



Brief article

Category contingent aftereffects for faces of different races, ages and species

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Abstract

Exposure to faces biases perceptions of subsequently viewed faces such that normality judgments of similar faces are increased. Simultaneously inducing such an aftereffect in opposite directions for two groups of faces might indicate discrete responding of the neural populations coding for those groups. Here we show such “category contingent” aftereffects following exposure to faces differing in eye-spacing (wide versus narrow) for European versus African faces, adult versus infant faces, and human versus monkey faces. As aftereffects reflect changes in responses of neural populations that code faces, our results may then suggest that functionally distinct neural populations code faces of different ages, races and species and that the human brain potentially contains discrete representations of these categories.

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1. Introduction

For each class of stimuli the human visual system encounters it may develop an individual representation, or prototype, made up of an average of the characteristics of all the different stimuli of that type that have been seen (Enquist & Arak, 1994; Giese & Leopold, 2005; Johnstone, 1994; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Valentine, 1991). Computer modelling has revealed that algorithms trained to discriminate different stimuli produce stronger responses to stimuli that represent the average of the training set, even though this average was not previously encountered (Enquist & Arak, 1994; Johnstone, 1994). These findings have been interpreted as evidence that prototype formation is a property of learning to recognize different stimuli as members of a class (Enquist & Arak, 1994; Johnstone, 1994).

Studies on category learning have a long history (e.g., Posner & Keele, 1968). Learning studies have examined how categorical perception develops using abstract stimuli. In classic studies it has been shown that exposure to different dot patterns with particular configurations results in abstraction so that the average of each of the patterns, while never previously seen, is recognised as belonging to the set of patterns from which it was derived (Posner & Keele, 1968). These results were originally taken as evidence for prototype formation but there is much debate about whether it does represent abstraction of a prototype or whether individuals store individual exemplars and use these to determine category (Ashby & Maddox, 2005; Nosofsky & Zaki, 2002; Smith & Minda, 2002).

Faces have been the focus of much research regarding recognition and prototype formation. While it has been proposed that faces may be coded as veridical representations of individuals or exemplars (Valentine, 1991), recent neuroimaging and single-cell recording studies have supported a prototype-referenced model of face coding (Giese & Leopold, 2005; Loffler et al., 2005). Exposure to faces biases subsequent perceptions of novel faces by causing faces similar to those initially viewed to appear more prototypical than they would otherwise be perceived as, presumably, a prototype or population of exemplars becomes updated (Leopold, O'Toole, Vetter, & Blanz, 2001; Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes, Halberstadt, & Brajkovich, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Rhodes et al., 2004; Webster, Kaping, Mizokami, & Duhamel, 2004). For example, adaptation to faces with contracted features causes novel faces with contracted features to be perceived as more normal than prior to this exposure (Rhodes et al., 2003; Rhodes et al., 2004). Analogous visual aftereffects have been observed following exposure to faces varying in identity (Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes et al., 2001), ethnicity (Webster et al., 2004), sex (Rhodes et al., 2004; Webster et al., 2004), expression (Webster et al., 2004) and sexual dimorphism (Little, DeBruine, & Jones, 2005). Such aftereffects are thought to reflect changes in the responses of neural mechanisms underlying face processing (Leopold et al., 2005; Moradi, Koch, & Shimojo, 2005; Rhodes et al., 2003; Rhodes et al., 2004; Webster et al., 2004).

While 'face' is a high order category, it remains to be determined the extent to which sub-categories exist. Faces share many visual properties and could theoretically be represented without category boundaries in a single 'face-space'. For exam-

ple, all faces regardless of categories such as race or age could be represented along continua of similarity. On the other hand, certain properties of faces may result in grouping of similar faces and categorical perception.

