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ORIGINAL ARTICLE

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Length of index and ring fingers differentially influence sexual attractiveness of men's and women's hands

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Abstract Humans show intra- and intersexual variation in second (2D) relative to fourth (4D) finger length, men having smaller 2D:4D ratio, possibly because of differential exposure to sex hormones during fetal life. The relations between 2D:4D and phenotypic traits including fitness components reported by several studies may originate from the organizational effects that sex hormones have on diverse organs and their concomitant effect on 2D:4D. Evolutionary theory posits that sexual preferences are adaptations whereby choosy individuals obtain direct or genetic indirect benefits by choosing a particular mate. Since sex hormones influence both fitness and 2D:4D, hand sexual attractiveness should depend on 2D:4D, a hypothesis tested only in one correlational study so far. We first presented hand computer images to undergraduates and found that opposite-sex hands with long 2D and 4D were considered more sexually attractive. When we experimentally manipulated hand images by increasing or decreasing 2D and/or 4D length, women preferred opposite-sex hands that had been masculinized by elongating 4D, whereas men avoided masculinized opposite-sex right hands with shortened 2D. Hence, consensus exists about which hands are attractive among different opposite-sex judges. Finger length may signal desirable sex hormone-dependent traits or genetic quality of potential mates. Psychological mechanisms mediating hand attractiveness judgments may thus reflect adaptations functioning to provide direct or indirect benefits to choosy individuals. Because the genetic mechanisms that link digit development to sex hormones may be mediated by *Hox* genes which are conserved in vertebrates, present results have broad implications for sexual selection studies also in nonhuman taxa.

Keywords Attractiveness · Digit length · Digit ratios · Hand esthetics · Mate choice · Sexual selection

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Introduction

In humans, males have consistently smaller length ratio between the index (2D) and the ring (4D) fingers compared to women (Manning 2002; McFadden and Shubel 2002; Peters et al. 2002; Romano et al. 2006; Saino et al. 2006). Studies of nonhuman primates and rodents have also documented sexual dimorphism in length ratios between 2D and 4D (2D:4D) (Manning et al. 2003a; McFadden and Bracht 2003; Roney et al. 2004; Leoni et al. 2005). Sex-related variation in 2D:4D has been attributed to differential exposure of the two sexes to androgens and estrogens during fetal life, with high levels of androgens resulting in small 2D:4D (Manning et al. 1998; Brown et al. 2002; Okten et al. 2002; Lutchmaya et al. 2004; but see Romano et al. 2005). However, variation in the hormone environment during early ontogeny may also explain within-sex variation in 2D:4D (Manning et al. 2003b; van Anders et al. 2006).

2D:4D correlates with several morphological, physiological, behavioral, and performance traits in humans (see Manning 2002 for a review; see also Putz et al. 2004 for references), and these relations have been attributed to the concomitant effects of sex hormones on 2D:4D and their organizational effects on diverse organ systems (Becker et al. 1992; Sisk et al. 2003). The possible positive association between prenatal and pubertal or adult androgens (e.g., Jamison et al. 1993) may also result in a correlation between 2D:4D and testosterone-dependent traits that are expressed at puberty or later. Consistent with this prediction, negative relations exist between masculinization of men's faces or perceived social dominance and 2D:4D (Neave et al. 2003; Bailey and Hurd 2005; but see

Koehler et al. 2004). Small 2D:4D in men and large 2D:4D in women have been shown to be associated with high phenotypic values of fitness components such as reproductive success, general vigor, aggressiveness, or intellectual skills (references in Putz et al. 2004). In addition, men with small 2D:4D have been shown to be more sexually attractive overall, in a study where hand attractiveness per se was not investigated (Roney and Maestripieri 2004).

Honest-advertisement evolutionary models of sexual selection posit that secondary sexual characters reliably signal genetic and/or phenotypic desirable traits (see Andersson 1994 for a review). Opposite-sex preference for such traits may have evolved because of direct fitness benefits accruing to the choosy individuals, such as acquisition of limiting resources, or indirect benefits, in terms of transmission to the progeny of high-quality genes that are advertised by secondary sex traits (see Andersson 1994 for a review).

Studies of humans have analyzed the role of face, anthropometric indexes (e.g., waist-to-hip ratio), fluctuating asymmetry, and other characters on sexual attractiveness (e.g., Penton-Voak et al. 2004; Fan et al. 2005; and references therein). Part of this research has focused on masculinity/femininity in an attempt to identify adaptive opposite-sex preferences for fitness-related traits dependent on sex hormones.

