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The neural representation of face space dimensions

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ABSTRACT

Functional neural imaging studies have identified a network of brain areas that are more active to faces than to other objects. However, it remains largely unclear how these areas encode individual facial identity. To investigate the neural representations of facial identity, we constructed a multidimensional face space structure, whose dimensions were derived from geometric information of faces using the Principal Component Analysis (PCA). Using fMRI, we recorded participants' neural responses when viewing blocks of faces that differed only on one dimension within a block. Although the response magnitudes to different blocks of faces did not differ in a univariate analysis, multi-voxel pattern analysis revealed distinct patterns related to different face space dimensions in brain areas that have a higher response magnitude to faces than to other objects. The results indicate that dimensions of the face space are encoded in the face-selective brain areas in a spatially distributed way.

1. Introduction

Recognizing faces is among the most important basic skills for social interaction. Although a typical human adult can identify a person from his/her face in a fraction of a second, this seemingly simple ability surpasses any computer system in its efficiency and robustness. Valentine (1991) suggested that underlying the ability to individuate faces is a system that encodes faces as points in a multidimensional space (the face space). This hypothesis has received support from numerous behavioral studies (e.g., Webster, Kaping, Mizokami, & Duhamel, 2004; Leopold, Rhodes, Müller, & Jeffery, 2005; Rhodes et al., 2011; Said & Todorov, 2011). However, little is known about how this multidimensional face space is represented in the human brain.

Neuroimaging studies have identified a network of brain areas that are involved in face perception. By comparing the magnitude of brain response to faces with the response to other categories of objects (e.g., houses), studies consistently report that the fusiform face area (FFA, Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992) and the occipital face area (OFA, Gauthier et al., 2000; see Pitcher, Walsh, & Duchaine, 2011 for a review) are more active to faces than to other objects. Although the heightened response to faces in these brain areas does not directly indicate the function of individuating faces, later studies have shed light on the role of these areas in encoding individual facial identity. Grill-Spector, Knouf, and Kanwisher (2004) reported a positive correlation between the blood oxygen level-dependent (BOLD) response magnitudes in the FFA with behavioral performance in identifying faces. Using the fMRI-adaptation paradigm, which exploits the observation that BOLD response is reduced after prolonged presentation of a stimulus, studies have shown that the FFA and the OFA are sensitive to changes of facial identity (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Grill-Spector et al., 1999; Loffler, Yourganov, Wilkinson, & Wilson, 2005). Another line of evidence comes from studies with prosopagnosia patients with focal lesion in the FFA (e.g., Barton, Press, Keenan, & O'Connor, 2002) or OFA (e.g., Buvier & Engel, 2006; Rossion et al., 2003; Steeves et al., 2006). Furthermore, by temporarily disrupting the function of the OFA (Pitcher, Walsh, Yovel, & Duchaine, 2007) through transcranial magnetic stimulation (TMS), people's accuracy in recognizing individual faces was reduced. Collectively, these findings suggest the important roles of the FFA and the OFA in individuating faces. Therefore, the FFA and the OFA are good candidates for the current investigation of the neural representations of the multidimensional face space.

A face space structure consists of two basic elements: the origin of the space and the dimensions. Valentine (1991) suggests that the origin of the face space represents the central tendency of all the faces encountered in one's life. There are two types of encoding mechanisms in relation to the origin of the face space that have been proposed. One hypothesis suggests that individual facial identities are encoded relative to the origin of the space (norm-based coding). The other hypothesis suggests that faces are encoded relative to the existing exemplars (exemplar-based coding) without referencing to the origin of the space. A recent study (Loffler et al., 2005) demonstrated that BOLD responses to faces in the FFA increase with increasing distance between the face and the origin of the face space (the average face) as would be predicted by the norm-based coding hypothesis but not by the exemplar-based coding hypothesis. The results indicate that the distance between an individual face and the origin of the face space is encoded as BOLD response amplitude in the FFA.

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Valentine (1991) suggests that the dimensions of the face space were formed through experience with faces, but no specific mechanism was proposed. The neural representation of the face space dimensions in the human brain remains largely unclear. Recent neuroimaging studies investigating the neural representations of individual facial identities have found that individual facial identities are encoded as patterns of neural responses in distributed cortical areas. Kriegeskorte, Formisano, Sorger, & Goebel (2007) recoded neural responses to one female and one male face, both of three quarter view. The two faces elicited different neural response patterns in the anterior inferotmeporal cortex (aIT). To maximize the discriminability of the facial identities, Natu et al. (2010) included face/anti-face pairs in their experiments. They found that a pattern classifier could reliably discriminate the neural response patterns to different facial identities in the ventral temporal cortex, including the fusiform gyrus and the lateral occipital areas, despite changes of point of view of the faces. A recent study (Nester, Plaut, & Behrmann, 2011) has confirmed the role of the FFA in individuating faces, as a searchlight analysis revealed that the fusiform area is one of the most informative areas in the neural response patterns for discriminating four facial identities with varying facial expressions. Since the face space dimensions are the basic elements encoding individual facial identity, one possibility is that the face space dimensions are also encoded as distributed patterns of neural activations in the face-selective cortical areas. Alternatively, it is possible that different face space dimensions are encoded in different loci in the brain. The collective pattern of activation of these loci encodes individual facial identity. To test these two hypotheses, we took a univariate approach and a multivariate approach to analyze the neural responses to changes of facial identities on different face space dimensions.

