By
LISA M. DEBRUINE, B.Sc, M.Sc.

A Dissertation
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

FACIAL RESEMBLANCE AFFECTS BEHAVIOUR AND ATTRIBUTIONS

DOCTOR OF PHILOSOPHY (2003)
(Psychology)

McMaster University
Hamilton, Ontario

TITLE: Facial Resemblance Affects Behaviour and Attributions

AUTHOR: Lisa M. DeBruine, B.Sc., M.Sc. (University of Michigan)

SUPERVISORS: Professors Margo Wilson and Martin Daly

NUMBER OF PAGES: xii, 97

Abstract

Two lines of reasoning predict that highly social species will have mechanisms to influence behaviour towards individuals depending on their degree of relatedness. First, inclusive fitness theory (Hamilton, 1964) leads to the prediction that organisms will preferentially help closely-related kin over more distantly-related individuals. Second, evaluation of the relative costs and potential benefits of inbreeding suggests that the degree of kinship should also be considered when choosing a mate. In order to behaviourally discriminate between individuals with different levels of relatedness, organisms must be able to discriminate cues of kinship. Facial resemblance is one such potential cue in humans. Computer-graphic manipulation of face images has made it possible to experimentally test hypotheses about human kin recognition by facial phenotype matching. I show that humans respond to facial resemblance in ways consistent with inclusive fitness theory and considerations of the costs of inbreeding, namely by increasing prosocial behaviour and positive attributions toward self-resembling images and selectively tempering attributions of attractiveness to other-sex faces in the context of a sexual relationship.

The four studies presented in this thesis use face images made to resemble either the experimental participants or unfamiliar people in order to test the impact of facial resemblance on behaviour and attributions. In Chapter 2, I demonstrated that people favour individuals represented by resembling faces in an economic game. In chapter 3, I tested the hypothesis that men, because of paternity uncertainty, should be more sensitive to phenotypic cues of relatedness to children than women should be. Although facial resemblance increased the attractiveness of and self-reported willingness to invest in pictured children, I found no evidence for a greater effect in men than women. To test whether responses to a kinship cue are sensitive to contexts in which the adaptive response should be different, I tested the perceived attractiveness of same-sex and other-sex self-similar faces in Chapter 4. Although self-resemblance increased the perceived "averageness" of male and female faces equally, self-resemblance increased the attractiveness of same-sex faces only. Additionally, in Chapter 5 I tested other-sex faces for trustworthiness, attractiveness in the context of a long-term relationship, and attractiveness in the context of a short-term relationship. Self-resemblance of other-sex faces increased attributions of trustworthiness, had no effect on attractiveness for a long-term relationship, and decreased attractiveness for a short-term relationship.

The results of these four studies indicate that humans respond to self-resembling faces in ways that are consistent with facial resemblance being a cue of kinship. Non-adaptive hypothesis explaining these results as byproducts of general perceptual mechanisms were tested and not supported. Specifically, the finding that same-sex faces were perceived as no more average than other-sex faces was evidence against the hypothesis that separate mental representations of male and female faces could explain the increased attractiveness of same-sex self-resembling faces relative to other-sex self-resembling faces in Chapter 4. The opposite responses to an other-sex self-resembling face for judgments of trustworthiness versus judgments of attractiveness in the context of a short-term relationship in Chapter 5 provided evidence against the "mere familiarity" hypothesis whereby exposure globally increases liking. Consequently, responses to facial resemblance seem best interpreted as evidence of specialized adaptations to the problems of kin recognition in the domains of mate choice and prosocial behaviour.

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Acknowledgements

I am sincerely grateful to my two wonderful advisors, Margo Wilson and Martin Daly. I've enjoyed every aspect of being involved in their lab. I am thankful to Bobbi Low, as well, for encouraging my scientific pursuits and for making me drive out to meet Martin and Margo when I thought I had made up my mind to study in a warmer climate. I never regretted it, even when the windchill was -40°C. I also wish to thank the past and present members of the Daly-Wilson lab: Andrew Clark, Pat Barclay, Nick Pound, Sean Myles, Danny Krupp, Alan Honey, Angela Chang, Paul Ramos, and Melanie McKenzie. I can't think of a better group of people to work (and juggle) with.

I would like to express appreciation to my friends and colleagues at McMaster. I've especially benefitted from the input of Sigal Balshine, Daphne Maurer, David Earn, Christopher Taylor, and Phil Cooper. I owe thanks to the entire McMaster Department of Psychology for providing such a supportive environment. Erie Long, Wendie Selbie, Sally Thompson, and Nancy Riddell were indispensable and made my life so much easier. Erie deserves special thanks for all the lovely brunches and American Thanksgiving dinners.

I owe a lot to my colleagues outside of McMaster, as well. Much of my research would not have been possible without the assistance of Ian Penton-Voak, Dave Perrett and Bernie Tiddeman. I am grateful for both the resources they kindly provided and all the other ways in which they benefitted my work. The past few months I've spent in Dave Perrett's lab have been wonderful and I wish to thank the lab members: Ben Jones, Dave Feinberg, Fhionna Moore, Miriam Law Smith, Elizabeth Cornwell, and Michael Stirrat. My talks with Tony Little are always educational and I thank him for that. I owe Steve Platek much gratitude for his help and correspondence.

My family also deserves thanks. They've always been supportive of my educational goals, even when the details of what I do perplex them. Finally, I'd like to specially thank Ben Jones. He knows what for.

Chapter 1

Introduction

As a highly social species, humans surely use some method to recognize their relatives. The identities of many relatives are distinguishable by environmental cues that reliably facilitate kin recognition, such as association with a parent or frequency and timing of contact (see section 1.4). However, reliably distinguishing other categories of relatives, such as maternal half-siblings from full-siblings, may require other mechanisms. Phenotype matching, the assessment of relatedness through the comparison of an individual's physical cues to a family template, is one possible mechanism. Although cross-fostering techniques have been successfully used to study phenotype matching in non-human animals (Holmes & Sherman, 1982; Penn & Potts, 1998; Todrank & Heth, 2001), it is difficult to use these techniques with humans. The recent development of sophisticated image transformation techniques that can manipulate facial similarity in a realistic manner allows for the investigation of whether and how humans use facial phenotype matching to recognize kin and how this affects social behaviour. In this thesis I will demonstrate that humans respond to experimentally manipulated facial resemblance in ways that are consistent with its use as a cue of kinship.

1.1 Why is it important to recognize kin?

Organisms can increase their fitness by recognizing and responding appropriately to kin. Such responses are said to be *context-dependent* because the fitness-enhancing response to kin is different in the contexts of nepotism and mate choice. Nepotism, in the biological sense, refers to the tendency to behave more altruistically toward relatives than toward non-relatives. Inclusive fitness theory (Hamilton, 1964) demonstrates the adaptive value of allocating effort toward others as a function of the probability they share copies of your genes that are identical by descent. This leads to the prediction that many organisms will direct their altruistic behaviour in response to cues of genetic relatedness. Recognition and categorization of kin are also important in a mating context due to the well-established costs of close inbreeding and the possible costs of extreme outbreeding.

In the next two sections I will present evidence for kin recognition and context-dependent differential treatment of kin and non-kin in the domains of nepotism and mate choice. Mammalian parental investment is discussed as one context in which cues of kinship are more or less reliably associated with genetic relatedness depending on individual circumstances.

1.1.1 Nepotistic Allocation of Altruism

Investment in others should be modulated by an assessment of how closely related they are, if at all. Examples of nepotism abound in nature, including insects (Greenberg, 1979), amphibians (Pfennig, Sherman, & Collins, 1994; Harris, Vess, Hammond, & Lindermuth, 2003), fish (Olsén, 1999), birds (van der Jeugd, van der Veen, & Larsson, 2002; Bukacinski, Bukacinski, & Lubjuhn, 2000), and mammals (Alberts, 1999; Heth, Todrank, Busquet, & Baudoin, 2003). Nepotism is expressed in many different ways, such as alarm calling in the presence of relatives (Sherman, 1977; Hauber & Sherman, 1998), kin-biased dominance interactions (Silk, 2002) and cooperative breeding (Griffin & West, 2003). Humans also show sensitivity to cues of genetic relatedness when making decisions about altruistic acts. For example, the rated probability of helping in a hypothetical situation (Burnstein, Crandall, & Kitayama, 1994) and the amount of imbalance tolerated in a reciprocal relationship (Hames, 1987) are both positively correlated with genetic relatedness.

While mammalian mothers have almost 100% confidence in their maternity, the same is not always true for fathers. Investment in young that varies with cues indiciating their probability of genetic relatedness is likely to have been favoured by natural selection. Consistent with this, Gaulin and Schlegel (1980) linked paternal confidence to investment in a cross-cultural sample of 186 preindustrial societies. Additionally, matrilateral kin, who have relatively high certainty of relatedness, invest more in children than patrilateral kin, who have greater reason to doubt their relatedness (Gaulin, McBurney, & Wartell, 1997; Euler & Weitzel, 1999).

These findings lead to the prediction that mammalian mothers use kin recognition methods such as regarding any infant who is present after childbirth as one's own child and are less affected by other, even conflicting, cues of relatedness such as lack of resemblance to self. On the other hand, fathers are predicted to rely on different cues, such as phenotypic similarity, to evaluate genetic relatedness. As a consequence, one might anticipate that men's investment in and relationships with offspring will vary with phenotypic similarity when other indicators of paternity (such as suspected maternal fidelity) are held constant, but women's investment will be relatively unaffected by phenotypic similarity.

1.1.2 Optimal Mate Choice

Another function of kin recognition is to avoid mating with close relatives and possibly even to obtain an optimal level of outbreeding. Mating between close relatives is associated with the risk of autosomal recessive genetic disorders and miscarriage (Bittles, 2001), although a positive association between consanguinity and fertility has been found due to other factors associated with consanguinous marriages, such as earlier age at first reproduction and longer duration of marriage (Bittles, Grant, Sullivan, & Hussain, 2002). In humans, a specialized mechanism for avoidance of inbreeding among close kin has been postulated in the form of the *Westermarck effect* (Westermarck, 1921; Wolf, 1995; Lieberman, Tooby, & Cosmides, 2003). This refers to the lack of sexual attraction between people who were closely associated as young children. In most circumstances, such people are likely to be close genetic relatives; thus, the Westermarck effect functions to prevent inbreeding.

While matings between closely related individuals can be deleterious, matings between too distantly related individuals can also carry costs such as the disruption of co-adapted gene complexes or suppression of genes adapted for specific environments (Bateson, 1983). The most extreme cost of outbreeding is hybrid sterility; traits functioning to prevent cross-species matings are likely to increase fitness. Organisms can regulate the genetic relatedness of mates through indirect means, such as the differential dispersal of the sexes (Pusey, 1987), or they can directly recognize relatives from familiarity or features characteristic of close kin and use this information when making decisions about mating partners.

1.2 Who should recognize kin?

Many species are likely to encounter individuals of differing relatedness to self in social or mating contexts. Without some method of recognizing kinship, such organisms cannot effectively direct nepotistic behaviour and are more vulnerable to the costs of inbreeding (and outbreeding). Put another way, the fitness benefits of directing altruism and mate choice as a function of genetic relatedness are unavailable to individuals who have no means to recognize kin. Natural selection should have favoured individuals who can both discriminate between individuals of differing relatedness to self and behave accordingly.

In certain situations, the costs and benefits of kin discrimination are different for different classes of individuals. One such situation is when the likelihood of encountering relatives differs for males and females because of sex-biased dispersal. For example, male Belding's ground squirrels disperse from their natal territory, but females do not. Thus, females are more likely than males to encounter kin as adults and females also show greater behavioural kin discrimination than males (Holmes & Sherman, 1982). To the degree that males and females both invest parentally in offspring, it behooves both to direct parental care preferentially toward genetically related young. However, the reliability of the association between kinship cues and genetic relatedness can differ according to sex.

1.3 Recognition vs. Discrimination

By "kin recognition", I do not mean that organisms have a cognitive representation of where individuals fit into a nested kinship structure or genealogical space, or even that they can recognize individual conspecifics. Instead, I use kin recognition to refer to the ability to direct different behaviours toward individuals based on cues associated with genetic relatedness (Porter, 1987).

Some authors distinguish kin recognition from kin discrimination, labeling recognition as a cognitive process of assessing relatedness and discrimination as a behavioural process (Gamboa, Reeve, & Holmes, 1991). Mateo (2002) demonstrated that Belding's ground squirrels (*Spermophilus beldingi*) showed recognition (in a habituation-recognition paradigm) of odour-based kinship cues of individuals with relatedness levels ranging from $r = 0.5$ (e.g. mother) to $r = 0.125$ (e.g. half-aunt), but only performed altruistic behaviour toward kin with relatedness levels greater than $r = 0.25$. For this reason, a failure to observe behavioural discrimination between individuals with different levels of relatedness cannot be used as evidence for the absence of an ability to perceptually discriminate between kin, although it is unclear why natural selection would have favoured such an ability if there were no fitness consequences.

Cues that are correlated with genetic relatedness can be utilized for kin recognition even in the absence of individual recognition. Kin recognition can be as simple as classing individuals based on proximity to one's home site and kin discrimination can operate to direct altruistic actions preferentially toward nearby individuals. For example, most "failures" of parent-offspring recognition (Beecher, 1991) are only seen in response to unnatural situations imposed by experimenters. If a certain species' offspring are reliably found only in the home nest, there is no reason to expect that species to evolve the ability to directly recognize offspring away from the nest. Indeed, Neff and Sherman (2002) developed a model defining the conditions under which kin recognition by indirect means would be favoured over kin recognition by direct means. The model uses the conditional (Bayesian) probabilities of correct and incorrect attribution of genetic relatedness to formalize the level of reliability that an indirect cue, such as presence in the nest, would require in order to outweigh the reliability of a direct cue, such as visual resemblance to self.

1.4 How do organisms recognize kin?

In order to direct behaviour discriminatively in a way that is contingent upon relatedness, organisms must have proximate mechanisms to detect cues that are reliably associated with differences in genetic relatedness. Cues and methods that are used for kin recognition have been variously categorized as *indirect* and *direct* (Hauber & Sherman, 2001); *spatial location*, *association/familiarity*, *recognition alleles*, and *phenotype matching* (Porter, 1987; Tang-Martinez, 2001); and *location*, *association*, and *situation* (Wells, 1987). Humans have available another type of cue, verbal communication.

Differential behaviour toward individuals based on indirect cues such as location or age does not require organisms to store a perceptual or cognitive representation of kin identity. For example, in species where the spatial distribution of relatives is highly predictable, such as when one sex disperses and the other remains in the natal area, location alone can indicate relatedness. The location of an individual can provide information about the probability of it being kin even in the absence of an ability to recognize specific individuals. If situational cues, such as a particular hormonal state, are reliably associated with the presence of kin they can also cause a general predisposition to behave altruistically. For example, female gerbils frequently cannibalize pups, but this tendency decreases in the latest stages of pregnancy (Elwood, 1977).

Direct methods of kin recognition require the learning of individual kin identities in response to an association or situation. Learning is constrained to a stage where only relatives are likely to be encountered (e.g. imprinting in newborn goslings; Lorenz, 1970) or is otherwise limited to avoid false kin recognition. Situational cues, such as the experience of mating, can cause animals to treat others experienced under those circumstances as kin. For example, male langurs refrain from infanticide if they had copulated with the mother of the infant (Hrdy, 1979).

The use of kinship terminology that indicates genetic relatedness is a universal feature of human societies (Daly, Salmon, & Wilson, 1997). In addition, most communities have certain members whose special function is to keep track of genealogies and even in the individualistic societies of North America, genealogy holds enormous interest for many people (Shoumatoff, 1985). Although it is unknown how terminological kinship cues are translated into assessments of genetic relatedness, nominal kinship cues have been shown to influence altruistic behaviour (Oates & Wilson, 2002) and agreement with political views (Salmon, 1998).

While there is convincing evidence for the use of the above methods of assessing kinship, it is more controversial whether any organisms use the other class of kin recognition, phenotype matching (Alexander, 1990; Grafen, 1990).

1.4.1 Phenotype Matching

Phenotype matching refers to the use of the sensory modalities (e.g. vision, audition, and olfaction) to recognize relatives through comparison to a mental "kin" template against which individuals are compared. Phenotype matching may be used for novel individuals or individuals who present ambiguous relatedness cues. In species where such individuals are commonly encountered this ability is likely to be adaptive, while in other species the favouring of individuals with phenotypes similar to kin is likely to be an incidental effect of imperfect recognition of individuals (Alexander, 1990). In other words, individuals may be treated as kin because they resemble known kin enough to be confused for them, not because selection favoured such an ability.

Phenotypic cues can indicate the presence of particular genes. If such genes also influence behavioural discrimination based on that phenotype, then selection is likely to increase their representation in a population. An adaptation for directly recognizing a particular genotype/phenotype (i.e. green-beard gene) has been shown to exist in some species (Grosberg & Quinn, 1976; Keller & Ross, 1998), but the phenotypic cue being matched is controlled by one or a few genes. More complex cues, such as general physical resemblance, are the result of the interaction of many genes which are frequently disrupted by sexual reproduction. Genes for complex phenotypic traits are unlikely to have the polymorphic effect of or be associated with genes influencing both the development of a corresponding mental template and adaptive behavioural responses to phenotypic similarity. Consequently, phenotype matching for complex polygenic traits is unlikely to involve direct assessment of genotype.

Kinship is predictive of the probability of sharing any autosomal gene. A gene that influences behavioural discrimination based on a reliable correlate of kinship should, on average, have the same effect as a gene directly detecting and favouring individuals possessing copies of itself (Hamilton, 1964). A kin template can be learned from observing one's own phenotype (*self-referential phenotype matching*) or that of others who are likely to be closely related (*familial imprinting*). Self-referential phenotype matching would be the least corruptible method, but learning a phenotype by familial imprinting may be easier and the opportunity to do so may be very reliable.

Hauber and Sherman (2001) delineate the circumstances under which self-referential phenotype matching would be favoured over other methods of kin recognition. These circumstances include multiple mating, dispersal and inter-brood aggregation. Without self-referential phenotype matching, the identity of maternal half siblings is not distinguishable from full siblings and the identity of paternal half-siblings is not distinguishable from non-relatives. In species with dispersal or overlapping generations, individuating methods of kin recognition are not sufficient because unfamiliar related individuals are encountered later in life. In circumstances where young are raised communally or by non-relatives, familial imprinting is likely to result in errors of kin recognition and even species recognition (e.g. in the case of brood parasitism).

Cross-fostering is a common research paradigm for distinguishing between self-referential phenotype matching and familial imprinting. Cross-fostered individuals are taken from their natal family and raised by a family with a different phenotype. Self-referential phenotype matching can be inferred if these individuals later show typically kin-directed behaviour toward their own unfamiliar genetic relatives. Familial imprinting can be inferred from such behaviour toward unfamiliar genetic relatives of the foster family.

Both phenotype-matching and kin recognition by association have been demonstrated in Belding's ground squirrels. Squirrels cross-fostered at birth have fewer aggressive interactions with familiar individuals than unfamiliar ones, regardless of their genetic relatedness, and also show less aggression toward genetic siblings than unrelated individuals, regardless of their familiarity (Holmes & Sherman, 1982). Sweat bees also exhibit familial imprinting; they will allow unfamiliar unrelated females into a hive if they have a phenotype similar to that of cross-fostered siblings (Greenberg, 1979). Similar experiments have demonstrated the existence of self-referential phenotype matching in several species of birds and mammals and one species of fish (see Hauber & Sherman, 2001, for a detailed review).

