
Sexual Selection and the Evolution of Human Physique

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Abstract

Charles Darwin proposed in *The Descent of Man and Selection in Relation to Sex* (1871) that traits which improve reproductive success, such as sexually attractive adornments, or weaponry that enhances fighting potential, have been selected for during the course of evolution. The field of evolutionary psychology has revitalized Darwin's hypotheses of sexual selection and human evolution through integrating the fields of anthropology, biology and psychology. In this thesis I investigate the potential for sexual selection to have acted upon sexual dimorphism in body composition and secondary sexual adornments in women and men.

In women, body fat accumulation around the hips, buttocks and thighs can be measured using the waist-to-hip ratio (WHR). Female body fat and body weight are critical as energy reserves for gestation, pregnancy and lactation. Female body shape, body weight and breast morphology have been implicated in male judgments of female physical attractiveness. Men from New Zealand (NZ), China, Samoa and the highlands of Papua New Guinea (PNG) rated images of women with low WHRs as most attractive, independent of changes in body weight. In studies of male preferences for female breast morphology, married men from NZ, Samoa and PNG preferred large breasts whereas unmarried men preferred medium-sized breasts. Darkly- and medium-pigmented areolae were preferred in each culture, as were symmetrical breasts. However, male preferences for female areolar size varied considerably across these cultures.

Eye-tracking techniques were used to measure attention to morphological traits as men made attractiveness judgments of female images that varied in WHR and breast morphology. In studies using full-length female images that varied in WHR and breast

size, men look most often and for longer at the regions of female physique in which fat deposits are greatest (i.e. the breasts followed by the waist). However, attractiveness judgments were driven primarily by WHR rather than breast size. In eye-tracking studies using female torsos as stimuli, men looked most often and for longest at the breasts and areolae, irrespective of differences in breast size and areolar pigmentation. Men rated large and medium size breasts, and medium and darkly pigmented areolae as most attractive. These eye-tracking studies show a possible discordance in male visual attention for morphological traits that appear to drive attractiveness decisions. However, when men were shown full-length images of women posed in back-view as well as in front-view there were significant differences in their viewing patterns. Men spent more time looking at the midriff region of back-posed images than front-posed images and, irrespective of body-pose, rated images with low WHRs as most sexually attractive.

Darwin suggested that the human male beard evolved via female choice as a highly attractive secondary sexual adornment. Other authors have proposed that the beard may augment aggressive displays and enhance perceptions of social dominance among males. To test these hypotheses I developed a new questionnaire that integrated facial expressions with the presence or absence of the beard. These questionnaires were administered in NZ and Samoa. The presence of a beard augmented male perceptions of aggressive facial expressions in Samoa and NZ. However, women in these cultures rated faces without beards as more attractive than bearded men. Men and women in both cultures rated bearded men as looking older and as having higher social status. The findings suggest that the beard plays a stronger role in intra-sexual competition rather than inter-sexual mate choice.

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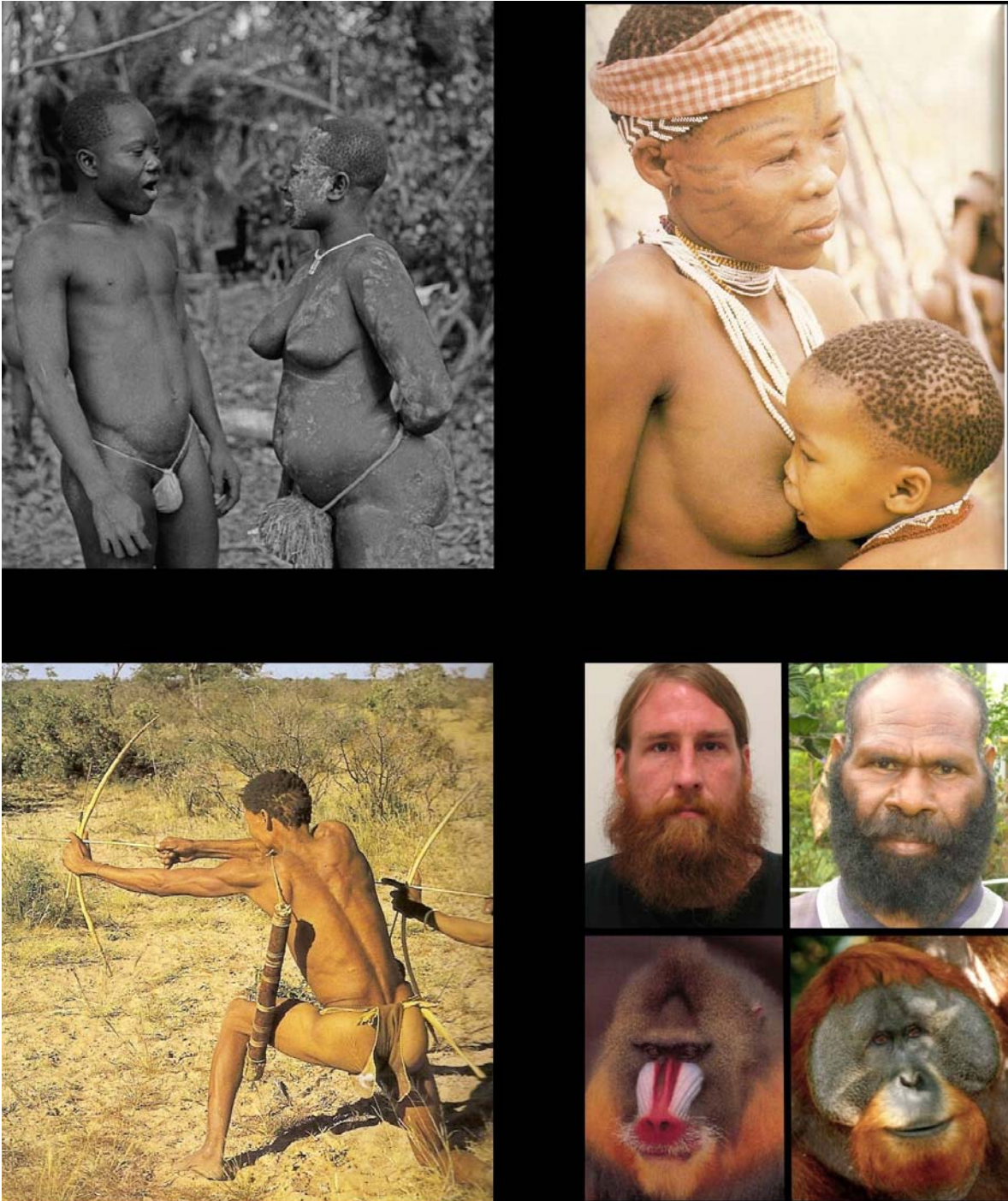
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Chapter One: Sexual Selection and the Evolution of Human Morphology.



Charles Darwin proposed in *The Descent of Man and Selection in Relation to Sex* (1871) that certain morphological and behavioural traits must have evolved in males and females due to sexual selection. Darwin suggested two mechanisms by which sexual selection might operate. Firstly, adornments that are perceived as highly attractive by members of the opposite sex may become enhanced via inter-sexual selection. Secondly, traits that enhance fighting ability or augment social rank among members of the same sex may have been favoured due to intra-sexual selection.

Darwin applied sexual selection hypotheses to describe sexual selection at the pre-copulatory level. Indeed, this has helped explain the evolution of sexually dimorphic behaviours and morphologies in many animals (Andersson, 1994). However, sexual selection also occurs at the copulatory and post-copulatory level. If a female mates with multiple males there is potential for sperm to compete within the female reproductive tract to fertilize the given set of ova (Parker, 1970). Detailed studies of the invertebrates have found strong evidence for sexual selection via sperm competition and on the morphology of male genitalia (Eberhardt, 1985; Simmons, 2001). Among the anthropoids the diversity in male genitalia, and the morphology of sperm gametes, may also have been strongly affected by sexual selection (Dixon, 1998; 2009). Given that the female reproductive tract is the arena in which sperm competition occurs, it is possible that a 'cryptic female choice' occurs so that females preferentially receive and transport the spermatozoa of males with particular genital morphologies, copulatory patterns or biochemical constitution of spermatozoa (Eberhard, 1996).

Darwin suggested that sexual selection applied to the evolution of morphology in *Homo sapiens*. However, many of his ideas remained neglected for many years after his

death. There has been a resurgence of interest in the effects of sexual selection on the evolution of human morphology and sexual behaviour with the birth of a new field called evolutionary psychology. Evolutionary psychology takes a multi-disciplinary approach by incorporating tools and concepts from anthropology, evolutionary biology and psychology, to understand how current behaviour might reflect the effects of selection in ancestral environments (Buss, 2005; Dunbar & Barrett, 2007). One of the recurring adaptive problems faced by human ancestral males and females was to assess 'mate value', i.e. the degree to which a potential partner might enhance his or her reproductive success (Symons, 1979; 1995). However, hominid fossils cannot tell us about sexual behaviour or soft tissue structures. Thus, evolutionary psychologists propose that selection has shaped human psychological faculties to attend to morphological features that signal competitive ability and fecundity (Buss, 2003; Grammer et al., 2003).

Reproduction involves substantial physical and emotional investment on the part of both men and women. Women also invest considerably through pregnancy, lactation and child rearing (Jasienska, 2009). Such investments may have led to highly selective sexual and social preferences in reproductive partners. Mens' mate value may be determined by morphological cues that signal competitive ability and potential to acquire resources, as well as nurturing social traits. Womens' mate value is determined by reproductive health, including post-partum care of offspring. While these traits cannot be directly observed, human morphology may convey biological information relating to competitive ability, health and fertility, which may have been important in mate selection in ancestral environments (Barber, 1995; Symons, 1995; Thornhill & Gangestad, 1996).

Selection, therefore, may have shaped the development of psychological mechanisms in people to increase attention to bodily features in order to assess mate value.

Hypotheses about sexual selection in humans could be tested by identifying bodily features known to be indicative of health and fertility, and then investigate whether variation in those features predictably determine judgments of attractiveness. Men and women across cultures state that physical attractiveness is an important trait when considering a potential partner (Buss, 1989). Further, physical attractiveness in men and women predicts their success in attaining short and long-term sexual partners (Rhodes, Simmons & Peters, 2005). In this Chapter, I will review the literature on male and female physical attractiveness in order to examine the extent to which sexual dimorphism in physique and secondary sexual traits arose via mechanisms of sexual selection. I will focus on the signaling value of morphological traits that may play a role in mate choice at the pre-copulatory level.

Sexual Selection and the Evolution of Male Physique.

Among many of the nonhuman primates, males are larger in body size than females (Martin, Willner & Dettling, 1994). Men are also larger than women, averaging 63.5kg compared to 52.3kg (Collard, 2002). However, the largest sex differences in people are reflected in body composition and body shape. Male physique is 38.8% muscle compared with 27.7% in women. Women have almost twice the amount of body fat as men. Typically 43.6% of the female physique is comprised of fat in comparison to 28.4% in men (Clarys et al., 1984). Muscle mass and body fat are stored in specific regions of the body that result in sexual dimorphism in body shape. Men have an android body shape, so that muscle mass is concentrated in the upper body, particularly the

shoulders. In contrast, women have a gynoid physique in which the waist is narrower and fat is stored in hips, buttocks and thighs (the gluteal/femoral region) and breasts.

Natural selection and sexual selection may be responsible for the male android body composition. *Homo sapiens* is thought to have evolved from small bands of hunter-gatherers in Africa (Marlowe, 2005). Hunting is primarily a male activity and prior to the advent of complex technology and the domestication of dogs, men used persistence hunting (Liebenberg, 2006). Persistence hunting involves a small group of men running down prey, sometimes over the course of several days, until the animal succumbs to heat exposure and exhaustion. This hunting technique survived, until recently, among the bushmen of the central Kalahari (Liebenberg, 2006). Persistence hunting requires a physique that is well adapted to the demands of distance running (Bramble & Lieberman, 2004; Liebenberg, 2006). It is conceivable that those men who were most successful at persistence hunting achieved greater reproductive success through the provision of resources that may have contributed to offspring survival (Buss, 2003).

Male physique has been measured using a system called somatotyping. Somatotyping is an anthropometric scale which defines physique by employing a three dimensional assessment of a person's mesomorphy (muscularity), endomorphy (fatness), and ectomorphy (leanness) (Carter & Heath, 1990; Sheldon, Depertuis, & McDermott, 1954). A muscular (mesomorphic) physique is indicative of greater strength, speed and cardiac function compared to an ectomorphic (lean) physique (Carter & Heath, 1990). In contrast, an endomorphic physique, characterized by more body fat and less muscular development, may be linked to weakened immune function and greater susceptibility to diabetes and cardiovascular diseases (Katzmarzyk *et al.*, 1998; Bolunchuk *et al.*, 2000).

Male somatotype may provide women with a visual cue to underlying health, fitness, provisioning skills and competitive ability. In support of this hypothesis, women from United Kingdom (U.K), Sri Lanka, China, Cameroon, New Zealand and United States of America (U.S.A), rate mesomorphic and average somatotypes as more attractive than ectomorphic and endomorphic somatotypes (Dixson *et al.*, 2003; 2007a, 2007b, 2008). Thus, the mesomorphic somatotype may have undergone intra-sexual and inter-sexual selection during evolution.

In addition to sex differences in body shape and composition, human populations also show sexual dimorphism in height. The ratio of adult male/female height is 1.06 across cultures (Collard, 2002). Stature also affects attractiveness. Men and women from Poland, Germany, Austria and the UK rate images depicting a couple in which a man taller than a woman by ratios of 1.04, 1.09 and 1.14 as more attractive (Fink et al., 2007; Pawlowski, 2003). Male height has been associated with reproductive success. Men in UK, Poland and USA who are taller than the population mean father significantly more offspring (Mueller & Mazur, 2001; Nettle, 2001; Pawlowski, Dunbar, & Lipowicz, 2000). While these studies show that sexual selection via female choice may drive sexual dimorphism in human stature, they reflect only the preferences of women from Western cultures. In studies conducted in rural Gambia, taller men did not have greater reproductive success (Sear, 2006). Further, among people from rural Gambia and the Hadza hunter-gatherers of Tanzania, taller men are not preferred as marriage partners (Sear & Marlowe, 2009). However, it may be that absolute height is of less importance than the components that contribute to height. For example, it has been shown that the length of the legs is an important predictor of female preferences for male stature in

Poland (Sorokowski & Pawlowski, 2008). It will be important for future studies to investigate this question among pre-industrialized cultures.

Androgens during pubertal development promote the growth of the larynx, which is markedly sexually dimorphic in adults. Men have a larger larynx than women (Beckford et al., 1985; Hollien, Green & Massey, 1994). This trait is responsible for the lowering of vocal pitch. Women have a vocal pitch that is twice as high as men (Titze, 2000). Men with higher levels of circulating testosterone have been shown to have the lowest vocal pitch (Dabbs & Mallinger, 1999) and masculine vocal pitch correlates with other measures of physique that are linked with male competition such as body size and upper body musculature (Evans, Neave & Wakelin, 2006). Women find men with low vocal pitches more attractive (Collins, 2000; Feinberg et al., 2005; Puts, 2005). Men with low vocal pitches are also judged as sounding more socially and physically dominant and men who judge themselves as physically dominant lower their vocal pitch in response to other male competitors (Puts, Gaulin & Verdolini, 2006). Among the Hadza hunter-gatherers, men with lower vocal pitches fathered significantly more offspring than men with higher vocal pitches (Apicella, Feinberg & Marlowe, 2007). Sexual dimorphism in vocal pitch in *Homo sapiens* may have undergone intra- and inter-sexual selection.

Sexually dimorphic facial features may also be sexually selected in men and women (Fink & Penton-Voak, 2002; Rhodes, 2006). In men, androgens during adolescent development stimulate the growth of a more prominent brow ridge, narrower eyes and larger jaw than is typically found in women (Swaddle & Reiersen, 2002). It has been suggested that because masculine traits develop under the actions of testosterone, which may have immunosuppressant effects on individuals (Grossman, 1985), those

males displaying these traits are advertising their genetic fitness through possessing physiologically costly ornaments (Folstad & Karter, 1992, Zahavi & Zahavi, 1997). However, studies of male facial attractiveness have shown that male faces with less pronounced masculine traits are generally rated as most attractive by women (Perrett et al., 1998). Further, while men with higher levels of circulating testosterone have more sexual partners, their faces are not judged as more attractive by women (Peters, Simmons & Rhodes, 2008). Recent studies have proposed that women may show temporal shifts in mate preferences during the menstrual cycle. Thus, research employing computer-generated faces as stimuli has found that women in the follicular (often termed 'fertile') phase of the menstrual cycle prefer more masculine faces (Gangestad & Thornhill, 2008). However, when unaltered photographs of male faces and bodies were used, no effect was found of the menstrual cycle on women's judgments of male attractiveness (Peters, Rhodes & Simmons, 2009). Male facial attractiveness may signal aspects of mate quality, however, it remains to be determined that 'good genes' models of sexual selection are driving sexual dimorphism in facial features.

Morphological traits can vary in symmetry due to environmental and genetic factors (Møller & Swaddle, 1997; Møller & Thornhill, 1998). Trait asymmetry has been described as either antisymmetry, directional asymmetry or fluctuating asymmetry (Van Valen, 1962). Antisymmetry refers to the enlargement of a bilateral trait on a random side of the body. For example, male fiddler crabs can develop one enlarged claw on either the right or left side (Pratt & McLain, 2002). Directional asymmetry is the enlargement of a trait on a specific side of the body such as occurs with the left testes of barn swallows (Møller, 1994). Fluctuating asymmetry involves small, random variations in bilateral

traits. In recent years there has been a lot of research into fluctuating asymmetry and human facial attractiveness (Rhodes & Simmons, 2007; Simmons et al., 2004). Among the Hadza hunter-gatherers, men and women state a higher preference for facial symmetry than people from the UK (Little et al., 2007). Numerous studies have shown that facial symmetry is a highly attractive trait in men and women (Rhodes, 2006). Rhodes & Simmons (2007) suggest that human preferences for facial symmetry may not be sexually selected because the evidence is weak that symmetry signals health. Rather, symmetry may be part of a suite of perceptual traits that play a role in human visual processes. Interestingly, eye-tracking research has shown that symmetry is a salient feature that captures people's attention to images of flowers, animals and buildings (Kootstra & Schomaker, 2009). It would be valuable to test whether this finding extends to perceptions of symmetry in the human face.

Compared to the nonhuman primates, human beings have less body hair. Nuclear genetic studies suggest that hairlessness in Hominids dates back to 1.2 million years ago (Rogers, Iltis & Wooding, 2004). Many hypotheses have been proposed for the loss of body hair (hirsuteism) in humans (for review see Rantala, 2007). For example, it has been suggested that as ancestral hominids transitioned from arboreal to savannah conditions, loss of body hair was adaptive for cooling (Morris, 1967; Wheeler, 1992a, 1992b). Another, more recent, hypothesis proposes that due the development of cooperative hunting and fixed home bases, loss of body hair may have lessened disease-carrying ectoparasites (Pagel and Bodmer, 2003; Rantala, 1999, 2007).

While humans have lost thermoregulatory pelage important in other anthropoid primates, men retain some body and facial hair. Hamilton and Zuk (1982) proposed that

female preferences for male secondary sexual adornments could be due to their signaling the male's ability to withstand or resist parasitic infection. Hair on the face and body are localized breeding sites for ectoparasites such as *Demodex folliculorum* and *Demodex brevis* which can result in skin diseases such as demodicosis (Nenoff *et al.*, 2009). Thus, hirsute men could be advertising their superior immune system through possessing a trait that is immunologically costly. Hirsuteism is driven by androgens (Randall, 2007). The immunocompetence-hypothesis proposes that androgen-dependant male secondary sexual adornments advertise superior immune function to females through the ability to tolerate the immunosuppressant effects of testosterone (Folstad & Karter, 1992). This hypothesis may also explain the evolution of facial and body hair in men.

Testing these hypotheses requires experiments to reveal female preferences for body and facial hair. A logical first test of hypotheses for sexual selection on masculine body hair would be to ask women in various cultures whether body and facial hair enhances male sexual attractiveness. Women from the UK rate images of men with pronounced body hair as highly attractive (Dixson *et al.*, 2003). However, women from Cameroon, China, New Zealand and California (USA) rate images lacking body hair as more attractive than those showing pronounced hirsuteism (Dixson *et al.*, 2007a, 2007b, 2008). These studies highlight the importance of cross-cultural replication and the danger of drawing strong conclusions when the preferences of only one culture have been quantified. Present evidence indicates that it is unlikely that masculine body hair evolved via female choice.

Darwin, however, argued that the male beard evolved via female choice. He cited cross-cultural examples of the role of the beard as a signal of masculine social status and

physical attractiveness. For example, “in the Pacific the Fijian’s beard is profuse and bushy, and his greatest pride” (Darwin, 1871, p 575). Like research on masculine trunk hair, a similar discordance occurs when women are asked to judge the attractiveness of male beardedness. Beards make a man look more masculine, socially mature, confident and older (Kenny and Fletcher 1973; Wood 1986; Addison 1989; Wogalter and Hosie 1991; Neave and Shields 2008). While women appear to value these characteristics in their mates (Buss 1989; Penton-Voak and Perrett 2001), studies of facial hair in relation to male facial attractiveness have produced contradictory results. Some studies have found a full beard to be attractive to women (Pelligrini 1973; Feinman and Gill 1977; Reed and Blunk 1990) while others have not (Wogalter and Hosie 1991; Muscarella and Cunningham 1996). Recently, Neave and Shields (2008) reported that women rated male faces with light stubble as most attractive; perceived age rose with increasing amounts of facial hair and a full beard was rated as most dominant. While these studies provide quantitative data on the role of the beard in perceptual judgments of masculine dominance and attractiveness, few cross-cultural comparisons have been made. Thus, cross-cultural research on female preferences for male beardedness remains a priority.

Studies of male physical attractiveness have advanced considerably in recent years. It is now known that women assess men for long-term relationships, so that a complex array of social traits may influence their assessments of attractiveness (Buss et al., 1990). Prior to courtship, physique and visually conspicuous adornments such as height, broad shoulders, muscularity, body and facial hair appear to be significant determinants of women’s attractiveness judgments of men. Understanding the effects of intra- and inter-sexual selection on the evolution of male morphology still has some way

to go before firm conclusions can be drawn. Cross-cultural research, in particular, is a priority if meaningful generalizations about the role of sexual selection on the evolution of male physique and secondary sexual adornments are to be made.

Sexual Selection and the Evolution of Female Physique.

Women have almost twice as much body fat as men (Clarys et al., 1984). Female body fat is stored primarily in the hips, buttocks, thighs (the gluteal/femoral region) and breasts (Lassek & Gaulin, 2006; 2007) resulting in a gynoid body shape. Natural selection in relation to biomechanical and thermoregulatory constraints may have favored gynoid deposition of fat in women (Cant, 1981; Pawlowski, 2001). Subcutaneous body fat may be critical for heat dispersal in colder climates (Cant, 1981). The evolution of bipedal locomotion places a biomechanical constraint on women as they must be mobile during gestation (Pawlowski, 2001). The deposition of gluteal femoral fat in the hips, buttocks and thighs correlates with the centre of body mass in women and thus may serve for balance required for bipedal locomotion during gestation (Pawlowski & Grabarczyk, 2003).

Variation in the distribution of body fat can be measured using the waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist by the distance around the hips and buttocks. A low WHR, characterized by a slimmer waist in relation to wider hips, fuller thighs and larger buttocks, is linked to earlier onset of menarche in girls (Lassek & Gaulin, 2007), and the maintenance of regular menstrual and ovulatory cycles in adulthood (Moran et al., 1999; Van Hooff et al., 2000). Women with larger breasts and low WHRs have been shown to have higher circulating levels of 17β -oestradiol and progesterone (Jasienska et al., 2004), which are predictors of the

probability of conception (Lipson & Ellison, 1996). Women with lower WHRs also have higher conception rates in artificial insemination (Zaadstra et al., 1993) and in *in-vitro* fertilization programs (Wass et al., 1997). Women with lower WHRs have also been found to be younger at first coitus and report having had more sexual partners (Hughes et al., 2004). The ‘hourglass’ female body constitution may therefore signal health and reproductive potential.

Evolutionary psychologist Devendra Singh hypothesized that sexual selection via male partner preference may have driven the evolution of low WHR in women (Singh, 1993; 2006). Cross-cultural research is critical for testing adaptive explanations for sexual preferences for traits such as female WHR, given that variations in human physique and mate preferences occur in different parts of the world. Singh’s original studies of WHR were carried out mainly in the USA. Subsequently, cross-cultural studies have found that men from industrialized societies rate female images, the majority of which are line drawings, with low WHRs (0.6-0.7) as most attractive in China (Dixson et al., 2007a), the USA and New Zealand (Dixson et al., 2008). Images depicting women with low WHRs are also preferred by men from Germany (Henss, 2000), England (Furnham et al., 1997) and Poland (Rozmus-Wrzesinska & Pawlowski, 2005). However, several studies conducted in less industrialized cultures have questioned whether a low female WHR of 0.7 is universally attractive to men. Among the Matsigenka of Peru a WHR of 0.9 was most attractive (Yu & Shepard, 1998). In Bakossiland, a community of subsistence farmers in rural Southwest Cameroon, a WHR of 0.8 was most attractive for both short and long-term relationships (Dixson et al., 2007b). Initial studies among the Hadza hunter-gatherers of Tanzania also found that a WHR of 0.9 was more attractive

(Wetsman & Marlowe, 1999). However, in a follow-up study using images in profile view so that the buttocks were visible, Hadza men preferred a WHR of 0.6 (Marlowe et al., 2005). Among the Shiwiar of the Ecuadorian Upper Amazon, men selected images of women with a high body weight as most attractive (Sugiyama, 2004). However, when body weight was controlled for, images with WHRs of 0.7 and 0.8 were selected as more attractive (Sugiyama, 2004). Thus, discordance in male preferences for images varying in WHR may be an artifact of the use of stimulus line drawings, which confound the effects of WHR on female body weight (Tovée & Cornellisen, 2001).

Singh (1993, 2002, 2006) argued that the role of WHR as a determinant of female physical attractiveness to men is not independent of body weight. Indeed, WHR is a measure of body fat distribution and is positively correlated with another anthropometric measure, the body mass index (BMI), which equates to weight scaled for height ($\text{BMI} = \text{weight in Kilograms} / (\text{height in meters} \times \text{height in meters})$). Women with BMIs of 20-22 are highly attractive to men in the UK (Tovée et al., 1999). Some cross-cultural investigations, employing photographs of women that varied in BMI and WHR as stimuli, have concluded that women's BMI exerts a greater influence than WHR on male ratings of female attractiveness (Japan: Swami et al., 2006; Malaysia: Swami and Tovée, 2005; Zululand in South Africa: Tovée et al., 2006). These authors reject the WHR hypothesis and propose that female BMI is a better predictor of female attractiveness to men (Swami & Furnham, 2007).

As WHR and BMI are positively correlated it has been very difficult to tease apart the contribution made by each variable to men's judgments of female attractiveness. Nevertheless, a recently developed surgical procedure called micrograft surgery provides

such an opportunity (Singh & Randall, 2007). In this procedure adipose tissue is harvested from the waist and used to re-shape the buttocks of female patients (Roberts, 2001). This surgical procedure reduces female WHR without altering BMI (Roberts et al., 2006; Singh & Randall, 2007). If female body fat distribution has been important in the evolution of male mate selection, images of women whose WHRs have been reduced should be more attractive independently of BMI. However, cross-cultural research using appropriate questionnaires and female images is required to test this hypothesis fully.

Women also store fat around the mammary glands to a much greater extent than men. The breasts are prominent morphological structures that enlarge during adolescent development. In other primates breast enlargement only occurs during pregnancy and lactation (Short, 1980). Breast fat provides an important energy reserve, given the requirements of pregnancy and lactation (Anderson, 1983). Some authors have argued that large breasts act as milk storage organs (Low et al., 1987). However, it is important to note that the size of the non-lactating breast is not indicative of its ability to produce milk because breast enlargement is due to the deposition of adipose and stromal tissue and not milk ducts (Vandeweyer & Hertens, 2002). Others have proposed that the breasts are critical in mother-infant bonding (LeBlanc & Barnes, 1974; Smith, 1986). However, these hypotheses are very difficult to test and, as such, they remain speculative (Caro, 1987; Jesser, 1971).

Biologists, anthropologists and psychologists often argue that womens' breasts are sexually attractive to men. Indeed, anthropological studies have found that men across cultures find female breasts and nipples to be sexually erotic characteristics (Ford and Beach, 1952). Male preferences for female breast morphology appear to vary between

cultures. For example, among the Sudanese Azande, men are said to prefer long pendulous breasts. Alorese men of the Alor Island in Indonesia prefer large breasts and men of the Kenyan Masai tribes prefer firm, upright breasts (Ford & Beach, 1952). However, these statements were sourced from qualitative ethnographies whose primary aim was not the study of human sexuality and physical attractiveness. Nevertheless, more empirical and replicated studies that have quantified male preferences for female breast size have also found considerably variable results. Men rate as most attractive line drawings and silhouettes of women with small breasts (Furnham & Swami, 2007; Furnham, Swami, & Shah, 2006), medium-sized breasts (Horvath, 1981; Wiggins et al., 1968) or larger than medium-sized breasts (Singh and Young, 1995). The variable nature of these results is clearly problematic.

While these studies provide some quantitative data on the role played by sexual selection in the evolution of the human breast, they are subject to significant methodological problems. Using line drawings and silhouettes is potentially problematic as they do not allow people to distinguish between changes in breast shape, size and areola configuration. Across the lifespan such changes may be used to gauge a woman's age and reproductive status (Gallup, 1982; Marlowe, 1998; Symons, 1995). Relatively few studies have been undertaken to test the role of such traits in male judgments of female attractiveness. Furthermore, it is perhaps surprising that there have been no studies conducted on male preferences for female breast size in pre-industrialized cultures. Thus, cross-cultural studies quantifying male preferences for female breast morphology are a priority for future research.

Darwin (1871) noted that across cultures women tend to have somewhat lighter skin than men and suggested that this sex difference arose during human evolution via sexual selection. Natural selection is likely to have been responsible for the striking differences in skin pigmentation and colour that occur in different parts of the world. The dark pigmentation that is found in African populations is likely to represent the skin colour of human ancestors as it provides protection from ultraviolet (UV) radiation. Skin acquires its colouration due to epidermal melanin. Melanocytes secrete either eumelanin, which causes darker skin, or pheomelanin, which creates red or yellow skin (Jablonski, 2006). The MC1R gene, which is responsible for darker skin, shows greatest variation among Europeans, little variation among Africans and is lacking among Asians (Sturm, 2006). Thus, as humans migrated out of Africa and occupied settlements in more northern latitudes with lower UV levels, skin colour lightened (Jablonski & Chaplin, 2000).

The decrease in melanin content in populations such as the Europeans may be adaptive for the cutaneous synthesis of vitamin D in response to UV rays (Jablonski, 2004; Jablonski & Chaplin, 2000). Thus, lighter skin allows for more efficient synthesis of vitamin D in conditions of lower exposure to UV levels. Vitamin D stimulates the absorption of calcium that is crucial for bone growth. The synthesis of UV into vitamin D therefore plays a crucial role in the development of the fetus. For example, developmental pelvic abnormalities and rickets occur, in part, due to vitamin D deficiencies (Jablonski, 2006). This may explain why women have lighter skin than men, as they must increase the synthesis of vitamin D during pregnancy. The vitamin D hypothesis was first proposed by Murray (1934). Additions were made by Loomis (1967)

and finally Jablonski & Chaplin (2000) have cemented this theory in the anthropological literature. Robins (1991), however, has argued that production and storage of vitamin D occurs seasonally, with peak synthesis in the summer for storage in the winter when levels of UV radiation decreases. Furthermore, people with darkly pigmented skin in parts of the world with low levels of UV produce the same amount of vitamin D as people with light skin (Robins, 1991). Interestingly, these arguments resurfaced recently in two review articles in the *American Journal of Physical Anthropology* (Chaplin & Jablonski, 2009; Robins 2009) and highlight the fact that the vitamin D hypothesis is as contentious today as it was when Murray (1934) first proposed it.

The secretion of androgens in men during pubertal development drives the deposition of epidermal melanin and stimulates increased production of haemoglobin. Thus, men tend to have darker pigmentation of the skin and a ‘ruddier’ complexion than women (Frost, 1994a). Interestingly, women rate photographs of men with darkly pigmented skin as more attractive than lightly pigmented skin (Frost, 1994b). Women have lighter skin than men, possibly as a by-product of increased oestrogen production during adolescence (Van den Bergue & Frost, 1986). In their summary of the anthropological literature, Van den Bergue and Frost (1986) found that men across human cultures judge women with lighter skin to be more physically attractive. However, these data were sourced from anecdotal accounts from ethnographies that did not directly quantify male preferences for female skin tone. Recent cross-cultural research has shown that men in China have a marked preference for light skin in women (Dixson et al., 2007a). A moderate preference for light skin was also observed in New Zealand and USA (Dixson et al., 2008), whereas among the Bakossi of Cameroon, female skin colour did

not influence male ratings of female attractiveness (Dixson et al., 2007b). The faces of Caucasian women with higher levels of oestrogen are judged to be more attractive (Law-Smith et al., 2006). How far this result is due to the effects of oestrogen on skin complexion, as distinct from other facial traits, remains to be clarified. This interesting study also requires cross-cultural replication, particularly in African or other populations where women have very darkly pigmented skin.

As has been mentioned previously, hormonal changes during pubertal development affects the growth of craniofacial traits which results in sexual dimorphism in facial shape in men and women. Androgens drive the expression of masculine facial traits such as thin lips, narrow and deeply set eyes and a brow ridge (Swaddle & Reiereson, 2002). Women have much lower levels of androgens and higher levels of oestrogen, which may inhibit the growth of masculine facial features and results in women retaining neotenous traits such as large eyes, full lips and a smaller chin. These traits enhance female facial attractiveness to men. Feminine faces are highly attractive to men irrespective of whether natural or computer-generated composite faces are employed as stimuli (Rhodes, 2006). Furthermore, faces in which feminine features have been enhanced are judged to be more attractive than faces depicting an average facial shape (Rhodes, 2006). Research on female facial attractiveness suggests that feminine facial shape may represent sexually selected traits that were important during the evolution of human sexual behaviour.

An empirical anthropological perspective is essential in the study of sexual selection and the evolution of human morphology. Questionnaires make it possible to collect comparative data in different parts of the world. However, this technique does not

measure peoples' behavioral responses to the morphological cues that are predicted to influence judgments of physical attractiveness. How do men analyze visual cues such as WHR and breast morphology when judging the attractiveness of female physique? A behavioural response can be measured precisely using new eye-tracking technology because it measures visual attention. In psychological studies, visual attention to stimuli is closely linked to motivation. For example, fear-related stimuli, such as snakes and spiders, capture people's attention (Öhman, Anders, & Esteves, 2001). Attractiveness, particularly in women, comprises a suite of morphological cues that have also been shown to capture male attention (Maner et al., 2007). Men look more often, and for longer, at faces they judge to be more attractive (Fink et al., 2008; Shimojo et al., 2003). Attractiveness may therefore influence attention, at least in studies of female facial attractiveness.

Recent eye-tracking studies have found that men spend a lot of time looking at the female body when viewing both erotic and non-erotic stimuli (Lykins, Meana, & Kambe, 2006; Lykins, Meana, & Strauss, 2008; Rupp & Wallen, 2007). Indeed, eye-tracking studies of the female body have consistently shown that the breasts receive a lot of visual attention even when images are shown fully or partially clothed (Hewig et al., 2008; Suschinsky et al., 2007). In such experiments, men may be examining the breast as a whole, or looking at specific features such as the areolae when making attractiveness judgments. However, it is difficult to obtain fine-grained measurements concerning eye-tracking and attention to female morphology when men view complex scenes and clothed, or partially clothed, images. Thus, if the goal of the study is to test male attention for female morphological traits that could be under sexual selection, it will be important

for future eye-tracking studies to employ stimuli that allow men to view female physique and not be distracted by clothing. If WHR and breast morphology are important visual signals of female youth and fecundity, men should spend the most time looking at these features when judging the attractiveness of a potential partner.

Goals of this thesis

I begin this thesis with studies of male preferences for female waist-to-hip ratio (WHR) and body mass index (BMI). In Chapter 2, Chapter 3 and Chapter 4 I present cross-cultural data that highlight the importance of female WHR in male attractiveness judgments when controlling for the effects of female BMI.

The importance of female breast morphology in male perceptions of female physical attractiveness has been proposed by several authors (Gallup, 1982; Marlowe, 1998; Symons, 1995). However, the few studies that have been conducted have used silhouettes or line drawings and data have been confined to the preferences of men from industrialized and Western cultures. In Chapter 5: *Male preferences for female breast morphology in New Zealand, Samoa and Papua New Guinea* I use a new questionnaire to test the role of breast size, areolar colour, areolar pigmentation and breast symmetry in male judgments of female attractiveness. I find cross-cultural differences in men's preferred breast size in women. However, when analyses take into account the marital status of men, married men prefer large breasts to a greater extent than unmarried men. Darker areolar pigmentation is preferred, as are symmetrical breasts. However, preferences for areolar size vary across the cultures examined.

Studies of human physique and physical attractiveness most often use questionnaires that contain images. These images are then rated for specific traits. The

prediction is that participants will actively respond to the characteristics of the images and that this will, in turn, influence their subjective attractiveness ratings of the images. However, despite the large numbers of questionnaire studies that have collected ratings of various traits of the body and face, relatively little is known about how much attention is given to these traits during attractiveness judgments. In Chapter Six, Chapter Seven and Chapter Eight, I use new eye-tracking techniques to collect data from men on the specific body parts that are looked at during attractiveness judgments of female physique.

Turning to the question of sexual selection and masculine secondary sexual traits, Darwin (1871) argued that the human beard had evolved via female choice. Other authors proposed that the beard plays a stronger role in male perceptions of aggressiveness, dominance and social status (Goodhart, 1960; Guthrie, 1970). It is possible that the beard might act in concert with particular facial expressions, which can express underlying emotional states among humans as well as nonhuman primates (Ekman, 1993; Ekman et al., 1969; Schmidt and Cohn, 2001). The beard might therefore augment facial expressions that signal masculine aggressiveness to men and attractiveness to women. In Chapter Nine: *Sexual selection and the evolution of the beard: A cross-cultural study*, I combine facial expressions with manipulations of facial hair to test the role of the beard in male and female perceptions of attractiveness, aggressiveness, social dominance and age of men in Samoa and New Zealand.

