ELSEVIER

Evolution and Human Behavior 28 (2007) 135–144

Evolution and Human Behavior

Differential facial resemblance of young children to their parents: who do children look like more?

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Initial receipt 14 June 2006; final revision received 18 August 2006

Abstract

In humans, paternal investment is highly variable and is modulated by paternity uncertainty. Facial phenotypic similarity between a father and a child is one possible paternity indicator. However, whether such paternal-biased traits are expressed in children is unclear, as previous empirical results are contradictory. Therefore, we quantified the facial resemblance between a child and each of his or her parents, from birth to 6 years old. Resemblance was assessed from pictures of the face by nonrelated judges. We found that, at all ages, children resemble both their parents more than would be expected by chance, although there is a differential resemblance toward one or the other parent depending on the age and sex of the child. For newborns, boys and girls resemble their mothers more, this differential resemblance persisting through time for girls. For boys, an inversion occurs and they resemble their fathers more between 2 and 3 years of age. The resemblance ascribed by the parents shows that, at birth, mothers ascribe a resemblance to the father, as previously found, although assessment by external judges revealed the opposite. These results suggest that facial appearance is a cue for kin recognition between a father and a child. Patterns of differential resemblance are discussed within the context of evolutionary theories on parental investment.

Keywords: Facial resemblance; Family conflict; Paternal investment; Paternity uncertainty

1. Introduction

Facial appearance is highly variable in humans. Some brain areas (left frontal cortex) are specifically involved in recognizing familiar faces, as lesions in these areas make individuals unable to recognize well-known faces (prosopagnosia, Malone, Morris, Kay, & Levin, 1982). This high facial variability and a specialized recognition area in the brain suggest that facial appearance plays a role in many social contexts. For example, facial resemblance increases both the attractiveness of same-sex individuals (DeBruine, 2004) and trustworthiness (DeBruine, 2002), leading to greater cooperation. Facial resemblance has also been implicated in the father–child relationship (Apicella & Marlowe, 2004; Platek, 2003), with the perceived resemblance of the child being more valued by men than by women (Platek et al., 2004; Volk & Quinsey, 2002). More strikingly, males who had committed infanticide often cited a lack of physical resemblance of the child revealing nonpaternity as an explanation (Daly & Wilson, 1984). Furthermore, the perception of nonresemblance by fathers is correlated with the incidence of sexual abuse and marital violence (Burch & Gallup, 2000). Controlled experiments have shown that when making hypothetical parental investment decisions, men are more sensitive to child resemblance than women (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al. 2004). Moreover, the neural activation in response to child facial resemblance is greater for men (Platek, Keenan, & Mohamed, 2005). The activated brain area, the left frontal cortex, is involved in response inhibition when making uncertain decisions. These results suggest that humans have been selected to be sensitive to self-referent phenotypic matching through facial recognition (Platek et al., 2004), with face appearance thus being a cue of relatedness.

Women have evolved counterstrategies that limit the problems of paternity uncertainty. One is to ascribe the

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doi:10.1016/j.evolhumbehav.2006.08.008

child's resemblance to the father (Daly & Wilson, 1982; McLain, Setters, Moulton, & Pratt, 2000; Regalski, J.M., & Gaulin, S.J.C., 1993). This has been studied for newborns and young babies, and is considered as a way to ensure men of their paternity: unfaithful mothers could reduce uncertainty, whereas faithful mothers could gain more paternal investment.

Another evolutionary possibility is a biased facial resemblance toward the father. A gene revealing paternity in children would thus confer more paternal care in some situations (no EPP) and less paternal care in others (EPP). Formal models have produced conflicting results for this possibility: when EPP increases in the population, such a gene would be either selected against (Bressan, 2002; Pagel, 1997) or selected for (Johnstone, 1997).

