An Evolutionary Perspective on Parental and Grandparental Investment

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An Evolutionary Perspective on Parental and Grandparental Investment

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(met een samenvatting in het Nederlands)

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Chapter 1

General Introduction

Whether, how, and to what extent parenting shapes and influences child development has been of longstanding interest to developmental psychologists and family scientists. A vast body of empirical evidence highlights the contribution of parenting to a wide range of cognitive, socio-emotional, and behavioral developmental outcomes in children (for a review see Bornstein, 1995). Although great effort has been spent on studying the effects of parenting, much less research has focused on factors that predict individual differences in parental investment. In his *Process Model of the Determinants of Parenting*, Belsky (1984) identified three general sources of influence on parental functioning: (1) individual personality and general psychological well-being of the parent, (2) characteristics of the child, and (3) contextual sources of stress and support. In this dissertation, we focus on the effect of the child on parenting behavior. An evolutionary psychological perspective is used to identify characteristics in children that stimulate their parents and grandparents into giving them the care, attention, and emotional support they need.

We begin this chapter by providing a short overview of the central tenets of evolutionary psychology. Next, we discuss parental investment and use an evolutionary psychological perspective to generate hypotheses about which characteristics in children would influence individual differences in investment by both parents and grandparents. We conclude this chapter by giving an outline of the rest of this dissertation.

Evolutionary Psychology

The relatively new field of evolutionary psychology (e.g., Buss, 1995, 1999; Cosmides & Tooby, 1987; Daly & Wilson, 1988; Tooby & Cosmides, 1992) is an *approach* to psychology, in which knowledge and principles from evolutionary biology are applied in research on the design of the human mind. It is not an *area* of psychology, like vision, reasoning, or social behavior. It is a *way of thinking* about psychology that can be applied to any topic within it.

Evolutionary psychologists argue that much of contemporary human behavior is generated by psychological mechanisms that were shaped by natural selection to solve specific adaptive problems faced by our hominid ancestors (such as choosing a good habitat, deciding which foods to eat, negotiating social hierarchies, selecting mates, and partitioning investment among offspring). Although these psychological mechanisms evolved to adequately solve the day-to-day problems faced by our ancestors, the behavior these mechanisms generate will not necessarily be adaptive in the present. Despite the

many differences in lifestyle between contemporary humans and our hunter-gatherer ancestors, there has been too little time for evolved psychological mechanisms to have changed since our ancestors abandoned the nomadic lifestyle they lived in for well over 99% of our species' evolutionary history. As a result, the psychological mechanisms evolved to adapt ancient humans to their environments may still leave traces in the behavior of modern people, even though that behavior may no longer be adaptive. Therefore, it is interesting to use an evolutionary psychological perspective in the study of contemporary human behavior.

Parental Investment

One of the human behaviors that can be studied from an evolutionary psychological perspective is parental investment. Whereas developmental psychologists and family scientists generally use the term parenting, in evolutionary psychology the more general term parental investment is used. Although the term *investment* can also imply financial or physical support, the term is used here to refer to parenting behavior such as emotional support, attention, time investment, and discipline.

From an evolutionary perspective parental investment in children is a means of optimizing the reproductive success of the parent by increasing one's inclusive fitness, that is, the number of copies of one's genes passed on to future generations through surviving offspring or descendent collateral kin (Hamilton, 1964).

On average, human mothers invest more in their children than fathers. This is partly due to the difference in potential rate of reproduction between men and women. Because of internal gestation and obligatory postpartum maternal care, the rate with which women can reproduce is considerably lower than the potential rate of male reproduction (Clutton-Brock, 1991). As a consequence, the reproductive success of women is more strongly influenced by investment in offspring, whereas men can benefit reproductively by directing their efforts towards gaining additional mates rather than investing in existing children (Trivers, 1972). In addition, whereas women are 100% sure of their maternity, men can never be fully certain of their paternity. Fathers who are unsure about their paternity may be reluctant to invest in their putative children.

Trivers (1972) defined parental investment as *"any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring"*. So defined, parental investment is limited, and parents have to make choices on how to allocate their resources among their offspring. (Although the word *choice* might imply that

parents take conscious decisions, it is important to stress that most investment decisions are taken non-consciously.) According to evolutionary theory, human parents are not expected to invest equally in each of the children in their household. Instead, parents are expected to favor children on the basis of their genetic relatedness and their reproductive value.

Genetic Relatedness

In order to maximize their own reproductive fitness, parents should prefer to invest in children to whom they are genetically related (Alexander, 1974; Trivers, 1972). Indeed, several studies have reported that parents favor their own biological children over genetically unrelated stepchildren. Stepchildren receive less care and investment compared to genetic children (e.g., Anderson, Kaplan, Lam, & Lancaster, 1999; Marlowe, 1999). In addition, children living with a stepparent are much more likely to be physically abused or neglected than children living with two biological parents (e.g., Daly & Wilson, 1996).

Besides investing in stepchildren (who are known to be unrelated to the parent), fathers face the problem of paternity uncertainty, and hence run the risk of unknowingly raising an unrelated child. Since men can never be fully certain of their paternity, they need to rely on indirect cues to assess whether they are likely to be the father of their putative children. One source of information contributing to a putative father's confidence of paternity is his confidence of the mother's sexual fidelity (Daly, Wilson, & Weghorst, 1982). Indeed, across cultures, discovery or suspicion of female infidelity is the leading cause of spouse abuse (Buss, 1996; Daly & Wilson, 1988) and divorce (Betzig, 1989). In 31% of the societies described by Betzig (1989) divorce followed from infidelity by either partner, in 67% it followed only from infidelity on the wife's part, and in 2% only from infidelity on the husband's part, suggesting that infidelity of their partner is a bigger issue for men than for women.

A second source of information a doubtful father could use to assess his relatedness to a putative child is father-child phenotypic similarity. One way a father could assess the resemblance of his putative child to himself is through phenotype matching. Phenotype matching involves learning particular phenotypic features of oneself (self-referent phenotype matching), or of familiar relatives (parents, siblings), thereby forming a mental template against which the phenotype of other individuals can be compared (Lacy & Sherman, 1983; Mateo & Johnston, 2000). It is predicted that the higher the degree of similarity between the father's mental template and his putative child, the more certain he will be of his paternity, and, consequently, the more willing he will be to invest in that particular child.

A first possible cue for parent-child phenotype matching is physical or facial resemblance. Several studies have examined parent-child resemblance. When asked to

identify a child's parent among three adults, unrelated judges correctly matched children to both of their parents at a significantly higher rate than expected by chance (Alvergne, Faurie, & Raymond, 2007; Brédart & French, 1999; Bressan & Grassi, 2004; McLain, Setters, Moulton, & Pratt, 2000). These findings indicate that there is a significant resemblance between parents and children, and thus suggest that physical resemblance is a potential cue for phenotype matching.

To assess child resemblance, a father may rely not only on his own perception of resemblance, but also on what others tell him (the "social mirror") (Burch & Gallup, 2000). If fathers use resemblance to assess genetic relatedness, and consequently adjust their investment in proportion to their perceived paternity, it would be in the mother's interest to assure paternity, and mothers should be especially motivated to claim resemblance of the child to the father (Kurland, 1979). Indeed, mothers are significantly more likely to ascribe resemblance of their newborn babies to the domestic father than to themselves, especially when they are in the presence of the domestic father (Daly & Wilson, 1982; McLain *et al.*, 2000; Regalski & Gaulin, 1993). This bias in how mothers ascribe resemblance does not reflect resemblance assessed by unrelated judges, who ascribed either no differential resemblance (Brédart & French, 1999; Bressan & Grassi, 2004), or a biased resemblance toward mothers (Alvergne *et al.*, 2007; McLain *et al.*, 2000). This observed contradiction between what mothers claim about resemblance and resemblance assessed by judges supports the hypothesis that women evolved a psychological mechanism to assure domestic fathers of their paternity by claiming paternal resemblance to promote paternal investment (Daly & Wilson, 1982; McLain *et al.*, 2000; Regalski & Gaulin, 1993).

Previous research on the link between parent-child resemblance and parental investment was mostly hypothetical and used college students as participants (e.g., Bressan, Bertamini, Nalli, & Zanutto, 2009; DeBruine, 2004; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek *et al.*, 2003, 2004; Volk & Quinsey, 2002, 2007). In *Chapter 2* of this dissertation we use a sample of Dutch parents and their school-age children to examine the link between parent-child resemblance and parental investment. In addition to physical resemblance, personality similarity between parents and their children may also give parents information on genetic relatedness. Therefore we examine both physical resemblance and personality similarity in relation to parental behavior of both mothers and fathers.

A second possible cue for parent-child phenotype matching is the child's olfactory signature. Humans, like other mammals, are capable of recognizing close biological kin by olfactory cues alone. Breast-feeding infants as young as two days old respond differentially to the characteristic odors of their own nursing mother (Macfarlane, 1975; Russell, 1976; Schaal, Montagner, Hertling, Bolzoni, Moyse, & Quichon, 1980), mothers can recognize

their newborn infants by olfactory cues after only a few hours of contact (Kaitz, Good, Rokem, & Eidelman, 1987; Porter, Cernoch, & McLaughlin, 1983; Russell, Mendelson, & Peeke, 1983; Schaal *et al.*, 1980), and fathers are able to identify the odor of a related infant, independent of prior experience with the child (Porter, Balogh, Cernoch, & Franchi, 1986). Unrelated judges can accurately match the odors of mothers to the odors of their biological children, indicating that mothers and their offspring share similar detectable odors (Porter, Cernoch, & Balogh, 1985). Failure to find comparable odor similarity among husbands and wives (Porter *et al.*, 1985) suggests that shared environmental factors (i.e., family members sharing similar basic diets and being exposed to comparable household odors) are insufficient for the development of olfactory resemblance among individuals who are not genetically related. Thus, the perceived olfactory similarity between mothers and children seems to be mediated (at least partially) by their shared genotypes (Porter *et al.*, 1985). If a person's unique odor is indeed genetically mediated, it follows that close relatives (who share a large proportion of their genes) should smell more alike than unrelated individuals, and parents may be capable of recognizing their kin by phenotype matching of these olfactory signatures.

Most research on humans has only focused on whether parents are able to recognize their children by smell, not whether parents use these olfactory cues when making investment decisions. The study presented in *Chapter 3* of this dissertation is among the first to examine whether parent-child olfactory recognition is linked to parental investment.

Given that men can never be fully certain of their paternity, and need to rely on indirect cues to assess whether they are likely to be the father of their putative children, both parent-child resemblance and olfactory recognition are expected to influence fathers' investment decisions more than mothers'.

Reproductive Value

A second factor that is expected to influence individual differences in parental investment is the reproductive value of the child (i.e., the child's probable future reproductive success). In order to maximize their own inclusive fitness, parents should allocate more care, resources, and attention to offspring who have the highest chance of future reproductive success (Mann, 1992; Scrimshaw, 1984). Indeed, evidence has been found that the degree of parental investment is influenced by a child's health status and reproductive value. For example, mothers of high-risk infants shorten the duration of breastfeeding and interbirth intervals compared to mothers of infants with higher survival prospects (Bereczkei, 2001). Also, when presented with both a healthy and an unhealthy twin, mothers bias their investment toward the healthy twin (Mann, 1992).

Not only information about current health of a child is important for parents when making investment decisions, also indirect cues can inform parents about the reproductive value of their child. Attractiveness is considered to accurately advertise fitness, health, and quality (Barber, 1995; Gangestad & Buss, 1993; Gangestad & Thornhill, 1997; Shackelford & Larsen, 1999; Thornhill, 1998; Thornhill & Gangestad, 1993). Attractive people, compared to less attractive people, display greater psychological well-being (Umberson & Hughes, 1987) and physical health (Shackelford & Larsen, 1999; but see Kalick, Zebrowitz, Langlois, & Johnson, 1998), and facial attractiveness predicts future longevity (Henderson & Anglin, 2003).

Like attractiveness, facial symmetry is considered to accurately advertise genetic quality and developmental stability (Gangestad & Thornhill, 1997; Møller & Thornhill 1997; Scheib, Gangestad, & Thornhill, 1999). Fluctuating asymmetry (i.e., small deviations from perfect symmetry in normally bilaterally symmetric traits) is presumed to be a measure of developmental instability and inability of an organism to cope with stress (e.g., Kowner, 2001; Little & Perrett, 2002). Facial asymmetry is thought to accumulate during development as a consequence of environmental or genetic stresses (Wilson & Manning, 1996). Only high-quality individuals can maintain symmetric development, therefore symmetry can serve as an indicator of the quality of an individual as well as the quality of its genes (Thornhill & Gangestad, 1996, 1999).

Although most research on attractiveness and facial symmetry has focused on preferences for mates, both attractiveness and facial symmetry may also signal to parents that their child has a high reproductive value, and, therefore, is worthy of investment. In *Chapter 4* of this dissertation we examine whether parental investment is influenced by child attractiveness and/or facial symmetry for our sample of Dutch parents and their school-age children.

Grandparental Investment

To this point our discussion has focused on factors that are expected to influence individual differences in parental investment. Kin selection theory, however, suggests that humans evolved to invest in other kin as well, to further increase their inclusive fitness. Grandparents, for example, can continue to contribute to their inclusive fitness by assisting their adult son or daughter in his/her parental effort. Several studies have shown that children benefit from the presence of grandparents (especially grandmothers), both in cognitive and health outcomes (Pope, Whiteside, Brooks-Gunn, Kelleher, Rickert, Bradley, & Casey, 1993), and psychological and sociological well-being (Al Awad & Sonagu-Barke,

1992; Wilson, 1986). Even though investment by grandparents clearly influences child health and well-being, and thus grandparental lifetime reproductive success, not all grandparents invest equally in their grandchildren. These differences in grandparental investment may be explained by certainty of relatedness (Smith, 1988).

Like paternal investment, grandparental investment might be affected by parental uncertainty, and because two generations of descendants are involved in grandparental solicitude, grandparents have a double chance of possible parental uncertainty. The most certain grandparent is the maternal grandmother, being certain of her own as well as her daughter's maternity. The most uncertain grandparent is the paternal grandfather, who can be certain of neither his own nor his son's paternity. The maternal grandfather and the paternal grandmother have intermediate levels of uncertainty of grandparenthood, both having one certain and one uncertain link. If discriminative grandparental solicitude varies as a function of certainty of relatedness, then maternal grandmothers are predicted to be the most caring grandparents, followed by maternal grandfathers and paternal grandmothers, with paternal grandfathers providing the least care. In *Chapter 5* of this dissertation we examine whether certainty of relatedness (as assessed by kinship lines) predicts differential grandparental investment by asking young grandchildren (8-10 years old) and their parents to rate the quality of the grandparent-grandchild relationship with each of the child's grandparents.

Outline of this Dissertation

The following chapters present four empirical studies addressing the key issues of this dissertation. *Chapter 2* describes two studies in which we examine the link between parent-child resemblance (both in looks and personality) and parental investment. *Chapter 3* examines whether parent-child olfactory recognition is associated with parental behavior. *Chapter 4* focuses on the effects of child attractiveness and facial symmetry on parental investment. *Chapter 5* assesses whether differential grandparental investment can be explained by certainty of genetic relatedness. The presentation of these empirical studies will be followed by a general discussion of the findings of these studies in *Chapter 6*.

Chapter 2

Parent-Child Resemblance and Kin Investment: Physical Resemblance or Personality Similarity?

Abstract

Resemblance between parents and children has been suggested as an indicator of kinship. Because men, unlike women, cannot be certain about parenthood, resemblance may influence men more than women when making investment decisions. In the present paper we describe two studies in which we examine the relation of physical resemblance and personality similarity with parental investment for 300 Dutch parents and their school-age children. The results of both studies indicate a link between personality similarity and parental investment for mothers. For fathers parental investment was linked to physical resemblance in one study but not in the other.

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Introduction

"It is a wise father that knows his own child", William Shakespeare wrote. And, at least from the perspective of evolutionary psychology, he was right. According to evolutionary theory, parents should prefer to invest in children to whom they are genetically related in order to increase their own reproductive fitness (Alexander, 1974; Trivers, 1972). Whereas women are sure of their maternity, men can never be fully certain of their paternity, but instead need to rely on indirect cues to assess whether they are likely to be the father of their putative children. Resemblance between parents and children, either in looks or personality, has been suggested as a possible cue of genetic relatedness (Alexander, 1974). Given the asymmetry in certainty of parenthood, men are predicted to be more sensitive to the resemblance of offspring to self than women when making investment decisions.

Conflicting results have been reported regarding the relation between physical resemblance and parental investment and the differences between men and women. In hypothetical adoption decisions, self-perceived cues of resemblance were significantly more important in men's decisions than in women's (Volk & Quinsey, 2002, 2007). In studies using images of child faces that were digitally manipulated to resemble the participants, three studies found that facial resemblance influenced men's investment decisions more than women's (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek *et al.*, 2003, 2004). Two independent attempts, however, failed to replicate these findings. One study found that facial resemblance increased hypothetical investment equally in men and women (DeBruine, 2004), whereas the other study found that the link between facial resemblance and investment was significant for women, but not for men (Bressan, Bertamini, Nalli, & Zanutto, 2009). Therefore, it remains unclear whether differences in hypothetical parental investment in reaction to facial resemblance reflect true differences between the sexes or whether these are due to differences in methodology across studies.

Evidence from studies on parental investment by actual fathers supports the hypothesis that men favor investing in children who are perceived as physically resembling them. Apicella and Marlowe (2004) reported that men's perceived resemblance to their offspring predicted their reported parental investment. Also, in a sample of convicted spouse abusers, men's ratings of physical resemblance were positively correlated with the self-reported quality of the men's relationships with their children and negatively correlated with the severity of injuries suffered by their spouses (Burch & Gallup, 2000). Unfortunately, both of these studies only included fathers, therefore it remains unclear

whether self-perceived cues of resemblance are more important in men's investment decisions than in women's.

Moreover, in measuring resemblance Apicella and Marlowe (2004) combined questions about physical resemblance and personality similarity into one measure of resemblance. Therefore it is not possible to determine whether it is physical resemblance, or personality similarity, or both, that contributes to the link with parental investment. The only study examining personality similarity in relation to parental investment found that personality similarity was linked to the quality of the parent-adolescent relationship (as reported by the adolescent) for mothers, but not for fathers (van Tuijl, Branje, Dubas, Vermulst, & van Aken, 2005). Physical resemblance was not included in this study, however. Therefore, it is important to investigate both physical resemblance and personality similarity in relation to parental investment in the same sample in order to determine whether one overrides the other for investment decisions or whether both are important.

In the present paper we describe two studies in which we attempt to disentangle physical resemblance and personality similarity in relation to parental investment and we investigate differences in investment between mothers and fathers. In the first study we examined the link between parental investment and a subjective measure of physical resemblance (self-report by the parent) and an indirect measure of personality similarity (Q-correlations between Big Five personality profiles of parents and their children) for a sample of 90 Dutch parents and their school-age children. In the second study we added an indirect measure of physical resemblance (a comparison of photographs by independent raters) and a subjective measure of personality similarity (self-report by the parent) for a sample of 210 Dutch parents.

Study 1

Method

Participants

Families were recruited via their 4th or 5th grade child (8-9 years) attending elementary schools in the Netherlands. Children were told about the study and were given letters describing the study to take home to their parents. In total 56 mothers, 34 fathers, and their children, representing 61 different families, agreed to participate and completed this first study. In 29 families both parents participated. All children were the purported biological offspring of the parents. In this sample 88% of the fathers and 75% of the mothers were currently married or cohabiting. The sample primarily represents Dutch

middle and upper middle class families. Among the fathers, 26% completed a lower educational training, 26% completed a higher technical degree, and 47% completed a university degree. Among the mothers, 21% completed a lower educational training, 35% completed a higher technical degree, and 43% completed a university degree.

Procedure

All families were visited twice in their own homes by two trained master's students studying developmental psychology. During the first visit parents completed a diverse battery of psychological and sociological measures designed to assess individual characteristics of parents and children, parental investment in each participating child, and perceived parent-child resemblance. Children were assessed on a number of social tasks (not relevant for the current research). The second visit was conducted three days later and included an odor recognition task and a computer recognition task (both not relevant for the current research).

Measures

Parental Investment

Three measures of parental investment were reported by the parents. The *emotional closeness of the relation* was measured using the mean of eight items adapted from existing Dutch parenting measures. Four items tapped how attached the parent feels to the child (de Brock, Vermulst, Gerris, & Abidin, 1992) and four items tapped how often the parent expresses affection towards the child (Gerris, Vermulst, van Boxtel, Janssens, van Zutphen, & Felling, 1993). Sample items from this scale include: 'I feel that I have a close bond with this child' and 'I regularly give this child a hug'. Cronbach's alphas were satisfactory (father $\alpha = .88$, mother $\alpha = .91$). Parents reported on their use of *physical punishment* on one item: 'I regularly give this child a slap'. For both the quality of the relation items and the physical punishment item parents rated the degree to which each item represented their behavior on a scale ranging from 1 (not at all true) to 7 (very true). The *amount of time* parents spend actively involved with the child each week was assessed by having parents estimate the amount of time engaged in six activities with the child on a daily basis (TV viewing, eating, assisting with homework, playing/reading, household tasks, and going out) (Dubas & Gerris, 2002).

