ORIGINAL PAPER

2D:4D and Sexually Dimorphic Facial Characteristics

Robert P. Burriss · Anthony C. Little · Emma C. Nelson

Received: 12 August 2005 / Revised: 24 May 2006 / Accepted: 23 June 2006 / Published online: 3 January 2007 © Springer Science+Business Media, LLC 2006

Abstract The second-to-fourth-digit ratio (2D:4D) may be related to prenatal testosterone and estrogen levels and pubertal face growth. Several studies have recently provided evidence that 2D:4D is associated with other-rated facial masculinity and dominance, but not with facialmetric measures of masculinity. We found that localized face shape differences, shown here to be sexually dimorphic and related to ratings of dominance, were associated with direct and indirect measurements of 2D:4D. In this study we examined various localized features of the face, showing nose width, jaw angle, and lip height to be sexually dimorphic. We then had faces rated for dominance and saw that the most dimorphic characteristics were those most associated with rated dominance, with typically masculine characteristics tending to be associated with high ratings of dominance. Finally, 2D:4D measurements were made using three different techniques. High (feminine) values of 2D:4D were associated with feminine facial characteristics in women, but not in men. It was concluded that certain aspects of facial development are governed by factors that are established prenatally. These aspects may be associated with perceptions of the self by others that are important in the social environment,

R. P. Burriss (⊠) · A. C. Little School of Biological Sciences, The University of Liverpool, Biosciences Building, Crown Street, Liverpool, L69 7ZB England e-mail: rob@oraclelab.co.uk

E. C. Nelson School of Archaeology, Classics and Egyptology, The University of Liverpool, Hartley Building, Brownlow Street, Liverpool, England

A. C. Little

Present address: Department of Psychology, Stirling University, Stirling, Scotland

particularly in terms of intra-sexual competition and mate acquisition.

Keywords 2D:4D · Digit ratio · Dominance · Face · Masculinity · Sexually dimorphic

Introduction

The second to fourth digit ratio (2D:4D) is a sexually dimorphic trait, with women tending towards larger ratios than men (Manning et al., 2000; Peters, Mackenzie, & Bryden, 2002; Phelps, 1952), a difference that appears early in life and remains stable throughout (Manning et al., 2000; Manning, Scutt, Wilson, & Lewis-Jones, 1998; Manning, Stewart, Bundred, & Trivers, 2004). Because finger length and the differentiation of the urinogenital tract are both controlled by the Homeobox genes Hox a and d, 2D:4D is thought to be a somatic marker of prenatal sex hormone exposure (Kondo, Zakany, Innis, & Duboule, 1997). Indeed, Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, and Manning (2004) have shown that high levels of fetal sex hormones derived from samples of amniotic fluid are correlated with 2D:4D at age two, with low 2D:4D associated with high fetal testosterone relative to fetal estradiol (though caution should be exercised regarding this study as the sample size was small, N = 29).

This evidence has led Manning et al. (2000) to suggest that 2D:4D may be associated with behavioral and physical adaptations made under sexual selection pressures. In support of this hypothesis, 2D:4D has been shown to be inversely related to male athletic performance (Manning & Taylor, 2001), semen quality (Manning et al., 1998; but also see Firman, Simmons, Cummins, & Matson, 2003), and musical ability (Sluming & Manning, 2000). Each of these characteristics may be adaptations that allowed our ancestors to better compete by increasing both success in intrasexual conflict and the likelihood of being chosen by potential mates (Faurie, Pontier, & Raymond, 2004; Kilgallon & Simmons, 2005; Miller, 2000). Associations between 2D:4D and measures of actual success at acquiring mates and reproducing are also evident. 2D:4D is inversely related to number of children fathered in men (Manning, Henzi, Venkatramana, Martin, & Singh, 2003), and positively related to female marital status (Manning et al., 2000).

