NeuroImage 157 (2017) 129–143

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Functional organization of the face-sensitive areas in human occipital-temporal cortex

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ARTICLE INFO

Keywords:
Face-sensitive areas
Face-category selectivity
Face-exemplar sensitivity
Response similarities
Regionally averaged activation
Multivoxel activation pattern

ABSTRACT

Human occipital-temporal cortex features several areas sensitive to faces, presumably forming the biological substrate for face perception. To date, there are piecemeal insights regarding the functional organization of these regions. They have come, however, from studies that are far from homogeneous with regard to the regions involved, the experimental design, and the data analysis approach. In order to provide an overall view of the functional organization of the face-sensitive areas, it is necessary to conduct a comprehensive study that taps into the pivotal functional properties of all the face-sensitive areas, within the context of the same experimental design, and uses multiple data analysis approaches. In this study, we identified the most robustly activated face-sensitive areas in bilateral occipital-temporal cortices (i.e., AFP, aFFA, pFFA, OFA, pcSTS, pSTS) and systemically compared their regionally averaged activation and multivoxel activation patterns to 96 images from 16 object categories, including faces and non-faces. This condition-rich and single-image analysis approach critically samples the functional properties of a brain region, allowing us to test how two basic functional properties, namely face-category selectivity and face-exemplar sensitivity are distributed among these regions. Moreover, by examining the correlational structure of neural responses to the 96 images, we characterize their interactions in the greater face-processing network. We found that (1) r-pFFA showed the highest face-category selectivity, followed by l-pFFA, bilateral aFFA and OFA, and then bilateral pcSTS. In contrast, bilateral AFP and pSTS showed low face-category selectivity; (2) l-aFFA, l-pcSTS and bilateral AFP showed evidence of face-exemplar sensitivity; (3) r-OFA showed high overall response similarities with bilateral LOC and r-pFFA, suggesting it might be a transitional stage between general and face-selective information processing; (4) r-aFFA showed high face-selective response similarity with r-pFFA and r-OFA, indicating it was specifically involved in processing face information. Results also reveal two properties of these face sensitive regions across the two hemispheres: (1) the averaged left intra-hemispheric response similarity for the images was lower than the averaged right intra-hemispheric and the inter-hemispheric response similarity, implying convergence of face processing towards the right hemisphere, and (2) the response similarities between homologous regions in the two hemispheres decreased as information processing proceeded from the early, more posterior, processing stage (OFA), indicating an increasing degree of hemispheric specialization and right hemisphere bias for face information processing. This study contributes to an emerging picture of how faces are processed within the occipital and temporal cortex.

Introduction

Neuroimaging studies in humans have identified several focal regions in the occipital and temporal cortex showing stronger responses to faces than other categories of objects, which are thought to be the biological substrate for face recognition. In particular, the posterior superior temporal sulcus [pSTS] (Puce et al., 1998; Pinsk et al., 2009; Pitcher et al., 2011), the occipital face area [OFA] (Gauthier et al., 2000; Weiner and Grill-Spector, 2010), and the fusiform face area [FFA] (Kanwisher et al., 1997) for the core network for face information processing (Haxby et al., 2000; Gobbini and Haxby, 2007; Atkinson and Adolphs, 2011). Recently, a more extensive and fine-grained map of face sensitivity within the occipital-temporal cortex emerged, in which the FFA could be subdivided into an anterior

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http://dx.doi.org/10.1016/j.neuroimage.2017.05.061
Received 18 January 2017; Accepted 27 May 2017
Available online 29 May 2017
1053-8119/

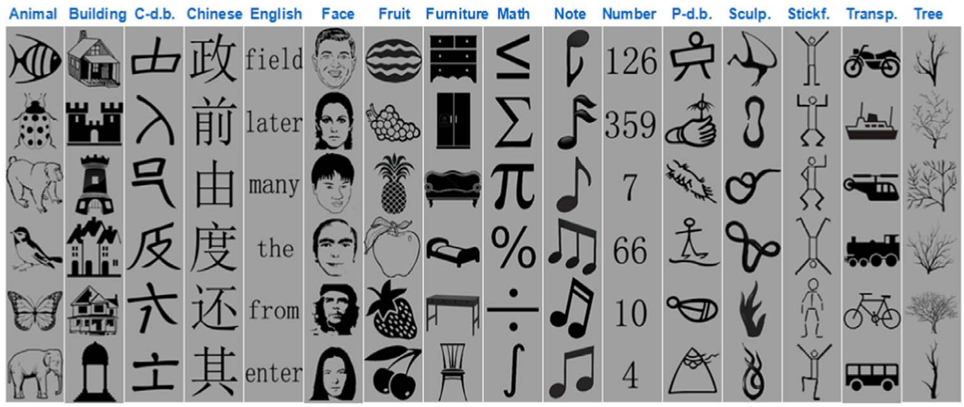

Fig. 1. Stimuli. The 96 object images presented to the participants. Sculp., Stickf., Transp., C-d.b. and P-d.b. stand for sculpture,stick figure,transportation ,characterlike-dongba and picturelike-dongba,respectively.