Previous published studies on differential resemblance of children toward their father or mother are disconcerting (see review in Table 1). Newborns are found to resemble preferentially their mother (McLain et al., 2000). At 1 year old, preferential resemblance is either toward the father (Christenfeld & Hill, 1995) or the mother (Bressan & Grassi, 2004), or there is none (Brédart & French 1999; Nesse et al., 1990). At later ages, no preferential resemblance has been reported (Brédart & French, 1999; Nesse et al., 1990). A close look at these published articles suggests that these divergent results could potentially be due to several types of bias in some studies. First, the source of the photograph (Bias category A in Table 1): the use of low-quality pictures could preclude or decrease the possibility to detect resemblance. This could explain, for example, why for most cases in Christenfeld and Hill (1995), children–parent resemblance was not detected. Second, the presence of backgrounds in the pictures (Bias category B in Table 1) is known to introduce unwanted cues that can be used by judges (Vokey, Rendall, Parr, de Waal & Tangen, 2004). It could be controlled for (different backgrounds for each parent and the child, as in McLain et al.) or removed. Third, a nonrandomization of the foil (or false) parents (Category C in Table 1): resemblance is detected by the judges by choosing, for a given child, one possible parent among three, one of which being the true one, the others being foil parents. It is essential that the identity of the foil parents, for a given true parent, be variable among the judges, in order to assess the child–parent resemblance relatively to a larger population, and not relatively to two particular foil parents. This randomization is not performed in Christenfeld and Hill (1995) and Brédart and French (1999). Fourth, in some studies the same individual could be used as a true parent, when the judge evaluates the resemblance of his/her child) and as a foil parent (when the same judge evaluates the resemblance of another child) (Category D in Table 1). This represents unwanted information that could affect, for a given judge, the probability of detecting the correct parent when the same face is seen another time. This bias is apparently present in Brédart and French (1999) and Christenfeld and Hill (1995), and is explicitly controlled for in Bressan and Grassi (2004). Finally, some data manipulation precludes a clear interpretation of the results (Category E in Table 1), such as selection of subsamples of pictures (precisely parent/child and foil parent/child picture pairs) for a better discrimination done in Nesse et al. (1990): the use of a nonrandom sample precludes inferences on the sampled population and, thus, results lack generality.

Some divergent results in Table 1 could also be explained by possible variation in differential resemblance with the age of the child. Indeed, costs and benefits of parental investment for each parent could change with age of the child (Clutton-Brock, 1991; Hagen, Hames, Craig, Lauer, & Price, 2001). The possibility that child differential resemblance may vary over time has been addressed in a study with a low sample size ($n \leq 6$), and in two studies with several methodological problems (see Table 1). They

Table 1
Overview of previous studies on child–parent resemblance, as estimated by nonrelated judges

Age class (years)	Sample size (families)	Judges/family	Resemblance to each parent	Differential resemblance	Possible biases	Reference
0.5–18 (different individual)	≤6	200	Yes	No	E[a]	Nesse, Silverman, and Bortz (1990)
1, 10, and 20 (same individual)	24	18–21	No[b]	Yes[b]	A[c], B, C D	Christenfeld and Hill (1995)
1, 3, and 5 (same individual)	28	30	Yes	No	A[d], B, C, D	Brédart and French (1999)
~0	160	10	Yes	Yes (mother > father)	D?	McLain et al. (2000)
1	40	20	Yes	Yes (mother > father)	A[e]	Bressan and Grassi, (2004)
~0, 1, 2–4, 4–6 (different individual)	83 (20–21/class)	51–55	Yes	Yes (age and sex variation)	–	This study

Only studies assessing independently mother–child and father–child resemblance are shown, ordered by year of publication. Age classes of children, number of families, and number of judges per family are indicated, and some key results. Possible biases are categorized: at the level of the source of the photograph (A), not removing or not controlling for the picture background (B), nonrandomization of the foil parents (C), allowing multiple occurrence of a parental face for a given judge (D), and others (E). See text for details.

[a] Parent/child and foil-parent/child pairs selected for better discrimination.

[b] No significant results except that at 1 year old, children resemble only their father.

[c] Photographs from family albums.

[d] Black and white photographs.

[e] Nonhomogenous sources of photographs (family albums and newly made pictures).

essentially disclosed negative results. Age variation of differential resemblance of the child remains an intriguing possibility not yet thoroughly investigated.

We explored parent–child facial resemblance during childhood through a systematic study on several age groups from birth to 6 years old. We aimed to quantify the resemblance of children to their parents, and how this resemblance varied with age of children. We compared this resemblance assessed by external judges to the ascription of resemblance by parents, to detect judgment biases within the family.

2. Methods

2.1. Face photographs

Families comprising at least one child and their mother and father were recruited publicly from Montpellier, Hyères, and Grenoble in France. We selected only families with a child 1, 2–4, or 4–6 years old. Families with a newborn child (1–3 days old) were recruited in maternity units (Montpellier and Hyères), with the formal agreement of the head of the obstetrics service. Individuals who have reached reproductive age (although information on parental status was not collected) were recruited publicly from Montpellier, Hyères, Grenoble, and Paris in France to act as either a "false father" or "false mother" in the experiment. For each family or individual, the general purpose of the study was explained (i.e., the resemblance between parents and children) and a formal voluntary agreement was requested to take pictures of the face of each family member and to use the picture for this project. All photographs of the front view of the face were taken with the same digital still camera (Canon EOS 20D), at a distance of about 1 m using the same general settings. Each individual was asked to express a neutral face and to look directly at the camera. Spectacle wearers were asked to remove them.