If these findings are correct, one might also expect 2D:4D to be associated with other sex-hormone dependent traits, such as subjective and objective measures of dominance and masculinity in the appearance of adults (Penton-Voak & Chen, 2004; Perrett et al., 1998; Verdonck, Gaethofs, Carels, & de Zegher, 1999). However, the evidence for such associations has been equivocal. Links have been shown between digit ratio and female-rated male dominance and masculinity (Neave, Laing, Fink, & Manning, 2003), but attempts to replicate these findings have been unsuccessful. Both Koehler, Simmons, and Rhodes (2004a) and Pound, Penton-Voak, and Kampe (2005) found no significant association between 2D:4D and perceptual and structural facial masculinity. These studies calculated different indices of structural masculinity, though both did so using principal components analysis of the relative locations of facial landmarks. Though this technique may produce indices that accurately reflect structural masculinity such indices will, by nature, be averages of masculinity. A face with a mixture of highly masculine and feminine characteristics may receive a score that suggests average masculinity. Therefore, it remains possible that 2D:4D is correlated with localized differences in face shape, i.e., differences that occur at specific regions of the face (such as the nose or jaw). Several studies have shown that men and women differ in localized face shape at several regions, though particularly at the lower jaw (Hennessy, McLearie, Kinsella, & Waddington, 2005; Penton-Voak et al., 2001). Some of these differences are apparent from an early age. Male nose width, for example, is significantly greater from about age eight (Nute, Orth, Moss, & Orth, 2000). Growth spurts at puberty further increase sex differences, particularly at the mandible (Snodell, Nanda, & Currier, 1993). Penton-Voak and Chen (2004) reported a positive correlation between salivary testosterone and other-rated facial masculinity in a sample of adult men (M age = 20 yrs), and adult facial masculinity may also be predicted well from face shape at ages 6-7 (Snodell et al., 1993).

A recent study by Fink et al. (2005) was the first to report a relationship between 2D:4D and face shape. Predicted face shapes for individuals with low digit 2D:4D were characterized by thinner lips, more robust jaws, and narrower noses. Though each of these regions is sexually dimorphic (e.g., Koehler, Simmons, Rhodes, & Peters, 2004b; Penton-Voak et al., 2001), Fink et al. reported that the shape differences associated with 2D:4D were not identical to those associated with sex. If the regions most associated with 2D:4D are not as strongly sexually dimorphic as are others, it may explain why correlations between 2D:4D and holistic measures of facial masculinity have yet to be identified.

Our aims were (1) to confirm that measures of jaw shape, lip size, and nose width are sexually dimorphic, i.e. that they differ significantly in size between the sexes, (2) to identify relationships between these measures of jaw shape, lip size, and nose width in male and female faces and other-rated dominance, using both male and female raters, and (3) to determine whether measures of jaw shape, lip size, and nose width in male and female faces were also associated with 2D:4D.

It has recently been reported that finger length measurements may differ according to the measurement technique used, with measurements made directly on the finger yielding higher 2D:4D ratios than measurements made on photocopies of the hand (Manning, Fink, Neave, & Caswell, 2005). Manning et al. (2005) suggested that this may be because of differences in the shape of fat pads on the tips of the fingers, which result in greater absolute sizes of 4D and 5D and lower absolute sizes of 2D and 3D in photocopies. Therefore, we employed three separate measurement techniques: direct measurement of digits using calipers and rule (the former measurement was made by an experimenter, the latter by the participant), and computer assisted measurement of digits from scans. Digit measurements using a rule were made by participants and not experimenters to assess this technique's suitability as a method of obtaining digit measurements remotely (e.g. in online experiments).

Study 1

Method

Participants

Photographs of 475 young adults, which were taken as part of several wider research projects, made up the pool of images used in this study. Photographs were taken under three different sets of conditions. A total of 91 men and 91 women were photographed under the first set of conditions: in variable environments (both indoors and outdoors) with the camera positioned approximately one meter from the face of the standing participant. A total of 67 men and 50 women were photographed under the second set of conditions: indoors

and under standardized lighting, with the camera positioned approximately three meters from the face of the seated participant. A further 111 men and 65 women were photographed under the third set of conditions. These conditions were similar to those described for the second set, though photographs were taken in a different laboratory and with different equipment. This resulted in slight but consistent differences in brightness, hue, and shadow from those produced under the second set of conditions.