In this thesis my goal is to present an integrative approach to study of human physique, sexual attractiveness and mate choice. I have developed and applied new questionnaires to test the role of female breast morphology, body fat distribution and body weight in male judgments of female attractiveness in cultures where studies of

physical attractiveness have not been conducted. Further, these images are employed in psychological studies of attention and attractiveness using new eye-tracking techniques. Finally, I test Darwin's hypothesis that the human beard evolved via female choice. For this study I integrate facial expressions, with the experimental manipulation of facial hair, in a cross-cultural study of the role of facial hair in inter- and intra-sexual selection.

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Chapter Two

Male Preferences for Female Waist-to-hip Ratio and Body Mass Index in the Highlands of Papua New Guinea.



A man from the Okapa District in the Eastern Highlands of Papua New Guinea.

Authors note: Chapter Two is presented in the style of the American Journal of Physical Anthropology, where it was appears as the manuscript:

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The chapter is a modified version of this manuscript, adapted to the thesis.

ABSTRACT

The waist-to-hip ratio (WHR) and body mass index (BMI) have both been implicated in male judgments of female physical attractiveness. WHR and BMI are correlated and attempts to test the individual contribution of each of these traits on female attractiveness have been inconclusive. A surgical technique called micrograft surgery provides the means for examining male preferences for female WHR independently of BMI.

Micrograft surgery involves harvesting adipose tissue from the waist and reshaping the buttocks to produce a low WHR. In this study one hundred men, living in 3 villages in a remote region of the eastern highlands of Papua New Guinea were asked to judge the attractiveness of pre- and post-operative photographs of women who had undergone micrograft surgery. Some women gained, and some lost weight, post-operatively, with resultant changes in BMI. Men consistently chose post-operative photographs as being more attractive than pre-operative photographs of the same women. Post-operatively changes in BMI were not related to men's judgments of attractiveness. These results show that the hourglass female figure is rated as attractive by men living in a remote, indigenous community, and that when controlling for BMI, WHR plays a crucial role in their attractiveness judgments.

INTRODUCTION

While men are somewhat larger than women in body size, human beings show greater sexual dimorphism in muscularity and body fat (Carter and Heath, 1990). Women typically have a higher percentage of body fat than men (Clarys et al., 1984). This sex difference emerges at puberty, with increased levels of body fat being laid down in female hips, thighs, buttocks (the gluteal/femoral region) and breasts (Merzenich et al., 1993; Boot et al., 1997). The distribution of body fat can be measured using the waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist by the circumference of the hips and buttocks.

Both natural and sexual selection may have played a role in the evolution of female body fat. Biomechanical and thermoregulatory constraints may have favored greater deposition of fat in certain areas of body (Cant, 1981; Pawlowski, 2001). The evolution of upright gait and bipedalism as the principle mode of locomotion, coupled with the fact that women must be mobile during pregnancy, may have driven a low center of body mass in women, which correlates with low WHR (Pawlowski and Grabarczyk, 2003). A low WHR of approximately 0.7 has also been linked to the timing of menarche (Lassek and Gaulin, 2007), maintaining regular menstrual cycles (Van Hooff et al., 2000) and ovulatory cycles (Moran et al., 1999). In a sample of 119 Polish women, women with lower WHRs and larger breast volumes were shown to have higher circulating levels of 17- β -estradiol and progesterone (Jasienska et al., 2004), which are predictors of conception probability (Lipson and Ellison, 1996). In studies conducted in fertility clinics, women with lower WHRs had higher success rates in artificial insemination (Zaadstra et al., 1993) and in in-vitro fertilization programs (Wass et al., 1997).

Women's WHRs increase as they age, possibly due to reduction in estrogen production (Kirschner and Samojlik, 1991). The 'hourglass' female body constitution may therefore signal health and reproductive status.

Human morphology that conveys biological information relating to health and fertility may have been important to mate selection in ancestral environments (Barber, 1995; Symons, 1995; Thornhill and Gangestad, 1996). Although these claims cannot be directly tested in modern-day human societies, it follows that, if true, selection has also shaped human psychological faculties to attend to morphological features that honestly signal health and reproductive status (Buss, 2003; Grammer et al., 2003). Sexual selection via male partner preference may have driven the evolution of low WHR in women (Singh, 2006). Men rate stimulus images with low WHRs of 0.6 as most attractive for both short and long-term relationships in North America (Dixson et al., in press) and China (Dixson et al., 2007a). Images of women with low WHRs of 0.6-0.7 are also attractive to men from Germany (Henss, 2000), England (Furnham et al., 1997), Poland (Rozmus-Wrzesinska and Pawlowski, 2005) and in New Zealand, where a female WHR of 0.7 was rated as most attractive by men when considering both short and long-term relationships (Dixson et al., in press).

Adaptive claims about sexual preferences for traits such as female WHR are difficult to validate in the absence of cross-cultural support. Several studies in less industrialized cultures have questioned whether a low female WHR of 0.7 is universally attractive to men. For example, among the Shiwiar of the Ecuadorian Upper Amazon, men selected images of women with a high body weight and a slightly higher WHR of 0.8 as most attractive (Sugiyama, 2004). Among the Matsigenka of Peru a WHR of 0.9

was most attractive (Yu and Shepard, 1998). In Bakossiland, a community of subsistence farmers in rural Southwest Cameroon, a WHR of 0.8 was most attractive for both short and long-term relationships (Dixson et al., 2007b). Initial studies among the Hadza hunter-gatherers of Tanzania found that a WHR of 0.9 was more attractive to Hadza men (Wetsman and Marlowe, 1999). However, in a follow-up study using images in profile view in which the buttocks were visible, Hadza men preferred a WHR of 0.6 (Marlowe et al., 2005). Therefore, the angle of the body pose may contribute to the differing male preferences across these cultures for female images varying in WHR.

Discordance in male preferences for images varying in WHR could also be due to the presentation of line drawings to participants that confound the effects of WHR on female body mass index (BMI) (Tovée and Cornellisen, 2001). BMI is calculated as weight in kilograms divided by (height in meters X height in meters). Women with a BMI of 20 are more attractive to men in the UK (Tovée et al., 1999). In a recent series of cross-cultural studies, differences in women's BMI were found to exert a greater influence than WHR on male ratings of female attractiveness in Japan (Swami et al., 2006), Malaysia (Swami and Tovée, 2005) and Zululand in South Africa (Tovée et al., 2006). However, there are some shortcomings in study design that may have affected their results. For example, in these studies men rated 50 images of women varying in BMI from 15 (emaciated) to over 30 (clinically obese). The relevance of these images is questionable, because men were asked to rate images that show women with a range of WHRs and BMIs that may not be typical of their daily experiences. It is perhaps not surprising that WHR becomes less important, if not irrelevant, when men are presented with images depicting emaciated and obese women. Thus, results in these studies may

also have been affected by the nature of the stimuli employed to measure female attractiveness.

WHR and BMI are positively correlated and therefore it is difficult to test the contribution made by each of these traits to men's judgments of female attractiveness. A recently developed procedure called micrograft surgery provides an opportunity to test these traits independently as in this procedure adipose tissue is harvested from the waist and used to re-shape the buttocks of female patients. The outcome for the patient is a reduction of WHR without modifying BMI (Roberts et al., 2005; Singh and Randall, 2007). If female fat distribution and body shape have been important in the evolution of mate choice then post-operative images with lower WHRs should be more attractive than pre-operative images of the same women. To test this hypothesis, one hundred men from three remote villages in the Okapa district of the highlands of Papua New Guinea completed a questionnaire in which they judged the attractiveness of photographs of women before and after micrograft surgery.

METHOD

Study site and participants

Papua New Guinea (PNG) is the eastern half of the island of New Guinea and has a population of 4.5 million people. The Okapa district is located in the Eastern Highlands Province of PNG (Fig. 1). There are approximately 54,000 people living in the Okapa district. These people form five separate ethnic groups: Fore, Auyana, Kimi, Keagana and Kanite. We conducted surveys among the Kanite, which is the language spoken by people who live north of the Wanevinti mountains. There are approximately 8,000 Kanite people living in the Okapa district. We interviewed a hundred Kanite men (mean age \pm

s.d = 27.55 years \pm 8.365, range = 18 – 58 years) from three small villages; Kimiagomo, Yafanagomo and Foseya, located in the Northern part of Okapa, the capital of the Okapa district. Kimiagomo village has a population of 486, Yafanagomo village and Foseya village each have approximately 200 residents. In this region polygynous marriages can occur. Of the 100 men interviewed, 42% were unmarried, 48% were married to one wife and 10% had two or more wives.

These villages have no mains water supply, electricity, television, or land phone lines (although recently mobile phones can be used). There is a road from the provincial capital, Goroka to Kimiagomo village but it is rarely used as it can only be accessed by four-wheel drive vehicles. These villages are typical of the highland region of PNG, where all the residents are subsistence farmers who sustain their livelihood through tilling the land. Small plots of bush are slashed for gardening and planting coffee trees. The main income in these villages comes from selling coffee. The villages and the surrounding areas do not support large animals, therefore hunting is a rare activity.

Procedure

Pre- and post-operative measurements were made of women's height and weight (in order to calculate BMI). Waist-to-hip ratios were also measured in all subjects in a standardized way (Singh and Randall, 2007). All subjects were North American in origin and included 5 Caucasians and 5 African Americans or Hispanic Americans (Table 1). Permission to use these images was given by Dr Roberts and Dr Singh and this study was preapproved by the Human Ethics Committee at Victoria University of Wellington. We selected five patients (Group A) whose BMIs had increased and five (Group B) whose BMIs decreased after surgery. All women had significantly lower WHRs after surgery (t

$= 7.364$, $df = 9$, $p < .001$) but group A had significantly higher post-operative BMI measures than group B ($t = 3.559$, $df = 4$, $p < .05$) (Table 1).

Participants completed questionnaires with the aid of one of the researchers (KS), who is from this region of PNG and is fluent in both English and Kanite. All the men were interviewed individually, either in their homes, at their farms or in communal huts. Participants completed a questionnaire containing color photographs of 10 women who had undergone cosmetic micrograft surgery. Pre- and post-operative photographs of the same patient were presented on a single page, but their positions in the questionnaire (right or left) were randomized. Participants viewed each pair of images for 10 seconds and selected only the image they found most attractive. To examine possible effects of body pose on judgments of attractiveness, the photographs of patients before and after surgery were taken using back-posed and oblique views. Only the torso, including the waist, hips and buttocks, was shown in each photograph (Figure 2A).



Figure 1. A map showing where the Okapa district is located on the Island of Papua New Guinea.

Table 1. Waist-to-hip ratio (WHR) and body mass index (BMI) measurements of patients before and after micrograft surgery. All patients have lower post-operative WHRs. Group A have higher post-operative BMI whereas in Group B, BMI decreased slightly.

Patient No	WHR		BMI		Patient Ethnicity
	Pre-op	Post-op	Pre-op	Post-op	
Group A					
1	0.84	0.75	21.13	21.46	Caucasian
2	0.93	0.78	22.84	23.92	Caucasian
3	0.84	0.75	25.06	25.32	Hispanic
4	0.78	0.68	26.31	26.47	Caucasian
5	0.80	0.69	26.36	26.66	African American
Group B					
6	0.74	0.70	25.18	24.05	Caucasian
7	0.76	0.68	22.53	19.99	African American
8	0.78	0.74	23.71	21.44	Hispanic
9	0.77	0.71	25.74	23.51	Caucasian
10	0.80	0.75	21.95	20.82	African American
Mean	0.80	0.72	24.80	23.36	
SEM	0.01	0.01	0.60	0.748	

STATISTICAL PROCEDURE

Wilcoxon signed rank tests were used to determine whether male preferences for the ten pre or post-operative images were statistically different at $\alpha = 0.05$. Mann-Whitney U tests were conducted to test whether selections for post-operative images were affected by increases (Group A) or decreases (Group B) in female BMI. Spearman Rank correlation coefficients were calculated in order to test for possible correlations between

the magnitude of post-operative changes in female WHR and BMI and men's judgments of female attractiveness.

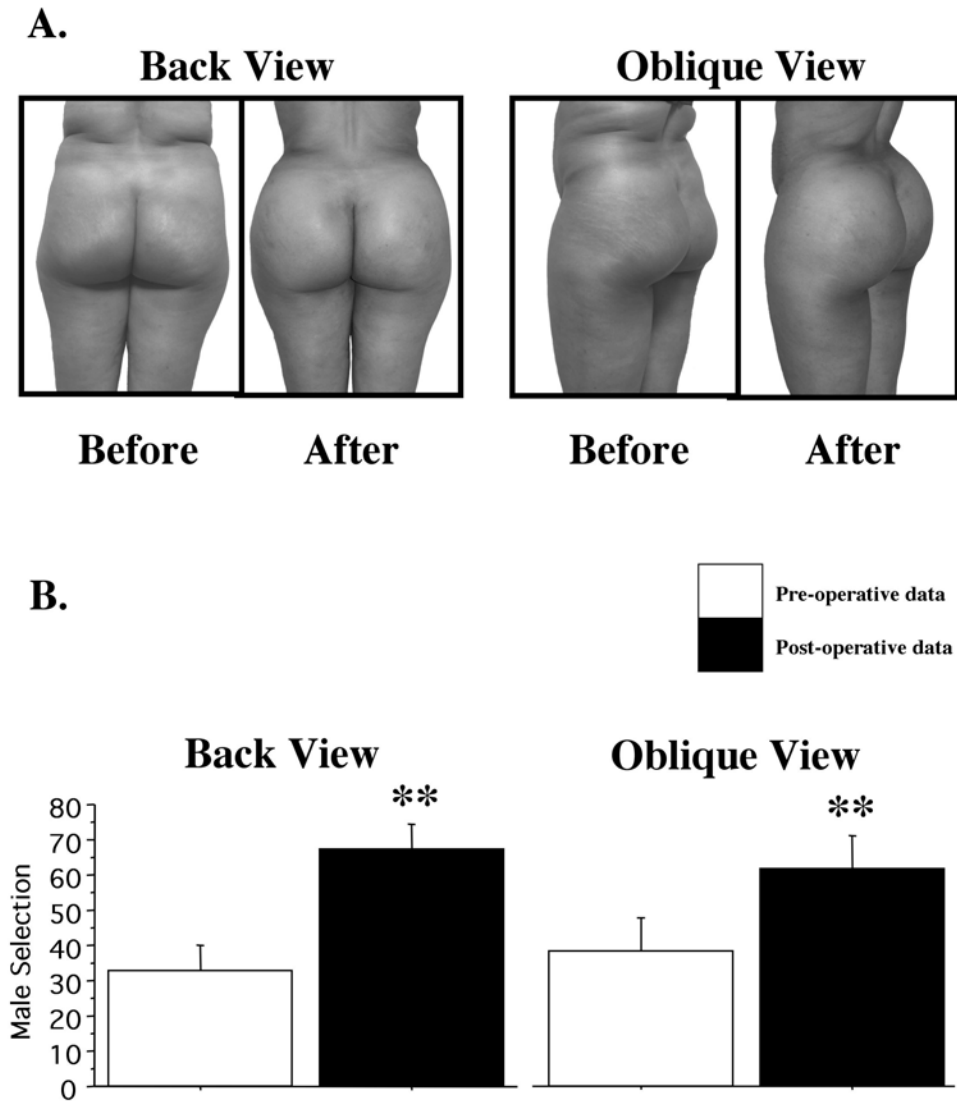


Figure 2. (A) An example of a patient who has undergone micrograft surgery. Images show the same woman pre and post-operatively, from back and oblique view. (B) Men's preferences for pre- and post-operative female images. Data are the mean number of subjects (\pm se).** $p < .01$.

RESULTS

Post-operative images were chosen significantly more often, ($z = 3.461$, $df = 9$, $p < .001$). There was also a significant effect of body pose on attractiveness judgments. More post-operative images were selected when images were presented in back views as opposed to oblique views ($z = 2.497$, $df = 4$, $p < .01$). We compared the preferences for the five women whose BMI increased post-operatively (Group A) to the five women who decreased in BMI post-operatively (Group B). Due to the significant differences between selection rates for back and oblique-posed images, these data were analyzed separately. A minimum U-value of 23 is required for significance at the 5% level. U-values were well below those required for significance for images in both back ($U = 11$) and oblique ($U = 11.5$) views. Thus, changes in BMI after micrograft surgery did not affect selection rates for post-operative images.

Men's preferences for post-operative images were not correlated with the magnitude of post-operative changes in female WHR (back view: $R_s = -.221$, $p = .507$; oblique view: $R_s = -.209$, $p = .531$) or BMI (back view: $R_s = .315$, $p = .344$; oblique view: $R_s = .382$, $p = .252$). To further examine possible differences in the attractiveness of images, dependant upon the amount of post-operative changes in WHR and BMI, we compared a specific pair of images. Patient 1 and patient 7 had very similar changes in WHR (0.09 and 0.08 respectively). However, patient 1 increased in BMI by 0.33 and patient 7 decreased in BMI by 2.54. Interestingly men's choices of post-operative images of these women were very similar (patient 1 = 67/100 and patient 7 = 63/100). Chi-square tests revealed that selections for these images achieved the same degree of statistical significance (patient 1: $\chi^2 = 5.78$, $p < .05$; patient 7: $\chi^2 = 3.38$, $p < .05$).

It is possible that the ethnicity of the subjects in the photographs might have influenced male selections. Five women were Caucasian and five were of African American or Hispanic descent. We compared men's selections of post-operative images of the five Caucasian women to their choices of the five women of African American or Hispanic descent. A minimum U-value of 23 would be required for significance at the 5% level. However, U-values were well below those required for significance, for images in both back ($U = 8.5$) and oblique ($U = 8.5$) views. Therefore, differences in ethnicity between the subjects in the photographs are unlikely to account for selection rates for post-operative images.

DISCUSSION

The current study tested whether body shape (WHR) affected male preferences for female physique when controlling for body mass index (BMI). Men from the highlands of Papua New Guinea (PNG) expressed a preference for an hourglass-shaped female physique with a low WHR, irrespective of changes in BMI. These results are consistent with Singh's (1993) theory that male preferences for low female WHRs evolved as an important 'first pass filter' used in mate selection.

The role of WHR and BMI in determining female physical attractiveness has been debated since Singh's (1993) publication. A large number of studies using line drawings have shown that a low WHR (0.7) is most attractive to men (for review see Singh, 2006). However, these studies have been criticized for presenting participants with unrealistic images and for confounding the effects of WHR and BMI, as the two traits are positively correlated (Tovée and Cornallisen, 2001).

A series of cross-cultural studies has been conducted in which photographs of women varying in BMI and WHR were rated for attractiveness (Swami and Tovée, 2005; Swami et al., 2006; Tovée et al., 2006). These studies question the validity of the WHR hypothesis by showing BMI as a better predictor of female attractiveness. Tovée et al (2006) suggested that human mate preferences may depend on the environmental context. This was posited to be the case for Zulu men in South Africa who stated a greater preference for women with high BMIs (over 30), whereas Zulu men living in the UK had very similar preferences to British Caucasians for women with BMIs in the range 20-22 (Tovée et al., 2006). These authors propose that human sexual preferences are plastic, that low WHR is not a trait that is universally preferred, and that male preferences for female BMI will account for cross-cultural variations in mate choice.

Data in the current study were collected in three villages in the highlands of Papua New Guinea. These villages existed in relative isolation until the 1950's, when doctors, anthropologists and Australian government officials began establishing contact with local people (Anderson, 2008). They have remained isolated from modern cultural influences such as the Internet, television, advertising and Hollywood films. Indeed, the area remains extremely challenging to contact, as one researcher recounts “ Poor (to appalling and impassable in the wet season) road conditions hampered work. The roads have significantly deteriorated in recent years. It takes 36 hours to cover 40 km in the wet season with heavy vehicle rescue equipment and a six-man team” (Collinge, 2008). Thus, this study reports data on human mate choice from a remote and culturally isolated community and provides important comparisons, and contrasts, with similar studies conducted in industrialized cultures.

A significantly larger proportion of men in the current study selected post-operative images with a lower WHR as most attractive, irrespective of body pose or post-operative changes in BMI. This questionnaire has recently been applied in several less remote and isolated cultures, with similar results reported from Cameroon, Indonesia, Samoa and New Zealand (Singh et al., in press). Therefore, across a diverse range of cultures, which vary in socioeconomic status and exposure to Western media, it appears that WHR is a trait that defines female attractiveness.

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Chapter Three

Female Waist-to-hip Ratio, Body Mass Index and Sexual Attractiveness in China.



A view of the city of Xi'an in the Shaanxi Province in China.

Authors note: Chapter Three is presented in the style of the journal *Current Zoology* where it appears as the manuscript:

Dixson, B. J., Li, B., Dixson A. F. Female waist-to-hip ratio, body mass index and sexual attractiveness in China. (2010). *Current Zoology*, 56, 175-181.

The chapter is a modified version of this manuscript, adapted to the thesis.

Abstract Men and women at Northwest University ($n = 751$), Xi'an, China were asked to judge the attractiveness of photographs of female patients who had undergone micrograft surgery to reduce their waist-to-hip ratios (WHR). Micrograft surgery involves harvesting adipose tissue from the waist and reshaping the buttocks to produce a low WHR and an 'hourglass' female figure. This gynoid distribution of female body fat has been shown to correlate with measures of fertility and health. Significantly larger numbers of participants, of both sexes, chose post-operative photographs, with lower WHRs, as more attractive than pre-operative photographs of the same women. Some patients had gained, and some had lost weight, post-operatively, with resultant changes in body mass index (BMI). However, these changes in BMI were not related to judgments of attractiveness. These results show that the hourglass female figure is rated as attractive in China, and that WHR, rather than BMI, plays a crucial role in such attractiveness judgments.

Key words China, Waist-to-hip ratio, Body mass index, Female attractiveness, Sexual selection.

INTRODUCTION

Uniquely among the Primates, adult female human beings have large stores of body fat in their breasts, thighs, hips and buttocks (Dufour & Slather, 2002; Pond, 1997). Body composition is highly sexually dimorphic (Carter & Heath, 1990), so that women typically have 43.6% of their physique comprised of fat in comparison to 28.4% in men (Clarys et al., 1984). Sexual dimorphism in human body composition is also reflected by sex differences in overall body shape. During adolescent development, secretion of oestrogen promotes storage of fat in the gluteofemoral region and breasts of girls (Merzenich et al., 1993; Boot et al., 1997). This gynoid distribution of body fat can be measured using the waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist by the distance around the hips and buttocks.

A low WHR, characterized by a slimmer waist in relation to wider hips, fuller thighs and larger buttocks, is linked to the onset of menarche in girls (Lassek & Gaulin, 2007), and the maintenance of regular, ovulatory cycles in adulthood (Moran et al., 1999; Van Hooff et al., 2000). Women with larger breasts and low WHRs have been shown to have higher circulating levels of 17β -oestradiol and progesterone (Jasienska et al., 2004), which are predictors of the probability of conception (Lipson & Ellison, 1996). Women with lower WHRs have higher success rates in artificial insemination (Zaadstra et al., 1993) and in *in-vitro* fertilization programs (Wass et al., 1997). Women with lower WHRs have been found to have a younger age of first coitus and report having had more sexual partners than women with high WHRs (Hughes et al., 2004). Women's WHRs increase as they age, possibly due to reduction in estrogen production (Kirschner and

Samojlik, 1991). The 'hourglass' female body constitution may therefore signal health and reproductive status.

Human morphology which may convey biological information relating to health and fertility was important in mate selection in ancestral environments (Barber, 1995; Symons, 1995; Thornhill and Gangestad, 1996). Evolutionary psychologists have proposed that selection has shaped human psychological faculties to attend to morphological features that honestly signal health and reproductive status (Buss, 2003; Grammer et al., 2003). Thus, sexual selection via male partner preference may have driven the evolution of low WHR in women (Singh, 1993; 2006). Cross-culturally, men rate images of women with low WHRs (0.6-0.7) as most attractive in China (Dixson et al., 2007a), the U.S.A and New Zealand (Dixson et al., in press). Images depicting women with low WHRs are also preferred by men from Germany (Henss, 2000), England (Furnham et al., 1997) and Poland (Rozmus-Wrzesinska and Pawlowski, 2005).

Cross-cultural studies are critical for testing adaptive claims for sexual preferences for traits such as female WHR. Several studies conducted in less industrialized cultures have questioned whether a low female WHR of 0.7 is universally attractive to men. Among the Matsigenka of Peru a WHR of 0.9 was most attractive (Yu and Shepard, 1998). In Bakossiland, a community of subsistence farmers in rural Southwest Cameroon, a WHR of 0.8 was most attractive for both short and long-term relationships (Dixson et al., 2007b). Initial studies among the Hadza hunter-gatherers of Tanzania found that a WHR of 0.9 was more attractive to Hadza men (Wetsman and Marlowe, 1999). However, in a follow-up study using culturally appropriate images, Hadza men preferred a WHR of 0.6 (Marlowe et al., 2005). Among the Shiwiari of the

Ecuadorian Upper Amazon, men selected images of women with a high body weight as most attractive (Sugiyama, 2004). However, when body weight was controlled for, images with WHRs of 0.7 and 0.8 were selected as more attractive (Sugiyama, 2004). Discordance in male preferences for images varying in WHR may be an artifact of the use of line drawings, which confound the effects of WHR on female body weight (Tovée & Cornellisen, 2001).

WHR is a measure of body fat distribution and is positively correlated with another anthropometric measure, the body mass index (BMI), which equates to weight scaled for height ($BMI = \text{weight in Kilograms} / (\text{height in meters} \times \text{height in meters})$). Women with a BMI of 20 are highly attractive to men in the UK (Tovée et al., 1999). Recently in a series of cross-cultural studies, which employed photographs of women that vary in BMI and WHR, differences in women's BMI were found to exert a greater influence than WHR on male ratings of female attractiveness (Japan: Swami et al., 2006; Malaysia: Swami and Tovée, 2005; Zululand in South Africa: Tovée et al., 2006). Thus, the roles played by BMI and WHR in determining female attractiveness to men remain highly debated (Swami & Furnham, 2007).

As WHR and BMI are positively correlated it is very difficult to tease apart the contribution made by each variable to men's judgments of female attractiveness. A recently developed surgical procedure called micrograft surgery provides such an opportunity. In this procedure adipose tissue is harvested from the waist and used to re-shape the buttocks of female patients. This surgical procedure reduces female WHR without altering BMI (Roberts et al., 2005; Singh & Randall, 2007). If female body fat distribution is important in male mate selection, then images with lower WHRs should be

more attractive. To test this hypothesis, men and women from Xi'an, China, completed a questionnaire quantifying their preferences for photographs of women who had undergone micrograft surgery to reduce the waist-to-hip ratio.

1 Materials and methods.

1.1 *Patients and photographic images.*

Plastic surgeons obtained pre-operative measurements of the waist-to-hip ratio (WHR) and body mass index (BMI) of ten North American women, who had requested micrograft surgery for cosmetic reasons (Singh & Randall, 2007). The measurements were repeated post-operatively, once healing was complete (Table 1). Five patients were of Caucasian and five were of African/Hispanic descent. Pre-operative and post-operative colour photographs were obtained of these same patients, directly from the back, and from an oblique angle (Fig. 1). Although the stimulus set varies in ethnicity, if WHR is of importance in mate choice, then images with low WHRs should be more attractive irrespective of ethnicity. Furthermore, low WHR in women should also be attractive when the body is viewed from different angles. As such, two views were taken of each woman in order to control for possible effects of pose upon attractiveness judgments. The post-operative photographs were taken a few months after surgery, in order to allow for healing of any scars. To control for any differences in skin blemishes between the pre- and post-operative photographs, the images were scanned into a computer and modeled using Adobe Photoshop version 7.0 in order to remove imperfections.

1.2 *Participants.*

This study was conducted at Northwest University, in the city of Xi'an, Shaanxi Province, China. Students were asked to participate by completing a questionnaire in

which they judged the attractiveness of photographs of women before, and after, micrograft surgery. Each questionnaire had a cover sheet (written in Mandarin Chinese) for demographic data, including the respondent's sex, age, and marital status. A total of 376 men (mean age 22.41 ± 3.25 years, range 18-52), none of whom were married, and 375 women (mean age 22.53 ± 3.46 years, range 18-45) completed the same questionnaire. Of these women, only 4% were married. Hence our sample consisted predominantly of unmarried university students, in their late teens and early twenties.

Table 1. Waist-to-hip ratio (WHR) and body mass index (BMI) measurements of patients before and after micrograft surgery. All patients have lower post-operative WHRs. Group A have higher post-operative BMI whereas in Group B, BMI decreased slightly.

Patient No	WHR		BMI		Patient Ethnicity
	Pre-op	Post-op	Pre-op	Post-op	
Group A					
1	0.84	0.75	21.13	21.46	Caucasian
2	0.93	0.78	22.84	23.92	Caucasian
3	0.84	0.75	25.06	25.32	Hispanic
4	0.78	0.68	26.31	26.47	Caucasian
5	0.80	0.69	26.36	26.66	African American
Group B					
6	0.74	0.70	25.18	24.05	Caucasian
7	0.76	0.68	22.53	19.99	African American
8	0.78	0.74	23.71	21.44	Hispanic
9	0.77	0.71	25.74	23.51	Caucasian
10	0.80	0.75	21.95	20.82	African American
Mean	0.80	0.72	24.80	23.36	
SEM	0.01	0.01	0.60	0.748	

1.3 Procedure.

A questionnaire was compiled which contained 20 pairs of images, in colour. Each pair of images was of one patient, showing her pre-operative and post-operative appearance, either in back-pose, or oblique-pose (Figure 1). The position of each photograph in a pair was randomized (appearing on either the right or left side of the page) and likewise the order in which the pairs were presented to subjects who judged their attractiveness was randomized. Each subject was asked to view one pair of photographs at a time, and to choose the image that they judged to be more attractive. Subjects had no knowledge of the rationale for the study, or that the pairs of photographs were of the same individuals. Permission to use the photographs was given by Dr Roberts and Dr Singh and this study was preapproved by the Human Ethics Committee at Victoria University of Wellington.

1.4 Statistical Analyses.

Wilcoxon signed rank tests were used to determine whether male preferences for pre- or post-operative images were statistically different at $\alpha = 0.05$. Mann-Whitney U tests were conducted to test whether selections for post-operative images were affected by increases (Group A in Table 1) or decreases (Group B in Table 1) in female BMI. Spearman Rank correlation coefficients were calculated in order to test for possible correlations between the magnitude of post-operative changes in female WHR and BMI and judgments of their attractiveness.

2 Results

2.1 Postoperative changes in WHR and BMI.

Micrograft surgery resulted in reductions in WHR in all ten women, from an average of 0.8 ± 0.017 to 0.72 ± 0.011 ($t = 7.364$; $df = 9$; $p < 0.001$). However, pre-operative and post-operative measurements of BMI for these same subjects did not differ significantly

(Pre-op: Mean \pm SEM 24.8 ± 0.60 ; Post-op: 23.36 ± 0.75 , $t = 1.731$; $df = 9$; $p = 0.118$).

Five women increased slightly in weight and five lost weight during the post-operative period (see Groups A and B, in Table 1). Group A had significantly higher post-operative BMI measures than group B ($t = 3.559$, $df = 4$, $p < .05$).

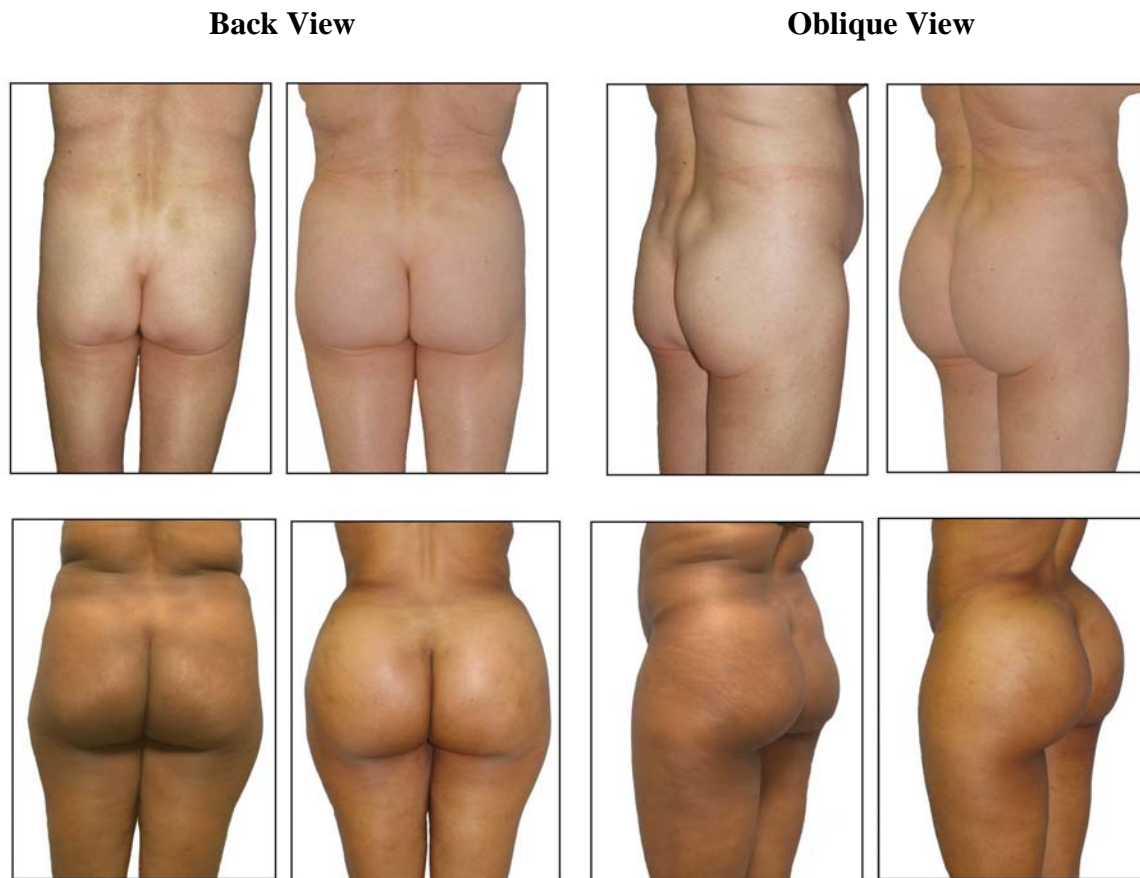


Figure 1. Representative pre- and post-operative images of patient No. 1 (upper images) and patient No. 3 (lower images) who underwent micrograft surgery. Post-operative images of these patients were consistently selected as most attractive by men and women in China.

2.2 Judgments of Attractiveness.

Judgments of attractiveness were not significantly influenced by the different views of the body (back-posed versus oblique-posed) depicted in the photographs (Men: $z = -1.478$, $df = 4$, $p = 0.139$; Women: $z = -1.325$, $df = 4$, $p = 0.185$). Thus, the data for both

views were combined for further analysis. Men and women selected post-operative photographs significantly more often, as determined by Wilcoxon Signed Rank tests (Men: $z = 3.061$, $df = 9$, $p < 0.001$; Women: $z = 3.603$, $df = 9$, $p < 0.0001$) (Fig. 2). Post-operative increases, or decreases, in BMI in the women who were photographed for this study had no significant effect on attractiveness judgments. Thus, five women increased slightly in BMI after micrograph surgery, whilst five showed small decreases (Table 1). Mann-Whitney U tests were conducted to compare the attractiveness judgments of men and women concerning these two groups. A minimum U value of 23 would be required for such comparisons to be significant at the five percent level. Both U values were well below this minimum (Men, $U = 8$; Women, $U = 6$) and hence were not statistically significant.

2.3 Attractiveness and post-operative changes in WHR and BMI.

It is possible that male and female judgments of attractiveness might be affected by the magnitude of changes in post-operative WHR or BMI. Therefore, we tested whether the differences between pre- and post-operative WHR and BMI for each of the 10 patients used in this study correlated with numbers of selections for post-operative images. For WHR, this correlation was not significant for male preferences for either back-posed ($R_s = .039$, $p = .906$) or oblique-posed photographs ($R_s = .227$, $p = .495$). Likewise, there was no correlation between female selections for back-posed ($R_s = .176$, $p = .598$) or oblique-posed images ($R_s = .048$, $p = .884$). Nor did male preferences for post-operative images correlate with the degree of post-operative changes in BMI (back-posed: $R_s = .552$, $p = .098$; oblique-posed: $R_s = .627$, $p = .060$). Women's judgments were not correlated with the magnitude of post-operative changes in BMI for oblique-posed images ($R_s = .039$, p

= .906). However, there was a small, significant effect regarding back-posed images ($R_s = 670$, $p < .05$). Thus, larger numbers of women showed a significant tendency to select back-posed images of patients whose post-operative BMI had increased slightly.

