

Sex-specific norms code face identity

Gillian Rhodes

FaceLab, School of Psychology, University of Western
Australia, Crawley, Australia



Emma Jaquet

FaceLab, School of Psychology, University of Western
Australia, Crawley, Australia, &
University of Bristol, UK



Linda Jeffery

FaceLab, School of Psychology, University of Western
Australia, Crawley, Australia



Emma Evangelista

FaceLab, School of Psychology, University of Western
Australia, Crawley, Australia



Jill Keane

MRC Cognition and Brain Sciences Unit, Cambridge, UK



Andrew J. Calder

MRC Cognition and Brain Sciences Unit, Cambridge, UK



Face identity aftereffects suggest that an average face, which is continuously updated by experience, functions as a norm for coding identity. Sex-contingent figural face aftereffects indicate that different norms are maintained for male and female faces but do not directly implicate them in coding identity. Here, we investigated whether sex-specific norms are used to code the identities of male and female faces or whether a generic, androgynous norm is used for all faces. We measured identity aftereffects for adapt–test pairs that were opposite relative to a sex-specific average and pairs that were opposite relative to an androgynous average. Identity aftereffects are generally larger for adapt–test pairs that lie opposite an average face, which functions as a norm for coding identity, than those that do not. Therefore, we reasoned that whichever average gives the larger aftereffect would be closer to the true psychological norm. Aftereffects were substantially and significantly larger for pairs that lie opposite a sex-specific than an androgynous average. This difference remained significant after correcting for differences in test trajectory length. These results indicate that, despite the common structure shared by all faces, identity is coded using sex-specific norms. We suggest that the use of category-specific norms may increase coding efficiency and help us discriminate thousands of faces despite their similarity as patterns.

Keywords: face perception, perceptual adaptation and aftereffects, norm-based coding of identity

Citation: Rhodes, G., Jaquet, E., Jeffery, L., Evangelista, E., Keane, J., & Calder, A. J. (2011). Sex-specific norms code face identity. *Journal of Vision*, 11(1):1, 1–11, <http://www.journalofvision.org/content/11/1/1>, doi:10.1167/11.1.1.

Introduction

Many theorists propose that faces are coded relative to a perceptual norm that represents the central tendency (average) of our perceptual diet of faces (Diamond & Carey, 1986; Goldstein & Chance, 1980; Hebb, 1949; Hochberg, 1978; Leopold, O’Toole, Vetter, & Blanz, 2001; Rhodes, 1996; Rhodes, Brennan, & Carey, 1987; Rhodes & Leopold, *in press*; Valentine, 1991). Norm-based coding makes explicit what is distinctive about each face, allowing us to readily discriminate and recognize thousands of faces despite their similarity as visual patterns.

Several findings are consistent with norm-based coding of face identity. First, people can abstract averages or prototypes from sets of seen faces, a process that operates from early infancy (Bruce, Doyle, Dench, & Burton, 1991;

Cabeza, Bruce, Kato, & Oda, 1999; Cabeza & Kato, 2000; De Haan, Johnson, Maurer, & Perrett, 2001; Haberman & Whitney, 2007; Inn, Walden, & Solso, 1993; MacLin & Webster, 2001; Reed, 1972; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Rhodes, Jeffery, Watson, Jaquet, Winkler, & Clifford, 2004; Solso & McCarthy, 1981a, 1981b; Strauss, 1979; Walton & Bower, 1993; Webster & MacLin, 1999). Second, distinctive faces (far from average) are recognized better than typical ones (close to average; Valentine, 1991, 2001). Third, exaggerating how a face differs from the average, by caricaturing, can facilitate recognition (Benson & Perrett, 1994; Byatt & Rhodes, 1998; Calder, Young, Benson, & Perrett, 1996; Lee, Byatt, & Rhodes, 2000; Rhodes, 1996; Rhodes et al., 1987).

The most direct evidence for norm-based coding, however, comes from face identity aftereffects (Anderson & Wilson, 2005; Leopold et al., 2001; Leopold, Rhodes,

Müller, & Jeffery, 2005; Rhodes & Jeffery, 2006; Rhodes, Jeffery, Clifford, & Leopold, 2007; Tsao & Freiwald, 2006). Viewing a face for a few seconds biases us to perceive an identity with opposite characteristics to the adapting face (Figure 1). This aftereffect seems to result from a (transient) shift of the average/norm toward the adapting face, so that low identity strength versions of the opposite identity look more distinctive and are therefore easier to identify (Rhodes & Jeffery, 2006; Rhodes et al., 2005). The aftereffect can even cause an initially “identity-neutral” average face to be perceived as different identities after adapting to different antifaces (Leopold et al., 2001, 2005; Rhodes et al., 2007). Importantly, perception is *selectively* biased toward the identity that lies *opposite* (defined relative to the average) the adapting face in face space, providing strong evidence that the average face functions as a perceptual norm against which identity is coded (Rhodes & Jeffery, 2006; Tsao & Freiwald, 2006).

