

## Body Odor Quality Predicts Behavioral Attractiveness in Humans

S. Craig Roberts PhD<sup>1,2,7</sup>, Alexandra Kravovich BSc<sup>1</sup>, Camille Ferdenzi PhD<sup>1,3</sup>, Tamsin K. Saxton PhD<sup>1,4</sup>, Benedict C. Jones PhD<sup>5</sup>, Lisa M. DeBruine PhD<sup>5</sup>, Anthony C. Little PhD<sup>2</sup>, and Jan Havlicek PhD<sup>6</sup>

<sup>1</sup>School of Biological Sciences, University of Liverpool, Crown St, Liverpool L69 7ZB, UK

<sup>2</sup>School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK

<sup>3</sup>Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

<sup>4</sup>Division of Psychology, School of Social and Health Sciences, University of Abertay Dundee, Bell Street, Dundee DD1 1HG, UK

<sup>5</sup>School of Psychology, William Guild Building, University of Aberdeen, Aberdeen AB24 2UB, UK

<sup>6</sup>Department of Anthropology, Charles University, Prague, Czech Republic

<sup>7</sup>To whom correspondence should be addressed at School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK; e-mail: craig.roberts@stir.ac.uk

**In press: Archives of Sexual Behavior, Dec 2011**

## ABSTRACT

Growing effort is being made to understand how different attractive physical traits covary within individuals, partly because this might indicate an underlying index of genetic quality. In humans, attention has focussed on potential markers of quality such as facial attractiveness, axillary odor quality, the second-to-fourth digit (2D:4D) ratio and body-mass index (BMI). Here we extend this approach to include visually-assessed kinesic cues (nonverbal behavior linked to movement) which are statistically independent of structural physical traits. The utility of such kinesic cues in mate assessment is controversial, particularly during every day conversational contexts, as they could be unreliable and susceptible to deception. However, we show here that the attractiveness of nonverbal behavior, in 20 male participants, is predicted by perceived quality of their axillary body odor. This finding indicates covariation between two desirable traits in different sensory modalities. Depending on two different rating contexts (either a simple attractiveness rating, or a rating for long-term partners, by 10 female raters not using hormonal contraception), we also found significant relationships between perceived attractiveness of nonverbal behavior and BMI, and between axillary odor ratings and 2D:4D ratio. Axillary odor pleasantness was the single attribute that consistently predicted attractiveness of nonverbal behavior. Our results demonstrate that nonverbal kinesic cues could reliably reveal mate quality, at least in males, and could corroborate and contribute to mate assessment based on other physical traits.

**Key words:** mate choice, nonverbal behavior, sexual selection, smell, face, good-genes

## INTRODUCTION

Many different physical human traits are associated with higher attractiveness judgments and mate preferences (for reviews, see Gangestad & Scheyd, 2005; Grammer, Fink, Moller, & Thornhill, 2003; Rhodes, 2006; Roberts & Little, 2008). Judgements of facial attractiveness have received most intense attention in view of the face's role in human social interactions (Little & Perrett, 2002; Rhodes, 2006; Roberts, Little et al., 2005; Thornhill & Gangestad, 1999). Other attributes contributing to attractiveness judgments include measures of body dimensions, such as body-mass index (BMI) (Maisey, Vale, Cornelissen, & Tovee, 1999; Pawlowski & Jasienska, 2008) and traits in other sensory modalities, such as voice (Feinberg, DeBruine, Jones, & Little, 2008; Feinberg et al., 2005; Saxton, Caryl, & Roberts, 2006; Saxton, DeBruine, Jones, Little, & Roberts, 2009) and body odor (Havlicek, Dvorakova, Bartos, & Flegr, 2006; Havlicek, Roberts, & Flegr, 2005; Rikowski & Grammer, 1999).