The kin template used in phenotype matching can be represented in any perceptual system, including vision, audition and olfaction. For example, Japanese quail (*Coturnix coturnix*) have been shown to discriminate between different degrees of relatives by visual cues alone (Bateson, 1982). One of the most interesting methods of kin recognition utilizes a highly variable segment of the genome ideally suited for allowing discrimination between varying degrees of relatives: the major histocompatability complex (MHC). This polymorphic region codes for parts of the immune system that function to discriminate between self and non-self. It also affects odour, as shown by the ability of mice to discriminate between the urine odours of individuals who are genetically identical at every locus except a single one in the MHC region (Yamazaki et al., 1983). House mice (*Mus musculus*) have been extensively studied in this context and have been shown to use MHC cues for both mate choice and nepotism. Several studies have demonstrated MHC disassortative mating preferences (Potts, Manning, & Wakeland, 1991; Penn & Potts, 1999; Yamazaki et al., 1988) which could function to reduce inbreeding or to maintain diversity in the immune system. Cross-fostering studies have shown that MHC preferences are most likely a result of familial imprinting since fostered mice avoid mating with individuals matching the MHC type of their foster family and do not avoid mating with individuals with their own MHC type (Penn & Potts, 1998). Responses to MHC-similar individuals are not uniformly negative, however. House mice, who form communal nests and nurse all pups in the nest, prefer to nest with MHC-similar individuals (Manning, Wakeland, & Potts, 1992). This demonstration of context-dependent preferences more decisively implicates the MHC in kin recognition.

1.5 Phenotype Matching in Humans

1.5.1 Odour-Based Matching

The human sense of smell is not highly salient in most of our conscious social interactions. Nevertheless, studies have found that people are remarkably good at determining the identity of relatives from their odour. Wallace (1977) demonstrated that participants could discriminate between two people on the basis of hand smell alone. The participants were also more accurate at distinguishing unrelated people than siblings or twins, suggesting that related individuals have more similar odours. In another study, Porter, Cernoch, and Balogh (1985) found that participants could match the odours of mothers with their children, but not husbands with their wives, indicating that shared genes contribute more to similarity of odours than shared environment. The T-shirt odours of children can be correctly identified by their siblings and mothers at levels greater than chance, and mothers are able to correctly discriminate between T-shirts worn by two of their children (Porter & Moore, 1981). Mothers can even identify their newborn infants' odours after a mean of 2.4 hours of exposure after birth (Porter, Cernoch, & McLaughlin, 1983). These differences in odour may be related to the major histocompatability complex (MHC).

Preference studies indicate that MHC-odours affect attractiveness judgments and possibly mate choice in humans. Wedekind, Seebeck, Bettens, and Paepke (1995) found that women who were not taking oral contraceptives preferred the smell of T-shirts from men with few MHC alleles in common with themselves, while women taking oral contraceptives exhibited the opposite preference. They explained this by likening the hormonal state caused by oral contraceptives to that of pregnancy and comparing it to nursing mice's preference for MHC-similar nestmates. A second study by Wedekind and Furi (1997) replicated these results and found that T-shirts that reminded participants of a mate or ex-mate came from people who shared fewer MHC alleles with those participants than expected by chance. Ober et al. (1997) addressed the distribution of MHC alleles in actual matings using a sample of married Hutterite couples. They found that couples shared fewer MHC alleles than expected by chance. Of those who did share haplotypes, in 50 out of 79 cases it was the paternally inherited haplotype, indicating that the MHC phenotype may be learned primarily from the mother.

1.5.2 Vocal Recognition

Anecdotally, family members are often told that they sound alike, especially on the phone. Whether this reflects the phenotypic expression of genetic similarity or is a consequence of shared environment is unknown. Apparently, no studies have investigated vocal resemblance in humans as a method of assessing genetic relatedness. A lack of such studies probably reflects people's intuition about the methods humans use to assess relatedness.

1.5.3 Facial Resemblance

An obvious candidate for a phenotypic indicator of relatedness in humans is facial resemblance. Most of the existing research on facial resemblance relevant to phenotype matching falls into one of two conceptual categories: paternity assessment and assortative mating based on resemblance between mates.

Paternity Assessment

Evidence from attributions of the resemblance of newborn babies suggests that people regularly assess putative fathers' facial resemblance to a child (Daly & Wilson, 1982; Regalski & Gaulin, 1993). While modern men can check these assertions by looking in the mirror and making their own assessment, men in the past would have had to rely on others' reports or assessment of the infant's resemblance to other kin. Humans have a conscious understanding of the implications of paternal non-resemblance that can have real impacts on a child, as evidenced by a study of the purported rationales for infanticide in a sample of 60 societies, in three of which it was reported that infants were killed because their appearance indicated inappropriate paternity (Daly & Wilson, 1984).

Much interest has been expressed in a finding that babies resemble their fathers more than their mothers (Christenfeld & Hill, 1995). On one hand, this is theoretically plausible, since men face the problem of paternity uncertainty and infants could benefit from proving their relatedness to the putative father. On the other hand, infants are not expected to advertise their paternity if cuckoldry is common or the cost of reliably cuing paternity is high (Pagel, 1997; Bressan, 2002). Despite numerous attempts to replicate Christenfeld and Hill's findings, the only consistent conclusion is that people can match children to their parents at levels significantly above chance. No other researchers have found that children resemble their fathers more than their mothers (Brédart & French, 1999; Bressan & Martello, 2002; Bressan & Grassi, in press; McLain, Setters, Moulton, & Pratt, 2000; Nesse, Silverman, & Bortz, 1990; Oda, Matsumoto-Oda, & Kurashima, 2002; Porter, Cernoch, & Balogh, 1984).

A pair of studies assessing hypothetical reactions to pictured children whose images had been manipulated to resemble adult participants found that men had more positive responses to self-resembling children than did women (Platek, Burch, Panyavin, Wasserman, & Gallup Jr., 2002; Platek et al., 2003). The methodology of these studies leaves open the possibility that men and women differed in responses to self-resemblance because they differed in the propensity to favour one child in a group versus treat them equally. Chapter 3 summarizes these studies by Platek et al. and presents an experiment that improves upon their methodology and replicates their results in some details but not others.

Assortative Mating

The evidence for facial resemblance between human mating partners is mixed. Some studies have found that both engaged couples and those married for many years are rated as more similar than randomly paired couples (Hinsz, 1989; Griffiths & Kunz, 1973). On the other hand, Zajonc, Adelmann, Murphy, and Niendenthal (1987), using photographs of the same couples during their first and twenty-fifth years of marriage, found that similarity was only present after many years of marriage. Although these studies attempted to control for factors such as similarities in attractiveness, health, and ethnicity that could account for the above-chance matching of couples' faces, it is a difficult task in a non-experimental study. These issues are discussed in greater depth in Chapter 4 which addresses preferences for self-resemblance in computer-generated faces lacking the above confounding factors.

1.6 Face Recognition and Processing

Humans have extraordinary face recognition capabilities and the study of the visual perception of faces is an active area in psychology. Responses to facial self-resemblance must be mediated by perceptual phenomena associated with face processing. Most relevant to kin recognition by facial phenotype matching are the phenomena of preference for familiarity and prototype formation.

1.6.1 Averageness and Familiarity

People find average faces attractive (Langlois & Roggman, 1990), although not all attractive faces are average (Perrett, May, & Yoshikawa, 1994). Mere exposure to a face or other object reliably increases liking upon later presentation of that same stimulus (Zajonc, 1968; Bornstein, 1989). Halberstadt and Rhodes (2003) argue that averageness judgments reflect perceived familiarity which has been found to statistically account for the correlation between averageness and attractiveness for the artifactual category of wristwatches, although not for the biological categories of dogs and birds (Halberstadt & Rhodes, 2000).

A preference for familiarity, combined with a tendency to form prototypes from individual examples by mentally averaging those examples, may account for the attractiveness of average faces. To test this hypothesis Rhodes, Halberstadt, and Brajkovich (2001) tested the effect of exposure to a set of individual faces on liking and attractiveness ratings of subsequently presented composite faces (averages of several individual faces). Liking and attractiveness ratings of composites that were composed of the previously presented individual faces were increased relative to composites made from previously unseen faces. Similar results were found in an experiment in which infants were familiarized with a set of female faces and tested with the composite average of these faces and novel female faces. Infants looked longer at the novel faces than either the familiar faces or the composite, indicating that the composite face was perceived as a familiar stimulus (Rubenstein, Langlois, & Kalakanis, 1999). Rhodes et al. (2001) argue that effects of familiarity and mere exposure necessarily imply changes to a mental prototype.

1.6.2 Prototyping

One possible proximate explanation for responses to facial resemblance is found in a model of how humans represent faces. Prototype-based coding involves the representation of faces as deviations from a mean that is constructed by averaging the faces one sees.

Blanz, O'Toole, Vetter, and Wild (2000) provided support for prototype-based coding using faces manipulated to be perceptually opposite target faces. These "anti-faces" were manipulated in shape and colour relative to an average face. For example, if a target face has a wider nose and thinner lips than the average, its anti-face will have a narrower nose and thicker lips than the average. Blanz et al. (2000) found that pairs of faces differing in shape and colour by the same amount are perceived as less similar if they are on different sides of the average than if they are on the same side. Complex perceptual adaptation effects in relation to the average (Leopold, O'Toole, Vetter, & Blanz, 2001) are also evidence of prototype-based coding. Brief presentation of an anti-face caused subsequent recognition of anti-caricatures (morphs intermediate to the target face and the average face) of the same face to increase and even caused greater than chance perception of the target face when the unmanipulated average was shown. These two studies provide evidence that the average face has some psychological salience and that faces may be encoded in relation to a mental prototype. Further explanation of perceptual adaptation to faces and its relevance to facial phenotype matching are discussed in Section 6.3 of Chapter 6.

Prototyping models of face processing have implications for kin recognition by facial phenotype matching because the faces one sees, either over a lifetime or during a critical period, influence the encoding of all faces. Thus, it makes sense that one's own face and the faces of one's family members might be represented to a greater extent than they are actually present in the population. Since people prefer average faces to non-average faces (Langlois & Roggman, 1990), if one's mental prototype is biased toward one's own face, it would follow that one would favor faces resembling one's own face. Thus, any preference for self-similar faces may simply be an artifact of prototype formation and a general preference for familiarity. Alternatively, prototyping may be one proximate mechanism involved in a more complex adaptive mechanism for facial phenotype matching. This issue is addressed further in Chapters 4 and 5.

1.7 Image Manipulation Techniques

The studies in the following chapters are experimental in nature and use computer imaging techniques to manipulate facial resemblance between subjects and the faces they viewed during the experiments. Two different methods were used, *averaging* and *transforming*. Specific details are described in the methods section of each experiment, but the general procedures are as follows.

1.7.1 Averaging Faces

The basic procedure for averaging images is illustrated in Figure 1.1a-d. A number of corresponding points, such as the centre of the pupils and the corners of the lips, are defined on two images. These images are termed *endpoint images* because they can be conceptualized as the 0% and 100% endpoints of a continuum. An algorithm is used to divide the endpoint images into triangular sections with the points as vertices (Fig. 1.1a,b). Two images can be combined (also termed *averaged* or *morphed*) by calculating the weighted average of the point coordinates. This results in new coordinates that are a specified percent of the distance between corresponding points along a vector connecting those points (Fig. 1.1c). This percent can be positive or negative: positive values move the points from the first image toward those from the second and negative values move them away. The triangular sections of the original images are warped into the shape of the new triangular sections defined by these calculated points. Colour values of corresponding pixels from the resulting warped images are combined in a specified ratio to make the finished morph (also termed *average* or *composite*, Fig. 1.1d). If the colour values from only one image are used, it is termed a *shape-only* morph.

1.7.2 Transforming Faces

Transforming images involves calculating the differences between two *endpoint* images and applying those differences to a *base* image. The basic procedure is much like

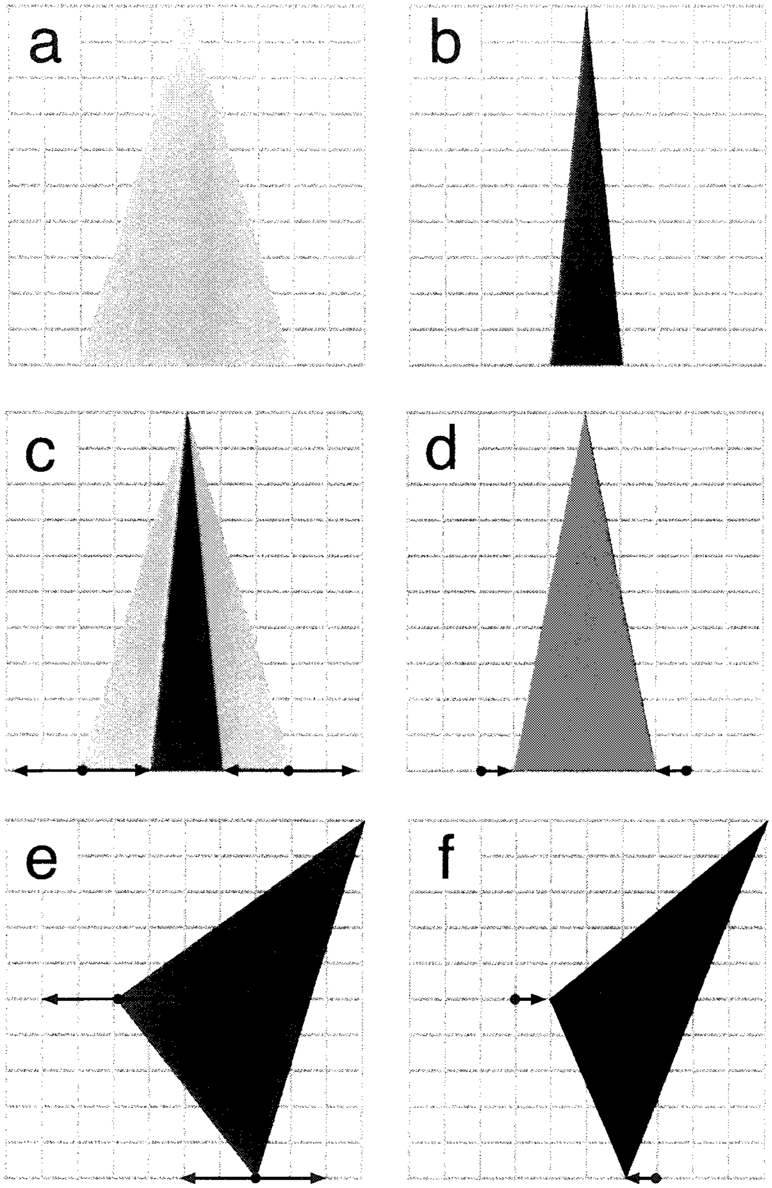

Figure 1.1: Averaging and transforming procedure examples. *Averaging* combines endpoint images (a, b) by calculating vectors through corresponding points (c), warping the endpoint images by moving these points to a specified position along the vector, and/or averaging colour values to make a *morph* (d). *Transforming* applies a percentage of the shape and/or colour differences between the two endpoint images to a third base image (e) to make a *transform* (f). These examples use 50% values for both shape and colour of each of the endpoint images. Notice that the morph (c) is a colour that is halfway between the endpoint images (a, b), but the transform (f) is darker than its base image (e) to 50% of the extent that the second endpoint image (b) is darker than the first (a).

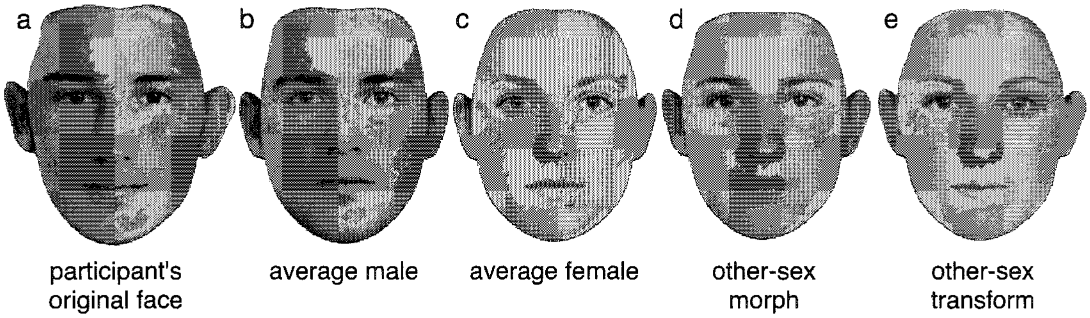

Figure 1.2: Other-sex morph versus other-sex transform. The other sex morph (d) was made by averaging the shape and colour of the participant's face (a) and an average female face (c). The other-sex transform (e) was made by applying 50% of the difference in shape and colour between the participant's face (a) and the average male face (b) to the average female face (c). Notice how androgynous the morph (d) appears compared to the transform (e).

morphing (see Tiddeman, Perrett, & Burt, 2001, for computational details); the same corresponding points are defined on each of the three images and these images are divided into triangular sections. The base image (Fig. 1.1e) can be transformed by moving the points on the base image a percentage of the distance between corresponding points on the endpoint images along the vector defined by the corresponding points on the endpoint images (Fig. 1.1c). Colour can also be transformed by changing the pixel colour values of the base image by a percentage of the extent that corresponding pixel colour values of the endpoint images differ. The resulting transform (Fig. 1.1f) is different from the base image in the same way that the second endpoint image is different from the first endpoint image. For example, if the second endpoint image (Fig. 1.1b) is thinner and darker than the first endpoint image (Fig. 1.1a), the transformed image (Fig. 1.1f) will be thinner and darker than its base image (Fig. 1.1e).

While the averaging technique is useful under certain conditions and software for averaging images is readily available, the transforming technique has several advantages for testing reactions to self-resemblance. First, averaging makes the resulting face more symmetrical and prototypical than either of the endpoint faces. Increasing averageness

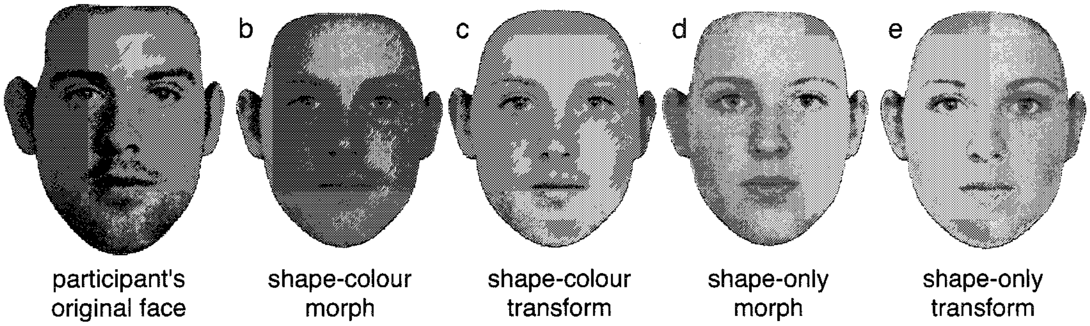

Figure 1.3: Shape-colour versus shape-only morphs and transform. The shape-colour morph (b) and transform (c) were made by averaging or transforming using 50% of the shape and colour information from the endpoint faces. The shape-only morph (d) and transform (e) were made by using 50% of the shape information from the endpoint faces and colour information only from the average female face. Notice how the shape-colour images (b, c) have the appearance of facial hair, while shape-only images (d, e) do not.

increases perceptions of attractiveness (Langlois & Roggman, 1990) and using averaged faces could cause ceiling effects for attractiveness judgments. More importantly, the transforming technique makes the production of other-sex self-resembling faces possible (Figure 1.2). Averaging participants with other-sex faces would produce androgynous, unrealistic morphs (e.g. Fig. 1.2d, Fig. 1.3b, d). Transforming other-sex faces to the extent that the participant faces differ from a prototypical same-sex face does not masculinize or feminize the resulting other-sex transform (Fig. 1.2e, Fig. 1.3c, e).