Forty-two of the images in the pool were discarded due to excessive head-tilting or manifest facial expressions. Also, in order that an equal number of male and female faces from each condition set be included in the analysis (to minimize the effects of differing photographic conditions on sexual dimorphism measures), excess images of men (57) were randomly selected and discarded. The total number of images used in the current analysis was 376.

Procedure and measures

Nine feature points were marked onto the 188 male and 188 female facial photographs by means of a dedicated computer program (Tiddeman, Burt, & Perrett, 2001). Using these points, the program rendered measurements as a percentage of interpupilary distance. Upper lip height was defined as the vertical distance between the stomion (the midpoint of the line at which the upper and lower lips meet when lips are gently closed) and the labiale superius (the midpoint of the upper vermilion line), and lower lip height as the vertical distance between the stomion and the labiale inferius (the midpoint of the lower vermilion line). Nose width was defined as the horizontal distance between the left and right alares (the most lateral points on each alar contour or curve of the nostril). Jaw angle was calculated as the mean "angle at the gonion" for two right-angled triangles placed on either side of the face. The vertices of each triangle were at the (1) gonion (the most lateral point on the mandibular angle, normally identified by palpation but estimated here as the most lateral points on a horizontal line intersecting the stomion), (2) zygion (the most lateral point of each zygomatic arch, or cheekbone), and (3) the intercept point of two lines, one of which was drawn vertically intersecting point (a) and the other horizontally intersecting point (b). A smaller angle would indicate a steeper jaw line (see Fig. 1).

All measurements (except jaw angle) were rendered as percent of interpupilary distance so that a distance equal to interpupilary distance would be given a value of 100.

Results

Table 1 shows the means of each facialmetric measure as a function of sex. Means were compared using independent-



Fig. 1 Points used for the measurement of the putative sexually dimorphic and dominance related features. Al = Alare, Ls = Labiale superius, Sto = Stomion, Li = Labiale inferius, (a) = Gonion, (b) = Zygion, (c) = 3rd point in right-angled triangle, abc. The zygion, impossible to locate on a front-on photograph, was estimated as lying on a horizontal line intersecting the stomion. Anthropometrical definitions are taken from Farkas (1981).

samples *t*-tests. The measure of upper lip height was not significantly sexually dimorphic, though women possessed heights that were, on average, 5.43% greater than those of men. Lower lip height was significantly sexually dimorphic, with women possessing heights that were, on average, 5.97% greater than those of men. Nose width was also significantly sexually dimorphic, with the mean male nose width 3.93% greater than the female, as was jaw angle, with the mean female angle 15.71% greater than the male (see Table 1).

Discussion

Previous studies have shown that nose width and measures of jaw shape (though not specifically angle) are sexually dimorphic (e.g., Koehler et al., 2004a; Penton-Voak et al., 2001), and the current findings were confirmatory. Koehler et al. (2004a) found that men had larger lip areas. However, large lips are thought to be a neotonous feature (Cunningham, Barbee, & Pike, 1990) and so might, therefore, be considered

	Ν	M (SD)	t	р	d
Upper lip height					
Female	188	10.48 (3.60)	-1.65	.01	.17
Male	188	9.94 (2.73)			
Lower lip height					
Female	188	17.93 (4.03)	-2.48	.013	.26
Male	188	16.92 (3.82)			
Nose width					
Female	188	58.17 (4.35)	5.12	.001	.53
Male	188	60.55 (4.63)			
Jaw angle					
Female	188	10.68° (2.32)	-5.98	.001	.62
Male	188	9.23° (2.36)			

^{*a*}All measurements, except jaw angle, were proportions of horizontally measured interpupilary distance df = 374.

feminine. Lip height is also negatively correlated with age, and, because youthfulness is more attractive in women than in men (Kozieł & Pawłowski, 2003; Peters, Shackelford, & Buss, 2002), one would expect there to have been a greater selection pressure upon women during recent evolutionary history to retain the neotonous features of large lips. The current finding that lower lip height was greater in women than in men is, therefore, in line with evolutionary predictions, though it does contradict the earlier finding of Koehler et al. (2004a).