Because hand morphology depends on fetal sex hormones, and variation in exposure to sex hormones affects development and possibly fitness, morphology of hands should predict their sexual attractiveness. However, we are aware of only one preliminary study of hand attractiveness. In his seminal book on human digit ratios, Manning (2002) summarized evidence showing positive correlations between opposite-sex ratings of hand attractiveness and 2D or 4D length (Manning 2002, p. 48; see also "Discussion"). This substantial lack of information seems surprising because people are apparently paying attention to own and others' hand esthetics, as witnessed by the considerable, although hardly quantifiable, amount of money that are spent on hand cosmetics and ornaments. In a preliminary survey of undergraduates, the vast majority of the respondents rated hands as either moderately or quite important in the judgment of the overall attractiveness of potential sexual partners, whereas very few considered them as negligible (our unpublished data).

In the present paper, we report on two studies. In the first study (study 1), we tested whether sexual attractiveness of opposite-sex hands is influenced by 2D and 4D length. We asked undergraduates to judge computer scans of hands and analyzed the correlation between attractiveness scores and length of 2D and 4D, and 2D:4D.

In the second study (study 2), we produced replicas of hand images by increasing or decreasing 2D and 4D length to alter 2D:4D within the natural range of variation as recorded in the same population of students under scrutiny. We then asked other undergraduates to judge the different versions of the hands for attractiveness.

We predicted that if opposite-sex preference exists for hands with extreme, sex-specific 2D:4D: (1) in the correlational study, men would have opposite-sex preference for large 2D:4D while the reverse would be true for women; (2) in the manipulative study, we predicted that males would judge females' hands with elongated 2D and shortened 4D as more attractive, whereas the reverse would be the case when females judged males' hands.

Materials and methods

Measurement of digits and digit ratios (2D:4D)

In both study 1 and study 2, before computer scanning of hands, (see below), a thin black line was drawn in the basal crease of the fingers while holding the second to fifth fingers parallel and forming an angle of 100–120° with the plane of the palm. A ruler with 1 mm ticks was always visible in the image (the ruler was canceled from the image that was presented for judgment). Images were analyzed using Adobe Photoshop 7.0 software. Length of fingers was measured from the distal tip to the midpoint of the line in the basal crease with an approximation of 0.1 mm (this approximation is reliable; see Romano et al. 2005). 2D:4D was computed for each hand (hereafter $2D:4D_L$ and, respectively, $2D:4D_R$ for the left and the right hand). At the time of enrollment, we also measured total body height to obtain measures of 2D and 4D corrected for an index of body size, height (H). The ratios between 2D or 4D and H will be indicated as $2D_L$:H or $4D_L$:H (left hand), and $2D_R$:H or $4D_R$:H (right hand).

Consistency of length ratio estimates was obtained by marking and measuring the same 19 left and 19 right hands four times on different days. One-way analyses of variance showed that all length ratios were highly repeatable within individual, indicating that the measures were reliable (repeatability calculated according to Falconer (1981): left hand: R=0.932; right hand: R=0.862; see Romano et al. 2005).

Study 1. Correlation between attractiveness scores and length ratios

The individuals (136 males and 136 females) whose hands were included in the correlational study were undergraduate or recently graduated Caucasian students from the Natural Sciences or Biology courses at the University of Milano. Ventral images of their hands due to be shown to judges were obtained using a computer scanner (Espon Perfection 1670) by placing the hand in a standard position relative to the body of the subject. The same image acquisition settings were applied to all hands. Color hand images were presented to 20 male and 26 female judges (see also below) who were asked to score hand attractiveness on a 0.5 (low)–10 (high) 20-level scale, by asking the following question: "How sexually attractive would you rate a man/women according to his/her hand shown here?" The images were shown each for 10 s by projecting them on a vertical white screen in the following order: males'

right hands; females' right hands; males' left hands; females' left hands. The order of presentation of the test hands was randomized within each sex by side group. All judges saw the hands in the same order. Judges were informed of the sex of the test individuals.