and a posterior part [aFFA, pFFA], and is accompanied by one or two more anterior face areas [AFP] (Weiner and Grill-Spector, 2012; Tsao et al., 2008; Pinsk et al., 2009). And in STS, besides regions around the junction of the ascending and descending limbs of the STS [pSTS], regions in the posterior continuation of the STS [pcSTS] have also been reported to be sensitive to faces (Pitcher et al., 2011).

Although all of these face-sensitive areas show, by definition, higher responses to faces than to other categories of objects, the respective roles of these areas in face perception remain unclear. To date, piecemeal insights on the functional organization of these regions abound. They have come, however, from studies that are far from homogeneous with regard to the areas involved, the experimental design, and the data analysis approach. In order to provide an overall view of the functional organization of these regions, it is necessary to conduct a study that taps into the pivotal functional properties of all the regions, within the context of the same experiment design, using both coarse and fine-grained data analysis approaches.

The current study therefore aims to comprehensively investigate the functional properties of the face-sensitive areas in human occipital-temporal cortex within the same paradigm to avoid potential confounding factors. Specifically, we ask the following three questions: (1) how do these areas differ in their face-category selectivity? (2) Do they have differential face-exemplar sensitivity? (3) The extent to which these areas process visual object information in a similar way? These questions are asked because (1) face-category detection and face-exemplar discrimination are two pivotal dimensions of face perception; and (2) the neural responses in each distinct area are not independent but might constitute transformations of each other; investigating the functional similarities between these areas provide information about the relationship between these areas.

To address these questions, we (1) identified face-sensitive areas in the entire occipital-temporal cortex in each individual, using relatively high-resolution fMRI (1.72 × 1.72 × 2 mm); and (2) measured single-image fMRI activity elicited by 96 images from 16 categories. This approach densely samples the functional profile of a neural system, allowing for measurements of category selectivity at a single image level and also at the exemplar level of sensitivity (Kriegeskorte et al., 2008; Kravitz et al., 2011; Mur et al., 2012; Liu et al., 2013; Silson et al., 2015); and (3) systematically investigated the functional similarities of these areas by examining the correlational structure of neural responses to the 96 images. Overall, the neural activity associated with an image was characterized with two complementary measures: the mean activity of voxels within an area (univariate), and the patterns of activation across the voxels (multivariate). Whereas the mean activity shows how strongly an area is engaged in processing a type of input, the spatial pattern of activation in that area provides more details about the nature of representations for a type of stimulus. Below we report the experimental results and analysis aimed at answering these questions.

Materials and methods

Subjects

15 healthy human volunteers participated in the fMRI experiment (mean age = 27 years; nine females). Subjects were right-handed and had normal or corrected-to-normal visual acuity. Before scanning, the subjects received information about the procedure of the experiment and gave their written informed consent for participating. The experiment was conducted in accordance with the Institutional Review Board of the Hangzhou Normal University.

Experimental stimuli, designs and tasks

Experiment runs

We used 96 greyscale photos of isolated objects spanning a wide range of categories, including faces and nonfaces (Fig. 1). Overall, the faces are not systematically different from other types of stimuli in basic spatial properties (Kardan et al., 2015; Berman et al., 2014), including entropy (Entropy), edge density (ED), straight edge density (SED) and non-straight edge density (NSED). Detailed information about these stimulus properties is provided in Table S1. Stimuli were presented using a rapid event-related design (stimulus duration: 300 ms, inter stimulus interval: 3700 ms) while subjects performed a fixation-cross-color detection task. Stimuli were displayed at fixation on a uniform gray background at a width of 3° visual angle. Each of the 96 object images was presented once per run in a random order. Each run included 32 randomly interleaved baseline trials where no stimulus was shown. Additionally, three and two baseline trials were inserted at the beginning and at the end of each run respectively. A total run lasts 532 s.

Localizer runs

Subjects participated in an independent block-design experiment that was designed to localize regions of interest (ROIs). The localizer experiment used the same fMRI sequence as the event-related experiment and a separate set of stimuli. Stimuli were greyscale photos of faces, flowers, characters, limbs, houses, tools and scrambled objects displayed within ± .3° around the fixation point. Subjects performed a position judgment task (left or right). The photos were presented in 12 s category blocks (stimulus duration: 1000 ms, interstimulus interval: 500 ms, four blocks for each category), intermixed with six 12 s fixation blocks (one at the beginning and one at the end of each run), for a total run time of 408 s.