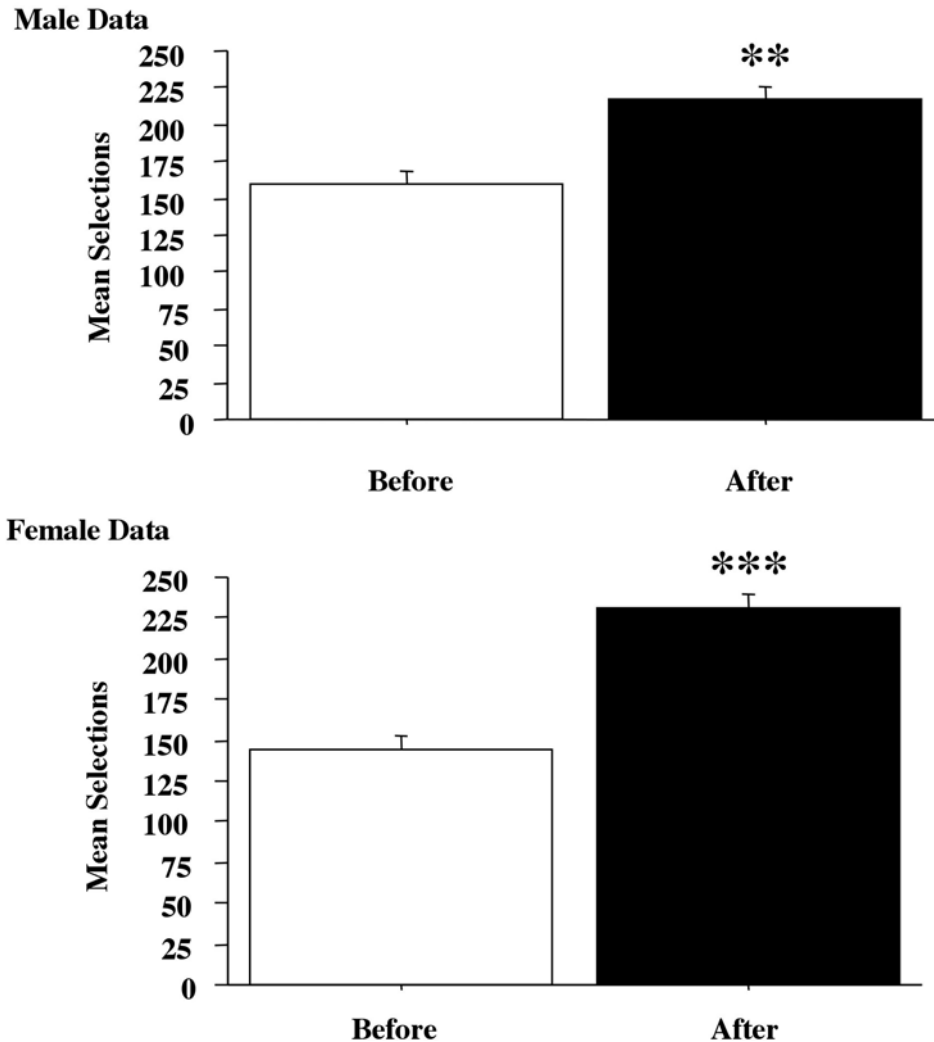


Figure 2. Male and female preferences for pre- and post-operative images of women who had undergone micrograft surgery. Open histograms = pre-operative data. Black histograms = post-operative data. Data are the mean number of subject (+standard errors). ** $p < .001$, *** $p < .0001$.

2.4 Female attractiveness as a function of ethnicity.

It is possible that selections might be affected by the ethnicity of the patients that were rated for attractiveness. Five women were of African American or Hispanic descent,

while the remaining five patients were Caucasian. Mann-Whitney U tests were conducted to compare attractiveness judgments concerning these two groups (i.e. African American/Hispanic versus Caucasian). A minimum U value of 23 would be required for such comparisons to be significant at the five percent level. However, both U values were well below this minimum and hence were not statistically significant (Men, $U = 6.5$; Women, $U = 10$). Thus, it is unlikely that the ethnicity of the patients used in this study affected attractiveness judgments.

2.5 Some variable effects concerning individual images.

The current study has shown that Chinese men and women, given the choice of pre-operative and post-operative images of women who underwent micrograft surgery, are more likely to choose the post-operative images. These statistical effects refer to data on all 10 female patients, considered as a group. However, there was considerable variability regarding judgments of certain individual patients. Thus, images of 4 women were not consistently judged to be significantly more attractive post-operatively, by either male or female subjects. The back-posed images of these four patients are shown in Figure 3. Patient no. 8 received 45% of post-operative selections from men and 52% from women. Post-operative images of patient no. 3 received 50% of selections from men and 58% from women. Similarly, the post-operative image of patient no. 4 was chosen by 52% by men and 51% of women. Finally, the post-operative image of patient no. 9 received 50% of male selections and 54% of female selections. Some possible reasons for these individual variations are considered in the discussion section.

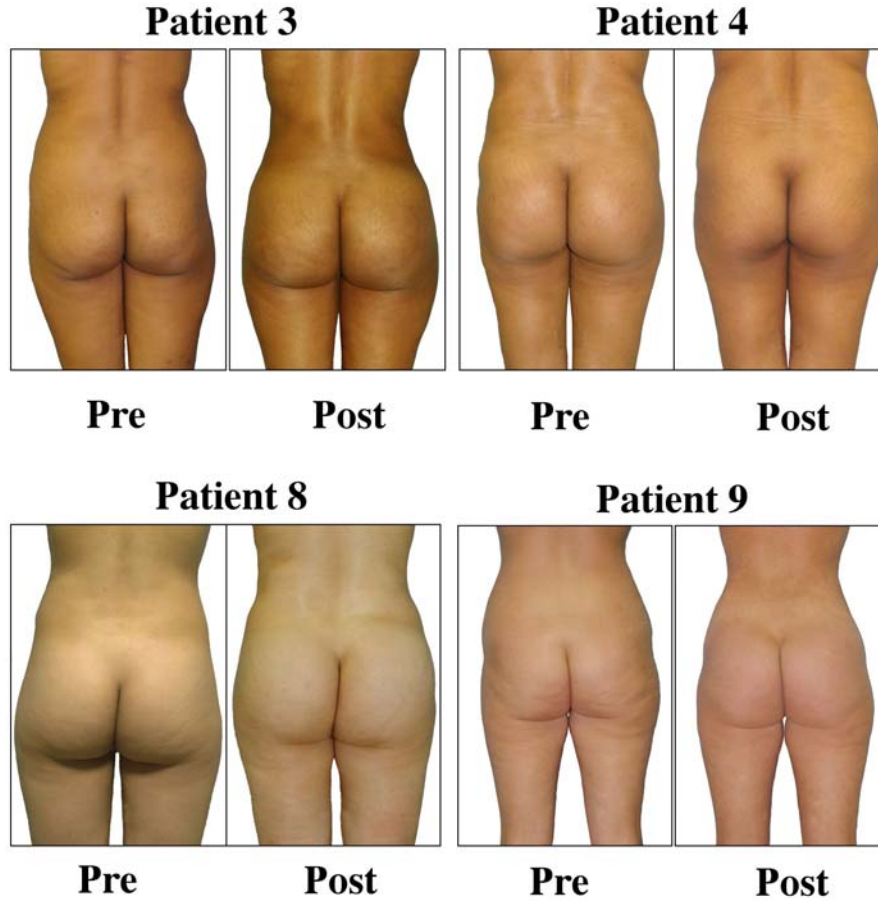


Figure 3. Images of the four patients that were not consistently judged to be more attractive post-operatively.

4 Discussion.

This study tested the role of waist-to-hip ratio (WHR) and body mass index (BMI) as possible determinants of female attractiveness, as judged by a sample of young Chinese men and women. In general, post-operative images with low WHRs were preferred over pre-operative images. Post-operative changes in BMI, by contrast, did not affect attractiveness judgments. These results are consistent with the hypothesis that low female WHR is a trait that is preferred as it may signal health, youth and fertility (Singh, 1993; 2006).

The role of WHR in male judgments of female physical attractiveness has been heavily critiqued in recent years (Swami & Tovée, 2005; Tovée et al., 1999). Previous research may have confounded the effects of WHR and BMI by using line drawings as stimulus images (Tovée & Cornellisen, 2001). In response, these authors used photographs of women that ranged in BMI from 15 (severely underweight) to 30 (clinically obese), while WHRs fell in a range of 0.68-0.98 (e.g. Tovée et al., 1999). In the current study, photographs of women with a narrower range of BMIs, from 19.99-26.66, and a comparable range of WHRs (0.69-0.93) were used. The effect of BMI (i.e. the variance that BMI accounted for when measuring male preferences) that has been shown in previous studies may be due to the extreme range of BMIs in the stimulus sets. In the current study, Chinese men's preferences for post-operative images did not correlate with the magnitude of post-operative changes in BMI. Interestingly, larger numbers of women showed a significant tendency to select back-posed images of patients whose post-operative BMI had increased slightly. Thus, when controlling for BMI, men in China show a significantly higher preference for images of women with low WHRs.

These findings agree with results of recent work, conducted using the same questionnaire but with much smaller numbers of subjects, in Samoa, Komodo Island (Indonesia), New Zealand (NZ) and in Cameroon (Singh et al., in press). These effects referred to the overall selections by subjects for pre-operative or post-operative images of the ten women. Interestingly, Chinese men and women showed considerable variability regarding judgments of certain individual patients. Because the sample sizes in the current study are relatively large (751 men and women) it is possible to examine these individual variations in more detail. Of the four most problematic sets of images (Patients

3, 4, 8 and 9, shown in Fig 3) two are Caucasian (patients 8 and 9) and two are darker-skinned. Thus, ethnicity alone is not likely to provide an explanation for differences in attractiveness judgments, especially as there were no significant differences for such judgments of the 5 Caucasian versus the 5 African American/Hispanic patients.

Patient No. 8 showed only a very small post-operative reduction in her WHR (from 0.78-0.74). Cross-culturally, men's preferences for the post-operative images of this patient were quite low, ranging from 47% in Samoa to 63% in NZ and Cameroon. Thus, in this case, the findings in China are not unexpected. Patient No. 4 showed a larger post-operative decrease in WHR (from 0.78-0.68) but this did not result in a truly 'hour-glass' body shape (see Fig 3). This patient was not rated as highly attractive by men in other cultures; post-operative scores ranged from 45% in NZ to 67% in Indonesia. Thus, again, the findings in China, involving much larger numbers of subjects, follow the pattern observed elsewhere. However, Patients 3 and 9 present a different picture since their post-operative images were not rated as more attractive in China (50% of choices in both cases) and this was not the case cross-culturally. Patient No. 3 was given ratings of between 69%-85% in Samoa, Cameroon, Komodo Island and NZ. Patient No. 9 received ratings of between 78%-88% in these same cultures. Examination of Figure 3 shows that both patients underwent a marked change in body shape as a result of micrograft surgery and achieved an 'hour-glass' figure with low WHR. Patient 3 showed a post-operative increase in BMI whereas Patient 9 showed a decrease. Thus, at the present time, we can offer no explanation as to why Chinese men and women's attractiveness judgments were evenly distributed between the pre and post-operative images of these patients.

The current study extends previous research (using computer-morphed drawings), showing that a female WHR of 0.6 is rated as most attractive by Chinese men (Dixson et al., 2007a). The use of photographic images of women who have undergone cosmetic micrograft surgery has made it possible to test the effects of altering WHR on female attractiveness, while controlling for BMI. Significantly larger numbers of Chinese men and women chose as most attractive the post-operative images of women who had undergone micrograft surgery, with resultant reductions in their waist-to-hip ratios. This study contributes to a growing body of scientific evidence indicating that a low female WHR (in the range from 0.6-0.8) is a trait that men find physically attractive throughout a wide range of cultures.

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Chapter Four

Male Preferences for Female Waist-to-hip Ratio and Body Mass Index: Further Evidence from New Zealand and Samoa.

Authors note: In this Chapter I present data on female body shape and attractiveness. For this study I was responsible for the experimental design and the construction of the questionnaires. I was also responsible for data collection in New Zealand and during fieldwork on Upolu Island in Western Samoa. These data were combined with data from Cameroon and Indonesia in the manuscript:

Singh, D., Dixon, B. J., Jessop, T. S., Morgan, B., Dixon, A. F. Cross-cultural consensus for waist-to-hip ratio and women's attractiveness'. (2010). *Evolution and Human Behavior*, 31, 176-181.

Dr Devendra Singh is the first author of this paper. Therefore in this Chapter I have included only the data that I was responsible for collecting. The full manuscript is included as Appendix 1 of this thesis.

Abstract

In women of reproductive age, a gynoid body fat distribution as measured by the size as the waist-hip ratio (WHR), is a reliable indicator of their sex hormone profile, greater success in pregnancy, and less risk for major diseases. According to evolutionary mate selection theory, such indicators of health and fertility should be judged as attractive. Previous research confirms this prediction as men in various societies judge women with a low WHR as attractive. WHR, however, is positively correlated with body weight or body mass index (BMI), and some researchers have argued that it is changes in BMI rather than the size of WHR which affects the judgments of attractiveness. To resolve this issue, we use photographs of women who have gone through micrograft surgery for cosmetic reasons. This surgery entails removal of fat cells from the waist and transplantation of these cells on the buttocks. After surgery, these women have lower WHR independent of changes in BMI. If sexual selection during human evolution favored adaptations, such as low WHR, that enhance attractiveness, then men in diverse modern day cultures should judge women with low WHR as more attractive. In this study, Polynesian men from Samoa and New Zealand men and women preferred post-operative images of women with low WHRs. These judgments were unaffected by gain (or loss) in body weight. This suggests that WHR is an important determinant of female sexual attractiveness.

Key words: Waist-to-hip ratio, body weight, female attractiveness, sexual selection.

1. INTRODUCTION

According to evolutionary-based theories of mate selection, one of the recurring adaptive problems faced by human ancestral males was to assess a woman's mate value, or the degree to which she would enhance his reproductive success (Symons, 1995). Women's mate value is determined by numerous variables, such as hormonal status, reproductive age, fecundity, parity, and a resistance to diseases, none of which can be directly observed. Information about some of these variables may be reliably conveyed through specific characteristics of the female body. It is the fundamental assumption of evolutionary mate selection theories that physical attractiveness is largely reflective of such reliable cues of woman's mate value (Buss, 1994; Grammer et al., 2003). Selection, therefore, shaped the development of psychological mechanisms in men to increase attention to women's bodily features and to assess their mate value.

One straightforward test of the validity of this assumption would be to identify bodily features that are known relate to genetic quality, health, and fertility, and then to investigate whether the variation in such bodily features systematically effect judgments of attractiveness. One such bodily feature, which reliably signals women's reproductive age, hormone profile, fecundity, and susceptibility to diseases, is sexually dimorphic fat distribution as measured by the waist-hip ratio (WHR).

WHR becomes distinctively sexually dimorphic during pubertal development, with a low WHR being linked to triggering menarche in adolescent girls (Lassek & Gaulin, 2007). In healthy women of reproductive age low WHRs (0.80 or less) are dependant on sex hormone levels (Jasienska et al., 2004). Women's WHRs increase pre-menopausally, with parity and may increase further post-menopausally (Bjorkelund et al.,

1996; Kosková et al., 2007; Tchernof & Poehlman, 1998; Toth et al., 2000). The fact that a woman's WHR lowers during adolescence and remains low during the pre-menopausal years, suggests that it is a reliable cue to her reproductive age. Low WHR is correlated with an optimal sex hormone profile (Jasienska et al., 2004) and endocervical pH, which favors sperm transport (Jenkins et al., 1995). Low WHR predicts successful pregnancy in women attending an artificial insemination clinic (Zaadstra et al., 1993) and in women undergoing *in-vitro* fertilization and embryo transfer (Wass et al., 1997).

In the first study examining the effect of WHR on female attractiveness Singh (1993) developed twelve line drawings representing three body weight categories (underweight, normal, overweight) and four levels of WHR (0.70, 0.80, 0.90, 1.00) in each weight category. Men and women of various ages (19-86 years old), educational background (college undergraduates to white collar professionals), and ethnicity (Mexican-American, African-American, and Euro-American) judged the normal weight figure with 0.7 WHR as most attractive and healthy. There was an important effect of the body weight, as the overweight figure, in spite of 0.7 WHR, was not judged to be attractive. These findings have since been replicated with men from Indonesia (Singh & Lewis, 1995), Azore Islands, and Guinea Bissau (Singh, 2004). The preference for low WHR has been shown in Chinese men (Dixson et al., 2007a) and men of Shiwiar tribe of Ecuador (Sugiyama, 2004), in addition to men from Western countries like the UK, Germany and New Zealand (Dixson et al., 2008; Furnham, Tan, & McManus, 1997; Henss, 2000).

Many researchers in non-Western society have reported a preference for low waist-hip ratio, even in some cases where heavier figures are preferred. For example,

Furnham, Moutofi, and Baguma (2002) found that Ugandan men prefer a low waist hip ratio in women of a higher body weight. As BMI and WHR are positively correlated, it is important to determine the relative role of BMI and WHR in judgments of female attractiveness. Tovée and Cornelissen (1999) have even suggested that an attractiveness judgment based on WHR is an artifact of changes in BMI. They argue that reducing the size of WHR in stimulus line drawing and images, for example, from 0.80 to 0.70 reduces BMI, and that this reduction in BMI is responsible for the attractiveness ratings for stimulus images with low WHR.

A potential solution to resolve this issue is to use a stimulus where WHR and BMI are independent. Micrograft surgery provides the means for examining the role of WHR in male attractiveness judgments, independently from BMI. This surgical procedure involves liposuction of the circumference of the waist and transplantation of fat cells into the buttocks (Roberts, Weinfeld, & Nyuyen, 2005; Singh & Randall, 2007). This procedure both narrows the waist and enhances the buttocks, lowering WHR without altering BMI. In this study photographs of pre- and post-surgical patients are used to examine whether people in New Zealand and Samoa judge women's attractiveness on the basis of their WHR or BMI.

2. METHODS

2.1 Stimulus Material

Pre-operative measurements of the waist-to-hip ratio (WHR) and body mass index (BMI) were made of ten women who had requested micrograft surgery. The measurements were repeated post-operatively, once healing was complete. Pre-operative and post-operative colour photographs were obtained of these same patients from the

back and an oblique angle. The post-operative photographs were taken a few months after surgery, in order to allow for healing of any scars. To control for any differences in skin blemishes between the pre- and post-operative photographs, the images were scanned into a computer and modeled using Adobe Photoshop version 7.0 in order to match their skin tones.

Procedure

A questionnaire was compiled containing 20 pairs of images, in colour. Each pair of images was of one patient, showing her pre-operative and post-operative appearance, either in back-pose, or oblique-pose. Thus, photographs of 10 patients in both views were used. The position of each photograph in a pair was randomized (appearing on either the right or left side of the page) and likewise the order in which the pairs were presented to participants was randomized. Each participant was asked to view one pair of photographs at a time, and to choose the image that they judged to be more attractive. Once the choice was made, the page was turned and they viewed the next pair. Participants had no knowledge of the rationale for the study, or that the pairs of photographs they viewed was of the same individuals. This study was preapproved by the Human Ethics Committee at Victoria University of Wellington.

Participants were recruited from independent Samoa and the North and South Island of New Zealand. The Samoan sample was recruited from Upolu Island (N= 78 men; mean age 27.55 ± 8.37 years). They were fishermen, farmers, laborers and others living in, and around, the city of Apia. Young Caucasian men (N= 113; mean age 20.6 ± 5.98 years) and women (N= 166; mean age = 19.8 ± 3.56 years) were recruited from the North Island (Victoria University of Wellington) and South Island (Otago University) of

New Zealand. The rationale for including young Caucasian women was that these women might be subject to greater media pressure concerning attractiveness and body shape, and that their judgments might differ from the other (exclusively male) groups tested.

Somatic data were analyzed using paired t-tests to determine whether micrograft surgery had resulted in significant changes in WHR or BMI. Behavioral data were analyzed using non-parametric statistics (Mann Whitney U tests and Wilcoxon signed rank tests, as detailed in the Results).

3. RESULTS

3.1 Postoperative effects on WHR and BMI

Micrograft surgery resulted in reductions in WHR in all ten women, from an average of 0.8 ± 0.017 to 0.72 ± 0.011 ($t = 7.364$; $df = 9$; $p < 0.001$). However, pre-operative and post-operative measurements of BMI for these same subjects did not differ significantly (Pre-op: Mean \pm SEM 24.8 ± 0.60 ; Post-op: 23.36 ± 0.75 , $t = 1.731$; $df = 9$; $p = 0.118$). Five women increased slightly in weight (Group A) and 5 lost weight (Group B) during the postoperative period. Group A had significantly higher post-operative BMI measures than group B ($t = 3.559$, $df = 4$, $p < .05$). Descriptive data for the ten patients used in this study are detailed in Table 1 of Chapters 2 and 3 of this Thesis.

3.2 Judgments of Attractiveness

Both populations judged post-operative photographs to be significantly more attractive, as determined by Wilcoxon signed rank tests (Samoan Islanders: $z = 2.865$, $df = 9$, $p < 0.0001$; New Zealand men: $z = 2.395$, $df = 9$, $p < 0.016$; New Zealand women: $z = 2.599$, $df = 9$, $p < 0.028$). To test for possible differences in the numbers of subjects who choose back-posed versus oblique-posed photographs, Wilcoxon tests were conducted for

each sample population. These paired comparisons were not statistically significant for Samoan Islanders ($z = 0.764$, $df = 4$, $p = 0.445$) although a trend towards preferences for the back-posed images was evident in New Zealand (for both sexes: $z = 1.784$, $df = 4$, $p = 0.074$). Mann Whitney U tests were conducted to compare judgments in each population concerning the group in which BMI increased with that which BMI decreased. All U values were well below the minimum of 23 required to be significant at the five percent level: Samoa, $U = 9.5$; NZ (men), $U = 12$; NZ (women), $U = 12.5$.

DISCUSSION

Despite pronounced ethnic and socio-economic differences between the people who participated in this study, they judged photographs of women who had lower waist-to hip ratios (WHR), as a consequence of micrograft surgery, as being more attractive than pre-operative photographs of the same women. It is striking that University students in New Zealand (NZ), who are frequently exposed to media depictions of what is desirable in female body shape and weight (e.g. in professional models) still responded in the same way as men in rural Samoa. Samoan people have a very high rate of obesity; surveys conducted during from 1978 - 1991 have found that 74% of urban women in Western Samoa were obese (Hodge et al., 1994). Despite this, subjects in Samoa rated the post-operative (low WHR) photographs as being most attractive.

The current study provides some resolution regarding the debate on the role of WHR and BMI in judgments of female attractiveness. Some authors have proposed that the judgment of attractiveness of WHR is due to changes in BMI. In that, BMI plays a more significant role than WHR (e.g. Tovée & Cornelissen, 1999; Swami et al., 2006). However, in the current study post-operative weight gain, or loss, which slightly altered

BMI in these women, had little effect on the attractiveness judgments of men in the two populations studied, or of women in NZ who judged the same photographs. Thus, the WHR, rather than BMI, was crucial in determining cross-cultural concordance in judgments of female attractiveness.

This is not to imply that BMI is of no importance in men's judgments of female attractiveness. On the contrary, it has long been clear that men judge images of women who have a healthy, average body weight, in combination with a low WHR, as most attractive (Singh & Luis, 1995). Nor should it be expected that men would universally rate one value of the female WHR as most attractive in all human populations. Rather it seems that the preferences expressed by men in different populations range from a female WHR of 0.60 (e.g. in the Hadza hunter gatherers of Tanzania: Marlowe, Apicella, & Reed, 2005), through to 0.80 (e.g. in the Bakossi people of Cameroon: Dixson et al., 2007b), with a WHR value of 0.70 being preferred in a number of populations (Singh, 2006).

Yu and Shepard (1998) have suggested that the preference for the WHR in non-Western societies is due their exposure to Western tourists, billboards, Western models, and printed media. The problem with this explanation is that investigators do not specify the conditions that may lead to changes in perceptions of attractiveness in local populations. For example, if notions of attractiveness change due to exposure of the Western media, how long does the local population need to be exposed to Western tourists to induce this effect? Would a single exposure to a Western fashion magazine, or a billboard, be sufficient to change the pre-existing standards of beauty in an isolated indigenous population? As presently constructed, it must be admitted that culturally-

based hypotheses of human attractiveness are virtually un-testable, as almost no human groups remain that have never seen such Westernized images.

This study has demonstrated that low female WHR, falling within the range 0.60 - 0.80, is attractive to men from two different cultures. These findings are very similar to those from the highlands of Papua New Guinea (Chapter 2) and China (Chapter 3). This provides cross-cultural support for the hypothesis that a low female WHR is attractive to men, perhaps as a cue to youth, health and fecundity in a potential partner. They also highlight the importance of cross-cultural replication. Human mate preferences may be highly variable and it would unwise to claim a trait is 'universally' preferred without collecting such comparative data from people living in different parts of the world.

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Chapter Five

Male Preferences for Female Breast Morphology in New Zealand, Samoa and Papua

New Guinea.



Authors note: Chapter Five is presented in the style of the journal Archives of Sexual Behavior where it was accepted for publication on March 24, 2010, as the manuscript:

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The chapter is a modified version of this manuscript, adapted to the thesis.

Abstract

Sexual selection via mate choice may have influenced the evolution of women's breast morphology. We conducted an image-based questionnaire quantifying and comparing the preferences of men from Papua New Guinea (PNG), Samoa, and New Zealand (NZ) for images, corrected for skin color, of women's breast size, breast symmetry, areola size, and areolar pigmentation. Results showed that men from PNG preferred larger breasts to a greater extent than men from Samoa and NZ, providing some support for the hypothesis that men from subsistence living cultures have a greater preference for morphological cues indicative of caloric reserves. Symmetrical breasts were most attractive to men in each culture. However, preferences were highest among NZ men, followed by men from Samoa, and were lowest among men from PNG. These results did not support the hypothesis that people living in higher pathogen environments have a greater preference for traits indicative of pathogen resistance and developmental stability. Large areolae were preferred among men from PNG, and to a lesser extent in Samoa, while in NZ men preferred medium-sized areolae. Thus, men's preferences for women's areolar size appear to be highly culturally specific. Darkly pigmented areolae were most attractive to men from Samoa and PNG, whereas men from NZ preferred areolae with medium pigmentation. These findings suggest that areolar pigmentation indicative of sexual maturity is preferred by men rather than lighter pigmentation, which may signal that a woman is in the early years of reproductive maturity. This study highlights the importance of cross-cultural research when testing the role of morphological cues in mate choice.

Key words: Attractiveness; female breasts; sexual selection; cross-cultural research.

INTRODUCTION

Uniquely among the primates, adult female human beings have large stores of body fat in their thighs, hips, and buttocks (the gluteal/femoral region) and breasts (Dufour & Slather, 2002; Pond, 1997). Body composition is sexually dimorphic (Carter & Heath, 1990); women may have up to 43.6% of their physique comprised of fat in comparison to 28.4% in men (Clarys, Martin, & Drinkwater, 1984). Sexual dimorphism in body composition results in marked sexual dimorphism in body shape (Wells, 2007). Women typically have a narrower waist in relation to wider hips, as reflected in their lower waist-to-hip ratios (WHR) compared to men. The physiological demands of pregnancy and lactation are such that natural selection has likely been the primary evolutionary cause for sexual dimorphism in body fat and body shape (Cant, 1981; Jasienska, 2009). The evolution of bipedal locomotion also places biomechanical constraints on women, as they must remain mobile during gestation (Pawlowski, 2001). This may have favored a lower center of body mass in women, which correlates with low WHR (Pawlowski & Grabarczyk, 2003). In addition to natural selection, sexual selection may have affected body shape and the distribution of body fat in women. Thus, a gynoid fat distribution and an “hourglass” body shape may be honest signals of female health and reproductive potential (Barber, 1995; Singh, 2002; Singh & Young, 1995; Thornhill & Grammer, 1999).

In contrast to female nonhuman primates, where breast enlargement only occurs during lactation (Short, 1980), women’s breasts enlarge at puberty due to increased deposition of adipose and stromal tissue (Vandeweyer & Hertens, 2002). The social and evolutionary significance of breast enlargement prior to pregnancy and lactation in

women has been a subject of much debate (Caro, 1987; Jesser, 1971). Some authors have argued that as humans evolved hairlessness and bipedal locomotion, the breasts were displayed more prominently and their pendulous morphology was adaptive for breast-feeding babies (LeBlanc & Barnes, 1974). Smith (1986) suggested that the breasts provide a soft cushion that is psychologically comforting to the infant. Large breasts may serve as storage organs for milk (Low, Alexander, & Noonan, 1987). However, it is important to note that the size of the non-lactating breast is not indicative of its potential to produce milk (Anderson, 1988; Caro, 1987; Caro & Sellen, 1990; Mascia-Lees, Relethford, & Sorger, 1986). While localized fat storage is required as energy reserves for gestation and lactation in women (Anderson, 1983; Jasienska, 2009), fat in the breasts may have evolved in parallel with gluteal/femoral fat reserves (Pawlowski, 1999).

It has been suggested that sexual selection via mate choice may have enhanced the expression of permanently enlarged breasts in women (Barber, 1995). However, while men may become sexually aroused by images of female breasts (Freund, Langevin, & Zajac, 1974), male preferences for female breast size appear to be highly variable. Ford and Beach (1951) identified cross-cultural differences in male preferences for breast size and morphology. For example, among the Sudanese Azande, men prefer long pendulous breasts; Alorese men of the Alor Island in Indonesia prefer large breasts and men of the Kenyan Massai tribes prefer firm, upright breasts. Research quantifying male preferences for female breast size has also yielded mixed results. Studies have concluded that men in Western cultures rate images of women with small breasts (Furnham, Swami, & Shah, 2006), medium-sized breasts (Horvath, 1981) or larger than medium-sized breasts (Furnham, Dias, & McClelland, 1998; Singh & Young, 1995) as most attractive.

However, these studies are subject to methodological problems, as most have used line drawings of women in bathing suits or silhouettes as stimuli. Such images do not allow people to distinguish between changes in breast shape, size, and areolar configuration. Across the lifespan, such changes may be used to gage a woman's age and reproductive status (Gallup, 1982; Marlowe, 1998; Symons, 1995).

A further problem in research quantifying male preferences for female breast morphology concerns the lack of cross-cultural data. If selection has acted upon mate preferences from the earliest phases of human evolution, encouraging men to attend to certain morphological traits (Buss, 2003; Grammer, Fink, Møller, & Thornhill, 2003), one would predict concordance in preferences for those traits across societies that currently vary in socioeconomic status and exposure to Western mass media. The current study tested these ideas using a questionnaire survey quantifying attractiveness judgments for various aspects of female breast morphology among Melanesian men from Papua New Guinea (PNG), Polynesian men in Samoa, and men of European descent in New Zealand (NZ).

A number of theories propose either that breast morphology signals nubility in young women or that they are more important as signals of sexual maturity and fertility (Gallup, 1982; Marlowe, 1998; Symons, 1995). In a sample of 119 Polish women, women with larger breasts and lower WHRs had higher circulating levels of 17- β -estradiol and progesterone (Jasienska, Ziolkiewicz, Ellison, Lipson, & Thune, 2004), which are predictors of the probability of conception (Lipson & Ellison, 1996). Jasienska et al. found that women with larger breasts had higher levels of circulating estradiol,

independent of WHR. Therefore, we tested the hypothesis that men should judge large breasts as most attractive as a signal of fecundity.

Directional asymmetry in morphological traits may be strongly determined by genetic and environmental factors, as well as resistance to pathogens (Møller, 1999). Thus, symmetry in morphological traits may enhance attractiveness as a signal of mate quality (Møller & Thornhill, 1998). Women with more symmetrical breasts have been shown to have higher fecundity in the UK, the U.S., and Spain (Manning, Scutt, Whitehouse, & Leinster, 1997; Møller, Soler, & Thornhill, 1995). In contrast, women with greater breast asymmetry have a higher probability of developing breast cancer (Scutt, Lancaster, & Manning, 2006) and may experience difficulty lactating due to deficient glandular development (Niefert, Seacat, & Jobe, 1985). We tested the hypothesis that men should prefer symmetrical breasts as a signal of fecundity, maternal health, and pathogen resistance.

Breast maturation in girls is typically measured through fat deposition (Tanner, 1962). However, the maturation of the areolae may also be indicative of female sexual maturity. During adolescence in girls, areolar diameter increases and is larger at the onset of menarche than in pre-pubescence (Biro, Falkner, Khoury, Morrison, & Lucky, 1992). The size and shape of the areolae in women may influence men's attractiveness judgments of women's breasts (Barber, 1995; Guthrie, 1975). We examined the hypothesis that changes in areolar size should affect male judgments of female attractiveness, with men preferring breasts with large areolae as a sign of reproductive maturity.

Areolar pigmentation shows important variations with age, being lightest at the onset of menarche and darkening as women mature (Garn, Selby, & Crawford, 1956), particularly during pregnancy and lactation (Garn & French, 1963; Muzaffar, Hussain, & Haroon, 1998; Pawson & Petrakis, 1975). Areolar pigmentation may be an index of parity and lighter pigmentation of the areolae may be sexually attractive to men as a signal of youth (Goodhart, 1964; Guthrie, 1976; Montagna & Macpherson, 1974). Thus, we tested the hypothesis that lightly pigmented areolae might be most attractive to men.

METHOD

Participants

Each questionnaire had a cover sheet for demographic data, including the participant's sex, age, and marital status. Participants were interviewed individually and were not asked to give their names.

Papua New Guinea (PNG) is the eastern half of the island of New Guinea and has a population of 4.5 million people. Agriculture is the principle income in PNG. The Okapa district is located in the Eastern Highlands Province. There are approximately 54,000 people living in the Okapa district. These people form five separate ethnic groups, as defined on linguistic grounds: Fore, Auyana, Kimi, Keagana, and Kanite. We conducted surveys among the Kanite. There are approximately 8,000 Kanite people living in the Okapa district. We interviewed 100 men ($M \text{ age} \pm SD = 29.58 \text{ years} \pm 10.84$, range = 18-58 years) from three small villages: Kimiagomo, Yafanagomo, and Foseya. In this region, polygynous marriages can occur. Of the 100 men interviewed, 42% were unmarried, 48% were married to one wife, and the remaining 10% were married to two or more wives. The region is extremely remote and has no main water supply, electricity,

television, Internet access or land phone lines. All the participants were subsistence farmers.

Samoa is a chain of islands in Western Polynesia with a population of 182,548. Participants were recruited on the two main islands of Upolu and Savai'i. Agriculture is the main employment on the island. These islands are not as exposed to the kind of media influences that are common in industrialized Western cultures. For example, magazines (including fashion magazines) are not commonly found, even in the capital Apia. Equally, there are no large billboards advertising fashion. While Samoa has electricity and television, broadcasting is restricted to state run channels on which the bulk of programming focuses on local news and religious events. Outside of the capital, Internet access is extremely sparse. A total of 53 Polynesian men ($M \text{ age} \pm SD = 27.89 \text{ years} \pm 9.74$, range = 18-71 years), 23% of whom were married, completed questionnaires. We opportunistically recruited participants of various occupations. Some worked in restaurants or drove taxis in and around the capital Apia, while others were farmers and fisherman from more rural and remote areas of the islands.

New Zealand (NZ) has a population of 4 million people living on the North and South islands. It is an industrialized country where the principle incomes are the import and export trade, agriculture, and tourism. NZ is wealthier than PNG and Samoa and has much greater exposure to media influences such as magazines, television, cinemas, and billboard advertising. Seventy men of European descent ($M \text{ age} \pm SD = 24.63 \text{ years} \pm 6.20$, range = 18-46 years), 24% of whom were married, were recruited opportunistically from in and around Wellington city. Some men were students, worked in office jobs, some were manual laborers and some were servers in cafés and bars.

Measures

Participants were asked to rate the attractiveness of images of women that varied in breast size, breast symmetry, areolar size, and areolar pigmentation. Each page contained three images, as detailed below in Studies 1-4. Participants were asked to select only the image that they found most attractive. Alternatively, if none of the images was preferred, participants had the option to rate all the images as equally attractive. To construct the various images, two photographs of a Caucasian woman's torso were scanned from Simblet (2001). In one photograph, the woman was front-posed and in the second image the same woman was oblique-posed. These images are hereafter referred to as the standard image from which experimental manipulations were made using Adobe Photoshop version 7.0. The questionnaire format was identical in each culture except that the skin color of the entire image, including the areolae, was matched to that which was typical to the ethnic group being studied (Figs. 1-4). Using Adobe Photoshop, the desaturate function was employed to render the image to black and white. Then, using the hue and saturation function, the hue, saturation, and lightness levels were manipulated qualitatively to match the skin color of a photograph of a woman from Samoa and PNG. Examples of the images are included in Figs. 1-4. Study 1 measured male preferences for oblique-posed female torsos that varied in breast size. Breast size was assessed using anthropometric measures (Brown, Ringrose, Hyland, Cole, & Brotherston, 1999). Using Adobe Photoshop, the breasts were cropped out of the image. Breast size was then manipulated before the breasts were blended back into the image. Participants selected from three images, the standard image (medium-sized), one image in which medium-sized breasts were increased by 20% (large), and an image where the medium-sized

breasts had been reduced to 80% (small). Study 2 quantified male preferences for front-posed torsos that varied in breast symmetry. A bilaterally symmetrical image was created by dividing the standard image in two, vertically, from the suprasternal notch, and copying and pasting one side to create a mirror image. From this symmetrical image, two further images were created. In one image, the left breast alone was lowered in one increment (3% of the total height of the image). This procedure was repeated in a second image in which only the right breast was lowered by one increment. Thus, participants were shown three images, one in which the breasts were symmetrical and two in which the breasts were asymmetrical. Study 3 assessed male preferences for oblique-posed female torsos that differed in areolar size. The areolae were cropped out of the image in Adobe Photoshop. Size adjustments were made (+50% and -50% of the standard image) before the areolae were blended back into the image. Participants chose between the standard (medium-sized) image, an image with large areolae (+50% of the standard image), and an image with small areolae (-50% of the standard image). Study 4 examined male preferences for three oblique-posed female torsos that varied in areolar pigmentation. The areolae were cropped out of the image using Adobe Photoshop. From the standard image (medium-pigmented areolae), areolar pigmentation was then altered in a stepwise fashion (+15 units of brightness and -10 of contrast) to produce one image with darkly pigmented areolae and one with lightly pigmented areolae.

Data Analysis

In order to examine whether there were statistically significant differences within and between cultures for particular images, data from the three cultures were entered into a mixed logistic regression model, with culture, age, and marital status as factors. In a

logistic regression model, one of the four possible choices (Image 1, 2, 3, or “all images are equally attractive”) was selected as a baseline or reference point. The logistic regression model then calculated the odds of selecting each of the other choices as opposed to the reference choice, taking into account the culture, marital status, and age of a particular individual.

RESULTS

Comparison of age and marital status across cultures

A 3 (Culture) x 2 (Marital Status) chi-square test revealed significant differences in numbers of married and unmarried men among the three cultures, $\chi^2 = 27.50$, $df = 2$, $p < .001$. In NZ, 17/70 (24.3%) of participants were married, in Samoa 12/53 (22.6%) were married, and in PNG 58/100 (58%) were married. A one-way ANOVA for culture showed a significant main effect of age of the participants, $F(2, 125) = 7.80$, $p < .001$. Post-hoc Bonferroni tests revealed that men from PNG were significantly older on average than men from NZ ($p = .002$). Samoan men were slightly older on average than NZ men ($p = .057$). Mann Whitney U-test showed that married men were significantly older than unmarried men ($p < .001$).