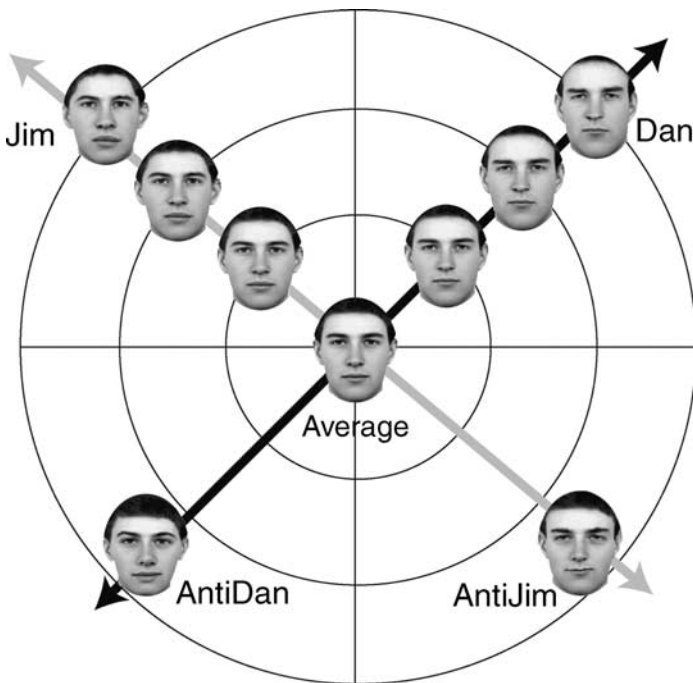


Figure 1. A simple 2-dimensional face space with two faces, Dan and Jim, and an Average face, created by morphing 20 males, Caucasian faces, at the center. Each face has a corresponding antiface (antiDan and antiJim), which occupies the opposite (relative to the average) location in face space. The antiface can be constructed by morphing the original face toward the average and beyond. Reduced identity strength versions of Dan and Jim, created by morphing those identities toward the average, are also shown. Viewing a face for a few seconds produces an identity aftereffect in which perception is biased toward the opposite identity. For example, viewing antiDan for a few seconds allows Dan to be identified from lower identity strength versions of Dan (e.g., Leopold et al., 2001; Rhodes & Jeffery, 2006).

Our face norm is continuously updated by experience and a few minutes exposure to consistently distorted faces shifts our perception of what is normal toward the adapting distortion (MacLin & Webster, 2001; Rhodes et al., 2003, 2004; Watson & Clifford, 2003; Webster & MacLin, 1999; Webster, Werner, & Field, 2005). For example, after viewing faces with “expanded” internal features, slightly expanded faces appear normal, and undistorted faces look “contracted.” In contrast, after viewing faces with “contracted” features, slightly contracted faces appear normal, and undistorted faces look “expanded” (e.g., Rhodes et al., 2003). Importantly, these figural aftereffects affect the perception of previously unseen faces, consistent with a change in the underlying norm that is used to code appearance.

So far we have talked as if there is a single face norm. However, the brain may maintain different norms for visually distinct categories of faces, such as male and female faces (for reviews, see Rhodes & Jaquet, 2010; Rhodes & Leopold, *in press*). Category-specific norms might enhance coding economy, because neural responses increase with distance from the norm and faces will generally lie further from an androgynous than a sex-specific average (Barlow, 1990; Bartlett, 2007; Leopold, Bondar, & Giese, 2006; for a review, see Rhodes & Leopold, *in press*). The use of category-specific norms to code identity could also improve discrimination by orthogonalizing identity vectors in a multi-dimensional face space (Rhodes, Watson, Jeffery, & Clifford, 2010).

The existence of sex-contingent figural face aftereffects suggests that different norms are maintained for male and female faces. These sex-contingent aftereffects occur when opposite aftereffects are induced simultaneously in male and female faces (Bestelmeyer, Jones, & DeBruine, 2008; Jaquet & Rhodes, 2008; Little, DeBruine, & Jones, 2005). For example, after adapting to contracted male faces intermixed with expanded female faces, undistorted male and female faces look slightly expanded and slightly contracted, respectively. Sex-contingent aftereffects are difficult to reconcile with a single norm, because viewing opposite distortions (contracted and expanded) would pull that norm in opposite directions, canceling to give no net aftereffect (e.g., Jeffery, Rhodes, & Busey, 2007).

These findings raise the possibility that facial identity is coded using sex-specific norms. However, this is by no means certain. For example, these norms could be used to assess facial beauty without playing a role in identity coding (Rhodes, 2006; Rhodes et al., 2003). Moreover, although sex-contingent figural aftereffects have been demonstrated, adaptation to faces of one sex can transfer (partially) to opposite-sex faces (Jaquet & Rhodes, 2008).¹ Such transfer reflects adaptation of traits that are common to faces of both sexes and highlights the alternative possibility that identity may be coded using a generic, androgynous face norm.

The current study sought to determine whether facial identity is coded using sex-specific norms or a generic

androgynous norm. To derive predictions, we exploited the finding that identity aftereffects are larger for adapt–test pairs that lie opposite an average face than those that do not (Leopold et al., 2001; Rhodes & Jeffery, 2006). These results indicate that aftereffects are larger when adapting faces are made relative to a face that is close to the underlying psychological norm (center of face space) rather than some other less central face. Therefore, we should be able to determine whether sex-specific or generic, androgynous averages function as a psychological norm, by comparing the size of identity aftereffects for adapt–test pairs that lie opposite (relative to) a sex-specific average and those that lie opposite (relative to) a generic average. If faces are coded relative to sex-specific norms, then identity aftereffects should be larger for adapt–test pairs that lie opposite a sex-specific average than those that lie opposite a generic average. Alternatively, if faces are coded relative to a generic norm, then the opposite pattern should be observed.

We created sex-specific (male and female) and generic (androgynous) averages (Figure 2), which were used to make antifaces for four test identities of each sex (Figure 3). For each test identity, we created two sets of reduced identity strength versions, one by morphing the face toward the same-sex average (Figure 3a) and one by morphing the face toward the generic average (Figure 3b). These images were used as test faces to measure identification thresholds for same-sex and generic trajectories, respectively.

On each trial, participants adapted to an antiface (e.g., antiAnne) for 5 s and then identified a briefly presented test face (e.g., 60% Anne). On match trials, the adapt and test faces came from the same identity trajectory (e.g., adapt antiAnne, test Anne), and on mismatch trials, they came from different identity trajectories (e.g., adapt antiBeth, test Anne). In both cases, the adapt–test pairs come from the same type of trajectory (same sex or

generic). Previous research has shown that adapting to a matching (opposite) antiface reduces identification thresholds whereas adapting to a mismatching (non-opposite) antiface increases them (by biasing perception toward an identity that lies opposite the mismatching antiface, i.e., toward an identity that is not the test identity), relative to no adaptation (Leopold et al., 2001; Rhodes, Evangelista, & Jeffery, 2009). Here we measured identity aftereffects directly as the difference between mismatch and match thresholds (cf., Pellicano, Jeffery, Burr, & Rhodes, 2007). Use of a mismatch condition rather than a no adapt baseline controls for any differences in alerting or arousal associated with the presence or absence of an adapting face. It also ensures that target identity is not predictable from the adapting identity. Larger aftereffects for adapt–test pairs made using sex-specific than generic averages, i.e., for sex-specific than generic trajectories, would indicate that male and female faces are coded using sex-specific norms. In contrast, larger aftereffects for pairs made using the generic average would indicate that a single androgynous norm is used.

