

### Original Article

## Redness Enhances Perceived Aggression, Dominance and Attractiveness in Men's Faces

Ian D. Stephen, School of Psychology, University of Nottingham Malaysia Campus, Semenyih, Malaysia.  
Email: [ian.stephen@nottingham.edu.my](mailto:ian.stephen@nottingham.edu.my) (Corresponding author).

Francesca H. Oldham, Evolutionary Anthropology Research Group, Durham University, Durham, UK.

David I. Perrett, School of Psychology, University of St Andrews, St Andrews, UK.

Robert A. Barton, Evolutionary Anthropology Research Group, Durham University, Durham, UK.

**Abstract:** In a range of non-human primate, bird and fish species, the intensity of red coloration in males is associated with social dominance, testosterone levels and mate selection. In humans too, skin redness is associated with health, but it is not known whether – as in non-human species – it is also associated with dominance and links to attractiveness have not been thoroughly investigated. Here we allow female participants to manipulate the CIELab  $a^*$  value (red-green axis) of skin to maximize the perceived aggression, dominance and attractiveness of photographs of men's faces, and make two findings. First, participants increased  $a^*$  (increasing redness) to enhance each attribute, suggesting that facial redness is perceived as conveying similar information about a male's qualities in humans as it does in non-human species. Second, there were significant differences between trial types: the highest levels of red were associated with aggression, an intermediate level with dominance, and the least with attractiveness. These differences may reflect a trade-off between the benefits of selecting a healthy, dominant partner and the negative consequences of aggression.

**Keywords:** attractiveness, face, men, aggression, dominance, perception.

---

### Introduction

Variation in skin redness due to the flow of oxygenated blood to the periphery conveys information about health, dominance and emotional state in birds and primates (Negro, Sarasola, Farinas and Zorrilla, 2006; Setchell, Smith, Wickings and Knapp, 2008). In birds, a phylogenetically diverse range of species have bare skin areas that flush deeper

red during agonistic encounters due to perfusion with oxygenated blood (Bamford, Monadjem and Hardy, 2010; Negro et al., 2006). Among primates, enhanced facial redness is associated with increased testosterone levels in male rhesus macaques (Rhodes et al., 1997) and with increased testosterone levels and dominance rank in male mandrills (Setchell and Dixson, 2001; Setchell et al., 2008). Male mandrills avoid conflict with other males with brighter red faces, suggesting that redness also signals aggression and fighting ability (Setchell and Wickings, 2005). Rhesus macaques of both sexes have been shown to attend and present preferentially to redder opposite sex faces (Waite et al., 2003; Waite, Gerald, Little and Kraisselburd, 2006) and female mandrills prefer to mate with redder males, irrespective of dominance rank (Setchell, 2005). Evidence that primate trichromatic color vision is optimized for perceiving changes in skin blood perfusion and oxygenation in conspecifics suggests that skin redness provides important cues to social and sexual status and changes in emotional state (Changizi, Zhang and Shimojo, 2006).

In humans too, facial skin redness is determined by perfusion with oxygenated blood, is sexually dimorphic (men are redder than women; Edwards and Duntley, 1939; Frost, 1994), and is strongly androgen-dependent in men (Edwards and Duntley, 1939; Edwards, Hamilton, Duntley and Hubert, 1941; Jeghers, 1944). Increased skin blood perfusion is associated with health: it is enhanced by physical training (Johnson, 1998) and reduced in patients with hypertension (Panza, Quyyimi, Brush and Epstein, 1990), diabetes (Charkoudian, 2003) and in smokers (Richardson 1987). Skin redness associated with increased blood perfusion and oxygenation enhances the healthy appearance of faces, even in dark-skinned people (Stephen et al., 2009a).

