

## Digit ratio (2D:4D) predicts facial, but not voice or body odour, attractiveness in men

Camille Ferdenzi, Jean-François Lemaître, Juan David Leongómez and S. Craig Roberts

*Proc. R. Soc. B* 2011 **278**, 3551-3557 first published online 20 April 2011

doi: 10.1098/rsob.2011.0544

---

### Supplementary data

["Data Supplement"](#)

<http://rsob.royalsocietypublishing.org/content/suppl/2011/04/19/rsob.2011.0544.DC1.html>

### References

[This article cites 51 articles, 12 of which can be accessed free](#)

<http://rsob.royalsocietypublishing.org/content/278/1724/3551.full.html#ref-list-1>

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Proc. R. Soc. B* go to: <http://rsob.royalsocietypublishing.org/subscriptions>

---

# Digit ratio (2D:4D) predicts facial, but not voice or body odour, attractiveness in men

Camille Ferdenzi<sup>1,\*</sup>, Jean-François Lemaître<sup>2</sup>,  
Juan David Leongómez<sup>3</sup> and S. Craig Roberts<sup>3</sup>

<sup>1</sup>Swiss Centre for Affective Sciences, University of Geneva, 7 rue des Batoirs, 1205 Geneva, Switzerland

<sup>2</sup>Unité Mixte de Recherche 5558, Biométrie et Biologie Evolutive, Université Lyon 1, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France

<sup>3</sup>School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK

There is growing evidence that human second-to-fourth digit ratio (or 2D:4D) is related to facial features involved in attractiveness, mediated by *in utero* hormonal effects. The present study extends the investigation to other phenotypic, hormone-related determinants of human attractiveness: voice and body odour. Pictures of faces with a neutral expression, recordings of voices pronouncing vowels and axillary odour samples captured on cotton pads worn for 24 h were provided by 49 adult male donors. These stimuli were rated on attractiveness and masculinity scales by two groups of 49 and 35 females, approximately half of these in each sample using hormonal contraception. Multivariate regression analyses showed that males' lower (more masculine) right 2D:4D and lower right-minus-left 2D:4D ( $Dr-1$ ) were associated with a more attractive (and in some cases more symmetrical), but not more masculine, face. However, 2D:4D and  $Dr-1$  did not predict voice and body odour masculinity or attractiveness. The results were interpreted in terms of differential effects of prenatal and circulating testosterone, male facial shape being supposedly more dependent on foetal levels (reflected by 2D:4D ratio), whereas body odour and vocal characteristics could be more dependent on variation in adult circulating testosterone levels.

**Keywords:** mate choice; finger ratio; testosterone; face symmetry; masculinity

## 1. INTRODUCTION

The relative length of the second (index) and fourth (ring) fingers, or 2D:4D ratio, is sexually dimorphic in several species, with lower 2D:4D ratios for males than females in mammals [1,2], while in birds it appears to be the reverse [3]. Although the precise genetic mechanism explaining this sexual dimorphism is still unclear, there is compelling evidence that *in utero* foetal testosterone and foetal oestrogen influence 2D:4D ratio in humans [1,4–6]. For example, males suffering from congenital adrenal hyperplasia (CAH), an enzymatic deficiency that entails excessive levels of androgens during the foetal period, have particularly low 2D:4D ratio [7]. More generally, men exposed to high levels of prenatal androgens develop low 2D:4D ratio [4,7].

Androgens such as testosterone are also involved in the development and maintenance of secondary sexual characters, and thereby in mate choice [8,9]. Because maintaining a high level of testosterone is costly for males (e.g. [10,11]), those that display enhanced sexual characters without suffering too much from immunosuppression are considered high-quality males [12]. Therefore, women should ultimately increase their reproductive success by choosing mates displaying testosterone-dependent sexual traits [12,13]. In humans, men with higher levels of circulating testosterone have voices with lower fundamental frequency

[14] and more masculine faces [15,16], two traits that are preferred by women when they become sexually mature (see [17] for voices and [18] for faces).

Since the growth of the fourth finger is dependent on the level of prenatal androgen, and since some authors have hypothesized a positive correlation between prenatal and adult testosterone levels [1,19], 2D:4D ratios might correlate negatively with some other testosterone-dependent traits [1]. If these traits such as vocal and facial features are sexually selected, then measures of 2D:4D should be a good predictor of men's attractiveness. To date, investigations of these putative relationships are scarce and remain principally focused on face and body masculinity of men (e.g. [20]), since these traits are testosterone-dependent [16] and preferred by women in a mate choice context [18]. Moreover, results from these studies are conflicting. For example, Neave *et al.* [20] found a negative correlation between 2D:4D ratios of the left and right hand and the female perception of male facial dominance and masculinity, but Koehler *et al.* [21] failed to repeat these results and found no relationship between 2D:4D and body and face masculinity. Furthermore, some authors found a link between 2D:4D and attractiveness [22–24], whereas others did not [20].

