The other-species effect in human perceptions of sexual dimorphism using human and macaque faces

P. J. Fraccaro, A. C. Little, C. C. Tigue, J. J. M. O'Connor, K. Pisanski & D. R. Feinberg

Published online: 18 Oct 2013.

Submit your article to this journal ⧉

Article views: 111

View related articles ⧉

Routledge
Taylor & Francis Group

The other-species effect in human perceptions of sexual dimorphism using human and macaque faces

P. J. Fraccaro[1], A. C. Little[2], C. C. Tigue[1], J. J. M. O'Connor[1], K. Pisanski[1], and D. R. Feinberg[1]

[1]Department of Psychology, Neuroscience and Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON, Canada L8S 4L8
[2]School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK

Humans are better able to discriminate among human faces than faces of other species. This difference in perceptual discrimination is known as the "other-species effect". Models of perception have posited that the ultimate functional significance of the other-species effect is a higher discrimination capability within an organism's most familiar and salient stimulus set while attenuating the ability to discriminate amongst unfamiliar stimuli. Here, human participants made masculinity judgements of human and macaque faces manipulated based on either human or macaque sexual dimorphism. Humans were more accurate at identifying masculine/feminine faces in species-congruent than species-incongruent transforms in both human and macaque faces. We observed an other-species effect whereby accuracy (correctly judging masculinized faces as more masculine) was highest for own-species faces. We also found that both men and women were better at judging the sex-typicality of male faces than female faces, regardless of the species of the face or the species of the manipulation. Our findings demonstrate an other-species effect for the perception of sex-typicality among human raters.

Keywords: Own-species bias; Face discrimination.

During infant development, humans typically retain and improve their ability to discriminate among familiar stimuli at some cost to the discrimination of stimuli that are less familiar (Cashon & DeNicola, 2011; Scott, Pascalis, & Nelson, 2007). For example, as human infants age it has been shown that a general ability to discriminate between faces of individuals belonging to different species becomes a more specific ability to discriminate among human faces, faces that are more relevant to human children (Pascalis et al., 2005). In other words, a general ability becomes more specialized for familiar stimuli, whereas unfamiliar stimuli become less able to be discriminated. One proximate mechanism by which this occurs is through differential experience as children receive different levels of exposure to native versus foreign stimuli sets (Scott et al., 2007). This effect of perceptual narrowing specific to important and frequently experienced stimuli in humans' environments occurs in multiple domains, including in the perception of language (Kuhl et al., 2006; Werker & Tees, 2005), the perception of voices across languages (Perrachione & Wong, 2007; Thompson, 1987; Winters, Levi, & Pisoni, 2008), faces (Meissner & Brigham, 2001; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005; Rhodes & Anastasi, 2012), and music (Hannon & Trehub, 2005a, 2005b; Lynch, Eilers, Oller, & Urbano, 1990).

One area in which this effect has been studied is in the development of species-specific discrimination abilities. Preferential looking tasks can be used to assess primates' ability to discriminate faces. In these tasks, familiar and unfamiliar faces are displayed to subjects, and time spent gazing at each face is tracked. Because primates tend to fixate on novel stimuli, attending to an unfamiliar face is interpreted as recognition of the adjacent familiar face. For example, adult humans and rhesus macaques (*Macaca mulatta*) show a novelty preference for own-species faces, suggesting that, by adulthood, facial discrimination abilities are limited to own-species faces (Pascalis & Bachavalier, 1998). In line with perceptual narrowing of abilities, infants have been shown to differentiate the faces of tonkean macaques (*Macaca tonkeana*) at 6 months of age, but lose this ability by 9 months of age (Pascalis et al., 2005). However, infants trained on images of named macaque faces were able to retain their ability to discriminate between macaque faces when 9 months old (Pascalis et al., 2005; Scott & Monesson, 2009). By adulthood, humans are better able to discriminate among own-race faces and own-species faces than they are at discriminating among other-race faces and other-species faces (e.g., Bothwell, Brigham, & Malpass, 1989; Meissner & Brigham, 2001; Pascalis & Bachavalier, 1998). These findings are thought to reflect substantial changes to perceptual systems that take place during the first year of life (Pascalis et al., 2005; Scott & Monesson, 2009).

The own-species advantage in the ability to discriminate among human faces and nonhuman faces is referred to as the "other-species effect". The ultimate functional significance of such effects resulting from perceptual narrowing may be to gain expertise in stimuli that are present in an individual's natal environment while minimizing the cost of learning less relevant perceptual

categories (Lewkowicz & Ghazanfar, 2006; Scott et al., 2007). Although experience in a perceptual category can increase perceptual discrimination within that category, primates may have the ability to discriminate among faces even when raised with no exposure to faces (Sugita, 2008). It is currently unknown whether humans can make similar judgements of other-species faces, compared to own-species faces, with little or no experience doing so. Therefore, we chose to investigate human participants' perceptions of human and macaque faces for facial sex-typicality (reflecting masculinity/femininity, or sexual dimorphism; Perrett et al., 1998), a dimension of facial variability relevant to the perception of facial attractiveness (see, for reviews, Feinberg, 2008; Little, Jones, & DeBruine, 2011; Rhodes, 2006), voting decisions (Little, Burriss, Jones, & Roberts, 2007), trustworthiness (Perrett et al., 1998; Smith et al., 2009), and many other socially relevant decisions. Thus, whereas past studies have tested for a disparity in recognition of the general identity of faces (e.g., Bothwell et al., 1989; Pascalis & Bachavalier, 1998), here we test for a similar disparity in recognition of the sex typicality of faces.