Parent-Child Resemblance

Two different measures of parent-child resemblance were used.

Physical Resemblance. Parents reported on *physical resemblance* on the item 'I think my child looks like me', on a scale ranging from 1 (not at all) to 5 (very much).

Personality Similarity. Personality was measured using a Dutch adaptation of the Big Five questionnaire (Goldberg, 1992). The original 100 markers were reduced to 30, six markers for each of the five personality factors (Gerris, Houtmans, Kwaaitaal-Roosen, de Schipper, Vermulst, & Janssens, 1998). Fathers and mothers filled out the shortened version about themselves and their child, on a scale ranging from 1 (not at all applicable) to 7 (very applicable).

Q-correlations were used to calculate parent-child similarity in personality dimensions. A Q-correlation reports on a dyad, and indicates profile similarity (van Tuijl *et al.*, 2005). The Q-correlation was computed over the 30 items of each child with father and mother, separately. The similarity between parent and child ranged from -.30 to .80 (Mean = .42, SD = .26, N = 34) for father-child dyads and from -.24 to .92 (Mean = .49, SD = .27, N = 56) for mother-child dyads.

Results

Descriptive Statistics and Simple Correlations

Table 2.1 presents descriptive statistics for the measures of parental investment and parent-child resemblance for mothers and fathers. No significant differences were found between mothers and fathers.

Table 2.1. *Means and standard deviations of parental investment and parent-child resemblance in study 1*

	Mothers (N = 56)		Fathers (N = 34)	
	Mean	SD	Mean	SD
Emotional Closeness	6.20	.90	6.13	.69
Physical Punishment	1.52	.79	1.58	.68
Time Investment	168.39	69.67	150.28	86.72
Physical Resemblance	2.56	1.02	2.53	.98
Personality Similarity	.49	.27	.42	.26

In Table 2.2 the correlations between the different measures of parental investment and parent-child resemblance are reported. Parents' report on emotional closeness was negatively correlated with physical punishment for both mothers (r = -.30, p = .02) and fathers (r = -.51, p < .01). For fathers physical punishment was positively correlated with

time investment (r = .33, p = .05). In addition, for mothers personality similarity was positively correlated with emotional closeness (r = .32, p = .01) and negatively with physical punishment (r = -.27, p = .04). For fathers physical resemblance was positively correlated with emotional closeness (r = .35, p = .03).

Table 2.2. *Correlations between parental investment and parent-child resemblance in study 1*

Variable	1.	2.	3.	4.	5.
1. Emotional Closeness	—	-.30*	.23	-.11	.32*
2. Physical Punishment	-.51**	—	-.06	-.06	-.27*
3. Time Investment	-.02	.33*	—	.03	.10
4. Physical Resemblance	.35*	-.24	-.10	—	.12
5. Personality Similarity	.09	.12	-.02	-.06	—

Note. Correlations for mothers are above the diagonal, correlations for fathers are below the diagonal
*$p < .05$, **$p < .01$

Resemblance and Parental Investment

Regression analyses were used to examine whether mothers and fathers invested more in children who resembled them in either looks or personality (Table 2.3). After controlling for age of the parent and gender of the child in the first step, in the second step of the analyses physical resemblance and personality similarity were entered. No significant effects were found for age of the parent and gender of the child. For mothers personality similarity was positively linked with emotional closeness (β = .39, $p < .01$). That is, higher personality similarity is linked with closer mother-child relations. For fathers physical resemblance was positively linked with emotional closeness (β = .39, p = .05, overall model not significant; ΔR^2 = .11, p = .12) and negatively with physical punishment (at the trend level: β = -.37, p = .06, overall model not significant; ΔR^2 = .11, p = .14). Thus, higher levels of physical resemblance seem to be linked with closer father-child relations and less punishment by fathers.

Table 2.3. *Regression analyses: physical resemblance and personality similarity predicting parental investment in study 1*

	Emotional Closeness		Physical Punishment		Time Investment	
	ΔR^2	β	ΔR^2	β	ΔR^2	β
Mothers (N = 56)						
Model 1	.02		.07		.02	
Age of Parent		.03		-.25$^{\#}$		-.15
Child Gender (girl = 1, boy = 2)		.14		.14		.03
Model 2	.14*		.04		.02	
Age of Parent		-.07		-.19		-.19
Child Gender (girl = 1, boy = 2)		.22$^{\#}$		.09		.07
Physical Resemblance		-.12		-.02		.03
Personality Similarity		.39**		-.20		.16
Fathers (N = 34)						
Model 1	.03		.00		.02	
Age of Parent		-.04		-.02		-.03
Child Gender (girl = 1, boy = 2)		.16		.06		-.14
Model 2	.11		.11		.00	
Age of Parent		-.07		.03		-.03
Child Gender (girl = 1, boy = 2)		-.05		.25		-.12
Physical Resemblance		.39*		-.37$^{\#}$		-.03
Personality Similarity		.10		.10		-.02

$^{\#}p < .10$, $^{*}p < .05$, $^{**}p < .01$

Discussion

In accordance with previous studies (Apicella & Marlowe, 2004, 2007; Platek *et al*., 2002, 2003, 2004; van Tuijl *et al*., 2005; Volk & Quinsey, 2002, 2007), we found a link between parent-child resemblance and parental investment for our sample of Dutch mothers and fathers. Mothers reported having a closer relation with children who resemble them in personality, whereas fathers tended to have a closer relation and used less punishment with children who resemble them in looks. These results suggest that fathers are influenced by physical cues when making investment decisions, whereas mothers are influenced by psychological cues.

In this first study we focused on an indirect match in personality characteristics of parents and children (Q-correlations between Big Five personality profiles) and a subjective (self-report) measure of physical resemblance. Replication of our findings in a design in

which parents directly report on the similarity in personality with their child and an indirect measure of physical resemblance would help clarify whether it is perception of resemblance, actual resemblance, or both, that contributes to the link with parental investment. Therefore, in our second study we include both indirect and self-reported measures of physical resemblance and personality similarity. In addition, we not only include parent-reported measures of investment, we also asked the children to report on their relationship with each of their parents.

Study 2

Method

Participants

Recruitment of families was similar to study 1. In total 117 mothers, 93 fathers, and their children, representing 121 different families, agreed to participate and completed this second study. In 89 families both parents participated. All children were the purported biological offspring of the parents. In this sample 97% of the fathers and 91% of the mothers were currently married or cohabiting. The sample primarily represents Dutch middle and upper middle class families. Among the fathers, 31% completed a lower educational training, 36% completed a higher technical degree, and 33% completed a university degree. Among the mothers, 42% completed a lower educational training, 30% completed a higher technical degree, and 27% completed a university degree.

Procedure

Similar to study 1, all families were visited twice in their own homes. During the first visit parents completed a diverse battery of psychological and sociological measures designed to assess individual characteristics of parents and children, parental investment in each participating child and perceived parent-child resemblance. In addition, children completed questionnaires about their relationship with each of their parents, and photographs were taken of all participating family members (using a Ricoh Caplio R2 5MP Digital Camera). Subjects were asked to try to maintain a neutral unexpressive face for the picture.

Measures

Parental Investment

As in study 1, parents reported on three measures of parental investment: *emotional closeness* (father α = .82, mother α = .84), *physical punishment*, and *time investment.* In addition, the children reported on their relationship with each of their parents on eight items adapted from the Parent-Child Interaction Questionnaire (PACHIQ; Lange, Blonk, & Wiers, 1998). Four items tapped authority and four items tapped acceptance. Children rated the degree to which each item represented their relationship with each of their parents on a 5-point scale ranging from either 'never' to 'always' (for the frequency items) or 'does not apply to me at all' to 'applies to me exactly' (for the feeling/behavior items). Sample items from this scale include: 'When I have a problem, I ask my mother for advice' and 'My father and I get along well'. We used the mean of the eight items. Cronbach's alphas were quite satisfactory (child on father α = .83, child on mother α = .72).

Parent-Child Resemblance

Four different measures of parent-child resemblance were used; two measures reported by the parent, and two indirect measures.

Self-Reported Resemblance. In addition to the self-reported *physical resemblance* in study 1, in study 2 parents also reported on *personality similarity* on the item 'I think my child resembles me in personality', on a scale ranging from 1 (not at all) to 5 (very much).

Indirect Personality Similarity. As in study 1, *indirect personality similarity* was calculated using Q-correlations between Big Five personality profiles of parents and their children. The similarity between parent and child ranged from -.36 to .84 (Mean = .31, SD = .27, N = 93) for father-child dyads and from -.34 to .79 (Mean = .31, SD = .29, N = 117) for mother-child dyads.

Indirect Physical Resemblance. One hundred undergraduate students (50 men, 50 women, mean age 21.7 years) were recruited to rate parent-child resemblance from photographs and received course credit for their participation. The photographs that were taken of the parents and children during the first home visit were converted to 256 shades of gray, cropped to reveal only the participant's face, and set to a standard size (10.0 x 13.3 cm). Photographs of parents were coupled to the photograph of their own child and to the photograph of a control child matched to the parent's child in age, gender, eye color and hair color. Each parent-child pair (related or control) was printed on standard office paper (21.0 x 29.7 cm). Each pair was rated by ten students (five men, five women). The students were told that there were real and randomly matched pairs, but they were not told which of the pairs were real. The students rated the resemblance of the pairs on six items using a rating scale ranging from 1 (not at all) to 5 (very much). Sample items include: 'This child

has facial traits which look like those of the parent', and 'This child has the same eyes as the parent'. First we calculated the mean of the six items per rater for each parent-child pair. For each pair we then calculated the mean of the ten raters. Interrater reliabilities (Cronbach's alphas) ranged from .81 to .93.

Results

Descriptive Statistics and Simple Correlations

Table 2.4 presents descriptive statistics for the measures of parental investment and parent-child resemblance for mothers and fathers. Mothers and fathers differed in the time they report spending with their children (mothers reported more time investment; $t(195) = 4.75$, $p < .01$).

Table 2.4. *Means and standard deviations of parental investment and parent-child resemblance in study 2*

	Mothers (N = 117)		Fathers (N = 93)	
	Mean	SD	Mean	SD
Emotional Closeness	6.26	.76	6.07	.68
Physical Punishment	1.43	.76	1.45	.79
Time Investment *	224.68	100.95	163.99	71.07
Child Reported Parenting	4.00	.54	3.98	.61
Indirect Physical Resemblance	2.86	.66	2.68	.64
Self-Reported Physical Resemblance	2.48	1.07	2.61	1.04
Indirect Personality Similarity	.31	.29	.31	.27
Self-Reported Personality Similarity	3.01	1.15	3.01	.96

Note. * Significant difference between mothers and fathers

In Table 2.5 the correlations between the different measures of parental investment and parent-child resemblance are reported. Parents' report on emotional closeness was negatively correlated with physical punishment for mothers ($r = -.32$, $p < .01$) and positively with time investment for fathers ($r = .24$, $p = .03$). For both mothers and fathers child-reported parenting was not correlated with any of the investment measures reported by the parents. Parent's report on personality similarity was positively correlated with parent's report on physical resemblance as well as to indirect personality similarity for both mothers (parent-report on physical resemblance $r = .43$, $p < .01$; indirect personality

similarity r = .35, p <. 01) and fathers (parent-report on physical resemblance r = .26, p = .01; indirect personality similarity r = .24, p =. 02). Also, for mothers indirect physical resemblance was positively correlated with indirect personality similarity (r = .22, p = .02). In addition, for mothers reported personality similarity was positively correlated with emotional closeness (r = .24, p = .01) and time investment (r = .20, p = .04), and indirect personality similarity was positively correlated with emotional closeness (r = .26, p < .01) and the quality of the parent-child relationship as reported by the child (r = .20, p = .05). For fathers physical resemblance and personality similarity were not correlated with any of the indicators of parental investment.

Table 2.5. *Correlations between parental investment and parent-child resemblance in study 2*

Variable	1.	2.	3.	4.	5.	6.	7.	8.
1. Emotional Closeness	—	-.32**	.11	.18	-.05	.02	.26**	.24*
2. Physical Punishment	-.18	—	-.15	-.08	.03	.04	.11	-.05
3. Time Investment	.24*	-.13	—	.05	-.10	-.06	.10	.20*
4. Child Reported Parenting	.06	.08	.12	—	.04	.09	.20*	.09
5. Indirect Physical Resemblance	.01	-.13	-.01	.14	—	.09	.22*	.02
6. Self-Reported Physical Resemblance	-.16	.04	.04	-.21	.05	—	.10	.43**
7. Indirect Personality Similarity	.10	-.03	.18	-.12	-.19	.08	—	.35**
8. Self-Reported Personality Similarity	.02	-.15	.08	-.05	.13	.26*	.24*	—

Note. Correlations for mothers are above the diagonal, correlations for fathers are below the diagonal
*p < .05, **p < .01

Resemblance and Parental Investment

Again, regression analyses were used to examine whether mothers and fathers invested more in children who resembled them in either looks or personality (Table 2.6). After controlling for age of the parent and gender of the child in the first step, in the second step of the analyses the measures of parent-child resemblance were entered. No significant effects were found for age of the parent and gender of the child. For mothers indirect personality similarity was positively linked with emotional closeness (β = .21, p = .04) and the quality of the parent-child relationship as reported by the child (β = .23, p = .04, overall model not significant; ΔR^2 = .05, p = .28). Also, self-reported personality similarity was positively linked with emotional closeness (at the trend level: β = .20, p = .07) and time investment (β = .26, p = .02, overall model just missed significance; ΔR^2 = .08, p = .09). Thus, higher personality similarity is linked with closer mother-child relations (as reported

by both mothers and children) and more time investment by mothers. For fathers no significant link was found between any form of resemblance and parental investment.

Table 2.6. *Regression analyses: physical resemblance and personality similarity predicting parental investment in study 2*

	Emotional Closeness		Physical Punishment		Time Investment		Child-Reported Parenting	
	ΔR^2	β	ΔR^2	β	ΔR^2	β	ΔR^2	β
Mothers (N = 117)								
Model 1	.00		.03		.00		.03	
Age of Parent		.02		.11		.03		-.10
Child Gender (girl = 1, boy = 2)		.03		.13		.04		-.14
Model 2	.11*		.02		.08$^{\#}$		.05	
Age of Parent		.02		.10		.03		-.11
Child Gender (girl = 1, boy = 2)		.03		.12		.05		-.16
Indirect Physical Resemblance		-.10		-.02		-.10		.01
Self-Reported Physical Resemblance		-.07		.10		-.16		.04
Indirect Personality Similarity		.21*		.13		.04		.23*
Self-Reported Personality Similarity		.20$^{\#}$		-.11		.26*		-.03
Fathers (N = 93)								
Model 1	.00		.02		.02		.00	
Age of Parent		.05		-.13		-.06		.00
Child Gender (girl = 1, boy = 2)		.03		.05		-.12		.04
Model 2	.04		.04		.04		.08	
Age of Parent		.02		-.14		-.07		.00
Child Gender (girl = 1, boy = 2)		.04		.02		-.16		.11
Indirect Physical Resemblance		.04		-.13		-.01		.14
Self-Reported Physical Resemblance		-.19		.06		.03		-.13
Indirect Personality Similarity		.10		-.02		.20		-.10
Self-Reported Personality Similarity		.05		-.14		.02		.02

$^{\#}p < .10$, $^{*}p < .05$

Discussion

In accordance with the study of van Tuijl and colleagues (2005), and the first study described in this paper, we found a link between personality similarity and parental investment for our second sample of Dutch mothers. Mothers had a closer relationship (as reported by both mothers and children) and spent more time with children who resemble

them in personality. Both self-perceived resemblance and indirect resemblance (Q-correlations based on personality profiles of parents and their children) were found to contribute to this link.

In contrast to previous studies (e.g., Apicella & Marlowe, 2004, 2007; Platek *et al*., 2002, 2003, 2004; Volk & Quinsey, 2002, 2007), and the first study described in this paper, no link was found between parent-child resemblance and parental investment for fathers in our second study.

General Discussion

Given the asymmetry in certainty of parenthood, men are presumed to be more sensitive to cues of genetic relatedness than women when making investment decisions. Resemblance between parents and children, either in looks or personality, has been suggested as a possible cue of kinship (Alexander, 1974). In this paper we described two studies in which we examined the relation between parent-child resemblance and parental investment for a sample of Dutch parents and their school-age children. We investigated differences between mothers and fathers and attempted to determine whether it is physical resemblance, personality similarity, or both, that contributes to the link with parental investment. The results of both studies indicate a link between personality similarity and parental investment for mothers. For fathers parental investment was linked to physical resemblance in the first study. In the second study these results were not replicated.

The differences in the results for fathers between our two studies cannot be explained based on methodology. Families were recruited in the same way in both studies, and the procedure was similar in all families. In post hoc tests no significant differences were found in age of the parents and measures of investment and resemblance between the two studies. Nor were there problems of restrictions of range on the variables of interest. Education level was slightly higher in the first study, but controlling for this did not change our results in either study. Thus, methodological differences cannot explain why parental investment by fathers was linked to physical resemblance in the first study but not in the second.

Apicella and Marlowe (2004, 2007) reported that fathers' perception of resemblance to their offspring predicted their investment in their children. Resemblance became a stronger predictor of investment when men were no longer in a relationship with the mother of their children. Separated fathers also reported lower fidelity in the mother of their children as compared to men who were still in a relationship with the mother. Thus, it seems that when fidelity is in doubt, men rely more heavily on other cues, such as

resemblance, to estimate paternity (Apicella & Marlowe, 2004, 2007). If this is true, the low percentage of separated fathers in our studies, 11.7% in the first and 3.2% in the second, compared to 22.4% in Apicella and Marlowe's study (2004, 2007), could explain our weaker findings compared to previous studies. Additional studies are needed that take into account perception of both parent-child resemblance and spouse fidelity to determine if the link between physical resemblance and parental investment is indeed moderated by the degree of paternity certainty.

An important difference that could explain the weaker findings for fathers in our studies compared to the studies that investigated hypothetical investment decisions (e.g., Platek *et al*., 2002, 2003, 2004; Volk & Quinsey, 2002, 2007) is the use of actual kin versus non-kin targets. Park and Schaller (2005) argue that although it makes sense to focus on perceptions of and reactions to actual kin when investigating kinship processes, in order to rigorously test the hypothesis that resemblance serves as a heuristic kinship cue, it is necessary to experimentally separate resemblance from other cues that may also be associated with genetic relatedness, such as shared history and familiarity, which could mitigate effects. Doing so requires using a methodology in which perceivers are presented with previously unknown non-kin targets (Park & Schaller, 2005), as was done in the hypothetical investment studies. This suggests that smaller effect sizes are expected when investigating real families.

For mothers parental investment was linked to personality similarity in both of our studies. Mothers can be sure of their maternity and do not need to rely on cues to assess relatedness. This raises the question whether the link between investment and personality similarity in mothers is driven by a mechanism other than kin recognition. Lerner (1993) suggests that parents' reactions to temperamental qualities of a child depend to some degree on the prevailing beliefs system of the parents with respect to the significance of the behavior in question, such that parenting of the child is a matter of goodness of fit. If the child's behavior fits with the expectations of the parent then problems are less likely to occur. Similarity may help a parent understand and read a child's behavior more accurately, resulting in more sensitive parenting (van Tuijl *et al*., 2005). Goodness of fit may be particularly relevant for mothers given that they are still responsible for the majority of childcare (Silverstein, 1996). This could explain why the link between parental investment and personality similarity was found for mothers but not for fathers in the present studies and the study by van Tuijl *et al*. (2005).

Several limitations with this research need to be acknowledged. First, because both of our studies use only cross-sectional data the direction of causal effects cannot be determined. Second, we restricted our sample to 8- and 9-year old children. At this age children are already less dependent on parental investment than younger children (Hagen,

Hames, Craig, Lauer, & Price, 2001). Therefore, in future research children of different age groups, particularly younger children, should be included. Third, we had a limited number of investment measures and none that was tapping overall investment. Stronger results may be found when a broader array of investment measures such as financial investment, educational involvement, and other indicators of time investment are taken into account (e.g., Anderson, Kaplan, & Lancaster, 2007; Apicella & Marlowe, 2004).

In conclusion, parental investment was found to be linked to personality similarity for mothers in both of our studies and to physical resemblance for fathers only in our first study. These results, combined with the results of Apicella and Marlowe (2004, 2007), suggest that it remains plausible that physical resemblance is more important for fathers than for mothers, especially when fathers are uncertain about their paternity.