We also sought to rule out an alternative account based on differences in test trajectory length. Target faces are likely to be more similar to a same-sex average than to an androgynous generic average (whose sex clearly differs from that of the target faces), making same-sex trajectories shorter than generic trajectories. Because aftereffects are measured as proportional shifts of identification thresholds along trajectories of unit length, larger aftereffects on same-sex than generic test trajectories might not represent larger shifts in face space (perceptual distance). For example, if same-sex trajectories were half the length of generic trajectories, then an aftereffect of 0.2 on a same-sex trajectory would represent the same shift in face space as an aftereffect of 0.1 on a generic-sex trajectory. To assess, and correct for, any difference in test trajectory



Figure 2. (Left) Male average, (center) female average, and (right) generic, androgynous average. The sex-specific averages were made by morphing together 24 male and 24 female faces, respectively. The generic average was made by morphing all 48 faces (24 males, 24 females).

lengths, we obtained ratings of perceived similarity of the target faces to the sex-specific and the generic averages.

Finally, we sought to rule out an alternative account based on differences in perceptual contrast between adapt and test faces on the two types of trajectory. Aftereffects can decrease as the adapting and test stimuli become more similar (Clifford, 2002; Robbins, McKone, & Edwards, 2007) and we wanted to rule out differences in adaptor–test similarity as an account for any observed differences in aftereffects between the two types of trajectory. We

obtained ratings of similarity of the adapting antifaes to the averages for each trajectory and used these to estimate adaptor–test similarity for each trajectory.

Methods

Participants

Twenty-four young Caucasian adults (4 males) from the University of Western Australia and the Cognition and Brain Sciences Unit in Cambridge participated.

Stimuli

Front-view photographs of four easily discriminable faces of each sex were used as target identities. All were young adult Caucasians, displaying neutral expressions. Sex-specific male (AvM) and female (AvF) average composites were created from 24 male and 24 female faces (including the test faces), respectively, using standard morphing procedures. A generic average (AvAll) was created from all 24 male and 24 female faces. We created two antifaes “adapters” for each target identity, by caricaturing the sex-specific and the generic average, respectively, away from the target identity, by 80% (i.e., –80% identity strength of the target) using Gryphon Morph. Two adapt–test trajectories were also created for each test identity: a sex-specific trajectory, in which the face was morphed toward the appropriate sex-specific average and a generic trajectory, in which it was morphed toward the generic average. Each trajectory consisted of 11 versions of the target face, varying in identity strength: –20%, –10%, 0%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80% (negative values represent antifaes, 0% represents an average face; partial trajectories shown in Figure 3). Only face shape (defined by landmark points) was varied (cf., Rhodes & Jeffery, 2006).² Faces were displayed in color, within a black oval mask that hid the

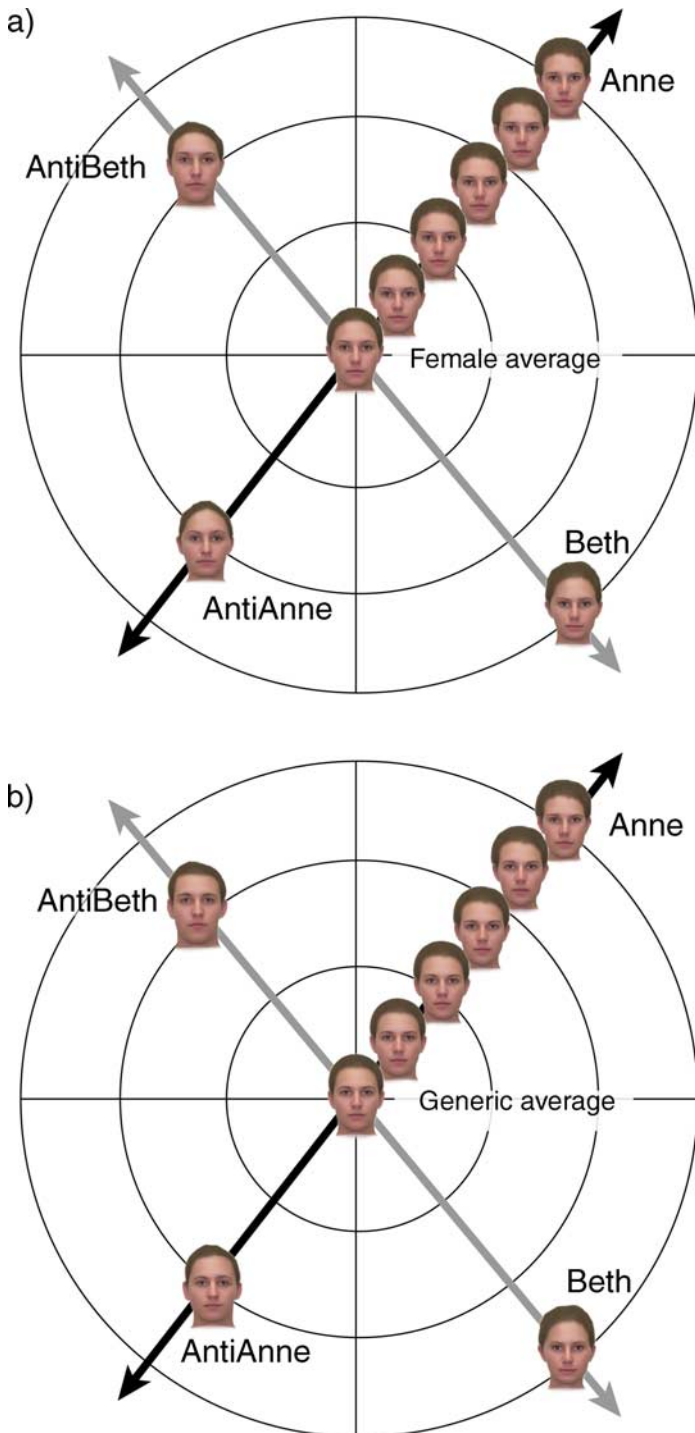


Figure 3. Simplified two-dimensional face spaces showing two identities, with matching antifaes made using a (a) sex-specific or (b) generic average. Each antifaes was made by morphing the target identity toward and beyond the relevant average to create a face with opposite properties. A subset of the test trajectory (–20 to +80 in 10% steps) used to measure Anne’s identification threshold is shown (0% is the average face for that trajectory). On match trials, participants adapted to matching antifaes (e.g., adapt antiAnne, test Anne), and on mismatch trials, they adapted to non-matching antifaes (e.g., adapt antiBeth, test Anne). Aftereffects were measured as the difference in identification thresholds between match and mismatch trials (mismatch minus match). These were calculated separately for adapt–test trajectories made using (top) sex-specific and (bottom) generic averages.