Study 2. Attractiveness of manipulated hands

We obtained color computer scans of hands of 25 male and 25 female students attending the Natural Sciences or Biology courses at the University of Milano as described for study 1, by always using the same scanner settings and an opaque black background to facilitate image editing and manipulation of apparent finger length. To manipulate hand morphology within the natural range of variation, we first estimated the standard deviation of 2D:4D for each sex and side in a large sample of undergraduates from the same university. The standard deviations of the mean 2D:4D recorded for 151 males were 0.027 for $2D:4D_L$ and 0.028 for $2D:4D_R$. The standard deviations for 182 female undergraduates were 0.026 for $2D:4D_L$ and 0.027 for $2D:4D_R$. Using Adobe Photoshop 7.0, we then produced six versions of each hand, modified as follows (see Fig. 1):

1) increased 2D:4D by 1 standard deviation by elongating 2D;
2) increased 2D:4D by 1 standard deviation by shortening 4D;
3) reduced 2D:4D by 1 standard deviation by shortening 2D;
4) reduced 2D:4D by 1 standard deviation by elongating 4D;
5) elongated 2D and 4D by the same length as in 1) and 4);
6) shortened 2D and 4D by the same length as in 2) and 3).

Hence, 2D:4D of the modified hands was within the natural range of variation.

The seven color versions (including the original, unmodified version) of each hand were presented consecutively, in random order, each for 10 s, to 16 male and 27 female unaware judges (see also below). The sexes by side groups were presented in the same order and scores of sexual attractiveness were given as in study 1. The order of the hands was randomized within each sex by side group. Judges knew that the seven versions presented consecutively belonged to the same individual and his/her sex.

Judges involved in both study 1 and study 2 were undergraduates from the Faculty of Sciences of the University of Milano. All judges declared of being unaware of the hypotheses being tested and having not read scientific or journalistic reports of studies of 2D:4D. In both studies, all judges scored the individuals of both sexes. However, only data for opposite-sex hand preferences are analyzed in the present study.

For each hand, mean scores given by individual opposite-sex judges were used in the analyses. Group statistics are given as mean followed by standard error in parentheses. Mixed model analyses of variance were run and least squares means (SE) were computed using "PROC MIXED" in SAS 9.0 (Littel et al.1996).

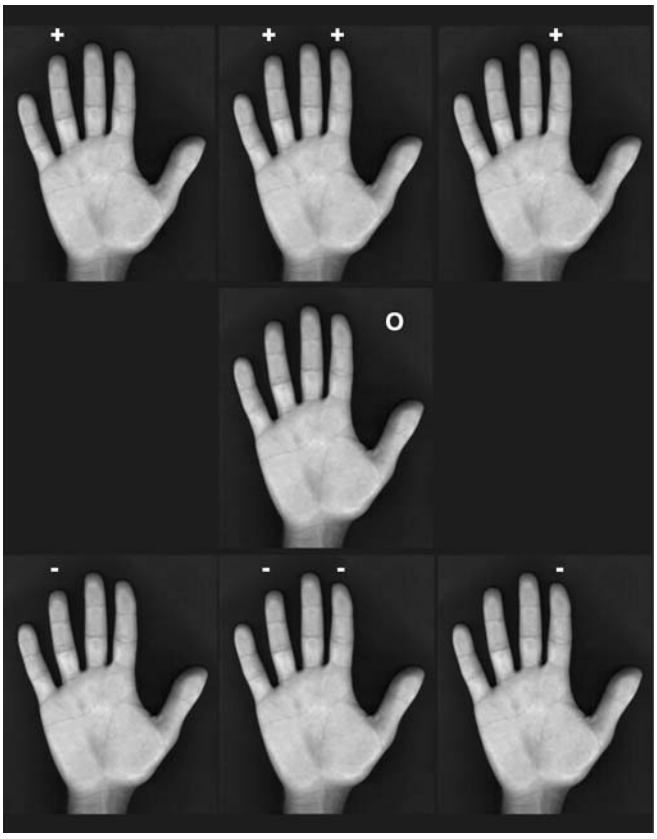

Fig. 1 Seven versions (in *gray scale*; color versions were presented to judges) of a male right hand presented to judges for attractiveness scoring. "O" indicates the unmodified hand. The *symbols* + *and* − indicate whether 2D or 4D was elongated or shortened so as to modify 2D:4D by 1 standard deviation (see "Materials and methods")

Results

Study 1. Correlation between attractiveness scores and length ratios

Judges of both sexes were highly consistent in their rating of hands. The mean of Fisher's *z*-transformed (Zar 1999) Pearson product–moment correlation coefficients resulting from correlation analyses between all possible pairs (n=190) of male judges was 0.458 [0.101 SD; range of the *z*-transformed correlation coefficients values: 0.213–0.737, mean p value associated to the correlation coefficients: 0.0003 (0.0015 SD)] for the left hands and 0.517 [0.124; range 0.219–0.868, mean p=0.0002 (0.0010 SD)] for the right hands of females. Mean correlation coefficients after *z*-transformation computed between all pairs (n=325) of female judges was 0.455 [0.114 SD; range: 0.087–0.927, mean p=0.0017 (0.019 SD)] for the left hands and 0.432 [0.134 SD; range 0.121–0.885, mean p=0.0036 (0.0178 SD)] for the right hands of males.