Chapter 3

Parent-Child Olfactory Recognition and Parental Investment

Abstract

In most mammalian species kin recognition and parental investment are mediated to a great extent by olfactory cues. Most research on humans, however, has only focused on whether parents are able to recognize their children by smell, not whether parents use these olfactory cues when making investment decisions. In the current study we show that fathers report spending more time with sons whose odor they are able to recognize and have a closer bond with sons whose odors they find pleasant. Mothers report having a closer bond with children whom they are able to recognize, and use less physical punishment with sons whose odors they are able to identify. These results provide evidence that olfactory cues may guide human parents in the allocation of parental care.

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Introduction

According to kin selection theory (Hamilton, 1964), organisms should preferentially aid more closely related kin over more distantly related kin or non-kin in order to increase their own reproductive fitness. Indeed, differential treatment of kin versus non-kin has been observed in a wide range of animal species (reviewed in Hepper, 1991), providing evidence for kin recognition. For many mammals, olfaction is their dominant sense (Wyatt, 2003), and it has been demonstrated that kin recognition and parental investment are mediated to a great extent by olfactory cues in most terrestrial mammals (Mateo, 2002; Yamazaki, Beauchamp, Curran, Bard, & Boyse, 2000). Even though the role of olfaction in parental investment is documented in many mammalian species, most research on humans has only focused on whether or not parents are able to recognize their children by smell, not whether parents use these olfactory cues when making investment decisions.

Humans, like other mammals, are capable of recognizing close biological kin by olfactory cues alone. Breast-feeding infants as young as two days old respond differentially to the characteristic odor of their own nursing mother (Macfarlane, 1975; Russell, 1976; Schaal, Montagner, Hertling, Bolzoni, Moyse, & Quichon, 1980). Likewise, mothers can recognize their newborn infants by olfactory cues after only a few hours of contact (Kaitz, Good, Rokem, & Eidelman, 1987; Porter, Cernoch, & McLaughlin, 1983; Russell, Mendelson, & Peeke, 1983; Schaal *et al*., 1980). Fathers, grandmothers and aunts have also been shown to be able to identify the odor of a related infant, independent of prior experience with the child (Porter, Balogh, Cernoch, & Franchi, 1986). Parental recognition of offspring odors is not restricted to infants. Parents can recognize the odors of their 3-11 year old children, and children of this age can identify their sibling's odor (Porter & Moore, 1981; Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003). Furthermore, both mothers and fathers can correctly distinguish between the odors of their biological children (Porter & Moore, 1981). They have difficulty, however, distinguishing the odors of identical twins (Wallace, 1977), suggesting that individual odors have a genetic basis.

The hypothesis that olfactory phenotypes are genetically mediated is supported by the fact that unrelated judges can accurately match the odors of mothers to the odors of their biological children, indicating that mothers and their offspring share similar detectable odors (Porter, Cernoch, & Balogh, 1985). Failure to find comparable odor similarity among husbands and wives (Porter *et al*., 1985) suggests that shared environmental factors (i.e., family members sharing similar basic diets and being exposed to comparable household odors) in themselves are insufficient for the development of olfactory resemblance among individuals who are not genetically related. Thus, the perceived olfactory similarity

between mothers and children seems to be mediated at least partially by their shared genotypes (Porter *et al*., 1985).

The mechanisms underlying olfactory kin recognition are not clearly understood (Halpin, 1991). Several studies have suggested that individual body odors are influenced by the major histocompatibility complex (MHC) (Boyse, Beauchamp, & Yamazaki, 1987; Yamazaki, Beauchamp, Singer, Bard, & Boyse, 1999; Yamazaki *et al*., 2000), a large and highly polymorphic family of genes also involved in immune response. If a person's unique odor is indeed genetically mediated, it follows that close relatives (who share a large proportion of their genes) should smell more alike than unrelated individuals. Humans might be capable of recognizing kin by phenotype matching of olfactory signatures.

If olfactory kin recognition serves to promote parental investment, then parental olfactory recognition of a child is expected to be positively associated with investment. Whereas women are sure of their maternity, men can never be fully certain of their paternity, but instead need to rely on indirect cues to assess whether they are likely to be the father of their putative children. Given the fact that olfactory recognition may increase certainty of genetic relatedness, the link between olfactory recognition and parental investment is expected to be stronger for men than for women.

Besides olfactory recognition, also pleasantness of a child's odor may be associated with parental investment. Pleasantness of an individual's odor may serve as a signal of lack of disease (Penn & Potts, 1998), and thus may indicate to parents that their child is genetically fit and, therefore, worthy of investment. Alternatively, however, child odor might serve a role in inbreeding avoidance, in which case parents are expected to have an aversion for their own child's odor (Weisfeld *et al*., 2003), particularly for their opposite-sex children.

In a preliminary study (Dubas, Heijkoop, & van Aken, 2009) we provided the first evidence that olfactory kin recognition and odor pleasantness are related to parental investment in humans. Our results suggested that fathers exhibit more affection and attachment and less ignoring behavior towards children whose odor they were able to identify compared to those whose odor they could not recognize. Mothers reported using higher levels of physical punishment with children whose odors they were unable to identify and independently also reported using higher levels of physical punishment with children whose odors they found pleasant. In the current study we examined whether the results of this first study would replicate, and thereby assess the reliability of its main findings using a larger sample. In addition, the larger sample of the current study allowed us to extend the first study to examine whether similar links are found when gender of the child is taken into account. If child odor serves a role in inbreeding avoidance, parents are expected to show an aversion for their own child's odor, especially for their opposite-sex

children. This could result in differences in parents' pleasantness ratings between boys and girls, which, in turn, could affect the link with parental investment. Finally, in the current study we conducted an odor threshold test to determine whether child recognition is associated with general olfactory function.

Method

Participants

Families were recruited via their 4th or 5th grade child (8-9 years) attending elementary schools in the Netherlands. Children were told about the study and were given a brief demonstration about olfaction. They were asked to take letters describing the study and consent forms home to their parents. Parent(s), the target child (8-9 years), and (if possible) one sibling (4-11 years) were invited to participate. In total 117 mothers, 93 fathers, and 195 children (88 boys and 107 girls), representing 121 different families, agreed to participate and completed the study. In 89 families both parents participated. All children were the purported biological offspring of the parents. In this sample 97% of the fathers and 91% of the mothers were currently married or cohabiting. Among the fathers, 31% completed a lower educational training, 36% completed a higher technical degree, and 33% completed a university degree. Among the mothers, 42% completed a lower educational training, 30% completed a higher technical degree, and 27% completed a university degree. Mean ages of participants were 42 years for fathers (SD = 4.89, range = 29-54), 40 years for mothers (SD = 3.91, range = 28-47), and 8 years for children (SD = 1.90, range = 4-11).

Procedure

All families were visited twice in their own homes by two trained bachelor students studying developmental psychology. All home visits were conducted in the same order, beginning with a general introduction and a general description of the study giving parents and children an opportunity to ask questions about the study. Subsequently, the t-shirts for the odor recognition task were distributed and the task was described. Parents were told that they would be tested on their ability to recognize their children during the second visit. Next, parents completed a diverse battery of psychological and sociological measures designed to assess individual characteristics of parents and children, and parental investment in each participating child. Children were assessed on a number of social tasks (not relevant for the current research). The second visit was conducted three days later and included the odor recognition task as well as a test to assess general olfactory function.

Measures

Parental Investment

We used three measures of parental investment reported by the parents. The *emotional closeness of the relation* was measured using the mean of seven items adapted from existing Dutch parenting measures. Four items tapped how attached the parent feels to the child (de Brock, Vermulst, Gerris, & Abidin, 1992) and three items tapped how often the parent expresses affection towards the child (Gerris, Vermulst, van Boxtel, Janssens, van Zutphen, & Felling, 1993). Sample items from this scale include: 'I feel that I have a close bond with this child' and 'I often let my child know that I love him/her'. Cronbach's alphas were satisfactory (father $\alpha = .78$, mother $\alpha = .82$). Parents also reported on their use of *physical punishment* on one item: 'I regularly give this child a slap'. For both the quality of the relation items and the physical punishment item parents rated the degree to which each item represented their behavior on a scale ranging from 1 (not at all true) to 7 (very true). The *amount of time* parents spend actively involved with the child each week was assessed by having parents estimate the amount of time engaged in six activities with the child on a daily basis (TV viewing, eating, assisting with homework, playing/reading, household tasks, and going out) (Dubas & Gerris, 2002).

Odor Recognition Task

A procedure similar to Porter and Moore (1981) was used. Each child received a new, 100% cotton t-shirt that was prewashed using odorless Neutral® brand laundry detergent and fabric softener. Parents were instructed to have their child wear the t-shirt to bed for three consecutive nights. To prevent t-shirts from absorbing ambient household odors during the day, they were kept in individual sealed plastic bags from the time the child woke up in the morning until bedtime. The children received Neutral® brand unscented soap to use during the study and were requested to refrain from using scented soaps and perfumes or having pets in their bedroom at night. If parents smoked, they were asked not to do so in and around the child's bedroom. On the day of the olfaction task they were asked not to smoke for at least one hour prior to the test. After three nights, the researchers returned for the odor recognition task, bringing two t-shirts worn by control children. Control children were recruited via work colleagues, family, and friends of the researchers and (as far as can be ascertained) were unknown to the participants in this study. In families with two children one control t-shirt was matched in age and gender to each of the children. In families with one child, one control t-shirt was matched in age and gender to the child, the other control t-shirt was chosen randomly.

The t-shirts were folded and rolled in such a manner that the axillary seams of the t-shirt were exposed. Each t-shirt was placed in a new plastic bag. T-shirts were then placed

in identical plastic beakers (H x D = 25 x 10 cm). Mothers and fathers were tested individually and were blindfolded during the task. For the *pleasantness rating task* parents were presented with a plastic beaker that held either their own child's t-shirt or a t-shirt worn by a control child. Parents were asked to smell the t-shirt and rate the pleasantness of the odor on a 5-point scale (1 = very unpleasant, 2 = unpleasant, 3 = neutral, 4 = pleasant, and 5 = very pleasant). Order of presentation of the t-shirts was random. For the *recognition task* parents were presented with two beakers; one containing their own child's t-shirt and one containing a t-shirt worn by a control child. Parents were asked to identify which beaker held the t-shirt worn by their own child. There was no time limit. Discrimination ability for each control t-shirt was tested three times, resulting in a total of six pair wise comparisons per child. To maintain independence of the six tests, parents were told about their performance only after completing the entire recognition task. All handling of t-shirts for the olfaction task was conducted with disposable vinyl gloves to obviate odor contamination.

Test of General Olfactory Function

General olfactory function was measured directly after the odor recognition task, by means of the Sniffin' Sticks odor threshold test (Burghart GmbH, Wedel, Germany; Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997; Kobal, Hummel, Sekinger, Barz, Roscher, & Wolf, 1996), using the method of constant stimuli (Lötsch, Lange, & Hummel, 2004). The odor threshold test consists of sixteen felt-tip pens containing phenyl ethyl alcohol diluted in propylene glycol in 1:2 dilution ratios (starting from 4%), and two pens containing only propylene glycol serving as blanks. Odors were presented in triplets of pens, one containing the odorant at a certain dilution, while the two other pens contained only the solvent. For odor presentation the cap was removed by the experimenter and the pen's tip was placed 1-2 cm in front of the nostril for ~3s. Employing a three-alternative, temporal forced-choice paradigm, the subject had to identify the pen that contained the odorant. Subjects were blindfolded to prevent visual identification of the odor containing pens (for details, see Hummel *et al*., 1997; Kobal *et al*., 1996; Lötsch *et al*., 2004). Triplets of pens were presented to the subject in a randomized order. Each triplet was presented only once.

Odor thresholds were calculated using the method of Lötsch *et al*. (2004); the logistic function (Linschoten, Harvey, Eller, & Jafek, 2001) of

$$P(x) = \gamma + (1- \gamma) \left(\frac{1}{1 + (\alpha / x)^{-\beta}} \right) \qquad (3.1)$$

was fitted to the data using a log-likelihood fitting technique. In this function x denotes the dilution step ($1 \leq x \leq 16$), γ the probability of correct identification by chance (0.33 for the three-alternative forced-choice paradigm), α the odorant dilution step half-way between chance and full probability (i.e., the odor threshold), and β the steepness of the function.

Confounding Factors Associated with Child Recognition

In addition, we examined several factors that possibly affect parents' ability to identify their children's odors. Parents reported on their current smoking status, as smokers have been found to have a higher olfaction threshold than non-smokers (Good, Martzke, Daoud, & Kopala, 2003). On average 17% of the parents currently smoked (20.4% of the fathers, 13.7% of the mothers). We also asked whether anyone else smoked in the home, as the ambient odor of smoke may permeate children's clothing, facilitating odor recognition. Households were then classified as smoke-free (72%) or non-smoke-free (28%).

We also examined whether mothers' menstrual cycle phase and use of oral contraception were possible confounds since the highest degree of olfactory sensitivity coincides with the ovulatory phase (Pause, Sojka, Krauel, Fehm-Wolfsdorf, & Ferstl, 1996), and women who use oral contraception lose this peak sensitivity (Caruso, Grillo, Agnello, Maiolino, Intelisano, & Serra, 2001). Mothers reported on their reproductive history including whether they were currently on oral contraception (yes: 19%) and their current menstrual status. Women indicated whether they had regular menstrual cycles, the length of their cycles in days, and the first day of their last menstrual cycle. Women with complete information on these questions (and who were not pregnant, menopausal, or using oral contraception) were classified as ovulatory (24%) if within three days of their midcycle or otherwise non-ovulatory (76%).

Statistical Analyses

Data from multiple children within the same family cannot be treated as independent observations, as it is likely that the responses given by the same parent about multiple children from the same family are more similar than the responses from different parents about unrelated children. Therefore multilevel analyses were conducted (using MLwiN version 2.02; Rasbash, Charlton, Browne, Healy, & Cameron, 2005), taking this nested structure of the data into account. Multilevel analysis partitions the variation in parental investment into two levels; the individual child level (level one) is nested within families (level two). The proportion of level two (or *between*-family) variance to total variance is an index of the intraclass correlation (i.e., the extent to which scores of investment between the parent and different children in the same family resemble one another as compared to parental investment scores from different families). The intraclass

correlation coefficients for the different measures of parental investment ranged between .27 and .87.

Interaction terms between child gender and odor recognition and child gender and pleasantness ratings were added to the model to determine whether the link between investment and odor recognition and investment and pleasantness ratings differed for boys and girls.

Results

Gender Differences in Olfactory Function and Child Recognition

Mothers and fathers did not significantly differ in their general olfactory function (mothers' mean odor threshold = 7.42, fathers' mean odor threshold = 7.78, t(332) = -1.05, p = .30). In addition, mothers and fathers did not significantly differ in their ability to identify their children's odors (mothers' mean accuracy = 4.65, fathers' mean accuracy = 4.43, t(332) = 1.16, p = .25). Children were classified as recognized or non-recognized based on the parent's olfactory recognition score. If parents correctly identified a child's t-shirt at least 5 out of 6 times the respective child was classified as recognized (binomial distribution P ($X \geq 5 \mid n = 6, p = .5$) = .05); if not, the child was labeled as non-recognized. A slightly higher percentage of mothers accurately recognized their children (65.1%) than did fathers (56.6%), although this difference was not significant (mothers' mean = .65, fathers' mean = .57, t(332) = 1.58, p = .12).

Pleasantness Ratings

Mothers and fathers did not significantly differ in their pleasantness ratings of their children's odor, neither for sons (mothers' mean pleasantness = 3.39, fathers' mean pleasantness = 3.22, t(148) = 1.34, p = .18) nor for daughters (mothers' mean pleasantness = 3.40, fathers' mean pleasantness = 3.33, t(182) = .69, p = .49). Mothers rated the odor of sons and daughters as equally pleasant (mean pleasantness sons = 3.39, mean pleasantness daughters = 3.40, t(187) = -.13, p = .90). Fathers rated the odor of daughters as slightly more pleasant than the odor of sons, although this difference was not significant (mean pleasantness sons = 3.22, mean pleasantness daughters = 3.33, t(143) = -.90, p = .37). Mothers rated the odor of both their sons and daughters as more pleasant than that of an age- and gender-matched control child (mean pleasantness sons = 3.39, mean pleasantness control boys = 2.87, $t_{paired}(84) = 4.04$, $p < .01$; mean pleasantness daughters = 3.40, mean pleasantness control girls = 2.92, $t_{paired}(103) = 3.91$, $p < .01$). Fathers rated the odor of their daughters as slightly more pleasant than that of a control girl (mean pleasantness daughters

= 3.33, mean pleasantness control girls = 3.08, $t_{paired}(79) = 1.94$, $p = .06$). Fathers' pleasantness ratings of their sons' odor did not significantly differ from that of a control boy (mean pleasantness sons = 3.22, mean pleasantness control boys = 3.23, $t_{paired}(64) = -.12$, $p = .90$). Thus, neither mothers nor fathers showed an aversion for their own child's odor, neither for same-sex nor for opposite-sex children.

Child Recognition, Pleasantness Ratings, and Parental Investment

Multilevel analyses were used to examine whether mothers and fathers invested more in children whom they were able to identify and/or children whose odor they rated as more pleasant (Table 3.1). Age of the parent and gender and age of the child were included in the analyses as control variables. For mothers a significant effect was found for both age and gender of the child. Specifically, mothers had a closer bond with their younger children ($\beta = -.16$, $p = .01$), and punished their sons more than their daughters ($\beta = .36$, $p < .01$). In addition, for mothers a near significant main effect was found for odor recognition; mothers reported having a closer bond with children whom they were able to recognize ($\beta = .14$, $p = .06$). For fathers a significant effect was found for age of both child and parent. Specifically, fathers had a closer bond with their younger children ($\beta = .-18$, $p = .02$), and younger fathers punished their children more than older fathers ($\beta = .-19$, $p = .04$). For fathers no significant main effects were found for odor recognition and pleasantness ratings.

Interaction terms between child gender and odor recognition and child gender and pleasantness ratings were added to the model to determine whether the link between investment and odor recognition and investment and pleasantness ratings differed for boys and girls. The interaction between child gender and recognition was significant for punishment for mothers ($\beta = -.26$, $p = .03$) and time investment for fathers ($\beta = .22$, $p = .04$). In addition, the interaction between child gender and pleasantness was significant for emotional closeness for fathers ($\beta = .17$, $p = .03$). To interpret these significant interaction terms, analyses were conducted for boys and girls separately. The link between recognition and punishment for mothers was significant for boys ($\beta = -.15$, $p = .05$), but not for girls ($\beta = .09$, $p = .19$), indicating that mothers use less physical punishment with sons whose odors they can recognize. The link between recognition and time investment for fathers was also significant for boys ($\beta = .20$, $p = .04$), but not for girls ($\beta = .10$, $p = .16$), indicating that fathers spend more time with sons whose odors they can recognize. The link between pleasantness and paternal emotional closeness was again significant for boys ($\beta = .21$, $p = .04$), but not for girls ($\beta = -.07$, $p = .23$), indicating that fathers have a closer bond with sons whose odors they find pleasant.

Table 3.1. *Multilevel analyses: olfactory recognition and pleasantness ratings predicting parental investment*

	Emotional Closeness		Physical Punishment		Time Investment	
	ΔR_1^2	β	ΔR_1^2	β	ΔR_1^2	β
Mothers (N = 117)	.05		.05		.02	
Age of Parent		.06		.04		.04
Child Gender (girl = 0, boy = 1)		.13		.36**		.04
Age of Child		-.16*		-.10		.07
Odor Recognition		.14#		.11		.05
Pleasantness Rating		.01		.05		-.02
Child Gender * Odor Recognition		-.11		-.26*		-.06
Child Gender * Pleasantness Rating		.03		.08		-.03
Fathers (N = 93)	.04		.14		.02	
Age of Parent		.09		-.19*		-.09
Child Gender (girl = 0, boy = 1)		.15		-.08		-.12
Age of Child		-.18*		-.05		-.04
Odor Recognition		-.05		.05		-.12
Pleasantness Rating		-.03		-.06		.06
Child Gender * Odor Recognition		-.13		.10		.22*
Child Gender * Pleasantness Rating		.17*		.02		.01

#$p < .10$, *$p < .05$, **$p < .01$

Factors Associated with Child Recognition

Additional multilevel analyses investigating several factors that possibly affect parents' ability to identify their children's odors revealed that mothers' (but not fathers') recognition was associated with general olfactory function ($\beta = .19$, $p = .05$). Specifically, mothers with higher olfactory function were better at recognizing their children's odors. Child recognition was not associated with gender and age of the child, parental smoking status, smoking status of the household (smoke-free or non-smoke-free), maternal oral contraception use, or maternal menstrual cycle phase.

Discussion

To our knowledge, this study is among the first to demonstrate that olfactory cues are associated with parental investment among humans. Our results suggest that fathers spend more time with sons whose odor they were able to recognize. Fathers also reported having a closer bond with sons whose odors they found pleasant. No reliable link was found between fathers' investment in their daughters and olfactory recognition or pleasantness. Mothers reported having a closer bond with children whom they were able to recognize. In addition, mothers reported using less physical punishment with sons whose odors they were able to recognize. No link was found between mothers' pleasantness ratings of their children's odors and investment.