hair (including inner hairline) but not the face outline or ears. Masked faces were approximately $8.0^\circ \times 7.2^\circ$, viewed from 50 cm.

Similarity ratings

Twelve additional participants (all female, Caucasian) rated the similarity of sequentially presented pairs of faces, using a 7-point scale, with 1 labeled “not at all similar” and 7 labeled “very similar.” Participants initiated each trial by pressing the space bar, which initiated the following sequence: a fixation point for 500 ms, a face for 200 ms, a blank ISI for 150 ms, a second face for 200 ms, a blank ISI for 150 ms, a response prompt screen. The exposure times and ISI durations matched those used in the main experiment. Trials were blocked by sex of face, counterbalanced across participants. Each block consisted of 0 vs. 80 and -80 vs. 0 pairs for each of the four identities and two trajectories.³ Each pair was shown twice, once in each sequential order. Trial order was randomized within blocks. At the beginning of each block, participants previewed the full set of trials for that block, without the screen asking for a response, to get a feel for the kind of variation they would see.

Procedure

Aftereffects for the sex-specific and generic trajectories were measured in separate 1-h sessions, conducted on different days, in counterbalanced order. Sex of target faces was varied between participants. Each session began with training on the appropriate target identities (male or female) and trajectory (sex-specific or generic).

Training

Participants began by learning to name the four test faces (male or female), by studying a printout of these faces and their names. Next, came three practice blocks, in which these faces were shown on the computer screen and had to be identified using labeled keyboard keys. Exposure duration was unlimited in the first block, 500 ms in the second block, and 200 ms in the third block. The correct answer was displayed after each response and incorrect responses received auditory feedback (beep). Each face was shown four times in random order in each practice block. Participants could consult the printout of the faces if necessary. Finally, participants practiced identifying the four test faces at weaker identity strengths (20%, 40%, 60%, 80%) in two blocks. Exposure duration was unlimited in the first block and 200 ms in the second block. Each face was shown four times at each identity strength, in random order, in each block, with feedback as above.

Adaptation

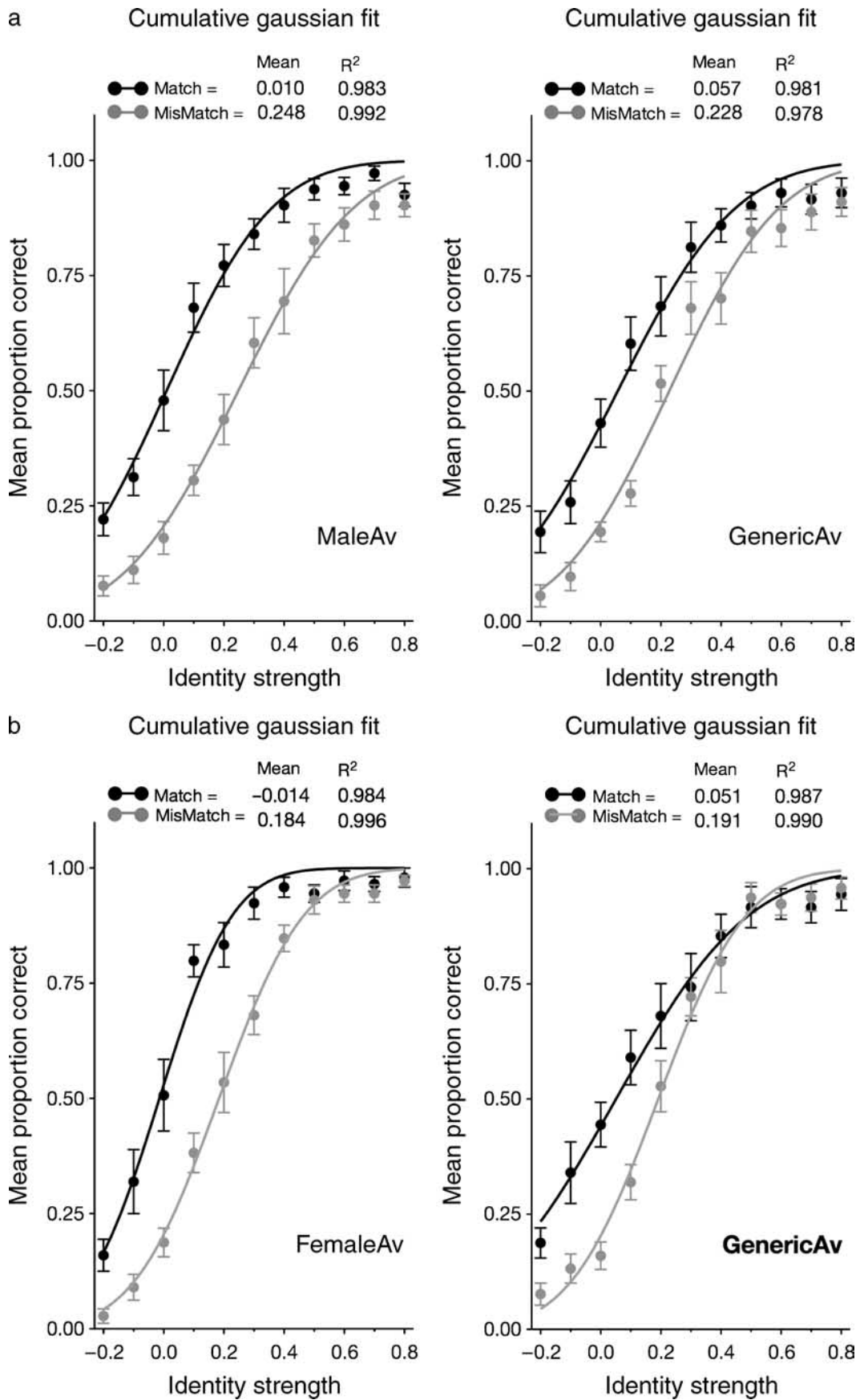
There were two kinds of adaptation trials for each trajectory: match and mismatch trials. On match trials, the adapt and test faces came from the same trajectory (e.g., adapt antiAnne, test Anne). On mismatch trials, the adapting and test faces came from different trajectories (e.g., adapt antiBeth, test Anne). One of the three possible non-matching antifaces was randomly assigned to each test identity. For each trajectory (test session), there were 264 trials, consisting of 4 test identities \times 2 adapting conditions (match, mismatch) \times 11 test identity strengths (-20% , -10% , 0% , 10% , 20% , 30% , 40% , 50% , 60% , 70% , 80%) \times 3 repetitions. Trial order was randomized. Participants pressed the space bar to initiate each trial. The trial sequence was a 5000-ms adapting antiface, 150-ms blank ISI, 200-ms test face, 150-ms blank ISI, screen prompt to identify the test face using labeled keyboard keys. Participants were told that it was important to look at the adapting face for the full 5 s. They were also told that some of the target faces would be hard to identify but to respond as accurately as possible and make their best guess if uncertain. Four practice trials illustrated the sequence.