To date, studies testing relationships between 2D:4D ratios and sexually selected traits have only focused on men's bodies and faces, although there is evidence that women use multiple testosterone-dependent cues to select mates, such as voice [25] and body odour [26,27]. As for faces [15], voice frequency and thus attractiveness are

\* Author for correspondence ([camille.ferdenzi@unige.ch](mailto:camille.ferdenzi@unige.ch)).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.0544> or via <http://rsob.royalsocietypublishing.org>.

related to the level of salivary testosterone [14]. Similarly, androgen level is likely to influence body odour since steroid compounds of axillary odour such as androstadienone are present more in males [28] and are products of testosterone transformation by underarm bacteria [29,30].

In this study, for the first time, we investigated, in three sensory modalities involved in human mate choice (voice, body odour and face), whether second-to-fourth digit ratio of left and right hands, and digit ratio difference between the two hands ( $Dr-1$ ; also related to prenatal testosterone sensitivity [31,32]), can predict male masculinity and attractiveness. We predicted that 2D:4D ratio and  $Dr-1$  would be negatively correlated with face, voice and odour masculinity and attractiveness, as evaluated by females. As voice frequency and face symmetry influence women's preference for men (deeper voices are preferred [33]; symmetrical faces are more attractive [34,35]), we also measured these two factors and linked them to 2D:4D ratios. Finally, we controlled for the use of hormonal contraceptives by the female raters, since this could alter women's preference for various male features, such as body odour, face and voice [36,37].

## 2. METHODS

### (a) *Participants*

Participants were 49 Caucasian male donors aged between 18 and 33 years old (mean  $\pm$  s.d. =  $22.3 \pm 4.0$  years), recruited among students of the University of Liverpool. From these, we obtained 2D:4D measures, a voice sample and a facial photograph. Axillary odour samples were collected for 28 of them who were non-smokers, as is standard in odour rating research because of the influence of smoking on body odour quality [38,39].

Male axillary odour samples were evaluated by 49 Caucasian female students of the University of Liverpool, aged between 19 and 34 years old (mean  $\pm$  s.d. =  $21.8 \pm 3.2$  years). Of these, 26 reported taking hormone-based contraception (hereafter named 'pill users') and 23 were not (hereafter named 'non-pill users'). Each odour sample was rated fresh by 9–10 women during one of five rating sessions at the University of Liverpool, between November 2007 and February 2008. Men's faces were judged by 27 of these women (mean  $\pm$  s.d. =  $21.8 \pm 3.4$  years old; 14 pill users, 13 non-pill users). Owing to experimental constraints, the voices were evaluated later (November and December 2010) by a separate group of female students at the University of Stirling ( $n = 35$ ; mean  $\pm$  s.d. =  $20.1 \pm 3.5$  years old, range = 18–34; 20 pill users, 15 non-pill users; Caucasian). Although both groups of raters were similar in terms of age, nationality (British) and occupation (students), we controlled for consistency of their evaluations. Hence, we asked the voice raters to rate the men's faces that were previously rated by the Liverpool group. Rating of both groups was highly consistent for face short-term attractiveness (intra-class correlation coefficient, ICC = 0.944,  $p < 0.001$ ), long-term attractiveness (ICC = 0.942,  $p < 0.001$ ), masculinity (ICC = 0.923,  $p < 0.001$ ) and symmetry (ICC = 0.889,  $p < 0.001$ ). Therefore, both groups were considered equivalent.

### (b) *Voice samples*

Participants' voices were recorded on a digital recorder (M-Audio Microtrack 24/96) with a cardioid condenser microphone (Technica ATR55 Telemike Shotgun), in a quiet room at

about 15 cm from the microphone. Participants were required to recite two sentences of *the rainbow passage* [40] and the monophthong vowels 'eh', 'ee', 'ah', 'oh' and 'oo'. This sequence was then repeated once. Female ratings and measure of voice frequency were performed on the second repetition (when participants are more relaxed) and on the three vowels in middle (ee, ah and oh; electronic supplementary material S1) to limit intonation variations. Voice frequency  $F_0$  was measured with PRAAT v. 4.6 ([www.praat.org](http://www.praat.org)). Voice attractiveness and masculinity ratings were collected on 1–7 scales with E-PRIME v. 2.0 (Psychology Software Tools), after equalizing the samples in intensity (in MATLAB v. 7.10) and length (2 s; in PRAAT).

### (c) *Axillary odour samples*

Axillary odour samples were collected on cotton pads ( $9.5 \times 6.5$  cm; Boots UK Ltd.) fastened onto both axillae for 24 h. Participants were instructed to refrain from eating strong food, drinking alcohol, smoking, doing sport and having sexual intercourse for 2 days before and during odour collection. They were also required to shower with a non-perfumed soap before fastening the pads, and not to use any scented products such as perfume or deodorant. Samples were presented fresh to female raters a few hours (range: 2–8 h) after pads were removed from the armpits. Odour samples were placed in glass flasks, presented in a random order to the raters, and evaluated for attractiveness and masculinity on 9-point scales. The variable used in this study was the average rating of the right and left side. For more details about the procedure of odour collection and rating, see [38].