Additionally, the use of shape-only transforms is required to eliminate unnatural colour artifacts caused by transforming female faces using male endpoint faces with differing amounts of facial hair. A man with more facial hair than the male average will have a female transform with the appearance of stubble (Fig. 1.3c), while a man with less facial hair than average will have a female transform with light blotches in the areas where facial hair differs on the endpoint faces.

Averaging was used to create the images for the experiments in Chapter 2. Because of the technical resources available at the time, only same-sex morphs were made. One subset of participants viewed morphs averaged in both shape and colour, while another subset viewed morphs averaged in shape only. Shape-only morphs were necessary for participants who were not of the same ethnicity as the unfamiliar faces and for men with facial hair, which would result in unnatural shadowy beards if averaged in colour. A combination of transforming and averaging was used to create the images for the experiments in Chapter 3. Adult faces were first transformed using average adult and infant faces as the endpoints in order to give the adult faces more baby-like proportions. The resulting transforms were averaged with infant faces to make the final images. Transforming was used to create the images for the experiments in Chapters 4 and 5 because they tested responses to other-sex faces, which can only be realistically made using shape-only transforming for the reasons described above. Specific details of the image manipulations can be found in each chapter.

1.8 Does facial resemblance affect human behaviour and attributions?

The following four chapters present experiments using averaged and transformed face images to elucidate how facial similarity between self and another moderates social inclinations, namely trust, altruism and sexual attraction.

In Chapter 2, I demonstrate that people are more likely to trust those who resemble themselves when playing an interactive investment game common to experimental economic research. This "trust game" gave the first player a choice between evenly splitting a small sum of money between self and the second player or entrusting a larger sum of money to the second player who could divide it equally or selfishly. When the pictured game partner had been subtly manipulated to resemble the experimental participant, he or she was more likely to trust the partner, although participants were no less likely to behave selfishly in the role of the second player.

Chapter 3 tests the prediction that men will have more positive responses than women in reaction to images of child faces that resemble self. Although I found that attractiveness judgements and self-reported probability of investment in children increased with self-resemblance, this effect was similar between men and women.

Since positive regard is likely to facilitate trust, increased perceptions of attractiveness may have mediated the finding in Chapter 2 that self-resemblance of same-sex game partners enhanced trusting behavior. In Chapter 4, I show that images of same-sex faces manipulated to resemble a viewer were judged as more attractive by that research participant than by others. In contrast, resemblance had a much smaller effect on the attractiveness of other-sex faces, in line with predictions derived from consideration of the costs of inbreeding.

Following this result, in Chapter 5 I show that self-resemblance increased attributions of trustworthiness to other-sex face images, but had a smaller or negative effect on attributions of attractiveness for long-term and short-term relationships. This result provides the most convincing evidence so far that responses to facial self-resemblance are context-dependent.

My findings demonstrate that facial resemblance can affect attributions and behaviour toward others. Divergent effects of facial resemblance in the domains of prosocial regard and mate choice clearly refute the hypothesis that responses to facial resemblance are non-adaptive byproducts of perceptual phenomena involved in face processing and support the existence of specialized adaptations for kin recognition by facial phenotype matching.

Chapter 2

Facial resemblance enhances trust

Preface

This chapter is reproduced from DeBruine (2002), which was published in the *Proceedings of the Royal Society of London, B* in volume 269 on pages 1307-1312.

Abstract

Organisms are expected to be sensitive to cues of genetic relatedness when making decisions about social behaviour. Relatedness can be assessed in several ways, one of which is phenotype matching: the assessment of similarity between others' traits and either one's own traits or those of known relatives. One candidate cue of relatedness in humans is facial resemblance. Here, I report the effects of an experimental manipulation of facial resemblance in a two-person sequential trust game. Subjects were shown faces of ostensible playing partners manipulated to resemble either themselves or an unknown person. Resemblance to the subject's own face raised the incidence of trusting a partner, but had no effect on the incidence of selfish betrayals of the partner's trust. Control subjects playing with identical pictures failed to show such an effect. In a second experiment, resemblance of the playing partner to a familiar (famous) person had no effect on either trusting or betrayals of trust.

2.1 Introduction

Humans undoubtedly learn who their relatives are by association and verbal communication, but these methods are not equally reliable for all classes of kin. Identification of one's mother and maternal siblings can be achieved by association, but distinguishing maternal half-siblings from full siblings, identifying one's father, or even recognizing offspring (for males), may require additional mechanisms such as phenotype matching (Hauber & Sherman, 2001; Pfennig & Sherman, 1995; Porter, 1987). Phenotype matching refers to an implicit evaluation of relatedness on the basis of some trait-based assessment of phenotypic similarity. This assessment of similarity may be either with reference to one's own phenotype (self-referent phenotype matching) or with reference to the phenotypes of individuals conveying other cues of kinship such as the patterns of social association characteristic of close family members. Evidence of phenotype matching has been found in several species, including ground squirrels (Holmes & Sherman, 1982), baboons (Alberts, 1999), golden hamsters (Mateo & Johnston, 2000), and rhesus monkeys (Meikle & Vessey, 1981), although seldom on the basis of visual cues. People, however, certainly attend to familial resemblances in appearance, especially on the paternal side (Daly & Wilson, 1982; Regalski & Gaulin, 1993), making facial resemblance a likely candidate for phenotype matching.

Digital morphing techniques provide an opportunity to manipulate facial resemblance experimentally and assess its effects on behaviour. Digital morphing allows photographs of two faces to be melded into a realistic virtual face by delineating corresponding points located at several standard landmarks (such as the corners of the eyes and the mouth) on each of the source faces, and generating a new face (the "morph") from a weighted average of landmark-specific parameters of the sources. Morphing may entail the averaging of both shape and colour information from the source faces, or shape alone. In shape-only morphing (also called warping), the morph retains the coloration of one specified source face. Otherwise, the color values of each pixel from matching locations on the two faces are also averaged to produce the morph. Morphs generally have smoother-looking skin and are more symmetrical than source faces, but appear realistic. In the present study, all experimental (self-similar) and control faces were morphs, so these effects of morphing were not confounded with cues of resemblance. Of course, facial averaging by digital morphing may not produce resemblances that are identical to those resulting from actual relatedness, but this consideration should only work against the hypothesis that experimental manipulation of resemblance in morphs will affect social responses as predicted. There has been little research on whether and how family members resemble each other. Unrelated people can detect resemblance between parents and infants or children, but their accuracy is far from perfect (Bressan & Martello, 2002; Nesse et al., 1990; McLain et al., 2000; Brédart & French, 1999). Understandably, even less has been done on the ability to assess resemblance of one's relatives to one's self, although Porter et al. (1984) found that, after only 15 minutes to 20 hours (average 4.7 hours) of post-natal contact, 22 of 24 mothers could correctly identify their infants from sets of four photographs of infants matched for sex, age, race, and amount of hair, and many of the mothers indicated that a family resemblance helped them to identify their child.

If humans use phenotype matching to guide their decisions and actions, they might be expected to exhibit higher levels of prosocial behaviours, such as trust and equitable sharing, towards those who resemble them. Economists have developed laboratory analogs of trust and selfish behaviour in the form of sequential bargaining games with monetary incentives. I report on the results of a computer-interactive "two-person" trust game (Figure 2.2) where Player 1 (P1) chooses either to dictate an equitable division of a small sum or to trust Player 2 (P2) to divide a larger sum equitably, even though the latter has a more selfish option. Standard game theory models of self-interested choice suggest that P2 should always act selfishly in an anonymous one-shot game of this sort, and therefore P1 should never trust P2. However, experimental studies have shown that P1 often does trust P2, and that P2 often rewards that trust with an unselfish division (Scharlemann, Eckel, Kacelnik, & Wilson, 2001; McCabe, Rassenti, & Smith, 1996; Berg & Know, 1995; Hoffman, McCabe, & Smith, 1998). The tendency to trust can be manipulated by framing effects, such as labeling the other player with terms implying cooperation or competition: in an experiment by Burnham, McCabe, and Smith (2000), the label "partner" produced twice as much trusting behaviour as the label "opponent". In light of this evidence, it is plausible that cues of relatedness will also increase prosocial behaviour in the trust game.

If the ultimate, evolutionary reason why payoffs to oneself have utility is because they enhance expected fitness, then payoffs to one's kin should also have utility because of inclusive fitness effects, and a cue of kinship with one's playing partner should imbue the partner's payoffs with utility proportionate to the degree of relatedness, r, that is implied by the cue (Hamilton, 1964). In the payoff structure of the current game, the expected effect of such an evolved psychology would be both to raise the incentive to trust, from 1 to $(1+r)$, and to lower the cost of betrayal, from 1 to $(1-r)$. According to this model of "nepotistic" social motives, people playing P1 should be more willing to trust a P2 that presents a cue of kinship, even if P1's subjective probability of unselfish reciprocation by P2 is unaffected by the cue (Figure 2.5). Moreover, by similar reasoning, a cue of kinship should reduce P2's incentive to betray a trusting P1, from 1 to $(1-r)$.

2.2 Methods

2.2.1 Preparation of facial stimuli

To create a cue of kinship, facial resemblance was manipulated using digital morphing techniques to combine same-sex faces of persons unknown to the subject (called "unknown" faces) with either the subject's own face ("self") or another unfamiliar same-sex face ("non-self").

The unknown and non-self faces were obtained by recruiting volunteers from another Ontario university. Photographs (neutral expression and centered) of 24 male and 24 female Caucasian students between the ages of 19 and 25 (mean age 21 years) were standardized for interpupillary distance and cropped to a standard size (320 x 400 pixels). Clothing and facial jewelry were removed digitally (Adobe Photodeluxe 2.0). The same procedure was used to prepare the images of the 24 research participants ("subjects"), who ranged in age from 18 to 24 (mean age 21 years). Photographs of the subjects were taken prior to the experiment, on the pretext that they were needed in order to show the subjects' faces to their playing partners at other universities.

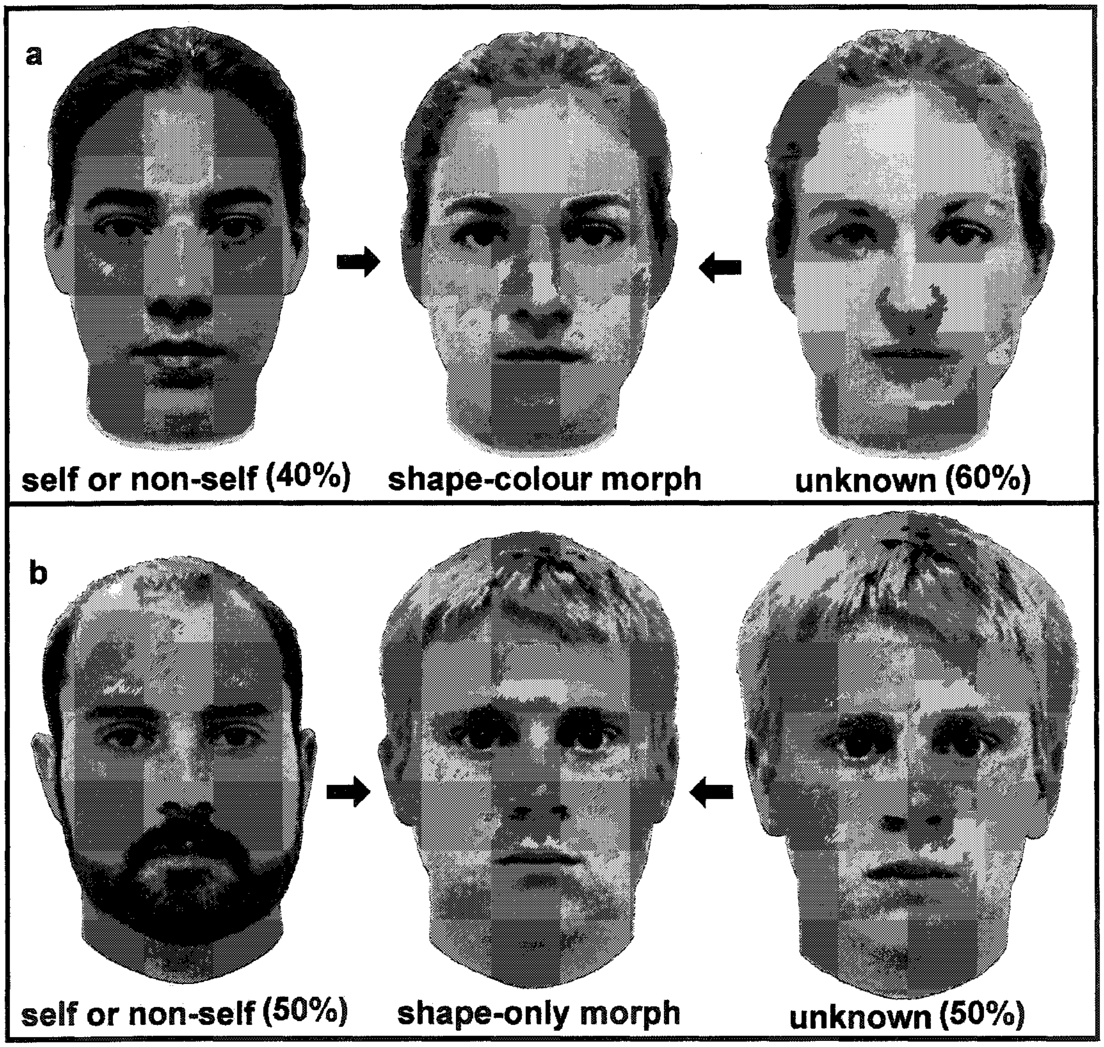

Figure 2.1: Sample morphs. Shape-colour morphs (a) were made by combining 40% of the shape and colour information from the self or non-self face with 60% of an unknown face to make the shape-colour morph. Note that the morph retains all of the unknown person's hair colour and style. Shape-only morphs (b) were made by combining 50% of the shape information from both faces and 100% of the colour information from the unfamiliar face. Note that the faces are standardized for interpupillary distance, which alters head size as a function of this distance.

Colour morphing of "white" with "non-white" persons creates conspicuously artificial images, but students at McMaster University who volunteer for research participation come from a diversity of ethnic backgrounds and it was not practical or fair to limit participation to Caucasians. Morphing bearded with non-bearded men also engenders an artificial appearance. For these reasons, two types of morphs were prepared: shape-colour morphs and shape-only morphs (Figure 2.1). The shape-colour morphs were based on pictures of Caucasians and non-bearded men (N=11), while the shape-only morphs were based on images of non-white persons (N=9) and men with facial hair (N=4). Furthermore, l.) combining colour information from different hairstyles led to unnatural-looking hair for the shape-colour morphs, so colour information in the hair area was always limited to that of the unknown face. Shape-colour morphs consisted of 40% of the self or non-self face and 60% of the unknown face, while shape-only morphs used 50% of each. These values were set at the highest level at which subjects in a pilot study did not spontaneously detect resemblance to self. Each unknown face served as a base for self morphs and non-self morphs an equal number of times, distributed equally across trials.

2.2.2 The trust game

The particular trust game used in this experiment is a two-node extensive form game (Figure 2.2), meaning that there are only two decisions that could be made and that the decisions are made in sequence, not simultaneously. The first node represents a decision by the first player (P1) to trust or not trust the second player (P2) to split a sum of money. The second node represents a decision by the second player to respond to P1's trust selfishly or unselfishly.

In the experiment, 24 subjects played 16 rounds of this bargaining game in sessions with 1-4 players at individual computer stations. Subjects played with what were ostensibly 16 different playing partners on-line at other universities, but in fact played against programmed choices associated with displayed facial morphs. The subjects' choices were scored as trusting or not trusting when playing P1 (6 rounds), and unselfish or selfish when playing P2 (6 rounds). In the remaining 4 rounds, subjects were assigned

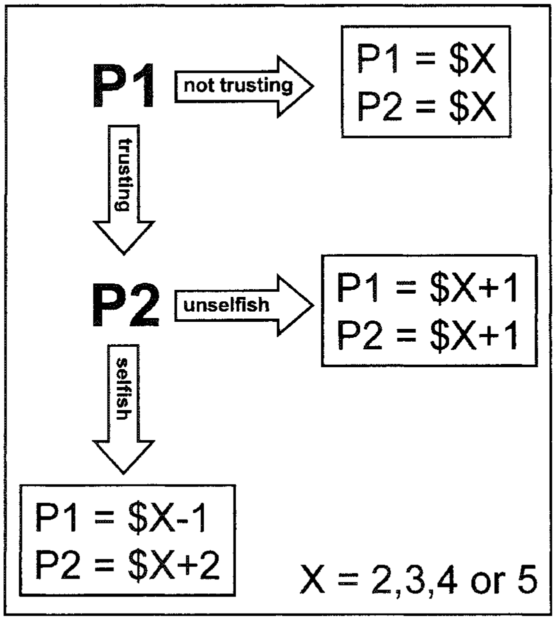

Figure 2.2: The trust game tree. Subjects were Player 1 (P1) for half the games and Player 2 (P2) for the other half. The order of games was chosen randomly and counterbalanced for order of self and non-self morphs. The monetary value of X ranged from \$2 to \$5 and was balanced between self and non-self morph trials. Subjects were presented with dollar values, not variables, and the arrows were not labeled.

the P2 role, but P1 was programmed to make a non-trusting move and terminate the game; these rounds generated no choice data, but were included to provide realism. Orthogonal to the above distinctions was the resemblance cue, with half the rounds played against self morphs and half against non-self morphs. Thus, each subject could make 0, 1, 2 or 3 prosocial decisions in each of four conditions: trusting self morphs and non-self morphs as P1, and responding unselfishly to trusting self morphs and non-self morphs as P2. To minimize differences in subjects' responses based on the sequence of roles or the other players' responses, both were kept constant. The payoff structure has been shown to affect responses (Bolton & Ockenfels, 2000), so payoff types were balanced equally between self and non-self morphs.

At the end of the session, subjects were paid the appropriate amount from one randomly chosen game, as promised at the beginning of the session. In debriefing interviews after each session, no subject revealed any suspicion that the images had been manipulated nor reported a perception of resemblance to self (although one subject remarked that one of his playing partners looked very much like his brother). Participants evidently believed that they were playing with real partners by internet, often commenting with apparent feeling about how a particular partner had played.

2.2.3 Control conditions

Three control conditions were included in this study.

1. To control for any peculiarities of the stimuli that may have caused subjects to trust self morphs more than non-self morphs, another 24 "race"-matched subjects played exactly the same virtual partners in the same sequence of roles as the players in the experimental condition. Besides providing a matched control for any idiosyncratic influences, this also controlled for effects of race, as any effects caused solely by the race of the experimental subject should also be seen in the same race control subject.

2. To assess the possibility that reactions toward self morphs might be mediated by perceptions of differential attractiveness, all stimulus faces were rated on a 10-point Likert scale (anchor adjectives were 1= "very unattractive" and 10="very

attractive") by an independent set of 10 undergraduates from the same pool of research volunteers.

3. Finally, to control for the effect of familiarity of self morphs, I repeated the procedure in this experiment using shape-only morphs of famous and non-famous faces in place of self and non-self faces. Eight images of famous and non-famous faces were taken from the internet and chosen to be approximately equal in attractiveness and picture quality. These faces served in place of the self and non-self faces, respectively, from the main experiment. Each subject played with eight morphs made from one of the same-sex famous faces and eight morphs made from one of the same-sex non-famous faces. After the games were played, subjects rated their familiarity with the original (unmorphed) famous and non-famous faces on a 5-point Likert scale. Only subjects who rated the famous faces as familiar (ratings of 4 and 5) and the non-famous faces as unfamiliar (ratings of 1 and 2) were included in the data analyses, although no other criteria for inclusion changed the conclusion.