Study 1: Male Preferences for Female Breast Size

Unmarried men from NZ selected medium-sized breasts more often (62.3%) than both unmarried and married men from Samoa (48.8% and 33.3%, respectively) and PNG (28.6% and 24.1%, respectively). Married men preferred large breasts in each culture (NZ = 58.8%; Samoa = 66.7%; PNG = 55.2%; Fig. 1). Logistic regression analyses

revealed that unmarried men were more likely than married men to select small breasts as most attractive, $\beta = 6.32$; $SE = 1.43$; 95% CI (3.52, 9.12), $p < .001$. Compared to men from NZ, the image with small breasts was less likely to be selected by men from Samoa ($\beta = -16.74$; $SE = 4.82$; 95% CI (-26.19, -7.29), $p < .001$) and PNG ($\beta = -14.09$; $SE = 4.59$; 95% CI (-23.10, -5.09). However, given the low number of selections for small breasts in NZ, the reliability of these comparisons is doubtful.

Study 2: Male Preferences for Female Breast Symmetry

In NZ, unmarried and married men preferred symmetrical breasts (69.8% and 76.5%, respectively). Similarly, in Samoa 58.5% of unmarried men and 58.3% of married men preferred symmetrical breasts. However, in PNG, unmarried men preferred symmetrical breasts more than married men (54.8% and 34.5%, respectively; Fig. 2). Logistic regression analyses showed that unmarried men were more likely than married men to select as most attractive the image in which the left breast was asymmetrical, $\beta = 5.28$; $SE = 1.62$; 95% CI (2.11, 8.45), $p < .001$. However, men in all three cultures were less likely to pick this image than the image depicting symmetrical breasts; NZ: $\beta = -21.89$; $SE = 4.12$; 95% CI (-29.97, -13.81), $p < .001$; Samoa: $\beta = -26.95$; $SE = 4.36$; 95% CI (-35.49, -18.41), $p < .001$; PNG: $\beta = -20.59$; $SE = 3.87$; 95% CI (-28.17, -13.01), $p < .001$.

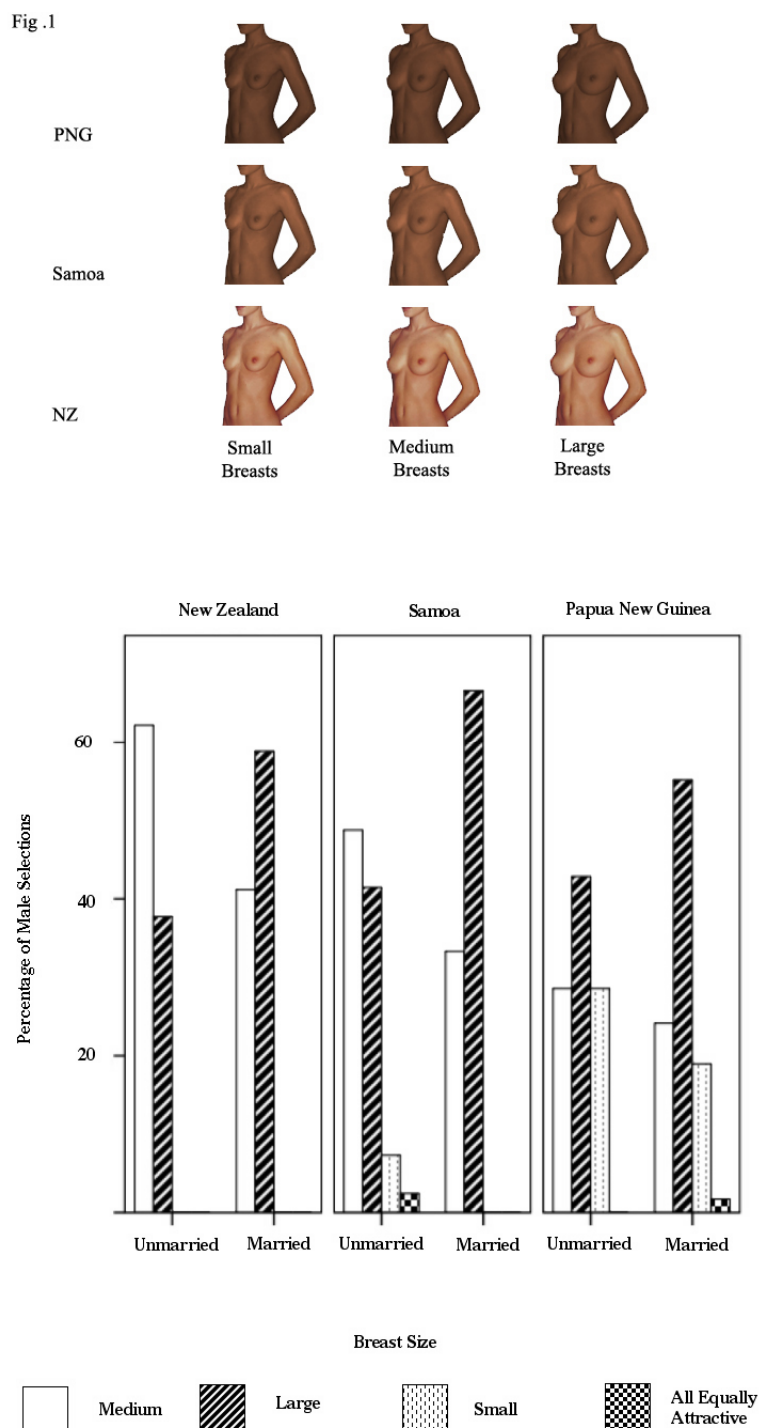


Fig. 1 Above the histograms are shown the stimuli used in PNG, Samoa and NZ to test the role of breast size in men's judgments of women's attractiveness. Data are the percentage of selections made by married and unmarried men in each culture for images of women varying in breast size.

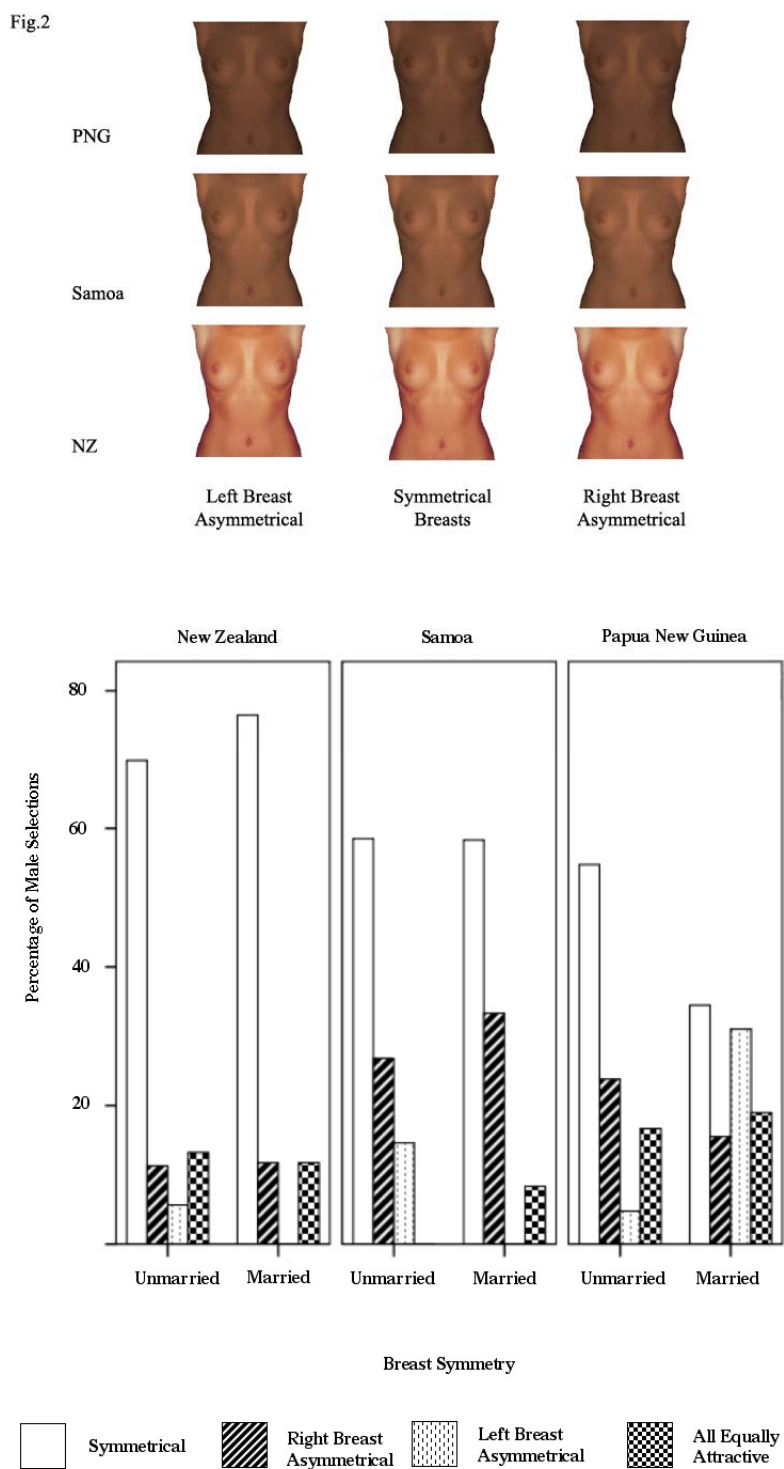


Fig. 2 The images used to test the role of breast symmetry in men's assessments of women's attractiveness are presented above the histograms. Each panel depicts the percentage of selections made by married and unmarried men in each culture for images of women varying in breast symmetry.

Study 3: Male Preferences for Female Areolar Size

In NZ, unmarried and married men selected medium-sized areolae more often (79.2% and 76.5%, respectively) than unmarried and married men from Samoa (48.8% and 33.3%, respectively) and PNG (42.9% and 22.4%, respectively). Preferences among married men from Samoa and PNG were greatest for the large areolar size (Samoa: 50.0%; PNG: 36.2%). As can be seen in Fig. 3, men in these cultures varied considerably in their preferences for female areolar size and the logistic regression yielded no statistically significant interactions.

Study 4: Male Preferences for Female Areolar Pigmentation

Unmarried men from NZ selected medium and darkly pigmented areolae evenly (47.2% and 47.2%, respectively). However, 82.4% of married men selected medium pigmented areolae. Among unmarried Samoan men, medium and darkly pigmented areolae were most attractive (41.5% and 48.8%, respectively). Married men from Samoa preferred darkly pigmented areolae (66.7%). In PNG, unmarried and married men preferred darkly pigmented areolae (47.6% and 53.4%, respectively) (Fig. 4). Logistic regression analyses revealed that unmarried men, compared to married men, chose medium pigmented areolae more frequently, $\beta = 5.07$; $SE = 2.27$; 95% CI (0.62, 9.52), $p = .026$. Men from each culture were less likely to choose lightly pigmented areolae than medium pigmented areolae, NZ: $\beta = -15.27$; $SE = 6.42$; 95% CI (-27.86, -2.69), $p = .017$; Samoa: $\beta = -15.86$; $SE = 7.21$; 95% CI (-29.99, -1.73), $p = .028$; PNG: $\beta = -12.91$; $SE = 4.82$; 95% CI (-25.43, -.38), $p = .043$). Older men were also less likely to pick the image with lightly pigmented areolea : $\beta = -.33$; $SE = .14$; 95% CI (-.60, -.06), $p = .017$.

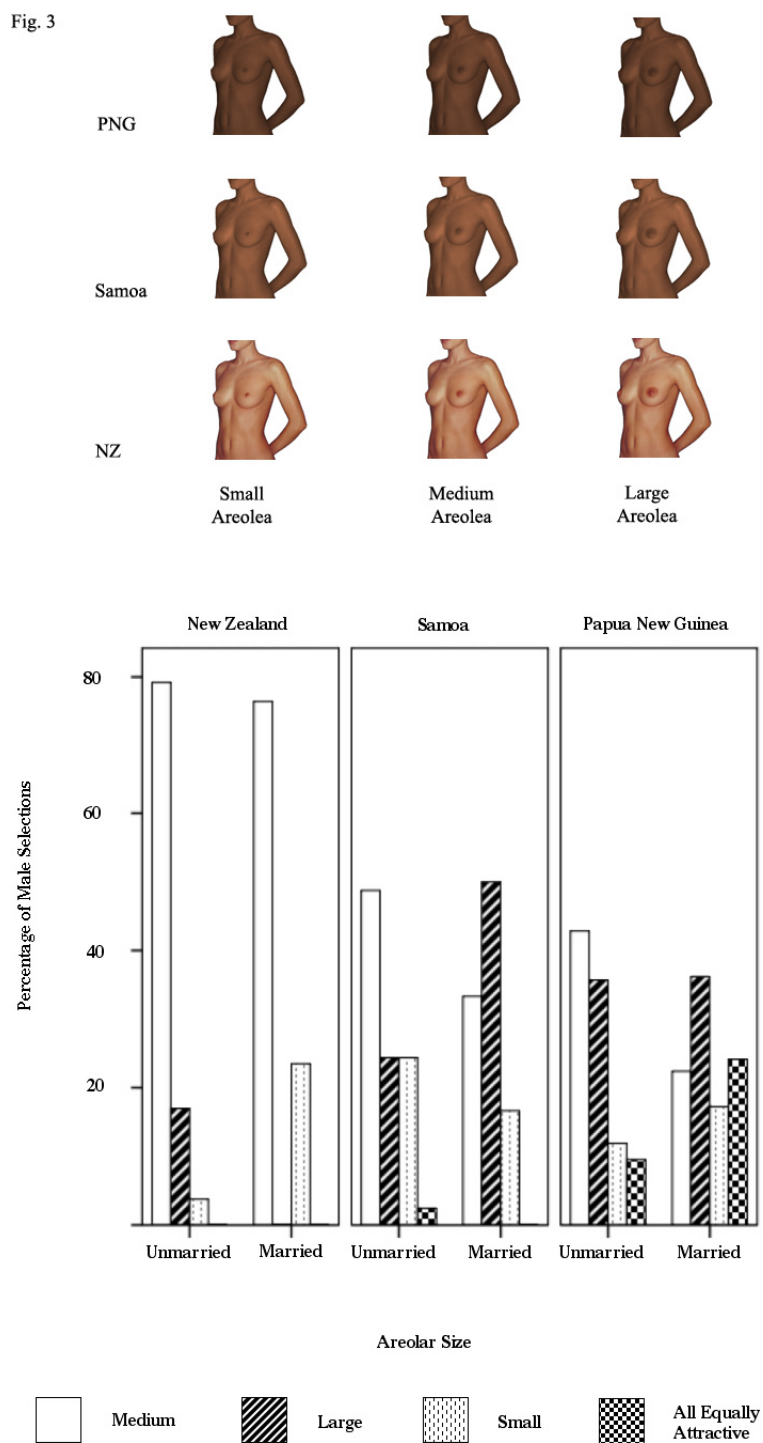


Fig. 3 Data are the percentage of selections made by married and unmarried men in each culture for images of women varying in areolar size. The images used in each culture are shown above the panels.

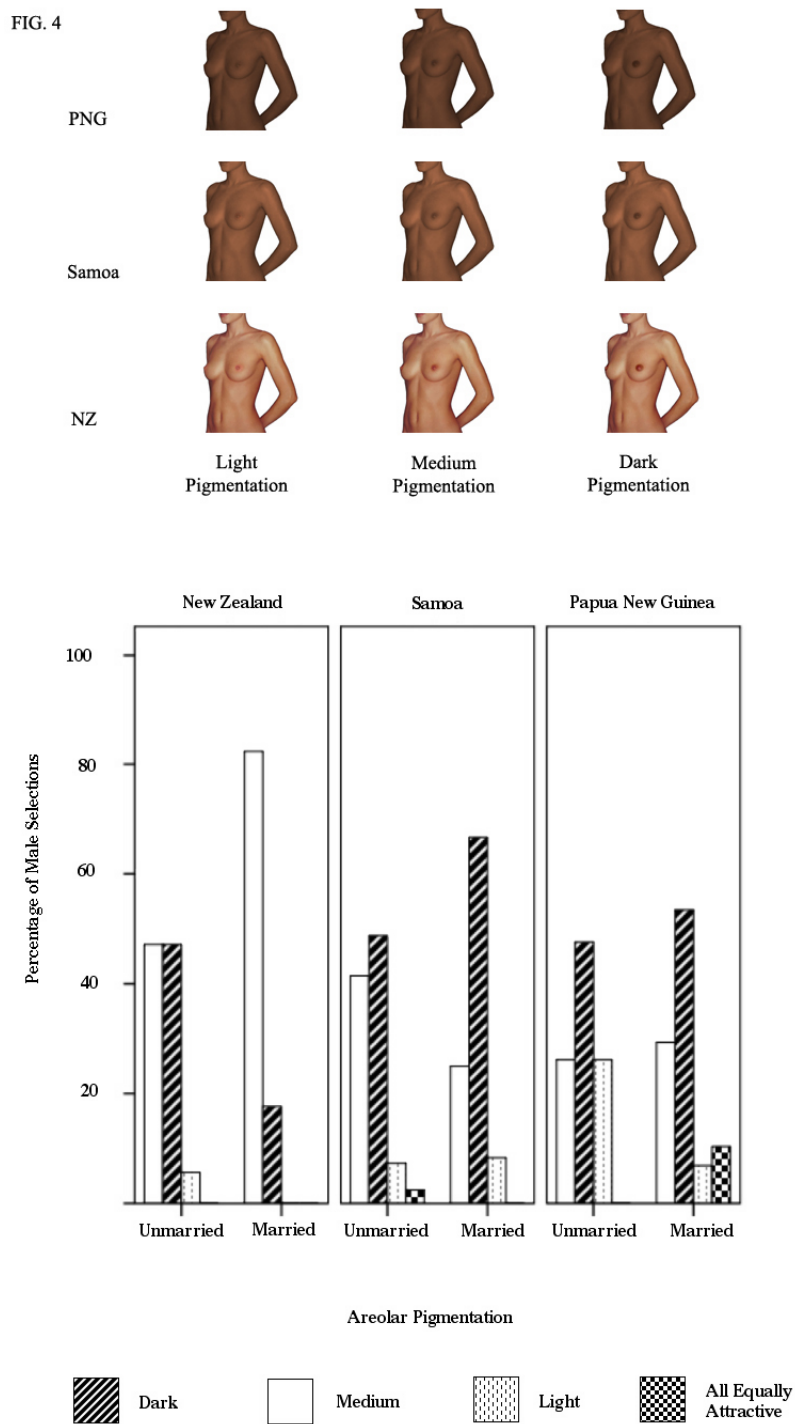


Fig. 4 The images used to test the role of areolar pigmentation in men's judgments of women's attractiveness are shown above the histograms. Data are the percentage of selections made by married and unmarried men in each culture for images of women varying in areolar pigmentation.

DISCUSSION

Given that variations in physique and sexual preferences may occur in different parts of the world, a challenge in studies of human morphology and physical attractiveness is to obtain cross-cultural data. The results reported here are the first of their kind for Polynesian and Melanesian men and they provide some useful comparisons, and contrasts, with the findings of studies among Caucasian men.

In the current study, men in each culture judged medium and large breasts as more attractive than small breasts. This provides some support for the hypothesis that men prefer large breasts as a cue to female fecundity, as women with larger breasts and narrow waists have significantly higher levels of estradiol during their menstrual cycles (Jasienska et al., 2004). The men we interviewed in PNG, all of whom were subsistence farmers, reported a greater preference for large breasts compared to men from Samoa and NZ. The physiological costs of pregnancy and lactation are considerable for women (Jasienska, 2009). Repeated pregnancies deplete energy reserves, which negatively affects female nutritional status (the maternal depletion syndrome) (Winkvist, Rasmussen, & Habicht, 1992). Maternal depletion has been documented among several ethnic groups in PNG (Garner, Smith, Baea, Lai, & Heywood, 1994; Tracer, 1991). Anderson, Crawford, Nadeau and Lindberg (1992) have provided evidence that, in developing nations and pre-industrial societies, men may prefer women who have higher levels of body fat as a cue to healthy storage of calories required for pregnancy and lactation. This may explain the greater preference for large breasts among subsistence farmers in PNG compared to men from Samoa and NZ. In such living conditions, where food is scarce and subsistence farming is very physically demanding, female fat

distribution may provide direct information to men of female fecundity that may be of somewhat less importance in better-nourished cultures such as NZ and Samoa.

Married men in each of these cultures stated a greater preference for large breasts than unmarried men. Why married men should be more sensitive to such traits is a difficult question, as evolutionary theory predicts that men, irrespective of marital status, should find young, healthy women most attractive as mates (Buss, 2003; Kenrick & Keefe, 1992; Symons, 1979). It may be that married men, whose partners have undergone changes in breast morphology due to pregnancy and lactation, have a learned preference for larger breasts. However, at present, this suggestion is purely speculative.

Bilateral symmetry may relate to underlying genetic quality and attractiveness in insects, birds, and mammals (Møller, 1999; Møller & Thornhill, 1998). In humans, symmetrical faces are rated as most attractive (Rhodes & Simmons, 2007). Female breast symmetry correlates with fecundity, as measured by the number of offspring, in samples from the UK, Spain, and, the U.S. (Manning et al., 1997; Møller et al., 1995). Caucasian men from North America rate symmetrical breasts as more physically attractive than asymmetrical breasts (Singh, 1995). We found that men in NZ, Samoa, and PNG rated symmetrical breasts as most attractive. It has been suggested that pathogens may negatively affect developmental stability which, in turn, reflects the degree of symmetry in morphological traits (Møller & Swaddle, 1997). People from cultures with high levels of pathogens may place a greater value on physical attractiveness in a potential partner as an indication of phenotypic quality (Gangestad & Buss, 1993). However, we found that men from NZ and Samoa reported the highest preferences for symmetrical breasts whereas in PNG, where there is comparatively a much greater incidence of diseases such

as malaria, only 34.5% of married men preferred symmetrical breasts. Thus, at present, our data did not support the hypothesis that men living in a high pathogen environment have greater preferences for traits indicative of stronger immunity during development.

The nipple and areola in women may be sexual signals to men (Goodhart, 1964; Guthrie, 1976; Montagna & Macpherson, 1974). Given the relationship between female sexual maturation and areolar configuration (Biro et al., 1992; Garn et al., 1956), it is plausible that areolar size and shape affects male preferences for female breasts. Barber (1995) suggested that because there is no ecological or adaptive argument for cross-cultural variation in areolar size and configuration, such variation in morphology “could be understood as a product of inter-sexual selection driven by arbitrary masculine tastes within reproductively, and culturally, isolated populations”. In the current study, male preferences for areolar size showed no distinct pattern across cultures. Men from PNG, the most culturally isolated group in this study, tended to prefer larger areolae. Similarly, in Samoa, unmarried men preferred medium-sized areolae and married men preferred the largest areolae. In contrast, the majority of men in NZ preferred the medium-sized areolae. To our knowledge, this study was the first attempt to quantify male preferences for female areolar size cross-culturally and our results suggest that male preferences for this female trait is culturally specific.

Women’s areolae are often lighter in the early stages of menarche, darken somewhat with age and considerably more during pregnancy and lactation (Garn & French, 1963; Garn et al., 1956; Muzaffar et al., 1998; Pawson & Petrakis, 1975). Thus, areolar pigmentation may be a signal of parity, with lighter pigmentation of the areolae signaling female nubility to men (Symons, 1995). In a study conducted in Austria and the

U.S., men preferred lighter, red-colored areolae (Grammer, Fink, Juetten, Ronzal, & Thornhill, 2001). In the current study, areolar pigmentation had a significant effect on male preferences for images of female breasts. However, unlike the study by Grammer et al. (2001), men in PNG, Samoa, and NZ preferred medium or darkly pigmented areolae, with lightly pigmented areolae being judged least attractive. These results suggest that male preference for female areolar pigmentation reflects a preference for sexual maturity rather than youth and nubility.

The use of computer-generated stimuli in studies of human morphology and physical attractiveness allows for the role of traits in mate choice to be studied in isolation from surrounding traits. However, this method may be problematic. Firstly, using computer programs to match the skin color of a stimulus image to that of the population from which data are being collected does not produce an exact replication of skin color seen in real life. Secondly, some cultures may be more or less familiar with computers, which, in turn, could affect the way they judge computer-morphed images. Indeed, men from PNG and Samoa are far less familiar with computers than men from NZ. Furthermore, women's breasts undergo considerable changes in their external appearance due to age and reproductive status (i.e., adolescent, adult, lactating). It has been suggested that these changes may affect female attractiveness (Gallup, 1982; Marlowe, 1998; Symons, 1995). Symons (1979, 1995), for example, suggested that the nulliparous breast shape should provide men with a signal of a woman's age, health, and fertility. Men across cultures may, therefore, have a profound preference for breast shape that signals nulliparity. It should be noted that in this study no attempt was made to specifically model features indicative of pregnancy, lactational status, and other traits that

may define multiparous breast morphology. The firmness of the breasts, which changes due to age and repeated pregnancies, may be a strong determinant of female attractiveness (Marlowe, 1998). However, relatively few studies have been conducted to test these ideas and the computer-generated stimuli utilized in the present study are not sufficiently realistic to model such changes in breast morphology. Areolar pigmentation darkens during pregnancy and lactation, and areolar color was modeled in our study. However, such changes do not occur in isolation, and may not be relevant in the absence of associated changes in breast firmness as well as size. A challenge for future work will be to collect quantitative data on how men assess these aspects of women's breast morphology using natural images.

The current study demonstrates the danger in drawing conclusions about the role of human morphology in mate preferences when data are restricted to one culture. It will be important for future studies to expand data collection to include other cultures if meaningful conclusions are to be drawn on the effects of sexual selection on evolution of female breast morphology. We hope that this study stimulates further cross-cultural research on human physique and sexual attractiveness.

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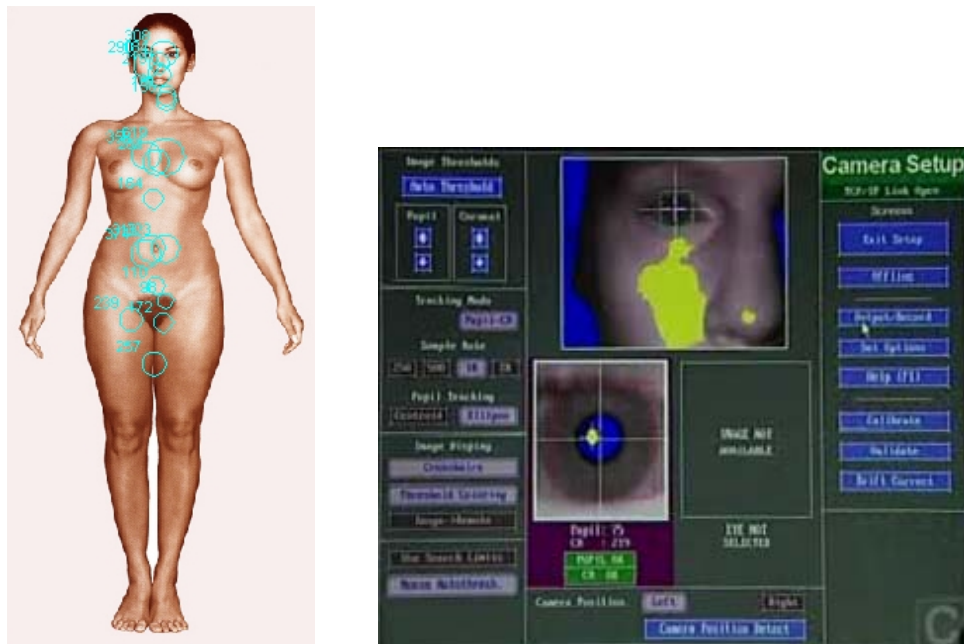
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Chapter Six

Eye-Tracking of Men's Preferences for Waist-to-Hip Ratio and Breast Size of Women.



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Archives of Sexual Behavior.

The chapter is a modified version of this manuscript, adapted to the thesis.

ABSTRACT

Studies of human physical traits and mate preferences often use questionnaires asking participants to rate the attractiveness of images. Female waist-to-hip ratio (WHR), breast size, and facial appearance have all been implicated in assessments by men of female attractiveness. However, very little is known about how men make fine-grained visual assessments of such images. We used eye-tracking techniques to measure the numbers of visual fixations, dwell times, and initial fixations made by men who viewed front-posed photographs of the same woman, computer-morphed so as to differ in her WHR (0.7 or 0.9) and breast size (small, medium, or large). Men also rated these images for attractiveness. Results showed that the initial visual fixation (occurring within 200 milliseconds from the start of each 5 second test) involved either the breasts or the waist. Both these body areas received more first fixations than the face or the lower body (pubic area and legs). Men looked more often and for longer at the breasts, irrespective of the WHR of the images. However, men rated images with an hourglass shape and a slim waist (0.7 WHR) as most attractive, irrespective of breast size. These results provide quantitative data on eye movements that occur during male judgments of the attractiveness of female images, and indicate that assessments of the female hourglass figure probably occur very rapidly.

KEYWORDS: Sexual attractiveness; Evolution; Female waist-to-hip ratio; Female breast size; Eye-tracking

INTRODUCTION

The nature of physical attractiveness has fascinated scholars for centuries. Indeed, attractiveness has often been shrouded in mystery. However, people across cultures state that physical attractiveness is an important trait in a potential partner (Buss, 1989). Evolutionary psychologists have suggested that selection has shaped human cognitive mechanisms to recognize physical traits that signal health and fertility (Grammer, Fink, Møller, & Thornhill, 2003). The attractiveness of such traits may therefore represent the results of sexual selection operating within ancestral human populations (Buss, 2003; Miller, 2000).

Men and women are strikingly sexually dimorphic in muscularity and body fat. Women have almost twice the amount of body fat of men (Clarys, Martin, & Drinkwater, 1984). The distribution of body fat is a secondary sexual characteristic in women. Body fat is laid down during pubertal development on the hips, buttocks, thighs (the gluteofemoral region), and breasts. Body fat distribution is important for triggering menarche in girls (Lassek & Gaulin, 2007) and maintaining regular ovulatory cycles (Singh, 2002). The distribution of women's body fat can be measured using the waist-to-hip ratio (WHR), which computes the ratio between body circumference at the waist and the hips (Singh, 1993). Women with lower WHRs have a body fat distribution consistent with greater health and reproductive potential (Singh, 2002, 2006) and, at the physiological level, it has been shown that larger breasts and slim waists are associated with higher estrogen and progesterone levels (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004), which are predictors of the probability of conception (Lipson & Ellison, 1996). Images of women with low WHRs (in the range 0.6-0.8) are more attractive to

men from Cameroon (Dixson, Dixson, Morgan, & Anderson, 2007), Germany (Henss, 2000), China (Dixson, Dixson, Li, & Anderson, 2007), the UK (Furnham, Tan, & McManus, 1997), the U.S., and New Zealand (Dixson, Dixson, Bishop, & Parrish, in press).

The evolutionary significance of prominent breasts in women has been much debated. Some authors have ascribed a functional role to large breasts. For example, as humans evolved hairlessness and bipedal locomotion, larger pendulous breasts were adaptive for breast-feeding babies (LeBlanc & Barnes, 1974) and provided a soft cushion that is psychologically comforting to the infant (Smith, 1986). During times of nutritional scarcity, breasts may act as milk storage organs (Low, Alexander, & Noonan, 1987) and fat reserves for breast-feeding babies (Anderson, 1983). However, many of these arguments have since been refuted. There is no relationship between larger breasts prior to pregnancy and improved lactation, as women with smaller breasts are able to feed their babies as effectively (Anderson, 1988; Pond, 1998). Breast enlargement may occur as a by-product of gluteofemoral fat deposition (Pawlowski, 1999) and theories ascribing a functional role to permanently enlarged breasts remain debatable. However, sexual selection via male partner choice may also explain the evolution of prominent breasts in women as a cue to adult sexual maturity (Gallup, 1982; Marlowe, 1998). Studies of male preferences for female breast size have produced mixed results. Some studies have found that men rate line drawings of women with medium sized breasts as most attractive (Horvath, 1981; Wiggins, Wiggins, & Conger, 1968) while other studies have found that men prefer smaller breasts (Furnham, Swami, & Shah, 2006) or larger breasts (Singh &

Young, 1995). The mixed responses from men reported in these studies suggest that further investigations of female breast size and sexual attractiveness would be valuable.

How do men analyze female morphological traits, such as WHR and breast size, when reaching decisions about the overall attractiveness of the female face and body? Eye-tracking provides a more objective measurement of the focus of attention during judgments of attractiveness than questionnaire-based studies. Attractiveness, particularly in women, comprises a set of physical traits that captures the attention of the opposite sex (Maner, Gailliot, & DeWall, 2007). Eye-tracking research has shown that participants of both sexes look preferentially at faces of attractive women (Fink et al., 2008; Maner, DeWall, & Gailliot, 2008). However, there is currently only limited information on how men process female WHR when making attractiveness judgments. Suschinsky, Elias, and Krupp (2007) conducted eye-tracking studies to measure men's responses to female images varying in WHR. The images were clothed, but a consistent finding was that men spent more time examining the breasts, irrespective of variations in WHR. Eye-tracking techniques have also been used to measure visual attention of both sexes to images depicting erotic heterosexual interactions (Lykins, Meana, & Kambe, 2006; Rupp & Wallen, 2007). However, in such cases, the visual scenes are complex, making it difficult to conduct fine-grained analyses of visual attention in relation to specific morphological traits.

In this study, we used eye-tracking procedures to measure how men examined images of front-posed naked women varying in WHR and breast size. Specifically, we measured the initial fixation, number of visual fixations, and the amount of time men spent looking at defined areas of the female body and face. Men were also asked to rate

the various images for sexual attractiveness. The purpose was to quantify eye movements and visual attention along with judgments of female attractiveness. Several hypotheses might be advanced regarding eye movements during judgments of female attractiveness. Men might spend significant time examining the face, the breasts, the waist or the pubic area given that all these areas are involved in female attractiveness and reproduction. However, the crucial issue was to obtain quantitative measures of which areas of the body men looked at and how frequently they examined them during eye-tracking experiments.

METHOD

Participants

A total of 36 men of European descent, ranging in age from 22-42 years ($M = 27.42$ years; $SD = 4.99$), were recruited opportunistically from the post-graduate student body at Victoria University. Participants were given individual verbal orientation before the start of data collection and allowed some time to familiarize themselves with the room and eye-tracking machine. The details of the study were not discussed with participants beforehand. However, when each participant had completed the experiments, they were provided with written details of the rationale for the research. Each participant was told of their right to withdraw themselves or their data from the study without prejudice. The project was pre-approved by the Human Ethics Committee of the School of Psychology at Victoria University.

Measures and Procedure

A photograph of a front-posed naked woman was scanned from Simblet (2001). Waist-to-hip ratio (WHR) and breast size were manipulated in this image using

Photoshop Version 7.0. Three different breast sizes were created using anthropometric measurements taken from Brown et al. (1999). Images with small breasts (80% of the original image), medium (unchanged), and large (120% of the original size) were made. Each breast size was shown on a figure with a waist-to-hip ratio of 0.7 or 0.9. Thus, six images were constructed in total. The experiment was programmed using the SR Research Experiment Builder (version 1.4.128 RC) and conducted on a 3-GHz Pentium D computer. Stimuli were presented on a 21 inch monitor at a resolution of 1024 x 768 pixels and with a refresh rate of 60 Hz.

Participants were seated in a comfortable chair in a quiet room facing the monitor at eye level at a viewing distance of 57 cm, maintained by a forehead and chin-rest. They underwent eye-tracking trials in which each image was presented individually, in random order on the computer screen for five seconds.

Attractiveness

At the end of each presentation, participants were instructed to rate the image for attractiveness using a keyboard with a six point Likert scale in which 1 = unattractive, 2 = somewhat attractive, 3 = moderately attractive, 4 = attractive, 5 = very attractive, and 6 = extremely attractive.

Eye-tracking

Using the EyeLink® 1000 Tower Mount Head Supported System (SR Research Ltd., Ontario, Canada), eye position and eye movements were determined by measuring the corneal reflection and dark pupil with a video-based infrared camera and an infrared reflective mirror. The eye tracker had a spatial resolution of 0.01° of visual angle and the signal was sampled and stored at a rate of 1000 Hz. While viewing was binocular,

recording was monocular, measuring right eye movements only as this is a standard procedure in eye-tracking studies (e.g., Lykins et al., 2006). Calibration and validation of measurements were performed before each experimental session.

The stimulus image was divided into six anatomical regions for subsequent analysis of eye-tracking data (Fig. 1). The six regions were defined as follows: (1) the face and neck, from the top of the head to the level of the clavicle; (2) breasts, from the top of the clavicle to the posterior border of each breast; (3) midriff, including the waist; beginning from the below the breasts to the widest part of the hips; (4) pubic triangle, as defined by the limits of the pubic hair; (5) the thighs, the upper portion of the leg ending at the knee and (6) lower leg and feet. The arms were not included in the analyses as they received so little visual attention.

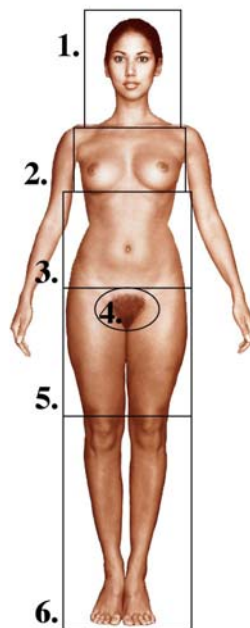


Fig 1. Female images were divided into six regions in order to analyze male visual attention during eye-tracking. 1 = head, 2 = breasts, 3 = midriff, 4 = pubic region, 5 = thighs and 6 = lower legs and feet.

In each of the six regions, three dependent variables of eye movement were measured: first fixation, number of fixations, and amount of time spent (dwell time) examining the area. The first region of the body to be examined, from 200 milliseconds after the start of the test, was defined as the first fixation. The lag time of 200 milliseconds was allowed in order to give sufficient time for the eye to move from its initial fixation point in the center of the screen. Each time the eye moved, the eye-tracking machine recorded a new fixation. Total fixations which occurred in each area were summed during the analysis. Likewise, the machine measured individual fixation times, so that it was possible to obtain the total time spent examining each of the six regions.

RESULTS

Attractiveness

Fig. 2 shows the mean attractiveness ratings as a function of WHR and breast size. A 2 (WHR: 0.7 vs. 0.9) x 3 (Breast Size: Small, Medium, Large) analysis of variance (ANOVA) yielded a significant main effect for WHR on attractiveness ratings, $F(1, 35) = 64.26, p < .0001$. Images with a 0.7 WHR ($M = 4.08, SD = 1.04$) were more attractive than images with a 0.9 WHR ($M = 2.93, SD = 1.07$).