### (d) *Face samples*

Full face pictures of the male participants were taken in standardized conditions of light with a Canon Powershot camera. Participants were asked to have a neutral expression and to look at the camera without any vertical or horizontal tilt of the head. Distance to the camera was constant and participants wore a dark gown. Images were resampled to  $400 \times 480$  pixels with 72 dpi resolution. Using PSYCHOMORPH v. 8.4 (Perrett and Tiddeman, University of Saint Andrews, UK), faces were normalized according to pupils and mouth position, and face symmetry was computed using seven bilateral points (pupils, outermost and innermost eye corners, leftmost and rightmost points of the nose, mouth corners, cheekbones and jaws; electronic supplementary material S2). The asymmetry index was the sum of the vertical and horizontal asymmetry indices. Vertical and horizontal asymmetries were, respectively, the sum of differences in vertical and horizontal locations of each of the seven facial features (see details in [41]). Placement of the points and computation of the asymmetry index were performed twice, and averaged, since the two asymmetry indices were highly consistent (ICC = 0.876,  $p < 0.001$ ). Men's faces were presented in random order with a Java applet. Female participants were asked to rate the faces for short-term attractiveness (i.e. considering the person as a dinner date or holiday romance), long-term attractiveness (i.e. considering the person as a long-term partner), masculinity and symmetry on 1–7 scales. They were asked to skip the ratings of the men they knew.

### (e) *Measures of 2D:4D*

The length of index and ring fingers of the male participants was measured to the nearest 0.1 mm using Vernier callipers, directly on fingers (more reliable than indirect measures

performed on a photocopy of the hands [42]). Measurement was taken from the most proximal ventral crease of the digit to the tip of the finger. To limit measurement errors, the procedure was repeated three times, and as the measures were highly correlated ( $ICC = 0.986$ ,  $p < 0.001$ ) they were averaged. The index-to-ring ratio (2D:4D) for the left and right hand separately were then computed, as well as the difference between right and left 2D:4D ( $Dr-1$ ).

#### (f) *Data analysis*

All variables had normal distributions (assessed by Kolmogorov–Smirnov tests) and parametric statistics were thus used. In addition, no extreme values were to be removed before performing analyses. Tests were two-tailed and were conducted using STATISTICA v. 9.0 and SPSS v. 18.0. The link between 2D:4D and visual, auditory and olfactory stimuli was investigated using multivariate simple regressions, with face, voice and odour characteristics (masculinity, attractiveness, etc.) as dependent variables and 2D:4D as predictor. The difference between pill users and non-pill users was tested with paired *t*-tests, and the relation between masculinity, attractiveness and other dimensions was assessed with Pearson correlation coefficients.

### 3. RESULTS

#### (a) *Voice*

First, correlations between male voice frequency and both rated attractiveness and rated masculinity were significantly negative ( $r = -0.69$  and  $r = -0.63$ , respectively;  $n = 48$ ,  $p < 0.001$ ). Attractiveness and masculinity correlated positively ( $r = 0.77$ ,  $n = 48$ ,  $p < 0.001$ ). Pill users gave slightly higher attractiveness ratings than non-pill users ( $t_{47} = 2.14$ ,  $p = 0.038$ ), but the two groups did not differ on the masculinity ratings ( $t_{47} = 0.95$ ,  $p = 0.35$ ; electronic supplementary material S3).

Multivariate simple regressions were performed to determine whether 2D:4D ratio of right hand, 2D:4D of left hand and difference between right and left 2D:4D ( $Dr-1$ ) were significant predictors of voice frequency, and rated attractiveness and masculinity. Voice frequency and voice attractiveness were predicted neither by the right 2D:4D ratio,  $Dr-1$  (table 1) nor left 2D:4D (electronic supplementary material S4). Voice masculinity was predicted only by left 2D:4D when non-pill users were taken into account (electronic supplementary material S4).

#### (b) *Body odour*

The correlation between masculinity and attractiveness of males' body odours was significantly negative ( $r = -0.54$ ,  $n = 28$ ,  $p = 0.003$ ). Average ratings of the pill users and non-pill users did not differ (attractiveness:  $t_{27} = 0.44$ ,  $p = 0.66$ ; masculinity:  $t_{27} = 0.01$ ,  $p = 0.99$ ; electronic supplementary material S3).

As for voice ratings, multivariate simple regressions were performed to determine whether 2D:4D ratio of right and left hand were significant predictors of body odour attractiveness and masculinity. There were significant effects for 2D:4D of the right hand only. Although masculinity was not predicted by 2D:4D (right, left,  $Dr-1$ ), attractiveness was (by right 2D:4D) when only non-pill users were taken into account (table 1; electronic supplementary material S4).

