# Computer Graphic Studies of the Role of Facial Similarity in Judgements of Attractiveness

# I.S. PENTON-VOAK, D.I. PERRETT and J.W. PEIRCE School of Psychology, University of St. Andrews

Anecdotally, spouses are often said to resemble one another. This study investigates the effects of similarity between participants and stimuli on judgements of facial attractiveness: does "like prefer like"? Using computer graphic techniques, opposite sex facial stimuli were generated from subjects' photographs. Experiment 1 showed a correlation between attractiveness and similarity but the effect can be explained by the attractiveness of average faces. Beyond this, there was a trend for individual subjects to rate opposite sex images with a similar face shape to their own face as more attractive than other subjects. Experiment 2 allowed subjects to interactively manipulate an opposite sex facial image along a continuum from a self-similar shape, through an average face shape, to a face with opposite characteristics. No significant preferences for self-similar or opposite characteristics were found. Preferences for average faces are stronger than preferences for self-similar faces.

Cross-population studies indicate that facial attractiveness reflects features that indicate good genetic quality, reproductive potential, and the likelihood of pro-social parenting behaviours, not arbitrary cultural values (Perrett et al., 1994; Jones 1995; Perrett et al., 1998).

Selection pressures operate against extreme genotypes, leading to the hypothesis that facial attractiveness is "averageness" (Symons, 1979). Composite faces with average features are judged as more attractive than the individual faces from which they are constructed (Langlois and Roggman, 1990; Grammer and Thornhill, 1994). These average faces, although attractive, can be improved upon (Perrett et al., 1994). "Good genes" theories predict that symmetrical, exaggerated secondary sexual characteristics will be found attractive in faces as they indicate developmental stability and immuno-competence in males and youth and fertility in females (Thornhill, 1994), exaggerated facial secondary sexual characteristics are not always preferred. Recent studies have shown that, although female faces that are artificially feminised are considered more attractive than average faces, masculinised male faces are not (Perrett et al., 1998). In fact, *feminised* male faces are preferred, possibly due to negative personality characteristics attributed to very masculine faces.

Despite cross-subject and cross-population agreement in judgements of attractiveness, individual differences exist in such preferences. One factor that may lead to such variation in attractiveness judgements is the similarity in physical appearance between judge and judged. We briefly review evolutionary theories of *assortative mating*: a mating pattern that occurs when similar phenotypes mate at levels above chance (Partridge, 1983). Data from many species indicate that positive assortment is the most common pattern found among animals (Burley, 1983; Thiessen and Gregg, 1980); it seems mates across many species are indeed more similar than chance predicts. This study investigates, for humans, whether or not like really does *prefer* like with respect to facial similarity.

Theoretical work by evolutionary biologists indicates that phenotypic similarity between partners may increase inclusive fitness (Thiessen and Gregg, 1980; Bateson, 1983). Most of the hypothesized benefits accrue from increasing the coefficient of parent-offspring relatedness, resulting in increased gene duplication and reduced costs of altruism (Thiessen and Gregg, 1980; Epstein and Guttman, 1982; Rushton, 1988, 1989). The advantage of extra-closely related offspring is, however, disputed (Dawkins, 1979).

Rushton presents controversial evidence (based on blood type analysis) that genetic similarity in human partnerships increases fecundity (Rushton, 1988). Clark and Spuhler (1959) proposed a similar link and found small positive correlations between spousal physical similarity and the number of children produced. Bateson (1988) examined fecundity of pairings between Japanese quail with varying levels of relatedness showing that first cousin partnerships produced fertile eggs earlier than unrelated pairs.

Some benefits of assortment may occur at the phenotypic level. For example, mating within local populations results in an assortative mating pattern that is beneficial as individuals avoid the costs of leaving the immediate environment to mate. Hill et al. (1976) found that human couples who were similar on a variety of traits were more likely to remain together than dissimilar partners. An increase in marital satisfaction may lead to an increase in fecundity without the need for any biological increase in fertility.

A limiting factor on any hypothesized increase in fitness associated with assortative mating is the *inbreeding depression*. Assortative mating will, to a greater or lesser extent, increase homozygosity leading to the expression of potentially lethal traits. Such effects have been observed in many non-human species (Partridge, 1983). In humans, the result of incestuous mating is high infant mortality, developmental disorders, and physical defects such as heart abnormalities, deafness, and dwarfism (Seemanova, 1971).