These and other sexually selected traits are thought to be potential indicators of underlying "good genes" and, as such, are predicted to co-vary within individuals (Roberts & Little, 2008; Thornhill & Grammer, 1999). Indeed, intercorrelations between traits are widely-reported. For example, correlations are seen between face and body attractiveness (Feinberg et al., 2005; Saxton, Burriss, Murray, Rowland, & Roberts, 2009), between facial and body odor attractiveness (Rikowski & Grammer, 1999; Thornhill et al., 2003), and between facial attractiveness and the second-to-fourth digit ratio (2D:4D, where low ratios are related to masculinity) (Ferdenzi, Lemaître, Leongómez, & Roberts, 2011). Beyond attractiveness, facial masculinity is related to facial symmetry (Gangestad & Thornhill, 2003; Little et al., 2008), and is also related to the second-to-fourth digit ratio (2D:4D, where low ratios are related to masculinity) (Burriss, Little, & Nelson, 2007; Fink, Manning, Neave, &

Grammer, 2004; Fink, Seydel, Manning, & Kappeler, 2007; Manning, 2002; but see Ferdenzi et al., 2011).

More recently, evolutionary approaches to human attractiveness have begun to focus on how judgements are formed when participants view stimuli that incorporate movement. That is, researchers are investigating attractiveness using judgements based on so-called dynamic images, including video-recordings and clips formed from motion-capture devices (e.g., Brown et al., 2005; Hugill, Fink, & Neave, 2010; Morrison, Gralewski, Campbell, & Penton-Voak, 2007; Penton-Voak, Allen, Morrison, Gralewski, & Campbell, 2007). In contrast with static images (e.g., photographs, line-drawings), dynamic stimuli contain information that is revealed by movement and includes gestures and other nonverbal behavior (collectively termed kinesic cues). However, the extent to which such cues might contain reliable information about individual quality, in the way that physical traits appear to do, remains somewhat controversial because they may be far less reliable in terms of biological signalling (Grammer et al., 1999; Roberts, 2008). For example, they may be temporally variable, context-dependent, culturally influenced, and potentially susceptible to manipulation and deception (Roberts, 2008). While this must be true to some extent, some evidence exists to suggest that such cues do reliably influence the perception and judgements of others. For example, in an observational study, the frequency of several specific behavioral patterns exhibited by men in a bar predicted their subsequent success in establishing conversational relationships with women (Renninger, Wade, & Grammer, 2004).

If such outcomes are meaningful in revealing genetic quality with a reasonable degree of reliability, then at least some of this information is also predicted to correlate with relevant physical traits used in mate choice (Hugill et al., 2010; Roberts, 2008). There exists some evidence for this, as Brown et al. (2005) showed that variation in attractiveness of dancing ability, a dynamic display used cross-culturally in human courtship, correlates with body

symmetry. Furthermore, men with low (i.e., masculine) 2D:4D ratios were judged to dance more attractively than men with more feminized ratios (Fink et al., 2007). While these studies provide important preliminary evidence for a link between kinesic information and physical indicator traits, the ability to dance in an attractive manner is likely linked to a measure of coordination and athleticism which is exhibited only in particular circumstances and relatively rarely compared to normal conversational contexts in day-to-day behavior. Here, we aimed to extend such research by investigating correlations between a set of phenotypic indicator traits and kinesic information within a more common scenario—simply observing someone talking.

A major obstacle for efforts to understand how behavioral cues affect quality perception by potential mates is that dynamic stimuli contain relevant information about both behavior and other influential physical attributes. It is, therefore, difficult to disentangle the effects of behavioral cues and those of the other traits on perceptions of judges. Thus, it is no surprise that ratings of human faces in static and dynamic form are intercorrelated (Riggio, Widaman, Tucker, & Salinas, 1991; Roberts, Saxton et al., 2009), even though some studies have suggested that the level of this correlation is lower than might be expected (Lander, 2008; Penton-Voak & Chang, 2008; Rubenstein, 2005). One solution to this problem is to employ new digital technologies to capture movement independently of shape or other information, by using wire-frame images or standardized models (Brown et al., 2005; Morrison et al., 2007). However, such approaches are not without their own problems. For example, generation of wire-frame images is best-suited to studies of gait (or dance) where the scale of movement is relatively expansive; it performs relatively poorly at capturing finer-scale movement, especially facial expressions. It also often requires markers to be attached to the body and time for spatial calibration (potentially altering or inhibiting normal behavior), and requires expensive motion-capture equipment. A more accessible solution is to statistically partial out the influence of structural physical features on judgements by

calculating residuals from static-dynamic image regression, providing researchers with a standardized measure of attractiveness based on movement cues alone (Roberts, Little et al., 2009; Roberts, Saxton et al., 2009).