#### (c) *Face*

First, masculinity was correlated neither with attractiveness (short-term attractiveness:  $r = 0.15$ ,  $p = 0.30$ ; long-term attractiveness:  $0.24$ ,  $p = 0.10$ ;  $n = 47$ ) nor with face symmetry (perceived by females:  $r = 0.20$ ,  $p = 0.17$ ; measured in PSYCHOMORPH:  $r = 0.05$ ,  $p = 0.73$ ;  $n = 47$ ). Long-term and short-term attractiveness were highly correlated ( $r = 0.96$ ,  $n = 47$ ,  $p < 0.001$ ), and symmetry rated and perceived were correlated too ( $r = 0.39$ ,  $n = 47$ ,  $p < 0.01$ ). Attractiveness was correlated with perceived face symmetry (short-term attractiveness:  $r = 0.67$ ,  $p < 0.001$ ; long-term attractiveness:  $0.66$ ,  $p < 0.001$ ;  $n = 47$ ), but not (or only marginally) with measured face asymmetry (short-term attractiveness:  $r = -0.22$ ,  $p = 0.14$ ; and long-term attractiveness:  $r = -0.28$ ,  $p = 0.06$ ;  $n = 47$ ). Contrary to odours, mean face ratings of the pill users and non-pill users significantly differed. Compared with pill users, non-pill users gave higher attractiveness (short-term:  $t_{46} = 1.99$ ,  $p = 0.052$ ; long-term:  $t_{46} = 6.06$ ,  $p < 0.001$ ), higher masculinity ( $t_{46} = 4.59$ ,  $p < 0.001$ ) and higher symmetry ratings ( $t_{46} = 8.03$ ,  $p < 0.001$ ; electronic supplementary material S3).

As for voice and odour ratings, multivariate simple regressions were performed to determine whether right 2D:4D, left 2D:4D and  $Dr-1$  were significant predictors of face attractiveness, symmetry and masculinity. There were significant effects for 2D:4D of the right hand and for the right–left difference  $Dr-1$  (table 1). Long-term and short-term attractiveness were significantly predicted by right 2D:4D and by  $Dr-1$ . Perceived symmetry was predicted by right 2D:4D only, and face masculinity was not predicted by any of the 2D:4D variables. These results remained unchanged when pill users and non-pill users are analysed separately.

### 4. DISCUSSION

In this study, we tested whether second-to-fourth digit ratio (2D:4D) of left hand, right hand and right-minus-left hand ( $Dr-1$ ), can predict male masculinity and attractiveness for three sensory modalities involved in human mate choice: voice, body odour and face. Our main finding is that right hand 2D:4D and  $Dr-1$  are significant predictors of attractiveness, but not masculinity of male faces, whether they are considered as short-term or long-term potential partners. Right hand 2D:4D also predicts perceived facial symmetry. The link between 2D:4D and facial attractiveness is consistent with previous studies investigating either self-evaluated attractiveness [22,23] or men's attractiveness rated by women [22,24]. This illustrates a female preference for men with a low 2D:4D ratio possibly driven by the fact that these have more symmetrical faces. Such a preference might have evolved because it increases females' reproductive success by gaining benefits from partners who are physically more robust [1] and who have more fertile ejaculates [43,44].

Our results differ from other studies that found a significant relationship between dominant/masculine personality traits and 2D:4D [45], and from a study by Neave *et al.* [20], who report a similar negative association between 2D:4D ratio (of both hands) and masculinity, but not attractiveness. However, our results and those of Neave *et al.* [20] are not necessarily contradictory. Indeed, men who are able to pay costs of high levels of testosterone [12] will

Table 1. Link between digit ratio (2D:4D) of the right-hand and right-minus-left 2D:4D (Dr-1), and voice, odour and face characteristics of 49 men, determined by a simple linear regression (voice pitch,  $r^2$ ) and multivariate linear regressions (other measures,  $\beta$ ). ST, short-term partner; LT, long-term partner; d.f., degrees of freedom. A negative  $\beta$ -value indicates an inverse relationship between 2D:4D ratio and the dependent variable. Results for left 2D:4D are presented in electronic supplementary material S4.