Individuals can be differentiated on the basis of facial characteristics (Haxby, Hoffman, & Gobbini, 2002; Kaminski, Dridi, Graff, & Gentaz, 2009; Morton, Johnson, & Maurer, 1990; Nelson & Ludemann, 1989; Schultz, 2005). One way in which human and nonhuman primate faces differ between individuals is the degree to which a face appears sex-typical or sex-atypical (Perrett et al., 1998). Within and between sexes, some faces appear more morphologically male-typical whereas others appear more female-typical. Research on the facial growth of nonhuman primate species suggests that these changes come about as a result of both ontogenetic scaling and divergence in male and female growth trajectories (O'Higgins & Collard, 2002). Male and female human faces differ in a number of ways (Bulygina, Mitteroecker, & Aiello, 2006). For example, female faces are flatter, with larger lips and smaller noses, when compared to male faces (Hennessy, Kinsella, & Waddington, 2002). In addition, the jaw, eyes and brows, and chin affect the perception of gender in faces (Brown & Perrett, 1993). Prior research on the other-species effect has only been able to determine whether the species of a face affects our ability to discriminate between individual faces. For example, Pascalis et al. (2002) investigated humans' ability to discriminate human and monkey faces, finding that monkey faces were less easily discriminated in adulthood compared to human faces. Another proximate mechanism for the other species effect is not visual experience with the species itself, but visual experience with the way features vary in other species. For example, learning a new category of faces may be aided by gaining experience with the way in which faces differ between the sexes (e.g., shape; Perrett et al., 1998), as well as the way in which faces vary during the production of various emotional expressions (e.g., de Gelder & Vroomen, 2000; Kaufmann & Schweinberger, 2004; cf. Fox, Oruç, & Barton, 2008). For example, the facial characteristics that set apart males and females (in addition to more general

individual differences in facial characteristics) may be encoded and used to categorize faces by sex or perceived sex-typicality. This is important because face perception is thought to be prototype based (Valentine et al., 1991). Furthermore, face aftereffects are larger when the orientation or category (e.g., sex, ethnicity) of the faces are congruent in the adaptation and test phases than when they are incongruent, suggesting a degree of neural specificity in the coding of face subcategories (Little, DeBruine, & Jones, 2005; Little, DeBruine, Jones, & Waitt, 2008; Rhodes et al., 2004; Webster & MacLeod, 2011).

Advances in computer technology have led to the development of computer software for manipulating face shape (Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001). This software enables the objective and systematic manipulation of sex-typicality in face shape (Perrett et al., 1998), and has been successfully applied in previous work on face perception (see, e.g., DeBruine, Jones, Smith, & Little, 2010; Jones, DeBruine, et al., 2010; Jones, Main, DeBruine, Little, & Welling, 2010). Additionally, the software is capable of quantifying the differences between male and female faces of one species, and using these differences to transform faces of a separate species. Here, we have used this technique to assess a novel topic: whether the other-species effect observed in the perception of faces is affected not only by the species of the faces viewed, but also the way in which the faces differ between the sexes of each species.

To test human raters' discrimination ability for sex-typical features in human and macaque faces, we manufactured four sets of faces varying in sex-typical face shape, with either a congruent or incongruent sexual dimorphism manipulation (Figure 1): (a) macaque faces manipulated by macaque sexual dimorphism, (b) macaque faces manipulated by human sexual dimorphism, (c) human faces manipulated by macaque sexual dimorphism, and (d) human faces manipulated by human sexual dimorphism. Previous studies suggest that human raters can reliably discriminate naturally occurring sexual dimorphism of macaque faces (e.g., Little, DeBruine, et al., 2008; Little, Jones, et al., 2008). Indeed, research suggests that the way in which humans and macaques process faces may be quite similar (Adachi, Chou, & Hampton, 2009; Dahl, Wallraven, Bülthoff, & Logothetis, 2009; Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003; for review, see Yovel & Freiwald, 2013). For example, humans and rhesus macaques both preferentially attend to the eye regions of faces (Guo et al., 2003), are impeded in recognizing inverted and "Thatcherized" faces (Adachi et al., 2009), and may employ similar holistic processing of faces (Dahl et al., 2009).

Here, sex-typicality was manipulated using systematic and objective methods (see the Stimuli section). It is apparent from our stimuli that several similarities exist between human and macaque sexual dimorphism. For example, increasing male-typicality of faces using either macaque sexual dimorphism or human sexual dimorphism increased jaw size, mouth width, and midpoint width, and
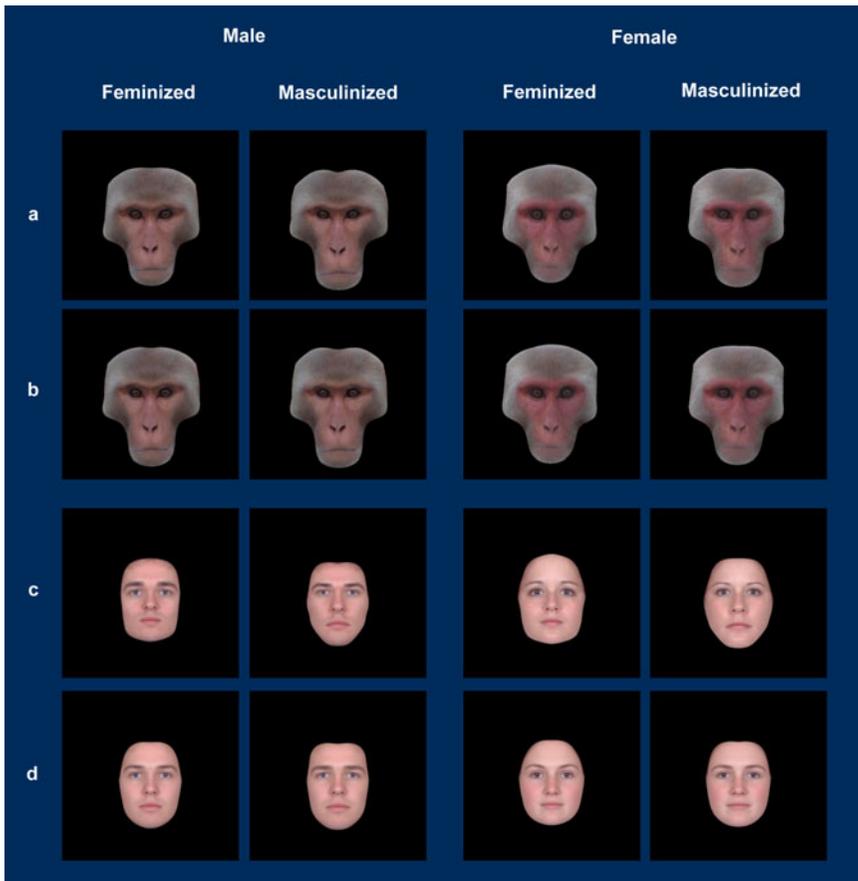
Figure 1.   The types of stimuli used in the experiment: (a) macaque faces manipulated by macaque sexual dimorphism, (b) macaque faces manipulated by human sexual dimorphism, (c) human faces manipulated by macaque sexual dimorphism, and (d) human faces manipulated by human sexual dimorphism. To view this figure in colour, please see the online issue of the Journal.