The results of the current study are consistent with the results of our preliminary study (Dubas *et al*., 2009) with respect to the fact that recognizing one's children is associated with an increase in investment for both mothers and fathers and a decrease in physical punishment by mothers. In the current study, the links between olfactory recognition and punishment by mothers, and olfactory recognition and time investment by fathers were significant only for sons, not for daughters. Mothers reported punishing their sons significantly more than their daughters, and the variance in punishment was larger for sons than for daughters, which could account for the link between recognition and punishment to be significant for sons, but not for daughters. Fathers, however, reported no difference in time investment between sons and daughters, nor was there a difference in variance. At this moment it is too early to speculate why the link between olfactory recognition and time investment by fathers was significant only for sons, not for daughters. More research is needed to verify whether this effect can be replicated.

In our preliminary study the most reliable links between olfactory recognition and parental investment were found for fathers, suggesting that olfactory cues were more important for fathers than for mothers. We proposed that olfactory recognition could be an indirect means by which fathers assess their genetic relatedness to their offspring, which, in turn, affects their degree of investment. In the present study, however, olfactory recognition was found to be equally important for mothers and fathers. Although this might seem strange, theoretically, sex differences would be unlikely to result from natural selection unless the costs of an adaptation to one sex outweigh the costs of maintaining dimorphism, even if one sex does receive greater benefits from a trait (Nesse, Silverman, & Bortz, 1990). Because many traits, like maintaining a large muscle mass or the ability to lactate, have substantial costs, it is easy to assume that sex differences will arise whenever benefits to the sexes differ. However, when the costs of maintaining a trait are small, and when the trait offers some benefits to both sexes, natural selection is not expected to favor sexual

dimorphism (Nesse *et al*., 1990). Although only men face direct paternity uncertainty, it would be adaptive for women to evaluate phenotypic cues of relatedness, such as odor recognition, when making investment decisions about children who are putatively related through a male (e.g., grandchildren through a son, or cousins through a brother) (DeBruine, 2004), and therefore mothers may use these cues even on their own children when making investment decisions.

In addition to olfactory recognition, we also investigated parents' reports on the pleasantness of their children's odor. We found only one significant link between pleasantness and parental investment; fathers reported having a closer bond with children whose odors they found pleasant, but only for sons. If pleasantness of a child's odor serves as a signal of health and genetic quality (Penn & Potts, 1998), these results are puzzling in that a link was only found for sons and not for daughters, and only for fathers' investment, not for mothers'. If instead pleasantness of a child's odor serves a role in inbreeding avoidance, parents are expected to show an aversion for their own child's odor (Weisfeld *et al*., 2003), particularly for their opposite-sex children. We compared parents' pleasantness ratings of their own child's odors to that of an age- and gender-matched control child and found no evidence that parents rate their own child's odor as less pleasant. In fact, mothers rated the odor of both their sons and daughters as more pleasant than the odor of control children. Fathers rated their daughter's odor as more pleasant than that of a control girl, and their son's odor as equally pleasant compared to a control boy. These results suggest that child odor does not serve a role in inbreeding avoidance in our study. Our sample, however, consisted of only pre-pubertal children, who are still dependent on their parents' investment. Child odor may still become important as a mechanism to avoid inbreeding when children reach sexual maturity and the risk of inbreeding increases.

Several limitations of the current study need to be acknowledged. First, we used only a limited number of investment measures and none that was tapping overall investment. Stronger results may be found when a broader array of investment measures such as financial investment, educational involvement, and other indicators of time investment are taken into account. Second, we only used parent report to assess the degree of parental investment. Future research should use additional methods, such as observations in the family situation, as using a multi-method measure gives a more complete and more objective impression of the investment made by parents. Finally, our results are correlational and therefore the cause-effect directions of our findings cannot be firmly established; investment may drive olfactory recognition rather than recognition driving investment. If this is true, however, we would expect a link between duration of co-residence and olfactory recognition; in the present study we found no such link if we use age of the child as a proxy for length of co-residence. Well-controlled experimental studies

could be used to establish the direction of cause and effect and further clarify whether olfactory recognition is facilitated when the child's odor represents a stronger match to the parent's own olfactory signature.

Despite the limitations of our study, our results suggest that olfactory cues are associated with parental investment for both mothers and fathers. Research that examines which characteristics of children predict parental behaviors, and that explores ways of modifying such unconscious parental biases could make important contributions to our understanding of parent-child interactions and child development.

Chapter 4

Child Attractiveness and Parental Investment: Do Looks Really Matter?

Abstract

In order to maximize their inclusive fitness, parents should adjust their investment depending on the child's fitness, quality and reproductive potential, investing more in higher quality offspring. Good-genes theory asserts that attractiveness and facial symmetry accurately advertise health and quality. If this is true, parents are expected to invest more in attractive and symmetrical children compared to less attractive and less symmetrical children. We examined the relation of child attractiveness and facial symmetry with parental investment in a sample of 121 Dutch families with school-age children. Both mothers and fathers reported having a closer bond with attractive children compared to less attractive children. Attractive children were also punished less often than less attractive children by both mothers and fathers. These results indicate that child attractiveness is a significant predictor of parental behavior.

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Introduction

From an evolutionary perspective parental investment in children is a means of increasing one's inclusive fitness, that is, the number of copies of one's genes passed on through surviving offspring or descendent collateral kin (Hamilton, 1964). Evolutionary theory asserts that in order to maximize their own inclusive fitness, parents should invest differently in children depending on the child's fitness, quality and reproductive potential (Buss, 1999; Daly & Wilson, 1980). Parents should allocate more care, resources, and attention to higher quality offspring (Mann, 1992; Scrimshaw, 1984). Indeed, evidence has been found that the degree of parental investment is influenced by a child's health status. For example, mothers of high-risk infants shorten the duration of breastfeeding and interbirth intervals compared to mothers of infants with higher survival prospects (Bereczkei, 2001). Also, using a hypothetical adoption paradigm, Volk, Lukjanczuk, and Quinsey (2005) found that both men and women were less willing to adopt infants and children whose facial photographs had been digitally manipulated to simulate cues of low body weight (low body weight reflects health problems in infants and children).

Not only is information about current health of a child important for parents when making investment decisions, also indirect cues can inform parents about the health and reproductive value of their child, and, in turn, be linked with investment decisions. Attractiveness and facial symmetry are considered to accurately advertise fitness, health, quality, and heterozygosity (Barber, 1995; Gangestad & Buss, 1993; Gangestad & Thornhill, 1997; Shackelford & Larsen, 1999; Thornhill, 1998; Thornhill & Gangestad, 1993), and thus may signal to parents that their child is genetically fit, and, therefore, worthy of investment.

Although initially developed to explain why individuals prefer romantic partners who are physically attractive, the good-genes theory posits that attractiveness is an honest cue of health, quality, and accordingly, reproductive value. The preference for an attractive partner may have evolved to favor healthy individuals due to direct and indirect benefits associated with the selection of a healthy partner (Andersson, 1994; Thornhill & Gangestad, 1993, 1999). Several lines of support have been found for this good-genes explanation of attractiveness. Different cultures share similar standards of attractiveness (Cunningham, Roberts, Wu, Barbee, & Druen, 1995; Langlois, Kalakanis, Rubenstein, Larson, Hallam, & Smoot, 2000), and infants as young as two months old prefer to look at faces that are judged as attractive by adults (e.g., Langlois, Roggman, Casey, Ritter, Rieser-Danner, & Jenkins, 1987), suggesting that the perception of attractiveness has a stable, innate component. Furthermore, several studies found evidence for a relationship between attractiveness and actual health. Attractive people, relative to less attractive people,

displayed greater psychological well-being (Umberson & Hughes, 1987) and physical health (Shackelford & Larsen, 1999; but see Kalick, Zebrowitz, Langlois, & Johnson, 1998), and facial attractiveness was found to predict future longevity (Henderson & Anglin, 2003). These findings are consistent with the good-genes theory that attractiveness is an honest cue of actual health.

Like attractiveness, facial symmetry is considered to accurately advertise genetic quality and developmental stability (Gangestad & Thornhill, 1997; Møller & Thornhill, 1997; Scheib, Gangestad, & Thornhill, 1999). Fluctuating asymmetry, that is, small deviations from perfect symmetry in normally bilaterally symmetric traits, is presumed to be a measure of developmental instability and inability of an organism to cope with stress (e.g., Kowner, 2001; Little & Perrett, 2002). Facial asymmetry is thought to accumulate during development as a consequence of environmental (e.g., parasites and toxins) or genetic (e.g., harmful mutations and homozygosity) stresses (Wilson & Manning, 1996). Only high-quality individuals can maintain symmetric development, therefore symmetry can serve as an indicator of the quality of an individual as well as the quality of its genes (Thornhill & Gangestad, 1996, 1999). In a range of species, including humans, individuals' fluctuating asymmetry negatively predicts their growth rate, survival, and fecundity (Møller & Pomiankowski, 1993; Watson & Thornhill, 1994).

If attractiveness and facial symmetry indeed are indicators of quality, parents should invest more in attractive and symmetrical children than in less attractive and less symmetrical children (Barden, Ford, Jensen, Rogers-Salyer, & Salyer, 1989; Field & Vega-Lahr, 1984; Langlois, Ritter, Casey, & Sawin, 1995). Research findings suggest that children really are treated differently on the basis of their attractiveness. Experimental laboratory studies have shown that attractive children, compared to less attractive children, are generally treated more favorably by adults who are unacquainted with them. Berkowitz and Frodi (1979), for example, found that female college students punished unattractive children more severely than attractive children despite identical child behavior. Volk and Quinsey (2002, 2007) studied how cuteness of infants and children influenced adults' hypothetical adoption decisions, and found that both men and women were more willing to adopt infants and children that were rated as more cute. Badr and Abdallah (2001) examined whether nurses caring for premature infants in the neonatal intensive care unit (NICU) were influenced by the attractiveness of the infants. Premature infants that were rated as physically more attractive spent fewer days in hospital and gained more weight than premature infants perceived as less attractive. Even though the amount and kind of nursing care was not directly measured in their study, Badr and Abdallah (2001) presumed that attractive infants received more nurturing than less attractive infants. These

investigations suggest that attractive children are more likely to receive more positive treatment by unacquainted adults than less attractive children.

Moreover, there are a few studies using parents as participants that suggest that the phenomenon is not restricted to unacquainted adults. Elder, Van Nguyen, and Caspi (1985) examined the relationship between fathers and their adolescent children during the Great Depression, and found that following the loss of a job or income, fathers were more harsh and punitive toward their unattractive daughters than toward their attractive daughters. Langlois, Ritter, Casey, and Sawin (1995) examined the relation between infant attractiveness and maternal behavior and found that mothers of more attractive infants were more affectionate and playful with their babies compared to mothers of less attractive infants. In addition, mothers of less attractive infants were more likely to be attentive to other people rather than to their infant and engaged in more routine caregiving rather than affectionate behavior with their infants (Langlois *et al*., 1995). These studies both suggest that a child's attractiveness may indeed influence parental behavior.

However, only a limited number of studies have examined the link between attractiveness and investment, and no study included both mothers and fathers. Moreover, to our knowledge there are no studies published to date that have examined the link between facial symmetry and parental investment. The present study was designed to address this lacuna. Here we examine the relation of child attractiveness and facial symmetry with parental investment in a sample of Dutch mothers and fathers and their school-age children. We also examine whether the relation of child attractiveness and facial symmetry with parental investment differs for boys and girls. According to human mate-selection theory attractiveness is more important for females, because men seek attractive women (as attractiveness signals youth and reproductive fitness), whereas women seek men with resources, rather than attractiveness, because such men are able to provide for offspring (Buss, 1998, 1999; Thornhill, 1998). Therefore, attractiveness might be a more important predictor of reproductive value, and, in turn, have a stronger link with parental investment for girls than for boys.

Method

Participants

Families were recruited via their 4th or 5th grade child attending elementary schools in the Netherlands. Children were told about the study and were asked to take letters describing the study and consent forms home to their parents. Parent(s), the target child (8-9 years), and (if possible) one sibling (4-11 years) were invited to participate. In total 117

mothers, 93 fathers, and 195 children (88 boys and 107 girls), representing 121 different families, agreed to participate and completed the study. In 89 families both parents participated. All children were the purported biological offspring of the parents. In this sample 97% of the fathers and 91% of the mothers were currently married or cohabiting. The sample primarily represents Dutch middle and upper middle class families. Among the fathers, 31% completed a lower educational training, 36% completed a higher technical degree, and 33% completed a university degree. Among the mothers, 42% completed a lower educational training, 30% completed a higher technical degree, and 27% completed a university degree. Mean ages of participants were 42 years for fathers (SD = 4.89; range = 29-54), 40 years for mothers (SD = 3.91; range = 28-47), and 8 years for children (SD = 1.90; range = 4-11).

Procedure

All families were visited twice in their own homes by two trained bachelor students studying developmental psychology. During the first visit parents completed a diverse battery of psychological and sociological measures designed to assess individual characteristics of parents and children, and parental investment in each participating child. Children were assessed on a number of social tasks (not relevant for the current research). During the first visit photographs were taken of all participating family members (using a Ricoh Caplio R2 5MP Digital Camera). Subjects were asked to try to maintain a neutral unexpressive face for the picture. The second visit was conducted three days later and included an odor recognition task (not relevant for the current research).

Measures

Parental Investment

We used three measures of parental investment reported by the parents. The *emotional closeness of the relation* was measured using the mean of eight items adapted from existing Dutch parenting measures. Four items tapped how attached the parent feels to the child (de Brock, Vermulst, Gerris, & Abidin, 1992) and four items tapped how often the parent expresses affection towards the child (Gerris, Vermulst, van Boxtel, Janssens, van Zutphen, & Felling, 1993). Sample items from this scale include: 'I feel that I have a close bond with this child' and 'I regularly give this child a hug'. Cronbach's alphas were satisfactory (father $\alpha = .79$, mother $\alpha = .84$). Parents also reported on their use of *physical punishment* on one item: 'I regularly give this child a slap'. For both the quality of the relation items and the physical punishment item parents rated the degree to which each item represented their behavior on a scale ranging from 1 (not at all true) to 7 (very true). The *amount of time* parents spend actively involved with the child each week was assessed by

having parents estimate the amount of time engaged in six activities with the child on a daily basis (TV viewing, eating, assisting with homework, playing/reading, household tasks, and going out) (Dubas & Gerris, 2002).

Child Attractiveness

We used three different measures of child attractiveness.

Parent-report. Parents reported on their child's attractiveness on two items: 'How attractive do you think your child is (1) with respect to his/her face, and (2) in total (body and face)?'. Attractiveness was rated on a 5-point scale ranging from 'very unattractive' to 'very attractive'. Reliability (Cronbach's alpha) was satisfactory (father $\alpha = .86$, mother $\alpha = .89$).

Observer-report. Child attractiveness was also observed during the first home visit. Each trained observer independently assessed attractiveness on the same two items as the parents. Inter-rater agreement as assessed by Pearson's correlation coefficient was .31 ($p < .01$). Mean attractiveness scores across the two observers were used in the analyses.

Independent Ratings. One hundred undergraduate students (50 men, 50 women, mean age 21.7 years) were recruited to rate child attractiveness from photographs and received course credit for their participation. The photographs that were taken of the children during the first home visit were converted to 256 shades of gray, cropped to reveal only the child's face, and set to a standard size (10.0 x 13.3 cm). Each photograph was printed on standard office paper (21.0 x 29.7 cm). Each photograph was rated by twenty students (ten men, ten women). The students rated attractiveness of the children using a 5-point rating scale ranging from 'very unattractive' to 'very attractive'. Interrater reliabilities (Cronbach's alphas) ranged from .73 to .92.

Factor analysis on the different measures of attractiveness (mother-report, father-report, observer-report, and independent ratings) yielded one factor accounting for 49.77% of the variance across ratings. Therefore mean attractiveness was used in the multilevel analyses.

Facial Asymmetry

Facial asymmetry was measured based on the method introduced by Grammer and Thornhill (1994). We used 14 morphological points on the face that can be identified reliably (Figure 4.1). The points were positioned on the outside (P1 and P2) and inside (P3 and P4) corners of the eyes, the cheekbones (widest horizontal part of the face below the eyes, P5 and P6), the widest points at the sides of the nostrils (P7 and P8), the left and right junctions where the lower part of the ear touches the head (P9 and P10), the corners of the mouth (P11 and P12), and the jaw (widest horizontal part of the cheeks at the mouth, P13

and P14). Each of these seven pairs of points were connected by a horizontal line (L1-L7, Figure 4.2). The midpoint of each line was calculated using the formula ([right point - left point]/2) + left point. The vertical midline of the face was calculated as the average midpoint across the seven lines. Facial asymmetry was then calculated as the sum of the nonredundant differences between the midpoints of the horizontal lines and the vertical midline of the face. On a perfectly symmetrical face, all midpoints lie on the same vertical line, and the sum of all possible nonredundant midpoint differences is zero.

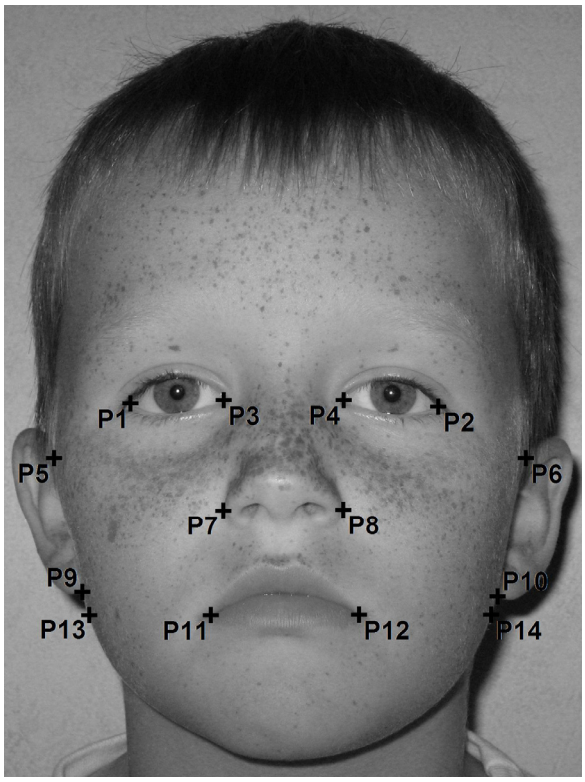

Figure 4.1. *Points used for measurement of facial asymmetry*

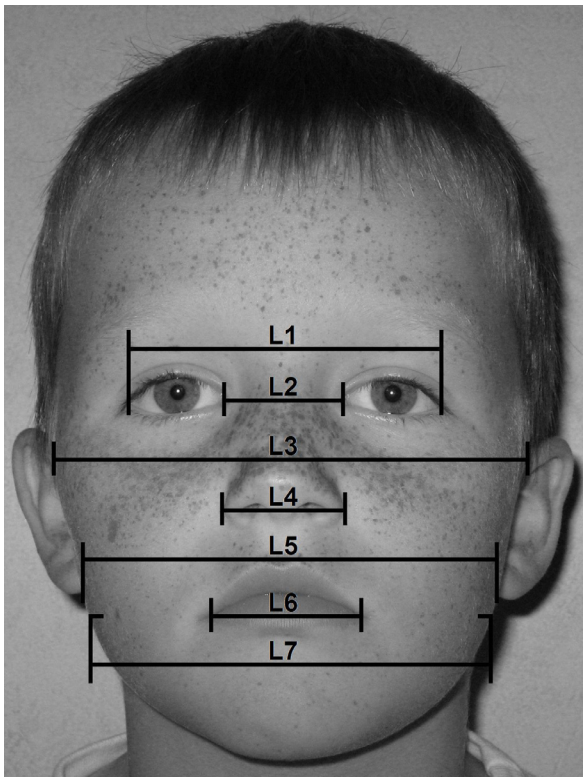

Figure 4.2. *Lines used for measurement of facial asymmetry*

The reliability of these measurements was examined by two methods. First, one of us placed the points on several faces two different times, two months apart; point locations did not differ more than two pixels. Second, a person unfamiliar with the research's hypotheses placed the points on each of 195 faces, and this was repeated by one of us without knowledge of the points placed by the naive assistant. The point locations had very high reliability; the zero-order correlations between the facial asymmetries calculated from the points of the two raters was .81 ($p < .01$). Mean facial asymmetry across the two observers was used in the analyses.

Statistical Analyses

Data from multiple children within the same family cannot be treated as independent observations, as it is likely that the responses given by the same parent about multiple children from the same family are more similar than the responses from different parents about unrelated children. Therefore multilevel analyses were conducted (using MLwiN version 2.02; Rasbash, Charlton, Browne, Healy, & Cameron, 2005), taking this nested structure of the data into account. The intraclass correlation coefficients for the different measures of parental investment ranged between .27 and .87.