2.2.4 Statistical analyses

For initial analyses of behaviour towards self morphs versus non-self morphs, the 11 subjects who saw shape-colour morphs and the 13 who saw shape-only morphs were treated as two independent experiments, affording a replication of the basic study with two slightly different methodologies. Since the effect on trusting was statistically significant in both cases and the pattern of results was identical (see Results), the data are pooled for further analyses.

To assess whether the effect of self morphs was modulated by sex, race or morph type, a difference score (number of prosocial responses to self morphs minus number to non-self morphs) was computed for each subject's play as P1, and these difference scores were submitted to a 3-way analysis of variance (ANOVA).

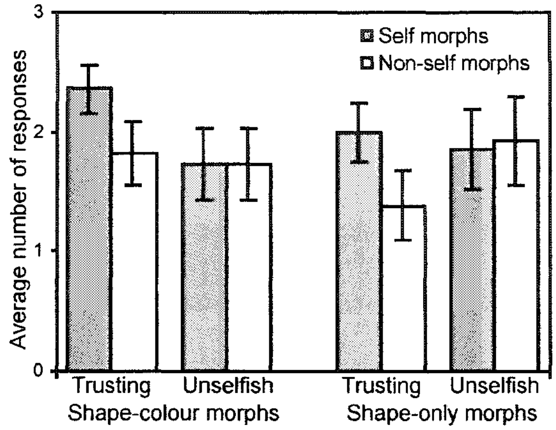

Figure 2.3: Differential behaviour towards self and non-self morphs. Average (± SE) number of prosocial responses ("trusting" as Player 1 and "unselfish" as Player 2) in resemblance experiments using shape-colour morphs ($n = 11$) and shape-only morphs ($n = 13$). Subjects for both morphing techniques showed more trust in self morphs than in non-self morphs ($p < 0.05$), but unselfish plays were not affected by facial resemblance.

2.3 Results

The 11 subjects who saw shape-colour morphs as stimuli were more trusting of self morphs than of non-self morphs when playing P1 ($t_{10} = 2.63, p = 0.013$), but as P2, they were equally unselfish towards both types of morph ($(t)_{10} = 0.00$, n.s.). The 13 subjects who saw shape-only morphs as stimuli behaved similarly, trusting self morphs more than non-self morphs as P1 ($t_{12} = 2.13, p = 0.028$), but failing to discriminate between self and non-self morphs as P2 ($t_{12} = 0.37$, n.s.) (Figure 2.3).

Combining the data for all 24 subjects, and using a difference score for number of prosocial plays to self-morphs minus non-self morphs, there were no significant effects of sex ($F_{1,23} = 0.13, p = 0.73$), "race" (white vs. non-white; $F_{1,23} = 0.83, p = 0.38$), or morph type (shape-colour morphs vs. shape-only morphs; $F_{1,23} = 0.13, p = 0.73$), nor were there any statistically significant interactions (all $p > 0.50$).

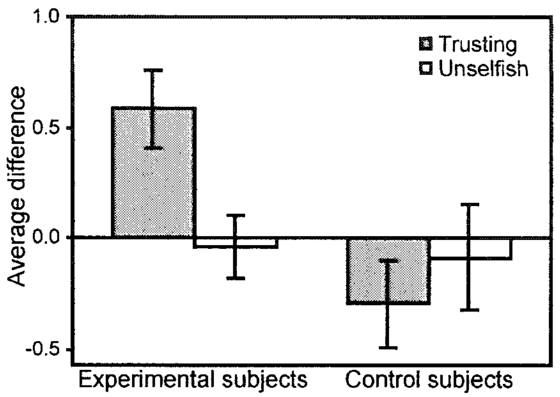

Figure 2.4: Resemblance effects. Average difference (± SE) between number of prosocial responses to self and non-self morphs for experimental and control subjects (both morphing methods combined). Scored as self minus non-self, so that positive differences indicate more prosocial responses towards self morphs and negative differences indicate more prosocial responses towards non-self morphs. An additional set of control subjects saw the same face stimuli as the experimental subjects. These control players showed no statistically significant differences in either trusting or unselfish behaviour, while experimental subjects were significantly more trusting of self than non-self morphs ($p < 0.005$).

There were no statistically significant differences in the behaviour of the matched-control subjects who played the same sets of faces in the same sequence as the experimental subjects. In other words, these control players did not play differentially towards faces that had been self morphs versus non-self morphs for the original subjects, neither in their trusting responses as P1 ($t_{23} = -1.50$, n.s.) nor their selfish choices as P2 ($t_{23} = -0.35$, n.s.) (Figure 2.4).

The attractiveness ratings by the independent set of 10 judges also showed no difference; the faces that had served as self morphs for the original subjects were actually rated slightly less attractive ($M = 4.11 \pm 1.17$ s.d. on a 10-point scale) than the non-self morphs ($M = 4.27 \pm 1.13$ s.d.), but the difference was not significant. Moreover, there was no difference in attractiveness ratings between morphed images that did or did not elicit trust from subjects playing P1 ($M_{trusting} = 4.11 \pm 1.06, M_{nottrusting} = 4.11 \pm 1.22, t_{141} = 0.00$, n.s.), nor between those that elicited selfish and unselfish moves by subjects playing P2 ($M_{selfish} = 4.30 \pm 1.18, M_{unselfish} = 4.26 \pm 1.20, t_{142} = -0.18$, n.s.). If we confine attention to the non-self morphs, there was still no significant difference, and those faces that elicited trust were actually rated slightly less attractive than those that did not ($M_{trust} = 4.14 \pm 1.04, M_{notrust} = 4.28 \pm 1.25, t_{142} = -0.53$, n.s.).

Finally, subjects in control condition 3 played against morphs based on famous or non-famous faces, without significant effects. In the P1 role, subjects trusted "famous" opponents 1.40 times on average and non-famous opponents 1.25 times ($t_{19} = 0.51$, n.s.). In the P2 role, subjects responded unselfishly to a trusting move by a famous P1 1.70 times and by a non-famous P1 1.80 times ($t_{19} = -0.42$, n.s.).

2.4 Discussion

Experimental subjects, who believed that they were playing against pictured opponents while unaware that information from their own faces had been incorporated into the "morphed" faces of some of those supposed opponents, trusted opponents who resembled themselves significantly more than they trusted other opponents, but did not reward trusting moves by their opponents differentially. These results were replicated in two independent groups of subjects, using two distinct facial morphing procedures.

These results show that facial resemblance can modulate social behaviour. An enhanced positive inclination towards individuals that resemble self was anticipated on the basis of kin selection theory (Hamilton, 1964), but this theory is mute with regards to the mechanisms by which such an inclination is elicited. One possibility is that self morphs are perceived as more attractive (Penton-Voak, Perrett, & Peirce, 1999) by the subjects and that more attractive people are trusted more. However, analysis of the subjects' game choices in relation to the independent ratings of the attractiveness of the stimulus faces does not support this possibility, as no effect of attractiveness on either trusting or selfishness was seen, even for non-self morphs.

The absence of an effect of familiarity using famous faces suggests that the relevant cue(s) modulating discriminative trusting moves may be more than simply familiarity. However, this is only weak evidence against familiarity as a mediator of the effect of resemblance on trusting behaviour, since the familiarity that one can gain through television and movies may be insufficient or of a different quality than that gained through personal experience.

The fact that self morphs were treated preferentially by subjects playing P1 but not by the same subjects playing P2 may be explicable in terms of the different payoff structures in the 2-person bargaining game. Following the logic of inclusive fitness theory (Hamilton, 1964), P1 is expected to be indifferent between trusting and not trusting if the coefficient of relatedness between the players is zero ("r" $= 0$) and P2's probability of a selfish betrayal of trust is equal to the probability of reciprocating trust (that is, if $p = .5$ for both moves), because the expected payoff is the same in each case. Any increase in the probability of P2 reciprocating trust or in the utility that P1 derives from P2's payoffs as a result of kinship cues would then raise P1's expected payoff from trusting above that from not trusting. However, P2's expected utility from the results of an unselfish decision will exceed that from a selfish decision only if $r > 0.5$ (the equivalent of full siblings). Clearly, subjects did not behave in full accord with such a model, since it cannot explain why they sometimes rewarded the trust of non-self morphs with unselfish responses. However, in conjunction with the additional considerations needed to explain why non-nepotistic generosity ever occurs, this asymmetry may help explain why resemblance affected only the subjects' initial gestures of trust and not the reciprocation of trust by their opponents.

If humans are indeed using phenotype matching to make decisions about social behaviour, several interesting questions are raised. Foremost is whether humans use self or others as a referent. Our human ancestors did not have mirrors until relatively recently, and reflections in water would provide quite degraded information. Using a genetically-encoded template of what one's face looks like seems highly implausible. Hence, the most likely mechanism for phenotype-matching is expected to depend on familial referents. The weakness in relying on facial resemblance of an unknown person to that of a relative identified as such by association or family history such as mother and maternal siblings, is that this mechanism would not provide reliable information about paternal relatives nor allow one to differentiate full siblings from half siblings.

It would be interesting to replicate the present study using "genetic" siblings and adopted unrelated siblings. If people use self-referential phenotype matching, self

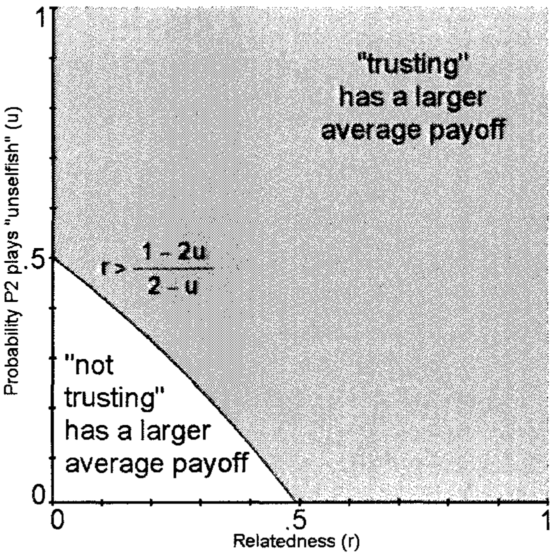

Figure 2.5: Game theoretical analysis. The payoff to P1 who plays “not trusting” is X(1+r) and the payoff to P1 who plays “trusting” is $u[(X+1)(1+r)]+(1-u)[(X-1)+r(X+2)]$. The shaded area of the graph represents all combinations of r and u where “trusting” results in a greater average payoff to P1, i.e. when $r > (1-2u)/(2-u)$. The payoff to P2 who plays “selfish” is $(X+2)+r(X-1)$ and the payoff to P2 who plays “unselfish” is $(1+r)(X+1)$. Playing “unselfish” results in a greater payoff to P2 than does playing “selfish” only when $r > 0.5$. (X = the payoff if P1 terminates the game at the first move, r = relatedness between P1 and P2, u = the probability of P2 playing “unselfish”)

morphs made from adopted and non-adopted siblings should elicit similar effects on trusting behaviour. If shown morphs made from their genetic or adopted siblings, the effect on trust should be completely absent or only present for morphs made from genetic siblings, inasmuch as they resemble the subject. However, if humans instead use other kin as referents, the data should exhibit the opposite pattern. Self morphs should elicit little effect on trust for adopted subjects, but morphs made from both genetic and adopted siblings should elicit at least as large an effect as self-morphs do for non-adopted subjects. Of course, both types of phenotype matching could occur at the same time, as has been shown to be the case in Belding's ground squirrels (Holmes & Sherman, 1982). Alternatively, only other-referent phenotype matching may occur, but the advent of mirrors has caused humans to experience their own phenotypes as they would experience a sibling's. Either alternative would result in an effect on trust of morphs made from both self and siblings and would be observed in both adopted and non-adopted subjects. To distinguish this pattern from one resulting from simple familiarity, morphs made from non-family members, such as close friends, should be assessed for their ability to influence trust. To conclude, the results discussed in this paper indicate that facial resemblance is a candidate cue for human visual phenotype matching; this is a first step in assessing whether and how we recognize kin by facial resemblance.

Chapter 3

Resemblance to self increases the appeal of child faces to both men and women

Preface

This chapter was accepted by *Evolution and Human Behavior* on March 29, 2004 (DeBruine, in press).

Abstract

Platek et al. (2002, 2003) reported that facial resemblance between self and a child increases professed willingness to invest in that child, and does so much more for men than for women. Because facial resemblance is a possible cue of kinship and men, unlike women, can be mistaken about parenthood, Platek et al. predicted and interpreted this sex difference as an adaptation whereby men allocate parental investment in proportion to cues of the likelihood of paternity. Extending their approach using a more realistic technique for manipulating facial resemblance and eliminating some of the confounds in their methodology, facial resemblance was found to increase attractiveness judgments and hypothetical investment decisions, although the published sex difference was not

found. This could not be explained by differences in resemblance between the participants and the morphed images because a separate group of observers could match the original adult images to the new morphs as accurately as to morphs made using Platek et al.'s method. In addition, composite scores indicating positive regard toward an image were correlated with resemblance as judged by these independent observers.

3.1 Introduction

Men are predicted to be more sensitive or responsive than women to the resemblance of offspring to self because of the asymmetry in certainty of parenthood. While women, throughout most of human history, could be absolutely certain which children were their own and which were not, men faced greater uncertainty. Situational cues of paternity, such as the appropriate timing of sexual contact, a strong emotional bond with the mother, and sequestration of the mother during the time of conception, as well as assessment of relatedness through the matching of physical cues may affect paternal investment decisions (Neff & Sherman, 2002).

It might seem adaptive for infants to unequivocally resemble their fathers (sensu Christenfeld & Hill, 1995), but little evidence exists for such an adaptation, although infants and children are consistently found to resemble both their mothers and fathers to a small degree (Nesse et al., 1990; Brédart & French, 1999; McLain et al., 2000; Bressan & Grassi, in press). However, even a small amount of paternity uncertainty can favor a strategy on the part of infants to camouflage any paternal resemblance (Pagel, 1997) and it is theoretically adaptive under some conditions for men to ignore physical resemblance when making investment decisions (Bressan, 2002). Although men and women do favor adult self-resembling faces with regard to trusting behavior (DeBruine, 2002) and attributions of attractiveness (DeBruine, under review), no sex differences have been found.

Evidence from self-report studies supports the hypothesis that men favor children who are perceived as facially resembling them (Burch & Gallup Jr., 2000; Volk & Quinsey, 2002). Platek et al. (2002, 2003) provided some of the first experimental evidence consistent with the hypothesis that men are more sensitive than women are to children's resemblance to self, reporting a series of results based on reactions to images of child faces that were digitally manipulated to resemble the experimental participants. They found in two separate studies that men favored children who resembled themselves in response to hypothetical investment questions, such as, "Which child would you be most likely to adopt?" and did so to a significantly greater extent than women did.

The first study (Platek et al., 2002) established a sex difference in professed willingness to invest in children who resemble self; men were much more likely than women to choose the self-morphs in response to positive investment questions. The second study (Platek et al., 2003) replicated and extended these findings, showing that the sex difference held for a lower level of resemblance (child faces made using 25% as opposed to 50% of the participant's image) and that men, but not women, preferred children with a greater degree of resemblance to self than expected by chance. Despite consistent significant sex differences in the two separate experiments, several methodological issues raise questions about the main result that facial resemblance influences men more than women when making investment decisions about children.

3.1.1 Methodology of Platek et al. (2002, 2003)

Both studies followed a similar method. Each participant was photographed directly facing the camera with a neutral expression. After the researchers morphed the participant's image with that of a male or female child, the participant viewed a display with five morphed child-faces and was asked a number of questions in response to which he or she was requested to choose one child. In the first experiment (Platek et al., 2002), two sets of arrays were presented, one set which included the image of the participant morphed with the child plus four images of unfamiliar male and female adults morphed with the same child, and one set which included five images of five unfamiliar adults morphed with the same child and did not include the participant's morph. In the second experiment (Platek et al., 2003), five additional sets were shown: four sets with varying degrees of morphing which included one image made from the participant and four images made from unfamiliar faces, and one set with five images made from the participant, each of which varied in the percent of the participant's image included in the morph (25% vs. 50%). Ten hypothetical investment questions were asked of each set. The order of presentations of the questions, the array sets, the position of images within the arrays, and the identity of the unfamiliar faces were all randomized. Unfamiliar faces were chosen from a pool consisting of morphs made from 15-30 men and 15-30 women. In the second experiment, the sex of the child image used in the morphs was also randomized across sets and questions.

3.1.2 Methodological Critique

My methodological concerns are the following: (a) The unfamiliar morphs included faces made from both male and female adults. (b) In the second study, the self-morph was shown with greater frequency than any other morph. (c) Each participant was asked ten questions about the same set of child faces, allowing preferences for equitable treatment of each child to mask preferences for any particular child. (d) The morphing procedure used by Platek et al. produced images that did not resemble real children. These concerns are described in detail in the following paragraphs.

Unfamiliar morphs were randomly chosen from a pool of approximately 30-60 images made from 15-30 male and 15-30 female adults (faces were added to this pool throughout the experiment), and the same group of unfamiliar morphs was shown for each question. Although the morphing procedure "tended to limit greatly the determination of gender" (Platek, personal communication), it is still possible that the inclusion of child morphs made from both male and female adult faces affected the results. For example, if both male and female participants preferred child morphs made from adult males, this would bias men toward choosing their own face and bias women away from their own face. Although this possibility could be addressed through the analysis of the control condition, that analysis was not reported.

In the second study, the self-morph was shown in an extra array in which each face in the set included a different percent of self, making it more familiar than any other individual morph. Even familiarity gained over a short duration can increase liking for a face (Rhodes et al., 2001), so care should be taken to provide equal exposure to all faces.

The sex difference found by Platek et al. could simply be a result of a sex difference in willingness to favor one child over others. Since participants were asked ten different questions about the same set of five child faces, some participants may have been reluctant to choose the same child too many times. If this is more true of women than men, it could account for the sex difference. Research indicates that women tend to conform to an ideal of equality, giving the same reward to all members of a group, while men tend to conform to an ideal of equity, distributing rewards in proportion to merit (Austin & McGinn, 1977; Kahn, O'Leary, Krulewitz, & Lamm, 1980). In fact, Platek (personal communication) conceded that "females tended to select different faces from trial to trial; at least that was what they reported". Although analyses of the control conditions in Platek et al.'s studies show that in arrays that did not include the participant's morph men did not choose one particular unfamiliar face more often than others, this type of analysis does not address the issue. It could be that each man tended to choose one face for most of the ten questions but this face was different for each man, resulting in no face being chosen more often than the others overall.

Lastly, the procedure used by Platek et al. (2002, 2003) to produce their morphs may have resulted in images that did not accurately represent children's faces. Directly morphing a child and adult face produces a very unnatural shape, so they instead uniformly compressed the adult faces by cropping the images at the chin, ears and hairline, and resizing the resulting image to 200 pixels wide by 150 pixels tall (see Figure 3.1b). This changes the face proportions to be somewhat closer to those of a child, but the resulting child morph (Figure 3.1d) may not satisfactorily resemble a real child.

3.1.3 The Present Study

The current study addresses the above four methodological issues by (a) only presenting morphs made from adults of the same sex as the participant, (b) presenting individual unfamiliar morphs as many times as self-morphs, (c) using a different set of child faces for each question, and (d) using a different morphing procedure that produced more realistic-looking children (see Figure 3.1).