There is a distinction between upright and inverted faces in terms of configural processing (Yin, 1969). Rhodes et al. (2004) found that opposite aftereffects could be induced for upright and inverted faces simultaneously and concluded that distinct neural populations code upright and inverted faces. The perception of normal shape for upright faces and inverted faces could be moved in opposite directions when observers were exposed to upright and inverted faces which had been manipulated to appear different in shape along a particular axis (Rhodes et al., 2004). While people have significantly more experience with upright faces than inverted ones, different neural populations may also code subcategories of faces for which expertise is more equivalent. Inverted faces also may or may not be processed by the Fusiform Face Area, the area of the brain proposed to be specialized for face perception (Kanwisher, McDermott, & Chun, 1997), but different categories of upright face are. Sex is an important classification and it has been shown that adaptation to eye-spacing, face shape, and sexual dimorphism does not cross the category of sex for judgements of both normality and attractiveness (Little et al., 2005). In other words, adapting to traits in male faces does not influence subsequent perceptions of female faces and vice versa. Indeed, it has been shown that simultaneous adaptation to male faces with increased eye spacing and female faces with decreased eye spacing can induce opposite aftereffects for male and female faces (Little et al., 2005). As distinct representations can occur for categories of faces for which configural processing is equal (Little et al., 2005), it is possible that different neural populations may also code other salient subcategories of upright faces. While such behavioural data does not demonstrate the existence of separable neural representation there is reason to believe that such adaptation reflects neuronal responses. For example, recent neuroimaging evidence has shown that adaptation reveals that specific neural populations respond to faces falling along specific identity axes (Loffler et al., 2005). Behavioural studies of adaptation of left and right eye gaze suggesting discrete neural populations for each (Jenkins, Beaver, & Calder, 2006) have recently been confirmed as indeed having different dedicated neural substrates using brain imaging techniques (Calder et al., 2007).

We note it is unlikely that neurons are predetermined to code face sex and that such selectivity is more likely the result of experience. It is also unclear the extent to which such effects reflect spatial separation of neurons as there is evidence in non-human primates that neurons coding different directions of gaze may be intermixed in the same cellular regions (Perrett, Hietanen, Oram, & Benson, 1992). Adaptation here, if involved in neural tuning, then addresses the issue of functional and not spatial dissociation of category coding neurons.

The current study investigated whether visual aftereffects cross the three salient categories of race, age and species. We exposed European adult participants to male faces transformed for eye-spacing (wide versus narrow) so that each potential category possessed opposite traits. For example, we exposed participants to either male European faces with narrow spaced eyes and male African faces with wide spaced eyes or European faces with wide spaced eyes and African faces with narrow spaced eyes

(Experiment 1). After the adaptation phase we then presented pairs of novel faces from within category (one of which had narrow spaced eyes and one of which had wide spaced eyes) for normality judgements. For example, the post adaptation test for the above example involved choosing which of a pair of European faces with differently spaced eyes appeared more normal and which of a pair of African faces with differently spaced eyes appeared more normal. This procedure was repeated as presented here but with European male adult versus European male infant faces (Experiment 2) and European male adult versus male monkey faces (Rhesus macaques, Experiment 3).

If each face group represents a separate category, we would expect exposure to faces of one category to affect perceptions of that category only. On the other hand, if the faces do not represent different face categories, we would expect exposure to have no effect, as judges are presented with an equal number of faces with wide and narrow eye-spacing making both images in our post test look equally normal.

2. Experiments

2.1. Methods

2.1.1. Participants

Participants in Experiment 1 were 52 women and 38 men (mean age = 29.4, $SD = 9.8$). Participants in Experiment 2 were 47 women and 35 men (mean age = 27.8, $SD = 9.0$). Participants in Experiment 3 were 56 women and 43 men (mean age = 34.1, $SD = 10.6$). Different participants took part in each experiment. All participants were volunteers and were selected for being between the ages of 16–60 and white in ethnicity.

2.1.2. Stimuli

All stimuli were constructed using established (Little, Burt, Penton-Voak, & Perrett, 2001; Little et al., 2005; Perrett et al., 1998) techniques for manipulating the appearance of face images in an objective, systematic manner (for technical details including mathematical algorithms see Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001). Eye-spacing was manipulated by transforming all images relative to a pair of face images, one original image and one image where all the points delineating the eyes had been moved outwards (Fig. 1). The distance change in eye-spacing distance from original (measured from the centre of the eye) in the presented images was 21 pixels for each individual face, either wider or narrower. We note that images still appear realistic and plausible as real faces. The same transform was applied to all starting images ensuring the wide and narrow eye-spacing images differed from the real starting images in an identical manner but in opposite directions. This procedure for manipulating eye spacing in face images is methodologically similar to that used to test for sex-contingent face aftereffects in previous studies (Little et al., 2005).