decreased eye size of the resulting image. By contrast, images manipulated with macaque sexual dimorphism displayed increased angularity of the jaw line and midpoint (see Figure 1). Because there is some overlap between human and macaque dimorphism, humans using a template of human facial sex-typicality to assess macaque faces may perform at above-chance levels with no experience viewing macaque faces. Therefore, following Sugita (2008), we also predicted that humans would be able to discriminate between instances of both human and macaque faces at levels above chance. Although similarities in sexually dimorphic features between the species may aid in judgements of sex-typicality, we predicted that participants would make more accurate judgements overall

when viewing human stimuli than macaque stimuli, owing to their increased experience with human faces (Cashon & DeNicola, 2011).

METHODS

Stimuli

For the human images, white male ($n = 50$) and white female ($n = 50$) participants had their photographs taken in the laboratory with a digital camera under standardized lighting conditions. Participants were asked to pose with a neutral expression and to look directly into the camera to produce front-on facial photographs. Participants were asked not to smile and to relax their face during photographs. All individuals were less than 30 years old and were randomly selected from a larger face set. Participants were UK-based university students who volunteered to take part in psychology studies.

For the macaque images, a digital video camera was used to capture images of adult males ($n = 45$) and females ($n = 45$) from the free-ranging population of rhesus macaques on Cayo Santiago, Puerto Rico. Only full-face images with neutral expressions were used, taken from video footage. All individuals were young adults and were randomly selected from a larger face set. Images were collected from Cayo Santiago field station, the Primate Ecology Section of the National Institutes of Health Laboratory of Perinatal Physiology, which abides by US laws and practices in the ethical treatment of animals. All images were standardized for interpupillary distance and cropped to a standard size with a standardized background.

Creating male and female composites.   A composite of male and female faces was made for humans and macaques separately for each sex and species. All respective images were used to create each composite (i.e., 50 each for male and female humans; 45 each for male and female macaques). For each set of face images a single composite face was produced reflecting the average shape and colour of the constituent images. The composite faces were created using Psychomorph, specially designed face manipulation software. Key locations (174 points) were manually marked around the main features and the outline of each face. The average location of each point in the faces for each composite was then calculated. The features of the individual faces were then morphed to the relevant average shape before superimposing the images to produce a photographic quality result. For more information on this technique, see Benson and Perrett (1993), Perrett et al. (1998), and Tiddeman et al. (2001). Because facial symmetry may be associated with facial sex-typicality (see, e.g., Little, Jones, et al., 2008; Scheib, Gangestad, & Thornhill, 1999; but see Koehler, Simmons, Rhodes, & Peters, 2004; Van Dongen, 2012), all images were then made perfectly symmetric.

Transforming the images based on facial sexual dimorphism. Base composite faces were created on which transforms were applied. For each face type (human male, human female, macaque male, macaque female), five target faces were created (i.e., faces on which a manipulation was later applied). These were made from five images each for human faces and four images each for macaque faces. The overall composites (50 human male/female, 45 macaque male/female) were used as end points to transform composite target faces. The five target faces were created using a random five images for humans and four images for macaques drawn from the pool of images used to create the overall composites. In total, 20 target composite images were created as base faces (five for each of human male, macaque male, human female, and macaque female) using the methods described previously. Using composites of multiple identities as target faces as opposed to one average image allows us to maintain separate identities for each of the stimuli, while representing a relatively large portion of natural variation in sex-typicality, whilst reducing the appearance of anomalous facial features (Perrett et al., 1994; Tiddeman et al., 2001). We can also eliminate the potential effects of an anomalous stimulus by using a repeated measures design. All stimuli were manipulated using established techniques for manipulating the appearance of face images in an objective, systematic manner (for technical details including mathematical algorithms, see Rowland & Perrett, 1995, and Tiddeman et al., 2001). To address the effect of starting sex on judgements, we included both male and female stimuli. Because skin colour is sexually dimorphic in humans (e.g., Correnti, Testa-Bappenheim, & Granata, 1964; for review, see Madrigal & Kelly, 2007) and macaques (Waitt et al., 2003), we used shape-only transformations to create our stimuli. Next, ±50% of the differences in linear two-dimensional shape between the male and female averages are applied to a third target face (here, our composite faces of either species). This method quantifies the differences in linear two-dimensional face shape between the male and female facial averages for a given species. Consequently, we can move landmark points on a third face towards the exact locations on the female average or male average face, thus manipulating the degree of sex-typicality in two-dimensional face shape. For each of the 20 target faces, two transforms were applied: (1) the linear shape difference between human male and female faces and (2) the linear shape difference between macaque male and female faces. This resulted in 80 faces in total (five for each example image in Figure 1). Transformations were ±50% of the difference between male and female composite images described earlier. This created four shape-transformed versions of each target face: species congruent +50% sex-typical, species congruent −50% sex-typical, species incongruent +50% sex-typical, and species incongruent −50% sex-typical. Transforming facial sexual dimorphism in this way (i.e., using between-sex differences in facial morphology) produces the same result as alternative manipulation methods, such as using pre- and postpubertal differences, and differences in perceived masculinity