Homozygosity may also prove disadvantageous for passive immune system resistance to parasites and pathogens that are generally best adapted to common proteins in the host population. Heterozygous individuals are more likely to carry rare alleles and may therefore possess more passive genetic resistance to pathogens (Thornhill and Gangestad, 1993). Individuals may seek to maximize heterozygosity in offspring by *negative* assortative mating. Indeed, Wedekind et al. (1995) demonstrate that women respond preferably to male odours that indicate a different major histocompatability complex from their own. Ober et al. (1998) demonstrate that fetuses that share HLA alleles with their mothers are less likely to survive to full term, providing evidence that assortative mating may have fitness costs.

Individuals could optimize the costs and benefits of assortative mating (Wright, 1933). "Optimal outbreeding" requires that individuals must assess the phenotype of a potential mate, estimate the likely genotypic similarity between themselves and the possible partner, and "decide" whether they are too closely or too distantly related to be an "optimal" mate. Processes of kin recognition may be used in mate choice to avoid excessive inbreeding and to allow optimal mate choice, as well as to direct altruistic behavior (Bateson, 1983; Waldman, 1987).

Lorenzian sexual imprinting during a critical sensitive period early in life seems a likely mechanism for establishing later mate preferences, including incest avoidance (Immelman, 1975). Repeated social interaction between proximate individuals (e.g., nest mates) at early stages of development seems to foster altruistic acts while inhibiting sexual interaction (Holmes and Sherman, 1983; Waldman, 1987). Placing infants in surrogate families at appropriate stages of development and observing kin-directed behavior of these non-related "offspring" reveal the involvement of learning in the identification of "kin" for many species including fish, mice, and goats (Holmes and Sherman, 1983).

Evidence for familial characteristics influencing future sexual behaviour comes from fostering studies of ungulates (Kendrick et al., 1998), rodents (D'Udine and Alleva, 1983), and birds (e.g., Vos, 1994, 1995a,b). Bateson (1982) attempted to test the optimal outbreeding hypothesis: that the preferred level of relatedness in a partner for Japanese quail lies between close relatives and unrelated birds. He found that quail spent significantly more time in front of first cousins than unrelated birds and novel or familiar siblings—the first empirical evidence that birds avoid both excessive inbreeding and outbreeding.

Similar mechanisms that prevent incestuous mating, but promote some similarity between partners may exist in humans. Westermarck (1894) hypothesised that children have an innate tendency to learn a sexual aversion to individuals with whom they live closely in infancy and early childhood (normally biological siblings and parents). Ethnographic studies have formed natural experiments that support Westermarck's hypothesis. For example, there are very few cases of sexual interaction between unrelated peers co-socialised since infancy in Kibbutzim, even though sexual relationships are not actively discouraged (Talmon, 1964; Rabin, 1965; Spiro, 1965; (Shepher, 1971). Studies of *sim-pua* marriages in China, in which future husbands and wives were raised together from childhood (effectively as siblings), indicate that *sim-pua* marriages are 250 percent more likely to end in divorce than marriages between partners who have not been raised together. The fertility of *sim-pua* marriages is 25 percent lower than other marriages (Wolf, 1993).

The findings of the studies of spousal facial similarity could be attributed to the development of preferences for family-like facial characteristics. Weak, but significant effects from two studies indicate that parental characteristics could influence later choice of partner. Small positive correlations between father's age and husband's age

demonstrate that daughters of older men subsequently tend to choose older husbands (Zei et al., 1981; Wilson and Barrett, 1987). Wilson and Barrett also showed that females chose partners whose eye color resembled their fathers'.

Human partners assort strongly for a wide range of non-biological characteristics such as religion, educational level, and socioeconomic status (Vandenberg, 1972; Thiessen and Gregg, 1980; Epstein and Guttman, 1982; Rushton, 1988, 1989). There seems to be an inverse relationship between the genetic component of a trait and the amount of assortment that occurs for it (Thiessen and Gregg, 1980), although some evidence of assortment for heritable physical characteristics has been found.

