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A face is more than just the eyes, nose, and mouth: fMRI evidence that face-selective cortex represents external features

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ABSTRACT

What is a face? Intuition, along with abundant behavioral and neural evidence, indicates that internal features (e.g., eyes, nose, mouth) are critical for face recognition, yet some behavioral and neural findings suggest that external features (e.g., hair, head outline, neck and shoulders) may likewise be processed as a face. Here we directly test this hypothesis by investigating how external (and internal) features are represented in the brain. Using fMRI, we found highly selective responses to external features (relative to objects and scenes) within the face processing system in particular, rivaling that observed for internal features. We then further asked *how* external and internal features are represented in regions of the cortical face processing system, and found a similar division of labor for both kinds of features, with the occipital face area and posterior superior temporal sulcus representing the parts of both internal and external features, and the fusiform face area representing the coherent arrangement of both internal and external features. Taken together, these results provide strong neural evidence that a "face" is composed of both internal and external features.

1. Introduction

Faces are the gateway to our social world. A face alone is enough to reveal a person's identity, gender, emotional state, and more. But what is a "face", precisely? Common sense suggests that internal features like the eyes, nose, and mouth are particularly important, and dictionaries typically define a face based on these features. Moreover, behavioral experiments have widely demonstrated our remarkable sensitivity to internal features (e.g., Thompson, 1980; Tanaka and Sengco, 1997; Farah et al., 1998), computer scientists have designed vision systems that primarily process internal features (e.g., Brunelli and Poggio, 1993), and the vast majority of fMRI studies have tested representation of internal features only (Tong et al., 2000; Yovel and Kanwisher, 2004; Schiltz and Rossion, 2006; Maurer et al., 2007; Schiltz et al., 2010; Arcurio et al., 2012; Zhang et al., 2012; James et al., 2013; Lai et al., 2014; Zhao et al., 2014; de Haas et al., 2016; Nestor et al., 2016). Intriguingly, however, some behavioral evidence suggests that a face is more than the internal features alone (Young et al., 1987; Rice et al., 2013; Abudarham and Yovel, 2016; Hu et al., 2017). For example, in the classic "presidential illusion" (Sinha and Poggio, 1996), the same internal features are placed within the heads and bodies of Bill Clinton and Al Gore, yet viewers readily recognize "Bill Clinton" and "Al Gore" using the external features only. Further work suggests that external and internal features are processed in a similar manner; for example, external features, like internal features, are particularly difficult to recognize when inverted (Moscovitch and Moscovitch, 2000; Brandman and Yovel, 2012). Taken together, these findings suggest that a face is composed of external features, along with internal features.

However, despite such behavioral work suggesting that both internal and external features are part of face representation, the possibility remains that external features are not represented in the same neural system as internal features (i.e., within the cortical face processing system), but rather are represented in a different neural system (e.g., for object or body processing), and consequently, that only internal features, not external features, are represented as part of a face. Accordingly, a promising approach toward unraveling which features make up a face would be to test directly whether and how both internal and external features are represented in the brain. Indeed, a handful of studies have taken this approach, and claimed to have found external feature representation in face-selective cortex (Liu et al., 2009; Andrews et al., 2010; Axelrod and Yovel, 2010; Betts and Wilson, 2010). Critically, however, none of these studies has established whether external features, like internal features, are represented *selectively* within the cortical face processing system, leaving open the question of whether external features,

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like internal features, are part of face representation. More specifically, the majority of these studies did not compare responses to internal and external features with those to a non-face control condition (e.g., objects). Given that these studies generally find weaker responses to external than internal features, it is unclear then whether the weaker response to external features is nevertheless a selective response (i.e., with face-selective cortex responding significantly more to external features than objects). In fact, it could be the case that the response to external features is similar to the response to objects, and consequently that only internal features are selectively represented in face-selective cortex. Beginning to address this question, one of the above studies (Liu et al., 2009) found a greater response to external features than scenes. However, given that face-selective cortex is known to respond more to objects than scenes (of course, with a greater response to faces than to either of these categories), these findings still do not answer the question of whether this pattern reflects face selectivity per se, or a more general preference for any object over scenes. Closer still, one EEG study (Eimer, 2000) found larger N170 amplitudes for isolated internal and external features than for houses, and crucially, hands; however, this study investigated only the face-selective temporal electrodes (T5 and T6), and no control electrodes; thus, it is unclear whether this finding reflects actual face selectivity or general attention. Taken together then, the selectivity of the cortical face processing system for external features is not yet established, and thus the question remains whether external features, like internal features, compose a face.

Here we present the strongest test of the hypothesis that external features, not just internal features, are part of face representation, by comparing fMRI activation in the cortical face processing system to isolated internal and external features with that to objects and scenes. We predicted that if a “face” includes both internal and external features, then face-selective regions, including the occipital face area (OFA), fusiform face area (FFA), and posterior superior temporal sulcus (pSTS), should respond strongly and selectively to both isolated internal and isolated external features, compared to objects and scenes.