Attractiveness scores given by individual judges to opposite hands were positively correlated (males rating females: mean Fisher's z values=0.427 (0.133), range 0.191–0.829, mean p=0.0017 (0.0063 SD), n=20; females rating males: mean z=0.414 (0.115), range 0.138–0.688, mean p=0.0048 (0.0218 SD), n=26). However, the mean correlation coefficients were not as high as could possibly be expected, suggesting that the two hands were perceived as having different attractiveness. Asymmetry in judgment of opposite hands was confirmed in a comparison of scores given to the left and right hands of the same individual. Male judges scored females' left hands higher [mean score=5.26 (0.080)] than right hands [5.09 (0.091); t test for paired data: t_{135}=2.33, p=0.022]. Conversely, female judges scored males' left hands lower [4.95 (0.085)] than right hands [5.21 (0.093); t_{135}=3.34, p=0.001], implying that asymmetry in evaluation of opposite-sex hands varied according to sex. Side-related variation in ratings could be due to the order in which the hands of either side were presented, as raters scored all right hands before starting scoring left hands (see "Materials and methods"). However, this explanation seems unlikely because the side that was scored highest differed between the two sexes.

2D:4D of males or females did not predict opposite-sex attractiveness scores averaged among judges (Table 1). However, for individuals of both sexes, significant positive correlations were found between 2D or 4D length and mean attractiveness scores (Table 1; Fig. 2). Positive, statistically significant preference existed also for opposite-sex hands of both sides with large ratios between 2D or 4D and body height (2D:H or, respectively, 4D:H) (Table 1). These correlations were significant also after Bonferroni correction for ten simultaneous tests on the same individuals, with the exception of the correlation between the scores given by males and $2D_R$:H of females.

Table 1 Pearson r correlation coefficients between length of 2D or 4D, 2D:4D, or the ratio between 2D or 4D and body height (2D:H or 4D:H) and mean attractiveness scores given by male and female judges

Opposite-sex character	Correlation with scores given by	
	Males	Females
$2D_L$	0.266***	0.361****
$2D_R$	0.229**	0.339****
$4D_L$	0.321****	0.368****
$4D_R$	0.264***	0.320****
$2D:4D_L$	−0.130	−0.087
$2D:4D_R$	−0.088	0.001
$2D_L$:H	0.257***	0.282***
$2D_R$:H	0.198*	0.319****
$4D_L$:H	0.323****	0.306****
$4D_R$:H	0.243***	0.303****

All correlations are based on 136 males or females. All correlations marked as significant, except that between scores given by males and $2D_R$:H of females, would be significant also after sequential Bonferroni correction for ten simultaneous tests on the same individuals

*0.05>p≥0.01, **0.01>p≥0.005, ***0.005>p≥0.001, ****p<0.001; all tests have 134 degrees of freedom

Length of 2D was positively correlated with 4D in all sexes by side groups (r>0.85, n=136, p is always <0.001). This relationship was isometric, as demonstrated by reduced major axis (RMA) regression analysis (see Sokal and Rohlf 1995) on log-transformed measures of 2D on 4D (slope for males, left hand: 0.917, right hand: 0.960; females, left hand: 0.972, right hand: 0.968), because 95% confidence interval estimates based on a bootstrap procedure always included 1. However, RMA analyses of digit length on body height showed positive allometry for all digits in males (slope for $2D_L$: 1.408, $2D_R$: 1.426, $4D_L$: 1.536, $4D_R$: 1.486) and females (slope for $2D_L$: 1.536, $2D_R$: 1.544, $4D_L$: 1.607, $4D_R$: 1.595), as all 95% confidence intervals excluded 1.