Results

Simple Correlations

In Table 4.1 the correlations between the different measures of attractiveness and facial asymmetry are reported. Facial asymmetry was not correlated with any of the measures of attractiveness. We also calculated inter-correlations between the three different measures of parental investment. Parents' report on emotional closeness was negatively correlated with physical punishment for mothers (r = -.24, p < .01), and positively with time investment for fathers (r = .25, p < .01).

Table 4.1. *Correlations between the different measures of attractiveness and facial asymmetry*

Variable	1.	2.	3.	4.	5.
1. Attractiveness by Mother					
2. Attractiveness by Father	.45**				
3. Attractiveness by Observers	.22**	.27**			
4. Attractiveness by Raters	.23**	.34**	.37**		
5. Mean Attractiveness	.72**	.71**	.68**	.66**	
6. Facial Asymmetry	.12	-.03	-.02	.04	.05

*p < .05, **p < .01*

Table 4.2 shows that for mothers all different measures of attractiveness were positively correlated with emotional closeness. In addition, father-reported attractiveness was negatively correlated with physical punishment. Facial asymmetry was not correlated with any of the investment measures. Table 4.2 also shows that for fathers attractiveness was positively correlated with emotional closeness, accept for the independent rating of attractiveness. In addition, attractiveness was negatively correlated with physical

punishment. Also for fathers facial asymmetry was not correlated with any of the investment measures.

Table 4.2. *Correlations between parental investment and attractiveness and facial asymmetry*

	Emotional Closeness		Physical Punishment		Time Investment	
	Mothers	Fathers	Mothers	Fathers	Mothers	Fathers
Attractiveness by Mother	.33**	.23**	-.05	-.22**	-.05	.11
Attractiveness by Father	.31**	.29**	-.18*	-.23**	-.07	.12
Attractiveness by Observers	.34**	.20*	-.11	-.14#	-.03	.14#
Attractiveness by Raters	.20**	.06	.01	-.19*	-.06	-.08
Mean Attractiveness	.43**	.25**	-.10	-.30**	-.12	.10
Facial Asymmetry	-.05	.01	-.01	-.04	-.11	-.02

#$p < .10$, *$p < .05$, **$p < .01$

Multilevel Analyses

We used multilevel analyses to examine whether mothers and fathers invested more in children who were assessed as more attractive and/or had a more symmetrical face (Table 4.3). Age of the parent and gender and age of the child were included in the analyses as control variables. For mothers a significant effect was found for gender of the child. Specifically, mothers had a closer bond with their sons than with their daughters (β = .14, p = .02). Mothers also punished their sons more than their daughters (β = .16, p = .02). In addition, a significant effect was found for attractiveness and asymmetry; mothers reported having a closer bond with children who were rated as more attractive (β = .44, $p < .01$) and with children who were less asymmetrical (β = -.18, p = .02). For fathers a significant effect was found for age of the child. Specifically, fathers had a closer bond with their younger children (β = -.16, p = .02) and punished younger children more often than older children (β = -.16, p = .01). In addition, a significant effect was found for attractiveness; fathers reported having a closer bond with children who were rated as more attractive (β = .34, $p <$ .01), and attractive children were punished less often than less attractive children (β = -.31, $p < .01$).

Interaction terms between child gender and attractiveness and child gender and facial asymmetry were added to the model to determine whether the link between investment and attractiveness and investment and asymmetry differed for boys and girls. The interaction between child gender and attractiveness was significant for emotional closeness for both mothers (β = -.14, p = .03) and fathers (β = -.26, $p < .01$). In addition, the

interaction between child gender and facial asymmetry was significant for emotional closeness for mothers (β = .16, p = .03). To interpret these significant interaction terms, analyses were conducted for boys and girls separately. Concerning the link between attractiveness and emotional closeness, for mothers the link was stronger for girls (β = .36, p < .01), but still significant for boys (β = .30, p < .01), whereas for fathers this link was significant for girls (β = .32, p < .01), but not for boys (β = .05, p = .35). The link between facial asymmetry and maternal emotional closeness was significant for girls (β = -.14, p = .03), but not for boys (β = .01, p = .46).

Table 4.3. *Multilevel analyses: mean attractiveness and facial asymmetry predicting parental investment*

	Emotional Closeness		Physical Punishment		Time Investment	
	ΔR_1^2	β	ΔR_1^2	β	ΔR_1^2	β
Mothers (N = 117)	.21		.05		.01	
Age of Parent		.00		.06		.04
Child Gender (girl = 0, boy = 1)		.14*		.16*		-.02
Age of Child		-.11#		-.12#		.07
Mean Attractiveness		.44**		-.12#		-.02
Facial Asymmetry		-.18*		.00		-.01
Child Gender * Mean Attractiveness		-.14*		.04		-.02
Child Gender * Facial Asymmetry		.16*		.00		.02
Fathers (N = 93)	.12		.14		.00	
Age of Parent		.05		-.17#		-.06
Child Gender (girl = 0, boy = 1)		.10		-.08		.02
Age of Child		-.16*		-.16*		-.04
Mean Attractiveness		.34**		-.31**		-.07
Facial Asymmetry		.03		.00		.04
Child Gender * Mean Attractiveness		-.26**		-.05		.06
Child Gender * Facial Asymmetry		-.10		-.09		-.05

#p < .10, *p < .05, **p < .01

In order to avoid shared method variance when parents report on both investment and attractiveness of their child, and possible contamination of the observers' in-home ratings of attractiveness by the child's behavior, we also performed multilevel analyses using only the independent ratings (based on photographs) of child attractiveness. The

results remain essentially the same (Table 4.4) with the effects slightly weaker, but still significant. In addition, the same interaction terms are significant, and separate analyses for boys and girls again suggest that the link between parental investment and attractiveness/facial symmetry is more important for girls than for boys (maternal emotional closeness and attractiveness, girls β = .12, p = .03, boys β = .08, p = .20; maternal emotional closeness and asymmetry, girls β = -.11, p = .04, boys β = -.03, p = .39; paternal emotional closeness and attractiveness, girls β = .11, p = .04, boys β = -.04, p = .36).

Table 4.4. *Multilevel analyses: rated attractiveness and facial asymmetry predicting parental investment*

	Emotional Closeness		Physical Punishment		Time Investment	
	ΔR_1^2	β	ΔR_1^2	β	ΔR_1^2	β
Mothers (N = 117)	.07		.04		.02	
Age of Parent		.04		.04		.04
Child Gender (girl = 0, boy = 1)		.10		.18*		-.02
Age of Child		-.15*		-.09		.06
Attractiveness by independent raters		.13*		-.05		-.01
Facial Asymmetry		-.16*		-.01		-.01
Child Gender * Attractiveness by raters		-.16*		.09		-.07
Child Gender * Facial Asymmetry		.15*		.01		.03
Fathers (N = 93)	.04		.08		.02	
Age of Parent		.08		-.20*		-.05
Child Gender (girl = 0, boy = 1)		.05		-.05		.01
Age of Child		-.19*		-.13#		-.06
Attractiveness by independent raters		.08		-.16*		-.07
Facial Asymmetry		-.14#		-.01		.01
Child Gender * Attractiveness by raters		-.15*		-.09		.09
Child Gender * Facial Asymmetry		-.10		-.08		-.03

#$p < .10$, *$p < .05$, **$p < .01$

Discussion

Consistent with the evolutionary theory that parents should invest differently in children depending on the child's fitness, quality and reproductive potential (Buss, 1999; Daly & Wilson, 1980), the good-genes theory that asserts that attractiveness accurately advertises health and quality, and previous research (Elder *et al*., 1985; Langlois *et al*., 1995), our results suggest that attractiveness is a significant predictor of parental behavior. Both mothers and fathers reported having a closer bond with children who were rated as more attractive. In addition, fathers reported punishing their attractive children less often than their less attractive children.

We also found that the link between attractiveness and emotional closeness was stronger for girls than for boys for both mothers and fathers, indicating that attractiveness is more important for girls than for boys. This is consistent with human mate-selection theory, which states that men seek attractive women because attractiveness signals reproductive fitness (Buss, 1998, 1999; Thornhill, 1998). In contrast, women seek men with resources, rather than attractiveness, because such men are able to invest in offspring (e.g., Buss, 1998). More research is needed to investigate whether cues of future status, such as IQ, school achievement, and body build, are more important predictors of parental behavior for boys.

Modest support was found for facial symmetry as a predictor of parental investment. Symmetry was significantly linked to maternal emotional closeness, but only for girls. This finding could indicate that symmetry is less important for parents as cue of future reproductive success of their child than attractiveness. Indeed, attractiveness has been found to be stable over time (Sussman, Mueser, Grau, & Yarnold, 1983; Tatarunaite, Playle, Hood, Shaw, & Richmond, 2005; Zebrowitz, Olson, & Hoffman, 1993), and as such, can be seen as an honest cue of future attractiveness, and accordingly, reproductive value. Symmetry, however, is less stable over time. Wilson and Manning (1996) have shown that symmetry in children increases with age until age eleven. This is followed by a decrease in symmetry during early teens, after which symmetry increases again. They argue that rapid growth during early childhood and puberty may make it difficult to maintain symmetry. Asymmetries accumulated during periods of rapid change may be eliminated when growth rate reduces again. Symmetry may therefore be less reliable as an indicator of quality of the pre-pubertal child, and, consequently, a less important cue for parents when making investment decisions.

If indeed symmetry becomes a reliable indicator of quality only after secondary sexual characteristics are developed during puberty, this could explain why symmetry was not correlated with attractiveness in this study. However, previous research on adults has

produced conflicting results; some studies found a link between attractiveness and symmetry (e.g., Grammer & Thornhill, 1994; Jones, Little, Penton-Voak, Tiddeman, Burt, & Perrett, 2001), whereas others did not (e.g., Noor & Evans, 2003; Shackelford & Larsen, 1997, 1999; Swaddle & Cuthill, 1995). This study adds to the growing list of inconsistent findings regarding the relationship between attractiveness and facial symmetry. Additional research needs to be designed that could unravel under what conditions the link between attractiveness and symmetry is found.

Before drawing firm conclusions about the importance of attractiveness and symmetry as cues of child quality, we need to acknowledge the limitations of the current study. First, our results are correlational and therefore the cause-effect directions of the findings cannot be firmly established. Second, we used only a limited number of investment measures and none that was tapping overall investment. Stronger results may be found when a broader array of investment measures such as financial investment, educational involvement, and other indicators of time investment are taken into account. Finally, we only used parent report to assess the degree of parental investment. Future research should use additional methods, such as observations in the family situation, as using a multi-method measure gives a more complete and more objective impression of the investment made by parents.

Despite these limitations our results suggest that even in a contemporary Western society where the widespread availability of medical care may reduce the association between health and physical attractiveness (Thornhill & Gangestad, 1993), child attractiveness is still a significant predictor of parental investment. Research that examines which characteristics of children predict parental behaviors, both between and within families, and that explores ways of modifying such unconscious parental biases could make important contributions to our understanding of parent-child interactions and child development.

Finally, although our results suggest that attractiveness is a significant predictor of parental behavior, we do not suggest that the parents in this study treated their less attractive children badly. All of the children in this study received adequate caregiving, however, attractive children received slightly more positive treatment and less punishment from their parents than did less attractive children.

Chapter 5

Darwinian Grandparenting: An Evolutionary Perspective on the Grandparent-Grandchild Relationship

Abstract

Kin selection theory predicts that grandparents will differentially invest in their grandchildren as a function of certainty of relatedness. In the present paper we study this 'discriminative grandparental solicitude' by asking young grandchildren (8-10 years old) and their parents to rate the quality of the grandparent-grandchild relationship with each of the child's living grandparents in a sample of 121 Dutch families. Both mothers, fathers, and children reported the highest quality of the grandparent-grandchild relationship with maternal grandmothers (most genetically certain) and the lowest with paternal grandfathers (least genetically certain). Relationship quality with both maternal grandfathers and paternal grandmothers was rated as intermediate. These results are consistent with the prediction that discriminative grandparental solicitude varies as a function of certainty of relatedness.

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Introduction

In contemporary Western societies, advances in medicine and technology have extended the life expectancy of older adults dramatically. As a consequence of this increased longevity a greater percentage of parents become grandparents, and grandparents and grandchildren share more years of their lives, allowing the possibility of long-term relationships between them. Although most people enjoy being a grandparent (Fischer, 1983), not all grandparents invest the same amount of time and resources in their grandchildren. On average, maternal grandmothers are the most caring grandparents, followed by maternal grandfathers and paternal grandmothers, with paternal grandfathers providing the least care (e.g., Euler & Weitzel, 1996; Hoffman, 1979-1980; Smith, 1988).

This 'discriminative grandparental solicitude' (Euler & Weitzel, 1996) has been explained by the evolutionary theories of kin selection (Hamilton, 1964) and paternal uncertainty (Buss, 1999; Euler & Weitzel, 1996). According to kin selection theory, grandparents can continue to contribute to their own inclusive fitness by assisting their adult son or daughter in his/her parental effort. Whereas women are sure of their maternity, men can never be completely certain that they are the genetic father of their putative children. As a consequence, psychological adaptations may have evolved to regulate paternal investment according to the degree of paternal uncertainty (Alexander, 1979). Like paternal investment, grandparental investment might also be affected by parental uncertainty, and because two generations of descendants are involved in grandparental solicitude, grandparents have a double chance of possible parental uncertainty. The most uncertain grandparent is the paternal grandfather, who can be certain of neither his own nor his son's paternity. The most certain grandparent is the maternal grandmother, being certain of her own as well as her daughter's maternity. The maternal grandfather and the paternal grandmother have intermediate levels of uncertainty of grandparenthood, both having one certain and one uncertain link. Based on this, Smith (1988) predicted that grandparental investment should follow the order: (1) maternal grandmothers, (2) maternal grandfathers and paternal grandmothers, and (3) paternal grandfathers. He found support for this hypothesis when he questioned Canadian grandparents about the amount of time they spent with each of their grandchildren. Similar patterns of discriminative grandparental solicitude have been found in comparable studies (e.g., Euler & Weitzel, 1996; Pashos, 2000).

The most direct test of discriminative grandparental solicitude would be to ask grandparents to rate the quality of their relationship with their grandchildren, including their feelings of closeness to, and investment in each grandchild. However, when grandparents are directly questioned about the discriminative care directed to their grandchildren, they often claim that they invest equally in all of their grandchildren

(Fischer, 1983; Thomas, 1989). Due to social desirability pressures, grandparents may not be inclined to assert, or may not be aware of favoring some grandchildren over others. Ratings of *received* care, however, are presumed to be less influenced by social desirability (Euler & Weitzel, 1996). Consequently, most research on discriminative grandparental solicitude has focused on reports by adult grandchildren, either retrospectively on the care they received from their grandparents during childhood (e.g., Euler & Weitzel, 1996; Pashos, 2000), or on their current relationship with at least one living grandparent (e.g., Bishop, Meyer, Schmidt, & Gray, 2009; Dubas, 2001; Laham, Gonsalkorale, & von Hippel, 2005).

Even though reports by adult grandchildren are assumed to be a better indicator of discriminative grandparental solicitude than reports given by grandparents themselves, there are some disadvantages. Adult grandchildren's reports on current relationships with living grandparents suffer from differential grandparental mortality, making assessment of discriminative solicitude questionable. In Hoffman's (1979-1980) study, for instance, approximately 60% of the maternal grandmothers were still living at the time of assessment, whereas only 30% of the paternal grandfathers was still alive. Even though retrospective reports on grandparental care return to a period in the respondent's life when all grandparents were more likely to be alive, and hence, discriminative grandparental solicitude can be assessed, this report strategy may suffer from retrospective distortion (e.g., second-hand descriptions of grandparents) (Bishop *et al*., 2009).

In the current study, we wished to avoid these problems with adult grandchildren's reports. Therefore, we studied discriminative grandparental solicitude by asking young grandchildren (8-10 years old) and their parents to rate the quality of the grandparent-grandchild relationship with each of the child's living grandparents in a sample of 121 Dutch families. In this way, results are not influenced by differential grandparental mortality or retrospective distortion. If discriminative grandparental solicitude varies as a function of certainty of relatedness, we would expect both mothers, fathers, and children to rate the quality of the grandparent-grandchild relationship highest with maternal grandmothers, followed by maternal grandfathers and paternal grandmothers equally, and lowest with paternal grandfathers.

Method

Participants

Families were recruited to participate in a broad study on parenting and family relationships via their 4th or 5th grade child (8-10 years) attending elementary schools in the

Netherlands. Children were told about the study and were asked to take letters describing the study and consent forms home to their parents. In total 117 mothers, 93 fathers, and their children, representing 121 families, agreed to participate and completed the study. In 89 families both parents participated. All children were the purported biological offspring of the parents. In this sample 97% of the fathers and 91% of the mothers were currently married or cohabiting. Mean ages of the parents were 42 years for fathers (SD = 4.89; range = 29-54), and 40 years for mothers (SD = 3.91; range = 28-47).

Procedure

All families were visited twice in their own homes by two trained bachelor students studying developmental psychology. During the first visit parents completed a diverse battery of psychological and sociological measures designed to assess individual characteristics of parents and children, parental investment in each participating child, and parents' perceptions of the quality of the grandparent-grandchild relationship for each grandparent. Children were assessed on a number of social tasks (not relevant for the current research) and completed a questionnaire about their relationship with each of their grandparents. The second visit was conducted three days later and included an odor recognition task (not relevant for the current research).

Measures

Parent-report on the Grandparent-Grandchild Relationship.

Both parents reported on the quality of the relationship between their child and each of his/her (living) grandparents on three items: 'My child and his/her grandparent have a close bond', 'This grandparent is very involved with my child', and 'This grandparent is a nice grandparent for my child'. Each item was rated on a 7-point scale ranging from 'not at all true' to 'very true'. Cronbach's alphas were good (father α = .93-.96; mother α = .92-.95).

Child-report on the Grandparent-Grandchild Relationship.

Children reported on the quality of their relationship with each of their grandparents on one item: 'How is your relationship with your grandmother/grandfather?', on a 5-point scale ranging from 'not at all good' to 'very good'.

Statistical Analyses

Data about multiple grandparents within the same family cannot be treated as independent observations, therefore multilevel analyses were conducted (using MLwiN version 2.02; Rasbash, Charlton, Browne, Healy, & Cameron, 2005), taking the nested

structure of the data into account. Multilevel analysis partitions the variation in grandparent-grandchild relationship quality into two levels; the individual grandparent level (level one) is nested within families (level two). The proportion of level two (or *between*-family) variance to total variance is an index of the intraclass correlation (i.e., the extent to which scores of relationship quality between different grandparents within the same family resemble one another as compared to grandparent-grandchild relationship quality between different families). The intraclass correlation coefficients for the different measures of grandparent-grandchild relationship quality ranged between .23 (for mother-report) and .29 (for father-report). Residential distance and age and gender of the child were included in the analyses as control variables.

Results

Table 5.1 presents the average ratings of grandparent-grandchild relationship quality. Mothers, fathers, and children all reported the closest relationship with the maternal grandmother, followed by the maternal grandfather, the paternal grandmother, and the paternal grandfather. Mother-report, father-report, and child-report on grandparent-grandchild relationship quality were all positively correlated (mother-father range r = .57-.71; mother-child range r = .23-.40; father-child range r = .22-.41).

Table 5.1. *Means and standard deviations of grandparent-grandchild relationship quality reported by mothers, fathers, and children*

	Mothers (N = 117)		Fathers (N = 93)		Children (N = 121)	
	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N
Maternal Grandmother	5.71 (1.36)	101	5.76 (1.29)	83	4.55 (.58)	107
Maternal Grandfather	5.42 (1.50)	80	5.60 (1.30)	61	4.38 (.68)	84
Paternal Grandmother	5.37 (1.42)	93	5.46 (1.24)	73	4.40 (.64)	99
Paternal Grandfather	4.90 (1.41)	79	4.97 (1.54)	63	4.17 (.82)	86

Multilevel Analyses

Multilevel analyses were used to examine whether the quality of the grandparent-grandchild relationship differed between the four types of grandparents (Table 5.2). Residential distance and age and gender of the child were included in the analyses as control variables. Residential distance was logarithmically transformed to counter

distortions by a few grandparents living extremely far away (Euler & Weitzel, 1996). The logarithmic scale corresponds to the following distances: 0 = 0 km; 1 = .1-.3 km; 2 = .4-1.0 km; 3 = 1.1-4.0 km; 4 = 4.1-16.0 km; 5 = 16.1-64.0 km; and so on. For mothers a significant effect was found for both residential distance and gender of the child. Specifically, mothers reported a closer grandparent-grandchild relationship with grandparents who live closer (D = -.20, SE = .06, $p < .01$). Mothers also reported that their daughters had a closer relationship with their grandparents than their sons (D = -.54, SE = .19, $p < .01$). For fathers and children no significant effects were found for residential distance and age and gender of the child.