and femininity (DeBruine et al., 2006). All images were standardized for size on interpupillary distance prior to transformation. Images were also cropped around the face outline to display only facial information, as nonface cues can alter the perception of facial sex-typicality (DeBruine et al., 2010). This technique has been successfully applied in many other studies of face perception (e.g., DeBruine et al., 2006; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Perrett et al., 1998).

Procedure

Experimental protocols were approved by the McMaster Research Ethics Board. Seventy-four women (mean age ± SD = 19.12 ± 2.92) and 95 men (mean age ± SD = 18.91 ± 2.08) were recruited in exchange for course credit. Sex-typical and sex-atypical stimuli were presented in a two-alternative forced-choice paradigm. On each trial, a masculinized and feminized face of the same composite were presented side by side and participants were instructed to "choose the face that looks more masculine" (i.e., male-typical). Each stimulus pair belonged to the same species and sex. Participants made five sex-typicality judgements for each stimulus type (e.g., female human face with macaque sex-typicality manipulation), resulting in 40 judgements in total (one judgement for each pair of the 80 stimuli). The number of correct judgements (i.e., male-typical faces chosen) of each stimulus type were averaged across faces within each manipulation type. Therefore, high scores indicate that a participant was highly accurate in their judgements of sex-typicality. The order of trials and the side of screen presentation were fully randomized.

RESULTS

We conducted a mixed-design repeated-measures ANOVA with three within-subjects factors, with two levels each: species of target face (human or macaque), species of manipulation (human or macaque), and sex of face (male or female). We also entered a between-subjects factor: sex of rater (male or female) (see Table 1). The ANOVA uncovered a main effect of sex of face whereby participants demonstrated better accuracy in discriminating the sex-typicality of male faces than female faces, $F(1, 167) = 19.05$, $MSE = 1.303$, $p < .001$, partial $\eta^2 = .10$.

As predicted by the relative expertise that human raters have with human faces versus macaque faces, we found a main effect of species of target face whereby participants were more accurate in discriminating sex-typicality among human faces than among macaque faces, $F(1, 167) = 75.39$, $MSE = 2.13$, $p < .001$, partial $\eta^2 = .31$. The ANOVA also indicated a main effect of species of manipulation whereby participants were more accurate in discriminating sex-typicality when the manipulation used was based on macaque sex-typicality than

TABLE 1
Results from a repeated-measures ANOVA including all factors of interest

Effect	F (1, 167)	P-value	Effect size (partial η^2)
Sex of rater	0.586	.445	.003
Sex of face	19.053	<.001***	.102
Sex of face × Sex of rater	0.068	.749	<.001
Species of target face	75.393	<.001***	.311
Species of target face × Sex of rater	0.358	.550	.002
Species of manipulation	4.749	.031*	.028
Species of manipulation × Sex of rater	0.180	.672	<.001
Sex of face × Species of target face	7.588	.007*	.043
Sex of face × Species of target face × Sex of rater	0.033	.856	<.001
Sex of face × Species of manipulation	3.737	.055†	.022
Sex of face × Species of manipulation × Sex of rater	0.045	.832	.000
Species of target face × Species of manipulation	119.462	<.001***	.417
Species of target face × Species of manipulation × Sex of rater	2.895	.091	.017
Sex of face × Species of target face × Species of manipulation	5.195	.024*	.030
Sex of face × Species of target face × Species of manipulation × Sex of rater	19.658	<.001***	.105

***$p < .001$, **$p < .01$, *$p < .05$.

human sex-typicality, $F(1, 167) = 4.75$, $MSE = 2.18$, $p = .031$, partial $\eta^2 = .028$. The ANOVA also uncovered a number of significant interactions: (1) between sex of face and species of target face, $F(1, 167) = 7.59$, $MSE = 1.02$, $p = .007$, partial $\eta^2 = .043$, indicating a larger other-species effect (i.e., more accurate discrimination of human target faces relative to macaque faces) when judging female faces than male faces, $t(168) = 2.76$, $p = .006$, Cohen's $d = 0.24$; (2) between sex of face and species of manipulation, $F(1, 167) = 3.74$, $MSE = 1.15$, $p = .055$, partial $\eta^2 = .02$, indicating a larger difference in accuracy between human and macaque sex-typicality when judging male faces than female faces, $t(168) = 1.98$, $p = .049$, Cohen's $d = 0.28$; (3) between species of target face and species of manipulation, $F(1, 167) = 119.46$, $MSE = 2.00$, $p < .001$, partial $\eta^2 = .42$, indicating participants were more accurate at judging faces that were congruent for species of manipulation and species of target face than faces that were incongruent, $t(168) = 10.74$, $p < .001$, Cohen's $d = 1.060$; (4) among sex of face, species of target face, and species of manipulation, $F(1, 167) = 5.20$, $MSE = 0.946$, $p = .024$, partial $\eta^2 = .03$, indicating that the above congruency effect was larger for judgements of men's faces than women's faces; (5) a marginally significant three-way interaction among sex of rater, species of face, and species of manipulation, $F(1, 167) = 2.90$, $MSE = 2.00$, $p = .091$, partial $\eta^2 = .017$, indicating that the previous congruency effect was larger for male raters than female raters; and (6) a significant four-way interaction among sex of rater, sex of face, species of target face, and species of manipulation, $F(1, 167) = 19.66$, $MSE = 0.946$, $p < .001$,

partial $\eta^2 = .11$, suggesting that this sex-by-congruency effect is larger for female raters than for male raters. We did not find a significant between-subjects main effect of rater sex on sexual dimorphism judgements, $F(1, 167) = 1.70$, $MSE = 2.90$, $p = .45$, partial $\eta^2 = .003$. There were no other effects or interactions, all Fs < 0.36, all ps > .55.