modality	raters	dimension	right 2D:4D				right-minus-left 2D:4D (Dr-1)			
			Wilks' $\lambda$	$r^2/\beta$	F(d.f.)	p	Wilks' $\lambda$	$r^2/\beta$	F(d.f.)	p
voice	n.a.	frequency	0.96	0.02	(1,46) 0.88	0.353	0.01	(1,46) 0	0.949	
	total	attractiveness		0.19	(1,46) 1.78	0.198	0.05	(1,46) 0.10	0.749	
		masculinity		0.17	(1,46) 1.43	0.237	-0.04	(1,46) 0.09	0.771	
	pill users	attractiveness		0.97	0.18	(1,46) 1.58	0.215	0.01	(1,46) 0.01	0.924
masculinity			0.95	0.16	(1,46) 1.16	0.287	-0.02	(1,46) 0.02	0.881	
odour	non-pill users	attractiveness		0.20	(1,46) 1.82	0.183	0.09	(1,46) 0.37	0.547	
		masculinity		0.19	(1,46) 1.77	0.190	-0.07	(1,46) 0.24	0.625	
	total	attractiveness		0.89	0.25	(1,26) 1.78	0.193	0.09	(1,26) 0.24	0.632
		masculinity		0.90	-0.32	(1,26) 2.98	0.096	-0.27	(1,26) 2	0.169
face	pill users	attractiveness		0.05	(1,26) 0.06	0.811	-0.04	(1,26) 0.05	0.831	
		masculinity		0.85	-0.31	(1,26) 2.81	0.105	-0.06	(1,26) 0.11	0.745
	non-pill users	attractiveness		0.38	(1,26) 4.38	0.046*	0.36	(1,26) 3.96	0.057	
		masculinity		0.76*	-0.10	(1,26) 0.25	0.618	-0.23	(1,26) 1.45	0.239
total	attractiveness ST			-0.42	(1,45) 9.59	0.003**	-0.33	(1,45) 5.51	0.023*	
		attractiveness LT		-0.43	(1,45) 10.49	0.002**	-0.35	(1,45) 6.48	0.014*	
	symmetry perceived	asymmetry measured		-0.41	(1,45) 9.17	0.004**	-0.25	(1,45) 3.07	0.086	
		masculinity		0.79*	0.29	(1,45) 4.05	0.050	0.20	(1,45) 1.78	0.188
pill users	attractiveness ST			-0.20	(1,45) 1.79	0.187	-0.02	(1,45) 0.02	0.903	
		attractiveness LT		-0.41	(1,45) 8.86	0.005**	-0.30	(1,45) 4.61	0.037*	
	symmetry perceived	masculinity		-0.41	(1,45) 9.26	0.004**	-0.38	(1,45) 7.66	0.008**	
		masculinity		-0.40	(1,45) 8.45	0.006**	-0.25	(1,45) 3	0.090	
non-pill users	attractiveness ST			-0.21	(1,45) 2.17	0.148	-0.01	(1,45) 0.01	0.921	
		attractiveness LT		0.78*	(1,45) 8.83	0.005**	-0.34	(1,45) 5.94	0.019*	
	symmetry perceived	masculinity		-0.44	(1,45) 10.89	0.002**	-0.32	(1,45) 5.16	0.028*	
		masculinity		-0.38	(1,45) 7.51	0.009**	-0.23	(1,45) 2.47	0.123	
total	attractiveness		-0.19	(1,45) 1.71	0.198	-0.05	(1,45) 0.11	0.737		

\* $p < 0.05$ .\*\*\* $p < 0.01$ .

consequently develop masculine phenotypes [15]. At the same time, symmetric faces are likely to be found in individuals who have a better developmental stability [13], which reflects a better resistance to parasites and poor environmental conditions [46]. Therefore, some particularly good-quality males should express simultaneously masculine and symmetric faces. Thus, one could expect 2D:4D to predict both face masculinity and symmetry, and the fact that only one of these predictions was found in our study and that of Neave *et al.* [20] might be an effect of sampling or of differences in 2D:4D measurement procedure. These effects are likely to be subtle, since other studies failed, as we did, to find a link between 2D:4D ratio and masculinity features [21].

Replication of our findings, the direction of which contradicts another study on 2D:4D and facial symmetry [47], would thus be worthwhile. Furthermore, future research will be necessary to better understand the relationship between prenatal androgen exposure and adult face attractiveness. Our study cannot directly address the mechanism underlying this relationship, and the present results provide no evidence that prenatal testosterone is the causal factor of both low 2D:4D and high attractiveness (via face symmetry). Indeed, it may be possible that the causal factor that explains the relationship between 2D:4D and attractiveness is situated at another level. For example, a high level of parental attractiveness, because it reflects genetic quality, might provide the foetus with both 'good genes' (high level of testosterone) and a healthy prenatal environment allowing high developmental stability.

The significant link we found between male facial attributes and 2D:4D ratio was observed only for the right hand, which has a more male-like ratio than the left hand (right: mean = 0.97, s.d. = 0.03; left: mean = 0.98, s.d. = 0.02;  $t_{48} = 3.57$ ,  $p < 0.001$ ). This result supports the assumption of Tanner (1990, cited in [1]), according to which 'sexually dimorphic traits tend to be expressed in the male form more strongly on the right side of the body'. This side-related difference is also supported by Manning *et al.* [43], who found stronger association between testosterone levels and 2D:4D ratios on the right hand compared with the left hand, as well as by other authors [4]. These authors hypothesize a stronger action of androgens on the digits of the right hand (see [48] for a meta-analysis).

Surprisingly, we found a positive relationship between 2D:4D ratios of men and the evaluation of their body odour attractiveness and voice masculinity by the non-pill users. This result is contrary to our predictions and deserves further investigation, especially taking into account the impact of cycle stage on this kind of evaluation. In this respect, we found that spontaneously ovulating women gave higher facial attractiveness, masculinity and symmetry ratings than pill users, which is concordant with previous studies showing that fertile women prefer less feminized [49] and more symmetrical male faces [50] (but see [51]). However, this result was not confirmed in the second group of females who evaluated the faces, which might be due to the proportion of women being in their fertile phase during data collection, a factor that we did not control.