We defined the face space dimensions based on statistical regularities of a set of faces. Specifically, we ran Principal Component Analysis (PCA) on the geometric information of a set of male Caucasian faces. We used the average face as the origin and used the resulting Principal Components (PCs) as dimensions to set up a face space structure. PCs have proved effective in encoding images of faces for computer recognition (Sirovich & Kirby, 1987; Turk & Pentland, 1991) and in modeling human perception (Hancock, Burton, & Bruce, 1996; O'Toole, Deffenbacher, Abdi, & Bartlett, 1991). The dimensions represented by the PCs are orthogonal. They do not represent local facial features, such as the eyes or the nose; instead, they represent the global configuration of the faces, which has been demonstrated to be important in face recognition (e.g., Tanaka & Farah, 1993; Maurer, Le Grand, & Mondloch, 2002).

One important feature of the PCA approach is that the PCs explain different amount of variation in the face set. Therefore, some PCs are more "prominent" than the others, as they explain more variations in the face set. In the current study, besides investigating how the brain encodes the face space dimensions defined by PCA, we are also interested in comparing the brain response to PCs of different importance. We compared brain responses between two PCs, one with a high eigenvalue (PC1) and one with a low eigenvalue (PC16). In the current set of faces, PC1 explained eight times as much of the variance as PC16 explained. By collecting both behavioral and functional neural imaging data, we are able to measure both perceptual sensitivity and neural sensitivity to changes of facial identities along the two face space dimensions that differed statistically.

2. Material and methods

2.1. Participants

Participants were nine adults (4 females, mean age = 31 years, SD = 3.6 years). All (except one male) participants were right-handed. None of the participants reported any history of psychiatric or neurological disorders, or current use of any psychoactive medications. The data from one male participant were excluded from the final data analysis because this participant has unusually large ear canals, which caused artifacts in BOLD signals in the ventral part of the temporal lobe. The study is approved by York University Research Ethics Board. We obtained informed written consent from all the participants.

2.2. Stimuli

2.2.1. Synthetic faces

We used synthetic faces derived from digital photographs of 41 Caucasian males. The detailed description of the design of the synthetic faces has been reported in a previous study (Wilson, Loffler, & Wilkinson, 2002). Briefly, each synthetic face is defined by 37 parameters. Within the 37 parameters, 23 of them define the head shape and hairline, while the remaining 14 parameters define the locations and sizes of the facial features. All the 37 measures were normalized with the unit change on each measure representing a percentage relative to the mean head radius of the 41 synthetic faces. The reconstructed synthetic faces were grayscale and were filtered with a bandpass difference of Gaussians (DOG) filter centered on 10 cycles per face with a bandwidth of two octaves to keep the most important information for facial identity (Gao & Maurer, 2011; Gold, Bennett, & Sekuler, 1999; Näsänen, 1999). The synthetic faces capture the major geometric information of individual faces, while leaving out fine details such as color and skin texture. The synthetic faces simplified the representations of the real faces compared to pixel based coding, while they still carry sufficient information of individual identities as demonstrated by high accuracy in matching the identities between synthetic faces and photographs of individual faces (Wilson et al., 2002).

2.2.2. Face space structure

We submitted the 41 synthetic faces to PCA. Unlike the original 37 parameters that have a certain degree of correlation among them, the resulting 37 PCs are orthogonal to each other, making them good candidates for face space dimensions. We set up a multidimensional face space structure centered on the mean of the 41 synthetic faces with the 37 PCs as the dimensions. Distance in this face space structure is defined as the Euclidean distance between two faces in the 37-dimensional face space as a fraction of the mean head radius of the faces

2.2.3. Experimental stimuli

We created synthetic faces along two dimensions (PC1 and PC16). PC1 explained 13.2% of the total variance in the original 41 faces while PC16 explained only 1.7% of the total variance. On each direction (+ or −) of each PC dimension, the synthetic faces had distances of 0.1, 0.17, and 0.24 from the average face. We chose these three distances because a previous study (Wilson et al., 2002) has shown that discrimination threshold at 75% accuracy for the synthetic faces was at a distance of 0.06. Therefore in the current stimuli, the faces that were the closest (a distance of

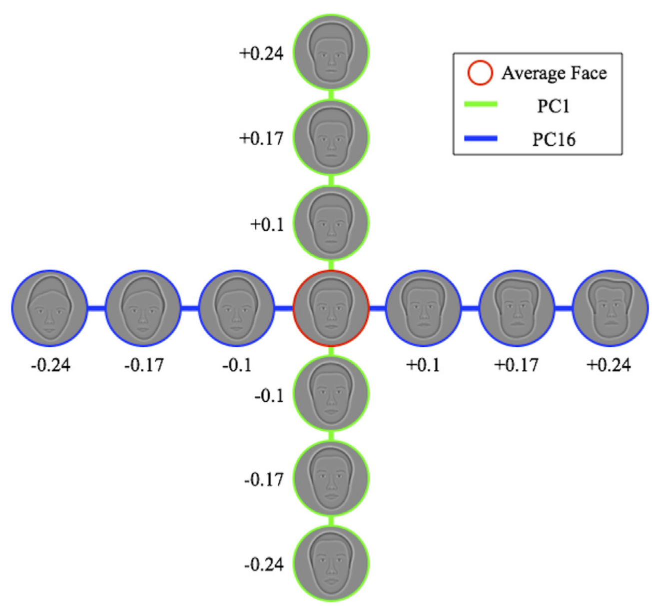

Fig. 1. A face space structure constructed based on PCA. The origin of the space (red) is the average of 41 Caucasian male faces. The two dimensions of the space are derived from PC1 (green) and PC16 (blue) of the 41 Caucasian male faces. On each direction of each dimension, three faces were created with a distance of 0.1, 0.17, or 0.24 from the average face, with the distances defined as the Euclidean distance between two faces in the 37-dimensional face space as a fraction of the mean head radius of the original 41 faces (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).