In order to determine whether the main effect of sex of face occurred in the perception of both species, we conducted separate ANOVAs for each stimulus type (see Table 2). Each ANOVA contained the within-subjects factor sex of face, and the between-subjects factor sex of rater. For human faces with human sexual dimorphism manipulation, the ANOVA indicated a main effect of sex of face, $F(1, 167) = 4.30$, $MSE = 0.697$, $p = .040$, partial $\eta^2 = .025$, a two-way interaction between sex of rater and sex of face, $F(1, 167) = 7.02$, $MSE = 0.697$, $p = .009$, partial $\eta^2 = .040$, and a between-subjects effect of sex of rater, $F(1, 167) = 6.79$, $MSE = 1.321$, $p = .025$, partial $\eta^2 = .030$. For human faces with macaque sexual dimorphism manipulation, a separate ANOVA similarly indicated a main effect of sex of face, $F(1, 167) = 40.00$, $MSE = 0.908$, $p < .001$, partial $\eta^2 = .193$, a two-way interaction between sex of face and sex of rater, $F(1, 167) = 5.97$, $MSE = 0.908$, $p = .016$, partial $\eta^2 = .035$, but no between-subjects effect of sex of rater, $F(1, 167) = 0.05$, $MSE = 3.67$, $p = .824$. A separate

TABLE 2
Results from repeated-measures ANOVAs performed for each stimulus type

Stimulus type	Effect	F(1, 167)	P-value	Effect size (partial η^2)
Human target faces with human manipulation	Sex of face	4.303	.040*	.025
	Sex of rater	5.145	.025*	.030
	Sex of face × Sex of rater	7.018	.009**	.040
Human target faces with macaque manipulation	Sex of face	39.998	<.001***	.193
	Sex of rater	0.050	.824	<.001
	Sex of face × Sex of rater	5.969	.016*	.035
Macaque target faces with human manipulation	Sex of face	0.894	.346	.005
	Sex of rater	0.265	.607	.002
	Sex of face × Sex of rater	3.385	.068	.020
Macaque target faces with macaque manipulation	Sex of face	0.839	.361	.005
	Sex of rater	0.488	.486	.003
	Sex of face × Sex of rater	2.550	.112	.015

***$p < .001$, **$p < .01$, *$p < .05$.

ANOVA for macaque faces with human sexual dimorphism manipulation indicated a marginally significant two-way interaction between sex of face and sex of rater, $F(1, 167) = 3.39$, $MSE = 1.53$, $p = .068$, partial $\eta^2 = .020$, but no other significant effects or interactions, all $Fs < 0.894$, all $ps > .346$. No significant effects or interactions were detected in a separate ANOVA conducted for macaque faces with macaque sexual dimorphism manipulation, all $Fs < 3.25$, all $ps > .112$. These findings suggest that the greater accuracy in sexual dimorphism judgements in male faces than female faces may be relatively specific to human faces.

DISCUSSION

Our study demonstrates that individuals were more often correct in judging masculinized faces as more masculine for own-species faces, indicating an own-species effect for the judgement of sex-typicality. Previous studies have suggested that the other-species effect occurs due to visual experience (Mondloch, Maurer, & Ahola, 2006; Pascalis et al., 2005). Our data are consistent with a new other-species bias in the perception of macaque faces. This effect may contribute to—or act independently of—biases in the recognition and discrimination of other-species faces. We show that the other-species effect is not only influenced by the species of the face itself, but is also related to the way in which male and female faces differ in each species: Individuals were more accurate at identifying masculinity in species-congruent than -incongruent transforms in both human and macaque faces. Thus, visual experience with the way facial features vary between sexes in other species (i.e., between-sex variability in facial morphology) may play a relatively minor role in the other-species effect observed in the perception of heterospecific faces. It is possible that the way faces differ within species in other domains, such as the way in which faces vary during the production of various emotional expressions (Kaufmann & Schweinberger, 2004; cf. Fox et al., 2008), accounts for some variance in the perception of other-species faces versus own-species faces.

Participants were more accurate in identifying facial masculinity in humans than macaques. Because experience facilitates facial discrimination ability (e.g., Pascalis et al., 2005), this result is likely a consequence of human participants' greater expertise with human faces than with macaque faces. Furthermore, this result is in line with previous findings suggesting that primates have better perceptual discrimination abilities when viewing their own-species versus another species. For example, both humans and monkeys are more accurate at recognizing individual faces of their own species versus other species (Dufour, Pascalis, & Petit, 2006), and infants prefer to view same-species faces over other-species faces (Pascalis et al., 2002). We also discovered an effect of species of manipulation, whereby participants were more accurate in identifying masculinity when the

manipulation used was based on macaque sexual dimorphism than human sexual dimorphism. It is possible that this effect is due to a higher degree of sexual dimorphism between the sexes in macaque faces than human faces. For example, sexual dimorphism in body weight, and mandible and maxilla size is lower in humans than in rhesus macaques (Plavcan & van Schaik, 1997). Further, this effect was much smaller than the effect of species of target face (species of target face partial η^2 = .31; species of manipulation partial η^2 = .028). We can infer from these effect sizes that the species of a target face impacts the perception of sex-typicality in primate faces to a greater extent than the way in which faces differ between the sexes in a given species. This finding constitutes an important increase in knowledge, as it broadens our understanding of how the way faces differ affects our ability to discriminate among them.