Preference for long digits in males' hands may reflect a preference for tall men. In fact, directional selection on body height mediated by mate choice has been suggested to occur in men (e.g., Pawlowski et al. 2000; Mueller and Mazur 2001) but not women (e.g., Nettle 2002). Allometric variation of the length of 2D and 4D with body size may suggest that female raters used digit length as a clue to body height of males, using as reference characters other hand traits isometrically related to body height. While we have no data to directly test this idea, if perceived digit length indicates body height, a preference for long fingers should translate into higher rates for hand attractiveness being assigned to tall individuals. However, we found only weak evidence supporting this hypothesis because the correlation coefficient with body height was small, albeit statistically significant for scores given by females to left hands of males (r=0.20, p=0.022, n=136), whereas the correlation was nonsignificant for attractiveness scores given to males' right hands (r=0.13, p=0.14, n=136). Scores given by males to both hands of females were not significantly related to body height (left hand: r=0.08, p=0.36, n=136; right hand: r=0.09, p=0.28, n=136).

In none of the sexes by side groups did 2D:4D significantly predict body height (details not reported).

Study 2. Attractiveness of manipulated hands

The effect of finger length manipulation on mean attractiveness scores was analyzed in mixed-model analyses of variance where manipulation of 2D or 4D was included as fixed effects factors. In these analyses, a factor 'individual' was also included whose levels identified the seven hand versions from the same student. The effect of 'individual' was considered as random because we intended to consider the individuals whose hands were judged to be a random sample from all possible students in the population (see Zar 1999, p. 184). The sample included seven versions of hands of each side of 25 males and 25 females (see "Materials and methods").

Manipulation of 2D length had a significant effect on male judgment of females' right hands (Table 2; Fig. 3). Males scored females' hands with a reduced 2D length as

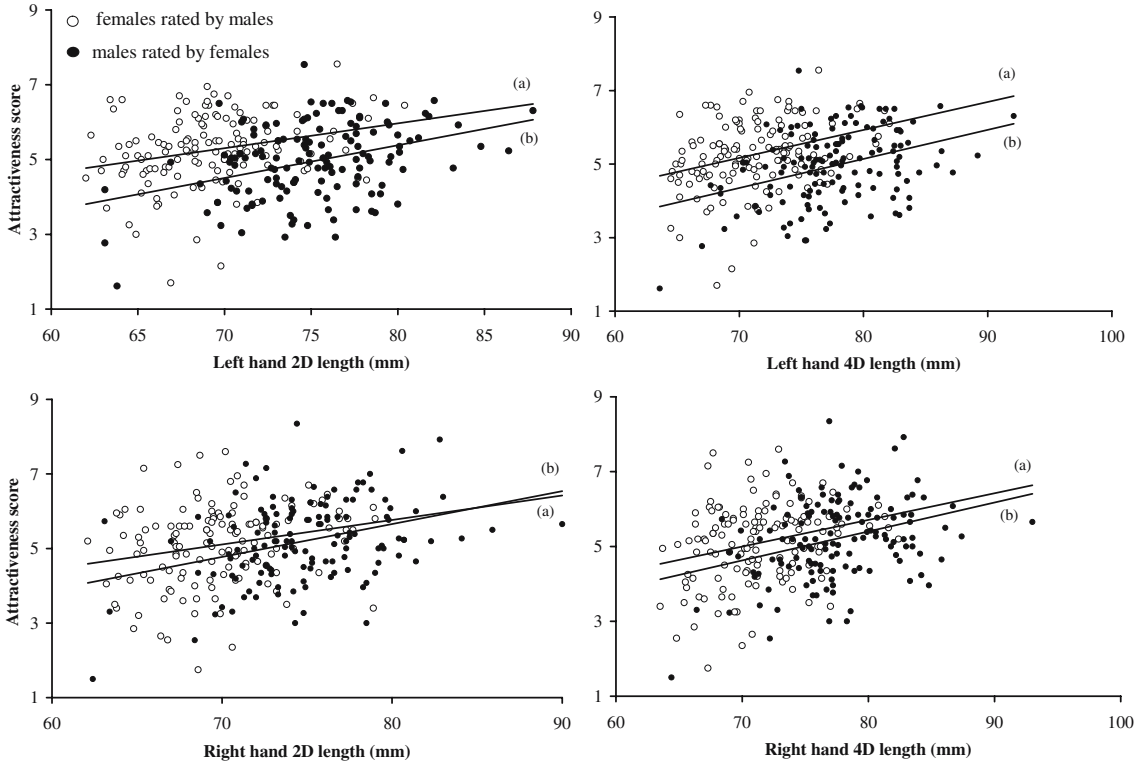

Fig. 2 Mean among-judges opposite-sex attractiveness scores given to hands of 136 females and 136 males in relation to 2D or 4D length (see Table 1). Linear regression lines for females (**a**) or males (**b**) are shown

less attractive than hands with unmodified or elongated 2D while controlling for manipulation of 4D. Thus, males scored as less attractive opposite-sex hands that had been masculinized. The effect of manipulation of left hand 2D or 4D on attractiveness scores given to females, however, was far from being statistically significant (Table 2).