Table 5.2. *Multilevel analyses: type of grandparent predicting grandparent-grandchild relationship quality reported by mothers, fathers, and children*

	Mother Report	Father Report	Child Report
Intercept	5.93** (.16)	5.89** (.18)	4.51** (.08)
Level 1			
Distance	-.20** (.06)	-.09 (.06)	.00 (.03)
Type of Grandparent (Ref. is Maternal Grandmother)			
Maternal Grandfather	-.30* (.18)	-.33* (.19)	-.18* (.09)
Paternal Grandmother	-.34* (.17)	-.31* (.18)	-.15* (.08)
Paternal Grandfather	-.79** (.18)	-.76** (.19)	-.40** (.09)
Level 2			
Child Age	.08 (.08)	-.04 (.09)	.00 (.05)
Child Gender (girl = 0, boy = 1)	-.54** (.19)	-.28 (.21)	.11 (.10)

Note. Standard errors are in parentheses

*$p < .05$, **$p < .01$

Both mothers (M), fathers (F), and children (C) reported a significantly closer grandparent-grandchild relationship with maternal grandmothers (used as reference category in Table 5.2), compared to both maternal grandfathers (M: D = -.30, SE = .18, p = .05; F: D = -.33, SE = .19, p = .04; C: D = -.18 , SE = .09, p = .02), paternal grandmothers (M: D = -.34, SE = .17, p = .03; F: D = -.31, SE = .18, p = .04; C: D = -.15, SE = .08, p = .03), and paternal grandfathers (M: D = -.79, SE = .18, $p < .01$; F: D = -.76, SE = .19, $p < .01$; C: D = -.40, SE = .09, $p < .01$). The quality of the grandparent-grandchild relationship did not differ between maternal grandfathers and paternal grandmothers (M: D = -.03, SE = .19, p = .43; F: D = .02, SE = .19, p = .45; C: D = .03, SE = .09, p =. 37). Maternal grandfathers had a significantly better relationship with their grandchildren than paternal

grandfathers (M: D = -.49, SE = .19, p < .01; F: D = -.43, SE = .20, p = .02; C: D = -.22, SE = .10, p = .01), and so did paternal grandmothers (M: D = -.45, SE = .19, p < .01; F: D = -.45, SE = .19, p < .01; C: D = -.25, SE = .09, p < .01).

Discussion

In the current study we examined discriminative grandparental solicitude by asking young grandchildren (8-10 years old) and their parents to rate the quality of the grandparent-grandchild relationship with each of the child's living grandparents. Both mothers, fathers, and children rated the quality of the grandparent-grandchild relationship highest with maternal grandmothers and lowest with paternal grandfathers. Relationship quality with both maternal grandfathers and paternal grandmothers was rated as intermediate. These results add to the growing body of literature consistent with the prediction from the evolutionary theories of kin selection and paternal uncertainty that grandparental solicitude varies as a function of certainty of relatedness. By asking young grandchildren and their parents about the grandparent-grandchild relationship this study improves previous research as it avoids problems with adult grandchildren's reports (i.e., either differential grandparental mortality when reported about current relationships, or retrospective distortion when reported on relationships in childhood). Children of 8-10 years old are able to accurately rate the quality of relationships (Lange, Blonk, & Wiers, 1998), which is confirmed by the significant correlations between parent- and child-reports in the present study.

In the current study the difference in relationship quality between maternal grandfathers and paternal grandmothers was not significant. There are some studies, however, that found that maternal grandfathers provided significantly more care than paternal grandmothers (e.g., Euler & Weitzel, 1996; Pashos, 2000), although these two should not differ according to the kin selection/paternal uncertainty hypothesis, as both carry the same presumptive level of certainty of relatedness. Laham, Gonsalkorale, and von Hippel (2005) hypothesized that the difference in solicitude between maternal grandfathers and paternal grandmothers is caused by the fact that paternal grandmothers often have the possibility to invest in genetically more certain kin (i.e., grandchildren through their daughter). Paternal grandmothers are expected to invest less in their son's children when they also have grandchildren through a daughter. Under these circumstances, maternal grandfathers are predicted to make a greater investment in their grandchildren compared to paternal grandmothers. Contrary to predictions, however, grandchildren did not rate maternal grandfathers consistently higher on caregiving or closeness when more certain

investment outlets were available to paternal grandmothers (Bishop *et al*., 2009), calling this 'preferential investment hypothesis' into question.

An alternative explanation for the difference in solicitude between maternal grandfathers and paternal grandmothers is that it is a consequence of co-residence of grandparents. Given that maternal grandmothers are the most caring grandparents, and that grandparents frequently care for the grandchild as a couple (Euler & Weitzel, 1996), it may be that maternal grandfathers become more involved in the care of their grandchildren when living with a caring partner. Conversely, paternal grandfathers, who are less genetically certain of their grandchildren, may resist investing in their grandchildren and so paternal grandmothers may be discouraged from investing as much as they otherwise would. Euler and Weitzel (1996) attempted to disentangle the effects of co-residence by examining the solicitude ratings of widowed grandparents. Widowed maternal grandfathers showed less solicitude compared to maternal grandfathers living with their partners, whereas widowed paternal grandmothers showed greater solicitude than paternal grandmothers living with their partners. More research is needed to determine whether these results are replicable and to examine why significant differences in solicitude between maternal grandfathers and paternal grandmothers are found in some studies but not in others.

More evidence in support of the hypothesis that differences in certainty of genetic relatedness lead to differences in investment by distal kin is found by looking at extended families. Maternal aunts and uncles (both certain of genetic relatedness) are significantly more caring to their nieces and nephews than paternal aunts and uncles (who are less certain of genetic relatedness) (Gaulin, McBurney, & Brakeman-Wartell, 1997; McBurney, Simon, Gaulin, & Geliebter, 2002). A similar matrilateral bias in kin investment has also been reported for relationships among cousins (Jeon & Buss, 2007).

Although the results of the current study as well as findings from previous research are consistent with the prediction that grandparental solicitude varies as a function of certainty of relatedness, we do not imply that differential grandparental investment is necessarily a direct reflection of grandparental certainty. Social environments have also been shown to affect grandparental caregiving. For instance, in rural Greece, a society with predominantly patrilateral cultural traditions (e.g., patrilocal residence and patrilineally inherited lands), paternal grandparents provided more care for grandchildren than maternal grandparents (Pashos, 2000), suggesting that the effect of a patriarchal system can override the (universal) matrilateral bias. Thus, an evolutionary explanation should not be seen as an alternative to an environmental explanation of grandparental behavior, but as providing another level of explanation to complement sociocultural approaches (Smith, 1988).

Although the current study shows that an evolutionary perspective is helpful in predicting discriminative grandparental solicitude, the proximate causes of biased kin investment remain unclear. For instance, do grandparents prefer to invest in their daughter's children simply because they are their daughter's children? Or do they use some sort of recognition mechanism to discriminate kin from non-kin? Do grandparents, for instance, (non-consciously) assess their grandchildren's resemblance to themselves, and develop preferences according to those perceived similarities? Future research should focus on these questions to determine how evolved dispositions and cultural influences work together to produce the observed kin investment patterns. Despite the fact that important questions remain, our findings add to a growing body of evidence demonstrating the robust nature of discriminative grandparental solicitude.

Chapter 6

General Discussion

Although great effort has been spent on studying the effects of parenting on child development (for a review see Bornstein, 1995), much less research has focused on factors that predict individual differences in parental investment. In this dissertation, an evolutionary psychological perspective was used to identify characteristics in children that stimulate their parents and grandparents into giving them the care, attention, and emotional support they need. The four empirical studies presented in the previous chapters all addressed a part of this overall goal. In this concluding chapter the main findings of the four studies will be discussed, followed by a general conclusion. In addition, we will discuss the strengths and limitations of the studies presented in this dissertation and suggest directions for future research.

Genetic Relatedness

A first factor that was expected to influence individual differences in parental investment is the genetic relatedness of the child to the parent. In order to maximize their own reproductive fitness, parents should prefer to invest in children to whom they are genetically related (Alexander, 1974; Trivers, 1972). Whereas women are sure of their maternity, men can never be fully certain of their paternity, but instead need to rely on indirect cues to assess whether they are likely to be the father of their putative children. Given this asymmetry in certainty of parenthood, men are predicted to be more sensitive to cues of genetic relatedness than women when making investment decisions.

Chapter 2 and *Chapter 3* both examined whether parental investment was influenced by possible cues of genetic relatedness. *Chapter 2* described two studies in which the relation between parent-child resemblance and parental investment was examined. We attempted to determine whether it is physical resemblance, or personality similarity, or both, that contributes to the link with parental investment. The results of both studies indicated a link between personality similarity and parental investment for mothers. For fathers parental investment was linked to physical resemblance in one study. In the other study these results were not replicated.

Apicella and Marlowe (2004, 2007) reported that fathers' perception of resemblance to their offspring predicted their investment in their children. Resemblance became a stronger predictor of investment when men were no longer in a relationship with the mother of their children. In addition, separated fathers reported lower confidence in the fidelity of the mother of their children as compared to men who were still in a relationship with the mother. Thus, it seems that when fidelity is in doubt, men rely more heavily on other cues, such as resemblance, to estimate paternity (Apicella & Marlowe, 2004, 2007). We argued

that the low percentage of separated fathers in our studies (11.7% and 3.2%, compared to 22.4% in Apicella & Marlowe, 2004, 2007) could explain our weaker findings for fathers compared to previous studies, and also why paternal investment was linked to physical resemblance in one of our studies but not in the other.

For mothers parental investment was linked to personality similarity in both of the studies presented in *Chapter 2*. Because mothers can be sure of their maternity and do not need to rely on cues to assess relatedness, this raised the question whether the link between investment and personality similarity for mothers is driven by a mechanism other than kin recognition. Lerner (1993) suggests that parents' reactions to temperamental qualities of a child depend to some degree on the prevailing beliefs system of the parents with respect to the significance of the behavior in question, such that parenting of the child is a matter of goodness of fit. If the child's behavior fits with the expectations of the parent then problems are less likely to occur. Similarity in personality may help a parent understand and read a child's behavior more accurately, resulting in more sensitive parenting (van Tuijl, Branje, Dubas, Vermulst, & van Aken, 2005). Goodness of fit may be particularly relevant for mothers given that they are still responsible for the majority of childcare (Silverstein, 1996).

Chapter 3 examined parent-child olfactory recognition as a cue of genetic relatedness. Most research on humans has only focused on whether parents are able to recognize their children by smell, not whether parents use these olfactory cues when making investment decisions. The study presented in *Chapter 3* is among the first to examine whether parent-child olfactory recognition is linked to parental investment. In our study, the ability to recognize one's children by smell was associated with an increase in investment for both mothers and fathers, and a decrease in physical punishment by mothers.

The results of *Chapter 2* and *Chapter 3* provide evidence that both mothers and fathers are sensitive to cues of genetic relatedness when making investment decisions. Contrary to our expectations, we found no convincing evidence that cues of genetic relatedness influence fathers' investment decisions more than mothers' investment decisions. Although we argued that the link we found in *Chapter 2* between parental investment and personality similarity for mothers might be driven by goodness of fit rather than kin recognition, the results of the study presented in *Chapter 3* suggest that mothers and fathers are equally sensitive to olfactory cues when making investment decisions. As we mentioned earlier, the percentage of separated parents in our sample was relatively low. Fathers may have felt confident about their partner's sexual fidelity, and consequently may have relied less on cues of genetic relatedness, such as resemblance or olfactory recognition, to estimate their paternity, resulting in correlations of similar strength compared to mothers.

Alternatively, mothers may be sensitive to cues of genetic relatedness, even though they can be sure of their maternity. Although this might seem strange, theoretically, sex differences would be unlikely to result from natural selection unless the costs of an adaptation to one sex outweigh the costs of maintaining dimorphism, even if one sex does receive greater benefits from a trait (Nesse, Silverman, & Bortz, 1990). Because many traits, like maintaining a large muscle mass in males or the ability to lactate in females, have substantial costs, it is easy to assume that sex differences will arise whenever benefits to the sexes differ. However, when the costs of maintaining a trait are small, and when the trait offers some benefits to both sexes, natural selection is not expected to favor sexual dimorphism (Nesse *et al*., 1990). Although only men face direct paternity uncertainty, it would be adaptive for women to evaluate phenotypic cues of relatedness such as resemblance or olfactory recognition when making investment decisions about children who are putatively related through a male (e.g., grandchildren through a son, or cousins through a brother) (Bressan, Bertamini, Nalli, & Zanutto, 2009; DeBruine, 2004), and therefore mothers may use these cues even on their own children when making investment decisions.

Reproductive Value

A second factor that was expected to influence individual differences in parental investment is the reproductive value of the child (i.e., the child's probable future reproductive success). In order to maximize their own inclusive fitness, parents should allocate more care, resources, and attention to offspring who have the highest chance of future reproductive success (i.e., healthy, high quality offspring) (Mann, 1992; Scrimshaw, 1984). *Chapter 4* examined whether parental investment was influenced by cues of reproductive value of the child. Both attractiveness and facial symmetry were considered to advertise reproductive value. Attractiveness is considered to accurately advertise health and quality (Barber, 1995; Gangestad & Buss, 1993; Gangestad & Thornhill, 1997; Shackelford & Larsen, 1999; Thornhill, 1998; Thornhill & Gangestad, 1993). Attractive people display greater physical health (Shackelford & Larsen, 1999; but see Kalick, Zebrowitz, Langlois, & Johnson, 1998) and psychological well-being (Umberson & Hughes, 1987), and facial attractiveness predicts future longevity (Henderson & Anglin, 2003). Facial asymmetry is presumed to be a measure of developmental instability and inability of an organism to cope with stress (e.g., Kowner, 2001; Little & Perrett, 2002). Facial asymmetry is thought to accumulate during development as a consequence of environmental or genetic stresses (Wilson & Manning, 1996). Only high-quality individuals can maintain symmetric

development, therefore symmetry can serve as an indicator of the quality of an individual as well as the quality of its genes (Thornhill & Gangestad, 1996, 1999).

Although several studies have focused on attractiveness and facial symmetry with respect to preferences for mates, very few studies examined attractiveness and facial symmetry with respect to parental investment. The results of the study presented in *Chapter 4* suggest that attractiveness is strongly associated with parental behavior. Both mothers and fathers reported having a closer bond with children who were rated as more attractive, and fathers punished attractive children less often than less attractive children. No consistent support was found for facial symmetry as a predictor of parental investment. We argued that symmetry may be less reliable as an indicator of quality of the pre-pubertal child, because it is less stable over time compared to attractiveness (Sussman, Mueser, Grau, & Yarnold, 1983; Tatarunaite, Playle, Hood, Shaw, & Richmond, 2005; Zebrowitz, Olson, & Hoffman, 1993; Wilson & Manning, 1996). Consequently, facial symmetry may be less important as a cue for parents when making investment decisions.

Although our results suggest that attractiveness is a significant predictor of parental behavior, we do not suggest that the parents in this study treated their less attractive children badly. All of the children in this study received adequate caregiving, however, attractive children received slightly more positive treatment and less punishment from their parents than less attractive children.

Grandparental Investment

In addition to individual differences in parental investment, in *Chapter 5* we examined differential investment by grandparents. Grandparents can continue to contribute to their inclusive fitness by assisting their adult son or daughter in his/her parental effort. Even though investment by grandparents positively influences child health and well-being (Al Awad & Sonagu-Barke, 1992; Pope, Whiteside, Brooks-Gunn, Kelleher, Rickert, Bradley, & Casey, 1993; Wilson, 1986), and thus grandparental lifetime reproductive success, not all grandparents invest equally in their grandchildren. Like paternal investment, grandparental investment might be affected by parental uncertainty. The most certain grandparent is the maternal grandmother, being certain of her own as well as her daughter's maternity. The most uncertain grandparent is the paternal grandfather, who can be certain of neither his own nor his son's paternity. The maternal grandfather and the paternal grandmother have intermediate levels of uncertainty of grandparenthood, both having one certain and one uncertain link.

Chapter 5 examined whether differences in grandparental investment can be explained by certainty of relatedness (as assessed by kinship lines). Most research on discriminative grandparental solicitude has focused on reports by adult grandchildren, either retrospectively on the care they received from their grandparents during childhood (e.g., Euler & Weitzel, 1996; Pashos, 2000), or on their current relationship with at least one living grandparent (e.g., Bishop, Meyer, Schmidt, & Gray, 2009; Dubas, 2001; Laham, Gonsalkorale, & von Hippel, 2005). There are some problems with adult grandchildren's reports, however (i.e., either differential grandparental mortality when reported about current relationships, or retrospective distortion when reported on relationships in childhood). To avoid these problems with adult grandchildren's reports, the study presented in *Chapter 5* examined discriminative grandparental solicitude by asking young grandchildren (8-10 years old) and their parents to rate the quality of the grandparent-grandchild relationship with each of the child's grandparents. Both mothers, fathers and children rated the quality of the grandparent-grandchild relationship highest with maternal grandmothers (the most certain grandparent) and lowest with paternal grandfathers (the least certain grandparent). Relationship quality with maternal grandfathers and paternal grandmothers was rated as intermediate. These results add to the growing body of literature consistent with the prediction that discriminative grandparental solicitude varies as a function of certainty of relatedness.

General Conclusions

The studies presented in this dissertation show that parental investment is associated with cues of both genetic relatedness (i.e., parent-child resemblance and olfactory recognition) and reproductive value of the child (i.e., child attractiveness) for both mothers and fathers, and that grandparental solicitude varies as a function of certainty of relatedness (as assessed by kinship lines).

Even though it would have been adaptive for ancient humans to invest their limited resources based on the genetic relatedness and reproductive value of their children, in contemporary Western societies families are relatively small and emotional and economic resources are more than enough for parents to invest equally in all of the children in their household. Nevertheless, our results suggest that even in a contemporary Western society, such as the Netherlands, parents are still sensitive to cues of genetic relatedness and reproductive value when making investment decisions.

Although the studies presented in this dissertation show that an evolutionary psychological perspective contributes to our understanding of individual differences in

parental and grandparental investment, we stress that an evolutionary explanation should not be seen as an alternative to explanations from environmental, cultural, or socioeconomic perspectives. An evolutionary perspective provides an additional level of explanation to complement existing models, and, by considering factors that are generally ignored by other perspectives, could make important contributions to our understanding of individual differences in parental behavior.

Strengths and Limitations

Each chapter already addressed the strengths and limitations of the study presented in that chapter. In this section we will focus on some more general strengths and limitations of the studies presented in this dissertation.

One of the major strengths of the current dissertation is the fact that we made use of a sample of real parents with school-age children to examine the relation between actual parental investment and possible cues of genetic relatedness and reproductive value of the child. In contrast, previous research was mostly hypothetical and used college students as participants in their experiments (Bressan *et al*., 2009; DeBruine, 2004; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek *et al*., 2003, 2004; Volk & Quinsey, 2002, 2007), or relied upon retrospective accounts of investment (Apicella & Marlowe, 2004, 2007). In addition, we included both mothers and fathers in our study, whereas many studies of parental investment focus only on mothers.

Nevertheless, we also need to acknowledge some limitations concerning the participating families. Our sample was relatively homogeneous, consisting of relatively small, well-functioning, primarily white families, with mostly middle to high socioeconomic status. Therefore, we cannot be certain that our results can be generalized to families of other social backgrounds. However, we believe that it is most likely that the associations that might be found in samples including larger families and/or families with lower socioeconomic status will be even stronger than the findings reported in this dissertation. In these families, resources are more limited and choices must be made regarding which children will receive more investment (Lawson & Mace, 2009).

Another strength of this dissertation is the use of many objective measures of genetic relatedness and reproductive value (e.g., Q-correlations to calculate parent-child similarity in personality dimensions, and independent ratings of parent-child resemblance and child attractiveness based on photographs), thereby reducing the likelihood of shared method variance. In addition, the use of objective measures avoids other possible

confounds associated with parent reports, such as that parents' prior experiences with their children may influence their reports (Sawyer, Streiner, & Baghurst, 1998).

A limitation of the measures used in this dissertation is the fact that we relied only on questionnaires filled out by parents to assess parental investment. Due to socially desirable responses, these parent reports may not always correspond with the parent's actual behavior (Silverman, 1977). Additional methods, such as observations in the family situation, might give a more complete and more objective impression of the investment made by parents. However, family observations are very time consuming, which, under the constraints of this study, would have meant a serious decrease in sample size.

Furthermore, we used only a limited number of investment measures and none that was tapping overall investment. Stronger results may be found when a broader array of investment measures such as financial investment, educational involvement, and other indicators of time investment are taken into account. In addition, parents can also invest in their children by working outside the family in order to supply the resources necessary to adequately raise their offspring. This indirect investment should also be taken into account.

The studies presented in this dissertation are among the first to provide empirical evidence that cues of genetic relatedness and reproductive value of the child are associated with actual parental behavior. A final limitation, however, concerns the correlational nature of our results. Because we only used cross-sectional data, the cause-effect directions of our findings cannot be firmly established.

Directions for Future Research

Although the studies presented in this dissertation give important insights in which characteristics of children stimulate their parents and grandparents into giving them the care, attention, and emotional support they need, several interesting questions remain unanswered.