Eye-tracking

First Fixation

Chi-square tests were conducted for each image to determine whether these fixations occurred on specific body regions more frequently than predicted by chance (Table 1). Due to the absence of first fixations on the lower legs and feet this body region

was not included in the analyses. In each image the breasts received the highest number of first fixations. First fixation counts on the breasts reached statistical significance for images with 0.7 WHRs with small ($p < .05$) and medium sized breasts ($p < .01$), and images with 0.9 WHRs and medium ($p < .01$) or large sized breasts ($p < .001$). The midriff was also looked at very frequently in all images (Table 1). Although these effects were not statistically significant it was noteworthy that 33% of first fixations overall involved the midriff, while 47% involved the breasts. Thus, 80% of first fixations were on the breasts and midriff of the figures, while the remaining body regions accounted for only 20% of first fixations.

Table 1. Number of men ($N = 36$) who made their first visual fixations on each of the five body regions. Data are shown for all six female images.

Image No.	Head χ^2	Midriff χ^2	Breast χ^2	Thighs χ^2	Pubis χ^2
1.	2 3.76	13 4.67	16 10.76*	1 5.34	4 1.42
2.	2 3.76	9 0.45	17 13.34**	1 5.34	7 0.09
3.	3 2.45	13 4.67	15 8.45	3 2.45	2 3.76
4.	3 2.45	13 4.67	15 8.45	0 7.20	5 0.67
5.	2 3.76	11 2.01	18 16.20 **	1 5.34	4 1.42
6.	0 7.20	13 4.67	20 22.76 ***	1 5.34	2 3.76

WHR/Breast Sizes are as follows: Image 1. = 0.7/small; 2. = 0.7/medium; 3. = 0.7/large; 4. = 0.9/small; 5. = 0.9/medium; 6. = 0.9/large. Chi-square analyses compared observed number of men fixating on a given region to the numbers expected by chance (7.20). * $p < .05$; ** $p < .01$; *** $p < .001$.

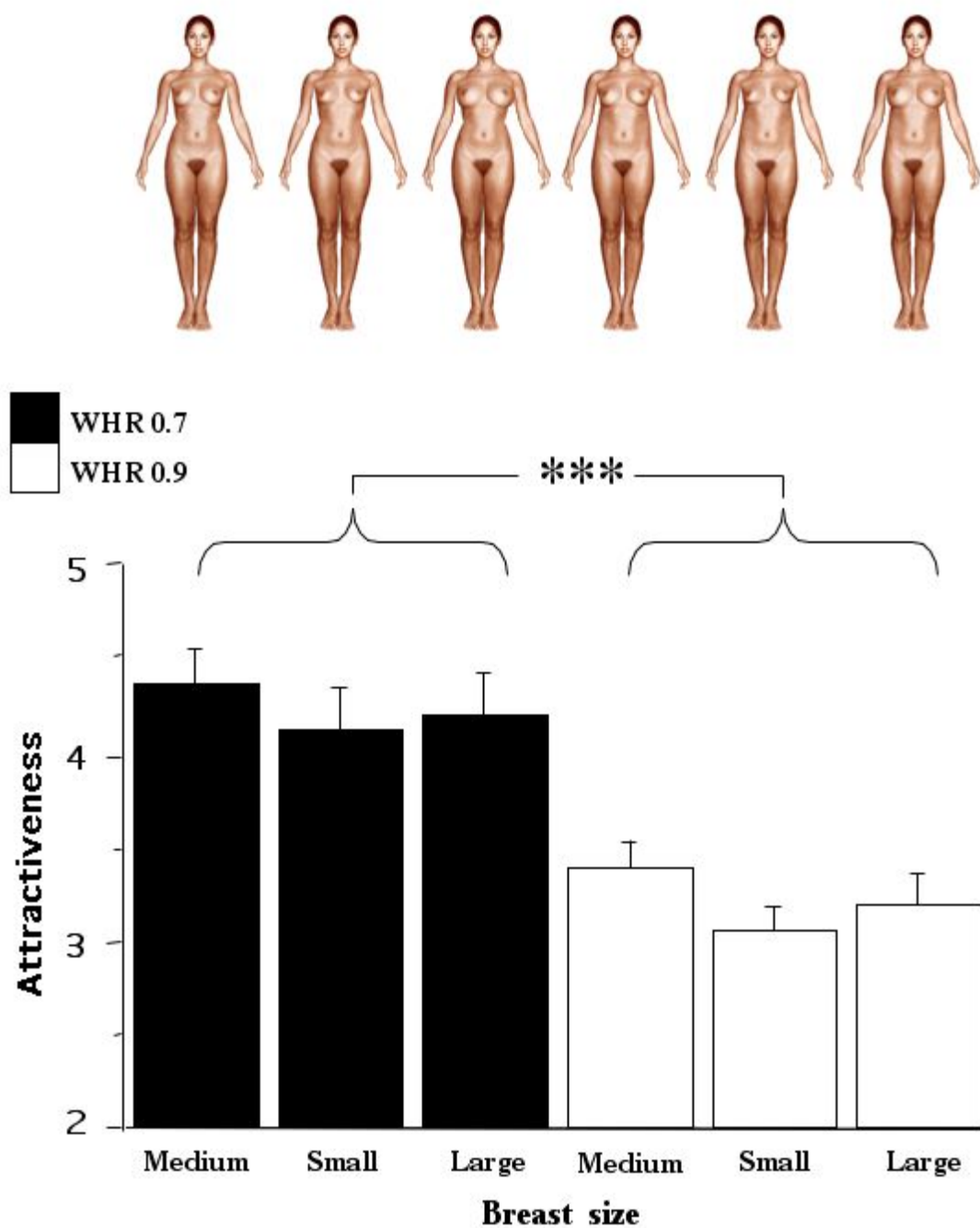
Fig 2.

Fig 2. Mean ratings (+SEM) for sexual attractiveness of six front-posed female figures varying in WHR (0.7 or 0.9) and breast size (small, medium or large). *** $p < .001$.

Number of Fixations and Dwell Times

A 2 (WHR) x 3 (Breast Size) x 6 (Body Region) x 5 (Time: Seconds 1-5) repeated measures ANOVA yielded a significant main effect of time for number of fixations, $F(4, 840) = 5.62, p = .001$, and dwell times, $F(4, 840) = 8.71, p = .001$. As illustrated in Fig. 3, a rapid drop in both number of fixations and dwell times occurred after the first three seconds. Therefore, subsequent analysis was based only on the first three seconds of the eye-tracking experiment.

Fig 3.

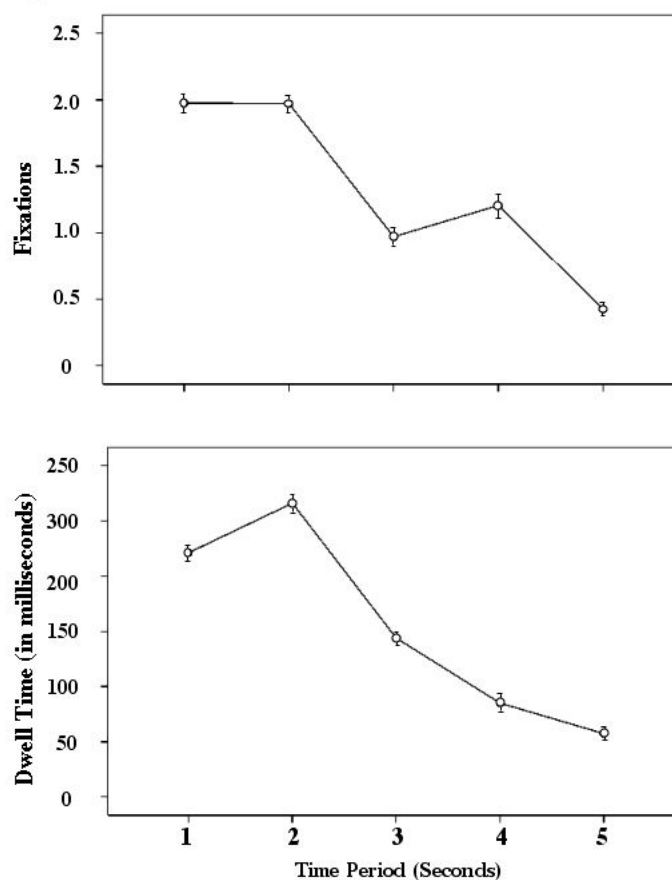


Fig 3. Combined means (+SEM) across the six images for number of fixations (upper graphs) and dwell times (lower graphs) made over the five seconds of the eye-tracking study.

For number of fixations, a 2 (WHR) x 3 (Breast Size) x 6 (Body Region) x 3 (Time: Seconds 1-3) mixed model repeated measures ANOVA yielded a significant Body Region x Time interaction, $F(10, 350) = 7.38, p = .001$ and a significant Breast Size x Time interaction, $F(4, 140) = 3.23, p = .014$. These two-way interactions were qualified by a three-way interaction between Breast Size, Body Region, and Time, $F(20, 700) = 4.07, p = .001$. Fig. 4 shows that this interaction was driven primarily by attention to the breasts and head during the first second of the eye-tracking session. When looking at images with large breasts, participants made significantly more fixations on the breasts than the head ($t = -10.21, df = 35, p < .001$) and the midriff ($t = 7.94, df = 35, p < .001$). When participants looked at figures with small breasts, fixations were more often on the breasts than the head ($t = -2.45, df = 35, p < .01$) and the midriff ($t = 3.09, df = 35, p < .01$). When looking at images with medium sized breasts, participants looked at the head more than the breasts, although this was not statistically significant ($t = 1.37$). The breasts were looked at more than midriff ($t = 5.68, df = 35, p < .001$), as was the head ($t = 6.47, df = 35, p < .001$).

For dwell times, a 2 (WHR) x 3 (Breast Size) x 6 (Body Region) x 3 (Time: Seconds 1-3) mixed model repeated measures ANOVA yielded a significant Body Region x Time interaction, $F(10, 350) = 4.20, p = .001$, and a Breast Size x Body Region interaction, $F(10, 350) = 8.34, p = .001$. These two-way interactions were qualified by a three-way interaction between Body Region, Breast Size, and Time, $F(20, 700) = 1.57, p = .053$. These interactions reflect the fact that the amount of time spent looking at either the head or the breasts was most pronounced during the first second of the eye-tracking experiment (Fig. 5). When images had small breasts, participants spent longer looking at

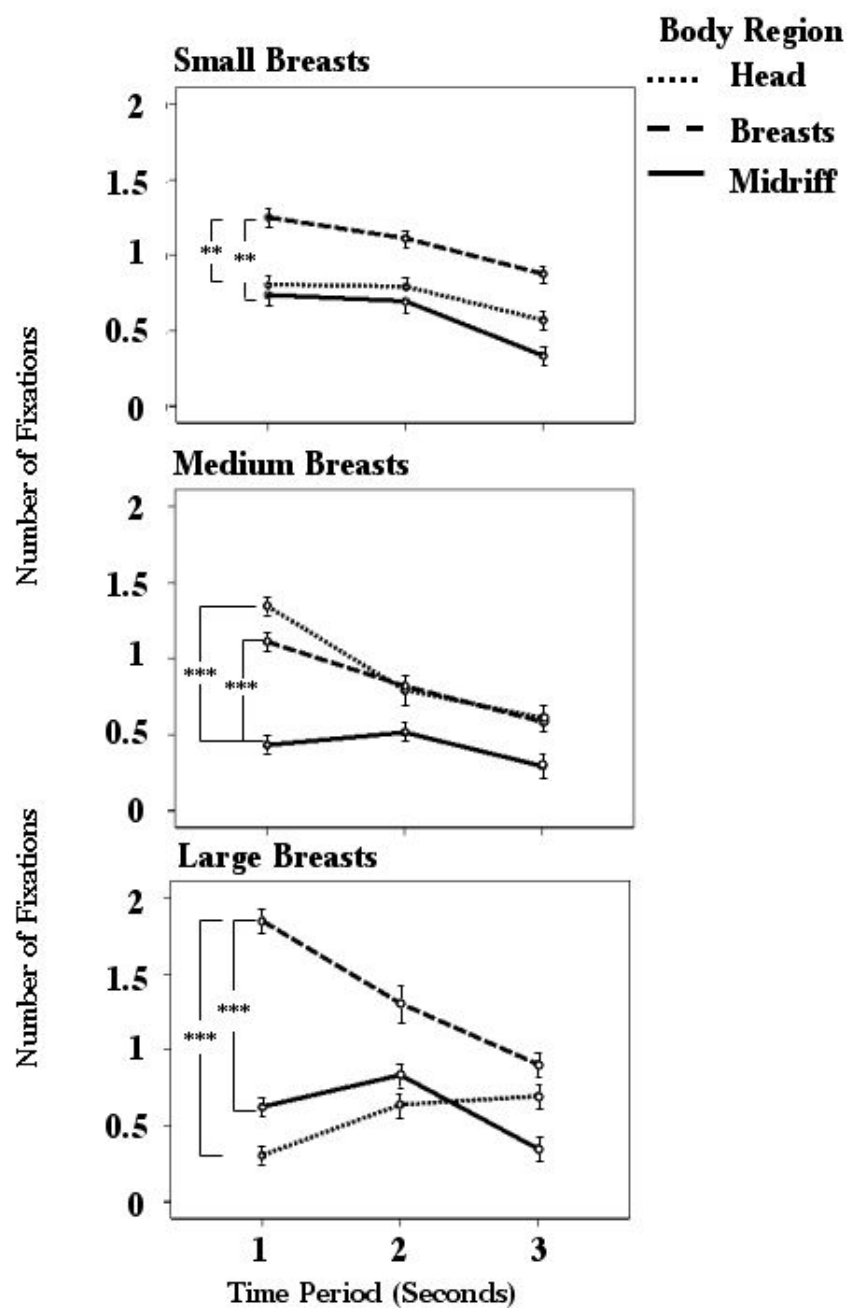
Fig 4.

Fig 4. Mean number of fixations (+SEM) made on images with small, average or large breasts for the first three seconds of the eye-tracking study. Separate lines indicate the body region (head, breasts and midriff) within the image being looked at. ** $p < .01$. *** $p < .001$.

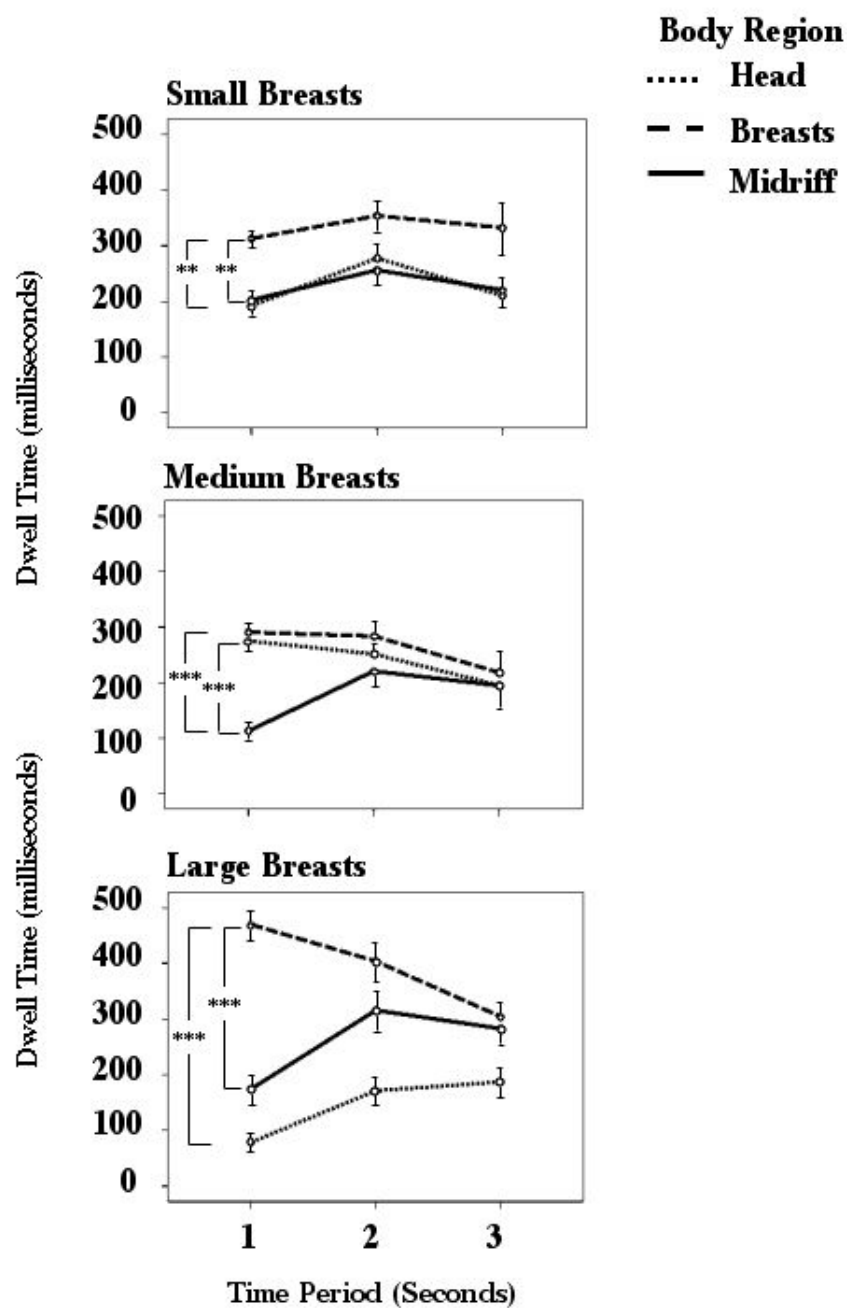
Fig 5.

Fig 5. Mean dwell times (+SEM) made on images with small, average or large breasts for the first three seconds of the eye-tracking study. Separate lines indicate the body region (head, breasts and midriff) within the image being looked at. ** $p < .01$. *** $p < .001$

the breasts than the head ($t = 2.62$, $df = 35$, $p < .01$) and the midriff ($t = 2.42$, $df = 35$, $p < .01$). When looking at images with large breasts, men spent more time looking at the breasts than the head ($t = 10.77$, $df = 35$, $p < .001$) and the midriff ($t = 5.53$, $df = 35$, $p < .001$). When the images had average sized breasts, participants spent more time looking at the breasts than the midriff ($t = 4.63$, $df = 35$, $p < .001$). The head was also looked at for longer than the midriff ($t = 4.35$, $df = 35$, $p < .001$). However, men spent almost as much time looking at the head as the breasts ($t < 1$).

DISCUSSION

Eye-tracking techniques provide novel insights in the study of male preferences for female body shape. Men spent consistently more time looking at the breasts of front-posed female images and also made significantly more fixations upon the breasts than other regions of the body or head. The midriff and thighs received less attention. However, men in general allocated more attention to the upper body, including the face, breasts, and midriff, than to the thighs, pubic area, legs, and feet. These effects were most pronounced during the first three seconds of a five second eye-tracking session. By the fourth and fifth second, men paid significantly less attention to all regions of the female body and head.

Despite the large amount of attention paid to the breast area, it was the WHR that primarily determined male ratings of female attractiveness. Thus, images having WHRs of 0.7 were consistently rated as more attractive than the 0.9 WHR images, irrespective of breast size. The *initial* visual fixation of a session most frequently involved either the breasts or the midriff, including the waist. The initial eye-movement occurs within the

first 200 milliseconds and was followed by longer and more frequent fixations upon adjacent areas.

It appears, therefore, that men may make assessments of female WHR very rapidly during the eye-tracking procedure, but spend most time examining those areas where secondary sexual deposition of fat has occurred (i.e., the breasts). The gluteofemoral region is also an important site of fat accumulation in women. The buttocks were not visible in the images used for these experiments. Anthropological studies of the Hadza hunter-gatherers in Tanzania have shown that men find the female buttocks to be highly attractive and rate images with a low WHR and larger buttocks as most sexually attractive (Marlowe, Apicella, & Reed, 2005). This leads us to predict that eye-tracking studies using back-posed images of women varying in WHR should provide further insights concerning how men make visually-based judgments of female attractiveness. We predict that numbers of fixations and dwell times will be highest for the buttocks when men view back-posed images of women.

A potential shortcoming of the current research was that the face was identical in each figure presented. Facial features are important in male assessment of female physical attractiveness (Hassebrauck, 1998). Novel or unique features capture attention during eye-tracking studies (Sütterlin, Brunner, & Opwis, 2008). As facial features were not manipulated in the current study, one could argue that men paid more attention to the breasts and midriff as these were the novel items that were manipulated. This is a valid criticism; however, in a recent eye-tracking study where participants viewed photographs depicting complex erotic and non-erotic heterosexual scenes, men spent more time looking at women's bodies than their faces (Lykins, Meana, & Strauss, 2008).

Interestingly, women with higher levels of estrogens have been rated as having more attractive faces (Law-Smith et al., 2006). Thus, facial features may signal healthier levels of estrogens to potential partners in the same way as breast size and WHR (Jasienska et al., 2004). Therefore, it would be valuable in future studies to manipulate facial features as well as body morphology to gain a more complete understanding of male assessments of female sexual attractiveness.

In a previous eye-tracking study, Johnson and Tassinari (2005) found that men used WHR in assessing the sex of people when walking. However, it is crucial to note that these researchers employed as stimuli figures from which “all observable sex characteristics had been removed.” Thus, the figures used lacked cues such as pubic hair, breasts, and genitalia. In the absence of these cues, subjects paid particular attention to the waists of moving images. In another study, Suschinsky, Elias, and Krupp (2007) presented men with sets of three clothed images of identical women, varying only in WHR. Despite the possible distraction of the clothing, Suschinsky et al. found that men attended more to the breasts as well as the face of such images. Both the studies cited above produced results that were consistent with our findings concerning the importance of the breast and waist (midriff) for male assessments of female attractiveness.

It is likely that a constellation of traits influences female sexual attractiveness to men. WHR is instrumental as a pre-copulatory cue to female health and fertility. Eye-tracking research suggests that men dwell longest on those areas of the female body where fat reserves are greatest (i.e., the breasts and gluteofemoral region), but also achieve an overall or gestalt appreciation of the hourglass body shape incorporating a narrow waist and full breasts. Results of the current study indicated that men began to

analyze essential components of the hourglass feminine shape, including the midriff and breasts, during the first 200 milliseconds of viewing. This provides further evidence that the WHR is rapidly processed and that it represents a “first pass filter” in men’s ratings of female attractiveness (Singh, 1993). Men may be looking more often at the breasts because they are simply aesthetically pleasing, regardless of the size. However, breast morphology is more complex than size alone. Breast shape and firmness, as well as nipple and areola configuration, may signal age and reproductive status (Gallup, 1982; Marlowe, 1998; Symons, 1995). Thus, it would be valuable for future eye-tracking research to manipulate more aspects of female breast morphology. The results presented here provide additional evidence confirming that female WHR and breasts represent important sexually selected traits that are highly attractive to men.

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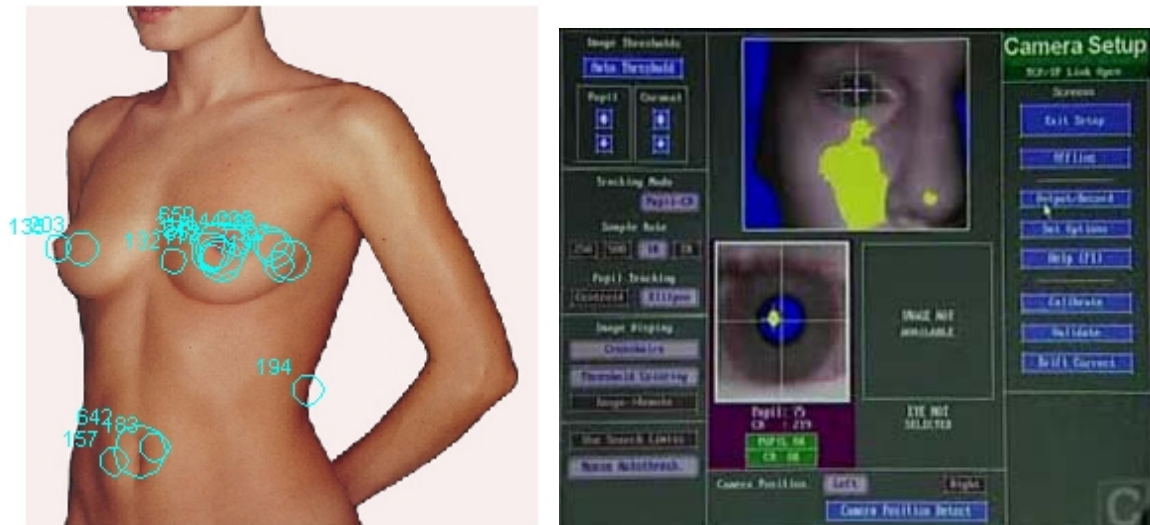
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Chapter Seven

Eye-Tracking of Men's Preferences for Female Breast Size and Areola Pigmentation.



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The chapter is a modified version of this manuscript, adapted to the thesis.

ABSTRACT

Sexual selection via male mate choice has been implicated in the evolution of permanently enlarged breasts in women. While questionnaire studies have shown that men find female breasts visually attractive, there is very little information about how they make such visual judgments. In this study we used eye-tracking technology to test two hypotheses: 1) that larger breasts should receive the greatest number of visual fixations and longest dwell times, as well as being rated as most attractive; 2) that lightly pigmented areolae, indicative of youth and nubility, should receive most visual attention and be rated as most attractive. Results showed that men rated images with medium-sized or large breasts as significantly more attractive than small breasts. Images with dark and medium areolar pigmentation were rated as more attractive than images with light areolae. However, breast size had no significant effect on eye-tracking measures (initial visual fixations, number of fixations and dwell times). While the majority of initial fixations during eye-tracking tests were on the areolae, areolar pigmentation did not affect measures of visual attention. These results demonstrate that cues indicative of female sexual maturity (large breasts and dark areolae) are more attractive to men. However, patterns of eye movements did not differ based on breast size or areolar pigmentation. Hypotheses that visual attention on morphology should be correlated with attractiveness judgments may be overly simplistic.

KEY WORDS: female attractiveness; breast size; areola pigmentation; eye-tracking.

INTRODUCTION

Women appear to be unique among mammals in developing enlarged breasts prior to pregnancy and lactation (Short, 1976). Breast size in women increases during puberty due to deposition of adipose tissue (Linzel, 1959). Mammary adiposity varies substantially between women independent of total body fat (Vandeweyer & Hertens, 2002). The morphology and pigmentation of the areolae and nipples also change during pubertal development in girls (Biro, Falkner, Khoury, Morrison, & Lucky, 1992; Garn, Selby, & Crawford, 1956). The areola is the area of pigmented skin that surrounds the nipple. The areolae acquire their coloration due to increased deposition of melanin. Indeed, the areolae contain twice the amount of melanin that occurs in the skin of the surrounding breast (Dean, Haynes, Brennan, Neild, Goddard, Dearman, & Cooter, 2005). The pigmentation of the areolae also changes with reproductive status in women. Thus, the areolae are often lighter in girls at the onset of menarche, darken somewhat during consecutive ovulatory cycles, and become much darker during pregnancy and lactation (Garn & French, 1963; Garn et al., 1956; Montagna & Macpherson, 1974; Muzaffar, Hussain, & Haroon, 1998). In a study of skin reflectance of the breast, the areola was darkest in pregnant women, and also in non-pregnant women during the final week of the menstrual cycle (Pawson & Petrakis, 1975).

It has been suggested that breast size may have undergone sexual selection via mate-choice (Barber, 1995). However, findings on the relationship between breast size and attractiveness are inconsistent; some studies have found that men rate line drawings of women with average-sized breasts as most attractive (Horvath, 1981; Wiggins,

Wiggins, & Conger, 1968), while other studies have concluded that men prefer smaller breasts (Furnham, Swami, & Shah, 2006) or larger breasts (Singh & Young, 1995).

Eye-tracking techniques can provide data on attention that may shed light on the relative importance of morphological traits when people make attractiveness judgments. In eye-tracking experiments, attentional capture may be an endogenous process, in which participants actively control how they allocate attention in order to achieve a goal (Ruz & Lupiáñez, 2002). Alternatively, attention may be exogenous, whereby participants allocate their attention to stimuli unintentionally (Ruz & Lupiáñez, 2002). Attention is influenced by the motivation of the individual. For example, stimuli that are associated with fear and reward have been shown to capture attention (Castellanos, Charboneau, Dietrich, Park, Bradley, Mogg, & Cowan, 2009; De Martino, Kalisch, Rees, & Dolan, 2009; Raymond & O'Brien, 2009). There is growing evidence that facial attractiveness actively captures attention (Maner, DeWall, & Gailliot, 2008; Maner, Gailliot, & DeWall, 2007) and that participants purposefully use facial features when judging the attractiveness of female faces (Shimojo, Simion, Shimojo, & Scheier, 2003). Female faces with an even complexion are judged to be highly attractive and also receive the most visual attention during eye-tracking studies (Fink, Matts, Klingenberg, Kuntze, Bettina, & Grammer, 2008).

Recent eye-tracking studies have shown that men spend a lot of time looking at the female body when viewing both erotic and non-erotic stimuli (Lykins, Meana, & Kambe, 2006; Lykins, Meana, & Strauss, 2008; Rupp & Wallen, 2007). The breasts in particular are the focus of male attention. A recent eye-tracking study (Dixson, Grimshaw, Linklater, & Dixson, 2009) presented men with individual front-posed nude

images of women that had been manipulated to show small, medium or large breasts and either low (0.7) or high (0.9) waist-to-hip ratios (WHR). Although ratings of attractiveness were related primarily to WHR, men spent more time and looked more frequently at the breasts compared to other areas of the body. Indeed, eye-tracking studies of the female body have consistently shown that the breasts receive a lot of visual attention irrespective of whether the stimulus images are shown fully clothed (Hewig, Trippe, Hecht, Straube, & Milner, 2008), wearing dresses and bathing suits (Suschinsky, Elias, & Krupp, 2007) or nude (Dixson et al., 2009). In such experiments, men may be examining the breast as a whole, or looking at specific features such as the areolae when making attractiveness judgments. However, it is difficult to obtain fine-grained measurements concerning eye-tracking and breast morphology when men view clothed images or images of the entire female body and face. Therefore, in the current study, eye-tracking procedures were employed to obtain such measurements by using images of nude female torsos as stimuli. Specifically, the first visual fixation, number of fixations, and the amount of time (dwell time) men spent looking at defined areas of the female breast and torso were measured. Men were also asked to rate the various images for sexual attractiveness.

The current study was undertaken to examine the relative importance of two features of breast morphology in attentional capture and male judgments of female attractiveness; breast size and areola pigmentation. Women with larger breasts and lower WHRs have been shown to have higher circulating estradiol and progesterone (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Women with higher circulating levels of estradiol and progesterone have higher rates of conception compared to women with

lower levels of estradiol and progesterone (Lipson & Ellison, 1996). In the Jasienska et al. (2004) study the relationship between breast size and estradiol was independent of WHR, so that women with larger breasts had higher levels of estradiol compared to women with smaller breasts. Therefore, the first hypothesis we examined was that men should direct most visual attention to larger breasts and rate them as being most sexually attractive. Turning to the question of areola pigmentation, this is lightest at the onset of menarche, darkens as women age and particularly during pregnancy and lactation (Garn & French, 1963; Garn et al., 1956; Montagna & Macpherson, 1974; Muzaffar et al., 1998). It has been suggested that morphological features of the breast that signal youth should be most attractive to men, as they seek to maximize their reproductive success by selecting mates who exhibit traits of youthfulness as well as sexual maturity (Symons, 1995). Several authors have suggested that areola pigmentation may be a signal to men of female age and reproductive status (Goodhart, 1964; Grammer, Fink, Juetten, Ronzal, & Thornhill, 2001; Guthrie, 1976). Because lighter areolae may signal youth and nubility to men, the second hypothesis we tested was that a lighter-colored areola should be most attractive to men and the focus of their visual attention.

METHOD

Participants

Thirty-seven heterosexual men of European descent, ranging in age from 22-47 years ($M = 30.05$ years; $SD = 6.21$), were recruited opportunistically from the staff and post-graduate student body at Victoria University. Ten of these men were married. Participants were given individual verbal briefing before the start of data collection and allowed some time to familiarize themselves with the room and eye-tracking machine.

The details of the study were not discussed with participants beforehand. However, when each participant had completed the experiments, they were provided with written details of the rationale for the research. Each participant was told of their right to withdraw themselves or their data from the study without prejudice. All participants had normal vision or correction by contact lenses. None wore glasses. The project was approved by the Human Ethics Committee of the School of Psychology at Victoria University.

Apparatus and materials

A color photograph of an oblique-posed torso of a naked woman was scanned from Simblet (2001). This image was used to model overall breast size (three sizes) and areolar pigmentation (three levels) as detailed below. Thus, there were six stimulus images based on the same photograph.

Breast size was manipulated using Photoshop Version 7.0. Three sizes were created using anthropometric measurements taken from Brown et al. (1999). Images with small breasts (80% of the original image), medium (unchanged), and large (120% of the original size) were made. Each of these images had the same areolar pigmentation. In another set of images, areola pigmentation was altered in a step-wise fashion by adding or subtracting 10 units of brightness and 15 units of contrast to create two further images; one image that had lighter areolae and one with darker areolae. All three images had medium breast size.

The experiment was programmed using SR Research Experiment Builder (version 1.4.128 RC) and run on a 3-GHz Pentium D computer. Stimuli were presented on a 21 inch monitor at a resolution of 1024 x 768 pixels and with a refresh rate of 60 Hz.

Procedure

Participants were seated in a comfortable chair in a quiet room facing the monitor at eye level at a viewing distance of 57 cm, maintained by a forehead and chin-rest. They underwent eye-tracking trials in which each image was presented individually, in random order on the computer screen for five seconds.

Attractiveness measurements

At the end of each presentation, participants were instructed to rate the image for sexual attractiveness using a keyboard with a six point Likert scale in which 1 = unattractive, 2 = somewhat attractive, 3 = moderately attractive, 4 = attractive, 5 = very attractive, and 6 = extremely attractive.

Eye-tracking

Using the EyeLink® 1000 Tower Mount Head Supported System (SR Research Ltd., Ontario, Canada), eye position and eye movements were determined by measuring the corneal reflection and dark pupil with a video-based infrared camera and an infrared reflective mirror. The eye tracker had a spatial resolution of 0.01° of visual angle and the signal was sampled and stored at a rate of 1000 Hz. While viewing was binocular, recording was monocular, measuring right eye movements only as this is a standard procedure in eye-tracking studies (e.g. Lykins et al., 2006). Calibration and validation of measurements were performed before each experimental session.

The stimulus image was divided into five anatomical regions for subsequent analyses of eye-tracking data (Fig. 1). The five regions were defined as follows: (1) the jaw and neck, from the jaw to the bottom of the clavicle; (2) breasts (excluding the areolae and nipples), from the bottom of the clavicle to the lower border of each breast; (3) the nipple and areola, the area of pigmented skin surrounding the nipple; (4) midriff,

including the waist; beginning from below the breasts extending to the widest part of the hips and (5) the arm, from the top of the shoulder to the wrist.

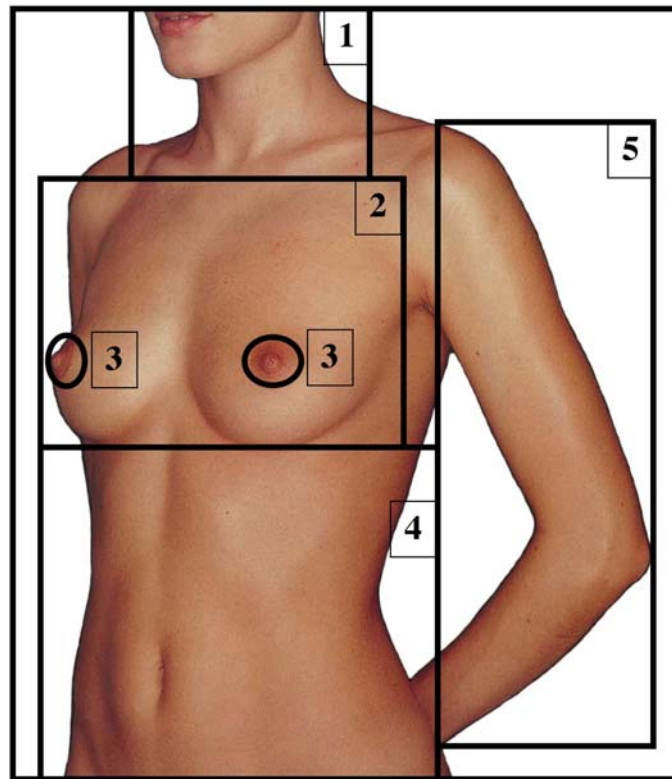


Fig. 1 Female stimulus images were divided into five anatomical regions in order to analyze male visual attention during eye-tracking. 1 = neck and jaw; 2 = breasts; 3 = nipples and areolae; 4 = midriff; 5 = arm.

From the eye-tracking data, three dependant variables, first fixation, number of fixations, and dwell time (total time spent looking), were recorded for each of the five body regions. The first region of the body to be examined, starting 200 milliseconds after the start of the trial, was defined as the first fixation. The lag time of 200 milliseconds was allowed in order to give sufficient time for the eye to move from its initial fixation point in the center of the screen. Each time the eye moved, the eye-tracking machine

recorded a new fixation. Total fixations which occurred in each area were summed during the analysis. Likewise, the machine measured individual fixation times, so that it was possible to calculate the total time spent examining each of the five regions.

RESULTS

Attractiveness

Fig. 2 shows the mean attractiveness ratings as a function of breast size. A single factor (Breast size: Small, Medium, Large) repeated measures analysis of variance (ANOVA) yielded a significant main effect for breast size on attractiveness ratings, $F(2, 72) = 25.20, p < .001$. Post-hoc Scheffé's tests revealed that large and medium-sized breasts were significantly more attractive than small breasts ($p < .001$). There was no statistical difference in attractiveness ratings between the images with medium and large breasts ($p = .454$).