Roberts (1977) and Spuhler (1968) review early research of spousal correlations from large-scale measurement studies of anthropometric characteristics (arm length, ear lobe length, etc.). Overall, these studies reveal positive correlations (0.01–0.35) between spouses on many physical features. The validity of these early studies is questionable. Few take into account the age of partners (physical features vary systematically with age), or the effects of environmental coexistence (diet, etc.) on similarity. Recent studies of assortative mating (Malina et al., 1993; Allison et al., 1996), however, have found significant correlations in measures of weight and physical strength between spouses that could not be explained by cohabitation or age. It seems reasonable to conclude that some physical similarity occurs in human marriage.

Three studies have reported facial similarity between couples at the perceptual level. Griffiths and Kunz (1973) found observers could match spouses married for less than ten years or more than twenty years at above chance levels, though subjects failed to match couples married for between ten and twenty years. The small stimuli sets used (n=5) may explain the inconsistent results. Zajonc et al. (1987) obtained two photographs (one from the first year and the second from the twenty-fifth year of the partnership) from each individual in married couples. Older, but not young partners were ranked as more similar and more likely to be married than predicted by chance. This indicates that couples do not get together due to similarity, but become more alike over time, perhaps due to shared environmental and emotional experiences. Hinsz (1989) used photographs of individuals from engaged couples and couples who had been married for around twenty-five years. Real couples were rated as more similar than randomly generated couples. Unlike Zajonc et al. (1987), Hinsz (1989) did not find that couples that had been together for longer periods of time were perceived as more similar than new couples.

It is important to note that an assortative *pattern* is not necessarily caused by assortative *preferences* (Burley, 1983). Assuming that "like mates with like" because "like prefers like" is an oversimplification; in a population where a certain characteristic is universally considered attractive (a *type* preference) an assortative pattern can still develop. For example, Berscheid et al. (1971) showed that, although college students prefer to date highly attractive people, (a type preference) they actually find themselves with dates of similar attractiveness to themselves (leading to assortment for attractiveness despite a type preference). Likewise, Shepherd and Ellis (1972) found that married couples have similar attractiveness rating. Thus, one problem with studies



FIGURE 1 Average composite images

Note: Female average (left, 40 females) and male average (right, 21 males).

assessing perceived facial similarity of real couples is that similarity may be more due to attractiveness matching rather than actual facial similarity.

## **EXPERIMENT 1**

The study of similarity of real life couples has obvious validity in the study of assortative mating for facial appearance, but it also has drawbacks; studying partnerships is not the same as studying preferences (Burley, 1983), and studies can have confounding factors such as a common source of photographs for partners.

A computer graphic study is well placed to investigate assortative preferences for facial characteristics. Experiment 1 employs techniques that change the apparent sex of an individual's face, while maintaining their own characteristics (Rowland and Perrett, 1995). This creates an image of a hypothetical opposite sex "sibling." As there can be no Westermarckian impediment to an individual finding a synthesized facial image attractive, these sibling images can be used as test stimuli in studies of similarity and facial attraction.

# Method

*Stimuli*. Fifty-two female and twenty-three male participants (students at St. Andrews University, mean age twenty-one, were photographed and the images digitised. The positions of 174 feature points were marked on each image to define the shape of the eyes, mouth, etc. Component images were then blended to form average or prototype images (Benson and Perrett, 1992; Perrett et al., 1994; Rowland and Perrett, 1995).

An opposite sex image that retained shape information from the individual source faces as generated for each of the fifty-two female participants photographed. The vector difference between the feature points of an individual (e.g., female subject) and the same sex (female) prototype specifies the shape information unique to the indi-

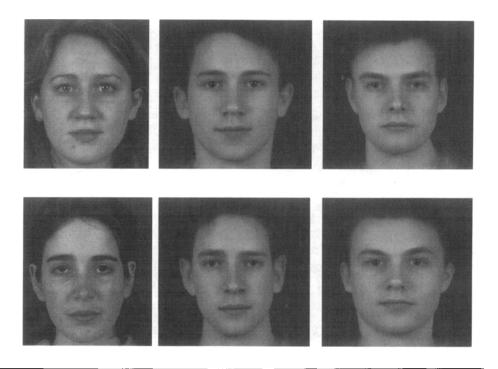


FIGURE 2 Examples of original faces and synthetic stimuli

Note: Original female (left), "similar" male face stimuli (centre, experiments 1 & 2) and "opposite" male face stimuli (right, experiment 2).

vidual. This identity information can be added to the shape of the opposite sex (male) prototype to create a synthetic male with a "similar" face type to the subject (Figure 2, left versus centre; Rowland and Perrett, 1995).

