identified seven basic categories of facial expression that can be distinguished and classified; these include neutral, fearful, angry, sad, disgust, surprise and happy (Ekman, 1992). Each category of facial expression produces a unique combination of facial musculature, thereby conveying unique social information to the viewer (Ahs et al., 2014). What might be the neural substrates for the classification of emotional facial expressions? One brain structure widely reported to be involved in the representation of emotional expression is the amygdala. Patient S.M., who has bilateral amygdala damage resulting from Urbach–Wiethe syndrome, is impaired in recognizing fearful, angry and surprised facial expressions; the patient's performance in recognizing fearful faces is especially poor (Adolphs et al., 1994). Another patient, D.R., who sustained partial amygdala damage after undergoing bilateral stereotaxic amygdalotomy for the relief of epilepsy, similarly shows deficits in recognizing several categories of facial expression, including fearful, angry, sad, disgust, surprise and happy (Young et al., 1995). Consistent with these behavioral results, functional magnetic resonance imaging (fMRI) studies in healthy subjects have found that emotional faces, especially fearful expressions, evoke greater activation than neutral faces in the amygdala (Breiter et al., 1996; Whalen et al., 1998; Pessoa et al., 2002, 2006). Imaging studies have also reported that patients with amygdala lesions show reduced fMRI responses to fearful faces in fusiform and occipital areas as compared with healthy subjects, indicating the critical role played by the amygdala in conveying this information back to visual processing areas (Vuilleumier et al., 2004).

In addition to the amygdala, many studies have suggested that the human posterior superior temporal sulcus (STS) is involved in the discrimination of facial expressions (see Allison et al., 2000 for review). For example, patients with posterior STS damage are reported to have impaired recognition of fearful and angry faces as compared to healthy subjects (Fox et al., 2011). Similarly, TMS to right posterior STS has been shown to impair recognition of facial expressions (Pitcher, 2014). Several fMRI studies (Narumoto et al., 2001; Engell and Haxby, 2007) have also found that STS is more strongly activated when subjects viewed faces with emotional expressions than when they viewed neutral faces, and several fMRI adaptation studies (Winston et al., 2004; Andrews et al., 2004) have shown an increased response in STS when the same face was shown with different expressions, indicating the involvement of STS in the processing of facial expressions. In addition, recent multi-voxel pattern analysis (MVPA) of fMRI data has shown that different categories of emotional expression elicit distinct patterns of neural activation in STS (Said et al., 2010a, 2010b).

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In addition to the amygdala and posterior STS, a third region, the fusiform face area (FFA) has also been implicated in the processing of facial expressions. Several neuroimaging studies in healthy participants (Dolan et al., 1996; Vuilleumier et al., 2001; Surguladze et al., 2003; Winston et al., 2003; Ganel et al., 2005; Pujol et al., 2009; Pessoa et al., 2002, 2006; Furl et al., 2013) and electrocorticography recordings in patients (Kawasaki et al., 2012) have found significantly greater responses in FFA to several categories of emotional faces compared to neutral faces.

Taken together, these studies have provided evidence that emotional faces, compared with neutral faces, may be preferentially represented in several face-selective regions, such as the amygdala, STS, and possibly FFA. However, since most of these studies compared activations evoked by emotional faces to activations evoked by neutral faces, they did not directly address whether these brain regions differentiate among the different categories of emotional expression. Additionally, most previous studies have focused only on one or two face-selective regions and very few (Harris et al., 2012; Harris et al., 2014a) have comprehensively examined all face selective regions in the brain.

Our current work investigates the contribution of each face-selective region in the human brain to the classification of four categories of facial expression: fearful, angry, happy and neutral. We hypothesized that different categories of facial expression would evoke different patterns of neural activity within the different face-selective regions, and these different patterns could be decoded by combining fMRI with a multivariate machine classification analysis. The advantage of using multivariate classification analysis over the traditional univariate approach is that the former is more efficient at classifying fine-scale spatial differences in neural representations and therefore is expected to yield better classification performance (Kriegeskorte et al., 2006; Misaki et al., 2010).