Results

Identification responses were scored as correct if they corresponded to the identity from which the test face was made. Following Leopold et al. (2001), a quarter of the 0% test faces was randomly assigned to each identity trajectory, allowing “performance” to be measured. For each participant, we plotted mean proportion correct as a function of identity strength for each trajectory and type of trial (match, mismatch). We then fitted cumulative Gaussian curves to these identification data. Curve fits were very good (mean $R^2 = 0.914$, $SD = 0.072$, range = 0.680 to 0.998). The means of the fitted cumulative Gaussians provided an identification threshold for each condition. For each participant, we calculated an identity aftereffect for each trajectory, by subtracting the identification threshold on match trials from the identification threshold on mismatch trials. Half the participants were tested on male target faces and half on female target faces.

Comparing aftereffects

Mean proportions correct for same-sex and generic trajectories are shown in Figure 4a for male faces and Figure 4b for female faces. Aftereffect size (differences between curves) is shown in Figure 5. It is clear from both Figures 4 and 5 that aftereffects were larger for same-sex



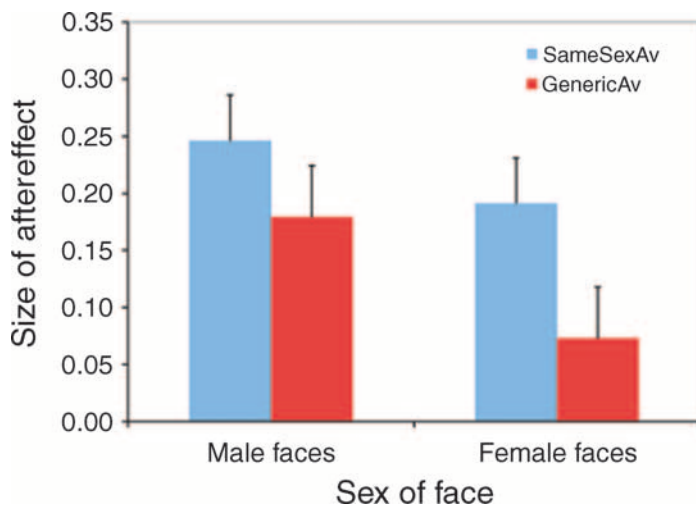


Figure 5. Mean size of aftereffect (mismatch threshold minus match threshold) for sex-specific and generic average trajectories, for male and female target faces. SE bars are shown.

than generic trajectories. A two-way ANOVA on the aftereffects, with trajectory (same-sex, generic) as a repeated measures factor and face sex (female, male) as a between-participants factor, confirmed that the aftereffects were significantly and substantially larger for the same-sex ($M = 0.219$, $SD = 0.139$) than generic trajectories ($M = 0.126$, $SD = 0.162$), $F(1,22) = 8.02$, $p < 0.01$ (partial $\eta^2 = 0.27$). There was no main effect of face sex, $F(1,22) = 2.52$, $p = 0.13$ (partial $\eta^2 = 0.103$) and no interaction between trajectory and face sex, $F < 1$.

Correcting for differences in test trajectory length

Mean similarity ratings for target–average (80% vs. 0%) pairs (Table 1) were used to assess the length of sex-specific and generic trajectories. A two-way ANOVA on these ratings, with trajectory and face sex as repeated measures factors, showed a significant effect of face sex, $F(1,11) = 7.371$, $p = .020$ (partial $\eta^2 = .401$). There was also a significant effect of trajectory, $F(1,11) = 9.518$, $p = .010$ (partial $\eta^2 = .464$), which did not interact with face sex, $F(1,11) = 3.020$, $p = .110$ (partial $\eta^2 = .215$). Similarity ratings were 12% lower for generic ($M = 4.38$, $SD = 0.89$) than same-sex trajectories ($M = 5.03$, $SD = 0.66$), indicating

Figure 4. (a) Mean (SE) proportion correct for male target faces on sex-specific (MaleAv) and generic (GenericAv) trajectories. Cumulative Gaussian identification curves are shown for match (e.g., adapt antiAnne, test Anne) and mismatch (adapt antiBeth, test Anne) trials for each trajectory. (b) Mean (SE) proportion correct for female target faces on sex-specific (FemaleAv) and generic (GenericAv) trajectories. Cumulative Gaussian identification curves are shown for match (e.g., adapt AntiAnne, test Anne) and mismatch (adapt antiBeth, test Anne) trials for each trajectory.