Red also has behavioral and psychological effects in humans, consistent with it being a signal of dominance and aggression: wearing red enhances the probability of winning in individual combat sports (Barton and Hill, 2005; Hagemann, Strauss and Leißing, 2008; Hill and Barton, 2005), team sports (Attrill, Gresty, Hill and Barton, 2008; Greenlees, Leyland, Thelwell and Filby, 2008), and virtual combats (Ilie, Ioan, Zagrean and Moldovan, 2008). Attributions of increased dominance are even made to abstract shapes when these are colored red rather than blue (Little and Hill, 2007). Subjects show physical avoidance reactions to red stimuli, moving their body away from red-covered IQ test booklets more than from green- or grey-covered booklets (Elliot, Maier, Binser, Friedman and Pekrun, 2009) and perform worse on cognitive tests after exposure to red than to other colors (Elliot, Maier, Moller, Friedman and Meinhardt, 2007).

Anger increases the blood flow to faces in Caucasian and Chinese samples (Drummond and Quah, 2001; Montoya, Campos and Schandry, 2005), and there is evidence that the association of red with anger, danger, strength, activity and aggression is consistent across cultural boundaries (Adams and Osgood, 1973; Hupka, Zaleski, Otto, Reidl and Tarabrina, 1997). Hence, a wide range of evidence suggests that redness is associated with testosterone, health, physical dominance and anger, and is perceived as such in a range of stimuli. We hypothesize therefore that increased skin redness will enhance the dominant and aggressive appearance of men's faces.

We also investigate the relationship between redness and attractiveness, since increased blood coloration enhances apparent health (Stephen et al., 2009a), attractiveness is linked to apparent health (Jones, Little, Burt and Perrett, 2004) and previous research

suggests a role for blood color in attractiveness (Re, Whitehead, Xiao and Perrett, 2011). Research on facial shape suggests that trade-offs exist between dominance or masculinity and attractiveness. Dominant face shape has been suggested as an honest signal of male quality (Mueller and Mazur, 1998), and might therefore be expected to be considered attractive by women. Indeed, military officers with more dominant facial features were found to have more offspring if they also achieved high military rank (but did not have more children if they remained low rank; Mueller and Mazur, 1998). Teenage boys with more dominant faces report sexual activity at a younger age and report more copulation opportunities than those with less dominant faces (Mazur, Halpern and Udry, 1994). Men displaying more dominant behaviors are considered more attractive by women (Sadalla, Kenrick and Vershure, 1987). Interestingly, images of male faces manipulated to appear as though they have been more influenced by testosterone during puberty appear more dominant but not more attractive to women (Swaddle and Reiersen, 2002). In many species females prefer less dominant males, possibly because dominance is associated with aggression and low investment by males (Qvarnstrom and Forsgren, 1998). In humans, masculine facial features are weakly associated with increased attractiveness (DeBruine et al., 2006), though this is subject to individual and menstrual cycle variation (DeBruine et al., 2006; Frost, 1994; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Rupp et al., 2009). In particular, female preferences shift towards less masculine faces during phases of the menstrual cycle when they are at low risk of conception. Recent theoretical work has suggested that male masculinity may have evolved more in response to male-male competition than to female choice (Puts, 2010). Puts (2010) points out that the high degree of sexual dimorphism in muscle mass (similar to the dimorphism seen in gorillas; Zihlman and MacFarland, 2000), and ability to control access to females predict that male-male contest competition is more important in the evolution of masculine traits than female choice. This prediction is supported by the finding that male sex-typicality on a number of traits, including beard growth (Neave and Shields, 2008), masculine voice (Puts, Gaulin and Verdolini, 2006), masculine face (DeBruine et al., 2006) and brawny build (Frederick and Haselton, 2007), increase ratings of dominance more than they do attractiveness (Puts, 2010). It should be noted that women are able to control mating to an extent, for example by extra-pair copulations, and consequently are predicted to favor males with healthy appearance (Puts, 2010), which is enhanced by a slight increase in redness caused by increased oxygenated blood perfusion (Stephen et al., 2009a, 2009b).