Newborn humans prefer their mother's face to the face of a stranger shortly after birth (Bushneil, Sai, & Mullin, 2011) and infants discriminate female faces better and attend to them more than male faces (Quinn, Yahr, Kuhn, Salter, & Pascalis, 2002). Similarly, infant rhesus macaques preferentially orient towards, and show significantly more lipsmacking behaviour towards female faces than male faces (a social gesture of affiliation or appeasement; Paukner, Huntsberry, & Suomi, 2010). The higher accuracy in discriminating among men's faces in adult humans found here may reflect a change in the developmental trajectory of face processing. At birth and during infancy, mothers' faces are extremely important for survival, whereas men's faces are less important during infancy. Several other studies have also found that adults demonstrated higher accuracy in identifying the sex-typicality of men's than women's faces (e.g., Fink, Neave, & Seydel, 2007; Watkins et al., 2010). Future research may help clarify whether these findings reflect a general shift in discriminatory ability of male and female faces from infancy to adulthood.

In summary, we have explored the independent contributions of the species of face and species-typical sexual dimorphism on the other-species effect. Our study provides the first evidence to suggest that, although the species of face contributes more to the other-species effect than the way in which faces differ between the sexes of a particular species, species-typical facial sexual dimorphism also plays a key role in face discrimination. The relatively high degree of accurate sex-typicality judgements in both species suggests that the way in which male and female faces differ in a particular species may be conserved to some degree across primate taxa. Similarities in facial morphology among primates are hypothesized to reflect functional modifications for the chewing of highly resistant food and the production of emotions (Burrows, 2008; Preuschoft, 2000; Strait et al., 2008) as well as demonstrating mate-choice relevant qualities to members of the opposite sex (e.g., colour: Fink, Grammar, & Thornhill, 2001; Waitt et al., 2003; symmetry: Perrett et al., 1999; Rhodes, Proffitt, Grady, & Sumich, 1998; Waitt & Little, 2006). Thus, the characteristics used to perceive

sex-typicality in humans and macaque faces may be similar. Finally, we show for the first time that humans are better at discriminating between sex-typical and -atypical face pairs when the faces are male than female, and that this bias may be relatively specific to human faces.

REFERENCES

Adachi, I., Chou, D. P., & Hampton, R. R. (2009). Thatcher effect in monkeys demonstrates conservation of face perception across primates. *Current Biology*, *19*(15), 1270–1273. doi:10.1016/j.cub.2009.05.067

Benson, P. J., & Perrett, D. I. (1993). Extracting prototypical facial images from exemplars. *Perception*, *22*(3), 257–262. doi:10.1068/p220257

Bothwell, R., Brigham, J., & Malpass, R. (1989). Cross-racial identification. *Personality and Social Psychology Bulletin*, *15*(1), 19–25. doi:10.1177/0146167289151002

Brown, E., & Perrett, D. I. (1993). What gives a face its gender? *Perception*, *22*(7), 829–840. doi:10.1068/p220829

Bulygina, E., Mitteroecker, P., & Aiello, L. (2006). Ontogeny of facial dimorphism and patterns of individual development within one human population. *American Journal of Physical Anthropology*, *131*, 432–443.

Burrows, A. M. (2008). The facial expression musculature in primates and its evolutionary significance. *BioEssays*, *30*(3), 212–225. doi:10.1002/bies.20719

Bushneil, I. W. R., Sai, F., & Mullin, J. T. (2011). Neonatal recognition of the mother's face. *British Journal of Developmental Psychology*, *7*(1), 3–15.

Cashon, C. H., & DeNicola, C. A. (2011). Is perceptual narrowing too narrow? *Journal of Cognition and Development*, *12*, 159–162. doi:10.1080/15248372.2011.563483

Correnti, V., Testa-Bappenheim, I., & Granata, G. (1964). Riflettometria del colore della pelle e dei capelli in soggetti palermitani. *Zeitschrift für Morphologie und Anthropologie*, *56*, 118–131.

Dahl, C. D., Wallraven, C., Bülthoff, H. H., & Logothetis, N. (2009). Humans and macaques employ similar face-processing strategies. *Current Biology*, *19*(6), 509–513. doi:10.1016/j.cub.2009.01.061

DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., … Tiddeman, B. P. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society: Biological Sciences*, *273B*, 1355–1360. doi:10.1098/rspb.2005.3445

DeBruine, L. M., Jones, B. C., Smith, F. G., & Little, A. C. (2010). Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(3), 751–758. doi:10.1037/a0016457

de Gelder, B., & Vroomen, J. (2000). The perception of emotions by ear and eye. *Cognition and Emotion*, *14*(3), 289–311. doi:10.1080/026999300378824

Dufour, V., Pascalis, O., & Petit, O. (2006). Face processing limitation to own species in primates: A comparative study in brown capuchins, Tonkean macaques and humans. *Behavioural Processes*, *73*(1), 107–113. doi:10.1016/j.beproc.2006.04.006

Feinberg, D. R. (2008). Are human faces and voices ornaments signaling common underlying cues to mate value? *Evolutionary Anthropology: Issues, News, and Reviews*, *17*, 112–118. doi:10.1002/evan.20166

Fink, B., Grammer, K., & Thornhill, R. (2001). Human (Homo sapiens) facial attractiveness in relation to skin texture and colour. *Journal of Comparative Psychology*, *115*(1), 92–99. doi:10.1037/0735-7036.115.1.92

Fink, B., Neave, N., & Seydel, H. (2007). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, *19*, 82–87. doi:10.1002/ajhb.20583

Fox, C. J., Oruç, İ., & Barton, J. J. S. (2008). It doesn't matter how you feel: The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision*, *8*(3), 1–13. doi:10.1167/8.3.11

Guo, K., Robertson, R. G., Mahmoodi, S., Tadmor, Y., & Young, M. P. (2003). How do monkeys view faces?—A study of eye movements. *Experimental Brain Research*, *150*, 363–374.