For the adaptation phase, 10 composite images (each made up from 2 images) from each category were transformed plus and minus for eye-spacing. The same adult European images were used in all 3 experiments. This meant for Experiment

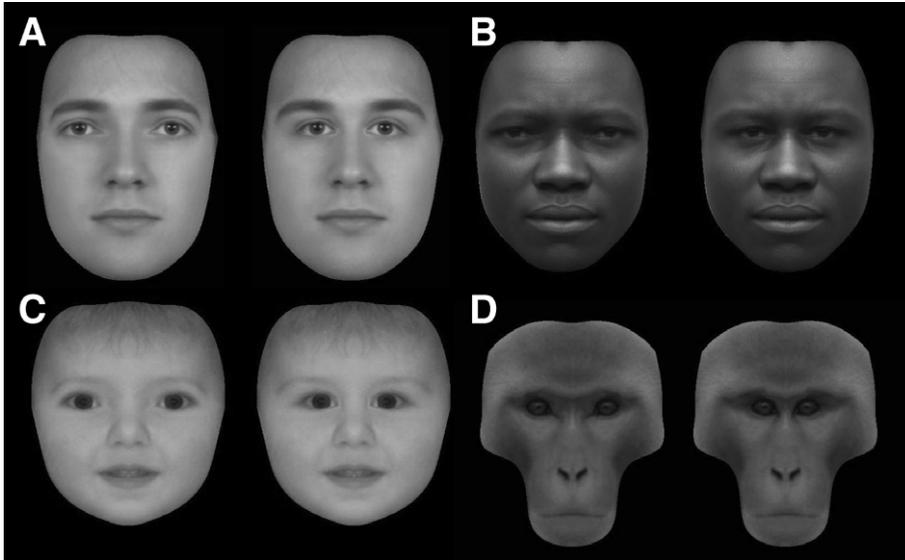


Fig. 1. Examples of face images varying in eye-spacing for Adult Europeans (A), Adult Africans (B), Infant Europeans (C) and Adult monkeys (D). Eye-spacing stimuli were manufactured by increasing (left, plus) or decreasing (right, minus) the distance between the eyes of an original image the same prescribed distance for all images. These images appeared as part of the post-adaptation tests for normality judgements.

1, 10 European and 10 African faces were transformed, for Experiment 2, 10 infant faces, and for Experiment 3, 10 monkey faces.

For the test conditions, 5 new composite images (each made up from random pairs of the adapting faces, 4 images each) from each category were transformed plus and minus for eye-spacing, creating pairs of images where one image had narrow-spaced eyes and wide-spaced eyes. Again, the same adult European images were used throughout.

All images were standardised for size on interpupillary distance prior to transformation. The magnitude of the deviation from average for the wide-set version was identical to the magnitude of deviation from average for the close-set version for each identity used in all parts of the experiment.

2.1.3. Procedure

The two adaptation conditions consisted of rating the attractiveness of 10 different faces of one category and 10 different faces of the other. In one adaptation condition, the 10 adult European faces were transformed plus eye-spacing and the 10 faces from the alternate category were transformed minus eye-spacing. In the other adaptation condition, transformation was reversed, the 10 faces from the alternate category were transformed minus eye-spacing and the 10 adult European faces were transformed plus eye-spacing. In the test phase, participants were shown 5 different novel pairs of faces from one category and 5 different novel pairs of faces from the other category and were asked to choose the more ‘normal-looking’ of the pair. Pairs

were of the same identity, one transformed plus eye-spacing and one transformed minus eye-spacing. Participants were randomly allocated to a category condition, race (Experiment 1), age (Experiment 2), and species (Experiment 3). This procedure and design follows that used by our previous studies (Little et al., 2005).

3. Results

3.1. Experiment 1 (race)

A repeated measures ANOVA [dependent variable: % of post-adaptation trials on which increased eye-spacing was judged as more normal; within-participant factor: test face race (European, African); between-participant factors: adaptation condition (Euro+/African–, Euro–/African+), sex of judge (male, female)] revealed a significant interaction between test face race and adaptation condition ($F_{1,86} = 60.7$, $p < 0.0001$, Fig. 2a). For both face races, the image with increased eye-spacing was