In this study, we examine whether red skin coloration is, like facial shape, perceived as an indicator of dominance and attractiveness. We also test for an association of skin redness with aggressiveness, and predict a similar trade-off between attractiveness and dominance or aggression as has been found for facial shape. Based on the comparative, physiological, behavioral and psychological evidence discussed above, we predict associations between skin redness and perceived dominance, aggression and attractiveness. We further predict that the association between redness and attractiveness will be limited by the negative implications of dominance and aggression, in a similar way to that found for facial shape.

## **Materials and Methods**

This work was approved by the Anthropology Department Ethics Committee, Durham University and UTREC at the University of St Andrews. All participants gave prior, informed consent in writing.

Female participants were allowed to manipulate the redness of the skin on color-calibrated images of men's faces in order to maximize the aggressiveness, dominance and attractiveness of those faces, in separate trials.

Skin portions of color-calibrated (Hong, Luo and Rhodes, 2001), male Caucasian facial images were transformed (Burt and Perrett, 1995) along the CIELab  $a^*$  (redness) axis (see Figure 1a). Female Caucasian participants were presented with facial images on a calibrated CRT monitor, and were asked to manipulate their color to "make the face as aggressive as possible", "make the face as dominant as possible" or "make the face as attractive as possible".

**(a) Photography.** 21 male Caucasian participants (aged 18-22) were photographed, without skin make-up and with neutral expressions, in a booth painted Munsell N5 grey, illuminated with three Verivide F20 T12/D65 daylight simulation bulbs in high-frequency fixtures (Verivide, UK), to reduce the effects of flicker. The booth was located in a room with no other lighting. A Munsell N5 painted board was placed over the shoulders and a GretagMacbeth Mini ColorChecker color chart was included in the frame. Images were color corrected after Stephen et al. (2009b).

Matlab was used to calculate mean CIELab values across skin pixels for each face image (defining initial CIELab face color), by converting RGB values to CIELab via the XYZ color space.

**(b) Image manipulation.** Face-shaped masks were produced in Matlab, one representing average face color +8 units of  $a^*$ , and one representing average face color -8 units of  $a^*$ . Each face image ( $n = 21$ ) was manipulated by the difference in color between the two masks (Burt and Perrett, 1995), producing thirteen images in equal steps from -16 to +16 units of  $a^*$  from the original face color. Hair, eyes, clothing and background remained constant (Figure 1a).

**(c) Experimentation.** Participants were 45 Caucasian women (aged 18-25). Participants were presented with the stimuli, one face at a time, in random order on a CRT monitor (color calibrated using a ColorVision Spyder 2Pro). A computer program allowed participants to manipulate the color of the facial skin along the CIELab  $a^*$  (redness) color axis by moving the mouse horizontally across the screen. The starting point of the transform was randomized and looped (so that holding the mouse cursor over the middle of the screen did not always display the mid-point of the transform), and the direction of color change (i.e. whether moving the mouse left increased and right decreased redness or vice versa) was randomized for each trial. They were asked to "make the face as AGGRESSIVE as possible", "make the face as DOMINANT as possible" or "make the face as ATTRACTIVE as possible". Dominance, aggression and attractiveness were not defined for the participants. Each participant saw each of the 21 faces once for each condition. Trials were grouped into blocks. For example, participants saw all aggressive trials in one

block. Face order within blocks was randomized and the order of the blocks themselves was randomized.

**(d) Statistical Methods.** Mean color changes applied to each face were calculated (by face dataset). One-sample t-tests ( $H_0$ : no color change) were used to evaluate the overall color changes. To test for the effects of initial face color on the amount of redness ( $a^*$ ) change applied to optimize aggressive, dominant or attractive appearance, Pearson's correlation was used. To test for the difference between the trial conditions (aggression, dominance and attractiveness), general linear mixed modeling was performed (DV = redness change applied; fixed factor = trial condition; to control for variation between participants, subject ID was included as a random factor). Tukey's HSD post-hoc tests were used to determine the differences between the three conditions.