Whereas women are sure of their maternity, men can never be fully certain of their paternity, but instead need to rely on indirect cues to assess whether they are likely to be the father of their putative children. Therefore, men were predicted to be more sensitive to cues of genetic relatedness than women when making investment decisions. Contrary to our expectations, however, we found no convincing evidence that cues of genetic relatedness influenced fathers' investment decisions more than mothers' investment decisions. It remains unclear whether mothers are sensitive to cues of genetic relatedness (even though they can be sure of their maternity), or whether the fathers in our study felt confident about their partner's sexual fidelity, and consequently relied less on cues of genetic relatedness,

such as resemblance or olfactory recognition, to estimate their paternity. Additional studies are needed that use larger samples of separated fathers (who might be less certain of their paternity) and take into account fathers' perceptions of the fidelity of the mother of their putative children, to determine whether the link between cues of genetic relatedness and paternal investment is moderated by the degree of paternity certainty. In addition, studies are needed that examine whether women use cues of genetic relatedness when making investment decisions about children who are putatively related through a male. Sensitivity of paternal grandmothers and paternal aunts to cues of genetic relatedness may provide the first clue that mothers too may be sensitive to cues of genetic relatedness when making investment decisions.

In addition, although we argued that the link between maternal investment and mother-child personality similarity might be driven by goodness of fit rather than kin recognition, the fact that this link was consistently found in three separate studies (i.e., van Tuijl *et al*., 2005; and the two studies presented in *Chapter 2* of this dissertation) suggests that this link and the possible mechanisms behind it are worthy of further investigation.

Finally, in the study on discriminative grandparental solicitude (*Chapter 5*), we used only kinship lines to assess certainty of genetic relatedness between grandparents and their grandchildren. Other cues of genetic relatedness, such as grandparent-grandchild resemblance (both in looks and personality) and olfactory recognition, might also contribute to a grandparent's perception of relatedness of a grandchild. Therefore, it would be an interesting extension to examine whether grandparental investment, like parental investment, is influenced by cues of genetic relatedness, and whether grandparents who are least certain of genetic relatedness based on kinship lines (i.e., paternal grandfathers) are more sensitive to these cues than grandparents who are more certain (i.e., maternal grandfathers and paternal grandmothers) or even completely certain (i.e., maternal grandmothers).

References

Al Awad, A.M.H., & Sonuga-Barke, E.J.S. (1992). Childhood problems in a Sudanese city: A comparison of extended and nuclear families. *Child Development*, 63, 906-914.

Alexander, R.D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325-383.

Alexander, R.D. (1979). *Darwinism and Human Affairs.* Seattle: University of Washington Press.

Alvergne, A., Faurie, C., & Raymond, M. (2007). Differential facial resemblance of young children to their parents: Who do children look like more? *Evolution and Human Behavior*, 28, 135-144.

Andersson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.

Anderson, K.G., Kaplan, H., Lam, D., & Lancaster, J. (1999). Paternal care by genetic fathers and stepfathers II: Reports by Xhosa high school students. *Evolution and Human Behavior*, 20, 433-451.

Anderson, K.G., Kaplan, H., & Lancaster, J.B. (2007). Confidence of paternity, divorce, and investment in children by Albuquerque men. *Evolution and Human Behavior*, 28, 1-10.

Apicella, C.L., & Marlowe, F.W. (2004). Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evolution and Human Behavior*, 25, 371-378.

Apicella, C.L., & Marlowe, F.W. (2007). Men's reproductive investment decisions. Mating, parenting, and self-perceived mate value. *Human Nature*, 18, 22-34.

Bahr, L.K., & Abdallah, B. (2001). Physical attractiveness of premature infants affects outcome at discharge from NICU. *Infant Behavior and Development*, 24, 129-133.

Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, 16, 395-424.

Barden, R.C., Ford, M.E., Jensen, A.G., Rogers-Salyer, M., & Salyer, K.E. (1989). Effects of craniofacial deformity in infancy on the quality of mother-infant interactions. *Child Development*, 60, 819-824.

Belsky, J. (1984). The determinants of parenting: A process model. *Child Development*, 55, 83-96.

Bereczkei, T. (2001). Maternal trade-off in treating high-risk children. *Evolution and Human Behavior*, 22, 197-212.

Berkowitz, L., & Frodi, A. (1979). Reactions to a child's mistakes as affected by her/his looks and speech. *Social Psychology Quarterly*, 42, 420-425.

Betzig, L. (1989). Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology*, 30, 654-676.

Bishop, D.I., Meyer, B.C., Schmidt, T.M., & Gray, B.R. (2009). Differential investment behavior between grandparents and grandchildren: The role of paternity uncertainty. *Evolutionary Psychology*, 7, 66-77.

Bornstein, M. (1995). *Handbook of Parenting*. Hillsdale, NJ: Erlbaum.

Boyse, E.A., Beauchamp, G.K., & Yamazaki, K. (1987). The genetics of body scent. *Trends in Genetics*, 3, 97–102.

Brédart, S., & French, R.M. (1999). Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld and Hill (1995). *Evolution and Human Behavior*, 20, 129-135.

Bressan, P., Bertamini, M., Nalli, A., & Zanutto, A. (2009). Men do not have a stronger preference than women for self-resemblant child faces. *Archives of Sexual Behavior*, 38, 657-664.

Bressan, P., & Grassi, M. (2004). Parental resemblance in 1-year-olds and the Gaussian curve. *Evolution and Human Behavior*, 25, 133-141.

de Brock, A.J.L.L., Vermulst, A.A., Gerris, J.R.M., & Abidin, R.R. (1992). *NOSI: Nijmeegse Ouderlijke Stress Index* [NPSI: Nijmegen Parental Stress Index]. Amsterdam/Lisse: Swets & Zeitlinger.

Burch, R.L., & Gallup, G.G. (2000). Perceptions of paternal resemblance predict family violence. *Evolution and Human Behavior*, 21, 429-435.

Buss, D.M. (1995). Evolutionary psychology. *Psychological Inquiry*, 6, 1-30.

Buss, D.M. (1996). Paternity uncertainty and the complex repertoire of human mating strategies. *American Psychologist*, 51, 161-162.

Buss, D.M. (1998). The psychology of human mate selection: Exploring the complexity of the strategic repertoire. In: C. Crawford & D.L. Krebs (Eds.), *Handbook of evolutionary psychology* (pp. 405-430). Mahwah, NJ: Erlbaum.

Buss, D.M. (1999). *Evolutionary psychology: The new science of the mind*. Boston: Allyn & Bacon.

Caruso, S., Grillo, C., Agnello, C., Maiolino, L., Intelisano, G., & Serra, A. (2001). A prospective study evidencing rhinomanometric and olfactometric outcomes in women taking oral contraceptives. *Human Reproduction*, 16, 2288-2294.

Clutton-Brock, T.H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Cosmides, L., & Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In: J. Dupre (Ed.), *The latest on the best essays on evolution and optimality* (pp. 277-306). Cambridge, MA: MIT Press.

Cunningham, M.R., Roberts, A.R., Wu, C.H., Barbee, A.P., & Druen, P.B. (1995). "Their ideas of beauty are, on the whole, the same as ours": Consistency and variability in

the cross-cultural perception of female physical attractiveness. *Journal of Personality and Social Psychology*, 68, 261-279.

Daly, M., & Wilson, M.I. (1980). Discriminative parental solicitude: A biological perspective. *Journal of Marriage and the Family*, 42, 277-288.

Daly, M., & Wilson, M.I. (1982). Whom are newborn babies said to resemblance? *Ethology and Sociobiology*, 3, 69-78.

Daly, M., & Wilson, M.I. (1988). *Homicide*. Hawthorne, NY: Aldine de Gruyter.

Daly, M., & Wilson, M.I. (1996). Violence against stepchildren. *Current Directions in Psychological Science*, 5, 77-81.

Daly, M., Wilson, M.I., & Weghorst, S.J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, 3, 11-27.

DeBruine, L.M. (2004). Resemblance to self increases the appeal of child faces to both men and women. *Evolution and Human Behavior*, 25, 142-154.

Dubas, J.S. (2001). How gender moderates the grandparent-grandchild relationship. A comparison of kin-keeper and kin-selector theories. *Journal of Family Issues*, 22, 478-492.

Dubas, J.S., & Gerris, J.R.M. (2002). Longitudinal changes in the time parents spend in activities with their adolescent children as a function of child age, pubertal status and gender. *Journal of Family Psychology*, 16, 415-427.

Dubas, J.S., Heijkoop, M., & van Aken, M.A.G. (2009). A Preliminary Investigation of Parent-Progeny Olfactory Recognition and Parental Investment. *Human Nature*, 20, 80-92.

Elder, G.H., Van Nguyen, T., & Caspi, A. (1985). Linking family hardship to children's lives. *Child Development*, 56, 361-375.

Euler, H.A., & Weitzel, B. (1996). Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, 7, 39-59.

Field, T.M., & Vega-Lahr, N. (1984). Early interactions between infants with cranio-facial anomalies and their mothers. *Infant Behavior and Development*, 7, 527-530.

Fischer, L.R. (1983). Transition to grandmotherhood. *International Journal of Aging and Human Development*, 16, 67-78.

Gangestad, S.W., & Buss, D.M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, 14, 89-96.

Gangestad, S.W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, 18, 69-88.

Gaulin, S.J.C., McBurney, D.H., & Brakeman-Wartell, S.L. (1997). Matrilateral biases in the investment of aunts and uncles. A consequence and measure of paternity uncertainty. *Human Nature*, 8, 139-151.

Gerris, J.R.M., Houtmans, M.J.M., Kwaaitaal-Roosen, E.M.G., de Schipper, J.C., Vermulst, A.A., & Janssens, J.M.A.M. (1998). *Parents, adolescents, and young adults in Dutch families: A longitudinal study*. Nijmegen, The Netherlands: Institute of Family Studies, University of Nijmegen.

Gerris, J.R.M., Vermulst, A.A., van Boxtel, D.A.A.M., Janssens, J.M.A.M., van Zutphen, R.A.H., & Felling, A.J.A. (1993). *Parenting in Dutch families*. Nijmegen, The Netherlands: Institute of Family Studies, University of Nijmegen.

Goldberg, L.R. (1992). The development of markers of the Big-Five factor structure. *Psychological Assessment*, 4, 26-42.

Good, K.P., Martzke, J.S., Daoud, M.A., & Kopala, L.C. (2003). Unirhinal norms for the University of Pennsylvania smell identification test. *Clinical Neuropsychology*, 17, 226-234.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, 108, 233-242.

Hagen, E.H., Hames, R.B., Craig, N.M., Lauer, M.T., & Price, M.E. (2001). Parental investment and child health in a Yanomamö village suffering short-term food stress. *Journal of Biosocial Sciences*, 33, 503-528.

Halpin, Z.T. (1991). Kin recognition cues in vertebrates. In: P.G. Hepper (Ed.), *Kin Recognition* (pp. 220-258). Cambridge: Cambridge University Press.

Hamilton, W.D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, 7, 1-52.

Henderson, J.J.A., & Anglin, J.M. (2003). Facial attractiveness predicts longevity. *Evolution and Human Behavior*, 24, 351-356.

Hepper, P.G. (1991). *Kin Recognition*. Cambridge: Cambridge University Press.

Hoffman, E. (1979-1980). Young adults' relations with their grandparents: An exploratory study. *International Journal of Aging and Human Development*, 10, 299-310.

Hummel, T., Sekinger, B., Wolf, S., Pauli, E., & Kobal, G. (1997). 'Sniffin' sticks': Olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. *Chemical Senses*, 22, 39-52.

Jeon, J., & Buss, D.M. (2007). Altruism towards cousins. *Proceedings of the Royal Society of London*, *Series B: Biological Sciences*, 274, 1181-1187.

Jones, B.C., Little, A.C., Penton-Voak, I.S., Tiddeman, B.P., Burt, D.M., & Perrett, D.I. (2001). Facial symmetry and judgements of apparent health: Support for a "good genes" explanation of the attractiveness-symmetry relationship. *Evolution and Human Behavior*, 22, 417-429.

Kaitz, M., Good, A., Rokem, A.M., & Eidelman, A.I. (1987). Mothers' recognition of their newborns by olfactory cues. *Developmental Psychobiology*, 20, 587-591.

Kalick, S.M., Zebrowitz, L.A., Langlois, J.H., & Johnson, R.M. (1998). Does human facial attractiveness honestly advertise health? *Psychological Science*, 9, 8-13.

Kobal, G., Hummel, T., Sekinger, B., Barz, S., Roscher, S., & Wolf, S. (1996). 'Sniffin' sticks': Screening of olfactory performance. *Rhinology*, 34, 222-226.

Kowner, R. (2001). Psychological perspective on human developmental stability and fluctuating asymmetry: Sources, applications and implications. *British Journal of Psychology*, 92, 447-469.

Kurland, J.A. (1979). Paternity, mother's brother and human sociality. In: N.A. Chagnon & W.G. Irons (Eds.), *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective* (pp. 145-180). North Scituate, MA: Duxbury Press.

Lacy, R.C., & Sherman, P.W. (1983). Kin recognition by phenotype matching. *American Naturalist*, 121, 489-512.

Laham, S.M., Gonsalkorale, K., & von Hippel, W. (2005). Darwinian grandparenting: Preferential investment in more certain kin. *Personality and Social Psychology Bulletin*, 31, 63-72.

Lange, A., Blonk, R., & Wiers, R.W. (1998). Assessment: The parent-child interaction questionnaire, PACHIQ. *Clinical Psychology and Psychotherapy*, 5, 187-198.

Langlois, J.H., Kalakanis, L., Rubenstein, A.J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, 126, 390-423.

Langlois, J.H., Ritter, J.M., Casey, R.J., & Sawin, D.B. (1995). Infant attractiveness predicts maternal behaviors and attitudes. *Developmental Psychology*, 31, 464-472.

Langlois, J.H., Roggman, L.A., Casey, R.J., Ritter, J.M., Rieser-Danner, L.A., & Jenkins, V.Y. (1987). Infant preferences for attractive faces: Rudiments of a stereotype? *Developmental Psychology*, 23, 363-369.

Lawson, D.W., & Mace, R. (2009). Trade-offs in modern parenting: A longitudinal study of sibling competition for parental care. *Evolution and Human Behavior*, 30, 170-183.

Lerner, J.V. (1993). The influence of child temperamental characteristics on parent behaviors. In: T. Luster & L. Okagaki (Eds.), *Parenting: An ecological perspective* (pp. 101-120). Hillsdale, NJ: Erlbaum.

Linschoten, M.R., Harvey, L.O., Eller, P.M., & Jafek, B.W. (2001). Fast and accurate measurement of taste and smell thresholds using a maximum-likelihood adaptive staircase procedure. *Perception and Psychophysics*, 63, 1330-1347.

Little, A., & Perret, D. (2002). Putting beauty back in the eye of the beholder. *The Psychologist*, 15, 28-32.

Lötsch, J., Lange, C., & Hummel, T. (2004). A simple and reliable method for clinical assessment of odor thresholds. *Chemical Senses*, 29, 311-317.

Macfarlane, A. (1975). Olfaction in the development of social preferences in the human neonate. In: *Parent-infant interaction*, Ciba Foundation Symposium 33 (pp. 103-113). New York: Elsevier.

Mann, J. (1992). Nurturance or negligence: Maternal psychology and behavioral preference among preterm twins. In: J.H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 367-390). New York: Oxford University Press.

Marlowe, F. (1999). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology*, 46, 57-64.

Mateo, J.M. (2002). Kin-recognition abilities and nepotism as a function of sociality. *Proceedings of the Royal Society of London*, *Series B: Biological Sciences*, 269, 721-727.

Mateo, J.M., & Johnston, R.E. (2000). Kin recognition and the 'armpit effect': Evidence of self-referent phenotype matching. *Proceedings of the Royal Society of London*, *Series B: Biological Sciences*, 267, 695-700.

McBurney, D.H., Simon, J., Gaulin, S.J.C., & Geliebter, A. (2002). Matrilateral biases in the investment of aunts and uncles. Replication in a population presumed to have high paternity certainty. *Human Nature*, 13, 391-402.

McLain, D.K., Setters, D., Moulton, M.P., & Pratt, A.E. (2000). Ascription of resemblance of newborns by parents and nonrelatives. *Evolution and Human Behavior*, 21, 11-23.

Møller, A.P., & Pomiankowski, A. (1993). Fluctuating asymmetry and sexual selection. *Genetica*, 89, 267-279.

Møller, A.P., & Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology*, 10, 1-16.

Nesse, R.M., Silverman, A., & Bortz, A. (1990). Sex differences in ability to recognize family resemblance. *Ethology and Sociobiology*, 11, 11-21.

Noor, F., & Evans, D.C. (2003). The effect of facial symmetry on perceptions of personality and attractiveness. *Journal of Research in Personality*, 37, 339-347.

Park, J.H., & Schaller, M. (2005). Does attitude similarity serve as a heuristic cue for kinship? Evidence of an implicit cognitive association. *Evolution and Human Behavior*, 26, 158-170.

Pashos, A. (2000). Does paternal uncertainty explain discriminative grandparental solicitude? A cross-cultural study in Greece and Germany. *Evolution and Human Behavior*, 21, 97-109.

Pause, B.M., Sojka, B., Krauel, K., Fehm-Wolfsdorf, G., & Ferstl, R. (1996). Olfactory information processing during the course of the menstrual cycle. *Biological Psychology*, 44, 31-54.

Penn, D.J., & Potts, W.K. (1998). Chemical signals and parasite-mediated sexual selection. *Trends in Ecology and Evolution*, 13, 391-396.

Platek, S.M., Burch, R.L., Panyavin, I.S., Wasserman, B.H., & Gallup, G.G. (2002). Reactions to children's faces: Resemblance affects males more than females. *Evolution and Human Behavior*, 23, 159-166.

Platek, S.M., Critton, S.R., Burch, R.L., Frederick, D.A., Myers, T.E., & Gallup, G.G. (2003). How much paternal resemblance is enough? Sex differences in hypothetical investment decisions but not in the detection of resemblance. *Evolution and Human Behavior*, 24, 81-87.

Platek, S.M., Raines, D.M., Gallup, G.G., Mohamed, F.B., Thomson, J.W., Myers, T.E., Panyavin, I.S., Levin, S.L., Davis, J.A., Fonteyn, L.C.M., & Arigo, D.R. (2004). Reactions to children's faces: Males are more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, 25, 394-405.

Pope, S.K., Whiteside, L., Brooks-Gunn, J., Kelleher, K.J., Rickert, V.I., Bradley, R.H., & Casey, P.H. (1993). Low-birth-weight infants born to adolescent mothers: Effects of co-residency with grandmother on child development. *Journal of the American Medical Association*, 269, 1396-1400.

Porter, R.H., Balogh, R.D., Cernoch, J.M., & Franchi, C. (1986). Recognition of kin through characteristic body odors. *Chemical Senses*, 11, 389-395.

Porter, R.H., Cernoch, J.M., & Balogh, R.D. (1985). Odor signatures and kin recognition. *Physiology and Behavior*, 34, 445-448.

Porter, R.H., Cernoch, J.M., & McLaughlin, F.J. (1983). Maternal recognition of neonates through olfactory cues. *Physiology and Behavior*, 30, 151-154.

Porter, R.H., & Moore, J.D. (1981). Human kin recognition by olfactory cues. *Physiology and Behavior*, 27, 493-495.

Rasbash, J., Charlton, C., Browne, W.J., Healy, M., & Cameron, B. (2005). *MLwiN Version 2.02*. Centre for Multilevel Modelling, University of Bristol.

Regalski, J.M., & Gaulin, S.J.C. (1993). Whom are Mexican infants said to resemblance? Monitoring and fostering paternal confidence in the Yucatan. *Ethology and Sociobiology*, 14, 97-113.

Russell, M.J. (1976). Human olfactory communication. *Nature*, 260, 520-522.

Russell, M.J., Mendelson, T., & Peeke, H.V.S. (1983). Mothers' identification of their infants' odors. *Ethology and Sociobiology*, 4, 29-31.

Sawyer, M.G., Streiner, D.L., & Baghurst, P. (1998). The influences of distress on mothers' and fathers' reports of childhood emotional and behavioral problems. *Journal of Abnormal Child Psychology*, 26, 407-414.

Schaal, B., Montagner, H., Hertling, E., Bolzoni, D., Moyse, A., & Quichon, R. (1980). Les stimulations olfactives dans les relations entre l'enfant et la mere. *Reproduction, Nutrition, Développement*, 20, 843-858.

Scheib, J.E., Gangestad, S.W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London*, *Series B: Biological Sciences*, 266, 1913-1917.

Scrimshaw, S.C.M. (1984). Infanticide in human populations: Societal and individual concerns. In: G. Hausfater & S.B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 439-462). Hawthorne, NY: Aldine.

Shackelford, T.K., & Larsen, R.J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology*, 72, 456-466.