Manipulation of 4D length of both hands of males had significant effects on mean rating by female judges (Table 2). Scores were maximal for hands with elongated 4D and minimal for hands with shortened 4D. Manipulation of 2D of either hands did not affect female opposite-sex preference (Table 2).

It must be emphasized that the effects of length manipulation of individual digits on attractiveness were tested while controlling statistically for the simultaneous effect of manipulation of the other digit (Table 2). Thus, for example, the evidence that elongation of 4D enhanced the attractiveness of males' right hands while 2D had no effect, in the absence of a significant interaction between treatments of 2D and 4D (see also Table 2), implies that for any given level of 2D treatment, 4D elongation resulted in higher attractiveness scores and, consequently, that hands with low 2D:4D were preferred because they displayed a relatively long 4D.

Discussion

The first main finding of this study is that judges were highly consistent in their appreciation of opposite-sex hand attractiveness. Thus, there appear to be a strict consensus among men and women about how attractive hands in the opposite sex look like. This may suggest that directional selection has led to the evolution of consistent judgment of hand attractiveness or, alternatively, that a sensory bias exists which enhances attractiveness of hands with a particular shape.

The second finding is that both men and women preferred hands with long fingers, despite the fact that no scaling elements were included in the hand images, and this was the case also when finger length was isometrically corrected for an index of body size, i.e., body height. This result suggests that judges assessed the absolute length of individual fingers relative to hand traits which are possibly allometrically related to each finger length. Consistent preference for long fingers then resulted in preference for hands with large finger length to height ratio.

We found no correlational support for the hypothesis that 2D:4D predicts opposite-sex ratings of hand attractiveness. Because digit length positively correlates with body height, the preference for males' hands with long digits in pictures with no scaling elements could reflect a preference for tall men (e.g., Mueller and Mazur 2001), if for example allometric variation of digit length with other hand traits provided information on the individual's height to the viewers. In addition, the possibility exists that other hand shape cues which covary with digit length to body height ratios provide information about an individual's stature. Martin and Nguyen (2004) have presented evidence that prenatal exposure to androgens may affect anthropometric

Table 2 Mixed-model analyses of variance of opposite-sex mean attractiveness scores given by male or female judges in relation to manipulation of the length of 2D or 4D (fixed effects)

Factor	*F*	Num *df*, Den *df*	*p*
Female left hands rated by males			
Manipulation of 2D	0.34	2, 146	0.71
Manipulation of 4D	0.45	2, 146	0.64
Female right hands rated by males			
Manipulation of 2D	11.45	2, 146	<0.0001[a]
Manipulation of 4D	0.70	2, 146	0.50
Male left hands rated by females			
Manipulation of 2D	0.44	2, 146	0.64
Manipulation of 4D	11.84	2, 146	<0.0001[b]
Male right hands rated by females			
Manipulation of 2D	2.59	2, 146	0.08
Manipulation of 4D	7.30	2, 146	0.0009[c]

Individual was included in the model as a random factor linking the seven versions of each hand. Each analysis is based on seven versions of the hands of 25 males or females

Results of pairwise comparisons with Bonferroni post hoc test:

[a]Shortening vs no manipulation: p=0.0001; shortening vs elongation: p<0.0001; no manipulation vs elongation: n.s.

[b]Shortening vs no manipulation: p=0.014; shortening vs elongation: p<0.0001; no manipulation vs elongation: p=0.011

[c]Shortening vs no manipulation: n.s.; shortening vs elongation: p=0.002; no manipulation vs elongation: p=0.004

Inclusion of the interaction between 2D and 4D manipulation showed that the effect of 4D manipulation depended on 2D manipulation only when females judged the left hands of males ($F_{1,144}$=6.52, p=0.002). The interaction arose because elongation of 4D resulted in higher scores when it was associated with no manipulation of 2D

indices such as hand width to length ratios and arm to body height ratios, suggesting that hand shape features may convey information about body size. However, we found only weak evidence that the pattern of hand preference resulted in variation of hand attractiveness scores in relation to body height, suggesting that either digit length was the actual target of the preference or, alternatively, that the information on body height provided by hand shape is not accurate enough to result in a strong positive correlation between hand scores and body height.