In this study, we used this approach for the first time to investigate the intercorrelations between attractive dynamic cues and putative indicator traits: axillary odor, 2D:4D ratio, and BMI. In addition, we examined the relationships between odor and either 2D:4D ratio or BMI, neither of which have been previously investigated. We photographed and video-recorded young men, collected samples of their body odor, and measured the relevant traits. We then asked a group of female raters to judge the photos, videos, and odors.

## **METHOD**

### **Participants**

Twenty men who reported being non-smokers were recruited as stimulus males from whom various physical traits would be measured or rated. Men were aged between 20 and 31 years ( $M = 22.0$ ;  $SD = 2.7$ ). In addition, 10 women (aged 25-31 years,  $M = 26.9$ ,  $SD = 2.2$ ) were recruited as raters; raters were not using hormonal contraception. Informed consent was collected beforehand and the study was approved by the University of Liverpool's Committee on Research Ethics.

### **Materials and Procedure**

Axillary odor samples were collected from all male participants. Cotton wool pads were taped with Micropore<sup>TM</sup> tape under both armpits after showering with non-perfumed soap, immediately before the men went to bed (see Roberts, Gosling, Carter, & Petrie, 2008; Roberts, Gosling et al., 2005), and were worn in bed for 8-10 h. In the morning, the men placed the pads in plastic bags and delivered them to the laboratory where they were stored in a  $-80^{\circ}\text{C}$  freezer until testing, which occurred within 1 month of collection. Freezing does not qualitatively alter subsequent perception of odors (Lenochova, Roberts, & Havlicek, 2009;

Roberts et al., 2008). Male participants were non-smokers, undertook to avoid using deodorants or aftershaves on the day of collection, and to refrain from consuming alcohol or certain strong-smelling foods, and from sexual activity during sample collection (for more details of such restrictions, see Roberts et al., 2008).

Digital color photographs were taken of the head and shoulders of all male participants from a distance of 2 m, in a room with fluorescent lighting but no natural light, to standardize lighting conditions (we used a Canon Powershot camera; images were resampled to  $400 \times 480$  pixels with resolution 72 dpi). The men were asked to adopt a neutral expression. Following this, they were asked to record a 1 min video, also capturing head and shoulders, in which they were asked to describe their most recent holiday (videos were edited to 15 s and muted when shown to female raters). Although some face-rating studies crop images to control for influences of hairstyle and clothing cues (e.g., Roberts et al., 2004), we did not do this here to maintain consistency with the video images. Note, however, that any confounding influence of clothing or hairstyle might reduce, but cannot enhance, a relationship between the phenotypic traits under study, particularly between the effect of odor and behavior; hence, the reported results likely underestimate the true underlying correlations.

We also took a photocopy of each man's hands, with both hands outstretched on the glass plate of the photocopier, and used these to measure 2D:4D ratios for each hand. Taking direct measurements from photocopies is a widely used approach in 2D:4D studies (e.g., McFadden et al., 2005), although the ratios are slightly lower compared to direct measurements (Manning et al., 2005). Digit lengths were means of three measurements done by one of the authors (AK) for each digit from the photocopy (working from the left 4<sup>th</sup> digit to the right 2<sup>nd</sup> digit, then repeating these measures twice over) to reduce measurement error. Left hand 2D:4D ratio ranged between 0.90 and 1.01 ( $M = 0.96$ ,  $SE \pm 0.01$ ), while right-hand

ratios ranged from 0.92 to 1.05 ( $M = 0.99$ ,  $SE. \pm 0.01$ ). In addition, height and weight measurements were recorded from each participant. Body-mass indices (weight in kg divided by height in  $m^2$ ) were calculated from these measures. BMI ranged from 17.9 to 26.0 ( $M = 22.7$ ,  $SE \pm 0.46$ ).