Fig. 3 shows the mean attractiveness ratings as a function of areola pigmentation. A single factor (Areola Pigmentation: Light, Medium, Dark) repeated measures ANOVA yielded a significant main effect for pigmentation on attractiveness ratings, $F(2, 72) = 5.75, p < .01$. Post hoc Scheffé's tests showed that the light areolae were significantly less attractive than the dark ($p < .01$) and the medium ($p < .5$) areolae. There was no statistical difference in the attractiveness ratings between medium and darkly-pigmented areolae ($p = .815$).

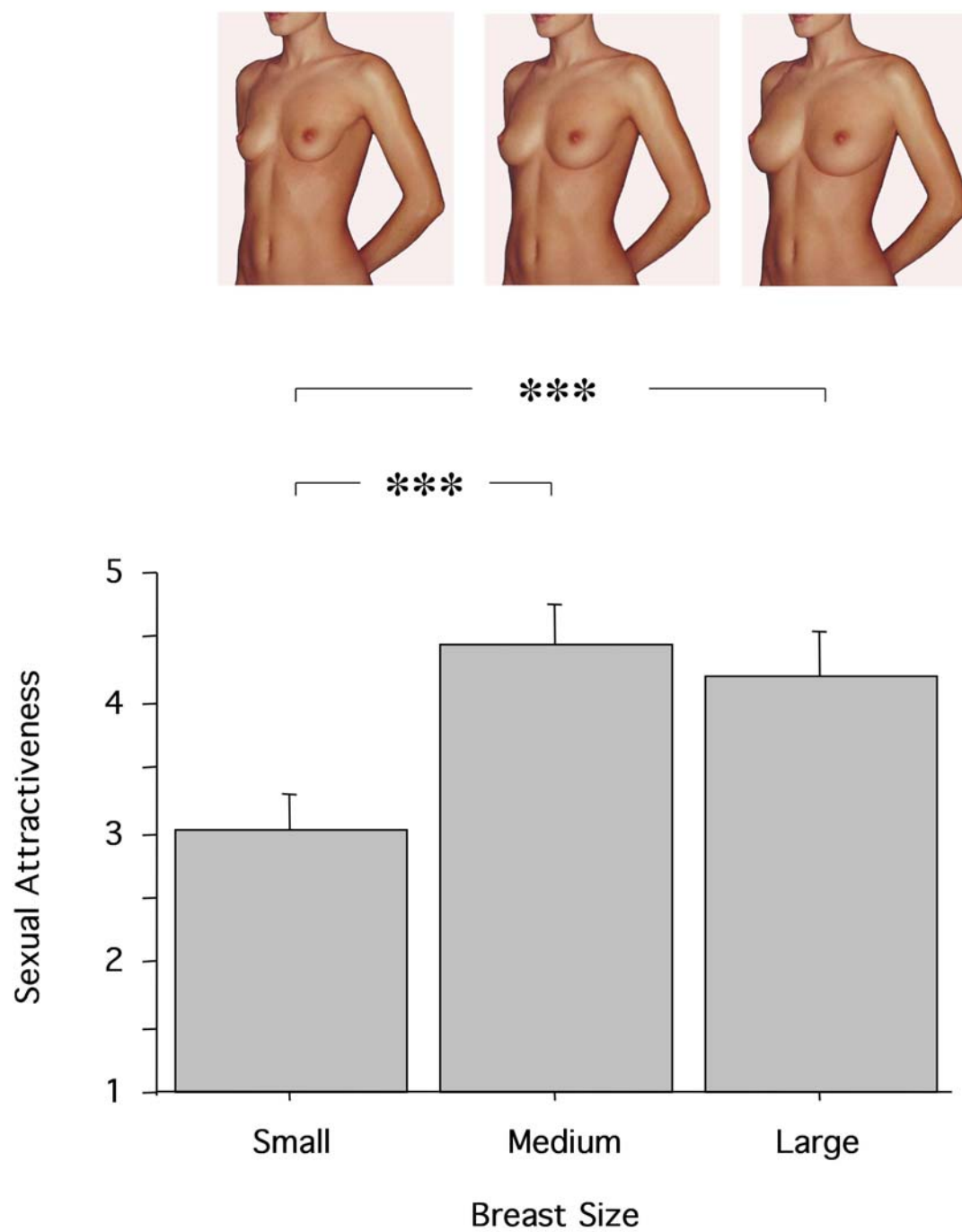
Fig. 2

Fig. 2 Mean ratings (+SD) of sexual attractiveness for three female torsos varying in breast size (small, medium or large). *** $p < .001$.

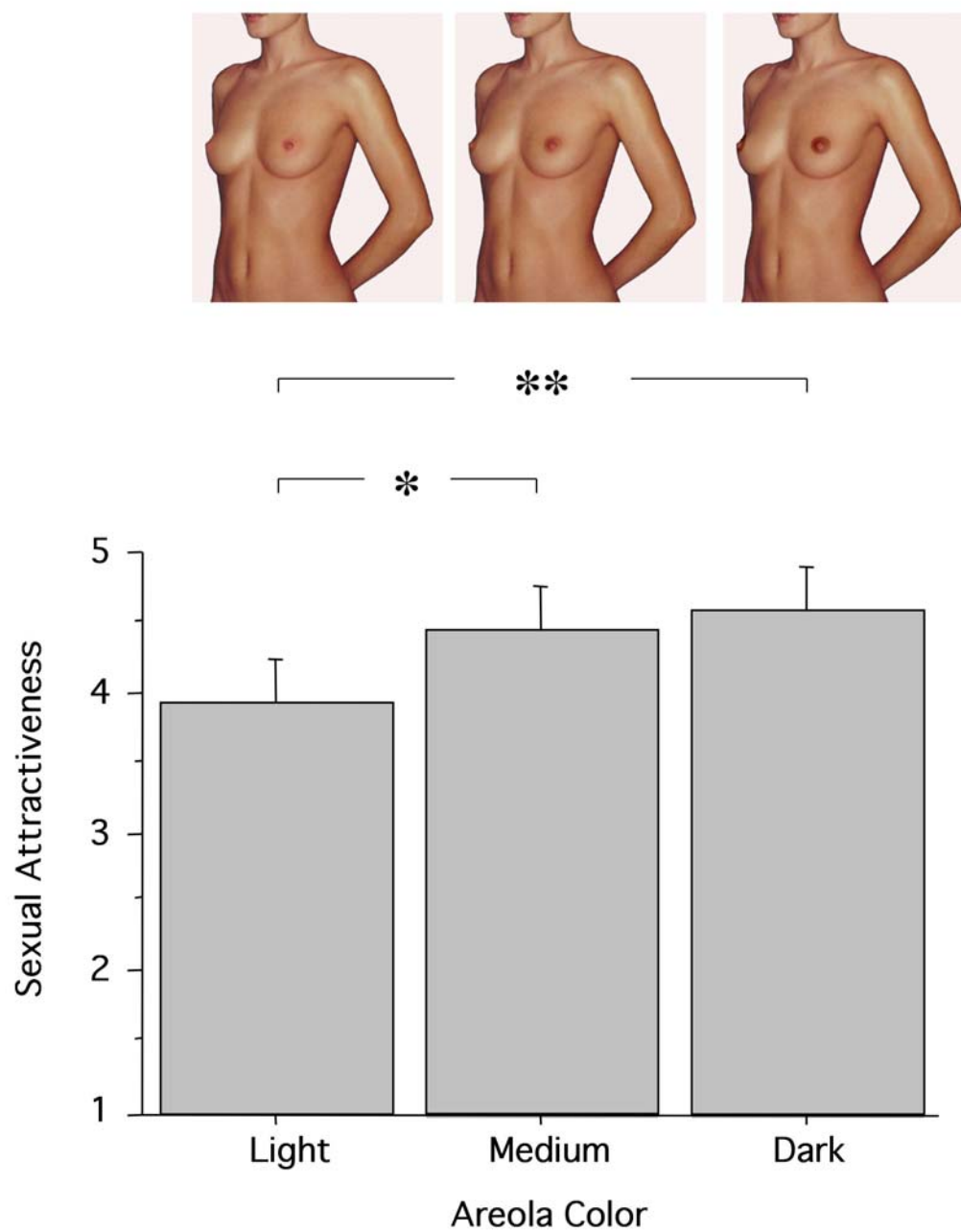
Fig. 3

Fig. 3 Mean ratings (+SD) of sexual attractiveness for three female torsos varying in areola color (light, medium or dark). * $p < .05$, ** $p < .01$.

Eye-tracking

First Fixations

Observations were made on the frequencies of first fixations on each body region for each of the six images. The areolae and nipples received the most first fixations, followed by the breast region, in all images irrespective of overall breast size or degree of areolar pigmentation (Table 1).

Table 1. Number of men ($N = 37$) who made their first visual fixations on each of the five body regions. Data are shown for all six female images.

Image	Jaw/Neck %	Breast %	Nipple/Areola %	Midriff %	Arm %
Small Breast	1 3%	9 24%	25 68%	2 5%	0 0%
Medium Breast	1 3%	10 27%	23 62%	2 5%	1 3%
Large Breast	2 5%	11 30%	22 59%	1 3%	1 3%
Light Areola	1 3%	7 19%	26 70%	1 3%	2 5%
Medium Areola	1 3%	10 27%	23 62%	1 3%	2 5%
Dark Areola	3 8%	10 27%	23 62%	1 3%	0 0%

Breast Size

Numbers of Fixations

For number of fixations, a 3 (Breast Size) x 5 (Body Region) repeated measures ANOVA yielded a significant Breast Size x Body Region interaction $F(8, 288) = 3.57, p < .001$. As can be seen in Figure 4, the pattern of fixations was very similar irrespective

of breast size. The breast as a whole was fixated on significantly more frequently than the areolae and nipples, $t(36) = 17.15, p < .001$, the jaw and neck, $t(36) = 21.92, p < .001$, the arm, $t(36) = 26.24, p < .001$, and the midriff, $t(36) = 20.47, p < .001$. The nipples and areolae were looked at significantly more often than the jaw and neck, $t(36) = 2.96, p < .01$, and the arm, $t(36) = 6.50, p < .001$. The image depicting small breasts attracted slightly more fixations to the jaw and neck area than when looking at the same area on images with large breasts, $t(36) = 2.72, p < .01$. Likewise, when viewing images with smaller breasts, men looked more often at the breast region than when they looked at this region of the images with medium-sized breasts, $t(36) = 2.75, p < .01$ (Fig. 4).

Dwell Times

For dwell times, a 3 (Breast Size) x 5 (Body Region) repeated measures ANOVA also yielded a significant Breast Size x Body Region interaction $F(8, 288) = 2.07, p = .039$. Similarly to data for numbers of fixations, the breast region was looked at for significantly longer than the areolae and nipples, $t(36) = 14.01, p < .001$, neck and jaw, $t(36) = 22.33, p < .001$, the arm, $t(36) = 27.17, p < .001$, and the midriff, $t(36) = 21.00, p < .001$. The nipples and areolae were looked at for significantly longer than the jaw and neck, $t(36) = 3.23, p < .001$, the midriff, $t(36) = 2.83, p < .001$, and the arm, $t(36) = 5.33, p < .001$. When men looked at images with smaller breasts, they dwelt for longer on the neck and jaw than when looking at images with large breasts, $t(36) = 3.48, p < .001$. Dwell times on the breasts were significantly longer when men viewed images of smaller breasts compared to medium-sized breasts, $t(36) = 2.71, p < .01$ (Fig. 1)

Areola Pigmentation

Numbers of Fixations

For number of fixations, a 3 (Areola Pigmentation) x 5 (Body Region) repeated measures ANOVA yielded a significant Areola Pigmentation x Body Region interaction $F(8, 288) = 2.83, p < .01$. The breast as a whole was fixated on significantly more frequently than the areolae and nipples, $t(36) = -16.61, p < .001$, jaw and neck, $t(36) = -21.19, p < .001$, the arm, $t(36) = -25.45, p < .001$, and the midriff, $t(36) = 20.51, p < .001$. The nipples and areolae were looked at significantly more often than the jaw and neck, $t(36) = 3.18, p < .01$, the midriff, $t(36) = 2.83, p < .01$, and arms, $t(36) = 6.55, p < .001$. Fixations were greater on the midriff of images with lightly-pigmented areolae compared to images with medium, $t(36) = -2.70, p < .01$, and darkly-pigmented areolae, $t(36) = -2.74, p < .001$ (Fig. 5).

Dwell Times

For dwell times, a 3 (Areola Pigmentation) x 5 (Body Region) repeated measures ANOVA yielded a significant Areola pigmentation x Body Region interaction $F(8, 288) = 4.80, p < .001$. These interactions reflect that the breast region was looked at for significantly longer than the areolae and nipples, $t(36) = 13.02, p < .001$, neck and jaw, $t(36) = 21.70, p < .001$, the arm, $t(36) = 26.88, p < .001$, and the midriff, $t(36) = 23.98, p < .001$. The nipples and areolae were looked at for significantly longer than the jaw and neck, $t(36) = 3.39, p < .01$, the midriff, $t(36) = 3.06, p < .01$, and arms, $t(36) = 5.50, p < .001$. When men looked at images with darkly-pigmented areolae, dwell times were significantly longer on the breast region compared to images with medium, $t(36) = 2.98, p < .01$ and lightly-pigmented areolae, $t(36) = 3.48, p < .001$ (Fig. 5).

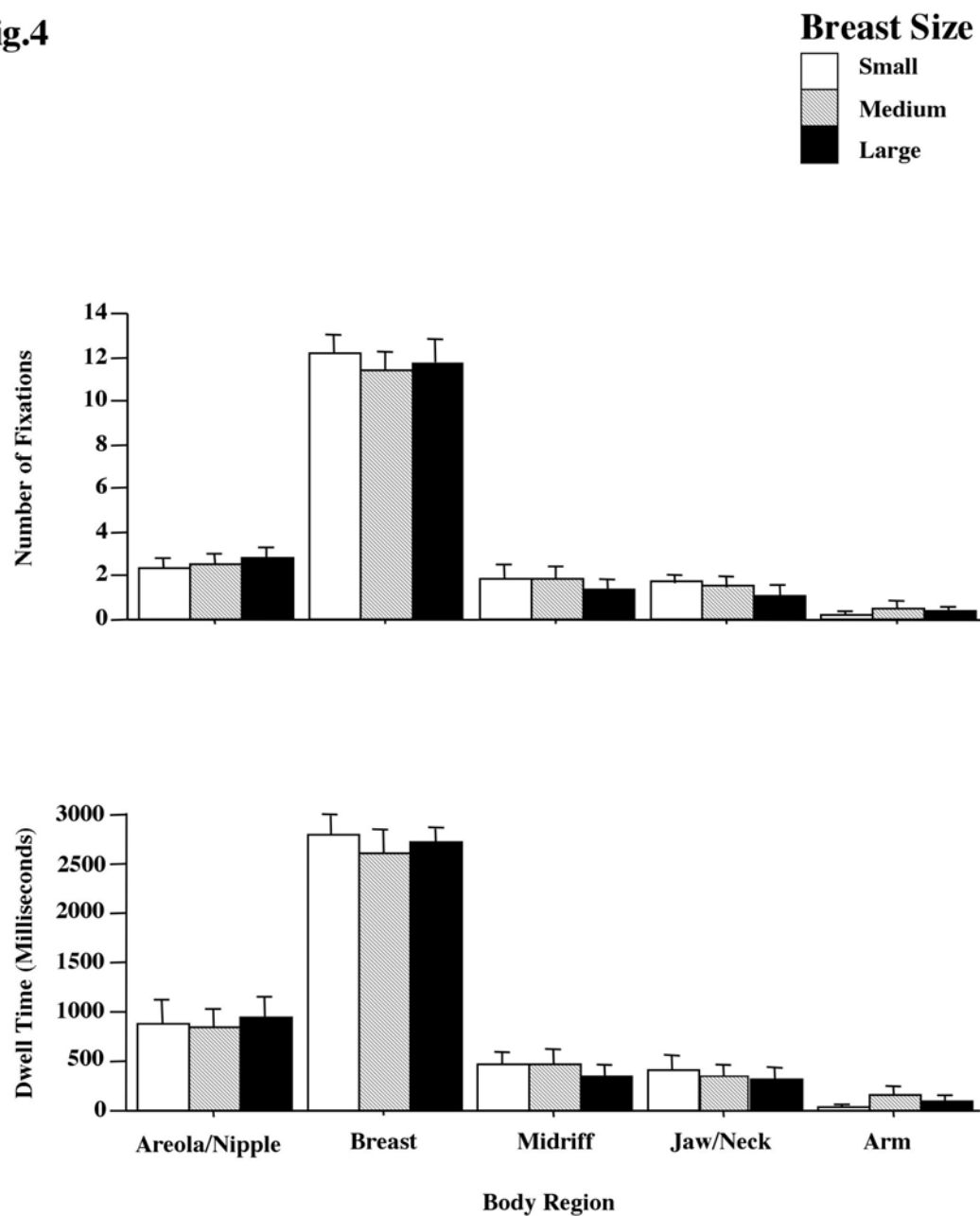
Fig.4

Fig. 4 Data are the means (+SD) of numbers of fixations (upper panel) and dwell times (lower panel) on the various body regions for the three images varying in breast size (small, medium, or large).

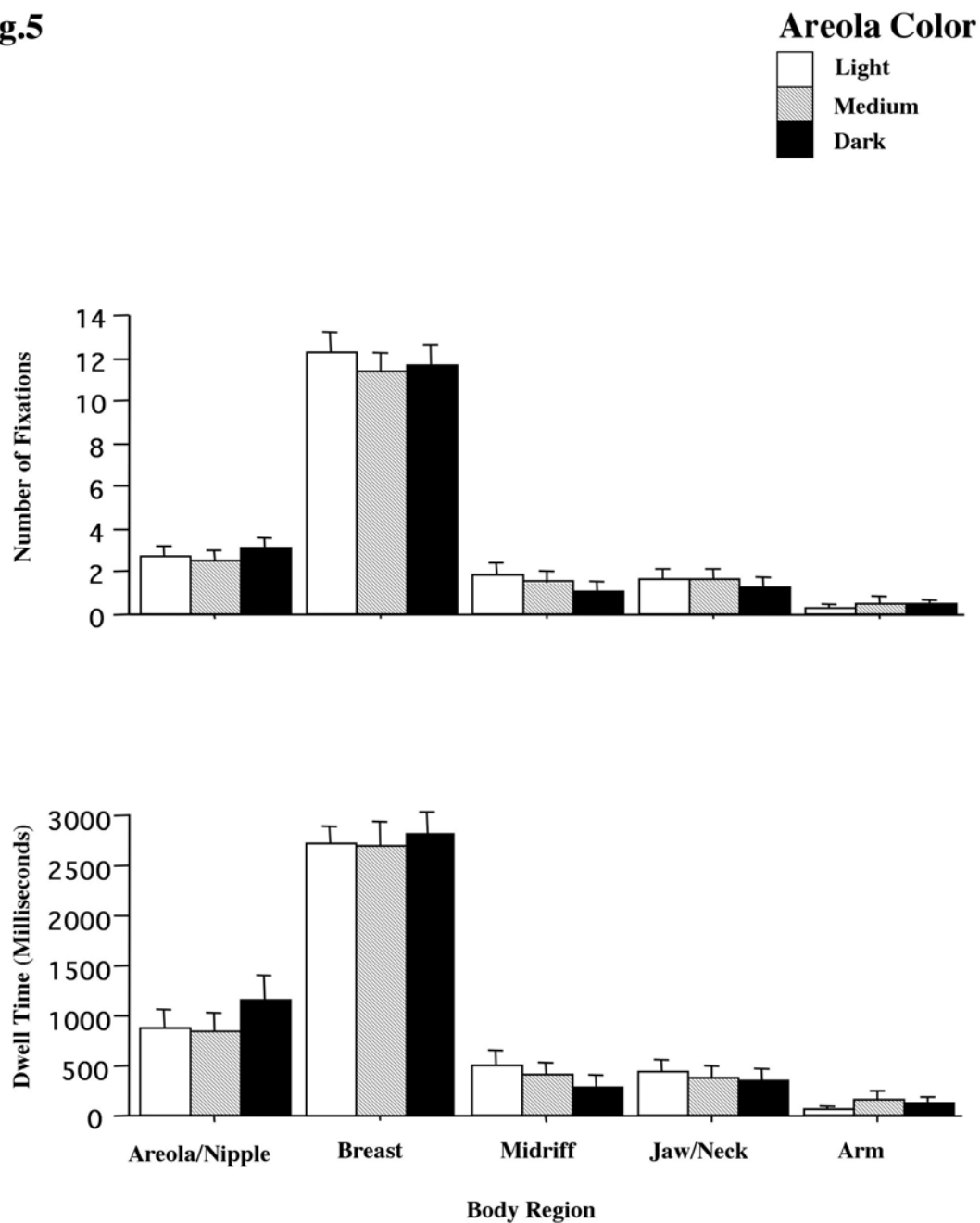
Fig.5

Fig. 5 Data are the means (+SD) of numbers of fixations (upper panel) and dwell times (lower panel) on the various body regions for the three images varying in areola pigmentation (light, medium, or dark).

DISCUSSION

The eye-tracking results reported here show that men attend to the overall shape of the breasts and also to the morphology of the areolae and nipples when making attractiveness judgments. Medium and large-sized breasts were rated as more attractive than small breasts. Medium and darkly-pigmented areolae were more attractive than lightly pigmented areolae. However, patterns of eye movements did not differ based on breast size or areolar pigmentation. These findings do not support hypotheses that visual attention on morphology should be correlated with attractiveness judgments.

Our first hypothesis that large breasts should be the focus of male attention and the most sexually attractive compared to smaller breasts was not supported. While medium and large breasts were rated as significantly more attractive than smaller breasts, frequencies of men's visual fixations, and dwell times were highest for the breast area, irrespective of overall breast size. However, this finding should be evaluated in the light of previous research on eye-tracking and breast size. Thus, in previous work (Dixson et al., 2009) using full-length images of women, there was no significant effect for breast size on male ratings of female attractiveness. These differing results may be due to the use of images of oblique-posed female torsos in the current study. Men may be more discerning in their preference for female breast size when viewing torsos because breast morphology is more prominently displayed than is the case when viewing full-length images of the female body. Numbers of fixations and dwell times were greater on the head and neck and breast region of images with small breasts compared to images with medium and large breasts. This may reflect an aversion to the breast region of the image that was judged to be less attractive. After their eye-tracking sessions, several participants

commented that images depicting smaller breasts appeared more immature. Marlowe (1998) has suggested that firmer and fuller breasts are more attractive to men because they signal sexual maturity. Thus, male preferences for medium and larger breasts in the current study might have been influenced by their more adult and sexually mature appearance.

Areola pigmentation was also a significant determinant of female sexual attractiveness in the current study. However, our second hypothesis concerning putative preferences for lighter areola pigmentation, such as occurs in young adulthood, was not upheld. Medium and darkly-pigmented areolae were rated as significantly more attractive than lightly pigmented areolae. The pigmentation of the areolae in women is lightest at the onset of menarche, and darkens somewhat with age, after repeated ovulatory cycles, pregnancies and lactation (Garn & French, 1963; Garn et al., 1956; Montagna & Macpherson, 1974; Muzaffar et al., 1998; Pawson & Petrakis, 1975). Grammer et al. (2001) have suggested that lighter pigmentation may be attractive to men as a signal of nubility in a potential female partner. However, that hypothesis was not supported in the current study. It is important to note that, irrespective of attractiveness judgments or degree of areolar pigmentation, men directed their first visual fixations most frequently to the areolae and nipples. As these are morphologically prominent traits at the center of the breast, it may be that attention is rapidly drawn to this feature as a passive response. As with effects of breast size discussed above, it is possible that male preferences for darker areolae were due to their significance as visual signals of female sexual maturity. Lighter areolae, by contrast, may be indicative of adolescence and of hormonal changes occurring during the period of adolescent sterility.

Studies of human physique and sexual attractiveness most often employ questionnaire surveys containing images, which are then rated by participants. The presumption is that participants will attend to the morphological cues that drive the attractiveness judgment. Eye-tracking can provide behavioral data on attention. The prediction is that those morphological cues that drive an attractiveness judgment will be the focus of attention during eye-tracking experiments. Indeed, attractiveness in women appears to capture male attention (Maner et al., 2007) and men bias their attention towards more attractive female faces (Fink et al., 2008; Maner et al., 2008; Shimojo et al., 2003). Given the relationship between attentional capture and facial attractiveness, attention and attractiveness may be correlated as men view other traits indicative of female health and fecundity such as female waist-to-hip ratio (WHR) and breast morphology.

In studies using full body images, men look at the breasts most frequently, but the breasts are not necessarily the principle determinants of female attractiveness, as WHR is crucial in this context (Dixson et al., 2009). A recent eye-tracking study has found that men do not attend to the same morphological cues when judging female waist-to-hip ratio as when they judge female attractiveness (Cornelissen et al., 2009). While the findings of the current study show male preferences for medium and large breasts, as well as darkly-pigmented areolae, behavioral measures of attention did not differ significantly based on breast size or areolae pigmentation. Eye-tracking studies have shown that novel, unique, attractive and unattractive traits capture attention (Sütterlin et al., 2008). Thus, it is interesting that such a disconnection in attention and attractiveness judgments occurred even when employing as stimuli a female torso, which one might argue displays the

experimentally manipulated trait quite obviously. It may be that the assumption that eye-tracking provides some implicit and bias-free measure of attractiveness is too simplistic. However, participants may be more attentive to the features they find more or less attractive when viewing pairs of stimulus images, as this would allow for a visual comparison. Future studies using paired images should investigate this question.

The current study has further implications for future research on human physique and sexual attractiveness using eye-tracking techniques. A challenge in any study of human morphology and mate preference is to isolate a variable and test its role in mate choice. However, this method has its drawbacks. For example, if one attempted to model the appearance of female breasts in regard to age or reproductive status (i.e. adolescent, adult, lactating) it would be necessary to alter multiple associated traits such as skin tone and body fat as well. This is because changes in breast morphology with reproductive status do not occur in isolation from other traits indicative of the ageing process. Various authors have stressed the possible importance of changes in breast morphology with age and reproductive status for male judgments of female attractiveness (Gallup, 1982; Marlowe, 1998; Symons, 1995). However, relatively few studies have been conducted to test these ideas and future work should aim to collect quantitative data on how men assess these aspects of female breast morphology.

Some authors have criticized the use of computer-generated stimuli and suggest that the use of sexually explicit stimuli is more ecologically valid when conducting studies investigating the possible effects of sexual selection on the evolution of human morphology (Voracek & Fisher, 2006, 2009). However, eye-tracking studies have shown that erotic pictures depicting female nudes with direct gaze illicit a startle effect in men

(as measured by the magnitude of eye blinks), the face then becomes the focus of attention, and the body receives less attention (Lass-Hennemann, Schulz, Nees, Blumenthal, & Schachinger, 2009). While other eye-tracking studies have confirmed the importance of the female body as a region that captures male attention in both erotic and non-erotic scenes (Lykins et al., 2006; Lykins et al., 2008; Rupp & Wallen, 2007; Tsujimura, Miyagawa, Takada, Matsuoko, Takao, Hirai, Matsushita, Nonomura, & Okuyama, 2009) these scenes are complex and may not allow for fine-grained analyses of attention on specific morphological traits. We suggest that, if the goal of the study is to test for attentional capture on traits that may be under sexual selection, a reasonable starting point is the use of stimuli in which the anatomical features can be standardized.

On a final note, it will be important in future to conduct cross-cultural studies concerning effects of breast size and areola pigmentation upon men's judgments of female attractiveness. Cross-cultural studies have shown discordance in male preference for female breast size. For example, Brazilian men prefer small breasts and large buttocks, whereas men from the U.S.A and Russia prefer large breasts and smaller buttocks in women (Jones, 1996). The current eye-tracking study included only men of European descent, living in New Zealand. Clearly men in other cultures may differ in their eye-tracking responses and attractiveness judgments. Thus for the moment it would be unwise to draw firm conclusions about human preferences for female breast morphology, as distinct from preferences within a single culture.

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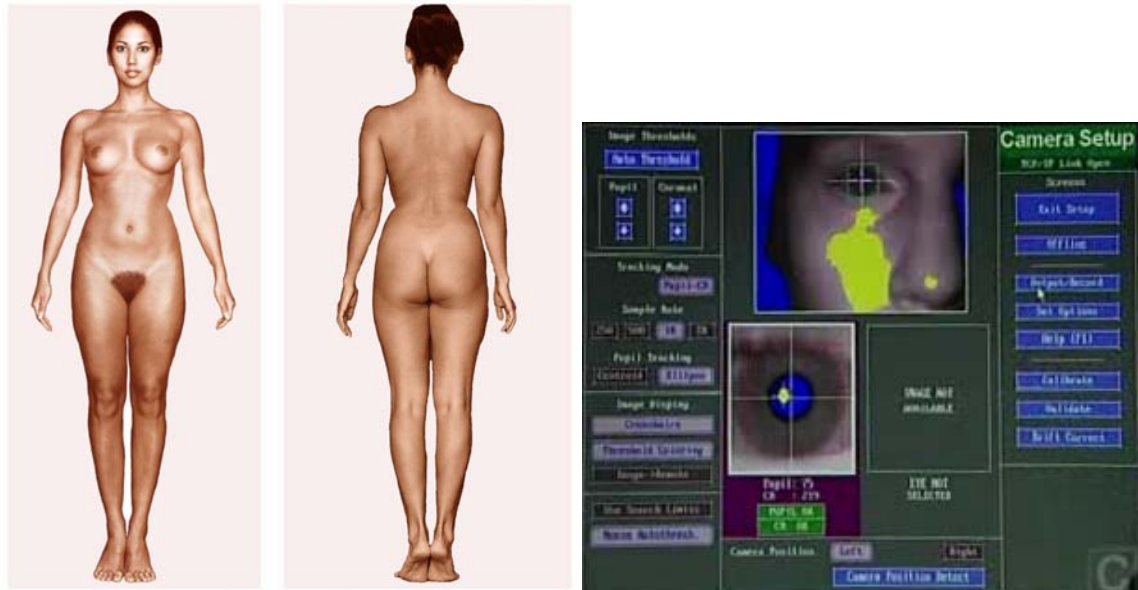
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Chapter Eight

Watching the Hourglass: Eye-Tracking Reveals Men's Appreciation of the Female Form.



Authors note: Chapter Eight is written in the style of the journal *Human Nature* where it was submitted on December 15, 2009, as the manuscript:

Dixon, B. J., Grimshaw, G., Linklater, L. W., & Dixon, A. F. Watching the Hourglass: Eye-Tracking Reveals Men's Appreciation of the Female Form. (Under Review). *Human Nature*.

The chapter is a modified version of this manuscript, adapted to the thesis.

ABSTRACT

Eye-tracking techniques were used to measure men's attention to back-posed and front-posed images of naked women. Irrespective of body-pose, men rated images having a 0.7 waist-to-hip ratio (WHR) as most attractive. For back-posed images, initial visual fixations (occurring within 200 milliseconds of commencement of the eye-tracking session) most frequently involved the midriff. Numbers of fixations and dwell times throughout each of the five-second viewing sessions were greatest for the midriff and buttocks. By contrast, visual attention to front-posed images (first fixations, numbers of fixations and dwell times) mainly involved the breasts, with attention shifting more to the midriff of images with a higher WHR. This report is the first to compare men's eye-tracking responses to back-posed and front-posed images of the female body. Results show the importance of the female midriff and of WHR upon men's attractiveness judgments, especially when viewing images in back-pose.

Keywords Attractiveness; Waist-to-hip ratio; Eye-tracking; Buttocks; Breasts; Sexual Selection.

INTRODUCTION

Human sexual attractiveness is often described as unique, complex, and thus exceedingly difficult to quantify. However, men and women across cultures state that physical attractiveness is an important trait in a potential partner (Buss 1989).

Morphological traits may be, by their very nature, more accessible to measurement than some other qualities of sexual attractiveness such as charm or sense of humor.

Morphology that conveys biological information relating to health and fertility may be of particular importance when people select their sexual partners (Grammer et al. 2003).

These processes of mate choice may be very ancient, and represent the effects of selection on cognitive processes within ancestral human populations (Buss 2003).

In comparison to nonhuman primates, female humans have much larger stores of body fat in their breasts, hips, thighs, and buttocks (Dufour and Slather 2002). Body composition is sexually dimorphic. Men tend to have a more mesomorphic muscular physique, whereas women have larger stores of body fat (Carter and Heath, 1990; Clarys et al. 1984; Wells 2007). Sexual dimorphism in body composition is reflected in sex differences in body shape. At puberty, under the actions of estrogens, female body fat is stored around the hips, thighs, buttocks (gluteal/femoral region) and breasts (Björntorp 1997). The distribution of body fat can be measured using the waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist by the distance around the hips including the buttocks. A low WHR is correlated with earlier onset of menarche in girls (Lassek and Gaulin 2007), and maintenance of regular menstrual cycles (Van Hooff et al. 2000) and ovulatory cycles in women (Moran et al. 1999). Women with low WHRs and large breasts have higher levels of circulating estrogen and progesterone (Jasienska et

al. 2004), and these hormones, in turn, are associated with higher rates of conception (Lipson and Ellison 1996). In studies conducted in fertility clinics, women with lower WHRs had the greatest success rates in artificial insemination (Zaadstra et al. 1993) and in in-vitro fertilization programs (Wass et al. 1997). Women's WHRs increase as they age, possibly due to reduction in estrogen production (Kirschner and Samojlik 1991; Wells 2007).

Sexual selection, via mate choice, may have favored the evolution of a low WHR in women as a signal of sexual maturity, health, and fecundity (Singh 1993). Numerous questionnaire studies have found that, in industrialized societies, stimulus images of women with low WHRs (0.6-0.7) are most attractive to men (in China: Dixson et al. 2007a; Germany: Henss 2000; UK: Furnham et al. 1997, Poland: Rozmus-Wrzesinska and Pawlowski 2005; New Zealand and U.S.A: Dixson et al. 2010a). However, there is some cross-cultural discordance in male preferences for female WHR. Matsigenka men in Peru rate higher WHRs (0.9) as most attractive in women (Yu and Shepard 1998). Men from Bakossiland in Cameroon select as most attractive a female WHR of 0.8 (Dixson et al. 2007b), as do Shiwiari men of the Ecuadorian Amazon (Sugiyama 2004). Research among the Hadza hunter-gatherers of Tanzania has produced some important findings with regard WHR and female attractiveness. Initial studies, which employed front-posed female images as stimuli, showed that men preferred a WHR of 0.9 (Wetsman and Marlowe 1999). However, in a follow-up study that used stimulus images in profile-view so that the buttocks were visible, Hadza men preferred a female WHR of 0.6 (Marlowe et al. 2005). The study by Marlowe et al. (2005) highlights an important methodological issue in research on female physique and sexual attractiveness. Studies of male

preference for female WHR most often use stimuli in which images of women are presented in front-pose only. It is important to consider that WHR is calculated by measuring not only the circumference of the body at the waist and hips, but also the buttocks. Therefore it may be that men's attractiveness judgments are affected by the body-pose of the female stimulus images, as they judge the waist region relative to the buttocks and breasts.

Eye-tracking techniques can provide data on attention to morphological traits when participants are making attractiveness judgments. Infants look for longer at the faces of attractive adults (Langlois et al. 1987). In adults, eye-tracking research has shown that men look more often and for longer at the faces of attractive women compared to faces they judge to be less attractive (Fink et al. 2008; Maner et al. 2008) and at the female body when viewing both erotic and non-erotic heterosexual scenes (Lykins et al. 2006; Lykins et al. 2008; Rupp and Wallen 2007). When viewing clothed full body images, men initially fixate on the women's faces, followed by long fixations on the breasts (Hewig et al. 2008). Similarly, the breasts in particular are the focus of attention when men are asked to judge the attractiveness of front-posed images of women wearing dresses, bathing suits, and underwear (Cornelissen et al. 2009; Suschinsky et al. 2007). In a recent eye-tracking study, in which men looked at nude full-length images of women that had been altered to show small, medium or large breasts, and either a WHR of 0.7 or 0.9, it was found that male attention was directed most often at the breasts. Initial visual fixations, occurring during the first 200 milliseconds of an eye-tracking session, most often involved either the female midriff, or the breasts (Dixon et al. 2009).

These eye-tracking studies have consistently shown that female breasts capture male attention when they are asked to make judgments of female physical attractiveness. However, the few studies conducted to date have presented participants with images in front-pose only. Male visual attention may show significant differences when viewing back-posed female images, as the lower body and buttocks are displayed prominently rather than the breasts. As such, we hypothesize that the female midriff region will receive greater visual attention from men when images are presented in back-view as compared to in front-view, but that low WHRs should still be judged as most attractive. To test this, men were presented with three front-posed images varying in WHR (0.7, 0.8 and 0.9). Images of the same woman were presented from a back-view showing the same range of WHRs. We measured the initial fixation, number of fixations and dwell times for six body regions during 5 second eye-tracking sessions. Men also rated the six images for sexual attractiveness.

METHOD

Participants

Thirty heterosexual men of European descent, ranging in age from 25-44 years ($M = 27.42$ years; $SD = 4.99$), 10 of whom were married, were recruited opportunistically from the staff and post-graduate student body at Victoria University. Participants were given individual verbal orientation before the start of data collection and allowed some time to familiarize themselves with the room and eye-tracking machine. The details of the study were not discussed with participants beforehand. However, when each participant had completed the experiments, they were provided with written details of the rationale for the research. Each participant was told of their right to withdraw from the study

without prejudice. All participants had normal vision or correction by contact lenses.

None wore glasses. The project was pre-approved by the Human Ethics Committee of the School of Psychology at Victoria University.

Apparatus and materials

A photograph of a naked woman, taken from front and back-views, was scanned from Simblet (2001). WHR was manipulated in this image using Photoshop Version 7.0 by narrowing or widening the waist to construct three levels of WHR (0.7, 0.8, 0.9) for the image in front-view and in back-view. Thus, six images were constructed in total. The experiment was programmed using SR Research Experiment Builder (version 1.4.128 RC) and conducted on a 3-GHz Pentium D computer. Stimuli were presented on a 21-inch monitor at a resolution of 1024 x 768 pixels and with a refresh rate of 60 Hz.

Procedure

Participants were seated in a comfortable chair in a quiet room facing the monitor at eye level at a viewing distance of 57 cm, maintained by a forehead and chin-rest. They underwent eye-tracking trials in which each image was presented individually, in random order on the computer screen for five seconds.