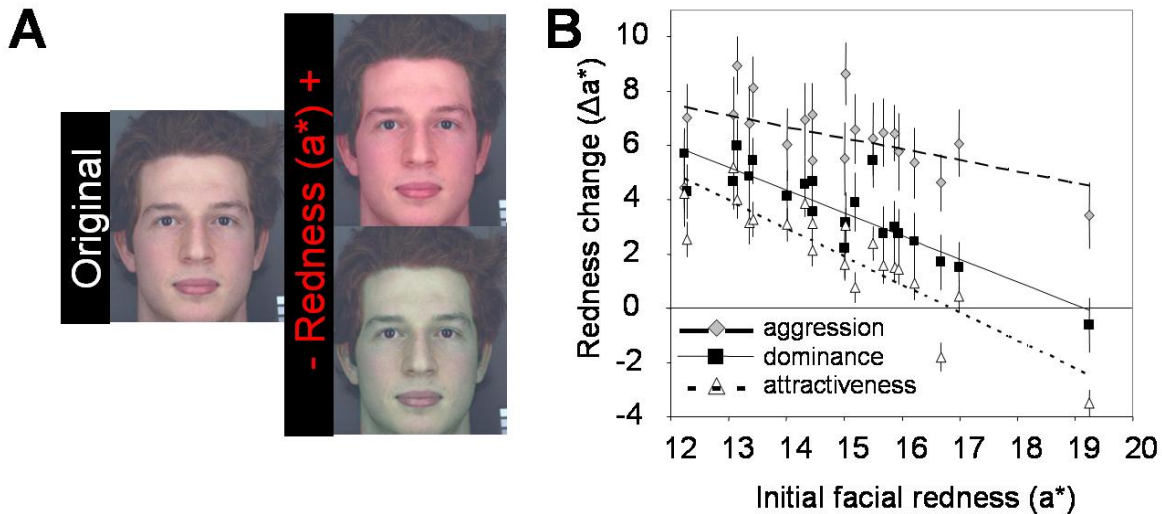


Figure 1a: Untransformed face photograph and high and low endpoints of the redness ( $a^*$ ) transform. Figure 1b: Amount of redness change applied ( $\Delta a^*$  mean $\pm$ SE) is greatest to optimize aggressive appearance (grey rhombi) is greater than for dominance (black squares) is greater than for attractiveness (white triangles).

## Results

Participants increased the redness of faces to optimize apparent aggression ( $\Delta a^*$   $M \pm SE = 6.24 \pm 0.30$ ;  $t(20) = 20.922$ ;  $p < 0.001$ ), dominance ( $\Delta a^*$   $M \pm SE = 3.66 \pm 0.36$ ;  $t(20) = 10.116$ ;  $p < 0.001$ ) and attractiveness ( $\Delta a^*$   $M \pm SE = 1.97 \pm 0.44$ ;  $t(20) = 4.500$ ;  $p < 0.001$ ). The redness change was negatively related to the initial redness of the faces for aggression, dominance and attractiveness, showing that more redness was added to faces initially low in red (Fig 1b, Table 1). Redness change ( $\Delta a^*$ ) was greater for initially lighter (higher  $L^*$ ) faces, in the aggression and attractiveness trials, though these effects were weaker than the effects of initial face redness ( $a^*$ ).

The trial condition (aggression, dominance or attractiveness) affected the amount of redness change applied ( $F(2,88) = 10.254$ ;  $p < 0.001$ ). Participants increased face redness the most for aggression, then dominance and least for attractiveness. All differences are significant ( $p < 0.001$ ; Fig. 1b).

**Table 1.** Statistical summary of the correlation analyses relating initial face lightness (L\*), redness (a\*) and yellowness (b\*) to redness change applied to optimize aggressive, dominant and attractive appearance.