Female participants rated the attractiveness of axillary odor from all male targets during two rating sessions on consecutive days (10 per day). We did this so as to avoid sensory overload effects resulting from olfactory adaptation to axillary odors. Odor samples consisted of both axillary pads (i.e., from both left and right axillae), because odor quality can vary according to handedness (Ferdenzi, Schaal, & Roberts, 2009). Samples were placed at the base of 500 ml conical flasks, capped with aluminium foil when not in use, and left on a bench for 2 h to thaw before use.

On each day, after rating the odors, women rated the photos and then videos of the same men they had just smelled. Order presentation of photos and videos was kept constant to avoid confounding photo judgements with behavioral attributes observed in videos, and because this mimics the logical sequence of impression formation. However, the order in which individual targets were presented was randomized within each test. Face photos were presented on a LCD screen using a java applet and order was randomized for each rater. Videos were presented using one of a series of four Powerpoint presentations, in each of which the image order was randomized; raters were allocated to one of these presentations in the order of testing (Raters 1 and 5 saw presentation 1, Raters 2 and 6 saw presentation 2, etc.). For each stimulus, women assigned a score for the following questions: "How attractive is this man?" using a 7-point rating scale (1 = not attractive, 7 = very attractive) and "How likely is it that you would consider having a long-term relationship with this man?" (1 = very unlikely, 7 = very likely). The two contexts were used because they can shift responses in subtle but statistically detectable manner (Little, Jones, Penton-Voak, Burt, & Perrett, 2002;

Roberts, Little et al., 2005) and give some insight into the selection pressure underlying the preference: those expressed more strongly in the long-term context indicate relatively higher attention to cues of paternal investment, while preferences more strongly expressed in the general attractiveness context may emphasize cues of good genes (Gangestad & Simpson, 2000).

### **Statistical analysis**

Mean ratings for each target man were calculated. These fulfilled assumptions of parametric statistical tests (Kolmogorov-Smirnov tests, all  $p > .05$ ). We used Pearson correlations to analyze relationships between variables. To obtain, for each target, our novel measure of attractiveness of kinesic cues independent of structural physical cues, we computed standardized residuals from a bivariate linear regression with video-rated attractiveness as the dependent variable and photo-rated attractiveness as the predictor. Positive residuals denote individual men who were rated as more attractive than predicted from their facial photograph alone, indicating that they move or behave in a more engaging manner than men with negative residuals (see also Roberts, Little, et al., 2009).

### **RESULTS**

For all measures, we found high levels of inter-rater reliability among our female raters. For attractiveness judgements and ratings as a long-term partner, respectively, we recorded Cronbach's alpha values of .90 and .85 for photo ratings, .86 and .82 for video ratings, and .86 and .86 for ratings of body odor.

Judgements of attractiveness correlated with judgements for a long-term partner for all measures (photo ratings: Pearson  $r = .926$ ; video,  $r = .854$ ; odor,  $r = .960$ ; residualised video-rated attractiveness,  $r = .689$ ). No correlations were found between the age of male participants and any of the measures reported in Tables 1 and 2.

Relationships between all rated traits (photo and video images, axillary odor, and residualized video-rated attractiveness) and other physical traits (left and right hand 2D:4D, BMI) are shown in Table 1. Not surprisingly, there was a significant positive correlation with attractiveness judgements from videos. More interestingly, and as predicted if these traits might form part of a common underlying index of genetic quality, we found a strong positive correlation between residualized video-rated attractiveness and body odor attractiveness, although neither 2D:4D nor BMI correlated with residualized video-rated attractiveness.

We also found significant correlations between photo and video-rated attractiveness (*contra* Lander, 2008; Penton-Voak & Chang, 2008; Rubenstein, 2005), and a non-significant tendency towards a correlation between both photo/video-rated attractiveness and BMI. Additionally, body odor ratings were negatively correlated with 2D:4D, although this was significant only for the right hand. As would be expected, left and right hand 2D:4D were positively correlated.