Other methodological differences were the use of younger children in the morphs (3.5 to 6 month-olds as compared to 2 year-olds in Platek et al.'s studies) and asking fewer questions (see Table 3.1). My choice of age category was based on both the availability of images and a theoretical argument that men should be most sensitive to the resemblance of infants to self. Because it is better to terminate investment early if it is going to be terminated at all, infancy is the most likely age at which the decision whether to invest would be made (Daly & Wilson, 1984). Five questions were asked instead of the original ten because several of those (1) produced no effect of resemblance in Platek et al.'s studies or (2) were negative questions (the experimental hypothesis was that self-morphs would be chosen less often than chance) which require a large number of participants to show any statistical effect. Four of the five questions were those with positive responses (the experimental hypothesis was that self-morphs would be chosen more often than chance) that produced reliable sex differences in Platek et al.'s two studies. The fifth question, "Which one of these children would you rather babysit?" was designed to be a more relevant question for first-year university students to answer.

In order to assess whether the new morphing technique produced child faces of comparable resemblance to the participants, I obtained a measure of resemblance by assessing the accuracy with which a separate group of judges matched the original participants' image to the correct child morph. The matching task was repeated for all five sets of child morphs used in the present study and 2 sets of child morphs made using the method and child images from the two previous studies (Platek et al., 2002, 2003).

3.2 Methods

3.2.1 Participants

Participants in the experiment were 53 (23 male, 30 female, mean age = 19) undergraduates taking an introductory psychology course at McMaster University who participated for course credit. All participants were Caucasian, as only pictures of Caucasian infants were available. The infants were three boys and two girls between the ages of 15 and

27 weeks.

Participants in the matching task were 20 (9 male, 11 female, mean age = 19) Caucasian introductory psychology undergraduates from McMaster University who also participated for course credit. Data from two of the women were excluded from the analyses due to decision times averaging less than one second, indicating meaningless responses. The remaining 18 participants had average decision times ranging from 2.4 to 10.0 seconds ($M = 5.6, SD = 2.3$).

3.2.2 Stimuli

Face stimuli were created by transforming the adult participants' faces to look more neotenous or infant-like, using techniques previously described to modify faces in masculinity, apparent age, and resemblance to a particular person (Perrett et al., 1998; Tiddeman et al., 2001; Penton-Voak et al., 1999). This transformation was necessary because the combination of unmanipulated adult and infant faces resulted in a much older and unnatural-looking child and is analogous to the vertical compression of adult faces used by Platek et al..

The transformation involved calculating the differences in shape between an averaged infant face (made from 18 male and female infants between the ages of three and six months) and an averaged male or female adult face (made from 20 same-sex Caucasian individuals with a mean age of 19 years). The participants' faces were transformed to the same extent that the averaged infant face differed in shape and color from the averaged same-sex adult face. The transformation did not warp the participant's face into the shape of an average child's face. Rather, it resulted in a face that was different from the average infant's face in the same way that the participant's face was different from the average same-sex adult's face.

This transformed version was separately blended with five different infants' faces using 50% of the shape and color information from each face (Figure 3.1). Finally, the hair and background were masked (as in Figure 3.1 e-g) to hide some artifacts of the morphing procedure that occurred at the hairline in order to facilitate the belief that these were real infant faces.

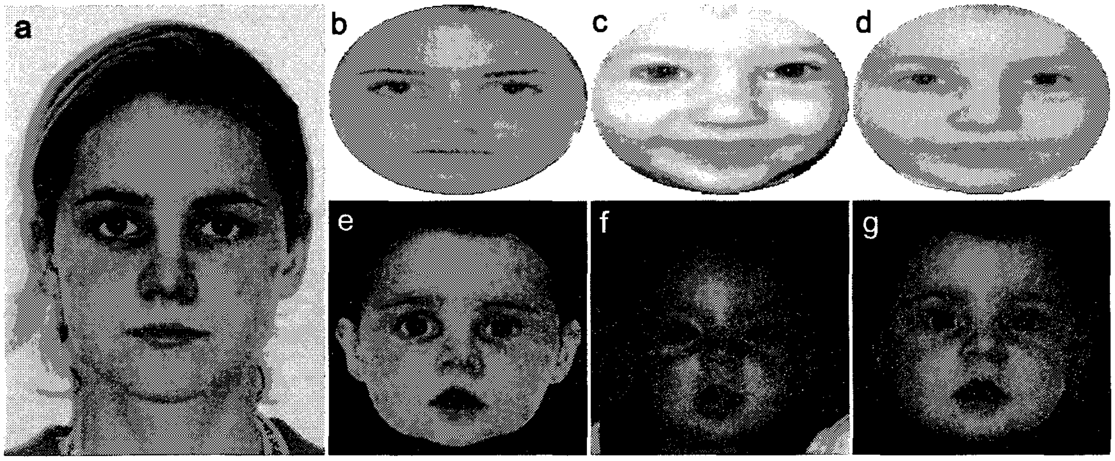

Figure 3.1: Comparison of the method used in Platek et al. (2002, 2003) to that used in this study. Platek resized an experimental participant's face (a, b) to the same aspect ratio as a child's face (c) and blended the two faces together in a 50/50 ratio to produce a child morph (d). In this study, I transformed a participant's face (a) to have neotenous proportions (e), and blended it in a 50/50 ratio with a child's face (f) to produce a more child-like morph (g).

Face stimuli for the assessment of resemblance were also made from the images of the 53 participants using a method identical to that used by Platek et al.. The adult images were made greyscale; cropped at the chin, hairline, and ears; resized to be 200 pixels wide by 150 pixels tall; and masked with a white oval (Figure 3.1b). The resulting images were separately blended in shape and color with the male and female child images used by Platek et al. (e.g. Figure 3.1c).

3.2.3 Procedure

Three photographs of participants were taken during an unrelated experiment for the purpose of calculating facial fluctuating asymmetry. Participants were asked to return one week later for the second part of the study. In a debriefing questionnaire, all participants were asked to write what they thought the study was about. No participants mentioned resemblance to self as a possible hypothesis.

The image with the most neutral expression was chosen to make the child morphs. Each participant was grouped with four other same-sex participants in a "testing unit". One of the participants failed to return for the second part of the experiment in two of the male testing units, resulting in two groups of four participants who still viewed the missing participant's morphs. Sets of child faces were the five morphs made from the same real child's image and the image of each participant in the testing unit. Since each participant was morphed with five different children, each testing unit viewed five sets of five faces.

Participants were asked five questions (Table 3.1) in the same order. A different set of five child faces was displayed with each question and the participant was instructed to choose one face in response to the question.

3.2.4 Resemblance Assessment by Independent Judges

The resemblance assessment task involved matching an image of each participant in the hypothetical decisions experiment to one of the five child images (one of which was a morph of the participant) from that participant's testing unit (Figure 3.2). The adult participant image was not the same image that was used to construct the child

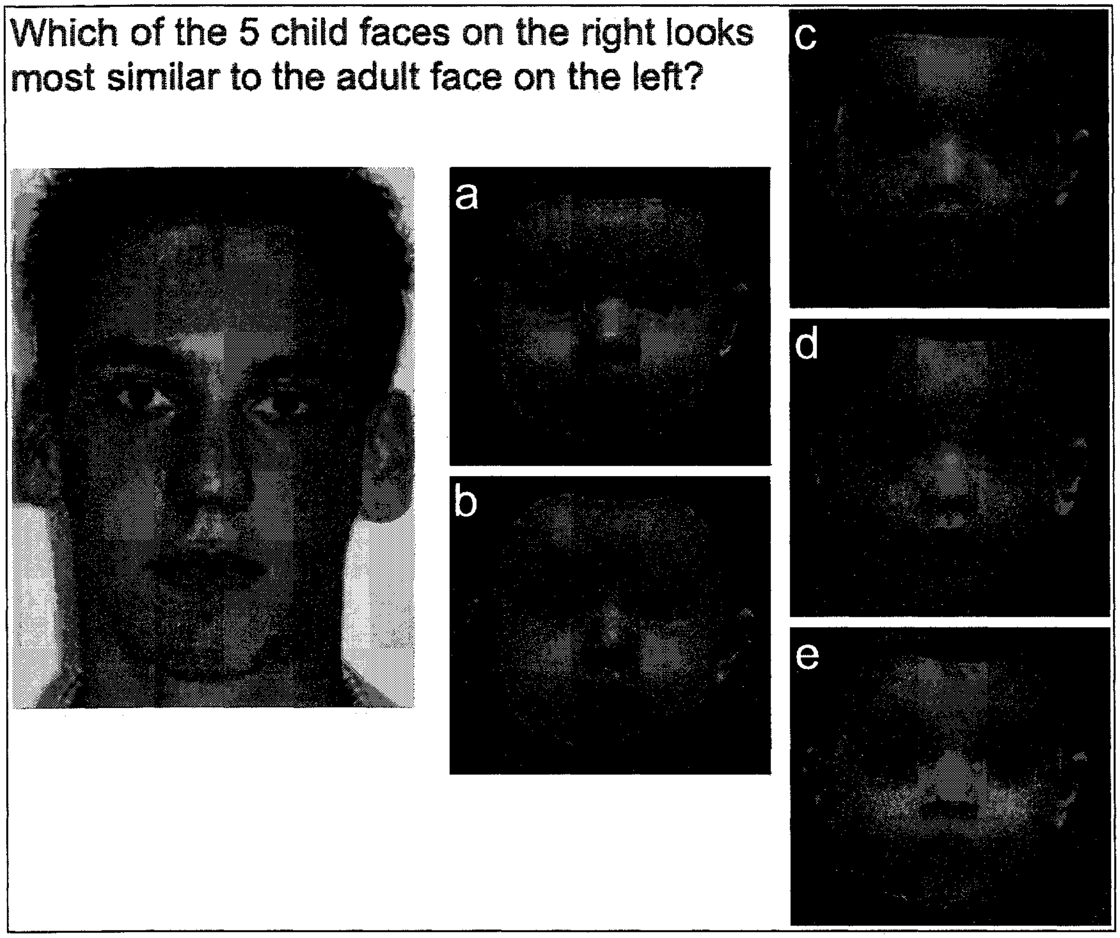

Figure 3.2: The stimulus presentation interface for the matching experiment. Each of the five child morphs was made from the same child face and one of five adult faces who were in the same testing unit and who had viewed the same stimuli. In seven randomized blocks, judges matched all 53 participant adults to one image from an array of the five. The seven blocks were the five image sets that the adult participant had viewed in the hypothetical investment decisions experiment and two image sets made from male and female child morphs using Platek et al.'s method. (The correct answer for this array is *d*.)

morph, but another, randomly chosen image from the three photographs taken of each participant. This was done in order to reduce the ability of judges to match images based on subtle differences in head orientation rather than global resemblance.

The matching task was repeated for all five sets of child faces used in the hypothetical decisions experiment and for two sets of faces made by a procedure identical to that of Platek et al. (2002, 2003). Judges matched all 53 participants to one set of morphs before moving on to the next set of morphs. Sets were presented in random order.

3.2.5 Statistical Analyses

Individual questions from the hypothetical investment decisions task were analyzed using binomial tests, as in Platek et al. (2002, 2003).

Composite scores were calculated for each participant by totaling number of times (out of five) that participant's morphs were chosen by each participant in a testing unit. The composite score for a particular morph given by the participant from whom that morph was made was termed the *self composite score* and the average of the composite scores for that morph given by other (unfamiliar) participants in the testing unit was termed the *control composite score.* Composite scores were normally distributed (all Kolmogorov-Smirnov $Z < 1.1, p > 0.19$), so a factorial repeated-measures ANOVA was used to determine the within-subjects effect of "resemblance" (self versus control composite scores) and the between-subjects effect of participant sex.

Resemblance assessments by independent judges were also normally distributed (all $Z < 1.0, p > 0.28$), so these data were analyzed using a factorial repeated-measures ANOVA with "morphing technique" (using Platek et al.'s method or the new method) and "judge sex" (the sex of the participant in the matching task) as within-subjects variables and "morph sex" (the sex of the adult image used to make the morph) as a between-subjects variable.

The difference between the composite scores described above (self minus control composite score, termed the *composite difference score*) gives a measure of the effect of resemblance on hypothetical investment decisions and is predicted to be correlated with the resemblance assessment. Pearson's correlations were used to assess this and

Table 3.1: Percentage of men and women who chose the self-morph from a choice of five child faces in response to the following questions. *P*-values were calculated using an exact binomial test with a chance value of 20%.

Question	men n=23 (p)	women n=30 (p)	total n=53 (p)
Which one of these children would you be most likely to adopt?	26% (.31)	23% (.39)	25% (.25)
Which one of these children do you find to be the most attractive?	30% (.16)	37% (**.03**)	34% (**.01**)
Which one of these children would you be comfortable spending the MOST time with?	22% (.50)	20% (.57)	21% (.50)
Which one of these children would you spend $50 on if you could only spend it on one child?	22% (.50)	33% (.06)	28% (.09)
Which one of these children would you rather babysit?	26% (.31)	33% (.06)	30% (**.05**)

one-tailed p-values are reported.

3.3 Results

3.3.1 Hypothetical Investment Decisions

Looking at individual questions, the proportion of self-morphs chosen was better than chance for each question, but this was only significant for the questions about attractiveness and willingness to babysit. If the appropriate correction for the number of statistical tests is applied ($p < 0.01$), only the question about attractiveness remained significant and only for both sexes combined (Table 3.1).

Analysis of the composite scores revealed that participants chose their own self-morphs more often than other participants did ($F_{1,51} = 7.24, p = 0.01$) and there was no statistically significant interaction with sex ($F_{1,51} = 0.52, p = 0.48$), although men chose slightly fewer self-morphs ($M = 1.26, SD = 1.25$) than women did ($M = 1.37, SD = 1.25$).

3.3.2 Resemblance Assessment

Figure 3.3 presents independent judges' accuracy at matching images of male and female adult participants with their child morph for morphs made using both my morphing method and Platek et al.'s method. Participants matched faces within each group at levels greater than chance (all $t_{17} > 5.2, p < .001$).

Judges matched images of female participants to their self-morphs somewhat more accurately than they matched male participants to their self-morphs ($F_{1,16} = 4.16, p < 0.06$) and female judges were no better than male judges at matching participants with their self-morphs ($F_{1,16} = 2.60, p = 0.13$). Judges were slightly, but not significantly, better at matching participants to self-morphs made using my morphing method than those made using Platek et al.'s method ($F_{1,16} = 3.12, p < 0.10$). No interactions were significant (all $F_{1,16} < 2.9$, all $p > 0.10$).

The correlation between independent judges accuracy of matching and the composite difference score (self minus control composite score) was significant ($r = 0.27, n = 53, p = 0.023$) and this correlation was not significantly different between men and women ($Z = .62, p = .54$, men: $r = .35$, women: $r = .18$). This suggests that the effect of resemblance on hypothetical investment decisions increases with increasing resemblance, as judged by independent observers.

3.4 Discussion

Consistent with the results of the two previous studies investigating the impact of computer-generated facial resemblance on hypothetical parental investment decisions (Platek et al., 2002, 2003), I also demonstrated that facial resemblance generates positive regard for images of children. Unlike these earlier studies, no evidence for a sex difference in this effect was found. The lack of a sex difference in preference for self-resembling child faces is consistent with the lack of sex differences in responses to similarly-produced adult self-morphs with regard to trusting behavior (DeBruine, 2002) and attributions of attractiveness (DeBruine, under review).

There are several possible reasons for the different results obtained by this and

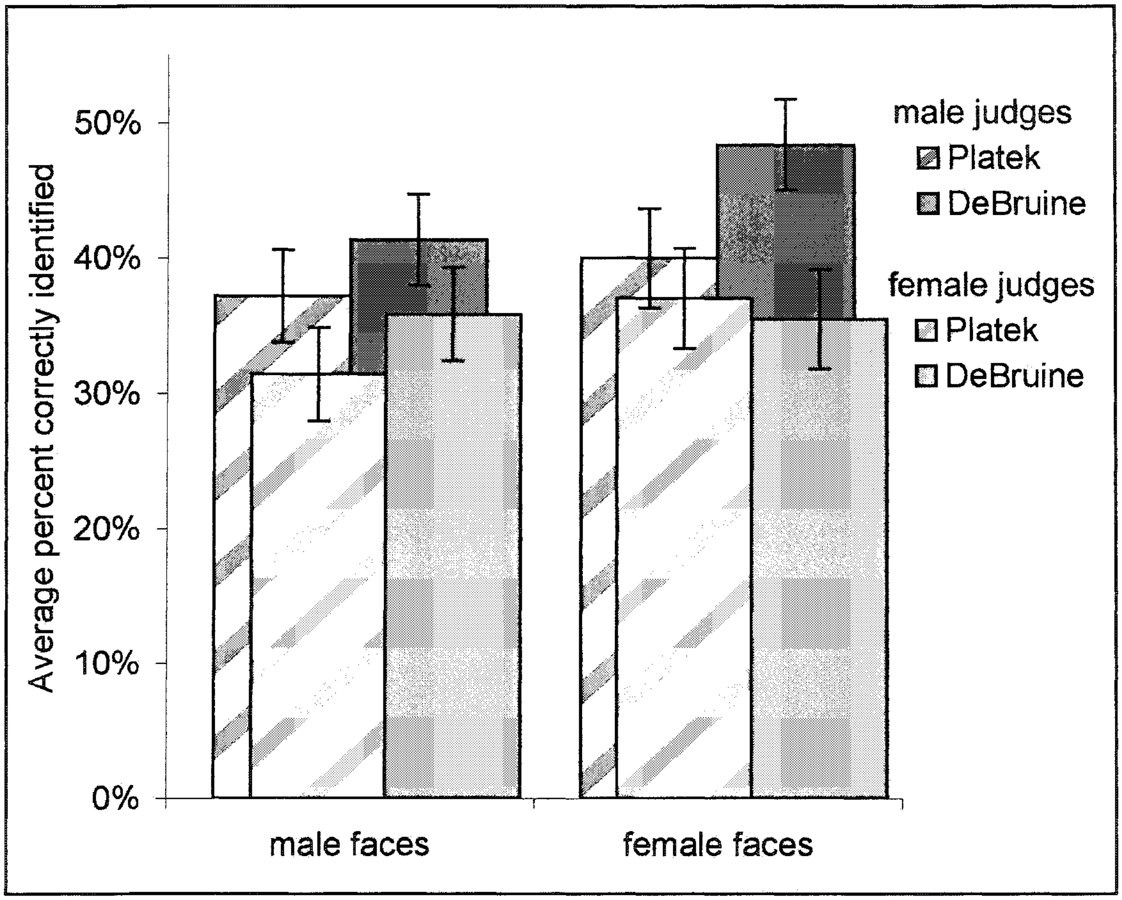

Figure 3.3: Matching task results. The average proportion of trials ($\pm SEM$) in which male ($n = 9$) and female ($n = 9$) judges correctly matched images of male and female participants with the child morph made from that participant (chance is 20%). Morphs were made using either the method used by Platek et al. or the method used in the current study.

the previous studies. It seems unlikely that Platek et al.'s original results were due to chance, given the level of significance and repeatability. This leaves a number of methodological differences between the two studies, the most important being my inclusion of images made only from same-sex adults as unfamiliar morphs and my use of different child faces for each question. More speculatively, differences in participant selection or morphing procedure could have produced a false sex difference in the previous studies or obscured a real sex difference in the current study.

There is no theoretical reason to believe that child morphs made from images of adult males would be preferred by both men and women to child morphs made from images of adult females. Nevertheless, such a bias could account for the consistent sex difference found by Platek et al., whose participants viewed child morphs made from images of both adult men and women, as well as the lack of a sex difference found in the current study, whose participants viewed only child morphs made using adult images of the same sex as the participant.

There is a reason to believe that women distribute rewards differently than men. Especially when future interaction is unlikely, men tend to distribute rewards in proportion to merit, while women tend to divide rewards equally (Austin & McGinn, 1977). This sex difference in preference for equity versus equality could explain the sex difference found by Platek et al., whose participants were given the chance to make ten different hypothetical investment decisions about the same set of five child images. This bias could not affect the results of the current study because a unique set of five child morphs was presented with each of the hypothetical investment questions.