Attractiveness Judgements. Thirty-six of the original fifty-two female subjects photographed rated the attractiveness of fifty-two transformed "male" faces on a sevenpoint Likert scale (1 = "very unattractive," 7 = "very attractive"). The order of presentation was randomised.

Similarity Assessment. Six different subjects rated the similarity (on a six-point Likert scale) of each of the synthetic male faces to each of the original photographs of the thirty-six female subjects making attractiveness judgments. Each subject rated the similarity of the complete set of fifty-two male faces to one original face before proceeding to repeat the task for a different original face (randomly chosen from the thirty-six). Ratings were self-paced in sessions spaced over several days.

## RESULTS

None of the subjects spontaneously recognized the stimuli as being derived from the face of themselves or their peer group. This might mean that the attempt to construct stimuli similar to subjects was unsuccessful. Analysis of similarity ratings showed this was not true. For each original female face, the fifty-two male faces were ranked by the average similarity rating across the six raters. For all but four of the thirty-six original faces, the male face constructed as an opposite sex version (Figure 2, center images) ranked highest in similarity from the set of fifty-two. Two synthetic male faces ranked fifth and two ranked second most similar to the original face from which they were derived.

Figure 3a plots the relationship between similarity of stimuli to the subjects and the subjects' judgments of stimulus attractiveness. Attractiveness and similarity ratings were transformed to allow comparisons among subjects. The thirty-six subjects' ratings of the male face most similar to themselves were averaged to give the extreme right data point. The extreme left point gives the average of the thirty-six subjects' ratings of the face least similar to themselves. Points in-between reflect the averaged attractiveness ratings of faces with intermediate rated levels of similarity.

The point on the extreme right appears an outlier, with a much higher similarity level than the average similarity of the second most similar face. This is not an artifact, but an indication of the success of the stimulus construction. The sex transformed stimulus was on average much more similar to the subject from which the face shape information was derived than any of the stimuli constructed to look like the fifty-one other female students.

The graph shows a clear relationship between similarity of faces to subjects and the subjects' ratings of attractiveness of the faces. Linear regression accounts for 58 percent of the variance in the data. Regression with a second order polynomial equation provides a better fit to the data and accounts for 65 percent of the variance. This indicates that although attractiveness ratings increase with similarity, this relationship asymptotes or declines when faces become very similar to the subject. This finding is consistent with the optimal outbreeding hypothesis, which postulates that intermediate levels of similarity should be most attractive.

Figure 3b plots the attractiveness ratings of subjects in isolation from the views of others. A critical question is whether subjects rate self-similar faces differently to other members of the population. This can be assessed by taking the difference between each subject's ratings of a face and the average rating of everyone else for the same face. This value (subject's view—others' view) gives the subject's "unique view" and is presented in Figure 3b. The graph displays no consistent relationship between the similarity of stimuli to subjects and their unique view of attractiveness.

The most exacting test of assortative preferences concerns the subject's ratings of the face most similar to themselves. This is analogous to testing whether the extreme right point in Figure 3b has a rating that is higher than zero. For each of the thirty-six subjects, two ratings were compared. The first of these was the rating given by a subject to the image rated as most similar to that individual (the "self-similar" rating). In thirty-two of the thirty-six cases, this was the opposite-sex image generated from the subject's own face. The second was the median of all the other subjects' ratings of that face (the "others" rating). A Wilcoxon signed ranks test showed a non-significant trend for self-similar ratings to be higher than others' ratings of that image (Z = -1.692, p = 0.091, n = 36).