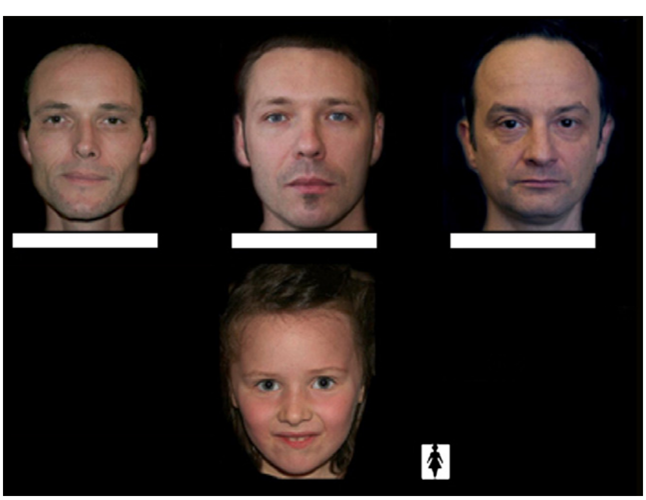

Fig. 1. Photographs presented to the judges: an example for assessing father–child resemblance. The small item on the lower right indicates the sex of the child.

Table 2
Number of children and judges for each sex and each age class

	Number of children			Number of judges		
Age classes	M	F	Total	M	F	Total
1–3 days	10	11	21	32	19	51
8 months to 1 year 10 months	10	11	21	26	25	51
2 years to 3 years 6 months	9	12	21	27	25	52
4 years to 6 years 2 months	9	11	20	35	20	55
Total	38	45	83	120	89	209

2.2. Personal information

We requested some personal information from the participants. After agreeing, the parents were questioned about the sex, age, birth order, and number of the child's siblings. They were also asked their own age, the duration of their relationship, and their monthly income (divided into nine classes from "less than 760 euros" to "more than 3618 euros"). Each parent was then asked to ascribe the resemblance of the child to either themselves (coded as 1) or the other parent (coded as 0). The resemblance was ascribed by the parent in the presence of the other parent. Judges were publicly recruited voluntarily in Montpellier, France. We recorded their sex, age, number of children, and number of siblings. The judges were unaware of the purpose of the study when assessing the resemblance.

2.3. Assessing resemblance

All photographs were electronically processed using Adobe Photoshop 7 to normalize the contrast and luminosity, and to turn all backgrounds into black. The general principle for assessing resemblance is taken from Christenfeld and Hill (1995). Resemblance is assessed by identifying the true parent (either the mother or the father) from three adults of the same sex. For each child, the resemblance to the father and mother was evaluated independently by the same judges. A computer program (written in Delphi, version 7) was used to present the photographs to judges, incorporating several useful statistical features such as randomization, and to record the results (Fig. 1). A given judge only evaluated the resemblance for one age class (newborn, 1, 2–4, or 4–6 years old). Within an age class, the photographs of children were presented randomly. The photographs of "false father" or "false mother" were also presented randomly, so that for each judge the true parents were randomly matched with the false parents. Each judge was allowed to see each adult photograph only once (true and false parents), and each child photograph twice (to assess the resemblance of the child once to the mother and once to the father). Whether resemblance was assessed first for the father or first for the mother was also randomized for each judge. The score for each judge was recorded (variable *score*) as 0 for failure or 1 for success. The resemblance of one child to a parent was expressed as the proportion of correct assignments from all the judges. Thus, the expected value varies between 1/3 (no resemblance) and 1 (perfect resemblance).

Table 3
Observed recognition rates by the judges for each age class

	Judges					
	% Rec mother			% Rec father		
Ages classes	Boys	Girls	All	Boys	Girls	All
1–3 days	48.9***	45.3***	47.0***	39.6***	34.6*	37.0**
8 months to 1 year 10 months	44.6***	45.9***	45.3***	40.5***	40.1***	40.3***
2 years to 3 years 6 months	49.5***	46.3***	47.9***	65.5***	43.0***	52.2***
4 years to 6 years 2 months	55.7***	55.0***	55.3***	53.7***	50.72***	52.1***

Under the null hypothesis of no resemblance (Ho), the expectation of % Rec is 33.3%.
* $p<.05$, significant departure from Ho.
** $p<.01$, significant departure from Ho.
*** $p<.001$, significant departure from Ho.