Attractiveness measurement

At the end of each presentation, participants were instructed to rate the image for attractiveness using a keyboard with a six point Likert scale in which 1 = unattractive, 2 = slightly attractive, 3 = moderately attractive, 4 = attractive, 5 = very attractive, and 6 = extremely attractive.

Eye-tracking

Using the EyeLink® 1000 Tower Mount Head Supported System (SR Research Ltd., Ontario, Canada), eye position and eye movements were determined by measuring the corneal reflection and dark pupil with a video-based infrared camera and an infrared reflective mirror. The eye tracker had a spatial resolution of 0.01° of visual angle and the signal was sampled and stored at a rate of 1000 Hz. While viewing was binocular, recording was monocular, measuring right eye movements only as this is a standard procedure in eye-tracking studies (e.g. Lykins et al. 2008). Calibration and validation of measurements were performed before each experimental session.

The front-posed stimulus image was divided into six anatomical regions for subsequent analysis of eye-tracking data (Fig. 1). The six regions were defined as follows: (1) the face and neck, from the top of the head to the level of the clavicle; (2) breasts, from the top of the clavicle to the posterior border of each breast; (3) midriff, including the waist; beginning from the below the breasts to the widest part of the hips; (4) pubic triangle, as defined by the limits of the pubic hair; (5) the thighs, the upper portion of the leg ending at the knee and (6) lower legs and feet. The arms were not included in the analyses as they received so little visual attention. The back-posed image was also divided into six anatomical regions, defined as follows: (1) the head and neck, from the top of the head to the base of the neck; (2) the back, from the bottom of the neck to the waist; (3) midriff, including the waist; beginning from the waist to the widest part of the hips; (4) the buttocks, from the bottom of the waist to below the buttocks; (5) the thighs, the upper portion of the leg ending at the knee and (6) lower legs and feet.

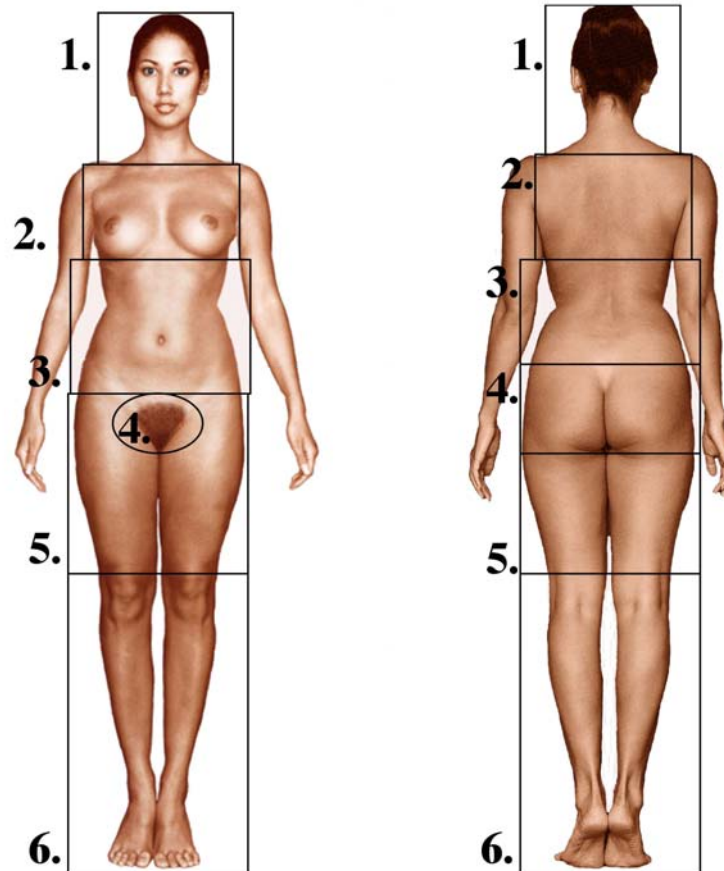
Fig 1.

Fig. 1 Female images were divided into 5 anatomical regions in order to analyze male visual attention during eye tracking. Front-posed image: 1 = head; 2 = breasts; 3 = midriff; 4 = pubis; 5 = thighs; 6 = lower legs and feet. Back-posed image: 1 = head; 2 = upper-back; 3 = midriff; 4 = buttocks; 5 = thighs; 6 = lower legs and feet.

In each of the six regions, three dependent variables of eye movement were measured: first fixation, number of fixations, and amount of time spent (dwell time) examining the area. The first region of the body to be examined, from 200 milliseconds

after the start of the test, was defined as the first fixation. The lag time of 200 milliseconds was allowed in order to give sufficient time for the eye to move from its initial fixation point in the center of the screen. Each time the eye moved, the eye-tracker recorded a new fixation. The number of fixations and duration of fixations made on each the six regions were summed during the analysis.

RESULTS

Attractiveness

A 2 (Body Pose: Front-Posed, Back-Posed) x 3 (WHR: 0.7, 0.8, 0.9) repeated measures ANOVA yielded a significant main effect for WHR on attractiveness ratings, ($F_{2,58} = 36.01, p < .001, \eta_p^2 = .554$). Images with 0.7 WHRs were significantly more attractive than images with 0.8 WHRs ($t = 2.90, df = 29, p = .007$) and 0.9 WHRs ($t = 7.02, df = 29, p < .001$) (Fig 2). Images with 0.8 WHRs were significantly more attractive than images with 0.9 WHRs ($t = 6.10, df = 29, p < .001$). The effect of Body Pose was almost significant ($F_{1,29} = 4.08, p = .053, \eta_p^2 = .123$), which reflects a trend toward images in front view ($M = 3.71, SD = 0.60$) being judged as more attractive than images in back view ($M = 3.49, SD = 0.74$). There was also a significant Body Pose x WHR interaction ($F_{2,58} = 7.34, p < .001, \eta_p^2 = .211$), which was due to back-posed 0.9 WHR image receiving significantly higher ratings of attractiveness than the front-posed 0.9 WHR ($t = 3.52, df = 29, p < .001$).

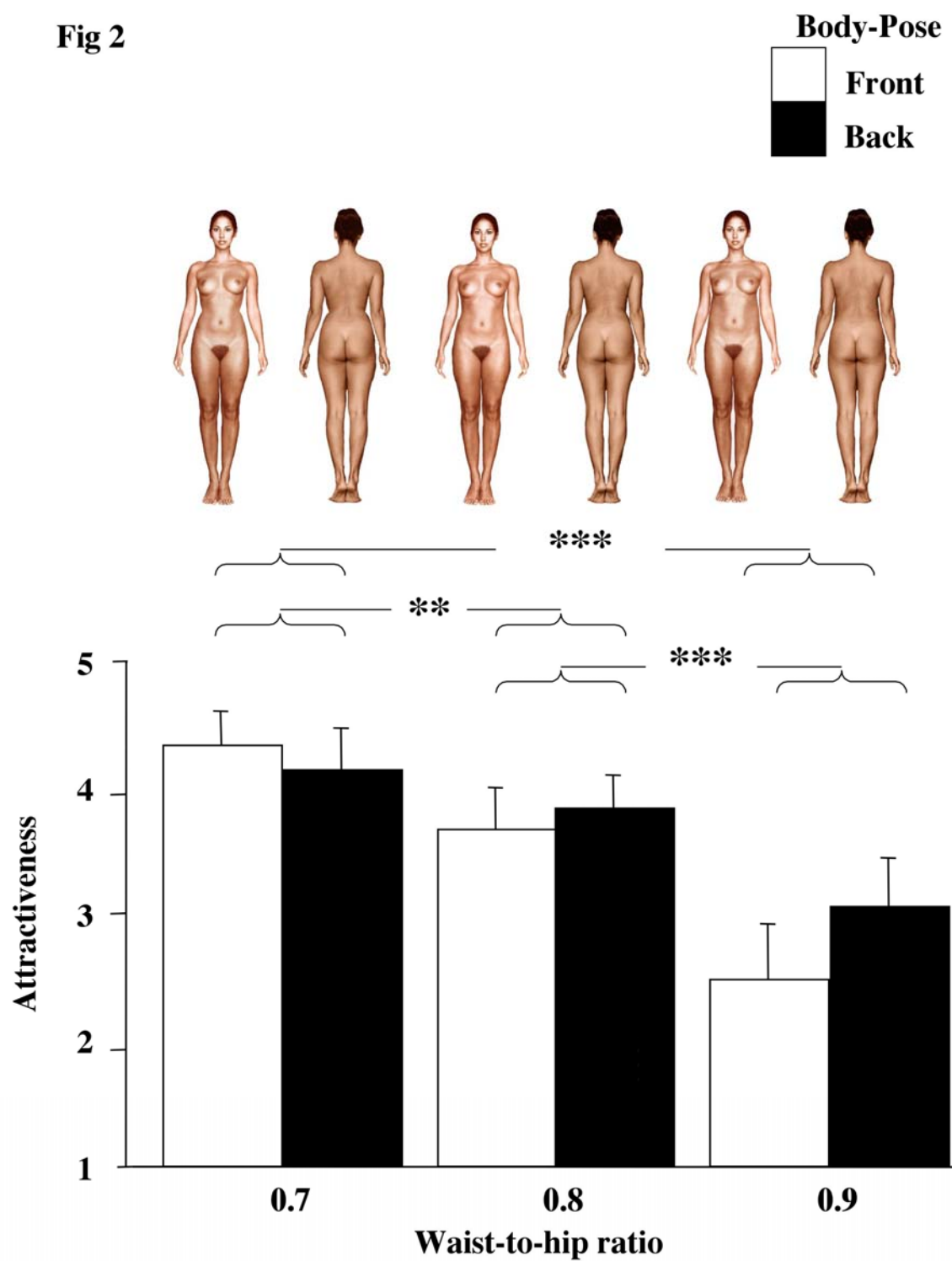
Fig 2

Fig. 2 Mean ratings (+S.E) for sexual attractiveness of 6 female images varying in WHR (0.7, 0.8 or 0.9) and body-pose (front and back). ** $p < .01$, *** $p < .001$.

Eye-tracking

First Fixation

When viewing front-posed images, the breasts received the highest number of first fixations for the image with a 0.7 WHR. The midriff received the highest number of first fixations for the image with a 0.8 WHR. When viewing the 0.9 WHR, the breasts and midriff received the majority of men's first fixations. When men looked at back-posed images, the midriff received more first fixations irrespective of WHR (Table 1).

Table 1. Number of men ($N = 30$) who made their first visual fixations on each of the five body regions. Data are shown for all six female images (3 in front-view; 3 in back-view).

Images in front-view

WHR	Head	Breasts	Midriff	Pubis	Thighs
0.7	5 (16.6%)	14 (46.6%)	7 (23.3%)	3 (10.0%)	1 (3.3%)
0.8	0 (0%)	7 (23.3%)	18 (60.0%)	2 (6.6%)	3 (7.0%)
0.9	2 (6.6%)	12 (40.0%)	13 (43.3%)	2 (6.6%)	1 (3.3%)

Images in back-view

WHR	Head	Upper back	Midriff	Buttocks	Thighs
0.7	3 (7.0%)	7 (23.3%)	13 (43.3%)	7 (23.3%)	0 (0%)
0.8	1 (3.3%)	7 (23.3%)	16 (53.3%)	6 (20.0%)	0 (0%)
0.9	0 (0%)	5 (16.6%)	15 (50.0%)	10 (33.3%)	2 (6.6%)

Number of Fixations

For number of fixations a 2 (Body Pose) x 3 (WHR) x 6 (Body Region) x 5 (Time: Seconds 1-5) repeated measures ANOVA yielded a significant main effect of time ($F_{4, 116} = 49.78, p < .001, \eta_p^2 = .632$), Body Region and Time ($F_{20, 580} = 6.75, p < .001, \eta_p^2 = .189$) and a significant three-way interaction between WHR, Body Region and Time ($F_{40, 1160} = 1.92, p < .001, \eta_p^2 = .062$). These interactions reflect that men fixated more often on the midriff of images with 0.8 and 0.9 WHRs than 0.7 WHRs during the first second of eye-tracking. There were no interaction between Time and Body Pose ($F_{4, 116} = .67, p = .614, \eta_p^2 = .023$) or Time and WHR ($F_{8, 232} = 1.43, p = .183, \eta_p^2 = .047$).

There were also no three-way interactions between Body Pose, WHR and Time

interaction ($F_{8, 232} = .151, p = .865, \eta_p^2 = .017$) or Body Pose, Body Region and Time ($F_{20, 580} = .1.55, p = .059, \eta_p^2 = .051$).

Table 2. Mean numbers of visual fixations \pm standard deviations, for each of the six body regions over the five seconds of the eye-tracking experiments. Data are shown for all six female images (3 in front-view; 3 in back-view).

Images in front-view						
WHR	Head	Breasts	Midriff	Pubis	Thighs	Legs/Feet
0.7	3.63 \pm	4.80 \pm	2.43 \pm	1.73 \pm	1.60 \pm	0.97 \pm
	2.68	2.34	1.48	1.41	1.54	1.03
0.8	3.37 \pm	5.57 \pm	3.23 \pm	2.07 \pm	1.73 \pm	0.53 \pm
	2.27	2.40	1.85	1.44	1.53	1.07
0.9	2.13 \pm	4.63 \pm	4.80 \pm	2.20 \pm	1.43 \pm	0.40 \pm
	1.19	1.19	2.12	1.27	1.57	0.85
Images in back-view						
WHR	Head	Upper back	Midriff	Buttocks	Thighs	Legs/Feet
0.7	1.17 \pm	2.07 \pm	3.77 \pm	4.80 \pm	0.87 \pm	0.90 \pm
	1.70	1.28	1.75	1.51	0.82	1.21
0.8	0.83 \pm	1.97 \pm	5.40 \pm	4.83 \pm	0.43 \pm	0.37 \pm
	1.02	1.45	2.01	1.84	0.68	0.67
0.9	0.87 \pm	1.67 \pm	4.70 \pm	4.53 \pm	0.70 \pm	1.07 \pm
	1.04	1.18	2.56	1.70	0.79	1.39

The ANOVA also yielded a significant Body Pose x Body Region interaction, ($F_{5, 145} = 65.49, p = .001, \eta_p^2 = .693$), and a WHR x Body Region interaction, ($F_{10, 290} = 6.25, p = .001, \eta_p^2 = .177$). These two-way interactions were qualified by a three-way interaction between Body Pose, Body Region and WHR ($F_{10, 290} = 4.05, p = .001, \eta_p^2 = .123$). Men directed more fixations towards the upper-body (head, breasts and midriff) than the lower body (pubis, thighs and lower legs) when viewing front-posed images. When looking at images in back-pose, the buttocks and midriff received more fixations (Table 2).

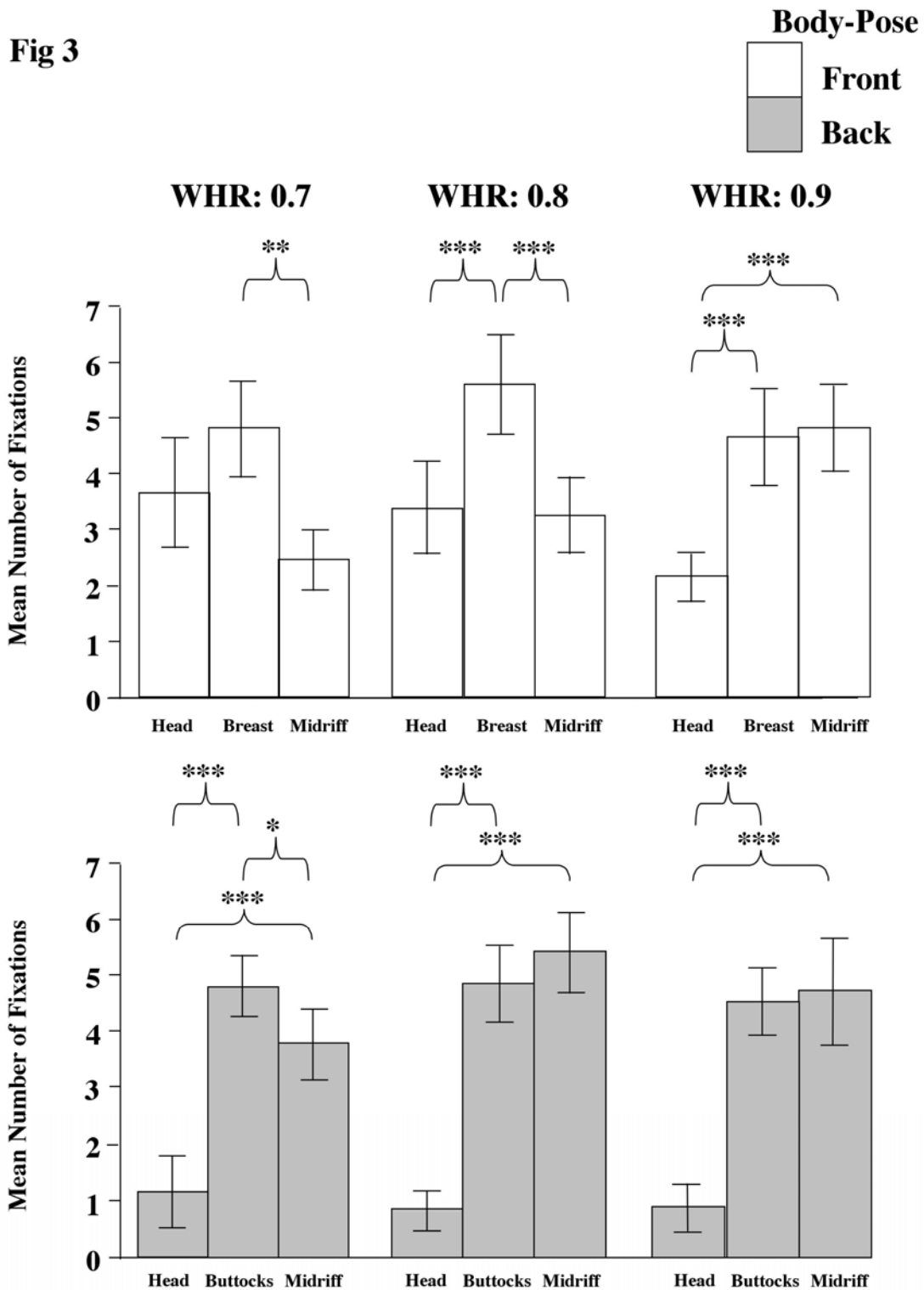


Fig. 3 Mean dwell times (\pm S.E.) made on the head, breasts and midriff of front-posed images (upper histograms) and the head, buttocks and midriff of back posed images (lower histograms). Symbols indicate the level of statistical significance from paired t-tests between the different body regions. * $p < .05$, ** $p < .01$, *** $p < .001$.

As represented in Figure 3, the interactions between Body Pose, Body Region and WHR uncovered in the ANOVA reflect that when men were looking at images with 0.7 and 0.8 WHRs in front pose, they looked more often at the breasts than the waist. However, when looking at front-posed images with a 0.9 WHR, men spent as much time looking at the midriff as the breasts. Similarly, when viewing back-posed images, number of fixations on the midriff increased as men viewed images with higher WHRs.

Dwell Times

For dwell times a 2 (Body Pose) x 3 (WHR) x 6 (Body Region) x 5 (Time: Seconds 1-5) repeated measures ANOVA yielded a significant main effect of Time ($F_{4, 116} = 13.14, p < .001, \eta_p^2 = .312$), Time and WHR ($F_{8, 232} = 2.16, p = .032, \eta_p^2 = .069$) and Time and Body Region ($F_{20, 580} = 1.67, p = .033, \eta_p^2 = .055$). There was also a trend toward a three-way interaction between Time, Body Region and WHR ($F_{40, 1160} = 1.37, p = .064, \eta_p^2 = .045$). These interactions reflect that when men looked at images with 0.8 and 0.9 WHRs they looked for longer at the midriff during the first second of eye-tracking than when they viewed images with 0.7 WHRs. There were no significant interactions between Time and Body Pose ($F_{4, 116} = .648, p = .630, \eta_p^2 = .022$), or three-way interactions between Body Pose, WHR and Time ($F_{8, 232} = 1.44, p = .182, \eta_p^2 = .047$) or Body Pose, Body Region and Time ($F_{20, 580} = 672, p = .855, \eta_p^2 = .023$).

The ANOVA also yielded a significant Body Pose x Body Region interaction, ($F_{5, 145} = 56.75, p < .001, \eta_p^2 = .662$), and a WHR x Body Region interaction, ($F_{10, 290} = 4.36, p < .001, \eta_p^2 = .131$). These two-way interactions were qualified by a three-way interaction between Body Pose, Body Region and WHR ($F_{10, 290} = 2.48, p = .007, \eta_p^2 = .079$). When viewing images in front-pose, men's visual attention was directed more to

the upper body (head, breasts and midriff) than the lower body (pubis, thighs and lower legs). When looking at images in back-pose, men's attention was most often towards the midriff and buttocks (Table 3).

Table 3. Mean dwell times \pm standard deviations, for each of the six body regions over the five seconds of the eye-tracking experiments. Data are shown for all six female images (3 in front-view; 3 in back-view).

Images in front-view						
WHR	Head	Breasts	Midriff	Pubis	Thighs	Legs/Feet
0.7	952.30 \pm	1477.70 \pm	923.20 \pm	486.13 \pm	537.03 \pm	376.70 \pm
	737.38	725.58	634.16	500.65	576.55	374.13
0.8	961.53 \pm	1691.73 \pm	1118.53 \pm	386.20 \pm	460.60 \pm	172.63 \pm
	739.39	768.78	628.00	372.97	431.88	356.79
0.9	556.23 \pm	1530.57 \pm	1610.00 \pm	528.57 \pm	397.933 \pm	124.23 \pm
	313.48	739.40	774.67	452.04	413.33	263.13
Images in back-view						
WHR	Head	Upper back	Midriff	Buttocks	Thighs	Legs/Feet
0.7	381.20 \pm	665.47 \pm	1475.57 \pm	1502.57 \pm	349.37 \pm	342.27 \pm
	502.86	380.50	682.22	523.08	345.17	445.89
0.8	288.90 \pm	677.33 \pm	1936.17 \pm	1548.57 \pm	187.43 \pm	124.50 \pm
	347.88	471.54	720.10	675.04	364.43	216.66
0.9	247.40 \pm	699.10 \pm	1776.90 \pm	1407.17 \pm	273.23 \pm	344.20 \pm
	323.17	553.12	948.63	732.09	365.45	444.68

As can be seen in Figure 4, the interactions between Body Pose, Body Region and WHR revealed in the ANOVA reflect that when men were looking at images in front-view with 0.7 and 0.8 WHRs, the breasts were looked at for significantly longer than the head and midriff. However, when front-posed images with 0.9 WHRs were examined, men spent as much time looking at the breasts as the midriff. When looking at back-posed images the buttocks and midriff were looked at for longer than the head irrespective of WHR.

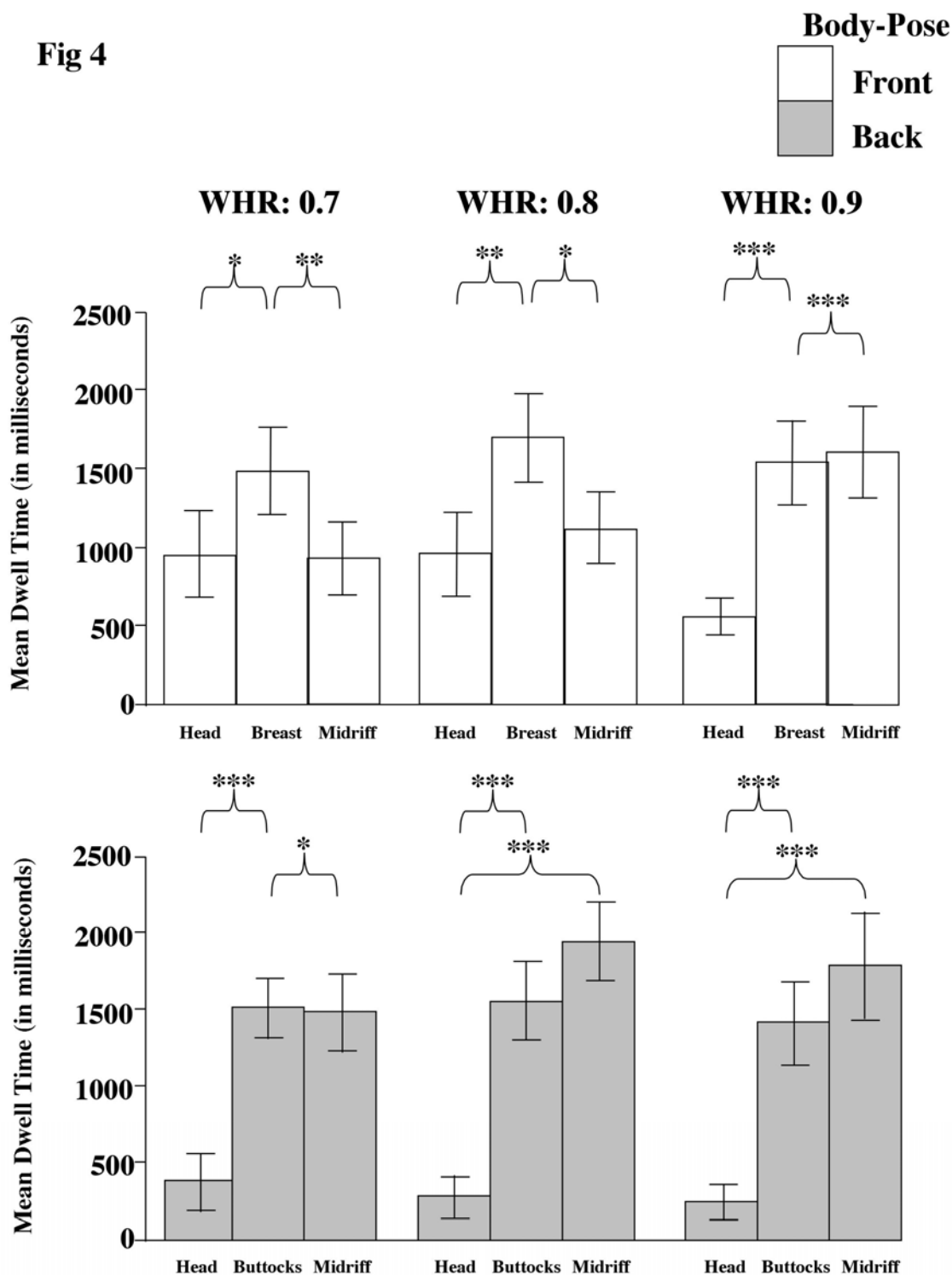


Fig. 4 Mean numbers of fixations (\pm S.E) made on the head, breasts and midriff of front-posed images (upper histograms) and the head, buttocks and midriff of back posed images (lower histograms). Symbols indicate the level of statistical significance from paired t-tests between the different body regions. * $p < .05$, ** $p < .01$, *** $p < .001$.

DISCUSSION

This study quantified eye-movements of men during attractiveness judgments of front and back-posed images of women varying in waist-to-hip ratio (WHR). Images with 0.7 WHRs were rated as most attractive, irrespective of body-pose. The initial fixation, occurring 200 milliseconds from the start of the eye-tracking experiment, most frequently involved the breasts for front-posed images with a 0.7 WHR, the midriff for 0.8 WHRs, while for 0.9 WHRs the first fixations fell most often on the breasts and midriff. For images in back-view, the midriff received the most first fixations for all WHRs. Over the full five seconds of the eye-tracking trials, men paid more attention to the midriff of images with 0.9 WHRs than images with 0.7 or 0.8 WHRs.

Previous eye-tracking studies, which have employed different methods to quantify attention on female WHR, did not reveal a relationship between eye movements towards the midriff and judgments of female attractiveness. Suschinsky et al. (2007) showed men three images (simultaneously) of the same clothed woman, computer-morphed to differ in WHR, and asked them to select the image they found most attractive. While men looked at the image with the lowest WHR more often and for longer than images with higher WHRs, and selected it as most attractive, relatively little attention was given to the midriff region. Cornelissen et al. (2009) presented men and women with images of individual women wearing bras and underwear and asked one group of participants to rate them for WHR, a second group to rate them for total body fat and a third group to rate them for attractiveness. Eye-movements when making attractiveness judgments were correlated with judgments of total body fat but not WHR, suggesting that the WHR region is of less importance than body fat when assessing female physical attractiveness.

Finally, Dixson et al. (2009a) showed that while the WHR was the primary determinant of male attractiveness ratings when judging full-length nude images, the midriff was not the main focus of their attention when they made attractiveness judgments. These studies indicate that there is discordance between male attention for traits that define female body shape and their subjective attractiveness ratings.

Attractiveness judgments involve complex processes in which a constellation of traits likely influences perceptions of physical beauty. The results of the current study suggest that in the case of female attractiveness and WHR, the midriff is, in fact, an important region that appears to be judged in relation to surrounding features such as the breasts and buttocks. In keeping with previous eye-tracking studies, the breasts were shown to capture the most male attention, particularly when the WHR is judged as more attractive. When the WHR is higher, male attention returns more frequently and remains for longer on the midriff than when looking at images with narrower waists. This suggests that men actively attend to those regions where female fat accumulation are greatest and achieve an appreciation of the 'hour-glass' shape. This process may occur very rapidly as men began to analyze the midriff within the first 200 ms of viewing. After this initial fixation the midriff is only more salient as a feature of attentional capture, relative to the head and breasts, if the WHR is higher. Singh (1993) hypothesized that female WHR represents a 'first pass filter' in male judgments of female attractiveness. Under this hypothesis, the WHR region is judged prior other traits as it represents an unambiguous signal of female gender, health, fertility and attractiveness (Singh 1993). The findings of the current study provide further support for Singh's hypothesis as men ultimately rated images with a low WHR of 0.7 as most attractive. Interestingly, when the

WHR is more attractive men are less reliant on the waist area to guide their behavioral and subjective judgments of female physical attractiveness than when viewing images with less attractive WHRs.

It is important to note that eye-movements are not implicit measures of perceived attractiveness. They are an index of attention and visual attention may depend very much on the motivation of the individual. For example, stimuli that are associated with fear and reward have been shown to capture attention (Castellanos et al. 2009; De Martino et al. 2009; Raymond and O'Brien 2009). In such circumstances attentional capture may be an active or endogenous process, so that participants control how they allocate attention in order to achieve a goal (Ruz and Lupiáñez 2002). Alternatively, attention may be passive or exogenous, whereby participants allocate their attention to stimuli without intention (Ruz and Lupiáñez 2002). There is some evidence that physical attractiveness actively captures attention. Shimojo et al. (2003) found that when judging the more attractive face among pairs of faces, participants' gaze was initially shared evenly between faces. However, as the experiment progressed, gaze was biased toward the face ultimately judged to be more attractive. Maner et al. (2007) found that attentional bias toward attractive female faces occurred within the first second of a visual cueing experiment and that participants showed reluctance to disengage from more attractive faces. However, that attractiveness is the primary motivation for such attentional capture may not be entirely accurate as novel, unique, attractive and unattractive traits have been shown to capture attention in eye-tracking studies (Sütterlin et al. 2008). In the current study, it is possible that the greater attention given to the midriff of the image depicting a 0.9 WHR was due to the use of computer-generated stimuli that resulted in a physical appearance

that was visually novel. Thus, attentional capture of the midriff for less attractive images may be an exogenous passive response to a novel or unique trait rather than an endogenous mechanism whereby participants are processing the features that make up an attractive female physique.

The use of computer-morphing to experimentally manipulate WHR may indeed be problematic as such techniques also alter the body mass index (BMI) (Tovée and Cornallisen 2001). BMI is calculated as weight in kilograms divided by (height in meters X height in meters). In a series of cross-cultural studies, differences in women's BMI were found to exert a greater influence than WHR on male ratings of female attractiveness in Japan (Swami et al. 2006), Malaysia (Swami and Tovée 2005) and Zululand in South Africa (Tovée et al. 2006). These authors question the validity of the WHR hypothesis based on the findings in these studies. However, WHR and BMI are positively correlated and as such it is very difficult to test the individual contribution made by each of these traits to men's judgments of female attractiveness. A recently developed procedure called micrograft surgery may provide such an opportunity, as in this procedure adipose tissue is harvested from the waist and used to re-shape the buttocks of female patients, which reduces WHR without altering BMI (Singh and Randall 2007). It has been shown that men in a wide variety of cultures select as most attractive post-operative images of women (Dixson et al. 2010b, 2010c; Singh et al. in press). Recently, Platek and Singh (2010) used fMRI scanning to measure men's neurological responses to images of women who had undergone micrograft surgery. They found that the right and left orbital frontal cortex (OFC) showed activation and that such activation was significantly greater when viewing post-operative, as compared to pre-

operative images. This research shows that responses to WHR are measurable at a central level in an area of the brain that is concerned with reward.

The application of eye-tracking technology in studies of sexual selection and the evolution of human physical attractiveness is relatively new. The current study confirms the importance of female WHR in male judgments of attractiveness and provides preliminary evidence that men's behavioral responses are mediated, in part, by WHR. The use of images that varied in body pose was an important addition to previous eye-tracking studies as it allowed to for analyses of attention to the WHR region when features known to capture attention (i.e. the face and breasts) were not visible. Eye-tracking may provide a key behavioral link in evolutionary studies of sexual selection and morphology. However, uncovering to what extent attractiveness judgments, attentional capture and morphology are interrelated is a complex challenge for researchers. Future research may seek to uncover whether an attractiveness judgment actively relates to morphology through the use of paired stimuli presented for comparison. A further question involves how women might respond to images that vary in WHR, perhaps as a consequence of intra-sexual mate competition. What is clear from this research is that the combination of psychological methods and evolutionary biology may yield significant advances in our knowledge of what constitutes physical attractiveness.

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Chapter Nine

Sexual Selection and Evolution of the Human Beard: A Cross-Cultural Study.



Participants completing questionnaire surveys in a rural village on Upolu Island, Samoa, August, 2008.

Authors note: Chapter Nine is written in the style of the American Journal of Human Biology where it was submitted for publication on December 17, 2009, as the manuscript:

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The chapter is a modified version of this manuscript, adapted to the thesis.

ABSTRACT

The beard is a strikingly sexually dimorphic, testosterone dependant, secondary sexual trait in humans. Darwin posited that it had evolved in human ancestors via inter-sexual selection as a highly attractive adornment. Others have proposed that beards evolved via intra-sexual selection a signal of male status and dominance. Here we show that women from two different ethnic groups, Europeans from New Zealand and Polynesians from Samoa, do not rate bearded male faces as more attractive than clean-shaven faces.

Women and men from both cultures judge bearded faces to be older and ascribe them higher social status than the same men who lack beards. Images of bearded men displaying an aggressive facial expression were also rated as significantly more aggressive than the same men when clean-shaven. Thus, the beard may also augment the effectiveness of human aggressive facial displays. These results are consistent with the hypothesis that the human beard evolved primarily via intra-sexual selection between males and as part of complex facial communication signalling status and aggressiveness.

INTRODUCTION

One of the most visually striking and sexually dimorphic of the secondary sexual traits in human beings is male facial hair (i.e., the beard including the moustache, hereafter, simply, “the beard”). Hair plays protective and insulative roles and there have been attempts to account for the evolution of the beard via natural selection, to assist in thermoregulation or protection against UV radiation (Cabanac and Brinnel, 1988; Cabanac and Brinnel, 2000; Green et al. 2006). However, the absence of facial hair in women argues against such explanations.

Darwin (1871) observed striking variations in male facial hair in different ethnic groups, from the slightly whiskered Asians to the extremely hirsute Ainos. To Darwin the beard represented a phylogenetically ancient trait, present in the nonhuman primate precursors of modern humans. He noted that some facial hair is present in both sexes of human fetuses and then posited that facial hair might have been secondarily lost in females. It is important to be clear, however, that the presence of hair on the face, as occurs at all ages in most monkeys and apes, is not equivalent to beard growth in men. Men’s beards (unlike the “beards” of monkeys and apes) are testosterone stimulated secondary sexual traits (Ewing & Rouse 1978; Farthing et al. 1982), which only develops from puberty onwards (Hamilton, 1958; Randall, 2007). The fine morphology of beard hair differs from that which occurs on the scalp and elsewhere on the head (Thozhur et al., 2006; Tolgyesi et al., 1983). Consequently, no vestiges of the human beard would be expected to occur in human fetus. As such, Darwin’s interesting observations do not provide evidence either for or against the proposition that beards ever occurred in both sexes in ancestral hominids. Despite these shortcomings in Darwin’s logic and absence of

data, he further hypothesized that the beard was an attractive adornment that had undergone sexual selection via female choice.

Testosterone may have suppressant effects on the immune system (Grossman, 1985). Thus, those males displaying androgen dependant traits may be advertising underlying genetic fitness to potential mates (Folstad and Karter, 1992). Zahavi and Zahavi (1997) suggested that the human beard may be a costly signal of male competitive ability as the beard may easily be grasped by a rival male during fights. Therefore, a man with a full beard may be advertising his confidence and higher competitive ability despite the handicap. Under these hypotheses, the beard may have evolved via inter- or intra-sexual selection as signal of masculine genetic fitness and competitive ability.

Research indicates that a beard makes a man look more masculine, socially mature, confident and older (Kenny and Fletcher, 1973; Wood, 1986; Addison, 1989; Wogalter and Hosie, 1991; Neave and Shields, 2008). Women appear to value these characteristics in male mates (Buss, 1989; Penton-Voak and Perrett, 2001). However, studies of facial hair in relation to male facial attractiveness have produced contradictory results. Thus, some studies have found a full beard to be attractive to women (Pelligrini, 1973; Feinman and Gill, 1977; Reed and Blunk, 1990), while other studies have not (Wogalter and Hosie, 1991; Muscarella and Cunningham, 1996). Recently Neave and Shields (2008) found that women rated male faces with light stubble as most attractive; perceived age rose with increasing amounts of facial hair and a full beard was rated as most dominant.