Finally, in order to ultimately understand face processing, we need to understand not only which features (e.g., internal and/or external) make up a face, but also the more precise nature of the representations extracted from those features. To our knowledge, no previous study has explored *how* external features are represented in the cortical face processing system. By contrast, studies of internal feature representation have found a division of labor across the three face-selective regions, with OFA and pSTS representing the parts of faces, and FFA representing the canonical, “T-shape” configuration of face parts (Pitcher et al., 2007; Harris and Aguirre, 2008, 2010; Liu et al., 2009). While this division of labor has been shown for internal features, it has never been tested for external features, allowing us to explore for the first time whether face-selective cortex exhibits a similar division of labor for external features as internal features, further supporting the hypothesis that internal features, like external features, are part of face representation.

2. Methods

2.1. Participants

Twenty participants (Age: 21–38; mean age: 27.6; 8 male, 11 female, 1 other) were recruited for this experiment. All participants gave informed consent and had normal or corrected-to-normal vision. Procedures for the study were approved by the Emory Institutional Review Board.

2.2. Design

We used a region of interest (ROI) approach in which we used one set of runs to localize category-selective regions (Localizer runs), and a second set of runs to investigate the responses of these same voxels to the experimental conditions (Experimental runs). For both Localizer and Experimental runs, participants performed a one-back task, responding every time the same image was presented twice in a row. In addition to the standard ROI analysis, we conducted a novel “volume-selectivity function” (VSF) analysis, which is described in the Data Analysis Section.

For the Localizer runs, a blocked design was used in which participants viewed images of faces (including internal and external features), bodies, objects, scenes, and scrambled objects. Each participant completed 3 localizer runs. Each run was 400s long and consisted of 4 blocks per stimulus category. The order of blocks in each run was palindromic (e.g., faces, bodies, objects, scenes, scrambled objects, scrambled objects, scenes, objects, bodies, faces, etc.) and the order of blocks in the first half of the palindromic sequence was pseudorandomized across runs. Each block contained 20 images from the same category for a total of 16 s blocks. Each image was presented for 300 ms, followed by a 500 ms interstimulus interval, and subtended 8 × 8° of visual angle. We also included five 16 s fixation blocks: one at the beginning, three in the middle interleaved between each palindrome, and one at the end of each run.

For the Experimental runs, participants viewed runs during which 16 s blocks (20 stimuli per block) of 8 categories of images were presented (six conditions were used for the current experiment, while two additional “scene” categories tested unrelated hypotheses about scene processing) (Fig. 1). Each image was presented for 300 ms, followed by a 500 ms interstimulus interval, and subtended 8 × 8° of visual angle. Participants viewed 8 runs, and each run contained 21 blocks (2 blocks of each condition, plus 5 blocks of fixation), totaling 336s. The order of blocks in each run was palindromic, and the order of blocks in the first half of the palindromic sequence was pseudorandomized across runs. As depicted in Fig. 1, the six categories of interest were: (1) arranged internal features with no external features (i.e. eyes, nose, and mouth only, arranged into their canonical “T” configuration); (2) rearranged internal features with no external features (i.e. the same eyes, nose, and mouth, but rearranged such that they no longer form a coherent T-shape); (3) arranged external features with no internal features (i.e. hair, head outline, and neck/shoulders only, arranged in a coherent configuration); (4) rearranged external features with no internal features (i.e. the same hair, head outline, and neck/shoulders, but rearranged such that they no longer form a coherent configuration); (5) objects (multiple objects, matching the multiple face parts shown in the internal and external feature conditions); and (6) scenes (empty apartment rooms). Images used to create stimuli for the four face conditions were drawn from the Radboud Faces Database (Langner et al., 2010), while the object and scene stimuli were the same as those used two previous studies (Epstein and Kanwisher, 1998; Kamps et al., 2016). Internal and external features were parcelated based on linguistic conventions and natural physical boundaries, which we established with pilot behavioral data. For example, there are clear words and natural physical boundaries between the hair, head, and neck/shoulders; indeed, pilot participants who were instructed to simply “label particular features on the image” (when viewing versions of our “face” stimuli that now included both internal and external features) spontaneously labeled the “neck,” “shoulders”, “chin”, and “hair.” Next, given that there is no clear physical boundary between the “neck” and “shoulders,” these features were grouped as a single unit. Likewise, given that there is no clear physical boundary between the chin and the rest of the head (sans internal features), this entire extent was treated as a single unit. Finally, the hair could clearly be separated from the rest of the head, leaving this as a third distinct unit.

2.3. fMRI scanning

All scanning was performed on a 3T Siemens Trio scanner in the Facility for Education and Research in Neuroscience at Emory. Functional images were acquired using a 32-channel head matrix coil and a gradient-echo single-shot echoplanar imaging sequence (35 slices, TR = 2 s, TE = 30 ms, voxel size = 3 × 3 × 3 mm, and a 0.3 mm interslice gap). For all scans, slices were oriented approximately between