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Reduced adaptability, but no fundamental disruption, of norm-based face-coding mechanisms in cognitively able children and adolescents with autism

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ABSTRACT

Faces are adaptively coded relative to visual norms that are updated by experience. This coding is compromised in autism and the broader autism phenotype, suggesting that atypical adaptive coding of faces may be an endophenotype for autism. Here we investigate the nature of this atypicality, asking whether adaptive face-coding mechanisms are fundamentally altered, or simply less responsive to experience, in autism. We measured adaptive coding, using face identity aftereffects, in cognitively able children and adolescents with autism and neurotypical age- and ability-matched participants. We asked whether these aftereffects increase with adaptor identity strength as in neurotypical populations, or whether they show a different pattern indicating a more fundamental alteration in face-coding mechanisms. As expected, face identity aftereffects were reduced in the autism group, but they nevertheless increased with adaptor strength, like those of our neurotypical participants, consistent with norm-based coding of face identity. Moreover, their aftereffects correlated positively with face recognition ability, consistent with an intact functional role for adaptive coding in face recognition ability. We conclude that adaptive norm-based face-coding mechanisms are basically intact in autism, but are less readily calibrated by experience.

1. Introduction

Adaptive, norm-based coding mechanisms play an important role in our ability to recognize faces (for reviews, see Rhodes & Leopold, 2011; Webster & MacLeod, 2011). These mechanisms code faces relative to norms that are continuously updated by experience. Their operation can be seen in identity aftereffects, in which exposure to a face (e.g., antiDan) shifts the average towards that face, selectively biasing us to see the opposite identity (e.g., Dan) in face space (Fig. 1) (Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006). These face identity aftereffects tap higher-level face-coding mechanisms, as indicated by findings that they are larger for upright than inverted faces (Rhodes, Evangelista, & Jeffery, 2009). Moreover, the selectivity of the bias for the opposite identity, with smaller aftereffects observed for equally perceptually dissimilar but non-opposite adapt–test face pairs, suggests that the average face functions as a perceptual norm for coding identity (Rhodes & Jeffery, 2006).

Norm-based coding is an efficient way to represent the distinctive information that allows us to recognize faces. In addition, the adaptation of face norms by experience calibrates face coding mechanisms to our diet of faces, which can enhance face discrimination and recognition (Armann, Jeffery, Calder, Bülthoff, & Rhodes, 2011; Wilson, Loffler, & Wilkinson, 2002) (although this is not always found; Nishimura, Doyle, Humphreys, & Behrmann, 2010; Rhodes, Maloney, Turner, & Ewing, 2007). Moreover, individuals with more adaptable face-coding mechanisms, as indicated by larger identity-related face aftereffects, have better face recognition (Dennett, McKone, Edwards, & Susilo, 2012; Rhodes, Jeffery, Taylor, Hayward, & Ewing, 2014). Taken together, these findings support a functional role for adaptive norm-based coding in face recognition ability.

Face identity aftereffects are reduced in children with autism (Ewing, Leach, Pellicano, Jeffery, & Rhodes, 2013; Pellicano, Jeffery, Burr, & Rhodes, 2007), in the relatives of individuals with autism (Fiorentini, Gray, Rhodes, Jeffery, & Pellicano, 2012) and in neurotypical men with high levels of autistic traits indicated by high Autism

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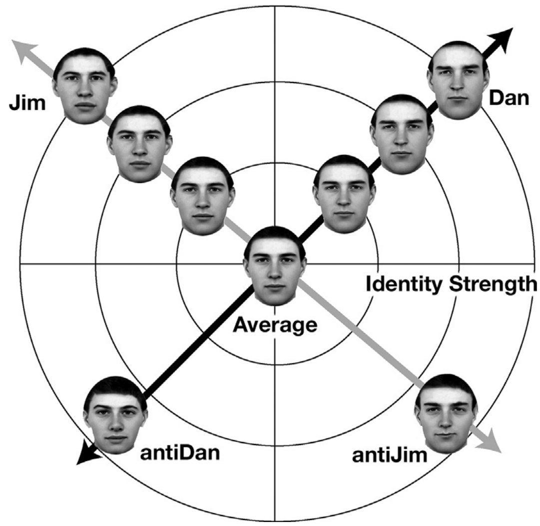

Fig. 1. A simplified (2 dimensional) face space with two faces, Dan and Jim, an average face, created by morphing 20 male, Caucasian faces, and two antifaces, antiDan and antiJim. An antiface is made by morphing a face towards, and beyond, the average, and has opposite properties to that face. Reduced-identity-strength versions of Dan and Jim, created by morphing those identities towards the average, are also shown. Identity aftereffects occur when exposure to a face biases subsequent perception towards a face with opposite properties. For example, after viewing antiDan for a few seconds, we are biased (briefly) to see Dan.

Quotient scores (Rhodes, Jeffery, Taylor, & Ewing, 2013). These results have led to the proposal that atypical adaptive coding of faces may be an endophenotype for autism (Fiorentini et al., 2012; Rhodes et al., 2013). Moreover, atypical adaptive coding of faces could potentially contribute to the face recognition difficulties often observed in autism (for reviews, see Dawson, Webb, & McPartland, 2005; Golarai, Grill-Spector, & Reiss, 2006; Sasson, 2006; Webb, Faja, & Dawson, 2011; Weigelt, Koldewyn, & Kanwisher, 2012).