Shackelford, T.K., & Larsen, R.J. (1999). Facial attractiveness and physical health. *Evolution and Human Behavior*, 20, 71-76.

Silverman, I. (1977). *The human subject in the psychological laboratory*. New York: Pergamon.

Silverstein, L.B. (1996). Fathering is a feminist issue. *Psychology of Women Quarterly*, 20, 3-37.

Smith, M.S. (1988). Research in developmental sociobiology: Parenting and family behavior. In: K.B. MacDonald (Ed.), *Sociobiological perspectives on human development* (pp. 271-292). New York, NY: Springer.

Sussman, S., Mueser, K.T., Grau, B.W., & Yarnold, P.R. (1983). Stability of females' facial attractiveness during childhood. *Journal of Personality and Social Psychology*, 44, 1231-1233.

Swaddle, J.P., & Cuthill, I.C. (1995). Asymmetry and human facial attractiveness: Symmetry may not always be beautiful. *Proceedings of the Royal Society of London*, *Series B: Biological Sciences*, 261, 111-116.

Tatarunaite, E., Playle, R., Hood, K., Shaw, W., & Richmond, S. (2005). Facial attractiveness: A longitudinal study. *American Journal of Orthodontics and Dentofacial Orthopedics*, 127, 676-682.

Thomas, J.L. (1989). Gender and perceptions of grandparenthood. *International Journal of Aging and Human Development*, 29, 269-282.

Thornhill, R. (1998). Darwinian aesthetics. In: C. Crawford & D.L. Krebs (Eds.), *Handbook of evolutionary psychology* (pp. 543-572). Mahwah, NJ: Erlbaum.

Thornhill, R., & Gangestad, S.W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature*, 4, 237-269.

Thornhill, R., & Gangestad, S.W. (1996). The evolution of human sexuality. *Trends in Ecology and Evolution*, 11, 98-102.

Thornhill, R., & Gangestad, S.W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, 3, 452-460.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In: J.H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–139). New York: Oxford University Press.

Trivers, R.L. (1972). Parental investment and sexual selection. In: B. Campbell (Ed.), *Sexual Selection and the Descent of Man, 1871-1971* (pp. 136-179). London: Heinemann.

van Tuijl, C., Branje, S.J.T., Dubas, J.S., Vermulst, A.A., & van Aken, M.A.G. (2005). Parent-offspring similarity in personality and adolescents' problem behaviour. *European Journal of Personality*, 19, 51-68.

Umberson, D., & Hughes, M. (1987). The impact of physical attractiveness on achievement and psychological well-being. *Social Psychology Quarterly*, 50, 227-236.

Volk, A.A., Lukjanczuk, J.M., & Quinsey, V.L. (2005). Influence of infant and child facial cues of low body weight on adults' ratings of adoption preference, cuteness, and health. *Infant Mental Health Journal*, 26, 459-469.

Volk, A.A., & Quinsey, V.L. (2002). The influence of infant facial cues on adoption preferences. *Human Nature*, 13, 437-455.

Volk, A.A., & Quinsey, V.L. (2007). Parental investment and resemblance: Replications, refinements and revisions. *Evolutionary Psychology*, 5, 1-14.

Wallace, P. (1977). Individual discrimination of humans by odor. *Physiology and Behavior*, 19, 577-579.

Watson, P.J., & Thornhill, R. (1994). Fluctuating asymmetry and sexual selection. *Trends in Ecology and Evolution*, 9, 21-25.

Weisfeld, G.E., Czilli, T., Phillips, K.A., Gall, J.A., & Lichtman, C.M. (2003). Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, 85, 279-295.

Wilson, J.M., & Manning, J.T. (1996). Fluctuating asymmetry and age in children: Evolutionary implications for the control of developmental stability. *Journal of Human Evolution*, 30, 529-537.

Wilson, M.N. (1986). The black extended family: An analytical consideration. *Developmental Psychology*, 22, 246-258.

Wyatt, T.D. (2003). *Pheromones and animal behaviour*. Cambridge: Cambridge University Press.

Yamazaki, K., Beauchamp, G.K., Curran, M., Bard, J., & Boyse, E.A. (2000). Parent-progeny recognition as a function of MHC odortype identity. *Proceedings of the National Academy of Sciences*, 97, 10500-10502.

Yamazaki, K., Beauchamp G.K., Singer, A., Bard, J., & Boyse, E.A. (1999). Odortypes: their origin and composition. *Proceedings of the National Academy of Sciences*, 96, 1522-1525.

Zebrowitz, L.A., Olson, K., & Hoffman, K. (1993). Stability of babyfaceness and attractiveness across the life span. *Journal of Personality and Social Psychology*, 64, 453-466.

Summary

Whether, how, and to what extent parenting shapes and influences child development has been of longstanding interest to developmental psychologists and family scientists. A vast body of empirical evidence highlights the contribution of parenting to a wide range of cognitive, socio-emotional, and behavioral developmental outcomes in children. Although great effort has been spent on studying the effects of parenting, much less research has focused on factors that predict individual differences in parental investment. In this dissertation, an evolutionary psychological perspective was used to identify characteristics in children that influence parental and grandparental investment. It should be noted that although the term *investment* can also imply financial or physical support, in this dissertation the term is used to refer to parenting behavior such as emotional support, attention, time investment, and discipline.

From an evolutionary perspective parental investment in children is a means of optimizing the reproductive success of the parent by increasing one's inclusive fitness (i.e., the number of copies of one's genes passed on to future generations through surviving offspring or descendent collateral kin). Parental investment was defined by Trivers (1972) as *"any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring"*. So defined, parental investment is limited, and parents have to make (non-conscious) decisions on how to allocate their resources among their offspring. According to evolutionary theory, human parents are not expected to invest equally in each of the children in their household. Instead, parents are expected to favor children on the basis of their genetic relatedness and their reproductive value. In this dissertation we examined whether possible cues of genetic relatedness (i.e., parent-child resemblance and olfactory recognition) and reproductive value of the child (i.e., child attractiveness and facial symmetry) were related to parental investment in a sample of Dutch parents with school-age children. In addition we examined whether differential grandparental investment could be explained by certainty of genetic relatedness.

The first factor that was expected to influence parental investment is the genetic relatedness of the child to the parent. In order to maximize their own reproductive fitness, parents should prefer to invest in children to whom they are genetically related. Whereas women are sure of their maternity, men can never be fully certain of their paternity, but instead need to rely on indirect cues to assess whether they are likely to be the father of their putative children. Given this asymmetry in certainty of parenthood, men are predicted to be more sensitive to cues of genetic relatedness than women when making investment

decisions. *Chapter 2* and *Chapter 3* of this dissertation examined parent-child resemblance and olfactory recognition as possible cues of genetic relatedness.

Chapter 2 described two studies in which we examined the relation between parent-child resemblance, in both looks and personality, and parental investment. We hypothesized that the higher the degree of similarity between parent and child, the more certain the parent - particularly the father - will be of genetic relatedness, and, consequently, the more the parent will invest in that particular child. The results of both studies described in *Chapter 2* indicated a link between personality similarity and parental investment for mothers. For fathers parental investment was linked to physical resemblance in one study. In the other study these results were not replicated.

Chapter 3 examined whether parent-child olfactory recognition was linked to parental investment. Several studies have shown that humans are capable of recognizing close biological kin by olfactory cues alone. In our study, the ability to recognize one's children by smell was associated with an increase in investment for both mothers and fathers, and a decrease in physical punishment by mothers.

The results of *Chapter 2* and *Chapter 3* provide evidence that both mothers and fathers are sensitive to cues of genetic relatedness when making investment decisions. Contrary to our expectations, we found no evidence that cues of genetic relatedness influenced fathers' investment decisions more than mothers' investment decisions.

The second factor that was expected to influence parental investment is the reproductive value of the child (i.e., the child's probable future reproductive success). In order to maximize their own inclusive fitness, parents should allocate more care, resources, and attention to offspring who have the highest chance of future reproductive success (i.e., healthy, high quality offspring). *Chapter 4* examined child attractiveness and facial symmetry as possible cues of reproductive value of the child. Attractiveness and facial symmetry are considered to accurately advertise fitness, health, and quality. Attractive people display greater physical health and psychological well-being, and facial attractiveness predicts future longevity. Facial asymmetry is presumed to be a measure of developmental instability and inability of an organism to cope with stress. Both attractiveness and facial symmetry might signal to parents that their child is genetically fit, and, therefore, worthy of investment.

Chapter 4 examined whether parental investment was influenced by child attractiveness and/or facial symmetry. Our results suggest that attractiveness is a significant predictor of parental behavior. Both mothers and fathers reported having a closer bond with children who were rated as more attractive, and fathers punished attractive children less often than less attractive children. No consistent support was found for facial symmetry as a predictor of parental investment.

In addition to individual differences in parental investment, in *Chapter 5* we examined differential investment by grandparents. Grandparents can continue to contribute to their inclusive fitness by assisting their adult son or daughter in his/her parental effort. Even though investment by grandparents positively influences child health and well-being, and thus grandparental lifetime reproductive success, not all grandparents invest equally in their grandchildren. Like paternal investment, grandparental investment might be affected by parental uncertainty. The most certain grandparent is the maternal grandmother, being certain of her own as well as her daughter's maternity. The most uncertain grandparent is the paternal grandfather, who can be certain of neither his own nor his son's paternity. The maternal grandfather and the paternal grandmother have intermediate levels of uncertainty of grandparenthood, both having one certain and one uncertain link.

In *Chapter 5* we examined whether differences in grandparental investment can be explained by certainty of relatedness (as assessed by kinship lines). Both mothers, fathers and children (8-10 years old) rated the quality of the grandparent-grandchild relationship highest with maternal grandmothers (most genetically certain) and lowest with paternal grandfathers (least genetically certain). Relationship quality with both maternal grandfathers and paternal grandmothers was rated as intermediate. These results are consistent with the prediction that discriminative grandparental solicitude varies as a function of certainty of relatedness.

Despite the fact that in a contemporary Western society, such as the Netherlands, families are relatively small and emotional and economic resources are more than enough for parents to invest equally in all of the children in their household, the studies presented in this dissertation show that both mothers and fathers are still sensitive to cues of both genetic relatedness (i.e., parent-child resemblance and olfactory recognition) and reproductive value of the child (i.e., child attractiveness) when making investment decisions. In addition, our results suggest that grandparental solicitude varies as a function of certainty of relatedness. Thus, an evolutionary psychological perspective seems helpful in predicting differences in parental and grandparental investment. It provides another level of explanation to complement existing models, and, as such, could make important contributions to our understanding of parent-child interactions and child development.

Samenvatting

(Summary in Dutch)

De manier waarop en de mate waarin opvoeding de ontwikkeling van een kind vormt en beïnvloedt, heeft al geruime tijd de interesse van ontwikkelingspsychologen en pedagogen. Diverse empirische studies hebben de invloed van opvoeding op de cognitieve, sociale en emotionele ontwikkeling van kinderen aangetoond. Hoewel er veel aandacht besteed is aan het bestuderen van de effecten van opvoeding, is er veel minder onderzoek gedaan naar factoren die individuele verschillen in ouderlijke investering voorspellen. In dit proefschrift werd een evolutionair psychologisch perspectief gebruikt om kindkenmerken te identificeren die van invloed zouden kunnen zijn op ouderlijke en grootouderlijke investering. Hoewel de term *investering* ook betrekking kan hebben op financiële en fysieke ondersteuning, wordt de term in dit proefschrift gebuikt om te verwijzen naar opvoedingsgedrag van ouders, zoals emotionele ondersteuning, aandacht, gezamenlijk doorgebrachte tijd en discipline.

Vanuit een evolutionair perspectief is ouderlijke investering in kinderen een manier waarop de ouder zijn/haar reproductieve succes kan optimaliseren, door zijn/haar inclusieve fitness (d.w.z., het aantal kopieën van iemands genen dat wordt doorgegeven aan toekomstige generaties door overlevende nakomelingen) te vergroten. Ouderlijke investering werd door Trivers (1972) gedefinieerd als *"elke investering door een ouder in een nakomeling die de overlevingskans (en dus het reproductief succes) van die nakomeling verhoogt ten koste van de mogelijkheid van de ouder om te investeren in andere nakomelingen"*. Volgens deze definitie is ouderlijke investering beperkt, en moeten ouders (onbewust) keuzes maken in hoe ze hun middelen, tijd en aandacht verdelen over hun kinderen. De evolutionaire theorie voorspelt dat ouders niet evenveel zullen investeren in ieder kind binnen hun gezin. In plaats daarvan wordt verondersteld dat ouders een voorkeur zullen hebben om te investeren in bepaalde kinderen op basis van hun genetische verwantschap en reproductieve waarde. In dit proefschrift werd onderzocht of mogelijke signalen van genetische verwantschap (d.w.z., gelijkenis tussen ouder en kind en geurherkenning door de ouder) en reproductieve waarde van het kind (d.w.z., aantrekkelijkheid van het kind en symmetrie van het gezicht) gerelateerd zijn aan ouderlijke investering in een onderzoeksgroep van Nederlandse ouders met kinderen in de basisschoolleeftijd. Bovendien werd onderzocht of verschillen in investering door grootouders verklaard kunnen worden door de mate van zekerheid van genetisch verwantschap.

De eerste factor waarvan verwacht werd dat deze ouderlijke investering beïnvloedt, is de genetische verwantschap van het kind aan de opvoeder. Om hun eigen inclusieve

fitness te maximaliseren, zouden ouders bij voorkeur moeten investeren in kinderen die genetisch aan hen verwant zijn. Terwijl vrouwen zeker zijn van hun moederschap, kunnen mannen nooit helemaal zeker zijn van hun vaderschap. In plaats daarvan zullen mannen moeten vertrouwen op indirecte signalen om in te schatten of zij werkelijk de biologische vader zijn van hun vermeende kinderen. Gezien de asymmetrie in zekerheid van ouderschap, wordt voorspeld dat mannen sterker beïnvloed zullen worden door signalen van genetische verwantschap dan vrouwen bij het nemen van (onbewuste) beslissingen over ouderlijke investering. In *Hoofdstuk 2* en *Hoofdstuk 3* van dit proefschrift werden gelijkenis tussen ouder en kind en het vermogen van ouders om hun kind te herkennen door middel van geur onderzocht als mogelijke signalen van genetische verwantschap.

In *Hoofdstuk 2* werden twee studies beschreven waarin de relatie tussen gelijkenis tussen ouder en kind (zowel in uiterlijk als in persoonlijkheid) en ouderlijke investering werd onderzocht. De hypothese was dat hoe groter de gelijkenis tussen ouder en kind, hoe zekerder de ouder - vooral de vader - zal zijn van het biologisch ouderschap. Deze zekerheid zal vervolgens leiden tot meer ouderlijke investering in dat specifieke kind. In beide studies in *Hoofdstuk 2* werd een verband gevonden tussen gelijkenis in persoonlijkheid en ouderlijke investering voor moeders. Voor vaders werd een verband gevonden tussen uiterlijke gelijkenis en ouderlijke investering in een van de studies. In de andere studie werden deze resultaten echter niet gerepliceerd.

In *Hoofdstuk 3* werd onderzocht of er een verband bestaat tussen ouderlijke investering en het vermogen van ouders om hun kinderen te herkennen door middel van geur. Verschillende studies hebben aangetoond dat mensen in staat zijn om biologische verwanten te herkennen aan hun geur. Uit onze studie bleek dat het vermogen van ouders om hun kind te herkennen door middel van geur gerelateerd is aan een toename van investering door zowel moeders als vaders, en een afname van fysieke straf door moeders.

De resultaten van *Hoofdstuk 2* en *Hoofdstuk 3* leveren bewijs dat zowel vaders als moeders gevoelig zijn voor signalen van genetische verwantschap bij het nemen van beslissingen omtrent ouderlijke investering. In tegenstelling tot onze verwachting, vonden we geen bewijs dat vaders sterker beïnvloed worden door signalen van genetische verwantschap dan moeders.

De tweede factor waarvan verwacht werd dat deze ouderlijke investering beïnvloedt, is de reproductieve waarde van het kind (d.w.z., het verwachte toekomstige reproductieve succes van het kind). Om hun eigen inclusieve fitness te maximaliseren, zouden ouders meer zorg, middelen en aandacht moeten besteden aan kinderen die de grootste kans hebben op toekomstig reproductief succes (d.w.z., gezonde, sterke kinderen). In *Hoofdstuk 4* werden aantrekkelijkheid van het kind en symmetrie van het gezicht onderzocht als mogelijke signalen van reproductieve waarde van het kind.

Aantrekkelijkheid en symmetrie van het gezicht worden beiden beschouwd als betrouwbare indicator van gezondheid en kwaliteit. Aantrekkelijkere mensen hebben een betere fysieke gezondheid en psychologisch welzijn, en aantrekkelijkheid van het gezicht voorspelt de levensduur van een persoon. Asymmetrie van het gezicht wordt verondersteld een maat te zijn voor een onnauwkeurige ontwikkeling en het onvermogen van het lichaam om om te gaan met stress. Zowel aantrekkelijkheid als symmetrie van het gezicht kan aan ouders het signaal geven dat hun kind genetisch gezond is, en dus de moeite waard om in te investeren.

In *Hoofdstuk 4* werd onderzocht of ouderlijke investering wordt beïnvloed door aantrekkelijkheid van het kind en/of symmetrie van het gezicht. Onze resultaten toonden aan dat aantrekkelijkheid een significante voorspeller is van ouderlijke investering. Zowel moeders als vaders rapporteerden een sterkere emotionele band te hebben met aantrekkelijkere kinderen. Bovendien straften vaders aantrekkelijkere kinderen minder vaak dan minder aantrekkelijke kinderen. Er werd geen overtuigend bewijs gevonden voor symmetrie van het gezicht als voorspeller van ouderlijke investering.

Naast individuele verschillen in ouderlijke investering onderzochten we in *Hoofdstuk 5* verschillen in investering door grootouders. Grootouders kunnen blijven bijdragen aan hun inclusieve fitness door hun volwassen zoon of dochter te assisteren in zijn/haar rol als ouder. Hoewel grootouderlijke investering de gezondheid en het welzijn van het kleinkind positief beïnvloedt, en op deze wijze bijdraagt aan het reproductieve succes van de grootouder, investeren niet alle grootouders even veel in hun kleinkinderen. Net zoals vaderlijke investering, zou ook grootouderlijke investering beïnvloed kunnen worden door onzekerheid over genetisch verwantschap. De meest zekere grootouder is de grootmoeder van moeders kant, die zeker kan zijn van zowel haar eigen als haar dochters moederschap. De meest onzekere grootouder is de grootvader van vaders kant, die zeker kan zijn van noch zijn eigen noch zijn zoons vaderschap. De grootvader van moeders kant en de grootmoeder van vaders kant zijn beiden gematigd onzeker, aangezien ze allebei één zekere en één onzekere stap in de lijn van verwantschap hebben.

In *Hoofdstuk 5* werd onderzocht of verschillen in grootouderlijke investering verklaard kunnen worden door de mate van zekerheid van genetisch verwantschap. Moeders, vaders en kinderen (8-10 jaar oud) beoordeelden allen de relatie met grootmoeders van moeders kant als beste, gevolgd door zowel grootvaders van moeders kant als grootmoeders van vaders kant. De relatie met grootvaders van vaders kant werd als minst beoordeeld. Deze resultaten komen overeen met de voorspelling dat grootouderlijke investering varieert als een functie van zekerheid van verwantschap.

In de huidige Westerse samenleving zijn de gezinnen relatief klein en hebben ouders ruim voldoende emotionele en economische middelen om in ieder kind binnen het gezin

even veel te investeren. Desondanks tonen de resultaten van de studies in dit proefschrift aan dat zowel moeders als vaders gevoelig zijn voor signalen van zowel genetische verwantschap (d.w.z., gelijkenis tussen ouder en kind en geurherkenning door de ouder) als reproductieve waarde van het kind (d.w.z., aantrekkelijkheid van het kind) bij het nemen van beslissingen over ouderlijke investering. Bovendien tonen onze resultaten aan dat grootouderlijke investering varieert als een functie van zekerheid van verwantschap. Een evolutionair psychologisch perspectief kan dus bijdragen aan het voorspellen van individuele verschillen in ouderlijke en grootouderlijke investering. Het levert een verklaring op een ander niveau, waarmee bestaande modellen aangevuld kunnen worden om een zo compleet mogelijk beeld te vormen. Een evolutionair psychologisch perspectief kan op deze wijze een belangrijke bijdrage leveren aan ons begrip van de interacties tussen ouders en kinderen en de ontwikkeling van het kind.

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Curriculum Vitae

Marianne Heijkoop was born in Gouda on July 18, 1981. After completing secondary education (Gymnasium, Emmauscollege, Rotterdam) in 1999, she studied Biology at Utrecht University. She received her master's degree in August 2004. In October 2004 she started her PhD project at the Department of Developmental Psychology at Utrecht University under the supervision of Prof. dr. Marcel van Aken and Dr. Judith Dubas. The results of this research are described in this dissertation.