The correlational part of this study (study 1) provided results partly consistent with those in a preliminarily report of human hands attractiveness (see Manning 2002, p. 48), and supplementary unpublished information kindly provided by the author of that study on a positive correlation between opposite-sex attractiveness scores and 2D or 4D length of male but not female hands (J.T. Manning, personal communication). In addition, similarly to the present study (see Table 1), in Manning's correlational data, no significant association between hand attractiveness and 2D:4D could be detected (J.T. Manning, personal communication).

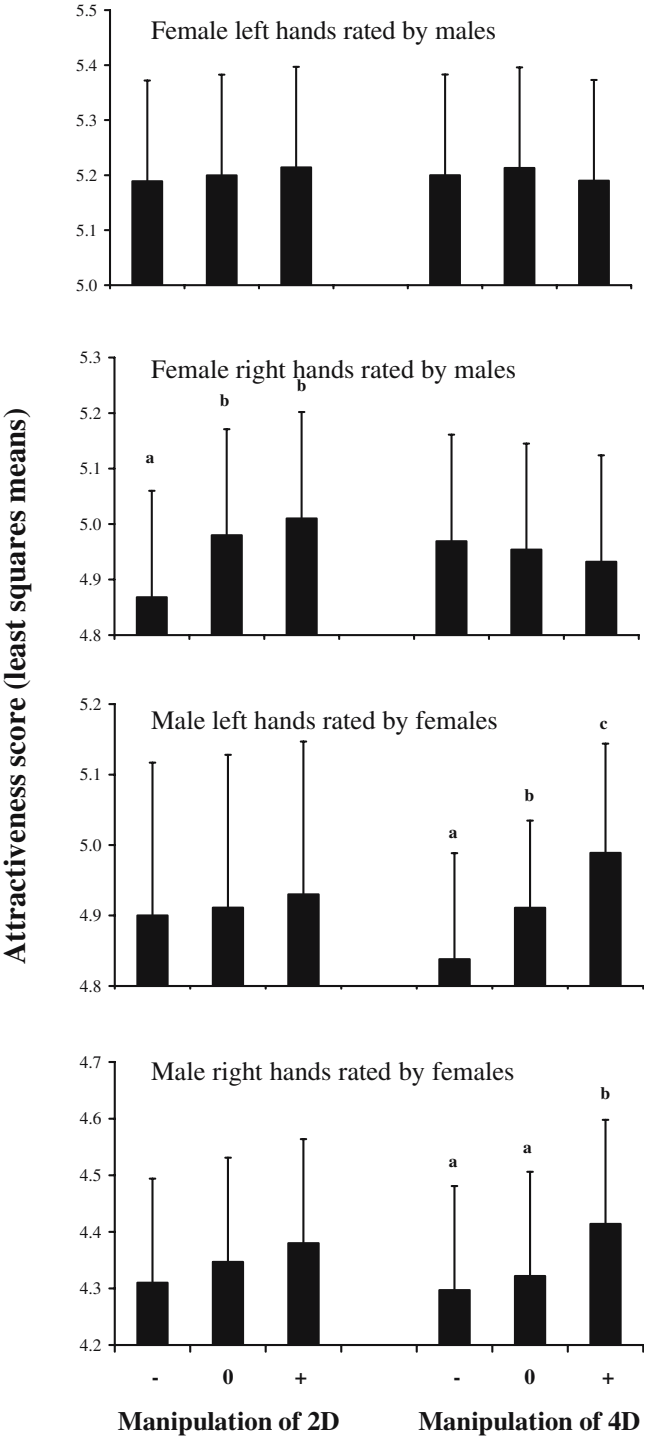

Fig. 3 Least square means (+SE) of attractiveness scores given by male or female judges to opposite-sex hands in relation to manipulation of 2D or 4D resulting from the mixed-model analyses of variance presented in Table 2. Least squares means estimate the marginal means over a balanced population. Fingers were shortened (−), elongated (+), or left unmodified (0) (see "Materials and methods"). *Different letters* in the body of the figure indicate that the difference between treatments was significant at a Bonferroni post hoc test according to the analyses presented in the footer of Table 2

These correlational studies, however, do not clarify which finger, if any in particular, was the target of the preference, as opposite-sex attractiveness scores were positively related to both 2D and 4D length in the present study as well as in the study of males' hands by Manning (see above). Direct preference could actually occur for either long 2D or 4D, and the correlation between attractiveness and the nonpreferred finger length could have arisen simply as a side effect of the relation between 2D and 4D length.