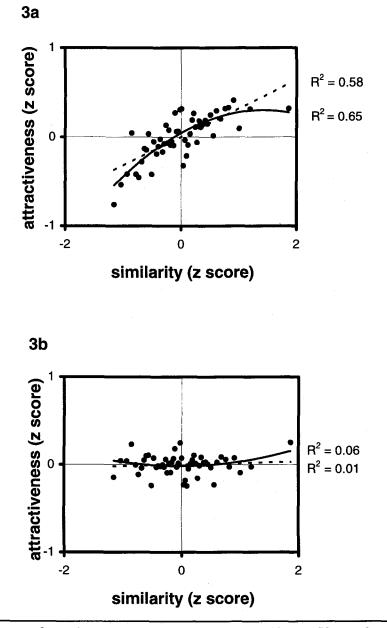


FIGURE 3 Facial similarity and judgements of attractiveness

Notes: (a) Average of attractiveness scores assigned by thirty-six subjects to fifty-two face stimuli ranked according to their similarity to each subject (for Method see text). Trend lines calculated by regression analyses using both linear (dashed line, accounting for 58% of the variance in the data) and second order polynomial models (solid line, accounting for 65% of variance). (b) Subjects' "unique view" of attractiveness, displaying the average difference between an individual's attractiveness rating of a face and the average ratings of all other subjects of that face. Linear and polynomial regression account for 1% and 6% of the variance respectively.

#### DISCUSSION

Figure 3a indicates that (a) subjects are attracted to others with similar faces and (b) preference peaks or asymptotes at a moderate level of similarity. Such evidence might be taken as support for the notion of optimal outbreeding and assortative mating. Figure 3b appears to contradict this.

It is not obvious how to reconcile Figure 3b with Figure 3a, in that it is not intuitive as to why subjects should be attracted to similar faces, but no more so than other members of the population. The results can be explained in terms of a preference for average face shapes. Consider faces that are very different from average; highly unusual faces are likely to receive low ratings of attractiveness but, by definition, such unusual faces are unlike most people. Subjects are not attracted to faces that look very different from themselves, but neither is anyone else. Now consider faces with an average shape that are viewed as attractive (Langlois and Rogman, 1990). A given subject's face will be more similar to an average face shape than to a face shape randomly chosen from the population. This means that average face shapes will have moderate levels of similarity to most subjects and will be rated relatively highly for attractiveness.

From these arguments, it can be seen that optimal outbreeding, positive assortative mating, and the averageness hypothesis all converge to make the same prediction: that like will prefer like (i.e., subjects will be attracted to similar looking others). While Burley (1983) notes that an assortative mating pattern need not be caused by assortative preferences, our data indicate that the corollary is also true: a *preference for similarity* (i.e., averageness) need not translate into a *pattern of similarity* in partners' faces. Consider a population of individuals of varying attractiveness (averageness) in which each individual competes to get the most attractive partner. The result is partnerships of equivalent levels of attractiveness (Berscheid et al., 1971). While highly attractive individuals should end up with similar (average) looking partners, there is no reason for unattractive couples to look alike: each partner may have a face shape that differs from average in unique ways. Thus, the averageness hypothesis predicts a preference for similar partners, but game theory predicts that this will not translate into a pattern of physical similarity in partners (positive assortative mating).

Figure 3b provides a measure of attractiveness relative to the opinion of others. Subjects may find faces that are slightly similar to themselves (i.e., average faces) attractive and faces very different from themselves (i.e., faces far from average) unattractive, but other members of the population are likely to have similar views about these same faces. From this analysis subjects will not have extra motivation (above other members of the population) to seek out partners with a similar face.

In summary, Experiment 1 found evidence for a positive relationship between facial similarity and judgements of attractiveness across a range of face stimuli (Figure 3a). This preference could simply reflect the relationship between averageness and attractiveness. There was, however, a trend for an assortative preference, i.e., subjects rated faces with the shape most similar to their own slightly higher than other subjects.

## **EXPERIMENT 2**

A more direct test of positive assortative preferences is to compare a subject's ratings of an opposite sex face that is constructed to have the same shape as that subject and an average face of the opposite sex. Experiment 2 was designed to allow this direct comparison. In addition, Experiment 2 addresses the concept of optimal similarity and investigates the possibility of negative assortative preferences for facial appearance. Negative assortative mating can be predicted from theories of parasite driven sexual selection since preference for partners with a dissimilar genotype should increase heterozygosity in offspring and, thereby, improve immunity (Thornhill and Gangestad, 1993). Human preferences for odour suggest negative assortative mating (Wedekind et al., 1995).

Novel interactive computer techniques allow warping between two different faces in real time giving subjects opportunity to select an optimum blend along a smooth continuum (Perrett et al., 1998). By constructing a continuum from an individual's sex transformed face through an average face to a face with dissimilar characteristics, the relative influence of similarity, averageness, and dissimilarity can be assessed. Thus, three competing hypotheses based on evolutionary concepts of fitness can be tested.