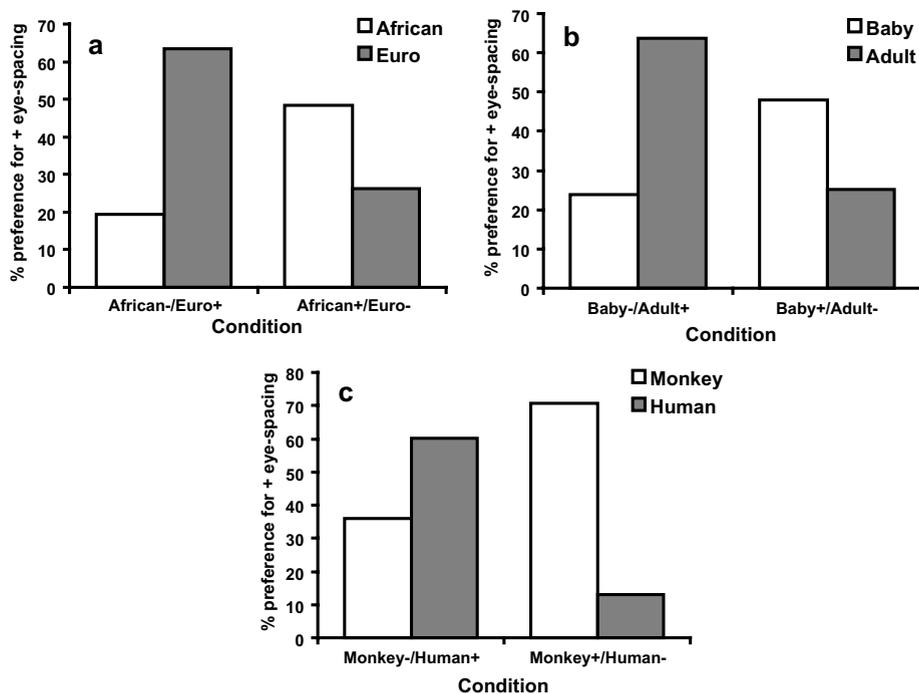


Fig. 2. Category-contingent visual aftereffects following exposure to faces manipulated in eye-spacing for race (African and European, a), age (infant and adult, b), and species (monkey and human, c). Figure shows % choice of plus (wide) eyespacing as most normal-looking across face categories for those exposed to wide-spaced eyes from one category and narrow-spaced eyes from the other category. There was a significant interaction between condition and category for all three face types (race: $F_{1,86} = 60.7$, $p < 0.0001$, $\eta_p^2 = .41$, age: $F_{1,78} = 48.7$, $p < 0.0001$, $\eta_p^2 = .38$, species: $F_{1,95} = 84.4$, $p < 0.0001$, $\eta_p^2 = .41$).

perceived as more normal after the adaptation condition in which the congruent-race face was presented with increased eye-spacing than after the adaptation condition in which the congruent-race face was presented with decreased eye-spacing. There was a theoretically unrelated main effect of test face race ($F_{1,86} = 6.7, p = 0.012$) indicating that wider eye-spacing was perceived as more normal for European than African faces. No other within or between participants effects or interactions were significant (all $F_{1,86} < 1.6, p > 0.21$).

3.2. Experiment 2 (age)

A repeated measures ANOVA [dependent variable: % of post-adaptation trials on which increased eye-spacing was judged as more normal; within-participant factor: test face age (Adult, Infant); between-participant factors: adaptation condition (adult+/infant–, adult–/infant+), sex of judge (male, female)] revealed a significant interaction between test face age and adaptation condition ($F_{1,78} = 48.7, p < 0.0001$, Fig. 2b). For both face ages, the image with increased eye-spacing was perceived as more normal after the adaptation condition in which the congruent-age face was presented with increased eye-spacing than after the adaptation condition in which the congruent-age face was presented with decreased eye-spacing. A theoretically unrelated main effect of face-age ($F_{1,78} = 6.7, p = 0.054$) indicated that wider eye-spacing was perceived as more normal for adult than infant faces. There was also a marginally significant interaction among sex of judge, test face age, and adaptation condition ($F_{1,78} = 3.9, p = 0.051$), suggesting that female judges show greater adaptation effects than male judges (test face age \times condition for women, $F_{1,45} = 42.4, p < 0.001$, for men, $F_{1,33} = 12.9, p = 0.001$). There was also a marginally significant overall effect of sex of judge ($F_{1,78} = 3.1, p = 0.085$), though this reflected the higher order interaction. No other within- or between-participants effects or interactions were significant (all $F_{1,78} < 1.2, p > 0.27$).

3.3. Experiment 3 (species)

A repeated measures ANOVA [dependent variable: % of post-adaptation trials on which increased eye-spacing was judged as more normal; within-participant factor: test face sex (Human, Monkey); between-participant factors: adaptation condition (human+/monkey–, human–/monkey+), sex of judge (male, female)] revealed a significant interaction between test face species and adaptation condition ($F_{1,95} = 84.4, p < 0.0001$, Fig. 2c). For both species, the image with increased eye-spacing was perceived as more normal after the adaptation condition in which the congruent-species face was presented with increased eye-spacing than after the adaptation condition in which the congruent-species face was presented with decreased eye-spacing. There was a theoretically unrelated main effect of face-species ($F_{1,95} = 14.1, p < 0.001$), indicating that wider eye-spacing was perceived as more normal for monkey than human faces. No other within or between participants effects or interactions were significant (all $F_{1,95} < 1.3, p > 0.25$).

