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Adaptive face space coding in congenital prosopagnosia: Typical figural aftereffects but abnormal identity aftereffects

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ABSTRACT

People with congenital prosopagnosia (CP) report difficulty recognising faces in everyday life and perform poorly on face recognition tests. Here, we investigate whether impaired adaptive face space coding might contribute to poor face recognition in CP. To pinpoint how adaptation may affect face processing, a group of CPs and matched controls completed two complementary face adaptation tasks: the figural aftereffect, which reflects adaptation to general distortions of shape, and the identity aftereffect, which directly taps the mechanisms involved in the discrimination of different face identities. CPs displayed a typical figural aftereffect, consistent with evidence that they are able to process some shape-based information from faces, e.g., cues to discriminate sex. CPs also demonstrated a significant identity aftereffect. However, unlike controls, CPs impression of the identity of the neutral average face was not significantly shifted by adaptation, suggesting that adaptive coding of identity is abnormal in CP. In sum, CPs show reduced aftereffects but only when the task directly taps the use of face norms used to code individual identity. This finding of a reduced face identity aftereffect in individuals with severe face recognition problems is consistent with suggestions that adaptive coding may have a functional role in face recognition.

1. Introduction

People with prosopagnosia have severe difficulty recognising the identity of familiar faces, despite intact low-level vision and unimpaired general cognitive abilities. Individuals with *acquired* prosopagnosia lose their ability to recognise faces after suffering a head injury, such as a stroke (e.g., Barton, 2008; Ramon, Busigny, & Rossion, 2010). In contrast, individuals with *congenital* prosopagnosia (CP; also referred to as developmental prosopagnosia) do not have a known brain injury but rather appear to have failed to develop adequate face recognition skills (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006a). Though individuals with CP do not report brain trauma, face recognition difficulties in CP are associated with reduced brain volumes (Behrmann, Avidan, Gao, & Black, 2007; Furl, Garrido, Dolan, Driver, & Duchaine, 2011; Garrido et al., 2009) and compromised white matter tracts (Thomas et al., 2009) in occipital and temporal areas involved in face processing. CP may affect as many as 2.5% of the educated population (Bowles et al., 2009; Kennerknecht et al., 2006) and often runs in families (Duchaine, Germine, & Nakayama, 2007; Grüter et al., 2007; Lee, Duchaine, Wilson, & Nakayama, 2010; Schmalzl, Palermo, & Coltheart, 2008). The inability to reliably recognise the faces of close friends, work colleagues and family members can have significant psychosocial consequences for individuals with CP, such as anxiety and avoidance of social situations (Yardley, McDermott, Pisarski, Duchaine, & Nakayama, 2008).

The source of CPs difficulty with face recognition is not yet clear. One possibility is that the key perceptual mechanisms of face recognition are disrupted in CP. There is evidence that CPs, as a group, show deficits in one of these mechanisms, namely holistic coding (Avidan, Tanzer, & Behrmann, 2011; Palermo et al., 2011) in which visual information across the whole of the face is integrated into a unified representation (Maurer, Le Grand, & Mondloch, 2002; McKone & Yovel, 2009; Rossion, Dricot, Goebel, & Busigny, 2011). However not all individual cases of CP appear to have a deficit with this perceptual mechanism (Le Grand et al., 2006; Schmalzl et al., 2008; Susilo et al., in press).

A second mechanism integral to the processing of faces, one which we examine in this study, is adaptive face coding (for reviews

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see Rhodes & Leopold, 2011; Webster & MacLeod, 2011). Adaptive face coding mechanisms are believed to generate face norms, which represent the average characteristics of faces that have been experienced (Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes & Leopold, 2011). Individual faces are coded relative to these norms, which are continually updated by experience. Adaptive coding is reflected by face aftereffects, in which prolonged exposure to a face biases subsequent perception in the opposite direction. Aftereffects are not simply the adaptation of low-level properties, but also involve some high-level, likely face-specific, properties (e.g., Afraz & Cavanagh, 2008; Rhodes, Evangelista, & Jeffery, 2009; Susilo, McKone, & Edwards, 2010). Adaptation may calibrate the face coding system to the current "diet" of faces so that discrimination is best among the kinds of faces an individual is currently experiencing (Chen, Yang, Wang, & Fang, 2010; Oruç & Barton, 2011; Rhodes & Leopold, 2011; Rhodes, Watson, Jeffery, & Clifford, 2010; Wilson, Loffler, & Wilkinson, 2002; Yang, Shen, Chen, & Fang, 2011). In this study, we examine whether abnormal adaptive face coding is associated with the face identity recognition impairments seen in CP.

Face aftereffects occur when perception of a face is influenced by exposure to a preceding face or faces. For example, adaptation to distorted faces (e.g., highly centre-contracted faces) causes a *face figural aftereffect* in which undistorted faces that are viewed subsequently appear slightly distorted in the opposite way (e.g., slightly centre-expanded) (see Fig. 1). Likewise, in the *face identity aftereffect*, adaptation to an individual face results in perception being biased toward an identity with opposite characteristics (see Figs. 2 and 3). Adaptation has been found for every facial attribute tested, including attributes that vary naturally among faces, such as sex, race, expression (Webster, Kaping, Mizokami, & Duhamel, 2004), identity (Leopold et al., 2001) and age (Schweinberger et al., 2010), and more arbitrary distortions of face shape (e.g., Carbon & Leder, 2006; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster & MacLin, 1999). A variety of evidence suggests that face aftereffects reflect adaptation of high-level coding mechanisms including face-specific coding mechanisms (Leopold et al., 2001; Rhodes et al., 2009, 2003; Watson & Clifford, 2003, 2006; Zhao & Chubb, 2001), though they also reflect contributions from low-level retinotopic adaptation (Afraz & Cavanagh, 2008, 2009; Dickinson, Almeida, Bell, & Badcock, 2010) and mid-level shape adaptation (Susilo et al., 2010), all of which contribute to face coding. Face aftereffects are therefore thought to reveal the underlying nature of the mechanisms of face perception.