As Fink et al. (2005) recently suggested that 2D:4D and sex do not appear to be related to face shape in an analogous fashion, dominance ratings of faces were collected in order to examine correlations between localized face shape differences and subjective perceptions of dominance.

Study 2

Method

Participants

Participants were 11 men (M age = 26.18 yrs; SD = 6.84) and 14 women (M age = 23.14 yrs; SD = 4.05), recruited via advertisements made on a university computer network messaging system. All were naïve as to the aim of the study.

Procedure and measures

A total of 67 of the male and 50 of the female facial photographs taken under condition set two were normalized on interpupilary distance and cropped so that clothing was not visible (50 of the male and all of the female faces had been used in Study 1). Images were presented on a computer monitor that was set to a screen resolution of 1024×768 and 32 bit color quality. Participants rated each image for dominance using a 7-point Likert scale. For the purposes of rating, a dominant person was defined as someone who "appears as though they can get what they want." Alpha reliability coefficient was high ($\alpha = 0.76$), demonstrating that participants were in agreement as to the cues that signaled a dominant appearance.

Results

Table 2 shows the correlations between male and female ratings of dominance and the four facialmetric measurements in male and female faces. Male ratings of male dominance were correlated significantly and negatively with upper lip height, lower lip height and jaw angle. Ratings were positively correlated with nose width. Dominance ratings made by women were correlated significantly and negatively with jaw angle alone. This means that male faces rated as dominant by men would tend to have thinner lips, wider noses, and steeper jaw angles; faces rated as more dominant by women would tend towards steeper jaw angles.

Male ratings of female dominance were significantly and negatively correlated with lower lip height, and jaw angle, while female ratings were correlated significantly and negatively with lower lip height. So, female faces rated as dominant by men and women would tend towards thinner lower lips. Additionally, faces rated as dominant by men would tend towards steeper jaw angles.

Discussion

Faces with a more masculine shape tended to be rated as more dominant. This was true for both male and female ratings of both male and female faces, although lower lip height and jaw angle seemed to be of particular importance. Relationships were in the expected direction, with greater ratings of dominance associated with greater facial masculinity. It is interesting to note that the measurements which were previously shown to be the most strongly dimorphic were the ones that were found to be most significantly correlated with dominance ratings.

Neave et al. (2003) have shown that 2D:4D was associated with rated facial dominance. Given the findings of Study 2, which showed that rated dominance and structural masculinity are related concepts, it is likely that 2D:4D is inversely related to masculinity in the face. However, it is important to note that Fink et al. (2005) have reported that 2D:4D and sex may not be related to face shape in an analogous fashion.

	Male fa	ces(n =	67)				Female faces $(n = 50)$							
	Male raters			Female raters			Male raters			Female raters				
	r	df	р	r	df	р	r	df	р	r	df	р		
Upper lip height	25	66	.041	03	66	ns	07	49	ns	16	49	ns		
Lower lip height	33	66	.006	10	66	ns	31	49	.029	42	49	.002		
Nose width	.27	66	.029	20	66	ns	.10	49	ns	.12	49	ns		
Jaw angle	37	66	.002	30	66	.015	35	49	.012	26	49	ns		

Table 2 Correlations between male and female ratings of dominance and four facialmetric measurements in male and female faces

Study 3

Method

Participants

Participants were 92 men (M age = 23.07 yrs, SD = 5.61) and 51 women (M age = 21.77 yrs, SD = 2.71) who were recruited via advertisements made on a university computer network messaging system. All were naïve as to the aims of the current investigation. These participants were part of the pool described above in Study 1.

Procedure and measures

Facial photographs of all participants were taken under condition set three and measurements made upon them as described above. Afterwards, images of hands were collected from participants using a Canonscan LiDE 50 computer scanner (2480×3407 pixels, 300 dpi). Hands were placed lightly on the surface of the plate with fingers together. If the creases at the base of the second and fourth digits were unclear, second scans were made. Scans were unavailable for three men and one woman because of computer errors or participant unwillingness to place hands in the scanner.