Here we ask exactly how the adaptive coding of face identity is compromised in individuals with autism. One possibility is that their adaptive face-coding mechanisms are simply less responsive to face inputs than are those of neurotypical individuals. Alternatively, however, there could also be some more fundamental alteration in their face-coding mechanisms. For example, abstraction of prototypes (norms) is impaired in autism (Gastgeb, Dundas, Minshew, & Strauss, 2012; Gastgeb, Rump, Best, Minshew, & Strauss, 2009; Gastgeb, Wilkinson, Minshew, & Strauss, 2011; Klinger & Dawson, 2001), raising the possibility that face-coding mechanisms may not be norm-based.

To determine more precisely how adaptive face-coding mechanisms are compromised in autism, we examined how face identity aftereffects vary with adaptor identity strength in cognitively able children and adolescents with autism and a group of age- and ability-matched neurotypical participants. In neurotypical children and adults, identity aftereffects generally increase with adaptor strength (Jeffery, Read, & Rhodes, 2013; Jeffery et al., 2011). This pattern is consistent with norm-based opponent coding of identity-related dimensions, where each face dimension is represented by activation in two neural populations, tuned to opposite ends of the dimension, with equal activation representing a neutral point or norm. More extreme adaptors shift the norm further, resulting in larger aftereffects (shifts in perception of average or low-identity-strength test faces), because they activate their preferred populations more strongly than less extreme adaptors. An alternative, non-norm-based model, is narrowband multichannel coding of identity, where each dimension is represented by activation in multiple populations (channels) tuned to distinct dimension values. With multichannel coding, aftereffects increase initially with adaptor identity strength, but then decrease, as adaptors become too extreme to affect the populations coding a given test stimulus (Blakemore & Sutton, 1969; Clifford, Wenderoth, & Spehar, 2000).

Studies of identity aftereffects in autism to date have not varied the identity strength of adaptors, but have instead used a single identity strength. With this design, the reduced aftereffects observed in autism could simply reflect weaker updating of norms by experience in an otherwise intact norm-based face-coding system. Alternatively, however, they could arise from a non-norm-based, multichannel coding system, in which strong-identity-strength adaptors have little effect on the channels coding (the weak-identity-strength) test faces. By examining how identity aftereffects change with increasing identity strength of adaptors, we should be able to distinguish between these possibilities. If face identity aftereffects increase with adaptor strength in our typically developing participants, but decrease with adaptor strength in our participants with autism, then we would conclude that face identity is not coded relative to perceptual norms in autism. Alternatively, an increase in aftereffects with increasing adaptor strength in both groups would be consistent with norm-based coding of face identity in both groups. We included a size difference between the adapt and test faces to minimize the contribution of low-level retinotopic adaptation to our aftereffects, and a change detection task during adaptation to ensure good attention to the adapting faces (Ewing, Leach, et al., 2013; Rhodes et al. 2011).

We also examined whether individual differences in adaptive coding strength are related to face recognition ability in our participants. In neurotypical adults, identity-related face aftereffects correlate positively with face recognition ability, consistent with a functional role for adaptive face-coding mechanisms (Dennett et al., 2012; Rhodes et al., 2014). We asked whether this link is already present in younger neurotypical individuals and whether it is disrupted in autism. Given that adaptive face-coding mechanisms appear to be mature in young children, we expected to see this link in our neurotypical participants (Jeffery et al. 2010; Jeffery et al., 2013). It was an open question, however, whether this link would also be seen in our participants with autism. Although face identity aftereffects are reduced in autism, they are not eliminated, and so adaptability might remain linked to face recognition ability. Alternatively, there might be some more fundamental dissociation between adaptability and recognition. We used an individual differences approach to assess the link between face adaptation and face recognition ability, including face-selective recognition ability, in each group.

2. Method

2.1. Participants

Twelve cognitively able children and adolescents with autism (11 boys) aged 9 years 2 months to 14 years 8 months were recruited from local schools and the West Australian Register for Autism Spectrum Disorders (See Table 1). All had received independent diagnoses of either Autistic Disorder ($n=7$), Asperger's Syndrome ($n=4$) or Pervasive Developmental Disorder Not Otherwise Specified ($n=1$) by a multidisciplinary team following DSM-IV criteria (American Psychiatric Association, 2013). They also completed Module 3 of the Autism Diagnostic Observation Schedule-2 (ADOS-2) (Lord et al. 2012) and all met the ADOS-2 criterion for autism spectrum disorder (cutoff score of 7). Moreover, all parents rated their child above the cut-off level for clinically-significant levels of autistic symptomatology on the Lifetime version of the Social Communication Questionnaire (SCQ) (Rutter, Bailey, & Lord, 2003).

Twelve typically developing children and adolescents (11 boys), who were well matched to our autism sample on chronological age ($p=.70$), non-verbal IQ ($p=.99$) and verbal IQ ($p=.51$), also participated (Table 1). They were selected from a larger sample of 48 typical participants (30 male; $M=12$ years, 0 month, $SD=2$ years, 3 months; range=8 years, 7 months to 16 years, 2 months), who provided reliability data for the measures used.

2.2. Tasks and measures

2.2.1. Face identity aftereffect task

This task was adapted from an identity aftereffect task used previously with children and adults (Ewing, Leach et al., 2013; Jeffery et al., 2013). Reliability was good;