Color dimension	Trial condition		
	Aggression	Dominance	Attractiveness
Lightness (L*)	$r(21) = 0.438$ $p = 0.047$	$r(21) = 0.347$ $p = 0.124$	$r(21) = 0.438$ $p = 0.047$
Redness (a*)	$r(21) = -0.509$ $p = 0.018$	$r(21) = -0.875$ $p < 0.001$	$r(21) = -0.868$ $p < 0.001$
Yellowness (b*)	$r(21) = 0.409$ $p = 0.065$	$r(21) = 0.095$ $p = 0.683$	$r(21) = 0.306$ $p = 0.177$

## Discussion

We have shown that increased redness (a\*), while holding lightness (L\*) and yellowness (b\*) constant, enhances the appearance of dominance, aggression and attractiveness in men's faces viewed by female participants. Participants increase redness more to maximize aggressive than dominant appearance, and more to maximize dominant than attractive appearance.

Our finding that apparent facial dominance and aggression are enhanced by increased skin redness is consonant with non-human primate studies that show associations between facial skin redness and social dominance (e.g., Setchell and Dixson, 2001). It also supports the explanation of color-related performance biases in humans that invokes an unconscious reaction associating red with dominance (Barton and Hill, 2005; Elliot et al., 2009; Hill and Barton 2005).

We find that facial skin redness enhances attractiveness, supporting the findings of a forced choice study by Re et al. (2011), but very high levels of redness increase perceived aggression to the detriment of attractiveness. These differences may reflect a trade-off between the benefits to females of choosing a healthy, dominant male and the costs of associating with an aggressive partner. Redness has associations with anger, both in faces (Drummond and Quah, 2001) and in abstract word association tasks (Hupka et al., 1997). In addition to health, dominance and aggression, facial redness is also associated with embarrassment. The fact that facial redness is associated with a range of social and emotional states does not mean that it is not associated with each individually; it need not be the case that facial redness is associated with only one, or only a limited number of, social and emotional states.

Facial redness is associated with high levels of testosterone and high dominance rank in non-human primates such as rhesus macaques (Rhodes et al., 1997) and mandrills (Setchell and Dixson, 2001). While dominance represents success in male-male competition, it is not always the case that female choice will favor the most dominant males (Qvarnstrom and Forsgren, 1998; Sadalla et al., 1987; Swaddle and Reiersen, 2002) or the most masculine males (Perrett et al., 1998; reviewed in DeBruine et al., 2006). Indeed, recent theoretical work has suggested that, in humans, male masculinity and sexual dimorphism may have evolved in response to male-male contest competition rather than in

response to female choice (Puts, 2010).

Dominance, moreover, is likely to explain only a portion of variance in attractiveness, with factors such as symmetry (Gangestad, Thornhill and Yeo, 1994; Grammer and Thornhill, 1994; Mealey, Bridgstock and Townsend, 1999; Penton-Voak et al., 2001; Perrett et al., 1999), health (Jones et al., 2004, 2005), averageness (Langlois and Roggman, 1990; Rhodes et al., 2001) and personality (Little, Burt and Perrett, 2006) also playing a role. Recent work has suggested that cues to current health, such as skin carotenoid levels, impact more strongly on men's attractiveness than does masculinity (Scott, Pound, Stephen and Penton-Voak, 2010; Stephen et al., 2012). Given that recent theoretical work suggests that male masculinity may have evolved more in response to selection from male-male competition than by female choice (Puts, 2010), further work exploring men's perception of the redness of other men's faces as aggressive and dominant would be desirable.

Physiological flushing responses to anger have been found in Chinese and Caucasian samples (Drummond and Quah, 2001). It has also been shown that skin color impacts similarly on perceptions of health in black African and Caucasian UK samples, with participants choosing similar levels of skin redness and yellowness adjustment to enhance perceived attractiveness (Stephen et al., 2009a; Stephen, Coetsee and Perrett, 2011). Affective attributions of red as strong and active have also been found to be consistent across a number of cultures (Adams and Osgood, 1973), suggesting that our results may generalize across cultures. Whilst the role of cultural influences in facilitating responses to red needs to be more fully investigated, such influences are not necessarily alternatives to a biological interpretation, but may interact with them. For example, the use of red as a warning signal in many contexts may itself reflect a predisposition as well as serving to reinforce that predisposition. Further cross-cultural work should therefore examine impacts of skin redness on perceptions of aggression, dominance and attractiveness in different cultures.