Hannon, E. E., & Trehub, S. E. (2005a). Metrical categories in infancy and adulthood. *Psychological Science*, *16*(1), 48–55.

Hannon, E. E., & Trehub, S. E. (2005b). Tuning in to musical rhythms: Infants learn more readily than adults. *Proceedings of the National Academy of Sciences*, *102*, 12639–12643. doi:10.1073/pnas.0504254102

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, *51*(1), 59–67.

Hennessy, R. J., Kinsella, A., & Waddington, J. L. (2002). 3D laser surface scanning and geometric morphometric analysis of craniofacial shape as an index of cerebro-craniofacial morphogenesis: Initial application to sexual dimorphism. *Biological Psychiatry*, *51*(6), 507–516. doi:10.1016/S0006-3223(01)01327-0

Jones, B. C., DeBruine, L. M., Main, J. C., Little, A. C., Welling, L. L. M., Feinberg, D. R., & Tiddeman, B. P. (2010). Facial cues of dominance modulate the short-term gaze-cuing effect in human observers. *Proceedings of the Royal Society of London*, *277B*, 617–624. doi:10.1098/rspb.2009.1575

Jones, B. C., Main, J. C., DeBruine, L. M., Little, A. C., & Welling, L. L. M. (2010). Reading the look of love: Sexually dimorphic cues in opposite-sex faces influence gaze-categorization. *Psychological Science*, *21*(6), 796–798. doi:10.1177/0956797610370756

Kaminski, G., Dridi, S., Graff, C., & Gentaz, E. (2009). *Proceedings of the Royal Society B*, *276* (1670), 3193–3200.

Kauffman, J. M., & Schweinberger, S. R. (2004). Expression influences the recognition of familiar faces. *Perception*, *33*(4), 399–408. doi:10.1068/p5083

Koehler, N., Simmons, L. W., Rhodes, G., & Peters, M. (2004). The relationship between sexual dimorphism in human faces and fluctuating asymmetry. *Proceedings of the Royal Society: Biological Sciences*, *271B*(Suppl. 4), S233–S236. doi:10.1098/rsbl.2003.0146

Kuhl, P. K., Stevens, E., Hayashi, A., Degushi, T., Kiritani, S., & Iverson, P. (2006). Infants show a facilitation effect for native language phonetic perception between 6 and 12 months. *Developmental Science*, *9*(2), F13–F21. doi:10.1111/j.1467-7687.2006.00468.x

Lewkowicz, D. J., & Ghazanfar, A. A. (2006). The decline of cross-species intersensory perception in human infants. *Proceedings of the National Academy of Sciences of the USA*, *103*(17), 6771–6774. doi:10.1073/pnas.0602027103

Little, A. C., Burriss, R. P., Jones, B. C., & Roberts, S. C. (2007). Facial appearance affects voting decisions. *Evolution and Human Behavior*, *28*(1), 18–27. doi:10.1016/j.evolhumbehav.2006.09.002

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*, *272B* (1), 1–5.

Little, A. C., DeBruine, L. M., Jones, B. C., & Waitt, C. (2008). Category contingent aftereffects for faces of different races, ages and species. *Cognition*, *106*, 1537–1547. doi:10.1016/j.cognition.2007.06.008

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011). Facial attractiveness: Evolutionary based research. *Philosophical Transactions of the Royal Society*, *366B*, 1638–1659. doi:10.1098/rstb.2010.0404

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society: Biological Sciences*, *269B* (1496), 1095–1100. doi:10.1098/rspb.2002.1984

Little, A. C., Jones, B. C., Waitt, C., Tiddeman, B. P., Feinberg, D. R., Perrett, D. I., … Marlowe, F. (2008). Symmetry is related to sexual dimorphism in faces: Data across culture and species. *PLoS ONE*, *3*(5), e2106. doi:10.1371/journal.pone.0002106

Lynch, M. P., Eilers, R. E., Oller, D. K., & Urbano, R. C. (1990). *Psychological Science*, *1*(4), 272–276.

Madrigal, L., & Kelly, W. (2007). Human skin-color sexual dimorphism: A test of the sexual selection hypothesis. *American Journal of Physical Anthropology*, *132*(3), 470–482. doi:10.1002/ajpa.20453

Meissner, C. A., & Brigham, J. C. (2001). Thirty years of investigating the own-race bias in memory for faces—a meta-analytic review. *Psychology, Public Policy, and Law*, *7*, 3–35. doi:10.1037/1076-8971.7.1.3

Mondloch, C. J., Maurer, D., & Ahola, S. (2006). Becoming a face expert. *Psychological Science*, *17* (11), 930–934. doi:10.1111/j.1467-9280.2006.01806.x

Morton, J., Johnson, M. H., & Maurer, D. (1990). *Infant Behavior & Development*, *13*(1), 99–103.

Nelson, C. A., & Ludemann, P. M. (1989). Past, current, and future trends in infant face perception research. *Canadian Journal of Psychology/Revue Canadienne de psychologie*, *43*(2), 183–198.