While a key goal in studies of physical attractiveness is to isolate morphological variables, the stimuli employed in some of these studies may not accurately reflect men's

faces and beards as they appear in real life. One reason for this is because beards do not exist independently of other facial traits. Thus, facial expression plays a most important role in many aspects of social and sexual communication, in human beings as in other anthropoids (Darwin, 1872). Ekman (1993) has shown on the basis of cross-cultural studies that all human populations share facial expressions indicative of fundamental emotions, such as fear, surprise, anger, happiness, sadness and disgust. It is thought that such facial expressions are phylogenetically ancient in humans (Ekman et al., 1969; Schmidt and Cohn, 2001). Morphologically very similar or identical facial expressions have also been described in the great apes (Burrows et al., 2006; Vick et al., 2007). Researchers have suggested that in primates the smile originated as a rejection response to noxious stimuli (i.e., drawing back the corners of the mouth), then evolved into a ritualized signal of fear and submission (i.e., a fear grimace) before finally differentiating into graded fearful, nervous and genuinely happy smiles in humans (Andrew, 1963; Van Hooff, 1972). In many species of nonhuman primates males have striking secondary sexual adornments involving the face and head (Dixson, 1998; Dixson et al., 2005). It is possible that certain facial expressions and secondary sexual adornments might act in concert for display purposes. In this study, we examine the effect of beardedness, or its absence, upon perceptions of facial expressions indicative of anger (aggression) and happiness (smiling).

The purpose of the present study is to assess the extent to which inter- and intra-sexual sexual selection may have influenced the evolution of the beard. Any evolutionary examination of the functional basis of beards requires establishing that perceptions of male beardedness are cross-culturally robust. As such, we carried out this research with

participants of European descent in New Zealand and with participants of Polynesian descent in Independent Samoa. New Zealand is a modern industrialized country with a population of four million people. It has the same exposure to ‘Western’ popular culture as would be typical in North American cities. Samoa is a chain of islands in Western Polynesia with a population of 182, 548. Compared to New Zealand, Samoa has far less exposure to ‘Western’ popular culture such as billboards, fashion magazines, movies and access to the internet is not widely available outside of the capital Apia. Bearded and clean-shaven men from both cultures were photographed posing neutral, smiling and angry facial expressions. The aim of this cross-cultural study was to test whether the beard enhances perceptions of attractiveness, dominance and aggressiveness of male faces, and thus to assess the extent to which inter- and intra-sexual sexual selection may have influenced the evolution of the beard.

On balance, the existing literature indicates that men with beards are perceived as being more masculine, older and socially dominant. In the current study we attempt to test four predictions as follows: Firstly, women viewing images of men with or without beards will find bearded images to be most attractive. Secondly, men who view images of clean-shaven and bearded men displaying an aggressive facial expression will judge bearded faces as more aggressive. Thirdly, participants of both sexes will judge bearded faces as indicative of higher social status. Finally, participants of both sexes will also judge images of bearded faces to be older than images of the same men when clean-shaven.

METHOD

Photographs

Ten New Zealand (NZ) men of European descent (age, $M = 23.50$, $SD = 3.44$, range 20-30 years) and nine Samoan men (age, $M = 23.00$, $SD = 2.78$, range 20-27 years) were recruited for this study. The men from these two cultures did not differ significantly in age ($F_{1,18} = .119$, $P = .733$). Participants were recruited with full beards, defined as not having shaved or trimmed the face for at least 8 weeks. Participants received monetary payment.

These men were photographed with a full beard and a clean-shaven face posing neutral, smiling and angry facial expressions using a Canon Power Shot digital camera with a resolution of 8.0 megapixels. The camera was set up 150 cm from the participant and all photographs were taken under the same controlled lighting.

The Facial Action Coding System (FACS: Ekman et al., 2002) was used to produce photographs of men with standardized angry and smiling facial expressions. During pilot studies a set of behavioral protocols was developed in order to instruct men how to pose the facial expressions. The instructions for facial movements were verbally administered by a researcher, who posed the facial expressions and provided examples of the facial expressions from FACS. Examples of the faces and facial expressions used in NZ and Samoa are provided in Figure 1.

Questionnaires

Each questionnaire began with a cover sheet to collect demographic information from each participant (sex, age, ethnicity). All questionnaires were submitted anonymously and participation was voluntary. Participants were interviewed at Victoria

University in Wellington. In the Samoan sample all the participants were Samoan citizens living on Upolu island. All participants were interviewed individually at their homes, in communal huts or at farms using a flipbook containing the photographs. Each photograph was cropped to show only the face, from the top of the head to below the jawline (Fig. 1). Three separate groups of participants completed one of three studies, as detailed below.

Study 1 quantified women's ratings of sexual attractiveness of men posing smiles with full beards and clean-shaven. The photographs were presented individually, in a random order and rated using a six-point Likert Scale where 0 = unattractive, 1 = only slightly attractive, 2 = moderately attractive, 3 = attractive, 4 = very attractive and 5 = extremely attractive.

Study 2 measured men's judgments of physical aggressiveness of bearded and clean-shaven men. Photographs of men posing angry facial expressions were presented individually in a random sequence and rated for aggressiveness using a six-point Likert Scale where 0 = not aggressive, 1 = only slightly aggressive, 2 = moderately aggressive, 3 = aggressive, 4 = very aggressive and 5 = extremely aggressive.

Study 3 assessed men and women's judgments of social status of men with beards or clean-shaven posing neutral expressions. Social status was defined as how likely the person in the photograph was to have a high ranking social position and commanding respect over other men in the community. To simplify this, after the definition of social status was explained to participants, the word 'importance' was used in the social status scale, which was as follows; 0 = low importance, 1 = only slightly important, 2 = moderately important, 3 = important, 4 = very important and 5 = extremely important.

Study 4 assessed men and women's perceived age (in years) of men photographed posing neutral facial expression with beards or clean-shaven.

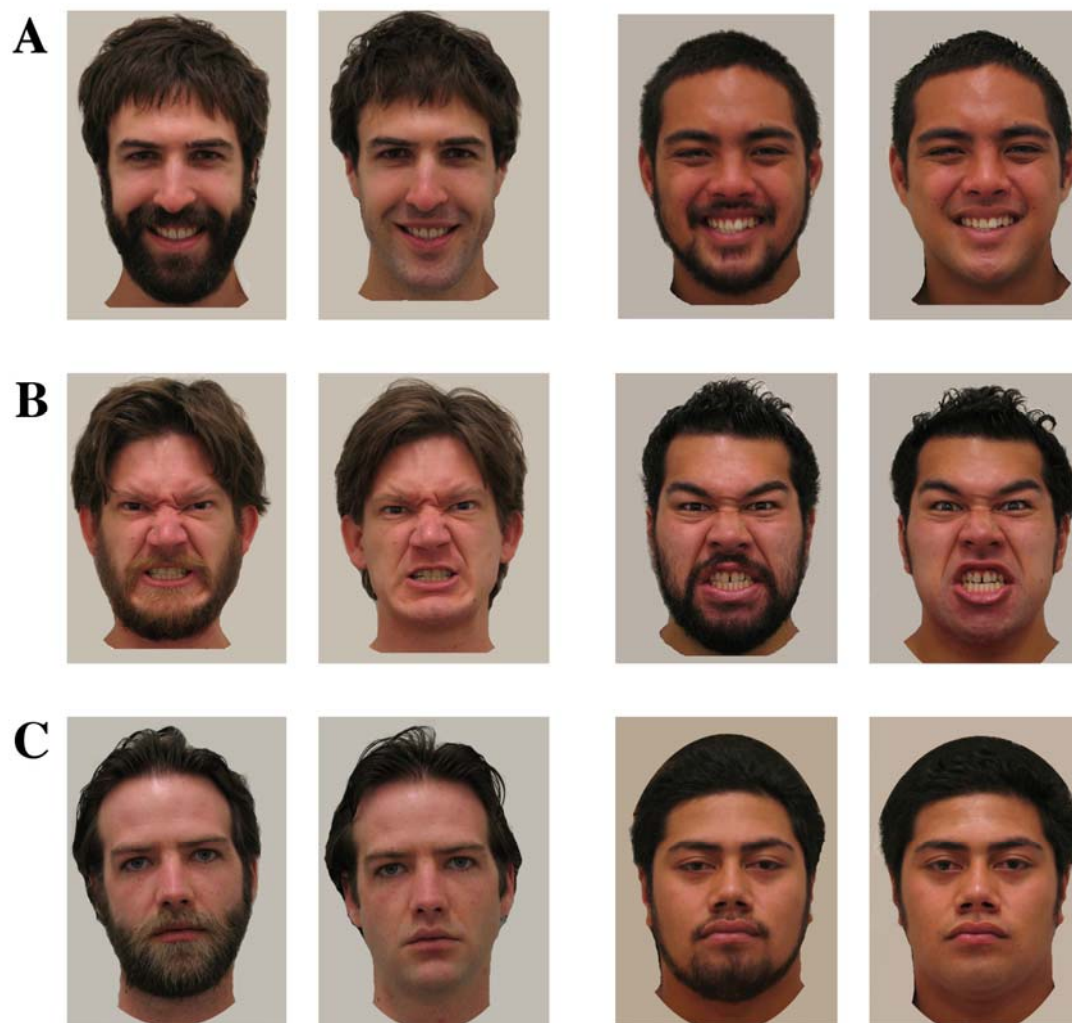


Figure 1. Examples of the facial expressions used to test the effect of the beard on perceptions of attractiveness (A), aggressiveness (B), social status and perceived age (C) in New Zealand and Samoa.

For the NZ sample, participants were of European descent and rated only the images of men who were of European descent. Samoan participants rated only the

photographs of Samoan men. In Samoa a linguistic interpreter, fluent in both English and Samoan, was present to ensure that participants understood the Likert scales. In both cultures, women, but not men, rated the photographs for attractiveness (Study 1) and men, but not women, rated the photographs for aggressiveness (Study 2). In both cultures, both men and women rated the designated photographic stimuli for social status (Study 3) and age (Study 4).

Statistical Analyses

Saville (1990) demonstrated that when testing *a priori* the most appropriate means of balancing the likelihood of Type I and Type II errors is to perform direct inferential tests. Consequently, we adopt this approach in testing the *a priori* predictions we generated in the Introduction using paired samples *t* tests on data from each culture.

RESULTS

Study 1: The beard, the human smile and attractiveness

129 women from NZ (mean age in years = 20.4, SD = 3.6, range = 18-38) and 100 Samoan women (mean = 21.4, SD = 3.3, range = 18-33) completed this study. NZ women's attractiveness ratings were significantly higher for smiling clean-shaven faces compared to smiling bearded faces ($t = -11.83$, $df = 128$, $P < .001$; Clean-shaven: mean \pm SD, $1.8 \pm .57$; Bearded: mean \pm SD: $1.07 \pm .75$). Similarly, Samoan women's attractiveness ratings were significantly higher for clean-shaven men compared to bearded men ($t = -12.01$, $df = 99$, $P < .001$; Clean-shaven: mean \pm SD: $2.94 \pm .89$; bearded: mean \pm SD: $1.86 \pm .95$) (Fig. 2A).

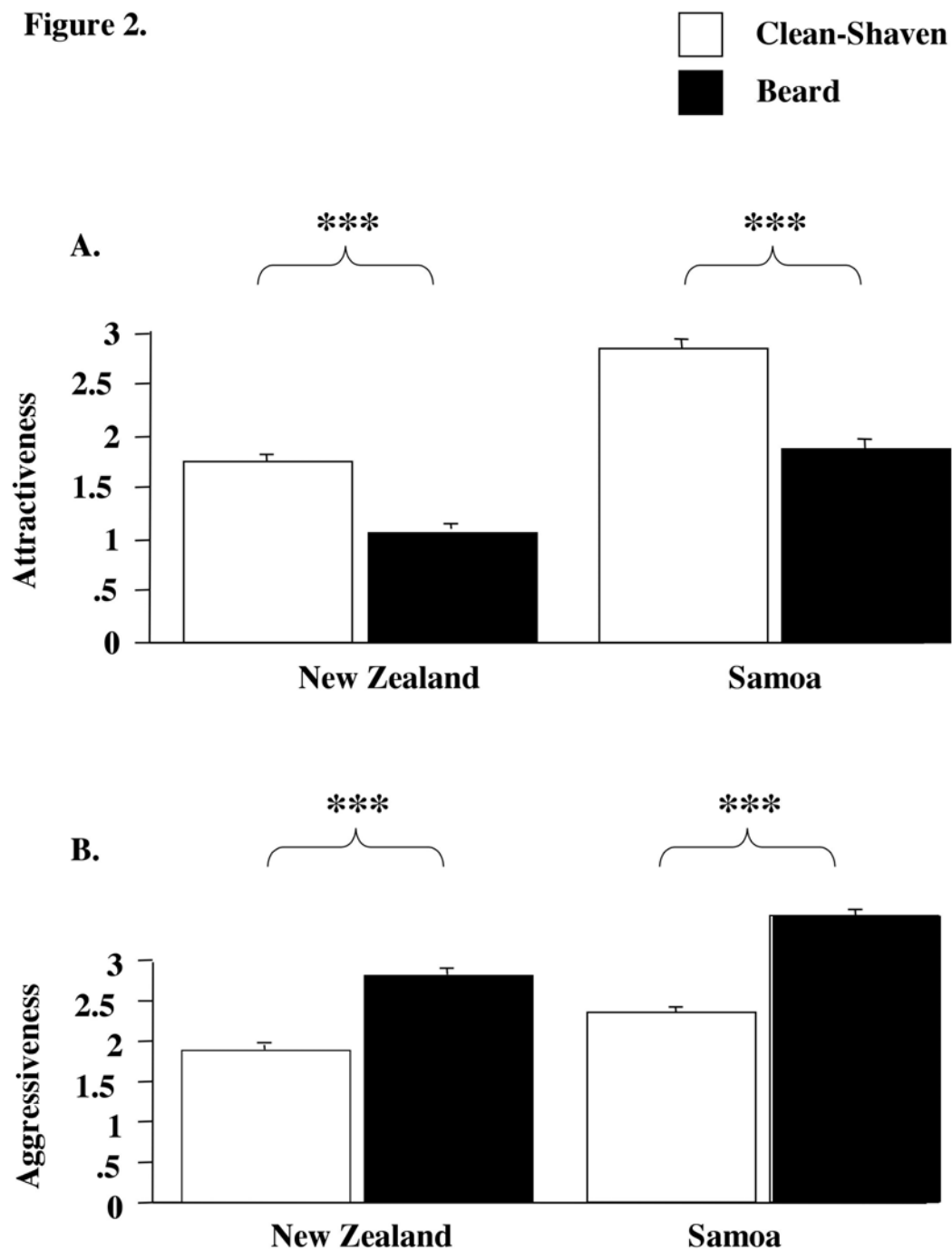
Figure 2.

Figure 2. Upper panels (A) show mean ratings (+SD) for attractiveness by women of men with beards and the same men clean-shaven. Lower panels (B) are the mean ratings (+SD) for physical aggressiveness by men of men with beards and the same men clean-shaven. *** = $P < .001$.

Study 2: Beardedness and aggressiveness

In total, 111 NZ men of European descent (mean age = 20.9, S.D. = 3.6, range = 18-39 years) and 117 Samoan men (mean = 28.6, S.D. = 11.0, range = 18-71 years) completed this study. NZ men's aggressiveness ratings were significantly higher for bearded men compared to clean-shaven men ($t = 18.26$, $df = 110$, $P < .001$; Clean-shaven: mean \pm SD: $1.85 \pm .67$; Bearded: mean \pm SD: $2.77 \pm .79$). Similarly, Samoan men's aggressiveness ratings were significantly higher for bearded faces compared to clean-shaven faces ($t = 20.87$, $df = 116$, $P < .001$; Clean-shaven: mean \pm SD: $2.30 \pm .51$; Bearded: $3.54 \pm .58$) (Fig. 2B).

Study 3: The Beard and Social Status.

A total of 52 NZ men (mean = 21.8, S.D. = 3.0, range = 19-40 years), 64 NZ women (mean = 21.3, S.D. = 5.2, range = 18-42 years), 119 Samoan men (mean = 28.6, S.D. = 11.0, range = 18-71 years) and 100 Samoan women (mean = 21.4, S.D. = 3.3, range = 18-33 years) completed this study. NZ men's social status ratings were significantly higher for bearded men compared to clean-shaven men ($t = 7.63$, $df = 51$, $P < .001$; Clean-shaven: mean \pm SD: $2.26 \pm .488$; Bearded: $2.88 \pm .411$). Similarly, Samoan men's social status ratings were significantly higher for bearded men compared to clean-shaven men ($t = 10.76$, $df = 118$, $P < .001$; Clean-shaven: mean \pm SD: $2.23 \pm .56$; Bearded: $2.97 \pm .76$) (Fig. 3A). NZ women's social status ratings were significantly higher for bearded men compared to clean-shaven men ($t = 3.68$, $df = 63$, $P < .001$; Clean-shaven: mean \pm SD: $2.12 \pm .57$; Bearded: $2.48 \pm .68$), as were Samoan women's social status ratings ($t = 6.0$, $df = 99$, $P < .001$; Clean-shaven: mean \pm SD: $2.22 \pm .44$; Bearded: $2.97 \pm .76$) (Fig. 3A).

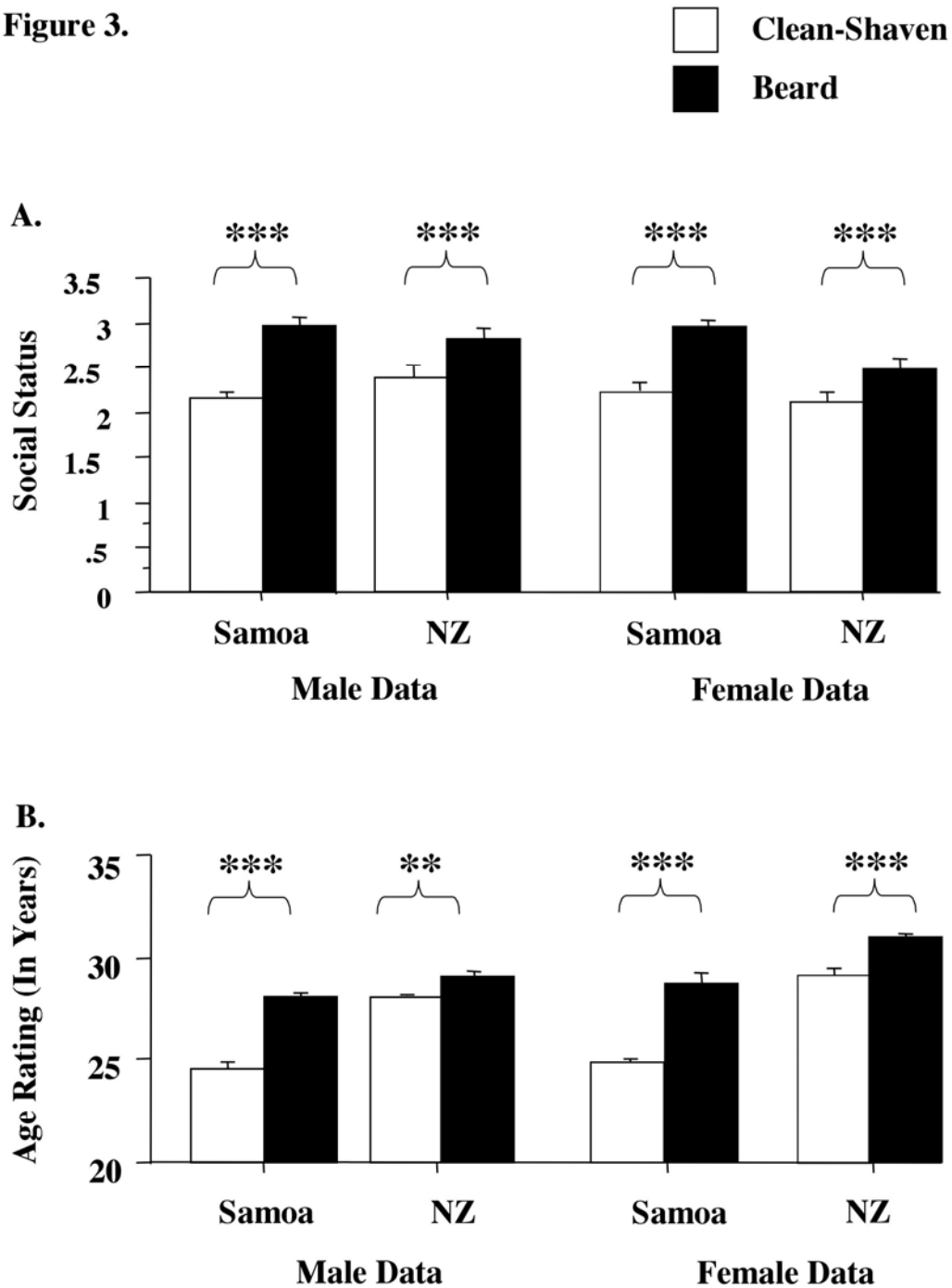
Figure 3.

Figure 3. Upper panels (A) are the mean ratings (+SD) for social status by men and women of men with beards and the same men clean-shaven. Lower panels (B) show the mean ratings (+SD) for perceived age by men and women of men with beards and the same men clean-shaven. ** = $P < .01$; *** = $P < .001$.

Study 4: The Beard and Perceived Age

In total, 52 NZ men (mean = 21.8, SD = 3.0, range = 19-40 years), 64 NZ women (mean = 21.3, SD = 5.2, range = 18-42 years), 119 Samoan men (mean = 28.6, SD = 11.0, range = 18-71 years) and 100 Samoan women (mean = 21.4, SD = 3.3, range = 18-33 years) completed this study. Men's perceived age ratings were significantly higher for bearded faces compared to clean-shaven faces in NZ ($t = 2.99$, $df = 51$, $P < .01$; Clean-shaven: mean \pm SD: 27.95 ± 1.83 ; Bearded: $28.73 \pm .1.91$). Similarly, Samoan men's perceived age ratings were significantly higher for bearded men compared to clean-shaven men ($t = 4.03$, $df = 118$, $P < .001$; Clean-shaven: mean \pm SD: 24.04 ± 1.44 ; Bearded: 27.69 ± 1.85) (Fig. 3B). Women's perceived age ratings were significantly higher for bearded men compared to clean-shaven men in NZ ($t = 11.66$, $df = 63$, $P < .001$; Clean-shaven: mean \pm SD: $28.51 \pm .19$; Bearded: $31.12 \pm .23$) and Samoa ($t = 20.08$, $df = 99$, $P < .001$; Clean-shaven: mean \pm SD: $24.19 \pm .15$; Bearded: $28.29 \pm .17$) (Fig. 3B).

DISCUSSION

The current study showed that in New Zealand (NZ) and Samoa facial hair augmented male and female perceptions of male age, aggressive facial displays, and social status. However, clean-shaven faces were rated as more attractive when smiling than bearded men. The use of facial expressions, combined with the presence or absence of the beard, also made it possible to test whether nonverbal displays of emotion were enhanced by this secondary sexual trait. Although the beard is not a trait that directly improves fighting ability, some authors have suggested it may intimidate rival males by increasing perceptions of the jaw size, overall length of the face and by enhancing

aggressive and threatening jaw-thrusting behaviors (Guthrie; 1970; Barber, 1995). The beard may handicap men during fighting as it may be easily clutched by rival men (Zahavi and Zahavi, 1997). Thus, bearded men may be advertising confidence as well as superior fighting ability. Several studies have found that images of bearded men, posing neutral facial expressions, are rated as highly self-confident (Pelligrini, 1973) and physically aggressive (Muscarella and Cunningham, 1996; Neave and Shields, 2008). The current study is the first to show that the beard augments a threatening behavioral display. Bearded men with angry facial expressions received significantly higher scores for aggressiveness compared with clean-shaven faces in both NZ and Samoa, suggesting that the beard plays an important role in inter-male aggression.

It is conceivable that secondary sexual traits such as the beard in *Homo sapiens* were also present in ancestral hominids. However, the fossil record cannot answer this question as cutaneous tissue does not fossilize. Thus, comparative studies of human beings and extant nonhuman primates may shed light on the possible functions of visually conspicuous secondary sexual traits (Dixson et al., 2005). Mature male gorillas (silverbacks) have a crest on top of the head; these crests are largest in those males having most females in their one-male units (Caillaud et al., 2008). In the orang-utan, adult males develop full expression of their ‘cheek flanges’ and beards only when they achieve dominant positions in the social system (Galdikas, 1985; Kingsley, 1982; Utami Atmoko and Van Hoof, 2004). Male mandrills (*mandrillus sphinx*) exhibit spectacular red and blue facial coloration, the red coloration being most pronounced in dominant males having higher testosterone levels (Wickings and Dixson, 1992; Setchell and Dixson, 2001). Dominant male hamadryas baboons (*Papio hamadryas*) develop large

androgen-dependent capes of hair that appear to be sexually selected as a dominance signal between males (Zuckerman and Parkes, 1939; Kummer, 1990). Although secondary sexual facial coloration and capes of hair in nonhuman primates are perhaps not strictly homologous to those of the human male, they may have arisen via similar selective mechanisms. Such traits are visually conspicuous and communicate an individual male's age and dominance status. Compared to many nonhuman primates, men exhibit relatively well developed secondary sexual traits (e.g. facial and body hair) such as occur in polygynous species (Dixon, 1998; Dixon et al., 2005). The results presented here on the human beard are consistent with the theory that sexual selection has enhanced via intra-sexual selection of visually conspicuous traits that communicate age, social status and aggressiveness between male primates.

Given that a beard makes a man look older than his real age and women typically prefer a partner who is 2-3 years older than themselves (Buss, 1989; Kenrick and Keefe, 1992), one might predict that facial hair should enhance male facial attractiveness to women. However, clean-shaven faces received significantly higher scores for attractiveness than bearded faces in both NZ and Samoa. Some previous studies have found that bearded men are rated as more socially mature, sincere, masculine, self-confident and courageous than clean-shaven faces by both men and women (Kenny and Fletcher, 1973; Pelligrini, 1973; Neave and Shields, 2008). However, studies of female preferences for male beardedness have produced different results. Some studies have concluded that beards enhance attractiveness to women (Pelligrini, 1973; Feinman and Gill, 1977; Reed and Blunk, 1990), whereas in other studies the opposite effect has been observed (Wogalter and Hosie, 1991; Muscarella and Cunningham, 1996). Studies of

male facial attractiveness have typically found that androgen-driven masculine facial features such as the large brow ridge and thicker jaw are not necessarily attractive to women (Perrett et al., 1998; Neave et al., 2003; Swaddle and Reiersen, 2002).

Furthermore, more masculine faces are ranked as less ‘warm’, honest and cooperative by women (Penton-Voak and Perrett, 2001). Consequently, although some studies have found that positive *social* traits are attributed to bearded men, these perceived qualities do not necessarily enhance their physical attractiveness to women.

Recent studies of male facial attractiveness have focused on female preferences for testosterone-dependant traits in men across the menstrual cycle. It has been found that women in the fertile phase of the menstrual cycle have a greater preference for masculine facial features (Gangestad and Thornhill, 2008). These traits may be energetically and immunologically costly, and only sustainable by those males of higher genetic quality or competitive ability (Folstad and Karter, 1992). Given that beard growth is androgen-dependant (Randall, 2007), it is possible that female preferences for male facial hair may vary dependant upon the phase of the menstrual cycle. However, it is worth noting that studies of female preferences for masculinity in male faces across the menstrual cycle most often use computer-generated stimuli. A recent study by Peters et al. (2009), which used as stimuli natural photographs of male faces and bodies, found no relationship between menstrual cycle phase and female preferences for masculinity in the face or body of men.

An alternative interpretation of female preferences for clean-shaven faces in the current study is that they are the result of modern day cultural practices of shaving the face. A study quantifying styles of facial hair (e.g. mustaches, sideburns, full beards) in

men photographed for the *Illustrated London News* between 1842-1971, showed that the popularity of facial hair, and particular styles of facial hair, may fluctuate over time within Western societies (Robinson, 1976). As such, it is possible that women from Wellington, New Zealand, which is a modern industrialized city with high exposure to ‘Western’ popular media, rated clean-shaven faces as more attractive than bearded faces because it is currently more fashionable for men to be clean-shaven in Western society. However, in Samoa, there is far less exposure to ‘Western’ popular media. For example, it is difficult, even in the capital of Apia, to find magazines of any sort (including fashion magazines) that can be easily acquired in Western societies. Equally, there are no large billboards advertising fashion. There is only one movie theatre in the entire country. Outside of the capital, access to the internet is sparse. Nevertheless, like NZ women, Samoan women also rated clean-shaven faces as more attractive. Indeed, Samoan women’s attractiveness ratings for clean-shaven male faces were higher than those of NZ women. This suggests that the finding that beards are not attractive to women may be cross-culturally robust and not simply due to the effects of contemporary popular media influencing women’s preferences. However, additional cross-cultural studies would be valuable as further tests of this hypothesis.

In conclusion, the results of this study did not find support for Darwin’s (1871) theory that the human beard evolved via female choice as a highly attractive secondary sexual adornment. Instead, our results indicate that beards increase perceptions of male age and social status, in addition to augmenting men’s aggressive facial displays. This suggests that the beard plays a strong role in intra-sexual signaling.

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Chapter Ten: Conclusions and Future Directions.

In this thesis I set out to use an integrative approach to test Darwin's (1871) theories of sexual selection on human morphology. I used questionnaire surveys in cross-cultural studies to collect data on male attractiveness judgments of female waist-to-hip ratio, body mass index and breast morphology. I also used eye-tracking techniques to measure male visual attention for female physique during attractiveness judgments. Turning to the question of whether sexual selection has enhanced masculine secondary sexual adornments, I developed an image-based questionnaire that combined facial expressions with manipulations of facial hair to test male and female perceptions of the beard in New Zealand and Samoa.

Female waist-to-hip ratio (WHR) is a bodily feature that reliably signals women's reproductive age, hormonal profile, fecundity, and susceptibility to diseases (Singh, 2002; 2006). Cross-cultural studies have found that men rate female images, the majority of which are line drawings, with low WHRs as more attractive than women with high WHRs (For review see Singh, 2006). However, some researchers have argued that male preferences for female images with a low WHR actually reflect preferences for a reduction in body mass index (BMI) (Tovée & Cornelissen, 1999; Swami, Antonakopoulos, Tovée, & Furnham, 2006). BMI may therefore be a more important determinant of female attractiveness to men than WHR.

WHR is positively correlated with BMI. Therefore it has proven challenging to experimentally tease apart the individual effect of these two traits on female attractiveness. In this thesis I used a new questionnaire to test the role of WHR and BMI

in male judgments of female attractiveness. I employed, as stimuli, photographs of women who had undergone micrograft surgery. In this procedure fat is removed from the midriff and grafted into the buttocks and thighs, resulting in a lower WHR and an 'hourglass' body shape (Roberts, 2001; Roberts et al., 2006). Pre- and post-operative photographs of five patients in which BMI increased post-operatively and five who decreased slightly post-operatively were used in questionnaires (Chapter two, three and four). This study design made it possible to evaluate the role of WHR in women's attractiveness independent of BMI. Men from the highlands of Papua New Guinea (PNG), China, Samoa and New Zealand (NZ) rated images of women with low WHRs as most attractive, when controlling for the effects BMI. These studies confirm the importance of female WHR as a cue used by men when judging female attractiveness.

Women's breasts undergo substantial changes in their external appearance due to age and reproductive status. Changes in female breast morphology and areolar configuration may influence male judgments of female attractiveness (Gallup, 1982; Marlowe, 1998; Symons, 1995). I investigated the role of breast size, breast symmetry, areolar pigmentation and areolar size in male judgments of female attractiveness to men from PNG, Samoa, and NZ (Chapter 5). Men from these cultures varied in their preferences for female breast size. However, when data were analyzed to take into account marital status, married men rated larger breasts as significantly more attractive than unmarried men did. Men across cultures preferred symmetrical breasts significantly more than asymmetrical breasts. Men in Samoa and PNG preferred darkly-pigmented areolae whereas in NZ men rated medium-pigmented areolae as most attractive. Male preferences for areolar size varied considerably across these cultures. These findings

demonstrate that men rate as most attractive female breast morphology indicative of sexual maturity and fecundity. However, further cross-cultural research evaluating the importance of breast morphology in male judgments of female physical attractiveness will be important.

Computer-generated stimuli allow for the controlled manipulation of traits in tests of mate choice. However, this method has several drawbacks. Women's breasts change in shape due to reproductive status (e.g. adolescent, adult, lactating). Gallup (1982) and Marlowe (1998) have suggested that changes in the breast morphology indicative of reproductive status and the ageing process may affect male judgments of female sexual attractiveness. It is very difficult to realistically model such morphological changes using computer-morphing programs because these changes in breast morphology do not occur independently of other changes associated with ageing. Thus, it will be important for future studies to use natural stimuli to test whether female attractiveness is influenced by changes in breast morphology due to age and reproductive status.

Studies of human morphology and physical attractiveness typically employ questionnaires in which participants rate images that have been experimentally manipulated to differ in morphological cues that may signal health, hormonal status and fertility. Eye-tracking technology makes it possible to obtain quantitative data on visual attention. The prediction is that those morphological cues that drive attractiveness judgments might command greater attention (number of fixations or durations of visual fixation) during eye-tracking experiments. Attention has been linked to attractiveness judgments of female faces so that men look more often and for longer at the faces of women they judge to be more attractive (Fink et al., 2008; Maner et al., 2007; 2008;

Shimojo et al., 2003). These studies suggest that male attention is correlated with perceptions of female physical attractiveness.

In this thesis eye-tracking techniques were used to quantify male attention to the female body and face during judgments of female physical attractiveness (Chapter 6, 7 and 8). When men were shown front-posed female images they spent longer and looked most frequently at the breasts, irrespective of female WHR. However, judgments of female attractiveness were driven primarily by WHR, and not breast size. Analyses of the first fixations, occurring within the first 200 milliseconds of the start of eye-tracking experiments, showed that men looked at the breasts and midriff more than other parts of the body (Chapter 6). Female WHR may be a trait that is rapidly analyzed after which the parts of the body where female fat deposits are greatest, such as the breasts, are the focus of male attention. When men were presented with female images in back-pose as well as front-pose, there were significant differences in viewing patterns. When participants looked at images in back-view they spent significantly more time looking at the midriff than when viewing images in front pose. The breasts also received a lot of visual attention, as did the buttocks. Irrespective of body-pose, female images with a low WHR were rated as most sexually attractive (Chapter 8).

Men may be examining the breast as a whole, or looking at specific features such as the areolae when making attractiveness judgments. Eye-tracking procedures were employed to obtain such measurements by using images of nude female torsos as stimuli (Chapter 7). Men looked most often at the breasts followed by the areolae, irrespective of differences in the breast size and areolar pigmentation. Images with large and medium-sized breasts were more attractive than smaller breasts. Darkly and medium-pigmented

areolae were more attractive than lightly pigmented areolae. These findings suggest that cues to female sexual maturity are attractive to men. However, male attention is not correlated in a simplistic way with the morphological features that are judged to be more attractive.

In eye-tracking studies of female facial attractiveness (Fink et al., 2008; Shimojo et al., 2003) participants have been presented with pairs of faces, which allows for a visual comparison during attractiveness judgments. The studies presented in this thesis were limited to quantifying male eye movements and perceptions of female physical attractiveness using images that were presented individually. It will be important for future eye-tracking studies to employ pairs of stimulus images that differ in WHR and breast morphology in order to measure whether men compare morphological features when judging female physical attractiveness.

Darwin suggested that the human beard evolved via female choice as a highly attractive adornment. However, studies of female preferences for male beardedness have produced variable results and conclusions. Thus, some studies have concluded that beards enhance male facial attractiveness (Pelligrini, 1973; Feinman & Gill, 1977; Reed & Blunk, 1990), while others have not (Wogalter & Hosie, 1991; Muscarella & Cunningham, 1996). I present the first cross-cultural data on female preferences for photographs of men with and without beards (Chapter 9). Women from Samoa and NZ rated faces without beards as more physically attractive than men with full beards. Interestingly, women from Samoa, where 'Western' media influences are much less abundant than in NZ, gave higher scores for the attractiveness of clean-shaven men than women did in NZ. This suggests that female preferences for clean-shaven faces may be

robust, although it will be important to replicate this study in other cultures. Sexual selection also acts on adornments that play a role in competition between males. The presence of a beard augmented male perceptions of men's aggressive facial expressions in Samoa and NZ. While the beard is not a trait that directly serves in fighting, it may make a man appear more aggressive and dominant through causing the face to appear longer and by enhancing threatening facial expressions (Barber, 1995; Guthrie, 1970). It was possible to measure the interaction between behavioral displays of aggressiveness and beardedness through employing stimuli in which facial expressions were standardized. The finding that a beard makes a man look older, more socially dominant and physically aggressive suggests that the beard played a stronger role in intra-sexual selection during human evolution rather than inter-sexual selection as posited by Darwin.

These findings are similar to other studies that have shown that androgen-driven facial traits such as a large brow ridge, deep-set eyes and thin lips are not necessarily attractive to women (Neave et al., 2003; Peters et al., 2008; Swaddle & Reiersen, 2002). However, only the preferences of women from two cultures were investigated in this thesis. Beards may enhance attractiveness in other human populations. Thus, further cross-cultural research will be valuable. The images used were of younger men aged 20 years – 30 years. Since beards augment age and social status, it may be that older men are more attractive to women when bearded.

Darwin's theories of natural and sexual selection changed the basis of our understanding of the origins of animal and plant life. Evolutionary biology and physical anthropology have contributed enormously towards an understanding of the origin of the human species. Darwin also suggested that man's mental faculties may have been subject

to the forces of selection during evolution. Many of these claims are now being tested as psychologists begin to apply their knowledge of the human psyche and cognitive processes to the study of the evolution of human behaviour. This thesis attempts to integrate these different fields in order to study human mate choice. As evolutionary psychology advances and becomes more successful at incorporating evolutionary biology and anthropology into psychological research, it should provide a deeper appreciation of the origins of sexual preferences in *Homo sapiens*.

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Appendix 1: Cross-Cultural Consensus for Waist-Hip Ratio and Women's Attractiveness.

Authors note: I collaborated on a cross-cultural study of male preferences for female body shape. The following is the paper we wrote together and contains the data reported in Chapter 4 of this thesis. For this study I was responsible for the experimental design, constructing the questionnaires and data collection in New Zealand and Independent Samoa. Professor Devendra Singh was first author on the manuscript that included further data collected on Komodo Island and Bakossiland in Cameroon. Therefore in Chapter 4 I reported only the findings from Samoa and New Zealand. This appendix includes the full manuscript, which has been accepted for publication in the journal *Evolution and Human Behavior*:

Cross-cultural consensus for waist-hip ratio and women's attractiveness. D. Singh^A; B.J. Dixon^B; T. S. Jessop^C; B. Morgan^D, and A.F. Dixon^B (In Press). *Evolution and Human Behavior*.

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