The fact that 2D:4D does not reliably predict voice and body odour attractiveness or masculinity is not

owing to the fact that different groups of females rated faces and voices. Indeed, not only were both groups highly correlated, but we also performed the regressions of table 1 and electronic supplementary material S4 again with the data of the 'voice raters' group and the results were replicated (the only difference being a lower level of significance for the effects in pill users; detail of the results not presented here). Rather, this absence of relationship between 2D:4D ratio and vocal and olfactory traits might stem from the fact that voice and body odour are by nature more variable than facial shape and more related to current circulating levels of testosterone in the adult individual (but see [52]). Consistent with this hypothesis, Evans *et al.* [14] found that voice frequency is related to the level of circulating testosterone but not to the indicator of prenatal testosterone level 2D:4D (see also [53,54]), whereas the reverse was found for faces [20] (but see [15]). Altogether, these results raise the question of the relative dissociation between organizational and activational effects of testosterone [8], organizational effects being irreversible and occurring during sensitive periods of early development, and activational ones being impermanent and occurring in adulthood. Foetal testosterone might serve to organize certain features of the face, like bones (jaws and cheek bones) that will subsequently be activated during puberty and remain relatively stable thereafter. On the contrary, voice is produced by the larynx, which is made of muscles and cartilage, and body odour consists in the degradation of products of the metabolism by skin bacteria; both of them are likely to change at any time under the influence of circulating hormones. Indeed, voice quality significantly changes with therapeutic administration of testosterone (e.g. [55]) or more subtly with normal daily variations of testosterone concentration [14], and some major compounds of axillary odours are by-products of androgen substances [29].

## 5. CONCLUSION

Our study suggests that both right 2D:4D and right-minus-left 2D:4D ( $Dr-1$ ) are good predictors of facial attractiveness in men, but not of their voice or body odour attractiveness. We showed, for the first time, that this effect might be supported by the link between 2D:4D and face symmetry, one indicator of male quality. Physical features closely linked to foetal levels of testosterone, such as face shape, are more likely to be correlated with second-to-fourth digit ratios than traits believed to be directly controlled by circulating testosterone later in life history (voice and body odour). We advocate that more research is needed to investigate the action of both early and adult testosterone levels on the development of sexually dimorphic traits involved in human attractiveness, including those we have examined here. The present study suggests that masculine and attractive features of voice and body odour might not be shaped *in utero* but later during life history: the timing (and even the existence, for body odour) of an action of testosterone on these two modalities remains to be elucidated in the future.

All participants gave their written informed consent, and the study was approved by the Committee on Research Ethics of the University of Liverpool and of the University of Stirling.

The authors wish to thank the participants, Kirsty Elliott and Marta Vondrova for their help in data collection, Rob Burriss, Hannah Rowland and Tamsin Saxton for technical advice, and Bernard Tiddeman and David Perrett for use of the PSYCHOMORPH software. One anonymous reviewer and Markus Rantala are also thanked for their constructive comments on the article. This research was supported by Fyssen Foundation, Paris.

