Neuropsychologia 48 (2010) 1828–1841

Contents lists available at ScienceDirect

Neuropsychologia

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

Probing the face-space of individuals with prosopagnosia

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ARTICLE INFO

Article history:
Received 5 June 2009
Received in revised form 2 March 2010
Accepted 6 March 2010
Available online 19 March 2010

Keywords:
Faces
Prosopagnosia
Face-space
Identity aftereffects
Distinctiveness
Caricature

ABSTRACT

A useful framework for understanding the mental representation of facial identity is face-space (Valentine, 1991), a multi-dimensional cognitive map in which individual faces are coded relative to the average of previously encountered faces, and in which the distance among faces represents their perceived similarity. We examined whether individuals with prosopagnosia, a disorder characterized by an inability to recognize familiar faces despite normal visual acuity and intellectual abilities, evince behavior consistent with this underlying representational schema. To do so, we compared the performance of 6 individuals with congenital prosopagnosia (CP), with a group of age- and gender-matched control participants in a series of experiments involving judgments of facial identity. We used digital images of male and female faces and morphed them to varying degrees relative to an average face, to create caricatures, anti-caricatures, and anti-faces (i.e. faces of the opposite identity). Across 5 behavioral tasks, CP individuals' performance was similar to that of the control group and consistent with the face-space framework. As a test of the sensitivity of our measures in revealing face processing abnormalities, we also tested a single acquired prosopagnosic (AP) individual, whose performance on the same tasks deviated significantly from the control and CP groups. The findings suggest that, despite an inability to recognize individual identities, CPs perceive faces in a manner consistent with norm-based coding of facial identity, although their representation is likely supported by a feature-based strategy. We suggest that the apparently normal posterior cortical regions, including the fusiform face area, serve as the neural substrate for at least a coarse, feature-based face-space map in CP and that their face recognition impairment arises from the disconnection between these regions and more anterior cortical sites.

Face-space is a useful conceptual framework for understanding how we represent facial identity (Valentine, 1991). Face-space is a multi-dimensional space centered on the average of previously experienced faces at its origin, and with individual identities represented as unique vectors from the origin. The distance from the origin represents the distinctiveness of a face because, by definition, typical faces should look more like the average face and, therefore, be located closer to the average. The direction from the origin represents *how* the face deviates from average, that is, along what particular facial dimension the face is distinct. These facial dimensions are ill-defined, as adults appear to use an amalgam of facial features that cannot be easily verbalized when making facial identity judgments (Nishimura, Maurer, & Gao, 2009). Sensitivity to both individual facial features as well as combinations of features has also been reported recently in face-selective neurons of the macaque temporal lobe (Freiwald, Tsao, & Livingstone, 2009). Nonetheless, such a coding scheme results in a face-space layout such that the distance between two faces represents the perceived similarity of those faces (the smaller the distance, the more similar the faces), and many faces cluster around the average whereas few faces sparsely occupy the periphery.

Face-space is a powerful and robust framework for understanding the underlying coding of facial identity and it has been adopted in many recent studies that explore the psychological and neural substrate of face processing. For one, it can account successfully for the apparently paradoxical effect of distinctiveness on face detection versus identification. The paradoxical finding is that adults demonstrate faster classification of *typical* faces as faces but faster individual recognition of *distinctive* faces (e.g., Johnston & Ellis, 1995; Lee, Byatt, & Rhodes, 2000; Rhodes, Byatt, Tremewan, & Kennedy, 1997; Valentine, 1991; Valentine & Bruce, 1986). According to the face-space framework, viewing a face activates an area of face-space that corresponds to the diagnostic dimensional values of that face. As such, distinctive faces will be better *recognized* because they are in a low-density region, making it less likely that neighboring faces will be erroneously activated. However, typical faces will be better detected or classified as a face, because, in a high-density region, activation may encompass several faces, lead-

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doi:10.1016/j.neuropsychologia.2010.03.007

Table 1
Performance of typical adults and individuals with prosopagnosia on a Famous Faces Questionnaire and a Face Discrimination Task (all results except for performance of MN from Behrmann et al., 2005).

Participant	Accuracy on famous face questionnaire	Median RT on upright face discrimination task	Median RT on inverted face discrimination task
Controls	86.5%(95% CI = ±10.4%)	2592 ms(95% CI = ±597 ms)	3549 ms(95% CI = ±962 ms)
CP mean	47.6%	4145 ms	3805 ms
IM	33.5%	4082 ms	5210 ms
MT	62.5%	8386 ms	7039 ms
WA	50%	1043 ms	5210 ms
TD	46.7%	1635 ms	1817 ms
IT	33.9%	7846 ms	5573 ms
MN	58.9%	1880 ms	1567 ms
AP	17.0%	5934 ms	5785 ms

ing to a stronger signal indicating that the stimulus is a face. The face-space framework also predicts that caricaturing a face (i.e., enhancing some distinctive facial feature, like Jay Leno's lower jaw), will enhance recognition because caricaturing moves the face away from the average and into an area of lower spatial density, and this is indeed true of adults' performance (e.g., Rhodes, Brennan, & Carey, 1987).