We asked whether CPs experience two types of face aftereffect, a figural aftereffect and an identity aftereffect. Figural aftereffects reflect adaptation of general shape information in faces and measure changes in perception without requiring identification or discrimination of individual faces, and as such do not explicitly tap face recognition processes. Figural aftereffects affect both perceptual judgements and early brain responses (190–260 ms after stimulus onset as measured with event-related potentials, Burkhardt et al., 2010). These aftereffects have not previously been studied in CP and so it is currently unknown whether impairments will be evident. In fact, there are several reasons to think that CPs may display typical figural aftereffects. First, most CPs are able to process some face shape information, such as those face attributes used as cues to discriminate sex (Le Grand et al., 2006; Nunn, Postma, & Pearson, 2001). Second, although face-specific coding does contribute to figural face aftereffects, mid-level shape coding mechanisms can contribute substantially (Susilo et al., 2010). Therefore CPs may show typical figural aftereffects because this aftereffect taps aspects of shape and face processing that are relatively unimpaired in CP. Either way, investigating face figural aftereffects will provide important insights into the nature of the face coding deficits in CP.

In contrast, identity aftereffect tasks require discrimination between individual faces and thus more directly tap the mechanisms involved in the recognition of facial identity (Rhodes et al., 2009). In these tasks, the perception of the identity of the face, rather than its general appearance, is changed by adaptation. This effect is most dramatically demonstrated when adaptation to a face causes a previously "neutral" average face to resemble the opposite identity. Therefore, CPs might be expected to show atypical identity aftereffects, given that the primary deficit in CP is recognition of individual faces. To date, one study has investigated face identity aftereffects in a group of CPs. In contrast to expectations, Nishimura, Doyle, Humphreys and Behrmann (2010) reported that face identity aftereffects for a group of CPs ($n = 6$) did not differ from those of typical participants. However, given the apparent heterogeneity of CP (Le Grand et al., 2006; Schmalzl et al., 2008), it may be premature to conclude that adaptive face coding is unimpaired on the basis of results from one study with a small sample of CPs.

We examined whether a larger sample of CPs show typical figural aftereffects ($n = 9$; Experiment 1) and typical identity aftereffects ($n = 14$; Experiment 2). We predicted that CPs would show typical figural aftereffects because this aftereffect taps aspects of shape and face processing that appear to be relatively unimpaired in CP. However, we predicted that CPs would show atypical identity aftereffects because this aftereffect taps the specific processes used to individuate faces. We used adaptation tasks in which the adapt and test faces were different sizes to minimise the contribution of low-level, retinotopic adaptation (Zhao & Chubb, 2001). It is possible that the apparently typical aftereffects Nishimura et al. (2010) found for CPs were driven by adaptation of low-level visual attributes because adapt and test images were the same size.

2. Methods and results

2.1. Participants

2.1.1. Congenital prosopagnosics

The CP group comprised 14 people (4 males, aged between 20 and 60 years, $M = 37.93$, $SD = 13.74$) who reported everyday face recognition difficulties and showed impaired performance on tests of facial identity recognition. Most contacted us via our online prosopagnosia register: http://www.maccs.mq.edu.au/research/projects/prosopagnosia/. Most of this group completed the screening tests used to confirm prosopagnosia (detailed below) at MACCS, although a few were tested at their home and one was assessed at the Australian National University (ANU). Data has been reported for some of these individuals previously (Bowles et al., 2009; Palermo et al., 2011; Rivolta, Palermo, Schmalzl, & Coltheart, in press; Susilo et al., in press).

All 14 CPs completed the identity aftereffect task, and ten of these also completed the figural aftereffect task (the latter task was not administered to F30, F33, F23-1, F50). However, the data from M53 was excluded from analysis of the figural aftereffect as no maxima could be obtained for one curve (see Experiment 1, Section 3.3). Ten CPs completed both the figural and identity aftereffect tasks at MACCS and were reimbursed at the rate of $30, one CP completed the identity aftereffect task at ANU and was reimbursed $15 and three CPs completed the identity aftereffect task at their home under the supervision of one of the researchers.

The CPs reported normal or corrected-to-normal vision, and demonstrated normal range contrast sensitivity (*Functional Acuity Contrast Test* [FACT], Vision Sciences Research Corporation, 2002), colour perception (*Ishihara Test for Colour Blindness*, Ishihara, 1925) and ability to judge the length, size and orientation of lines (*Birmingham Object Recognition Battery* [BORB], Riddoch & Humphreys, 1993).[3] None had any difficulty with basic level object recognition, as assessed with the BORB. IQ, as measured with the *Raven Coloured Progressive Matrices* (Raven, Raven, & Court, 1998), was within the normal range. No CP reported any psychiatric or neurological problems. Given that face processing problems are common in Autism Spectrum Disorders (ASD), the *Autism Spectrum Quotient* ([AQ], Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), a self-report questionnaire assessing the number of autistic traits was also adminstered. No CP scored 32 or above, which would be indicative of an ASD.

As in previous studies (e.g., Palermo et al., 2011; Rivolta et al., in press), prosopagnosia was determined via performance on two tests of face identity memory (*MACCS*

[3] The FACT was not administered to F47 and M57; The Ishihara Test for Colour Blindness was not administered to F23-1.