Using a computer program originally developed for the purposes of measuring distances between facial landmarks (Penton-Voak et al., 2001; Tiddeman et al., 2001), images were magnified to approximately 250% life-size (high res-

olution meant no loss of clarity at this magnification) and feature points were marked at the tip of the finger and at the center of the proximal crease on the second and fourth digits. Actual measurement was carried out automatically by the program (giving scanned 2D:4D or S-2D:4D). In addition, 52 of the men and 30 of the women self-measured digits using a transparent rule accurate to 0.1 cm (giving Se-2D:4D). Detailed instructions were given as to how digit length should be measured. These instructions included an explanation of how to hold the hand and a verbal and graphical description of the relevant landmarks. Also, 43 men and 21 women had digits measured directly from the hand by experimenters using digital Vernier calipers accurate to 0.01 cm (giving C-2D:4D).

2D:4D was calculated by dividing 2nd by 4th digit length. Associations between facialmetric measurements and 2D:4D were assessed separately for left and right 2D:4D, as previous research has suggested that hormone effects on hand-growth may differ (McFadden & Shubel, 2002).

Results

Previous studies have shown that 2D:4D is a sexually dimorphic trait, with women tending towards higher ratios than men (e.g. Manning et al., 2000; Peters, Mackenzie, & Bryden, 2002). Table 3 shows that the current study did not replicate this finding. In fact, it was found that men tended towards higher ratios than women. The difference was not significant for measurements made from computer scans,

Table 3 Differences between mean 2D:4D as rendered by the three measurement techniques as a functionof participant sex and hand

		Left hand			Right hand						
	Ν	$\overline{M(SD)}$	t	р	d	M(SD)	t	р	d		
S-2D:4D											
Female	50	.961 (.035)	.07	ns	.01	.972 (.032)	59	ns	.10		
Male	89	.961 (.027)				.969 (.030)					
Se-2D:4D											
Female	30	.964 (.042)	2.04	.045	.44	.983 (.044)	.63	ns	.14		
Male	52	.980 (.028)				.988 (.036)					
C-2D:4D											
Female	21	.975 (.034)	1.79	.078	.46	.969 (.033)	2.00	.049	.50		
Male	43	.989 (.027)				.983 (.024)					

Table 4Differences betweenmean 2D:4D as rendered by thethree measurement techniques,by participant sex and hand

	Comparison between S-2D:4D and Se-2D:4D			Compari and C-2	ison betwe D:4D	en S-2D:4D	Comparison between Se-2D:4D and C-2D:4D			
	t	р	d	t	р	d	t	р	d	
Men										
Right	-2.80	.007	.60	-2.69	.010	.55	.55	ns	.16	
Left	-3.88	.001	.67	-5.72	.001	1.02	-2.04	.048	.34	
Women										
Right	-1.13	ns	.28	.27	ns	.09	2.77	.012	.35	
Left	-2.11	.044	.08	-5.69	.001	.41	-2.99	.007	.28	

though left hand 2D:4D from self measurements using a rule and left and right hand 2D:4D from measurements using calipers were significantly greater in men than in women, with effect sizes of low to medium magnitude (Cohen, 1992).

There were significant correlations among mean digit ratios as calculated from measurements made using the different techniques (left S-2D:4D and left Se-2D:4D: r = .74, df = 77, p < .001; right S-2D:4D and right Se-2D:4D: r = .56, df = 77, p < .001; left S-2D:4D and left C-2D:4D: r = .70, df = 59, p < .001; right S-2D:4D and right C-2D:4D: r = .710, df = 59, p < .001; left C-2D:4D and left Se-2D:4D: r = .65, df = 63, p < .001; right C-2D:4D and right Se-2D:4D: r = .55, df = 63, p < .001). Manning et al. (2005) recently noted that digit ratios derived from photocopies tend to be lower than those derived from measurements made directly on the finger, and this also appeared to be the case for computerized scans: M S-2D:4D (.967 \pm .003) was significantly lower than M C-2D:4D (.981 \pm .003), $t(59) = -7.31, p < .001, and M Se-2D:4D (.979 \pm .004),$ t(77) = -4.44, p < .001. C-2D:4D and Se-2D:4D did not differ significantly, t(63) < 1. However, these effects were qualified by both hand and sex. Table 4 shows that there was evidence that the differences between S-2D:4D and the two direct measures of digit ratio were significant for men in both left and right hands, but for women only in the left hand. The finding relating to women supports that of Manning et al. (2005), who found that the difference between measurements of 2D:4D from direct and indirect methods was significant only for the left hand. Effect sizes for the differences in men were medium to large, while in women they were small, suggesting a greater magnitude of effect of technique on measured 2D:4D for men than for women. The difference between 2D:4D given by the two direct methods was non-significant for men in the right hand, but was significant for men in the right hand and for women in both hands, though effect sizes for these differences were small. It should be noted that for some analyses female sample sizes were low (Ns between 19 and 28), suggesting caution be exercised in the interpretation of these results.