Table 2 shows correlations between the same traits when ratings were carried out in the long-term partnership context (note that Table 2 does not show correlations between left or right 2D:4D and BMI, which are unaffected by differences in rating context and can be seen in Table 1). A similar pattern emerges, but with some interesting differences. In this longer-term context, residualized video-rated attractiveness was also correlated with male BMI, as was video-rated (but not photo-rated) attractiveness.

In view of the fact that our study is correlational and involves several traits, we subsequently applied Bonferroni correction to our 4 main tests (residualized video-rated attractiveness versus odor attractiveness, left and right 2D:4D, and BMI). The significance threshold for applying Bonferroni correction was therefore .0125 (although we reported other correlations, for completeness, we did not correct for all of these since these were exploratory and because this would likely inflate Type II error). Importantly, the relationship between

attractiveness scores of odor and nonverbal behaviour remains significant after Bonferroni correction.

In view of the fact that our study is correlational and involves several traits, we subsequently applied Bonferroni correction to our 4 main tests (residualized video-rated attractiveness versus odor attractiveness, left and right 2D:4D, and BMI). The significance threshold for applying Bonferroni correction was therefore .0125 (although we reported other correlations, for completeness, we did not correct for all of these since these were exploratory and because this would likely inflate Type II error). Importantly, the relationship between attractiveness scores of odor and nonverbal behaviour remains significant after Bonferroni correction.

## **DISCUSSION**

For the first time, our results revealed significant correlations between behavioral cues, independent of visual information available in photographs, and both attractiveness of body odor and BMI. No significant relationships were found between behavioral cues (i.e. residualized video-rated attractiveness) and 2D:4D ratio.

Men who were rated as more attractive in dynamic images than expected based on their photograph were found to have higher BMI. This result suggests that men who were relatively light for their height had more unattractive movement cues when observed in these videos than men who were relatively well-built. Since the men's body mass indices fell within the normal range (only 3 were over 25 and 1 under 18.5), this is unlikely to be unduly influenced by effects of being severely under- or overweight ( $p = .067$  when these men were excluded from the analysis). However, this requires further attention and it is not known whether this pattern would extend to men who fell further away from the normal range, in either direction. In addition, BMI correlated with residualized video-rated attractiveness when women judged the men in the explicit context of a long-term partnership. However, this

correlation did not hold in the general attractiveness context, and the difference between these two correlations was not significant (Steiger's  $z = 1.49$ ,  $p = .14$ ).

In contrast, we found correlations between residualized video-rated attractiveness and body odor in both the general and long-term attractiveness contexts. Individual men, who scored highly in residualized video-rated attractiveness (i.e. tending to display relatively more attractive nonverbal behaviour), also tended to have more attractive body odor. Attractiveness of body odor is also known to correlate with other putative good gene indicators, including body symmetry (Gangestad & Thornhill, 1999) and facial attractiveness (Rikowski & Grammer, 1999) and with psychometric dominance (Havlicek et al., 2005). The results on the association between axillary odor and dominance are perhaps especially pertinent, as it suggests that a possible mechanism for the relationship between behavior and odor attractiveness is movement associated with relative dominance and, perhaps, self-confidence. Indeed, it has been found repeatedly that dominance is expressed non-verbally (e.g., Schwartz, Tesser, & Powell, 1982).

Ratings of body odor in the general attractiveness context were also correlated with 2D:4D ratio. This correlation was stronger for the right hand (the left was only marginally significant), which is consistent with similar results between right-hand 2D:4D and facial symmetry and attractiveness reported by Ferdenzi et al. (2011), is interesting in view of recent studies suggesting heritability of 2D:4D ratio is higher in the right hand (Paul, Kato, Cherkas, Andrew, & Spector, 2006; the odor attractiveness-left 2D:4D ratio and odor attractiveness-right 2D:4D ratio correlations were not significantly different). The correlations suggest that individuals with more attractive odor were more likely to have lower (more masculine) ratios. Low 2D:4D ratios are thought to be an indicator of relatively high levels of exposure to testosterone *in utero* and are associated with health and vigor (Manning, 2002) as well as sexually dimorphic facial features related to perceptions of dominance

(Burriss et al., 2007; Neave, Laing, Fink, & Manning, 2003). Our results thus lend more support to evidence that axillary odors are meaningful cues of dominant and attractive traits.