Sex of face	Average/trajectory	
	Sex-specific	Generic
Male	5.48 (0.29)	4.54 (0.28)
Female	4.58 (0.27)	4.21 (0.22)
All	5.03 (0.26)	4.38 (0.19)

Table 1. Mean (SE) similarity of target faces to sex-specific and generic averages.

that the generic test trajectories were longer than the sex-specific ones. We, therefore, scaled the generic trajectory aftereffects (multiplying by 1.12) and reexamined the effect of trajectory in a two-way ANOVA with trajectory as a repeated measures factor and face sex as a between-participants factor. Nevertheless, the aftereffects remained significantly larger for same-sex ($M = 0.219$, $SD = 0.139$) than generic trajectories ($M = 0.141$, $SD = 0.182$), $F(1,22) = 4.862$, $p = 0.038$ (partial $\eta^2 = 0.181$).

Ruling out differences in adaptor–test contrast

To explain larger aftereffects for same-sex than generic trajectories, the perceptual contrast between adapt and test faces would have to be larger for same-sex trajectories, i.e., adaptor–average (and by extension, higher identity strength) test pairs should be rated as less similar for same-sex than generic trajectories. This was not the case. There was no significant difference between similarity ratings for the two trajectories, $F(1,11) = 4.229$, $p = 0.064$ (partial $\eta^2 = 0.278$) and the numerical difference was in the wrong direction (Table 2). Adapting antifaces were rated as slightly *more* similar to same-sex than generic averages, probably because the former face pairs appear to be the same sex.

Discussion

The sex of a face can be perceived rapidly and from minimal information (e.g., Cloutier, Mason, & Macrae, 2005; Gosselin & Schyns, 2001) and it provides important

Sex of face	Average/trajectory	
	Sex-specific	Generic
Male	4.46 (0.34)	4.17 (0.28)
Female	4.58 (0.19)	3.96 (0.24)
All	4.52 (0.24)	4.06 (0.24)

Table 2. Mean (SE) similarity of adapting antifaces to sex-specific and generic averages.

information that guides our interpersonal behavior. The present results suggest that it also determines how the identity of that face is coded, with male faces coded using a male norm (average) and female faces coded using a female norm.

Identity aftereffects were substantially and significantly larger for adapt–test pairs that lie opposite (relative to) a sex-specific average than opposite a generic androgynous average. This difference could not be explained by differences in adapt–test pair perceptual contrast or in test trajectory length. It remained significant when we corrected for a small difference in length between the two types of test trajectory. Because aftereffects are largest when adapt–test pairs lie opposite the average in face space (Leopold et al., 2001; Rhodes & Jeffery, 2006), these results indicate that sex-specific norms are used to code face identity.

One difference between the two kinds of trajectory is that the adapt and test faces appear to be the same sex on sex-specific, but not on generic, trajectories (see Figure 2). Could this difference explain why aftereffects are larger on the sex-specific trajectories? We think not. Aftereffects are measured as the improvement in performance (i.e., reduction in identification thresholds) when the identity of the adapt and test faces matches (e.g., adapt AntiAnne, test Anne) relative to when it does not (mismatch trials, e.g., adapt AntiBeth, test Anne). Any facilitation resulting from sex congruency of the adapt and test faces would be the same in both cases and would therefore be subtracted out when aftereffects are calculated. A similar argument also rules out any contribution of differences in sex adaptation (e.g., a bias to perceive the opposite sex to the adapting faces; Webster, Kaping, Mizokami, & Duhamel, 2004) on the sex-specific and generic trajectories.

Nor can the results be attributed to differences in the number of faces in the generic and same-sex averages. The generic average had twice the number of component faces as the sex-specific averages, and the average of a larger sample is a better estimator of the population mean than the average of a smaller sample. Therefore, *in the absence of any perceptual categorization into distinct male and female face populations*, the generic average should be closer to the center of face space than sex-specific averages. In that case, however, we should have seen larger aftereffects for the generic-average than the sex-specific trajectories. Instead, the reverse was found, providing strong evidence that the generic average is not the true psychological norm. Rather, male and female faces appear to form distinct (albeit overlapping on some dimensions) perceptual categories that are coded using different norms.

How might sex-specific coding operate in face space? One possibility is a functional and neural architecture in which male and female faces are represented in distinct face spaces with no common dimensions and coded by distinct (although not necessarily spatially separated) neural populations. However, such a scheme is implausible

given that male and female faces share many properties. Rather, we propose a *dissociable coding model* in which all faces are represented in a single face space that contains common as well as sex-selective dimensions (see Rhodes & Jaquet, 2010). Common dimensions code faces of both sexes (i.e., are represented in both male and female norms), whereas sex-selective dimensions code faces from one or other sex. A similar model has been proposed to handle the dissociable coding of facial identity and expression (Calder & Young, 2005) and the dissociable coding of faces of different races (Rhodes & Jaquet, 2010).

The present results may help solve a puzzle identified by Tsao and Freiwald (2006). They noted that the average face used to make adapting antifaes varied considerably across studies and yet identity aftereffects were always obtained and interpreted as evidence for a special role of the average face in coding faces (Anderson & Wilson, 2005; Leopold et al., 2001; Rhodes & Jeffery, 2006). More recently, identity aftereffects have even been reported when the endpoints of arbitrary identity continua between pairs of identities serve as adapt–test pairs (Benton & Burgess, 2008; Hills, Elward, & Lewis, 2008). The present results suggest that identity aftereffects occur whether or not adapt–test pairs span the center of face space, but that larger aftereffects are obtained when the adapt–test pairs lie opposite the true norm (see also Rhodes & Jeffery, 2006). Clearly, identity aftereffects per se are not evidence that the average face functions as a norm for coding identity. Rather it is their greater magnitude for opposite than non-opposite adapt and test identities in face space that provides strong evidence for norm-based coding.