Because relationships of specific directions were predicted after the findings of Fink et al. (2005), one-tailed statistical tests were employed. Table 5 shows the Pearson correlation coefficients that were obtained for relationships between 2D:4D (as measured on the left and right hand using the three measurement techniques) and the four facialmetric measures. Of the four measures, all but upper lip height showed significant correlations with measures of 2D:4D. However, none of these measures was correlated significantly with 2D:4D as rendered by all three of the measurement techniques. Also, none of the measures were

Table 5	Correlations among fe	male and male ratings	of dominance and	four facialmetric	measurements in	female and male faces
---------	-----------------------	-----------------------	------------------	-------------------	-----------------	-----------------------

	Left hand								Right hand									
	S-2D:4D		Se-2D:4D		C-2D:4D		S-2D:4D		Se-2D:4D			C-2D:4D						
	r	df	р	r	df	р	r	df	р	r	df	р	r	df	р	r	df	р
Upper lip height																		
Female	09	49	ns	.06	29	ns	07	20	ns	09	49	ns	.14	29	ns	09	20	ns
Male	.01	88	ns	12	51	ns	.24	42	.059	01	88	ns	17	51	ns	06	42	ns
Lower lip height																		
Female	06	49	ns	01	29	ns	11	20	ns	.02	49	ns	.40	29	.015	06	20	ns
Male	03	88	ns	14	51	ns	.17	42	ns	03	88	ns	15	51	ns	05	42	ns
Nose width																		
Female	24	49	.049	27	29	.079	48	20	.015	29	49	.022	15	29	ns	50	20	.011
Male	17	88	.057	.18	51	ns	.09	42	ns	11	88	ns	.21	51	.071	.16	42	ns
Jaw angle																		
Female	.21	49	.075	.21	29	ns	.56	20	.004	.004	49	ns	05	29	ns	.27	20	ns
Male	003	88	ns	.06	51	ns	.02	42	ns	.07	88	ns	.14	51	ns	06	42	ns

significantly correlated with male 2D:4D. Female S-2D:4D was significantly and negatively correlated with nose width (left and right hands), but with none of the remaining facialmetric measures. Female Se-2D:4D was significantly and positively correlated with lower lip height (right hand only), but with none of the remaining facialmetric measures. Female C-2D:4D was significantly and negatively correlated with nose width (left and right hands), and significantly and positively correlated with jaw angle (left hand only) (see Table 5). It should be noted, however, that none of the reported relationships survive Bonferroni correction (48 tests, p < .001).

Discussion

Though 2D:4D was not seen to be significantly related to any of the facialmetric measures in men, all significant relationships between female 2D:4D and the facialmetric measures were of the predicted valence. That is, high (feminine) values of 2D:4D were associated with feminine facial features, such as a narrower nose, thicker lower lip, and shallower jaw angle. The facialmetric measure most consistently correlated with 2D:4D was nose width, which was shown to differ significantly between the sexes but only to a small degree and to not be correlated with dominance ratings in female faces. This relationship would have been difficult to detect if an overall index of facial masculinity had been used rather than a number of individual localized measures. As these relationships would not survive Bonferroni correction, they must be interpreted with caution.