There are several prior studies that have used fMRI and multivariate machine classification methods to investigate facial expression discrimination. Said and colleagues (Said et al., 2010a, 2010b) used sparse multinomial logistic regression (SMLR) and its seven-way classification method to classify pairs of seven basic categories of facial expressions in STS. They found that facial expressions can be decoded in both posterior STS and anterior STS. Harry and colleagues (Harry et al., 2013) used single class logistic regression to classify each of six facial expression categories in FFA and early visual cortex (EVC), and found that facial expressions can be successfully decoded in both regions. Skerry and Saxe (2014) also examined the neural representations of facial expressions with binary SVM, and found that positive and negative expressions can be classified in right middle STS and right FFA. Because these studies used very different stimulus sets (both Said and colleagues, and Skerry and Saxe used dynamic videos, while Harry and colleagues used static images), and focused on different brain regions, it is difficult to compare the facial expression classification performance between these face-selective regions from different studies.

Our study, by contrast, examined the ability of each face-selective region to classify four different emotional expressions: fearful, angry, happy and neutral. Subjects participated in a slow event-related fMRI experiment, in which they were repeatedly shown 32 face images belonging to eight different identities. For each face-selective region of interest, we used a one-versus-all support vector machine (SVM) to classify the fMRI activation patterns evoked by each category of facial expression against all other categories, and then calculated the corresponding classification accuracy. The classification accuracy determined how well each category of facial expression was decoded in each face-selective brain region. We extended this one-versus-all classification process in a hierarchical fashion similar to Lee et al. (2011) to investigate how well each region discriminated between the different emotional expressions.

In addition to classification of emotional expressions, our experimental design gave us the opportunity to investigate the classification of facial identity using the same dataset, and allowed us to compare the performance of identity classification with that of expression classification in each face-selective region. One prominent idea in the face literature is that there are two distinct anatomical pathways for the visual analysis of facial expression and identity (Bruce and Young, 1990; Haxby et al., 2000). According to this conceptualization, the changeable aspects of a face, such as emotional expression, and the invariant aspects of a face, such as its identity, are processed in separate neural pathways: STS for expression and FFA for identity. Further, Haxby and his colleagues consider the amygdala as an extension of the system for processing emotional expression. However, the results of imaging studies have not been uniform in their support of this dual system idea (Calder and Young, 2005). We tested the idea in the current study.

Overall, the aim of our study was to uncover the ability of each face-selective region in the human brain to discriminate among four basic categories of facial expression. We also examined whether the discrimination of facial expression and identity are represented in distinct neural structures.

Materials and methods

Subjects

A total of 25 healthy subjects (12 male) aged 27.0 ± 5.0 (mean $\pm$ SD) years participated in our study. All subjects were right handed, had normal or corrected-to-normal vision, and were in good health with no past neurological or psychiatric history. All participants gave informed consent according to a protocol approved by the Institutional Review Board of the National Institute of Mental Health. Data from two subjects were discarded because of excessive head movement during the fMRI scan, leaving a total of 23 subjects (11 male), aged 26.4 ± 4.8 (mean $\pm$ SD) years, for further analysis.

Experimental procedure

Main experiment

Subjects performed a fixation cross color-change task during the presentation of face images with different expressions. The visual stimuli were shown in an event-related design. Each trial began with one of the 32 face stimuli (frontal view) presented simultaneously with a randomly generated colored fixation cross in the center of the image, for 300 ms, this was followed by a white fixation cross centered on the image for the rest of trial (7700 ms; see Fig. 1A). Subjects were instructed to press the left button if the fixation cross was red, and the right button if the fixation cross was green. Subjects were asked to respond as quickly as possible. Each trial lasted for a fixed duration of 8 s and there were 32 trials per run. At the beginning and end of each run, a gray fixation cross was presented at the center of the screen for 8 s. Each run lasted 4 min 32 s.

The 32 face images were selected from the Karolinska Directed Emotional Faces (KDEF) dataset (http://www.emotionlab.se/resources/kdef) and belonged to eight different individuals, each depicting four different facial expressions: neutral, fearful, angry, and happy. Half of the individuals were female and half were male. All face images were cropped beforehand to show only the face on a black background. These images were converted to gray-scale, normalized to have equivalent size, luminance and contrast, and resized to 330×450 pixels. (Fig. 1B). Each face image was presented once in each run. The order of the face images was randomized across runs, while the order of the runs remained the same across all the subjects.

Identification of face-selective brain regions

To identify face-selective brain regions for each subject, participants also performed a one-back matching task during separate localizer runs. During these runs, subjects viewed blocks of human faces, common objects and scrambled images, and were asked to press the left button if the current image matched the preceding one, and the right button if

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