In addition to the above, we found a very strong and positive correlation between attractiveness judgements of static and dynamic images. Some previous studies (Lander, 2008; Penton-Voak & Chang, 2008; Rubenstein, 2005) have not found a significant correlation between the two, suggesting that dynamic images are judged according to different standards. However, these differences are at least partly due to methodology (Roberts, Saxton et al., 2009) and, if each carries reliable information about male quality, we would expect them to be correlated. The fact that the correlation appears weaker in the long-term mate choice context might indicate that behavioral cues gain more importance in decisions emphasizing paternal investment compared to good genes, consistent with the strategic pluralism model of human mating strategies (Gangestad & Simpson, 2000). More investigation is needed into how context can affect judgements in these different kinds of stimuli and choice situations.

Our results provide some interesting insights into probable inter-relationships among different kinds of attractive traits. Our results partly support the idea of different facets of physical attractiveness being interwoven as a single ornament of quality (see Feinberg et al., 2005; Saxton, Burriss, Murray, Rowland, & Roberts, 2009; Thornhill & Grammer, 1999). However, this support is only partial. The lack, for example, of a correlation between ratings of facial and olfactory attractiveness might alternatively indicate that these components (at least) could be cues of different dimensions of underlying quality as suggested by Roberts, Little et al. (2005). Although this is intriguing, it should be noted that some other studies have reported positive correlations between these traits (e.g., Rikowski & Grammer, 1999), so further replications of these results are necessary to reach a firm conclusion. Furthermore, although our results were correlational, they demonstrate that a simple method for parsing

movement information from other physical cues is a useful approach to compare with other relevant traits. More research is now needed to characterize the specific kinds of movement that account for attractiveness perception and to explore further correlates with attractive phenotypic traits.

## REFERENCES

- Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Liu, C. K., Popovic, Z., & Trivers, R. (2005). Dance reveals symmetry especially in young men. *Nature*, *438*, 1148-1150.
- Burriss, R. P., Little, A. C., & Nelson, E. C. (2007). 2D : 4D and sexually dimorphic facial characteristics. *Archives of Sexual Behavior*, *36*, 377-384.
- Feinberg, D. R., DeBruine, L. M., Jones, B. C., & Little, A. C. (2008). Correlated preferences for men's facial and vocal masculinity. *Evolution and Human Behavior*, *29*, 233-241.
- Feinberg, D. R., Jones, B. C., DeBruine, L. M., Moore, F. R., Law Smith, M. J., Cornwell, R. E., ... Perrett, D. I. (2005). The voice and face of woman: One ornament that signals quality? *Evolution and Human Behavior*, *26*, 398-408.
- Ferdenzi, C., Lemaître, J-F., Leongómez, J. D., & Roberts, S. C. (2011). Digit ratio (2D:4D) predicts facial, but not voice or body odour, attractiveness in men. *Proceedings of the Royal Society B (in press)*.
- Ferdenzi, C., Schaal, B., & Roberts, S. C. (2009). Human axillary odor: Are there side-related perceptual differences? *Chemical Senses*, *34*, 565-571.
- Fink, B., Manning, J. T., Neave, N., & Grammer, K. (2004). Second to fourth digit ratio and facial asymmetry. *Evolution and Human Behavior*, *25*, 125-132.
- Fink, B., Seydel, H., Manning, J. T., & Kappeler, P. M. (2007). A preliminary investigation of the associations between digit ratio and women's perception of men's dance. *Personality and Individual Differences*, *42*, 381-390.
- Gangestad, S. W., & Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology*, *34*, 523-548.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*, 573-644.