**Acknowledgements:** We thank P. Hibbard, A. Hurlburt, Y. Ling, I. Penton-Voak and T. Troscianko for color calibration advice; R. Hill and J. Setchell for comments; P. Wilcox for booth fabrication; L. Ferrier for organizing participants; A. Perrett for proofreading. This work was supported by the BBSRC, Unilever Research and the ESRC.

**Received 1 December 2011; Revision submitted 8 April 2012; Accepted 2 August 2012**

## **References**

- Adams, F. M. and Osgood, C. E. (1973) A cross-cultural study of the affective meanings of color. *Journal of Cross-Cultural Psychology*, 4, 135-156.
- Attrill, M. J., Gresty, K. A., Hill, R. A. and Barton, R. A. (2008). Red shirt color is associated with long-term team success in English football. *Journal of Sports Sciences*, 26, 577-582.
- Bamford, A. J., Monadjem, A. and Hardy, I. C. W. (2010) Associations of avian facial flushing and skin colouration with agonistic interaction outcomes. *Ethology*, 116, Evolutionary Psychology – ISSN 1474-7049 – Volume 10(3). 2012. -568-

1163-1170.

- Barton, R. A. and Hill, R. A. (2005). Reply: Seeing red? Putting sportswear in context. *Nature*, 437, E10-E11.
- Burt, D. M. and Perrett, D. I. (1995). Perception of age in adult Caucasian male faces: computer graphic manipulation of shape and color information. *Proceedings of the Royal Society B*, 259, 137-145.
- Changizi, M. A., Zhang, Q. and Shimojo, S. (2006). Bare skin, blood and the evolution of primate color vision. *Biology Letters*, 2, 217-221.
- Charkoudian, N. (2003). Skin blood flow in adult human thermoregulation: how it works, when it does not, and why. *Mayo Clinic Proceedings*, 78, 603-612.
- DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., Cooper, P. A., Penke, L., Feinberg, D. R. and Tiddeman, B. P. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society of London B*, 273, 1355-1360.
- Drummond, P. D. and Quah, S. H. (2001). The effect of expressing anger on cardiovascular reactivity and facial blood flow in Chinese and Caucasians. *Psychophysiology*, 38, 190-196.
- Edwards, E. A. and Duntley, S. Q. (1939). The pigments and color of living human skin. *American Journal of Anatomy*, 65, 1-33.
- Edwards, E. A., Hamilton, J. B., Duntley, S. Q. and Hubert, G. (1941). Cutaneous vascular and pigmentary changes in castrate and eunuchoid men. *Endocrinology*, 28, 119-128.
- Elliot, A. J., Maier, M. A., Moller, A. C., Friedman, R. and Meinhardt, J. (2007). Color and psychological functioning: The effect of red on performance attainment. *Journal of Experimental Psychology: General*, 136, 154-168.
- Elliot, A. J., Maier, M. A., Binser, M. J., Friedman, R. and Pekrun, R. (2009). The effect of red on avoidance behavior in achievement contexts. *Personality and Social Psychology Bulletin*, 35, 365-375.
- Frederick, D. A. and Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness-indicator hypothesis. *Personality and Social Psychology Bulletin*, 33, 1167-1183.
- Frost, P. (1994). Preferences for darker faces in photographs at different phases of the menstrual cycle: Preliminary assessment of evidence for a hormonal relationship. *Perceptual and Motor Skills*, 79, 507-514.
- Gangestad, S. W., Thornhill, R. and Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, 15, 73-85.
- Grammer, K. and Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, 108, 233-242.
- Greenlees, I., Leyland, A., Thelwell, R. and Filby, W. (2008). Soccer penalty takers' uniform color and pre-penalty kick gaze affect the impressions formed of them by opposing goalkeepers. *Journal of Sports Sciences*, 26, 569-576.
- Hagemann, N., Strauss, B., Leißing, J. (2008). When the referee sees red. *Psychological Science*, 19, 769-771.