The current study examines the nature of "face-space" in individuals with prosopagnosia, a disorder in which face recognition is impaired. Specifically, prosopagnosia is characterized by the inability to recognize familiar faces despite intact low-level visual functions and general cognitive abilities (e.g., Behrmann & Avidan, 2005; Dobel, Bolte, Aicher, & Schweinberger, 2007). Because the condition appears to be associated specifically with recognizing individual faces, we hypothesized that the mental representation of faces in individuals with prosopagnosia may not adhere to the face-space framework. In congenital prosopagnosia (CP), where the condition has been present presumably since birth, it is unclear to what extent the mental representation of faces has an underlying structure, and/or to what extent compensatory mechanisms have developed for making facial identity judgments. The goal of this study is to explore for the first time whether the underlying coding of faces in CP individuals adheres to principles of face-space. In addition, we include a single acquired prosopagnosic (AP) individual in our sample whose performance provides a test for the sensitivity of our measures to reveal abnormalities in face processing. We compare the ability of the prosopagnosic individuals and matched controls to make decisions about morphed faces that are either more or less like the average face, as a means of tapping into the representation mediating their face perception. The nature and extent to which face-space is perturbed will shed important light on our understanding of the mechanisms giving rise to the recognition impairment in CPs.

We conducted three separate experiments to examine the mental representation of facial identity in individuals with prosopagnosia. In Experiment 1, to assess whether facial identity appears to be coded relative to the average or norm, we examined facial identity aftereffects (e.g., Leopold, O'Toole, Vetter, & Blantz, 2001). To assess the spatial density of the individuals' "face-space", we examined the effect of caricaturing on face perception (Experiment 2). Finally, to assess the underlying dimensions representing "face-space", we collected prosopagnosics' similarity ratings of pairs of faces and conducted multi-dimensional scaling analysis (Experiment 3).

1. General methods

1.1. Participants

Participants were 6 individuals with CP (age range 20–70 years), one individual with AP (age 34 years) resulting from a brain injury following a motor vehicle accident, and 14 typical participants matched to each of the prosopagnosics by age (±5 years), race, and gender (two per individual). Many of the CP individuals have participated previously in our studies, and details of their behavioral profiles can be found in Table 1 and in previous published reports (e.g., Avidan, Thomas, & Behrmann, 2008; Behrmann & Avidan, 2005). The AP individual, SM, has also participated in previous studies (Behrmann & Kimchi, 2003; Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005; Behrmann, Peterson, Moscovitch, & Suzuki, 2006; Behrmann & Williams, 2007). Briefly, SM sustained a lesion centered on the right inferotemporal lobe, and, despite good recovery from the accident (aside from a mild left hemiparesis), his major symptom is a profound impairment in face recognition. He also shows evidence of object agnosia, although this is not as pronounced as the prosopagnosia (Behrmann & Williams, 2007; Gauthier, Behrmann, & Tarr, 1999).

The control participants were recruited from the community. Additionally, the performance of this matched control group was compared to a group of approximately 20 university-aged participants (per experiment), to assess whether our control group's performance differed from previously established norms for adults because there is a wide age range in our matched control group. The expectation is that there would be no difference between them but this remained to be established.

1.2. Analysis

For each task, we first conducted ANOVAs to compare the performance between our matched control group and previously collected adult norms. Upon verifying that the performance between the two control groups did not differ, we proceeded to compare the matched control group and the CP group using ANOVAs. In addition, each CP and AP individual's score was compared to the matched control group, using Crawford's modified *t*-test for single cases (Crawford & Garthwaite, 2002). This last measure is becoming increasingly popular as a robust method of assessing whether a single individual's score diverges significantly from those of a control group.

2. Experiment 1: Identity aftereffects

A key characteristic of the face-space framework is that individual faces are coded relative to an average (i.e., norm-based coding). Recent adaptation paradigms provide supporting evidence that face-space is centered on the average face (Rhodes et al., 1987; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Valentine, 1991), and that individual identities are coded as deviations from the average or norm (Leopold et al., 2001; Rhodes & Jeffery, 2006; Webster & MacLin, 1999). The face identity aftereffect is demonstrated by creating pairs of "opposite" faces relative to the average. For example, if Dan has a large forehead (relative to average), "anti-Dan" is created to have a proportionately smaller-than-average forehead, and similarly all other facial characteristics in anti-Dan are morphed simultaneously to be opposite of Dan relative to