The images in this study differed from Platek et al.'s in several other ways. Platek et al.'s photographs were grayscale, the child images were of 2-year-olds, and the participants' faces were cropped and stretched to a standard size before morphing. My photographs were in color, the child images were of 3.5 to 6 month-olds, and the participants' faces were transformed to neotenous proportions instead of being uniformly compressed. I argue that color images are more realistic than grayscale images, that investment decisions are more likely to be made when children are very young than when they are older, and that the morphing procedure used in the current study produces independent observer resemblance judgments equal to or greater than Platek et al.'s procedure. Nevertheless, it would be useful to replicate this experiment using different combinations of methods and morphing procedures from this study and Platek et al. in order to determine exactly which changes eliminated the sex difference and resulted in a lower overall effect of resemblance to self on willingness to invest in hypothetical children.

Theoretically, natural selection is not expected to favor sexually dimorphic responses to resemblance unless the costs to one sex of such an adaptation outweigh the costs of maintaining dimorphism (Nesse et al., 1990). Although only men face direct paternity uncertainty, women may also respond to resemblance in infants who are putatively related through a male. Following the same logic, Euler and Weitzel (1999) predicted and found that maternal grandmothers, who have no uncertainty of relatedness to their daughters' children, provided more care and solicitude than paternal grandmothers, who have some uncertainty about their sons' paternity. As well, matrilateral aunts invest more in children than patrilateral aunts (Gaulin et al., 1997), lending further support to the idea that it would be adaptive for women to evaluate phenotypic cues of relatedness such as facial resemblance when making investment decisions about children not their own.

The results of the current extension of Platek et al.(2002, 2003) put in question the strength of the previous experimental findings that resemblance to self affects men more than it does women in the domain of investment decisions about children.

Chapter 4

Context-specific responses to a cue of kinship: Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces

Preface

This chapter is under review at the *Proceedings of the Royal Society of London, B* (DeBruine, under review).

Abstract

Reactions to facial self-resemblance could reflect either specialized responses to cues of kinship or byproducts of the general perceptual mechanisms of face encoding and mere exposure. The adaptive hypothesis predicts differences in reactions to self-resemblance in mating and prosocial contexts, while the byproduct hypothesis does not. Using

face images that were digitally transformed to resemble participants, I showed that the effects of resemblance on attractiveness judgments depended on both the sex of the judge and the sex of the face being judged: facial resemblance increased attractiveness judgments of same-sex faces more than other-sex faces, despite identical procedures being used to manipulate resemblance. A control experiment indicated that these effects were caused neither by lower resemblance of other-sex faces than same-sex faces, nor by an increased perception of averageness or familiarity of same-sex faces due to prototyping or mere exposure affecting only same-sex faces. The differential impact of self-resemblance on same-sex and other-sex faces supports the hypothesis that humans use facial resemblance as a cue of kinship.

4.1 Introduction

Judgments of facial attractiveness are highly consensual (Langlois et al., 2000), reflecting preferences for visible attributes such as bilateral symmetry, quality of the skin, averageness or typicality, and secondary sex characteristics (Thornhill & Gangestad, 1999). Attributes of the raters, such as own attractiveness, ovarian cycle stage, and romantic relationship status also affect judgments (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak et al., 1999; Johnston & Barry, 2001; Little, Jones, Penton-Voak, Burt, & Perrett, 2002). Another characteristic that may affect a face's attractiveness is its resemblance to the judge's own face.

Why might people be expected to respond to self-resemblance? One possibility is that self-resemblance is a cue of genetic relatedness (Hauber & Sherman, 2001) to which humans have evolved a specific sensitivity because kinship has affected the costs and benefits, in inclusive fitness, of social decisions (Hamilton, 1964). This hypothesis suggests that responses to self-resemblance may not be uniformly positive since the appropriate (fitness-enhancing) response to kin in ancestral environments was different in such distinct domains as altruism and mate choice. Indeed, self-resemblance has been shown to both increase affiliative behaviour in peacock brothers raised apart (Petrie, Krupa, & Burke, 1999) and decrease mating behaviour between baboon paternal half-siblings (Alberts, 1999). Alternatively, positive responses to self-resemblance could simply be non-adaptive byproducts of more general phenomena, such as liking what is familiar (Zajonc, 1968; Bornstein, 1989).

In this paper, I present evidence that attributions of attractiveness are enhanced by facial resemblance to self and that this enhancement is greater for same-sex faces than for other-sex faces. I also show that this same-sex bias is neither a result of low perceived resemblance to other-sex faces nor a functionless byproduct of a general preference for familiar stimuli. This suggests that the same-sex bias in attractiveness enhancement caused by self-resemblance is a product of specialized responses to facial resemblance as a cue of kinship, functioning to favour kin in a non-sexual prosocial context and avoid kin in a mating context.

4.1.1 Resemblance and Attractiveness of Other-Sex Faces

Negative consequences of inbreeding are well-documented in humans (Bittles & Neel, 1994). Many authors have argued that human sexual psychology includes adaptations for avoiding inbreeding, including the "Westermarck effect" whereby children reared together tend to find one another sexually unappealing (e.g. Wolf, 1995). Surprisingly, however, rather than selecting maximally dissimilar mates, human couples tend to resemble one another on both physical and personality traits (Keller, Thiessen, & Young, 1996; Buston & Emlen, 2003; Hinsz, 1989; Griffiths & Kunz, 1973; Bereczkei, Gyuris, Koves, & Bernath, 2002; Zajonc et al., 1987). This is puzzling in light of the documented costs of inbreeding. If people are attracted to others who physically resemble themselves despite those costs, this could be an incidental byproduct of a general preference for familiarity (Zajonc, 1968; Bornstein, 1989), evidence of preferences evolved to produce optimal inbreeding (Bateson, 1983), or it could indicate that the physical attributes on which couples are judged as similar (e.g. attractiveness, weight, demeanor) are not reliably correlated with genetic relatedness.

Penton-Voak et al. (1999) used computer-graphic image manipulation to investigate the impact of resemblance to self on perceptions of attractiveness. Male faces that resembled female participants were generated by changing the shape of an average male face to the same degree that the focal woman's face differed from the female average.

Participants rated the attractiveness of the transformed male faces and independent raters judged the resemblance between participants and each face. The average rating of the resemblance between a participant and a given face was positively and significantly correlated with the attractiveness rating the participant gave that face. Whether the results of this study bespeak a relationship between facial resemblance and sexual attraction or positive feelings that are independent of sex is unclear because the study was restricted to women's ratings of male faces.

4.1.2 Resemblance and Attractiveness of Same-Sex Faces

Although men's and women's attractiveness ratings of male and female faces correlate highly, attractiveness judgments of other-sex faces may carry a somewhat different connotation than attractiveness judgments of same-sex faces (Zebrowitz & Rhodes, 2002). Attractiveness judgments of other-sex faces are more likely to include an evaluation of desirability to the judge as a sexual or romantic partner, while judgments of same-sex faces are more likely to be evaluated on imagined desirability to other-sex people or on non-sexual, general positive regard.

Attractive people are judged positively in many domains, including intelligence, friendliness, sincerity and trustworthiness (e.g. Dion, Berscheid, & Walster, 1972; Eagly, Ashmore, Makhijani, & Longo, 1991). Attractive people even receive higher offers in economic games (Solnick & Schweitzer, 1999; Hancock & Ross, 2002). DeBruine (2002) reported that facial resemblance affected economic decisions when research participants had the option to divide a small sum of money equally between self and a same-sex pictured partner or to trust that partner with the division of a larger sum of money. Participants were more likely to trust partners whose images had been subtly manipulated to resemble themselves than partners whose images had been made to resemble others. Self-resembling faces may be judged more trustworthy, or people may be less concerned about whether they will reciprocate trust, much as kin are relatively unconcerned about equity in their interactions (Hames, 1987). Although they did not directly assess the impact of facial resemblance on the attractiveness of same-sex faces, these results suggest a general increase in positive regard towards such faces.

4.1.3 Evolved kin-recognition adaptations or byproducts of general processes?

Both familiarity with a face and its apparent averageness are known to enhance attractiveness judgments (Zajonc, 1968; Bornstein, 1989; Rhodes, Sumich, & Byatt, 1999; Langlois & Roggman, 1990). Moreover, it has been argued that judgments of averageness reflect familiarity with the images (Halberstadt & Rhodes, 2003; Rhodes et al., 2001). In the study reported here, the faces were experimentally transformed to resemble the participants using photographs of their own faces. Familiarity with one's own image may enhance judgments of attractiveness regardless of any relevance of resemblance as a kinship cue. On the assumption that one's mental model of an average face develops from familiarity with the faces one sees (Langlois & Roggman, 1990; Rhodes et al., 2001), experience with one's own face should influence this mental prototype. If familiarity alone accounts for an effect of self-resemblance on attractiveness, the effect of self-resemblance on same-sex and other-sex faces should be similar as long as one's mental model of a familiar or average face is sex-neutral. Alternatively, if people form discrete male and female facial prototypes of an average face then only the same-sex prototype should be influenced by one's own face.

In the first experiment, people were asked to make judgments about the attractiveness of same-sex and other-sex transformed faces in a two-alternative forced choice paradigm. I hypothesized that facial resemblance would enhance attractiveness judgments of same sex faces more than opposite sex faces on the assumption that an opposite sex image connotes personal sexual attraction while a same sex face cues a non-sexual evaluation of positive regard toward that person.

One might anticipate that resemblance would be more difficult to detect between faces of different sexes and self-resemblance would seem more familiar in a same-sex face than in an other-sex face. If so, effects of self-resemblance on judgments of attractiveness of same-sex and other-sex faces should also be reflected in other judgments of faces, such as familiarity. I could not ask directly about perceived familiarity because that question might reveal the nature of the manipulation I made to the faces. Since averageness or typicality judgments reflect perceived familiarity (Halberstadt & Rhodes, 2003), another experiment was carried out, with different participants, to determine whether resemblance to self affects averageness judgments as it does attractiveness judgments.

In this second experiment, participants were asked to make a judgment as to whether one face was more average than another face. The forced-choice paired comparisons were done with stimuli made in the same manner as in the first experiment where participants made judgments about attractiveness. If a same-sex-biased effect of self-resemblance on attractiveness is mediated by a self-biased same-sex mental prototype of faces (two-prototype hypothesis), perceptions of averageness will also be greater for same-sex faces than other-sex faces. Alternatively, the existence of a single, sex-neutral face prototype (single-prototype hypothesis) should lead to equal enhancement of perceived averageness for both same-sex and other-sex faces. This would demonstrate that the experimental manipulation of resemblance was sufficient to produce responses to both same-sex and other-sex faces. It would also support the hypothesis that a specific mechanism acts to temper the enhancement of attractiveness due to self-resemblance in the case of other-sex faces.

4.2 Methods

4.2.1 Experiment 1: Attractiveness Judgments

Participants

Digital photographs of the participants were taken one week prior to the experiment as part of a two-week study of facial symmetry and spatial ability. No data were collected from participants who did not wish to have their photographs taken or who did not return for the second week of the experiment. The remaining participants were 53 male and 55 female undergraduate students enrolled in introductory psychology (mean age=19.2 years, SD=1.6). They were of varying ethnic backgrounds, but were divided into the broad phenotypic categories of East Asian (14 male, 16 female), European (25 male, 32 female) and South/West Asian (including Indian and Middle Eastern; 14 male, 7 female) for the purposes of transforming faces.

Participants were grouped into testing units with one to six other same-sex, same-phenotypic-category students who acted as controls for each other. All participants in a testing unit viewed the same set of seven images, which included one transformed image made from each participant in the testing unit. For testing units with fewer than seven participants, images made from unknown same-sex, same-phenotypic-category participants were added to equate the number of images seen by each participant.

Transformed Facial Stimuli

Average composite faces were created using the images of 20 individuals of the same sex and phenotypic category with a mean age of 19 years. Male and female composite faces were made for East Asian, European and West Asian faces. The original head and shoulder photographs were taken using a digital camera under standard lighting conditions. The shape of each face was delineated using 171 facial landmarks and the average faces were constructed with image manipulation software (Rowland & Perrett, 1995; Tiddeman et al., 2001) by combining the shape, color and texture information from the individual images.

The same procedure was used to photograph and delineate the participants' images. To decrease the chance that participants would guess the nature of the experiment, their face photographs were taken one week before the experiment for an unrelated study about facial masculinity and spatial ability. Each participant's image was used to transform the composite male and female faces of the same phenotypic category. Transforms were made by calculating the shape differences between the participant's face and the same-sex composite face (Figure 4.1). To make same-sex transforms, 50% of this difference was applied to the same-sex composite face. To make other-sex transforms, 50% of the difference between the participant and same-sex composite was applied to the other-sex composite face. This is functionally identical to the procedure used by DeBruine (2002) to make 50% shape-only morphs and only different in the degree of transformation (50% vs. 100%) from that used by Penton-Voak et al. (1999) to make male transforms from images of female research participants. A 50% degree of transformation is the most one can use without participants noticing resemblance to self in same-sex images. I do not assume that 50% is equivalent to the degree of

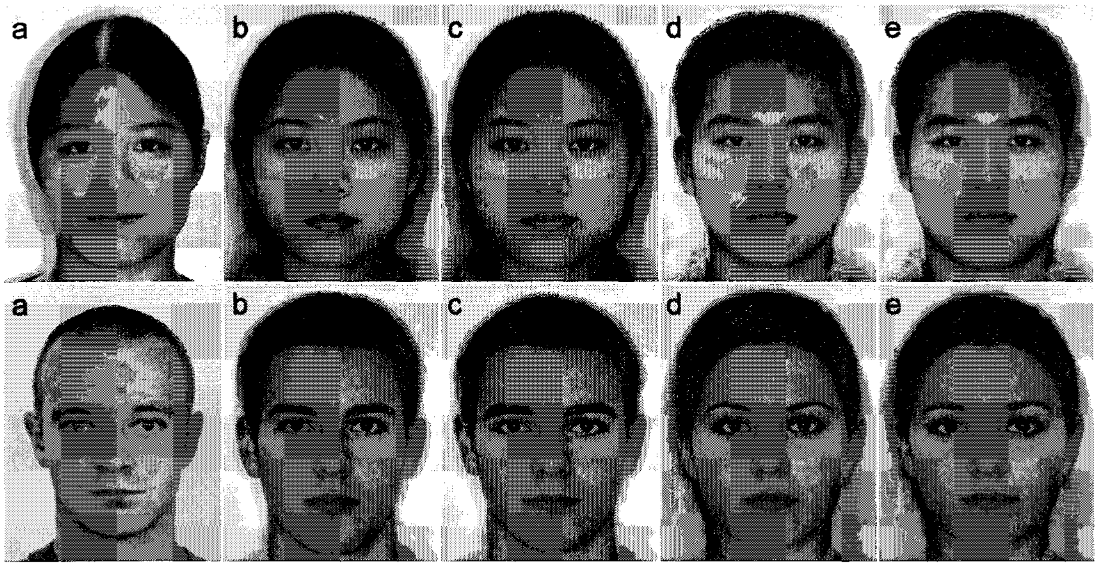

Figure 4.1: Same-sex transforms (c) were made by applying 50% of the shape difference between the participant's face (a) and the same-sex composite face (b) to the same-sex composite face (b). Other-sex transforms (e) were made by applying 50% of the shape difference between the participant's face (a) and the same-sex composite face (b) to the other-sex composite face (d). Transforms retained 100% of the color information from the composite face.

resemblance expected for siblings or first cousins, but I do assume it is sufficient to reach a threshold resemblance effect.

Although one might intuitively expect such a procedure to make male faces more feminine and female faces more masculine, this transformation only masculinizes or feminizes the resulting transform to the extent that the participant's face is more masculine or feminine than his or her same-sex composite face. In other words, only the *differences* between a participant's face and the same-sex composite face are used to transform the male and female composites.

Procedure

Participants made two-alternative forced-choice decisions between all 21 possible pairs of faces in each testing unit. Specifically, they were asked to, "Click on the face you find more attractive". Forced choice tests have been shown to be a more sensitive test of kin recognition than sequential discrimination in birds (Beecher, 1991) and were described by participants in pilot experiments for this study as easier than a Likert scale rating of the attractiveness of singly-presented faces.

Each participant thus made six decisions for each of the seven faces, including his or her own transformed image. Half the participants viewed a block of same-sex faces first, then repeated the procedure with the other-sex faces, and half viewed the stimuli in the opposite order. All participants in a given testing unit saw the stimuli in the same blocked order. The order of faces was randomized and then presented in an optimal order for two-alternative forced choice tasks (Ross, 1934), whereby each image was shown equally often in each position and the presentation of identical stimuli was maximally spaced.

After the experiment was completed, participants were asked to write down what they thought the experiment was testing and how the images were manipulated. No participants guessed that the images they viewed contained information from their own faces.

Statistical Methods

Two attractiveness scores were computed for each transformed image. The first (own-preference) was the number of times the participant whose face was used to make the transform chose this image. The second (other-preference) was the average number of times that others in the same testing unit chose that same image. These scores could range from zero (the image was never chosen as the more attractive of the pair) to six (the image was chosen as the more attractive in all six pairings).

Each participant's preference for self-resemblance was computed as the difference between the above-described attractiveness scores (i.e. own-preference minus other-preference). If participants judged their own transforms on the same criteria that others judged those faces, this difference score should average zero. Difference scores greater than zero will support the prediction that self-resemblance positively affects judgments of attractiveness.

A repeated-measures factorial ANOVA was used to determine the effects of three variables on the attractiveness scores for the transformed faces. Within-subjects effects of face sex and judge type (i.e. own-preference vs. other-preference) and the between-subjects effect of participant sex were assessed. An interaction among participant sex, face sex and judge type will support the prediction that resemblance will increase the attractiveness of other-sex faces less than same-sex faces. Paired t-tests were used to analyze the effect of judge type on men's and women's judgments of male and female face transforms separately. All reported p-values are two-tailed.

4.2.2 Experiment 2: Averageness Judgments

Participants

Participants were 33 male and 45 female undergraduates taking introductory psychology and participating in a two-week study on facial symmetry (mean age = 19.7 years, SD = 1.2). They were also grouped by phenotype (East Asian: 7 male, 10 female, European: 23 male, 32 female, South/West Asian: 3 male, 3 female).

Stimuli

Transformed facial stimuli were made as in Experiment 1.

Procedure

Participants were instructed, "You will be asked to choose which one is more average in each pair. By average, I mean most typical or ordinary." As in experiment 1, participants were grouped into testing units that viewed the same seven faces, but only 6 of those were transforms made from self or other participants. The seventh face was the unmanipulated composite, included to assess whether participants perceived their own transforms as more "average" than a statistically average composite.

Statistical Methods

To determine whether participants could detect averageness, a one-sample t-test was used to compare the number of times participants chose the unmanipulated composites against chance (half of the six forced-choice decisions in which the composite appeared). A repeated-measures factorial ANOVA was used to compare averageness scores of composites and self-transforms. Other results were analyzed as in Experiment 1. All reported p-values are two-tailed.