- Hill, R. A. and Barton, R. A. (2005). Red enhances human performance in contests. *Nature*, 435, 293.
- Hong, G., Luo, M. R. and Rhodes, P. A. (2001). A study of digital camera colorimetric characterization based on polynomial modeling. *Color Research and Application*, 26, 76-84.
- Hupka, R. B., Zaleski, Z., Otto, J., Reidl, L. and Tarabrina, N. V. (1997). The colors of anger, envy, fear, and jealousy: a cross-cultural study. *Journal of Cross-Cultural Psychology*, 28, 156-171.
- Ilie, A., Ioan, S., Zagrean, L. and Moldovan, M. (2008). Better to be red than blue in virtual competition. *Cyber Psychology and Behavior*, 11, 375-377.
- Jeghers, H. (1944). Pigmentation of the skin. *New England Journal of Medicine*, 231, 88-100.
- Johnson, J. M. (1998). Physical training and the control of skin blood flow. *Medicine and Science in Sports and Exercise*, 30, 382-386.
- Jones, B. C., Little, A. C., Burt, D. M. and Perrett, D. I. (2004). When facial attractiveness is only skin deep. *Perception*, 33, 569-576.
- Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., Tiddeman, B. P., Whiten, S., Pitman, R. M., Hillier, S. G., Burt, D. M., Stirrat, M. R., Law Smith, M. J. and Moore, F. R. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London B*, 272, 347-354.
- Langlois, J. H. and Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science*, 1, 115-121.
- Little, A. C., Burt, D. M. and Perrett, D. I. (2006). Assortative mating for perceived facial personality traits. *Personality and Individual Differences*, 40, 973-984.
- Little, A. C. and Hill, R. A. (2007). Attribution to red suggests special role in dominance signaling. *Journal Evolutionary Psychology*, 5, 161-168.
- Mazur, A., Halpern, C. and Udry, J. R. (1994). Dominant looking male teenagers copulate earlier. *Ethology and Sociobiology*, 15, 87-94.
- Mealey, L., Bridgstock, R. and Townsend, G. C. (1999). Symmetry and perceived facial attractiveness: A monozygotic co-twin comparison. *Journal of Personality and Social Psychology*, 76, 151-158.
- Montoya, P., Campos, J. J. and Schandry, R. (2005). See red? Turn pale? Unveiling emotions through cardiovascular and hemodynamic changes. *Spanish Journal of Psychology*, 8, 79-85.
- Mueller, U. and Mazur, A. (1998). Facial dominance in *Homo sapiens* as honest signaling of male quality. *Behavioral Ecology*, 8, 569-579.
- Neave, N. and Shields, K. (2008). The effects of facial hair manipulation on female perceptions of attractiveness, masculinity and dominance in male faces. *Personality and Individual Differences*, 45, 373-377.
- Negro, J. J., Sarasola, J. H., Farinas, F. and Zorrilla, I. (2006). Function and occurrence of facial flushing in birds. *Comparative Biochemistry and Physiology, Part A*, 143, 78-84.
- Panza, J. A., Quyyimi, A. A., Brush, J. R. and Epstein, S. E. (1990). Abnormal