- (1) Individuals will be attracted to some optimal degree of self-similarity in a face to realize the possible fitness benefits of positive assortative mating—the "like prefers like" hypothesis;
- (2) Individuals will be attracted to facial shapes dissimilar to their own to maximise heterozygosity—the "opposites attract" hypothesis; and
- (3) Individuals will prefer average faces to self-similar or dissimilar face shapes as selection acts against extreme, non-average genotypes—the averageness hypothesis.

# Method

Subjects and Procedure. Forty female and twenty-one male (mean age 21) participants were photographed and the images digitized as in Experiment 1. The identity information used to create the similar face type (Figure 2, centre) can be subtracted from the male prototype to create a synthetic male with an "opposite" face type (Figure 2, right). If the original female had a small nose and thick lips, the similar male face would have both characteristics, but the opposite male face would have a large nose and thin lips.

These two new face shapes (the similar and opposite face types) formed the end points of an interactive continuum, in which participants could manipulate the face shape displayed by moving a mouse controlled pointer left or right. Colour information from the appropriate sex prototype was rendered into the face shape in real time. Moving the computer mouse to the left or the right of the image showed the similar or the opposite face. Between these two points, the image displayed a face shape in proportion to the position of the pointer. The centre of the range displayed a prototype image (50% of the similar and 50% of the opposite face shape—mathematically equal to the average). The interactive software ran on a Silicon Graphics Indigo<sup>2</sup> Maximum Impact workstation, in twenty-four-bit color. Two examples of the end-points of face continua are shown in Figure 2.

Seventeen females and six males took part in testing, all of whom had been photographed. Subjects were instructed to move the mouse left and right to view the continuum and press the space bar when the image on the screen was, in their opinion, most attractive. The software recorded responses in terms of the proportion of the transform selected by the subjects. After a short training period using continua of the same sex as the subject, the experimental stimuli proper were presented.

Male subjects performed sixty-three trials in total. The stimuli (female faces generated from the 21 male photographs) were grouped into three blocks of twenty-one trials; within each block the order of stimulus presentation was randomized. Similar and the opposite face shapes had an equal probability of appearing at the right or left end of the continua. Female participants performed ninety trials in total, in three blocks of thirty trials. Ten of the original forty continua generated were not included in testing to reduce the duration of the testing. Order and left/right presentation was randomized as for male subjects.

Subjects were naïve as to the source of the stimuli; they were at no point informed that their own faces were used to generate the images.

#### RESULTS

The face shape selected by subjects in the continuum generated from their own facial characteristics is of primary interest. Subjects could select a face shape anywhere between a 100 percent similar to 100 percent opposite in shape. The mean level of similarity selected from this range was compared to the null hypothesis that the face shape selected would, on average, be neither similar nor dissimilar to the subject's own face (i.e., that the optimal face would be the prototype and 0% similar).

A one-sample *t*-test against a hypothesized mean of 0 percent similarity preferred demonstrated that subjects did not generate responses that were significantly different from the prototype when presented with a continuum generated from their own face (mean preference = 2% similar, t(22) = -0.44, p = 0.67). Separate analyses for each sex also yielded non-significant results (females, mean = 4.4% similar, t(16) = -0.90, p = 0.38; males, mean = 4.4% opposite, t(5) = 0.35, p = 0.74).

#### DISCUSSION

Experiment 2 found no preference for any significant level of self-similarity in opposite sex partners. The design of this study placed it in a position to investigate the relative importance of two processes in preferences for facial shape: preference for

average characteristics and preference for self-similar characteristics. Research has shown that average faces are, in general, more attractive than the individual faces from which they are synthesised. This effect remains when skin texture and blurring are controlled in both original and average face shapes (Langlois and Roggman, 1990; Benson and Perrett, 1992). It appears hard to improve on faces with average characteristics. It may be that the fitness benefits associated with averageness (e.g., immunocompetence and fertility) far outweigh the hypothesised fitness benefits that accompany an optimal amount of self-similarity in a partner.