## REFERENCES

- Manning, J. T. 2002 *Digit ratio: a pointer to fertility, behavior, and health*. New Brunswick, NJ: Rutgers University Press.
- Nelson, E. & Shultz, S. 2010 Finger length ratios (2D:4D) in anthropoids implicate reduced prenatal androgens in social bonding. *Am. J. Phys. Anthropol.* **141**, 395–405. (doi:10.1002/ajpa.21157)
- Burley, N. T. & Foster, V. S. 2004 Digit ratio varies with sex, egg order and strength of mate preference in zebra finches. *Proc. R. Soc. Lond. B* **271**, 239–244. (doi:10.1098/rspb.2003.2562)
- Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R. & Manning, J. T. 2004 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Hum. Dev.* **77**, 23–28. (doi:10.1016/j.earlhumdev.2003.12.002)
- Breedlove, S. M. 2010 Minireview: organizational hypothesis: instances of the fingerpost. *Endocrinology* **151**, 4116–4122. (doi:10.1210/en.2010-0041)
- van Honk, J., Schutter, D. J., Bos, P. A., Kruijt, A., Lentjes, E. G. & Baron-Cohen, S. 2011 Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proc. Natl Acad. Sci. USA* **108**, 3448–3452. (doi:10.1073/pnas.1011891108)
- Okten, A., Kalyoncu, M. & Yariş, N. 2002 The ratio of second- and fourth-digit lengths and congenital adrenal hyperplasia due to 21-hydroxylase deficiency. *Early Hum. Dev.* **70**, 47–54. (doi:10.1016/S0378-3782(02)00073-7)
- Neave, N. 2008 *Hormones and behaviour: a psychological approach*. Cambridge, UK: Cambridge University Press.
- Andersson, M. B. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Reed, W. L., Clark, M. E., Parker, P. G., Raouf, S. A., Arguedas, N., Monk, D. S., Snajdr, E., Nolan, V. & Ketterson, E. D. 2006 Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *Am. Nat.* **167**, 667–683. (doi:10.1086/503054)
- Mills, S. C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T. & Poikonen, T. 2010 Fitness trade-offs mediated by immunosuppression costs in a small mammal. *Evolution* **64**, 166–179. (doi:10.1111/j.1558-5646.2009.00820.x)
- Folstad, I. & Karter, A. J. 1992 Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**, 603–622. (doi:10.1086/281919)
- Thornhill, R. & Gangestad, S. W. 1999 The scent of symmetry: a human sex pheromone that signals fitness? *Evol. Hum. Behav.* **20**, 175–201. (doi:10.1016/S1090-5138(99)00005-7)
- Evans, S., Neave, N., Wakelin, D. & Hamilton, C. 2008 The relationship between testosterone and vocal frequencies in human males. *Physiol. Behav.* **93**, 783–788. (doi:10.1016/j.physbeh.2007.11.033)
- Penton-Voak, I. S. & Chen, J. Y. 2004 High salivary testosterone is linked to masculine male facial appearance in humans. *Evol. Hum. Behav.* **25**, 229–241. (doi:10.1016/j.evolhumbehav.2004.04.003)
- Pound, N., Penton-Voak, I. S. & Surridge, A. K. 2009 Testosterone responses to competition in men are related to facial masculinity. *Proc. R. Soc. B* **276**, 153–159. (doi:10.1098/rspb.2008.0990)
- Saxton, T. K., Debruine, L. M., Jones, B. C., Little, A. C. & Roberts, S. C. 2009 Face and voice attractiveness judgments change during adolescence. *Evol. Hum. Behav.* **30**, 398–408. (doi:10.1016/j.evolhumbehav.2009.06.004)
- Little, A. C., Saxton, T. K., Roberts, S. C., Jones, B. C., Debruine, L. M., Vukovic, J., Perrett, D. I., Feinberg, D. R. & Chenore, T. 2010 Women's preferences for masculinity in male faces are highest during reproductive age range and lower around puberty and post-menopause. *Psychoneuroendocrinology* **35**, 912–920. (doi:10.1016/j.psyneuen.2009.12.006)
- Jamison, S. C., Meier, R. J. & Campbell, B. C. 1993 Dermatoglyphic asymmetry and testosterone levels in normal males. *Am. J. Phys. Anthropol.* **90**, 185–198. (doi:10.1002/ajpa.1330900205)
- Neave, N., Laing, S., Fink, B. & Manning, J. T. 2003 Second to fourth digit ratio, testosterone and perceived male dominance. *Proc. R. Soc. Lond. B* **270**, 2167–2172. (doi:10.1098/rspb.2003.2502)
- Koehler, N., Simmons, L. W. & Rhodes, G. 2004 How well does second-to-fourth-digit ratio in hands correlate with other indications of masculinity in males? *Proc. R. Soc. Lond. B* **271**, S296–S298. (doi:10.1098/rsbl.2004.0163)
- Bogaert, A. F., Fawcett, C. C. & Jamieson, L. K. 2009 Attractiveness, body size, masculine sex roles and 2D:4D ratios in men. *Pers. Individ. Dif.* **47**, 273–278. (doi:10.1016/j.paid.2009.03.011)
- Manning, J. T. & Quinton, S. 2007 Association of digit ratio (2D:4D) with self-reported attractiveness in men and women: evidence from the BBC internet survey. *J. Individ. Dif.* **28**, 73–77. (doi:10.1027/1614-0001.28.2.73)
- Roney, J. R. & Maestripieri, D. 2004 Relative digit lengths predict men's behavior and attractiveness during social interactions with women. *Hum. Nat.* **15**, 271–282. (doi:10.1007/s12110-004-1009-5)
- Collins, S. 2000 Men's voices and women's choices. *Anim. Behav.* **60**, 773–780. (doi:10.1006/anbe.2000.1523)
- Havlicek, J., Saxton, T. K., Roberts, S. C., Jozifkova, E., Lhota, S., Valentova, J. & Flegr, J. 2008 He sees, she smells? Male and female reports of sensory reliance in mate choice and non-mate choice contexts. *Pers. Individ. Dif.* **45**, 565–570. (doi:10.1016/j.paid.2008.06.019)
- Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. J. 1995 MHC-dependent mate preferences in humans. *Proc. R. Soc. Lond. B* **260**, 245–249. (doi:10.1098/rspb.1995.0087)
- Bird, S. & Gower, D. B. 1981 The validation and use of a radioimmunoassay for 5 alpha-androst-16-en-3-one in human axillary collections. *J. Steroid Biochem.* **14**, 213–219. (doi:10.1016/0022-4731(81)90176-X)
- Rennie, P. J., Holland, K. T., Mallet, A. I., Watkins, W. J. & Gower, D. B. 1989 Testosterone metabolism by human axillary bacteria. *Biochem. Soc. Trans.* **17**, 1017–1018. (doi:10.1042/bst0171017)
- Havlicek, J., Murray, A. K., Saxton, T. K. & Roberts, S. C. 2010 Current issues in the study of androstenes in human chemosignalling. *Vitam. Horm.* **83**, 47–81. (doi:10.1016/S0083-6729(10)83003-1)
- Manning, J. T., Bundred, P. E., Newton, D. J. & Flanagan, B. F. 2003 The second to fourth digit ratio and variation in the androgen receptor gene. *Evol. Hum. Behav.* **24**, 399–405. (doi:10.1016/S1090-5138(03)00052-7)