- endothelium-dependent vascular relaxation in patients with essential hypertension. *New England Journal of Medicine*, 323, 22-27.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. and Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741-742.
- Penton-Voak, I. S. and Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39-48.
- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M. and Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society B*, 268, 1617-1623.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. and Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, 394, 884-887.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. and Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, 20, 295-307.
- Puts, D. A., Gaulin, S. J. C. and Verdolini, K. (2006). Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and Human Behavior*, 27, 283-296.
- Puts, D. A. (2010). Beauty and the beast: mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31, 157-175.
- Qvarnstrom, A. and Forsgren, E. (1998). Should females prefer dominant males? *Trends in Ecology and Evolution*, 13, 498-501.
- Re, D. E., Whitehead, R. D., Xiao, D. and Perrett, D. I. (2011) Oxygenated blood colour change thresholds for perceived facial redness, health and attractiveness. *PLOS One*, 6, e17859.
- Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R. and Akamatsu, S. (2001). Attractiveness of facial averageness and symmetry in non-Western cultures: In search of biologically based standards of beauty. *Perception*, 30, 611-625.
- Rhodes, L., Argersinger, M. E., Gantert, L. T., Friscino, B. H., Hom, G., Pikounis, B., Hess, D. L. and Rhodes, W. L. (1997). Effects of administration of testosterone, dihydrotestosterone, estrogen and fadrozole, an aromatase inhibitor, on sex skin color in intact male rhesus macaques. *Journal of Reproduction and Fertility*, 111, 51-57.
- Richardson, D. (1987). Effects of tobacco smoke inhalation on capillary blood flow in human skin. *Archives of Environmental Health*, 42, 19-25.
- Rupp, H. A., James, T. W., Ketterson, E. D., Sengelaub, D. R., Jansen, E. and Heiman, J. R. (2009). Neural activation in women in response to masculinized male faces: mediation by hormones and psychosexual factors. *Evolution and Human Behavior*, 30, 1-10.
- Sadalla, E. K., Kenrick, D. T. and Vershure, B. (1987). Dominance and heterosexual attraction. *Journal of Personality and Social Psychology*, 52, 730-738.
- Scott, I. M. L., Pound, N., Stephen, I. D. and Penton-Voak, I. S. (2010). Does masculinity matter? The contribution of sex-typical appearance to male attractiveness in

- humans. *PLoS one*, 5, e13585.
- Setchell, J. M. and Dixson, A. F. (2001). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior*, 39, 177-184.
- Setchell, J. M. (2005). Do female mandrills prefer brightly collared males? *International Journal of Primatology*, 26, 715-735.
- Setchell, J. M. and Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, 111, 25-50.
- Setchell, J. M., Smith, T., Wickings, E. J. and Knapp, L. A. (2008). Social correlates of testosterone and ornamentation in male mandrills. *Hormones and Behavior*, 54, 365-372.
- Stephen, I. D., Coetzee, V., Law Smith, M. J. and Perrett, D. I. (2009a) Skin blood perfusion and oxygenation color affect perceived human health. *PLoS ONE*, 4, e5083.
- Stephen, I. D., Law Smith, M. J., Stirrat, M. R. and Perrett, D. I. (2009b) Facial skin coloration affects perceived health of human faces. *International Journal of Primatology*, 30, 845-857.
- Stephen, I. D., Coetzee, V. and Perrett, D. I. (2011) Carotenoid and melanin pigment coloration affect perceived human health. *Evolution and Human Behavior*, 32, 216-227.
- Stephen, I. D., Scott, I. M. L., Coetzee, V., Pound, N., Perrett, D. I. and Penton-Voak, I. S. (2012). Cross-cultural effects of color, but not morphological masculinity, on perceived attractiveness of men's faces *Evolution and Human Behavior*, 33, 260-267.
- Swaddle, J. P. and Reiersen, G. W. (2002). Testosterone increases perceived dominance but not attractiveness in human males. *Proceedings of the Royal Society of London B*, 269, 2285-2289.
- Waite, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M. and Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male colouration plays a role in female primate mate choice. *Proceedings of the Royal Society of London B*, 270, S144-S146.
- Waite, C., Gerald, M. S., Little, A. C. and Krauselburd, E. (2006). Selective attention toward female secondary sexual color in male rhesus macaques. *American Journal of Primatology*, 68, 738-744.
- Zihlman, A. L., and MacFarland, R. K. (2000). Body mass in lowland gorillas: A quantitative analysis. *American Journal of Physical Anthropology*, 113, 61-78.