Our current experiments failed to reveal strong support for assortative preferences. One qualification of our studies is that they focused on female judgments of male attractiveness. Studies of sexual imprinting suggest stronger effects of early rearing on male subjects (Vos 1994, 1995a; Kendrick et al., 1998). Previous studies of spousal facial similarity have reported sporadic positive results; one possibility for these findings is that subjects have matched partners on attractiveness rather than physical resemblance.

Perhaps a better test of assortative mating theory would be to allow subjects to choose between faces that differ from average by equal amounts, but vary in similarity to the subject. If similarity between partners does correspond to a fitness advantage, and preferences for self-similar partners have evolved, subjects should prefer faces similar to themselves from a selection of equivalent non-average faces.

#### ACKNOWLEDGEMENTS

This work was supported by project grants to DP from Unilever Research and the ESRC-ROPA. IPV was supported by an ESRC Ph.D. studentship. We thank R. Edwards for help collecting similarity data, Dr. K. Lee, Dr. D. Rowland, and M. Burt for help in stimuli and test construction.

#### REFERENCES

- Allison, D.B., Neale, M.C., Kezis, M.I., Alfonso, V.C., Heshka, S., and Heymsfield, S.B. (1996). Assortative mating for relative weight: genetic implications. *Behavior Genetics*, 26, 103–111.
- Bateson, P. (1982). Preferences for cousins in Japanese Quail. Nature 295, 236-237.
- Bateson, P. (1983). Optimal outbreeding. In: *Mate Choice*, P. Bateson (ed.). Cambridge: Cambridge University Press, p. 257–277.

Bateson, P. (1988). Preferences for close relations in Japanese Quail. H. Ouellet. Ottawa: University of Ottawa Press. Acta XIX Congressus Internationalis Ornithologici, 1, 961–972.

Benson, P.J. and Perrett, D.I. (1992). Face to face with the perfect image. New Scientist, 133, 32-35.

Berscheld, E., Dion, K., Walster, E., and Walster, G.W. (1971). Physical attractiveness and dating choice: a test of the matching hypothesis. *Journal of Experimental Social Psychology*, 7, 173–189.

Burley, N. (1983). The meaning of assortative mating. Ethology and Sociobiology, 4, 191-203.

- Clark, P.J. and Spuhler, J.N. (1959). Differential fertility in relation to body dimensions. *Human Biology*, 31, 121–137.
- Dawkins, R. (1979). Twelve misunderstandings of kin selection. Zeitschrift fur Tierpsychologie, 51, 184– 200.
- D'Udine, B. and Alleva, E. (1981). Early experience and sexual preferences in rodents. In: *Mate Choice*, P. Bateson (ed.). Cambridge: Cambridge University Press, 311–330.
- Epstein, E. and Guttman, R. (1982). Mate selection in man: Evidence, theory, and outcome. Social Biology, 31, 243–276.
- Grammer, K. and Thornhill, R. (1994). Human (*homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology*, 108, 233–242.