The computerized method theoretically allowed for much greater accuracy in the placement of landmarks on the hand than did either of the direct methods. However, it may be that the measurements rendered from computer scans were not as reflective of "true 2D:4D": mean S-2D:4D was significantly lower than mean C-2D:4D and Se-2D:4D. This is precisely the pattern one would predict given previous findings by Manning et al. (2005), who suggested that 2D:4D derived from photocopies may be lower than that derived from direct measurements due to differences in the fat pads at the tip of the fingers. When compared to direct measurements, measurements derived from photocopies (and, presumably, computer scans, which also require the hand to be pressed against a glass plate) were lower for 2D and greater for 4D. This may explain why relationships involving S-2D:4D were not as strong as those involving C- and Se-2D:4D, and suggests the possibility that S-2D:4D does not reflect "true 2D:4D" as well as the direct measurement techniques.

An alternative explanation may be that spurious relationships were much more likely to be detected if sample sizes were small. Direct measurements of 2D:4D were only available for a small number of participants. Clearly, further studies, in which all measurement techniques are used on a large sample, are required in order to provide a complete answer.

Previous studies have found that indices of facial masculinity were not associated with 2D:4D (Koehler et al., 2004a; Pound et al., 2005). This may be true, though it remains possible that 2D:4D is associated with localized shape differences that are related, but not equivalent, to facial masculinity. The current findings, which support those of Fink et al. (2005), suggest that this hypothesis is correct. We found that localized differences in face shape, particularly at the jaw and lip, were associated with variation in perceived dominance, while nose width, a less strongly sexually dimorphic trait that is unrelated to dominance ratings in women, is most consistently related to 2D:4D.

Certain aspects of masculine facial development, though affected by pubertal sex hormone exposure (Snodell et al., 1993), are predictable before adolescence (Nute et al., 2000) and are here shown to be governed by factors that are in place before birth. These aspects may be associated with differing perceptions of the self by others that are important in the social environment, particularly in terms of intra-sexual competition and mate acquisition.

Acknowledgements The authors thank C. Hassell, R. Karadia, and A. D. Tufte for help with data collection, S. C. Roberts for allowing access to the facial photographs taken under condition set one, K. Kaskatis for advice on the sexual selection of musical ability, and D. I. Perrett and B. P. Tiddeman for the use of the Psychomorph program. We also thank three anonymous reviewers and B. Fink and J. T. Manning for their helpful comments. A. C. L. is supported by a Royal Society University Research Fellowship.

References

- Cohen, J. (1992). A power primer. *Psychological Bulletin*, 112, 155–159.
- Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical characteristics. *Journal of Personality and Social Psychology*, 59, 61–72.
- Farkas, L. G. (1981). Anthropometry of the head and face in medicine. New York: Elsevier.
- Faurie, C., Pontier, D., & Raymond, M. (2004). Student athletes claim to have more sexual partners than other students. *Evolution and Human Behavior*, 25, 1–8.
- Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Schaefer, K., Bookstein, F. L., et al. (2005). Second to fourth digit ratio and face shape. *Proceedings of the Royal Society of London, Series B*, 272, 1995–2001.
- Firman, R., Simmons, L. W., Cummins, J. M., & Matson, P. L. (2003). Are body fluctuating asymmetry and the ratio of 2nd to 4th digit length reliable predictors of semen quality? *Human Reproduction*, 18, 808–812.
- Hennessy, R. J., McLearie, S., Kinsella, A., & Waddington, J. L. (2005). Facial surface analysis by 3D laser scanning and geometric morphometrics in relation to sexual dimorphism in cerebralcraniofacial morphogenesis and cognitive function. *Journal of Anatomy*, 207, 283–295.

- Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, 1, 253–255.
- Koehler, N., Simmons, L. W., & Rhodes, G. (2004a). How well does second-to-fourth-digit ratio in hands correlate with other indications of masculinity in males? *Proceedings of the Royal Society of London, Series B*, 271, S296–S298.
- Koehler, N., Simmons, L. W., Rhodes, G., & Peters, M. (2004b). The relationship between sexual dimorphism in human faces and fluctuating asymmetry. *Proceedings of the Royal Society of London*, *Series B*, 271, S233–S236.
- Kondo, T., Zakany, J., Innis, J., & Duboule, D. (1997). Of fingers, toes and penises. *Nature*, 390, 29.
- Kozieł, S., & Pawłowski, B. (2003). Comparison between primary and secondary mate markets: an analysis of data from lonely hearts columns. *Personality and Individual Differences*, 35, 1849–1857.
- Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R., & Manning, J. T. (2004). 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Human Development*, 77, 22–28.
- Manning, J. T., Barley, L., Walton, J., Lewis-Jones, D. I., Trivers, R. L., Singh, D., et al. (2000). The 2nd:4th digit ratio, sexual dimorphism, population differences and reproductive success: Evidence for sexually antagonistic genes? *Evolution and Human Behavior*, 21, 163–183.
- Manning, J. T., Fink, B., Neave, N., & Caswell, N. (2005). Photocopies yield lower digit ratios (2D:4D) than direct finger measurements. *Archives of Sexual Behavior*, 34, 329–333.
- Manning, J. T., Henzi, P., Venkatramana, P., Martin, S., & Singh, D. (2003). Second to fourth digit ratio: ethnic differences and family size in English, Indian and South African populations. *Annals of Human Biology*, 30, 579–588.
- Manning, J. T., Scutt, D., Wilson, J., & Lewis-Jones, D. I. (1998). The ratio of 2nd to 4th digit length: A predictor of sperm numbers and concentration of testosterone, leutenizing hormone and oestrogen. *Human Reproduction*, 13, 3000–3004.
- Manning, J. T., Stewart, A., Bundred, P. E., & Trivers, R. L. (2004). Sex differences in the 2nd to 4th digit ratio of children. *Early Human Development*, 80, 161–168.
- Manning, J. T., & Taylor, R. P. (2001). Second to fourth digit ratio and male ability in sport: implications for sexual selection in humans. *Evolution and Human Behavior*, 22, 61–69.
- McFadden, D., & Shubel, E. (2002). Relative lengths of fingers and toes in human males and females. *Hormones and Behavior*, 42, 492–500.
- Miller, G. F. (2000). The evolution of music through sexual selection. In N. L. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 329–360). Cambridge, MA: MIT Press.

- Neave, N., Laing, S., Fink, B., & Manning, J. T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proceedings of the Royal Society of London*, B., 270, 2167– 2172.
- Nute, S. J., Orth, M., Moss, J. P., & Orth, D. (2000). Three-dimensional facial growth studied by optical surface scanning. *Journal of Orthodontics*, 27, 31–38.
- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution* and Human Behavior, 25, 229–241.
- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., et al. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London, Series B*, 268, 1617–1623.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, 394, 884–887.
- Peters, M., Mackenzie, K., & Bryden, P. (2002). Finger length and distal finger extent patterns in humans. *American Journal of Physical Anthropology*, 117, 209–217.
- Peters, J., Shackelford, T. K., & Buss, D. M. (2002). Understanding domestic violence against women: using evolutionary psychology to extend the feminist functional analysis. *Violence and Victims*, 17, 255–264.
- Phelps, V. R. (1952). Relative index finder length as a sex-influenced trait in man. American Journal of Human Genetics, 4, 72–85.
- Pound, N., Penton-Voak, I. S., & Kampe, V. (2005, June). Facial masculinity is not associated with digit masculinity. Paper presented at the annual conference of the Human Behavior and Evolution Society, Austin, Texas.
- Sluming, V. A., & Manning, J. T. (2000). Second to fourth digit ratio in elite musicians: Evidence for musical ability as an honest signal of male fitness. *Evolution and Human Behavior*, 21, 1–9.
- Snodell, F., Nanda, R. S., & Currier, G. F. (1993). A longitudinal cephalometric study of transverse and vertical craniofacial growth. *American Journal of Orthodontics and Dentofacial Orthopedics*, 104, 471–483.
- Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial texture for perception research. *IEEE Computer Graphics Applications*, 21, 42–50.
- Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. *European Journal of Orthodontics*, 21, 137– 143.