Our similarity ratings confirmed that faces lie further from the generic androgynous norm than from a sex-specific norm in face space. Given that neural responses generally increase with distance from the norm, the use of sex-specific norms may, therefore, increase coding economy (Barlow, 1990; Bartlett, 2007; Leopold et al., 2006; for a review, see Rhodes & Leopold, *in press*). It could also enhance discriminability of same-sex faces by maximizing directional differences between identity vectors for those faces (i.e., by orthogonalizing vectors). In contrast, same-sex face vectors originating from a generic norm would share some similar directions (representing any consistent sexual dimorphisms), making individual discrimination harder. Note that the use of sex-specific norms to code identity does not preclude a role for a generic norm in other contexts, where it may be useful to highlight differences between male and female faces, rather than differences between identities, for example in sex categorization.

Sex-contingent figural face aftereffects indicate that different norms are maintained for male and female faces (Bestelmeyer et al., 2008; Jaquet & Rhodes, 2008; Little et al., 2005). The present results implicate these norms in coding identity. Category-contingent aftereffects have also been reported for faces of different races (Jaquet, Rhodes, & Hayward, 2007, 2008; Little, DeBruine, Jones, & Watt,

2008), species (Little et al., 2008), and ages (Little et al., 2008). Generalizing from the present results, we suggest that category-specific norms may also be used to code identity for faces of different races, species, and even perhaps ages. More generally, we propose that mechanisms of perceptual adaptation may be able to tune face-coding mechanisms to any visually distinct categories that matter to us. Such tuning may improve coding economy and increase discrimination capacity over a system in which all faces are coded on the same dimensions (Rhodes et al., 2010).

Acknowledgments

This work was supported by the Australian Research Council and the Medical Research Council, UK (Project Code U.1055.02.001.00001.01 to AJC). We thank Marianne Peters for assistance with testing and data processing and Regine Armann for helpful comments on a draft of the manuscript.

Commercial relationships: none.

Corresponding author: Gillian Rhodes.

Email: gill@psy.uwa.edu.au.

Address: School of Psychology, The University of Western Australia, 35 Stirling HWY, Crawley 6009, Australia.

Footnotes

¹Note that if the adapted traits are sex-specific, then there may be little or no transfer. For example, adaptation to masculinized male faces affects preferences for male, but not female, faces (Little et al., 2005).

²All images had average colors, achieved by morphing the AvAll image into the shape of each target face, using standard morphing procedures, before test trajectories were created.

³A variety of other pair types was included but is not relevant here.

References

- Anderson, N. D., & Wilson, H. R. (2005). The nature of synthetic face adaptation. *Vision Research*, *45*, 1815–1828.
- Barlow, H. B. (1990). A theory about the functional role and synaptic mechanism of visual after-effects. In C. Blakemore (Ed.), *Vision: Coding and efficiency*. Cambridge, UK: Cambridge University Press.
- Bartlett, M. S. (2007). Information maximization in face processing. *Neurocomputing*, *70*, 2204–2217.
- Benson, P. J., & Perrett, D. I. (1994). Visual processing of facial distinctiveness. *Perception*, *23*, 75–93.
- Benton, C. P., & Burgess, E. C. (2008). The direction of measured face aftereffects. *Journal of Vision*, *8*(15):1, 1–6, <http://www.journalofvision.org/content/8/15/1>, doi:10.1167/8.15.1. [PubMed] [Article]
- Bestelmeyer, P. E. G., Jones, B. C., & DeBruine, L. M. (2008). Sex-contingent face aftereffects depend on perceptual category rather than structural coding. *Cognition*, *107*, 353–365.
- Bruce, V., Doyle, T., Dench, N., & Burton, M. (1991). Remembering facial configurations. *Cognition*, *38*, 109–144.
- Byatt, G., & Rhodes, G. (1998). Recognition of own-race and other-race caricatures: Implications for models of face recognition. *Vision Research*, *38*, 2455–2468.
- Cabeza, R., Bruce, V., Kato, T., & Oda, M. (1999). The prototype effect in face recognition: Extension and limits. *Memory & Cognition*, *27*, 139–151.
- Cabeza, R., & Kato, T. (2000). Features are also important: Contribution of featural and configural processing to face recognition. *Psychological Science*, *11*, 429–433.
- Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience*, *6*, 641–651.
- Calder, A. J., Young, A. W., Benson, P. J., & Perrett, D. I. (1996). Self-priming from distinctive and caricatured faces. *British Journal of Psychology*, *87*, 141–162.
- Clifford, C. W. G. (2002). Adaptation-induced plasticity in perception: Motion parallels orientation. *Trends in Cognitive Sciences*, *6*, 136–143.
- Cloutier, J., Mason, M., & Macrae, C. N. (2005). The perceptual determinants of person construal: Reopening the social-cognitive toolbox. *Journal of Personality & Social Psychology*, *88*, 885–894.
- De Haan, M., Johnson, M. H., Maurer, D., & Perrett, D. I. (2001). Recognition of individual faces and average face prototypes by 1- and 3-month-old infants. *Cognitive Development*, *16*, 659–678.
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107–117.
- Goldstein, A. G., & Chance, J. E. (1980). Memory for faces and schema theory. *The Journal of Psychology*, *105*, 47–59.
- Gosselin, F., & Schyns, P. G. (2001). Bubbles: A technique to reveal the use of information in recognition tasks. *Vision Research*, *41*, 2261–2271.