- Gangestad, S. W. & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society B*, 265, 927-933.
- Gangestad, S. W. & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior*, 24, 231-241.
- Grammer, K., Fink, B., Moller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews*, 78, 385-407.
- Grammer, K., Honda, M., Juette, A., & Schmitt, A. (1999). Fuzziness of nonverbal courtship communication unblurred by motion energy detection. *Journal of Personality and Social Psychology*, 77, 487-508.
- Havlicek, J., Dvorakova, R., Bartos, L., & Flegr, J. (2006). Non-advertized does not mean concealed: Body odour changes across the human menstrual cycle. *Ethology*, 112, 81-90.
- Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters*, 1, 256-259.
- Hugill, N., Fink, B., & Neave, N. (2010). The role of human body movements in mate selection. *Evolutionary Psychology*, 8, 66-89.
- Lander, K. (2008). Relating visual and vocal attractiveness for moving and static faces. *Animal Behaviour*, 75, 817-822.
- Lenochova, P., Roberts, S. C., & Havlicek, J. (2009). Methods of human body odor sampling: The effect of freezing. *Chemical Senses*, 34, 127-138.
- Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B*, 269, 1095-1100.

- Little, A. C., Jones, B. C., Waite, C., Tiddeman, B. P., Feinberg, D. R., Perrett, D. I., Apicella, C. L., & Marlowe, F. W. (2008). Symmetry is related to sexual dimorphism in faces: data across culture and species. *PLoS One*, *3*, e2106.
- Little, A. C., & Perrett, D. I. (2002). Putting beauty back in the eye of the beholder: Evolution and individual differences in face preference. *The Psychologist*, *15*, 28-32.
- Maisey, D. S., Vale, E. L. E., Cornelissen, P. L., & Tovee, M. J. (1999). Characteristics of male attractiveness for women. *Lancet*, *353*, 1500-1500.
- Manning, J. T. (2002). *Digit ratio: A pointer to fertility, behaviour and health*. New Brunswick, NJ: Rutgers University Press.
- 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.
- McFadden, D., Loehlin, J. C., Breedlove, S. M., Lippa, R. A., Manning, J. T., & Rahman, Q. (2005). A reanalysis of five studies on sexual orientation and the relative length of the 2nd and 4th fingers (the 2D:4D ratio). *Archives of Sexual Behavior*, *34*, 341–356.
- Morrison, E. R., Gralewski, L., Campbell, N., & Penton-Voak, I. S. (2007). Facial movement varies by sex and is related to attractiveness. *Evolution and Human Behavior*, *28*, 186-192.
- 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 B*, *270*, 2167-2172.
- Paul, S. N., Kato, B. S., Cherkas, L. F., Andrew, T., Spector, T. D. (2006). Heritability of the second to fourth digit ratio (2d:4d): A twin study. *Twin Research in Human Genetics*, *9*, 215-219.

- Pawlowski, B., & Jasienska, G. (2008). Women's body morphology and preferences for sexual partners' characteristics. *Evolution and Human Behavior*, 29, 19-25.
- Penton-Voak, I. S., Allen, T., Morrison, E. R., Gralewski, L., & Campbell, N. (2007). Performance on a face perception task is associated with empathy quotient scores, but not systemizing scores or participant sex. *Personality and Individual Differences*, 43, 2229-2236.
- Penton-Voak, I. S., & Chang, H. Y. (2008). Attractiveness judgements of individuals vary across emotional expression and movement conditions. *Journal of Evolutionary Psychology*, 6, 89-100.
- Renninger, L. A., Wade, T. J., & Grammer, K. (2004). Getting that female glance: Patterns and consequences of male nonverbal behavior in courtship contexts. *Evolution and Human Behavior*, 25, 416-431.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, 57, 199-226.
- Riggio, R. E., Widaman, K. F., Tucker, J. S., & Salinas, C. (1991). Beauty is more than skin deep—components of attractiveness. *Basic and Applied Social Psychology*, 12, 423-439.
- Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society B*, 266, 869-874.
- Roberts, S. C. (2008). Nonverbal communication of mate quality in humans. In P. D'Ettorre & D. P. Hughes (Eds.), *Sociobiology of communication: an interdisciplinary perspective* (pp.157-170). Oxford: Oxford University Press.
- Roberts, S. C., Gosling, L. M., Carter, V., & Petrie, M. (2008). MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proceedings of the Royal Society B*, 275, 2715-2722.