4. General discussion

Results from all three experiments indicated that face aftereffects occurred only when the category of the faces at exposure and post-adaptation testing were congruent. Previous studies have suggested that aftereffects following exposure to faces reflect change in the responses of distinct neural populations that code the stimuli viewed, such as orientation-contingent aftereffects (Rhodes et al., 2004) and sex-contingent aftereffects (Little et al., 2005). Our results extend these findings by suggesting that distinct neural populations code faces of different races, ages, and species. We note however that our data does not directly demonstrate neural tuning. Of course each of these categories will represent a continuum, with some faces closer to category boundaries than others. For example, age specific traits change with time and some age distinctions may be processed categorically while others are processed on a continuous basis. The average faces used here, however, are distinct enough to produce separable aftereffects, with experience of one category acting independently of experience with another.

Our data add to a burgeoning literature showing that exposure to faces biases subsequent perceptions of novel faces (Leopold, O’Toole, Vetter, & Blanz, 2001; Leopold et al., 2005; Rhodes et al., 2001; Rhodes et al., 2003; Rhodes et al., 2004; Webster et al., 2004) and literature on the general effects of exposure to other stimuli (Ashby & Maddox, 2005; Posner & Keele, 1968). Here we have used adaptation effects to examine representations in the brain with behavioural measures. Faces, as a category, can be subdivided into subcategories based on appearance and here we show that several natural categories appear to have discrete representations in the brain. The category-contingent effects observed in all three of our experiments are also further evidence that aftereffects due to exposure to faces cannot be explained simply by retinal adaptation as face aftereffects could be generated in opposite directions, rather than a global adaptation in a single direction. Additionally, studies of sex-contingent face aftereffects have shown that category-contingent aftereffects occur when adapting faces differ in category (e.g. male versus female) but do not occur when the same physical differences among adapting faces are presented within a category (i.e. female versus hyperfemale faces (Bestelmeyer et al., *in press*), showing that contingent aftereffects can not be induced for all pairs of groups that differ systematically. Likewise, neural responses to identity are sensitive to category differences rather than equivalent within-category changes (Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Such findings support the proposal that adaptation represents the coding of high-level aspects of faces (e.g. identity) rather than coding only simple physical aspects of different face patterns (Leopold et al., 2005).

The current findings are the first empirical evidence that the human brain can independently process faces of different race, age, and species. Within the broad class of ‘faces’ the human brain appears to possess at least separable representations of upright and inverted faces, male and female faces, European and African faces (or possibly own and other race faces), adult and baby faces, and human and non-human faces at the least. Potentially the visual system updates several other catego-

ries based on facial appearance, and future studies will usefully parse the boundaries of existing categories. Of course, adaptation studies could be used to examine categorical perception in other types of stimuli.

If categorical perception involves discrete neural responses for categories then this is likely the result of experience as it is unlikely that, for example, there are neurons in the brain predetermined to code face race. Rather, visual experience of faces of different races coupled with the salience of the category may recruit neurons to become selective to only one category. The notion of spatial segregation of neurons coding different categories is also open to question. As noted by [Jenkins et al. \(2006\)](#), in discussing their findings for eye-gaze adaptation, there are limitations in the spatial resolution of current functional imaging technology making it difficult to determine whether there are indeed spatially distinct neurons. There is even evidence in nonhuman primates that neurons coding different directions of gaze may be intermixed in the same cellular regions ([Perrett et al., 1992](#)) and potentially many categories may be represented via such distributed neural coding. We note though that recently it has been shown that discrete neural populations code for left and right eye gaze using adaptation techniques ([Calder et al., 2007](#)). Future research could usefully model whether a neural network trained to recognise stimuli using category compares well with human perception (see [Cheng, O'Toole, & Abdi, 2001](#)) and also note the relative advantages and disadvantages of spatially discrete versus distributed representations. The role of experience and the extent to which categories are represented by spatially distinct versus distributed neurons remain interesting avenues for future research.

We have also reported a marginally significant sex of judge effect, in that women showed a larger effect of adaptation than men when exposed to both adult and infant faces. This effect may be due to differential experience of men and women with infant faces and would then imply that, somewhat counter-intuitively, those with greater experience with a category have more malleable visual representations with that category. Alternatively, the different effect size in adaptation may reflect an influence of attention in adaptation, women may attend more to infant faces than men.

These results have important implications for the notion of face-space ([Valentine, 1991](#)), in which it is commonly conceived that we recognize faces based on deviations from a single average representation or their proximity to other specific faces within a single population of all faces encountered. Face-space may be better reconceptualised with distinct categories of faces as partially or fully independent subspaces with their own prototypes/norms or distributions. Multiple representations for subcategories are unlikely to be restricted to faces.

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