- 32 Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. *Behav. Genet.* (doi:10.1007/s10519-010-9404-7)
- 33 Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. *Anim. Behav.* **69**, 561–568. (doi:10.1016/j.anbehav.2004.06.012)
- 34 Grammer, K. & Thornhill, R. 1994 Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *J. Comp. Psychol.* **108**, 233–242. (doi:10.1037/0735-7036.108.3.233)
- 35 Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. *Evol. Hum. Behav.* **20**, 295–307. (doi:10.1016/S1090-5138(99)00014-8)
- 36 Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? *Trends Ecol. Evol.* **25**, 171–179. (doi:10.1016/j.tree.2009.08.003)
- 37 Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proc. R. Soc. B* **275**, 2715–2722. (doi:10.1098/rspb.2008.0825)
- 38 Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? *Chem. Senses* **34**, 565–571. (doi:10.1093/chemse/bjp037)
- 39 Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. *Chem. Senses* **31**, 747–752. (doi:10.1093/chemse/bjl017)
- 40 Fairbanks, G. 1960 *Voice and articulation drillbook*. New York, NY: Harper and Row.
- 41 Scheib, J. E., Gangestad, S. W. & Thornhill, R. 1999 Facial attractiveness, symmetry and cues of good genes. *Proc. R. Soc. Lond. B* **266**, 1913–1917. (doi:10.1098/rspb.1999.0866)
- 42 Manning, J. T., Baron-Cohen, S., Wheelwright, S. & Fink, B. 2010 Is digit ratio (2D:4D) related to systemizing and empathizing? Evidence from direct finger measurements reported in the BBC internet survey. *Pers. Individ. Dif.* **48**, 767–771. (doi:10.1016/j.paid.2010.01.030)
- 43 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 concentrations of testosterone, luteinizing hormone and oestrogen. *Hum. Reprod.* **13**, 3000–3004. (doi:10.1093/humrep/13.11.3000)
- 44 Auger, J. & Eustache, F. In press. Second to fourth digit ratios, male genital development and reproductive health: a clinical study among fertile men and testis cancer patients. *Int. J. Androl.* (doi:10.1111/j.1365-2605.2010.01124.x)
- 45 Manning, J. T. & Fink, B. 2008 Digit ratio (2D:4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet Study. *Am. J. Hum. Biol.* **20**, 451–461. (doi:10.1002/ajhb.20767)
- 46 Rhodes, G. 2006 The evolutionary psychology of facial beauty. *Annu. Rev. Psychol.* **57**, 199–226. (doi:10.1146/annurev.psych.57.102904.190208)
- 47 Fink, B., Manning, J. T., Neave, N. & Grammer, K. 2004 Second to fourth digit ratio and facial asymmetry. *Evol. Hum. Behav.* **25**, 125–132. (doi:10.1016/S1090-5138(03)00084-9)
- 48 Hönekopp, J. & Watson, S. 2010 Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand. *Am. J. Hum. Biol.* **22**, 619–630. (doi:10.1002/ajhb.21054)
- 49 Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Menstrual cycle alters face preference. *Nature* **399**, 741–742. (doi:10.1038/21557)
- 50 Little, A. C., Jones, B. C., Burt, D. M. & Perrett, D. I. 2007 Preferences for symmetry in faces change across the menstrual cycle. *Biol. Psychol.* **76**, 209–216. (doi:10.1016/j.biopsycho.2007.08.003)
- 51 Peters, M., Simmons, L. W. & Rhodes, G. 2009 Preferences across the menstrual cycle for masculinity and symmetry in photographs of male faces and bodies. *PLoS ONE* **4**, e4138. (doi:10.1371/journal.pone.0004138)
- 52 Rantala, M. J., Eriksson, C. J. P., Vainikka, A. & Kortet, R. 2006 Male steroid hormones and female preference for male body odor. *Evol. Hum. Behav.* **27**, 259–269. (doi:10.1016/j.evolhumbehav.2005.11.002)
- 53 Hughes, S. M., Harrison, M. A. & Gallup, G. G. 2002 The sound of symmetry: voice as a marker of developmental instability. *Evol. Hum. Behav.* **23**, 173–180. (doi:10.1016/S1090-5138(01)00099-X)
- 54 Puts, D. A., Gaulin, S. J. C., Sporter, R. J. & McBurney, D. H. 2004 Sex hormones and finger length. What does 2D:4D indicate? *Evol. Hum. Behav.* **25**, 182–199. (doi:10.1016/j.evolhumbehav.2004.03.005)
- 55 Akcam, T., Bolu, E., Merati, A. L., Durmus, C., Gerek, M. & Ozkaptan, Y. 2004 Voice changes after androgen therapy for hypogonadotrophic hypogonadism. *Laryngoscope* **114**, 1587–1591. (doi:10.1097/00005537-200409000-00016)