- Roberts, S. C., Gosling, L. M., Spector, T. D., Miller, P., Penn, D. J., & Petrie, M. (2005). Body odor similarity in non-cohabiting twins. *Chemical Senses, 30*, 651-656.
- Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., ... Petrie, M. (2004). Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proceedings of the Royal Society B (Suppl.)*, 271, S270-272.
- Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes and human mate choice. *Genetica, 132*, 309-321.
- Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D. I., Carter, V., & Petrie, M. (2005). MHC-assortative facial preferences in humans. *Biology Letters, 1*, 400-403.
- Roberts, S. C., Little, A. C., Lyndon, A., Roberts, J., Havlicek, J., & Wright, R. L. (2009). Manipulation of body odor alters men's self-confidence and judgements of their visual attractiveness by women. *International Journal of Cosmetic Science, 31*, 47-54.
- Roberts, S. C., Saxton, T. K., Murray, A. K., Burriss, R. P., Rowland, H. M., & Little, A. C. (2009). Static and dynamic facial images cue similar attractiveness judgements. *Ethology, 115*, 588-595.
- Rubenstein, A. J. (2005). Variation in perceived attractiveness: Differences between dynamic and static faces. *Psychological Science, 16*, 759-762.
- Saxton, T. K., Burriss, R. P., Murray, A. K., Rowland, H. M., & Roberts, S. C. (2009). Face, body and speech cues independently predict judgments of attractiveness. *Journal of Evolutionary Psychology, 7*, 23-35.
- Saxton, T. K., Caryl, P. G., & Roberts, S. C. (2006). Vocal and facial attractiveness judgments of children, adolescents and adults: The ontogeny of mate choice. *Ethology, 112*, 1179-1185.

- Saxton, T. K., DeBruine, L. M., Jones, B. C., Little, A. C., & Roberts, S. C. (2009). Face and voice attractiveness judgments change during adolescence. *Evolution and Human Behavior, 30*, 398-408.
- Schwartz, B., Tesser, A., & Powell, E. (1982) Dominance cues in nonverbal behavior. *Social Psychology Quarterly, 45*, 114-120.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Science, 3*, 452-460.
- Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCullough, J. K., & Franklin, M. (2003). Major histocompatibility genes, symmetry and body scent attractiveness in men and women. *Behavioral Ecology, 14*, 668-678.
- Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior, 20*, 105-120.

Table 1. Correlation matrix (Pearson's  $r$ ) between attractiveness ratings and other physical traits of 20 men.

	Video	Odor	L 2D:4D	R 2D:4D	BMI
RVA	.555*	.607**	-.291	-.326	.188
Photo	.832***	-.067	.127	.098	.400
Video		.281	-.056	-.099	.437*
Odor			-.411	-.463*	.120
Left 2D:4D				.616**	-.168
Right 2D:4D					.136

RVA (residualised video-rated attractiveness) is the standardized residual from a regression with video rating as the dependent variable and photo rating as the predictor. 2D:4D is the second-to-fourth digit ratio for either the left (L) or right (R) hand; BMI is Body Mass Index.

\*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < 0.001$

Table 2. Correlation matrix (Pearson's  $r$ ) between ratings of odor attractiveness and other traits in the context of a long-term relationship.

	Video	Odor	L 2D:4D	R 2D:4D	BMI
RVA	.831***	.449*	-.180	-.153	.455*
Photo	.556*	-.083	.065	-.024	.280
Video		.327	-.114	-.141	.533*
Odor			-.221	-.345	.068

RVA is residualised video-rated attractiveness. For explanations of other variables, symbols, and abbreviations, see Table 1.