In study 2, the experimental manipulation of apparent finger length we applied demonstrated sex-specific preference for either long 2D or 4D. In fact, our third main finding is that men avoided opposite-sex right hands manipulated as to look more masculine (i.e., with a shortened 2D), while females preferred males' hands with more masculine shape, i.e., with elongated 4D. It should be noted that the issue of the preference for tall individuals we discussed above is not relevant to the interpretation of the finding that individuals of the two sexes were differentially influenced by the same manipulations of opposite-sex hands because we did not alter the appearance of any other hand traits except 2D and/or 4D.

At present, we have no explanation for the difference in the effect of 2D manipulation on male preference for opposite hands. Previous studies of health signaling in humans have also demonstrated facial asymmetry in the appearance of beauty (see Reis and Zaidel 2001). The sex-related variation in the difference between attractiveness of opposite hands and the sexual difference in the effect of finger manipulation on preference for left hands might suggest that the two hands have different roles in visual sexual attraction. Alternatively, the order of presentation of opposite hands may have influenced the rating of attractiveness, leading to less accurate scoring of left hands of females, which were rated after the other groups of hands.

What is the function of highly consistent sex-specific preference for hands with particular features in terms of finger length? Opposite-sex hand preferences may reflect selection for adaptive mate preference. Remarkably, judgements by males disfavored females with masculinized hands, while females raters preferred masculinized hands, implying that judges of each sex rated as more attractive those hands where features of the opposite sex were relatively more expressed. If variation in 4D length partly depends on an effect of testosterone (Manning 2002), present results suggest that women prefer males who have been masculinized prenatally. In an evolutionary perspective, women may have been selected to prefer masculinized men for the sake of fitness benefits arising from mating with men expressing testosterone-dependent traits at high levels. Masculinized males have been shown to be more aggressive and have high testosterone levels (see Bailey and Hurd 2005). Aggressiveness could obviously have conferred social advantages in several contexts during human evolution. In addition, men with masculine hands have higher reproductive success and are more healthy (Manning et al. 2000; Manning 2002). A partly different interpretation is that 4D length functions as a conditional handicap (Zahavi 1977; Andersson 1994), whereby genetically high-quality males by showing long 4D reliably signal their ability to cope with the partly detrimental effects of androgens during development (e.g., Grossman 1985). Thus, the evolution of female preference for hands with long 4D may have been driven by the direct and/or indirect genetic benefits accruing to choosy women. Consistent with present results, Roney and Maestripieri (2004) have shown that a masculinized 2D:4D enhances overall attractiveness of men to women.

Reciprocal arguments can be formulated to interpret male avoidance for masculinized hands in women. A masculine 2D:4D, and thus relatively short 2D in women, is associated to low reproductive success (Manning et al. 2000) and high susceptibility to parasite infection (Flegr et al. 2005). The observed pattern of hand attractiveness therefore suggests that men prefer hands of healthy women with high fecundity.

In conclusion, this is the first experimental study where both men and women have been shown to exhibit consistent preferences for opposite-sex hands with emphasized sex-specific traits putatively dependent on fetal sex hormones. The function of such preference may be to acquire direct fitness benefits or indirect genetic benefits for the progeny. However, this study also prompts for more studies of the function of hand morphology and esthetics not only in visual but also in tactile sexual communication.

The remote mechanisms that link fetal hormone environment to digit development and thus relative finger length have been proposed to be mediated by *Hoxa* and *Hoxd* genes (Manning et al. 1998). Homeobox genes are highly conserved among vertebrates (Krumlauf 1994), suggesting that embryonic sex hormone environment may affect relative digit length also in nonhuman vertebrates. Present results therefore lead to predict that in species where highly expressed testosterone-dependent male traits are preferred by females, either because they provide choosy females with direct fitness benefits or because they function as conditional handicaps, females should prefer males with masculinized digit ratios, as we observed among undergraduates. Thus, digit ratios may provide a clue to sexual attractiveness of individual males also in studies of nonhuman vertebrates.

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