4.3 Results

4.3.1 Experiment 1: Effects of Resemblance on Attractiveness Judgments

As anticipated from the hypothesis that resemblance cues familiarity or kinship and evokes positive regard, the participant whom an image resembled chose it as the attractive face more often than other participants did (Figure 4.2a) and this result was confirmed as a main effect of judge type (own-preference vs. other-preference; $F_{1,106} = 20.9, p < 0.001$). There was no main effect of participant sex ($F_{1,106} = 0.01, p = 0.92$) or face sex ($F_{1,106} = 0.15, p = 0.70$). Confirming the hypothesis that resemblance

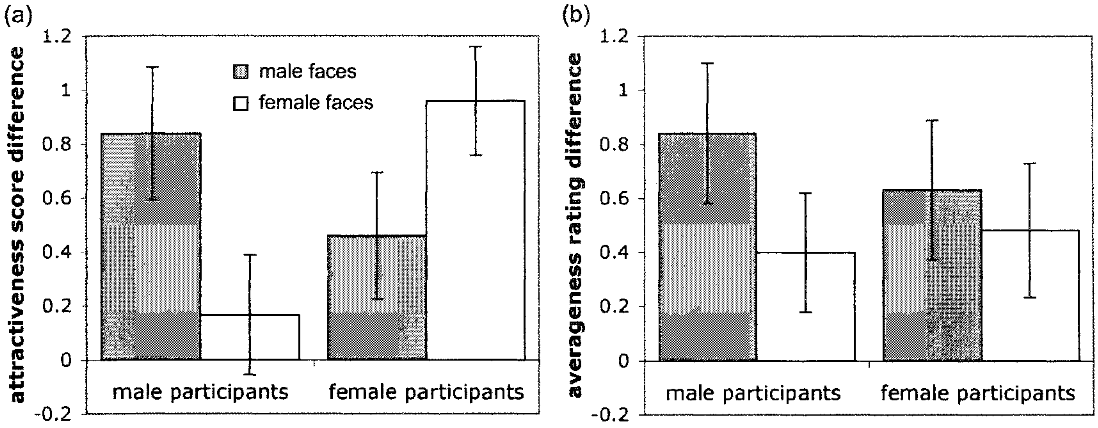

Figure 4.2: Mean attractiveness (a) and averageness (b) score differences (± s.e.) were calculated from the number of times a participant chose his or her own transformed image (own-preference) minus the average number of times other participants chose that image (other-preference). Self-resemblance increased the attractiveness of same-sex faces more than other-sex faces. In contrast, self-resemblance increased the perceived averageness of same-sex faces no more than other-sex faces.

will increase the attractiveness of other-sex faces less than same-sex faces, there was a significant three-way interaction among participant sex, face sex and judge type ($F_{1,106} = 10.57, p = 0.002$); both men and women preferred self-resembling transforms over non-self transforms more with same-sex faces than with other-sex faces.

Paired t-tests showed that both male and female participants judged their own same-sex transformed faces as more attractive than other participants judged them (men: $t_{52} = 3.40, p = 0.001$, women: $t_{54} = 4.75, p < 0.001$). Neither men nor women judged their own other-sex transformed faces as significantly more attractive than other participants judged them (men: $t_{52} = 0.71, p = 0.48$, women: $t_{54} = 2.06, p = 0.044$; Bonferroni-corrected critical $p = 0.0125$).

4.3.2 Experiment 2: Effects of Resemblance on Averageness Judgments

Both male and female participants chose male and female composites as the more average or typical face in a pair more often than chance (all $p < 0.01$) and more often than they chose self-transforms ($F_{1,76} = 8.0, p = 0.006$). This demonstrates that participants could indeed detect averageness,

Men and women selected both male and female self-transforms as more average than other participants did (main effect of resemblance: $F_{1,76} = 19.8, p < 0.001$). Face sex was not a statistically significant main effect ($F_{1,76} = 2.92, p = 0.092$), nor were there any significant main effects of participant sex or interactions among any of the main factors (all $F_{1,76} < 2.0, p > 0.15$).

Contrary to the results expected if people form male and female mental face prototypes and if resemblance to self affects only the perceived averageness or typicality of same-sex faces, there was no interaction among participant sex, face sex and resemblance ($F_{1,76} = 1.97, p = 0.165$, Figure 4.2b). Inasmuch as perceived averageness or typicality is influenced by familiarity, these results show that resemblance to self affects the familiarity of same-sex faces no more than it affects other-sex faces.

4.4 Discussion

Experimentally manipulated facial resemblance to self influences the perceived attractiveness of faces. Although same-sex and other-sex self-resembling transforms were produced by identical image manipulation techniques, attractiveness was enhanced for same-sex faces to a much greater extent than for other-sex faces. This result supports the hypothesis that facial resemblance is a cue of kinship to which humans respond differently in social and mating contexts and is consistent with the suggestion by Hauber and Sherman (2001) that highly social species are likely to have separate functional neural mechanisms to deal with these different contexts. Same-sex faces elicit judgments of non-sexual positive regard which cues of kinship should increase, while other-sex faces elicit judgments of sexual or romantic appeal to the judge, which cues of kinship should decrease. This could explain why other-sex self-resembling faces are not judged as aversive, since attractiveness judgments of other-sex faces may reflect a combination of prosocial regard and sexual appeal.

Experiment 2 determined whether the existence of separate male and female mental face prototypes can explain the same-sex bias in enhancement of attraction due to resemblance. A strong prediction of the two-prototype hypothesis is that familiarity with one's own face will only affect the same-sex prototype. The results of Experiment 2 clearly demonstrated that this is not the case, since resemblance to self increased the perceived averageness of other-sex faces as much as same-sex faces, supporting the single-prototype hypothesis. Moreover, this result provided evidence that the resemblance of other-sex faces to the participants from which they were made was sufficient to cause an effect equal to that for same-sex faces on perceptions other than attractiveness. While familiarity, at some level, must be driving the increased attractiveness of self-transforms, it cannot account for the differential effects of resemblance on same-sex and other-sex faces.

Although it is unlikely that our human ancestors would have experienced their own faces to the same extent that we now see ourselves in mirrors and photographs, resemblance to self may evoke kin-recognition mechanisms only to the extent that a person resembles family members (e.g. Penn & Potts, 1998). Alternatively, experience with one's own face may contribute to the development of a self or family template. The extent to which my findings can be attributed to matching to one's own phenotype versus matching to a template based on experience with family members was not addressed in this study. Further experiments comparing responses to self-resemblance between adopted and non-adopted people could elucidate these possibilities.

The present study has established that the attractiveness of faces is influenced by self-resemblance. This effect could contribute to stable individual differences in perceptions of attractiveness and may explain the increase in trust towards self-resembling same-sex faces found by DeBruine (2002). The greater enhancement of attractiveness due to self-resemblance for same-sex faces compared to other-sex faces reported in the present study cannot be explained as a functionless byproduct of general face-processing mechanisms, but may be a product of specific adaptations for kin recognition that are sensitive to cues of the costs and benefits of preference for kin in different circumstances.

Chapter 5

Context-specific effects of facial resemblance on attributions of trustworthiness and sexual attractiveness

Preface

This paper is being prepared for submission to *Proceedings of the Royal Society of London B*.

Abstract

If humans are sensitive to the costs and benefits of favouring kin in different circumstances, a strong prediction is that cues of relatedness will have a positive effect on prosocial feelings toward other-sex individuals, but will have an opposite effect on their sexual attractiveness. I show that images of other-sex faces that were subtly manipulated in the possible kinship cue of facial resemblance were judged as more trustworthy by the participants they resembled than by control participants. In contrast, the effects of self-resemblance on attractiveness were neutral in the context of long-term partners,

for whom both prosocial regard and sexual appeal are important criteria, and negative in the context of short-term partners, for whom sexual appeal is the dominant criterion. The differential impacts of self-resemblance on judgments of trustworthiness and sexual attractiveness provide evidence for the existence of specialized processing of cues of kinship in the form of facial resemblance.

5.1 Introduction

Cues of kinship should increase prosocial positive regard due to the inclusive fitness benefits of socially favouring kin (Hamilton, 1964) while decreasing sexual desirability due to the costs of inbreeding (Bittles & Neel, 1994). Judgments of same-sex individuals should elicit assessment in a prosocial context only, while judgments of other-sex individuals should also elicit assessment in a sexual context. Consistent with this hypothesis, experimentally produced resemblance to self increases trusting behavior (DeBruine, 2002) and attributions of attractiveness (DeBruine, under review) towards same-sex faces, but increases the attractiveness of other-sex faces to a much smaller extent (Penton-Voak et al., 1999; DeBruine, under review). These results could not be explained by resemblance to self being more difficult to detect in other-sex faces than in same-sex faces, since DeBruine (under review) found a significant increase in the perceived averageness of self-resembling faces that was no greater for same-sex faces than for other-sex faces. This suggests that the difference in attractiveness is due to specialized responses to kinship cues sensitive to contexts in which kin are expected to be favoured or avoided.

One way to further test the context-sensitive nature of preferences for self-resemblance is to assess more than one dimension of "attractiveness" of other-sex faces. If humans are sensitive to the costs and benefits of favouring kin in different circumstances, cues of relatedness will have a positive effect on prosocial attributions, such as the rated trustworthiness of other-sex individuals, but will have a neutral or negative effect on their sexual attractiveness. Sexual attractiveness can be further divided into attractiveness for a long-term relationship or a short-term relationship (Little et al., 2002; Penton-Voak et al., 2003). Since indirect benefits such as good genes are hypothesized to be of greater importance to sexual attraction in a short-term than a long-term context (Gangestad & Thornhill, 1998) and close inbreeding has demonstrable detrimental impacts on the fitness of offspring (May, 1979; Bittles, 2001), cues of relatedness should be considered less attractive in a short-term relationship partner than in a long-term relationship partner.

The present experiment tests the prediction that resemblance to self will increase attributions of trustworthiness to other-sex faces more than it will increase sexual attractiveness. A close genetic relationship between partners carries a risk of deleterious effects from inbreeding, but this cost may be offset by the increased cooperation and investment in a long-term relationship (Bittles et al., 2002). Thus, self-resembling faces are predicted to be less attractive for a short-term relationship than for a long-term relationship.

5.2 Methods

5.2.1 Participants

Digital photographs of the participants were taken one week prior to the experiment in order to measure facial symmetry as part of a study of symmetry preferences that they were participating in that week and the next. Only images from the participants who agreed to have their photograph taken and shown to others in the context of the experiment were used. The three women and nine men who did not agree to have their photograph taken were shown control images when they came back the next week and their results were not analyzed. Additionally, two women were excluded because there were not enough women in the African phenotypic group to analyze their results. Six more women were excluded because of an error in stimulus presentation whereby they did not view any self-morphs. Four women and two men did not return for the second week of the experiment. Results are reported for the remaining 144 participants.

Participants for whom data are reported were 66 male and 78 female undergraduate students enrolled in an introductory psychology course (mean age=19.1 years, SD=2.3). Participants were of varying ethnic backgrounds, but were divided for the purposes of transforming faces into the broad phenotypic categories of African (including Afro-Carribean; 6 male, 0 female), East Asian (13 male, 17 female), European (31 male, 52 female) and South/West Asian (including Indian and Middle Eastern; 16 male, 9 female).

Participants were grouped into 18 testing units of four to nine persons of the same sex and same phenotypic category who acted as controls for each other. All participants in a testing unit viewed the same set of nine images, which included one self-face of each participant in the testing unit. For the nine testing units with fewer than nine participants (6 with 8 participants and 1 each with 6, 5 and 4 participants), images of unfamiliar undergraduates of the same sex and same phenotypic category as the participants were added to equate the number of images seen by each participant.

5.2.2 Stimuli

Average composite faces were created for each combination of sex and phenotypic category using the images of 20 individuals with a mean age of 19 years. The original head and shoulder photographs were taken using a digital camera under standard lighting conditions. The shape of each face was delineated using 171 facial landmarks and the composite faces were constructed with image manipulation software (Rowland & Perrett, 1995; Tiddeman et al., 2001) by combining the shape, color and texture information from the individual images.

The same procedure was used to photograph and delineate the participants' images. Each participant's image was used to transform the composite male or female face of the same phenotypic category. Transforms were made (Figure 5.1) by calculating the shape differences between the participant's face and the same-sex composite face and applying 50% of this difference to the other-sex composite face (see Chapter 4). Colour was not transformed because female transforms made from men with more or less facial hair than the average male face would have the appearance of facial hair or white blotches where facial hair would be.

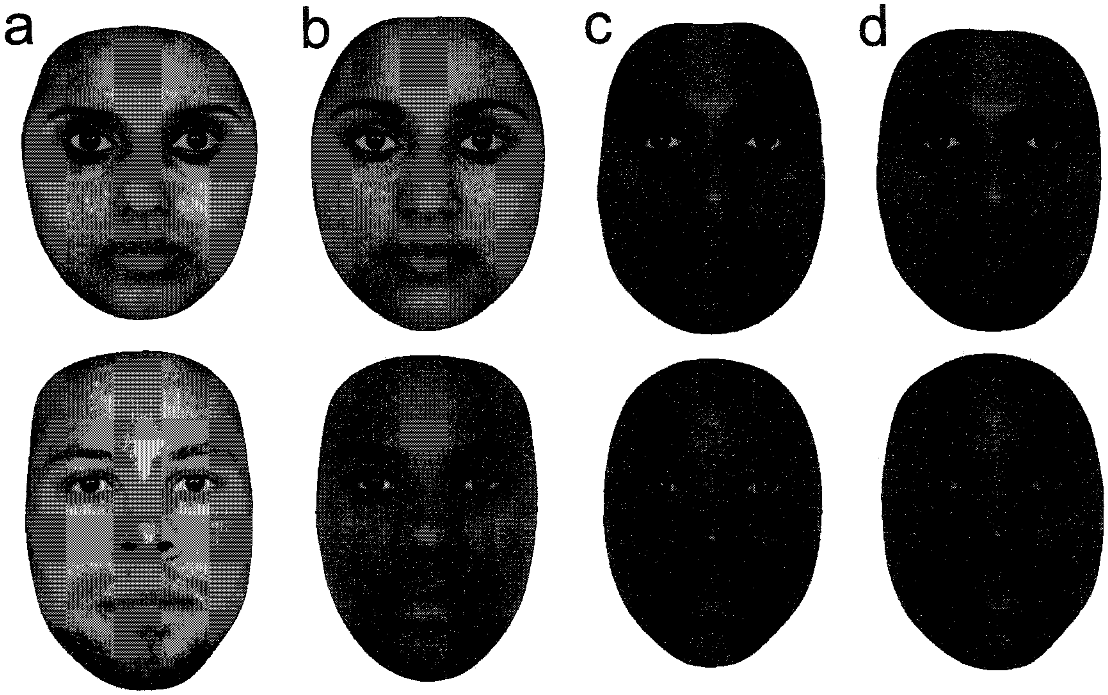

Figure 5.1: Transforms were made by applying 50% of the shape difference between the participant's face (a) and the same-sex composite face (b) to an other-sex composite face (c) to produce an other-sex self-transform (d). Transforms retained 100% of the color information from the other-sex composite face.

5.2.3 Procedure

Participants made two-alternative forced-choice decisions between all 36 possible pairs of the 9 faces in each testing unit for each question block. Each participant thus made eight decisions for each of the nine faces, including one self-resembling face. The order of faces was randomized and then presented in an optimal order for two-alternative forced choice tasks (Ross, 1934), whereby each image was shown equally often in each position and the presentation of identical stimuli was maximally spaced.

The same faces were presented for each of the three question blocks, which were presented in randomized order. Specifically, the three instructions presented were: (1) "Click on the face you find more trustworthy." (2) "Click on the face you find more attractive for a LONG-TERM relationship." and (3) "Click on the face you find more attractive for a SHORT-TERM relationship." A long-term relationship was defined as, "Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with, and someone you may, at some point, wish to marry (or enter into a relationship on similar grounds as marriage)." A short-term relationship was defined as, "This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship, and possibility of a one-night stand."

5.2.4 Statistical Analyses

Preference scores were calculated for each question by subtracting the average number of times each participant in a testing unit chose a particular face as the more trustworthy or more attractive of a pair (out of a possible 8 choices) from the number of times the participant from whom that face was made chose it.

Because Kolmogorov-Smirnov tests showed all variables to be normally distributed (all $Z < 1.2, p > .14$), a factorial repeated measures ANOVA was used to examine the within-subject differences in question type (trustworthiness, long-term attractiveness and short-term attractiveness), and the between-subjects effect of participant sex (two-tailed p-values are reported). Pearson's correlations were used to examine the relationships among preference scores for the three questions, with differences between correlations for control and self images assessed by Fisher r-to-z transformation (two-tailed p-values are reported). Independent samples t-tests were used to examine the predicted differences in men's and women's preferences for self-resemblance in the trustworthiness, long-term and short-term relationship contexts. One-tailed p-values were reported because resemblance was predicted to increase trustworthiness and decrease attractiveness.

5.3 Results

5.3.1 Preference Tests

Figure 5.2 shows a main effect of question type on preference for self-resemblance ($F_{2,284} = 6.94, p = .001$). Analysis of within-subjects contrasts revealed that self-resemblance increased attributions of trustworthiness more than attributions of attractiveness ($F_{1,142} = 9.48, p = .003$) and that preference for self-resemblance in a long-term relationship context was not significantly greater than in a short-term relationship context ($F_{1,142} = 2.95, p = .088$). There was no main effect of or interaction with sex of participant (all $F < 1.6$, all $p > 0.20$).

Because the ANOVA revealed no effect of sex, male and female responses were combined for t-tests assessing the strength of the effect of resemblance on preference scores for each of the three questions. Resemblance increased trustworthiness preference scores ($t = 2.69, p = .004$), had no effect on attractiveness for a long-term relationship ($t = 0.02, p = .493$), and decreased preference scores for attractiveness for a short-term relationship ($t = 1.80, p = .037$).

The average numbers of times that control participants chose a particular image were highly correlated for all question pairs for both men and women (Table 5.1). This indicates that, normally, trustworthiness, long-term relationship attractiveness, and short-term relationship attractiveness are influenced by similar criteria. In contrast, the correlations between the numbers of times the participant from whom an image was

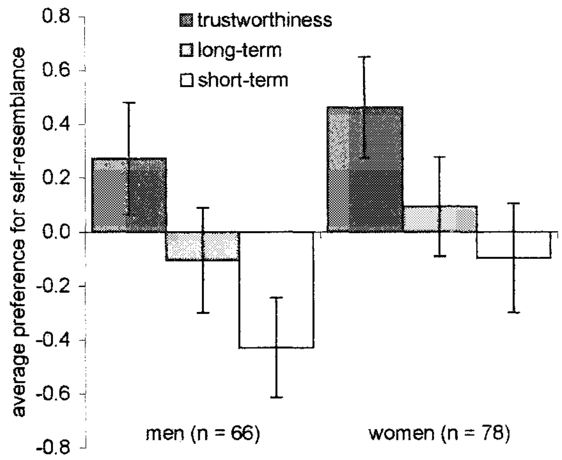

Figure 5.2: The average ($\pm SEM$) preference for self-resemblance in response to the trustworthiness, long-term and short-term relationship questions for men and women.

made chose that image for each question were significantly lower, suggesting that self-resemblance affected these responses in different ways. In other words, people judged most faces as attractive if they also judged them as trustworthy, but this tendency was much weaker if a face resembled the judge.