- Haberman, J., & Whitney, D. (2007). Rapid extraction of mean emotion and gender from sets of faces. *Current Biology*, *17*, R751–R753.
- Hebb, D. O. (1949). *The organisation of behaviour*. New York: Wiley.
- Hills, P. J., Elward, R. L., & Lewis, M. B. (2008). Identity adaptation is mediated and moderated by visualisation ability. *Perception*, *37*, 1241–1257.
- Hochberg, J. E. (1978). *Perception* (2nd ed.). Englewood Cliffs, NJ: Prentice-Hall.
- Inn, D., Walden, K. J., & Solso, R. L. (1993). Facial prototype formation in children. *Bulletin of the Psychonomic Society*, *31*, 197–200.
- Jaquet, E., & Rhodes, G. (2008). Face aftereffects indicate dissociable, but not distinct, coding of male and female faces. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 101–112.
- Jaquet, E., Rhodes, G., & Hayward, W. G. (2007). Opposite aftereffects for Chinese and Caucasian faces are selective for social category information and not just physical face differences. *Quarterly Journal of Experimental Psychology*, *60*, 1457–1467.
- Jaquet, E., Rhodes, G., & Hayward, W. G. (2008). Race-contingent aftereffects suggest distinct perceptual norms for different race faces. *Visual Cognition*, *16*, 734–753.
- Jeffery, L., Rhodes, G., & Busey, T. (2007). Broadly tuned, view-specific coding of face shape: Opposing figural aftereffects can be induced in different views. *Vision Research*, *47*, 3070–3077.
- Lee, K., Byatt, G., & Rhodes, G. (2000). Caricature effects, distinctiveness and identification: Testing the face-space framework. *Psychological Science*, *11*, 379–385.
- Leopold, D. A., Bondar, I., & Giese, M. A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*, *442*, 572–575.
- Leopold, D. A., O’Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89–94.
- Leopold, D. A., Rhodes, G., Müller, K.-M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society of London B*, *272*, 897–904.
- Little, A. C., DeBruine, L. M., & Jones, B. C. (2005). Sex-contingent face aftereffects suggest distinct neural populations code male and female faces. *Proceedings of the Royal Society of London B*, *272*, 2283–2287.
- Little, A. C., DeBruine, L. M., Jones, B. C., & Watt, C. (2008). Category contingent aftereffects for faces of different races, ages and species. *Cognition*, *106*, 1537–1547.
- MacLin, O. H., & Webster, M. A. (2001). Influence of adaptation on the perception of distortions in natural images. *Journal of Electronic Imaging*, *10*, 100–109.
- Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology*, *17*, 1508–1512.
- Reed, S. K. (1972). Pattern recognition and categorization. *Cognitive Psychology*, *3*, 382–407.
- Rhodes, G. (1996). *Superportraits: Caricatures and recognition*. Hove, UK: The Psychology Press.
- Rhodes, G. (2006). The evolution of facial attractiveness. *Annual Review of Psychology*, *57*, 199–226.
- Rhodes, G., Brennan, S., & Carey, S. (1987). Identification and ratings of caricatures: Implications for mental representations of faces. *Cognitive Psychology*, *19*, 473–497.
- Rhodes, G., Evangelista, E., & Jeffery, L. (2009). Orientation sensitivity of face identity aftereffects. *Vision Research*, *49*, 2379–2385.
- Rhodes, G., & Jaquet, E. (2010). Aftereffects reveal that adaptive face-coding mechanisms are selective for race and sex. In R. A. Adams Jr., N. Ambady, K. Nakayama, & S. Shimojo (Eds.), *Social vision* (pp. 347–362). New York: Oxford University Press.
- Rhodes, G., & Jeffery, L. (2006). Adaptive norm-based coding of facial identity. *Vision Research*, *46*, 2977–2987.
- Rhodes, G., Jeffery, L., Clifford, C. W. G., & Leopold, D. A. (2007). The time course of higher level face aftereffects. *Vision Research*, *47*, 2291–2296.
- Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W. G., & Nakayama, K. (2003). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science*, *14*, 558–566.
- Rhodes, G., Jeffery, L., Watson, T., Jaquet, E., Winkler, C., & Clifford, C. W. G. (2004). Orientation-contingent face aftereffects and implications for face coding mechanisms. *Current Biology*, *14*, 2119–2123.
- Rhodes, G., & Leopold, D. A. (in press). Adaptive norm-based coding of face identity. In A. J. Calder, G. Rhodes, M. H. Johnston, & J. V. Haxby (Eds.), *Handbook of face perception*. Oxford, UK: OUP.
- Rhodes, G., Robbins, R., Jaquet, E., McKone, E., Jeffery, L., & Clifford, C. W. G. (2005). Adaptation and face perception: How aftereffects implicate norm-based coding of faces. In C. W. G. Clifford & G. Rhodes (Eds.), *Fitting the mind to the world: Adaptation and*

- aftereffects in high-level vision* (pp. 213–240). Oxford, UK: Oxford University Press.
- Rhodes, G., Watson, T. L., Jeffery, L., & Clifford, C. W. G. (2010). Perceptual adaptation helps us identify faces. *Vision Research*, *50*, 963–968.
- Robbins, R., McKone, E., & Edwards, M. (2007). After-effects for face attributes with different natural variability: Adaptor position effects and neural models. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 570–592.
- Solso, R. L., & McCarthy, J. E. (1981a). Prototype formation of faces: A case of pseudomemory. *British Journal of Psychology*, *72*, 499–503.
- Solso, R. L., & McCarthy, J. E. (1981b). Prototype formation: Central tendency models vs. attribute frequency model. *Bulletin of the Psychonomic Society*, *17*, 10–11.
- Strauss, M. S. (1979). Abstraction of prototype information by adults and 10-month-old infants. *Journal of Experimental Psychology: Human Learning Memory*, *5*, 618–632.
- Tsao, D. Y., & Freiwald, W. A. (2006). What's so special about the average face? *Trends in Cognitive Sciences*, *10*, 391–393.
- Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion and race on face recognition. *Quarterly Journal of Experimental Psychology*, *43A*, 161–204.
- Valentine, T. (2001). Face-space models of face recognition. In M. J. Wenger & J. T. Townsend (Eds.), *Computational, geometric, and process perspectives on facial cognition: Contexts and challenges*. Hillsdale, NJ: Erlbaum.
- Walton, G. E., & Bower, T. G. R. (1993). Newborns form “prototypes” in less than 1 minute. *Psychological Science*, *4*, 203–205.
- Watson, T. L., & Clifford, C. W. G. (2003). Pulling faces: An investigation of the face-distortion aftereffect. *Perception*, *32*, 1109–1116.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural face categories. *Nature*, *428*, 557–560.
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, *6*, 647–653.
- Webster, M. A., Werner, J. S., & Field, D. J. (2005). Adaptation and the phenomenology of perception. In C. W. G. Clifford & G. Rhodes (Eds.), *Fitting the mind to the world: Adaptation and aftereffects in high-level vision* (pp. 241–277). Oxford: Oxford University Press.