- Griffiths, R.W. and Kunz, P.R. (1973). Assortative mating: A study of physiognomic homogamy. Social Biology, 20, 448-453.
- Hill, C.T., Rubin, Z., and Peplau, L.A. (1976). Breakups before marriage: The end of 103 affairs. Journal Social Issues, 32, 147-168.
- Hinsz, V.B. (1989). Facial resemblance in engaged and married couples. Journal of Social and Personal Relationships, 6, 223-229.
- Holmes, W.G. and Sherman, P.W. (1983). Kin recognition in animals. American Scientist, 71, 46-55.
- Immelman, K. (1975). Ecological significance of imprinting and early learning. Annual Review of Ecology and Systematics, 6, 15–37.
- Jones, D. (1995). Sexual selection, physical attractiveness, and facial neoteny. Current Anthropology, 36, 723-748.
- Kendrick, K.M., Hinton. M.R., and Atkins, K. (1998). Mothers may irreversibly determine male social and sexual preferences. *Nature*, 395, 229–230.
- Langlois, J.H. and Roggman. L.A. (1990). Attractive faces are only average. *Psychological Science*, 1, 115-121.
- Malina, R.M., Selby, H.A. Buschang, P.H., Aronson, W.L., and Little, B.B. (1983). Assortative mating for phenotypic characteristics in a Zapotec community in Oaxaca, Mexico. *Journal of Biosocial Science*, 15, 273–280.
- Ober, C., Hyslop, T., Elias, S., Weitkamp, L.R., and Hauck, W.W. (1998). Human Leukocyte antigen matching and fetal loss—results of a ten year prospective study. *Human Reproduction*, 13, 33–38.
- Partridge. L. (1983). Non-random mating and offspring fitness. In: Mate Choice, P. Bateson (ed.). Cambridge: Cambridge University Press, p. 227-256.
- Perrett, D.I., Lee, K.J., Penton-Voak, I.S., Rowland, D.R., Yoshikawa, S., Burt, D.M., Henzi, S.P., Castles, D.L., and Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, 394, 884– 887.
- Perrett, D.I., May, K.A., and Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature*, 368, 239-242.
- Rabin, I.A. (1965). Growing up in a Kibbutz. New York: Springer.
- Roberts, D.F. (1977). Assortative mating in man: Husband/wife correlations in physical characteristics. Supplement to the Bulletin of The Eugenics Society, 2.
- Rowland, D.A. and Perrett, D.I. (1995). Manipulating facial appearance through shape and color. IEEE Computer Graphics and Applications, 15, 70-76.
- Rushton, J.P. (1988). Genetic similarity, mate choice, and fecundity in humans. Ethology and Sociobiology, 9, 329-333.
- Rushton, J.P. (1989). Genetic similarity, human altruism, and group selection. Behavioral and Brain Sciences, 12, 503-559.
- Seemanova, E. (1971). A study of the children of incestuous matings. Human Heredity, 21, 108-128.
- Shepher, J. (1971). Mate selection among second generation Kibbutz adolescents and adults: Incest avoidance and negative imprinting. Archives of Sexual Behavior, 1, 293–307.
- Shepherd, J.W. and Ellis, H.D. (1972) The role of physical attractiveness in selection of marriage partners. *Psychological Reports*, 30, 1004.
- Spiro, M.E. (1965). Children of the Kibbutz. New York: Schocken Books.
- Spuhler, J.N. (1968). Assortative mating with respect to physical characteristics. Eugenics Quarterly, 15, 128-140.
- Symons, D. (1979). The evolution of human sexuality. Oxford: Oxford University Press.
- Talmon, Y. (1964). Mate selection in collective settlements. American Sociological Review, 29, 491-508.
- Thiessen, D. and Gregg, B. (1980). Human assortative mating and genetic equilibrium: An evolutionary perspective. *Ethology and Sociobiology*, 1, 111–140.
- Thornhill, R. and Gangestad, S.W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature*, 4, 237–269.
- Thornhill, R. and Gangestad, S.W. 1996). The evolution of human sexuality. *Trends in Evolution and Ecology*, 11, 98-102.
- Vandenberg, S.G. (1972). Assortive mating or who marries whom? Behavior Genetics, 2, 127-157.
- Vos, D.R. (1994). Sex recognition in zebra finch males results form early experience. Behaviour, 128, 1-14.
- Vos, D.R. (1995a). The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Animal Behavior*, 50, 645–653.
- Vos, D.R. (1995b). Sexual imprinting in zebra-finch females: Do females develop a preference for males that look like their father? *Ethology*, 99, 252–262.
- Waldman, B. (1987). Mechanisms of kin recognition. Journal of Theoretical Biology, 128, 159-185.
- Wedekind, C., Seebeck, T., Bettens, F., and Paepke, A.J. (1995). MHC-dependent mate preferences in humans. Proceedings of the Royal Society of London B., 260, 245-249.
- Westermarck, E. (1894). The History of Human Marriage. London: Macmillan.

Wilson, G.D. and Barrett, P.T. (1987). Parental characteristics and partner choice: Some evidence for Oedipal imprinting. *Journal of Biosocial Science*, 19, 157–161.

Wolf, A.P. (1993). Westermarck Redivivus. Annual Review of Anthropology, 22, 157-175.

Wright, S. (1933). The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the V1th International Conference on Genetics*, New York: Brooklyn Botanic Garden.

Zajonc, R.B., Adelmann, P.K., Murphy, S.T., and Niendenthal, P.M. (1987). Convergence in the physical appearance of spouses. *Motivation and Emotion*, 11, 335–346.

Zei, G., Astofli, P., and Jayakar. S.D. (1981). Correlation between father's age and husband's age: A case of imprinting? *Journal of Biosocial Science*, 13, 409–418.