5.4 Discussion

Due to the fitness benefits of helping kin, positive effects of kinship cues were predicted for prosocial attributions. In contrast, negative effects were predicted in the domain of mate choice due to the costs of inbreeding. Preferences for self-resembling faces were shown to be sensitive to context in ways that are predicted from considerations of inclusive fitness theory (Hamilton, 1964) and the costs of inbreeding. In the present study, facial resemblance, a putative cue of relatedness, increased judgments of trustworthiness, had no effect on attractiveness in the context of a long-term relationship, and decreased attractiveness for a short-term relationship. Attributions of trustworthiness were increased significantly more than attributions of attractiveness for a long-term or a short-term relationship. Attractiveness of resembling faces was decreased more in a

Table 5.1: Pearson's correlations between scores for trustworthiness (T) and attractiveness for long-term (LT) and short-term (ST) relationships. Correlations are given for control scores (the average of the number of times that the control participants chose an image) and self scores (the number of times that the participant from whom an image was made chose that image). Fisher r-to-z transformations showed that all correlations for control scores were significantly greater than all correlations for self scores. Two-tailed p-values are reported.

	correlated		control scores		self scores		difference	
sex	questions		r	p	r	p	z	p
male	T	LT	.996	$< .001$	.167	.181	16.49	$< .001$
(n=66)	T	ST	.998	$< .001$	.184	.139	18.34	$< .001$
	LT	ST	.998	$< .001$	.572	$< .001$	15.73	$< .001$
female	T	LT	.820	$< .001$	.322	.004	5.04	$< .001$
(n=78)	T	ST	.885	$< .001$	.313	.005	6.58	$< .001$
	LT	ST	.977	$< .001$	.544	$< .001$	9.90	$< .001$

short-term relationship context than in a long-term relationship context, although not significantly so ($p = .088$, two-tailed).

These results are consistent with the finding that players represented by same-sex self-resembling faces were trusted more in a two-person economic investment game than players represented by a face morphed to resemble an unknown person (DeBruine, 2002) and lend support to the conclusion that the greater preference for self-resemblance when judging the attractiveness of same-sex faces versus other-sex faces found by DeBruine (under review) was not an artifact of differential resemblance.

DeBruine (under review) found that other-sex faces were judged as slightly more attractive (although much less so than same-sex faces) by the participants they were made to resemble than by other participants. By contrast, in the present study identically-transformed faces were judged as trustworthy but unattractive. This apparent discrepancy may be explained by differences in the specificity of the attractiveness questions. In the previous study, participants were simply asked to choose the most attractive face and were presented with the same task for both male and female faces. It is likely, therefore, that attractiveness judgments about other-sex faces reflected both attractiveness in a mating context and non-sexual prosocial regard. In the present study, attractiveness was specifically defined in a mating context. Given that questions about attractiveness for a long-term and a short-term relationship produced differences in preferences for self-resembling faces that were close to significance, it is plausible that the differences in question specificity account for the differences in preference for self-resembling faces between the previous study and the present one.

One potential non-adaptive explanation for general preferential responses toward self-resembling individuals involves the *mere exposure* hypothesis. This refers to the idea that previous experience with stimuli, including faces, results in a preference for those familiar stimuli when they are later presented (Zajonc, 1968; Bornstein, 1989). This effect was also demonstrated for averaged composites of previously seen faces (Rhodes et al., 2001), suggesting that prior exposure can increase liking for faces both identical to those seen previously and those with a similar appearance. If the hypothesis of mere exposure was sufficient to explain my findings, preferences for self-resembling faces would be expected to be increased in all three contexts. Clearly, the significant aversion to self-resembling faces found for the short-term relationship context is not consistent with an explanation of mere exposure to one's own face producing a general preference for similar faces.

The differential effects of self-resemblance on judgments of trustworthiness and sexual attractiveness provide evidence against explanations invoking a general preference for familiar-looking stimuli. Instead, the results provide evidence for the existence of specialized adaptive information processing of cues of kinship in the form of facial resemblance.

Chapter 6

General Discussion

As the previous chapters indicated, humans respond to experimentally produced facial resemblance in ways consistent with predictions derived from inclusive fitness theory and consideration of the costs of inbreeding. The findings presented in this thesis address both of the theoretical reasons to recognize kin presented in Chapter 1: nepotistic allocation of altruism (including parental investment) and optimal mate choice. People had a greater likelihood of cooperating in an economic trust game when the game partner facially resembled them (Chapter 2), demonstrating an effect of facial resemblance on prosocial behaviour. An increase in positive prosocial attributions was shown for self-resembling same-sex adult faces (Chapter 4), other-sex adult faces (Chapter 5), and child faces (Chapter 3). In the domain of mate choice, facial resemblance had less positive effects: facial resemblance increased the perceived attractiveness of other-sex faces to a much smaller extent than same-sex faces in the experiment reported in Chapter 4, and actually detracted from attractiveness for a "short-term relationship" in the experiment presented in Chapter 5.

In line with theoretical predictions, facial resemblance was found to increase prosocial behaviour and attributions consistent with the kinds of contexts where favouring kin would have been adaptive. Moreover, resemblance had a detrimental effect on judgments of sexual attractiveness consistent with the optimal mate choice rationale that avoiding mating with close kin would have increased fitness in ancestral environments. These context-specific effects provide evidence that responses to facial resemblance are more specialized than would be expected if they were mere byproducts of general face-processing mechanisms. However, contrary to other adaptationist predictions, no sex differences were found in responses to facial resemblance.

In the remainder of this chapter I will discuss the aforementioned context-specificity and lack of a statistically significant sex difference, as well as their implications for understanding the proximate mechanisms governing reactions to self-resemblance. I will also outline new questions and areas for future research raised by the results presented in the previous four chapters.

6.1 Responses to Facial Resemblance are Context-Specific

The findings of Chapters 4 and 5 support the idea of context-specific effects of facial resemblance. Inclusive fitness theory suggests that traits resulting in behaviour that enhances the fitness of individuals who are likely to be kin will be favoured by natural selection. Given the fitness costs of inbreeding, traits reducing the sexual attractiveness of individuals likely to be kin are also predicted to be favoured by natural selection. In keeping with these predictions, facial resemblance had different effects on preferences in prosocial and mate choice contexts.

In line with the hypothesis that cues of kinship will increase prosocial behaviour and attributions likely to lead to prosocial behaviour, Chapter 2 demonstrated increased trusting behaviour toward individuals exhibiting facial resemblance. The results of Chapter 5 supported this earlier finding: facial resemblance increased attributions of trustworthiness. Self-reported parental inclinations toward children were also shown to be positively influenced by facial resemblance in Chapter 3.

Chapter 4 provided preliminary evidence that facial resemblance has a different impact in the domain of mate choice than in the domain of prosociality. Facial resemblance increased the perceived attractiveness of faces, but this increase was greater for same-sex faces than for other-sex faces, even though male and female faces were constructed identically. In contrast, self-resemblance increased the perceived averageness of same-sex faces no more than other-sex faces. This provided evidence against the hypothesis that the difference in attractiveness was due to a non-adaptive perceptual bias whereby self-resemblance was easier to perceive in same-sex faces or whereby experience with one's own face only affected processing of same-sex faces. The results indicated a difference in the judges' interpretation of "attractiveness", which has a more sexual implication when judging other-sex faces than same-sex faces. To test this hypothesis, I asked people to judge faces in explicitly prosocial and sexual contexts in the experiment presented in Chapter 5.

Chapter 5 provided more definitive evidence of context-specific responses: facial self-resemblance increased attributions of trustworthiness, had no effect on attractiveness in the context of a long-term relationship, and decreased attractiveness in the context of a short-term relationship. Participants in this experiment viewed the same set of faces for each of the three specified contexts. Attributions of attractiveness to other-sex self-resembling faces were tempered in the context of a short-term relationship relative to the context of a long-term relationship, lending further support to the idea that cues of relatedness in the form of facial resemblance influence adaptive mate choice processes.

The experiment presented in Chapter 5 was specifically designed to address attractiveness for a long-term or a short-term sexual relationship, making it inapplicable to same-sex images. Nonetheless, the neutral or negative effects of facial resemblance on sexual attractiveness are in stark contrast to the positive effect on general attractiveness seen in Chapter 4 for same-sex faces. This contrast supports the context-specificity of responses to facial resemblance.

How can the unaffected or decreased attractiveness judgments of other-sex self-resembling faces be reconciled with the reports of facial similarity between dating and marital partners (Hinsz, 1989; Griffiths & Kunz, 1973; Bereczkei et al., 2002)? First, the faces of dating and married couples may be seen as more similar than randomly paired faces not because of facial similarity per se, but because of similarity in clothing, weight, apparent health, age, attractiveness or subtle cues of ethnicity. Similarity between mates on such factors in likely for a variety of reason unrelated to kinship. The aforementioned studies partially controlled for these factors by matching images for attractiveness and comparing pairs of similar age and ethnicity, but the computer graphic methods in my experiments may be more effective at eliminating these potential biases because participants compared the attractiveness of face images that differed only in their resemblance to the participants' face shapes. Second, people may choose long-term partners who resemble themselves because many factors apart from sexual attraction are important in such relationships. The results of Chapter 5 indicate that the perceived trustworthiness of other-sex faces is positively affected by resemblance to self. Possibly, judgments of trustworthiness are more indicative of success in a long-term relationship than judgments of attractiveness, although attributions of trustworthiness were no more correlated to attractiveness for a long-term relationship than they were to attractiveness for a short-term relationship (Table 5.1).

Only the experiments presented in Chapter 4 directly compared attributions to same-sex and other-sex faces transformed to resemble the experimental participants. Self-resemblance increased the perceived averageness of same-sex and other-sex faces to a similar extent, which indicated that people could perceive resemblance in both same-sex and other-sex transforms. However, self-resemblance increased the attractiveness of same-sex faces to a greater extent than other-sex faces.

At the time of the experiment presented in Chapter 2, I did not have access to the computer graphic software needed to make other-sex self-resembling faces, but I would predict that similar results would be obtained using the same interactive trust game and other-sex game partners. Alternatively, strategies used when playing economic games with an other-sex partner may partially reflect mating strategies. In this case I would predict that men, who may be more likely to "court" a partner in an economic game because they have more to gain by offering resources, would be less inclined to cooperate with players represented by self-resembling female faces, given both men and women's negative responses to self-resembling other-sex faces in the context of short-term relationships seen in Chapter 5. I would expect women, who are less likely to pursue a strategy of offering resources for short-term matings, to be as cooperative with other-sex self-resembling partners as with same-sex self-resembling partners.

6.2 Men and Women Respond Similarly to Facial Resemblance

Sex differences in responses to facial resemblance were predicted in the contexts of parental investment and mate choice, but were not found in any of the contexts investigated in the previous four chapters. The experimental protocols I used may not be adequate to detect sex differences. Alternatively, although the theoretical reasoning behind these predictions may be sound, sex differences could be absent because the costs outweighed the benefits of maintaining sex differences in the mechanisms that detect and respond to facial resemblance. Maintaining a sex difference in a trait is potentially costly because the expression of that trait will depend on other sex-dependent traits such as testosterone levels. This dependence may cause maladaptive fluctuations in the expression of the trait or the added complexity may make it more susceptible to failure. If this cost is larger than the benefit of maintaining a sex difference, such as a slight reduction in metabolic cost to one sex, then sex-dependent expression of the trait will not be selected for.

6.2.1 Should men respond to children's facial resemblance more than women?

Theoretically, one would expect men to have a greater response than women to phenotypic cues of relatedness of putative children, as discussed in Chapters 1 and 3. Several studies have found this to be the case (Platek et al., 2002, 2003; Volk & Quinsey, 2002). In Chapter 3 I investigated the degree to which facial resemblance increased self-reported solicitude toward infants. While facial resemblance did increase attractiveness judgments and hypothetical investment decisions, it did not do so more for men than for women, as had been predicted because of the asymmetry in parental certainty.

The inconsistency with the previous studies could be explained by methodological differences. I argued that the methods used in Platek et al.'s studies were likely to produce a sex difference in response to facial resemblance as a consequence of women's greater tendency to distribute rewards equally (Austin & McGinn, 1977; Kahn et al., 1980). The methods used in my study eliminated this possibility and found no sex difference in responses to children's facial resemblance. These results agree with another study in which the use of Likert scale ratings made the assessment of each child relatively independent of the other children being judged (Paola Bressan, unpublished data), which also reduced the possibility of a sex difference due to a sex difference in equality of reward distribution.

In response to finding no difference in men's and women's ability to recognize family resemblance between unfamiliar adults and children, Nesse et al. (1990) postulated several reasons for the inaccuracy of the prediction that men should detect facial resemblance more accurately than women. For example, the requisite genetic diversity for a sex difference may have never arisen or women may use facial similarity assessments to direct behaviour toward non-descendant kin. In particular, they emphasized the relative costs and benefits of maintaining a sex difference in this trait. The ability to perceive facial resemblance and respond preferentially to individuals exhibiting resemblance to self may have very low costs to women, especially if such a bias were overridden by the presence of more reliable kinship cues, such as the experience of giving birth to an individual.

6.2.2 Should women avoid facial resemblance in sexual partners more than men?

One explicit prediction from Chapter 4 was that women would be less attracted to self-resembling men than men would be to self-resembling women. This prediction followed from the idea that women pay higher costs for an incestuous mating and would have been under stronger selection to avoid matings with potential relatives (Irons, 1986). Similarly, it would have been reasonable to predict in Chapter 5 that women would exhibit less attraction to self-resemblance than men, especially in the short-term relationship context. Neither of these predictions was supported by the evidence. Perhaps other adaptations, such as the Westermarck effect (Westermarck, 1921), suffice to prevent matings with close kin, making a female-specific aversion to phenotypic resemblance unnecessary. For example, women report significantly more disgust to descriptions of sexual acts involving siblings than do men (Lieberman, 2003).

In addition, women may acquire some benefits from pairing with a relative. Bittles et al. (2002) reported that the fertility of first cousin marriages was negatively affected by genetic factors causing fetal and infant death, but positively affected by social factors such as earlier marriage, longer duration of marriage, and greater family support. Perhaps women are less averse than would be predicted to cues of kinship in the context of a long-term relationship because of the direct material and social benefits such unions provide. It would be interesting to assess the level of extra-pair matings in such unions, especially given the finding that extra-pair paternity and maternity increase with the genetic similarity between mates in shorebirds (Blomqvist et al., 2002).

6.3 Implications for Understanding the Proximate Mechanisms Governing Reactions to Self-Resemblance

The demonstration of context-specific effects of facial resemblance rules out simplistic proximate mechanisms such as liking what appears familiar. Nevertheless, the actual proximate mechanisms almost certainly involve learning of one's own or family members' phenotypes. While not impossible, it is difficult to imagine how a mental template representing one's own facial configuration could be genetically encoded, given that facial attributes are influenced by the interactions among numerous genes that are recombined with sexual reproduction. If the template is learned, it could become fixed at a certain age or it could remain malleable by experience throughout the lifespan. Responses to self-resemblance in people whose facial appearance had been altered by environmental events at different times in their lives could test what kind of experiences influence the template and whether a critical period exists.

If responses to self-resemblance are a result of comparison to a learned template, it is another question whether that template is influenced only by one's own face or by the faces of people who are likely to be family members. The lack of a way to experience one's own face until the relatively recent invention of mirrors would suggest the latter. In that case, one's own face may still be included in a family template because it is experienced through mirrors and photographs in much the same way that family members' faces are. One way to investigate the composition of a family template is to test adopted people's responses to faces that are similar to self and to adopted family-members. If adopted people do not show the same effect of resemblance to self that non-adopted people do, one can conclude that the template is not exclusively based on self. If people respond to faces that resemble an adopted sibling in the same way as to faces that resemble a genetic sibling, one can conclude that the template includes familiar faces.

A current limitation of studies using computer-graphic techniques to manipulate facial resemblance is that it is not yet known how such resemblance compares to resemblance between actual genetic relatives. Blending 50% of the shape and colour of a face into another face is unlikely to be equivalent to the resemblance between people with genetic relatedness of 0.5. People judge genetic relatives as more facially similar than unrelated pairs (Brédart & French, 1999; Bressan & Martello, 2002; Bressan & Grassi, in press; Christenfeld & Hill, 1995; McLain et al., 2000; Nesse et al., 1990; Oda et al., 2002; Porter et al., 1984), but the exact cues they use to do this are unknown. Many anthropometric cranial measurements, such as head circumference and nose breadth, are correlated between family members and their inheritance is consistent with simple autosomal genes (Poosha, Byard, Satyanarayana, Rice, & Rao, 1984; Byard, Poosha, Satyanarayana, & Rao, 1985; Byard, Poosha, Satyanarayana, Rao, & Russell, 1985). It is possible that similarity of certain features is given more weight than overall similarity or that shape is more influential than colour in judgments of family resemblance. A series of experiments determining the accuracy with which people can make relatedness judgments between pairs of real faces and between morphs using either whole faces or parts of faces are among my future plans and will likely answer these questions.

Recent work on the phenomenon of perceptual adaptation to faces (Blanz et al., 2000; Leopold et al., 2001; Webster, Kaping, Mizokami, & Duhamel, 2004) suggests a possible proximate mechanism for perceiving facial resemblance. This high-level adaptation is analogous to seeing a yellow square against an all-white surface after staring at a blue square. What the perceptual "opposite" of a face looks like is less intuitive than the opposite of a colour, however. Opposite faces (termed *anti-faces*) are made by transforming the shape and colour of a face relative to an average face. For example, a face that is darker than average and has a wider nose than average will have an anti-face that is paler than average and has a thinner nose than average. Viewing an anti-face for several seconds has been shown to cause the perception of the corresponding face when later viewing an average face (Leopold et al., 2001) in the same way that viewing a red square for several seconds will cause the perception of a green square when later viewing a white surface. The same effect has been shown for several natural categories of "opposites": male vs. female, white vs. Japanese, happy vs. angry, disgust vs. surprise, and fear vs. contempt (Webster et al., 2004). For example, perceptual adaptation to male faces decreased the level of femininity required to categorize a face as female. In addition, Webster et al. (2004) reported that people differed in their pre-adaptation categorization of faces in a way that was consistent with long-term perceptual adaptation to their own sex or ethnic group (e.g. men required less femininity than women did to categorize a face as female). Perceptual adaptation to one's own face and the face of family members may underlie responses to facial resemblance. Evidence for this was shown in Chapter 4 where facial resemblance increased the perceived averageness of male and female faces. However, general preference due to perceived averageness cannot account for the context-specific responses to facial resemblance shown in Chapter 5. Additional specific adaptive mechanisms are needed to account for the different reactions to resemblance in different contexts.

Another area of research opened up by the results presented in this thesis is the interaction between facial resemblance and other potential cues of kinship, such as major histocompatability complex (MHC) odours, nominal kinship terms, and familiarity during a critical period. I am currently testing the influence of hormonal states on perception of and reactions to facial resemblance. Preliminary data suggest that women have a greater preference for self-similar faces during the luteal (non-fertile) stage of the menstrual cycle when the hormonal profile is similar to that during pregnancy. This is consistent with the report that pregnant female mice prefer to nest with others who share their MHC odour signature, a potential cue of kinship (Manning et al., 1992).

Although I did not find support for a male bias in the use of facial resemblance cues to make parental investment decisions, such a sex difference remains theoretically compelling. Perhaps the child images presented during the study in Chapter 3 were not responded to as if they were the participants' own children. If so, it would be interesting to replicate this study in expectant and new mothers and fathers who are presumably experiencing many of the cues that could predispose them to respond to infants as if they were their own. Before the birth of a child, men experience changes in hormones (Berg & Wynne-Edwards, 2001) and behaviour (Storey, Walsh, Quinton, & Wynne-Edwards, 2000) associated with parental care. After childbirth, women experience a surge in oxytocin that is presumed to facilitate bonding with the new infant (Kendrick, 2000). These cues of impending parenthood may facilitate processes for making adaptive decisions about the resulting infant. One such process may be a male-specific increased effect of facial resemblance on investment decisions.

6.4 Conclusions

Facial resemblance enhances prosocial behaviour and attributions in domains where nepotistic biases would have been favoured in our evolutionary past and decreases attractiveness in a mate choice context, especially in a short-term relationship context. The experiments presented in this thesis are among the first to provide experimental evidence that people respond to facial resemblance in ways that are consistent with expectations about kin recognition mechanisms. These results provide evidence for facial phenotype matching as a specialized kin recognition adaptation which motivates different responses to facial resemblance in different domains because of past adaptive consequences.

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