O'Higgins, P., & Collard, M. (2002). Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology*, *257*(2), 255–272. doi:10.1017/S0952836902000857

Pascalis, O., & Bachevalier, J. (1998). Face recognition in primates: A cross-species study. *Behavioural Processes*, *43*, 87–96. doi:10.1016/S0376-6357(97)00090-9

Pascalis, O., de Haan, M., & Nelson, C. A. (2002). Is face processing species-specific during the first year of life? *Science*, *296*, 1321–1323. doi:10.1126/science.1070223

Pascalis, O., Scott, L. S., Kelly, D. J., Shannon, R. W., Nicholson, E., Coleman, M., & Nelson, C. A. (2005). Plasticity of face processing in infancy. *Proceedings of the National Academy of Sciences*, *102*, 5297–5300. doi:10.1073/pnas.0406627102

Paukner, A., Huntsberry, M. E., & Suomi, S. J. (2010). Visual discrimination of male and female faces by infant rhesus macaques. *Developmental Psychobiology*, *52*(1), 54–61.

Perrachione, T. K., & Wong, P. C. M. (2007). Learning to recognize speakers of a non-native language: Implications for the functional organization of human auditory cortex. *Neuropsychologia*, *45*(8), 1899–1910. doi:10.1016/j.neuropsychologia.2006.11.015

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. A. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, *20*(5), 295–307. doi:10.1016/S1090-5138(99)00014-8

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., … Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*, 884–887. doi:10.1038/29772

Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgments of female attractiveness. *Nature*, *368*, 239–242.

Plavcan, J. M., & van Schaik, C. P. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of Human Evolution*, *32*, 345–374. doi:10.1006/jhev.1996.0096

Preuschoft, S. (2000). Primate faces and facial expressions. *Social Research*, *67*(1), 245–271.

Quinn, P. C., Yahr, J., Kuhn, A., Slater, A. M., & Pascalis, O. (2002). Representation of the gender of human faces by infants: a preference for female. *Perception*, *31*(9), 1109–1121.

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, *57*, 199–226.

Rhodes, G., Jeffery, L., Watson, T. L., Jaquet, E., Winkler, C., & Clifford, C. W. G. (2004). Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology*, *14*, 2119–2123. doi:10.1016/j.cub.2004.11.053

Rhodes, G., Proffitt, F., Grady, J. M., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin and Review*, *5*(4), 659–669. doi:10.3758/BF03208842

Rhodes, M. G., & Anastasi, J. S. (2012). The own-age bias in face recognition: A meta-analytic and theoretical review. *Psychological Bulletin*, *138*, 146–174. doi:10.1037/a0025750

Rowland, D. A., & Perrett, D. I. (1995). Manipulating facial appearance through shape and colour. *IEEE Computer Graphics and Applications*, *15*(5), 70–76. doi:10.1109/38.403830

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society: Biological Sciences*, *266B*(1431), 1913–1917. doi:10.1098/rspb.1999.0866

Schultz, R. T. (2005). Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience*, *23*, 125–141.

Scott, L. S., & Monesson, A. (2009). The origin of biases in face perception. *Psychological Science*, *20*, 676–680. doi:10.1111/j.1467-9280.2009.02348.x

Scott, L. S., Pascalis, O., & Nelson, C. A. (2007). A domain-general theory of the development of perceptual discrimination. *Current Directions in Psychological Science*, *16*(4), 197–201. doi:10.1111/j.1467-8721.2007.00503.x

Smith, F. G., Jones, B. C., Welling, L. L. M., Little, A. C., Vukovic, J., Main, J. C., & DeBruine, L. M. (2009). Waist-hip ratio predicts women's preferences for masculine male faces, but not perceptions of men's trustworthiness. *Personality and Individual Differences*, *47*, 476–480. doi:10.1016/j.paid.2009.04.022

Strait, D. S., Wright, B. W., Richmond, B. G., Ross, C. F., Dechow, P. C., Spencer, M. A., & Wang, Q. (2008). Craniofacial strain patterns during premolar loading: Implications for human evolution. In C. Vinyard, M. J. Ravosa, & C. Wall (Eds.), *Primate craniofacial function and biology* (pp. 173–198). New York, NY: Springer.

Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences of the USA*, *105*, 394–398. doi:10.1073/pnas.0706079105

Thompson, C. P. (1987). A language effect in voice discrimination. *Applied Cognitive Psychology*, *1*(2), 121–131. doi:10.1002/acp.2350010205

Tiddeman, B., Burt, M., & Perrett, D. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications*, *21*(5), 42–50. doi:10.1109/38.946630

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Quarterly Journal of Experimental Psychology*, *43A*, 161–204.

Van Dongen, S. (2012). Fluctuating asymmetry and masculinity/femininity in humans: A meta-analysis. *Archives of Sexual Behavior*, *41*(6), 1453–1460. doi:10.1007/s10508-012-9917-7

Waitt, C., & Little, A. C. (2006). Preferences for symmetry in conspecific facial shape among Macaca mulatta. *International Journal of Primatology*, *27*(1), 133–145.

Waitt, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M., & Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London: Biological Sciences*, *270B* (Suppl. 2), S144–S146. doi:10.1098/rsbl.2003.0065

Watkins, C. D., Fraccaro, P. J., Smith, F. G., Vukovic, J., Feinberg, D. R., DeBruine, L. M., & Jones, B. C. (2010). Taller men are less sensitive to cues of dominance in other men. *Behavioral Ecology*, *21*, 943–947. doi:10.1093/beheco/arq091

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society of London*, *366B*(1571), 1702–1725. doi:10.1098/rstb.2010.0360

Werker, J. F., & Tees, R. C. (2005). Speech perception as a window for understanding plasticity and commitment in language systems of the brain. *Developmental Psychobiology*, *46*, 233–251. doi:10.1002/dev.20060

Winters, S. J., Levi, S. V., & Pisoni, D. B. (2008). Identification and discrimination of bilingual talkers across languages. *Journal of the Acoustical Society of America*, *123*(6), 4524–4538. doi:10.1121/1.2913046

Yovel, G., & Freiwald, W. A. (2013). Face recognition systems in monkey and human: Are they the same thing? *F1000 Prime Reports*, *5*, 10.