2.4. Statistical analysis

We used logistic regression to test variation in the resemblance to parents according to the recorded variables. The dependent variable was *score* (binary variable). The independent variables concerning the child were *child* (child identification number; qualitative, random effect), *child-sex* (child sex; qualitative), *child-age* (the age of the child, quantitative), *father-rank* (paternal birth order; qualitative), *mother-rank* (maternal birth order; qualitative), and *sib* (number of siblings; quantitative). The independent variables concerning parents were *test* (mother or father test; qualitative), *father-age* (age of the father at child's birth; quantitative), *mother-age* (age of the mother at child's birth; quantitative), *father-income* (father's income; qualitative), and *relationship* (duration of parent's relationship at birth; quantitative). The independent variables concerning the judges were *judge* (judge identification number; qualitative, random effect), *sex-judge* (sex of the judge; qualitative), *age-judge* (age of the judge; quantitative), *children* (the number of children the judge has; quantitative), and *sib-judge* (number of siblings the judge has; quantitative). All variables are considered fixed-effect variables, except for *child* and *judge*, which are random-effect variables in this study; that is, the children and judges are considered random samples of a larger population of interest. Therefore, we used mixed-effect models, considering the random variable *judge* as grouped in the random variable *child*. We first considered a complete model, using all the single-effect variables, plus all the two-way interactions having a biological interpretation (*child-age*:*test*; *child-sex*:*test*; *child-sex*:*sex-judge*; *child-sex*:*child-age*). When correlations between some of the variables were higher than 30% (e.g., *father-age* and *mother-age*), we considered only one of the two variables in the model. The complete model was first simplified using the Akaike (AIC) criterion (Akaike, 1973). The selected model (smallest AIC) was then simplified by eliminating the remaining nonsignificant variables, as previously described (Crawley, 1993): the higher-order terms were first tested, with the least and nonsignificant ($p>.05$) terms being removed. We evaluated the significance of the removed terms using the χ^2 test. We also used logistic regression to analyze variation in the ascribed resemblance by each parent. As the data were paired (the ascribed resemblance by either the mother or the father concerned the same child), we built separate models for each parent. The dependent variables were *mother's ascription* (the ascribed resemblance of the child by his mother to either herself or the father, binary variable) and *father's ascription* (the ascribed resemblance of the child by his father to either himself or the mother, binary variable). The independent variables concerning children and parents were the same as those used in the previous analysis (except for the variables *judge* and *child*) plus resemblance toward mothers assessed by judges (*mother-resemblance*, continuous) and resemblance toward fathers assessed by judges (*father-resemblance*, continuous), and were considered as fixed effects. We used generalized linear models. All statistical analyses were carried out using version R.2.0.1. of the R software (The R development core team, http://www.r-project.org/).

3. Results

3.1. Descriptive statistics

We sampled 69 families with a total of 83 children, with at least 20 children per age class. For each age class,

Table 4
Observed percentage of ascription of resemblance of children to their fathers (% Ascription) by each parent, for each age class and child sex

	% Ascription by mothers		% Ascription by fathers	
Age classes	For boys	For girls	For boys	For girls
1–3 days	100% ($n=6$)	77% ($n=6$)	83% ($n=6$)	83% ($n=6$)
8 months to 1 year 10 months	86% ($n=7$)	72% ($n=7$)	83% ($n=6$)	28% ($n=7$)
2 years to 3 years 6 months	40% ($n=6$)	25% ($n=7$)	50% ($n=7$)	55% ($n=6$)
4 years to 6 years 2 months	36% ($n=5$)	100% ($n=8$)	42% ($n=6$)	83% ($n=9$)

Sample sizes are in parentheses. The percentage of ascription of the resemblance of children toward their mothers is 100 (percent of ascription toward fathers).

Table 5
Minimum models for differential resemblance

Dependent variable	Predictor variables	Estimate (S.E.)	*p* value
General model			
SCORE	Intercept	0.09 (0.24)	NS
	Test[a]	−0.02 (0.16)	NS
	Child-age	−0.02 (0.12)	NS
	Child-age^2	0.02 (0.02)	NS
	Child-sex[b]	−0.18 (0.13)	NS
	Test[a]:child-sex[b]	−0.24 (0.09)	**
	Test[a]:child-age	0.27 (0.08)	***
	Test[a]:child-age^2	−0.04 (0.01)	***
Analysis for boys			
SCORE	Intercept	−0.01 (0.17)	NS
	Test[a]	−0.51 (0.12)	***
	Child-age	−0.18 (0.17)	NS
	Child-age^2	0.04 (0.03)	NS
	Test[a]: child-age	0.66 (0.12)	***
	Test[a]: child-age^2	−0.11 (0.02)	***
Analysis for girls			
SCORE	Intercept	−0.34 (0.15)	*
	Test[a]	−0.26 (0.06)	***
	Child-age	0.11 (0.05)	*

Mixed generalized linear models have been used, considering *judge* and *child* as random effects. For each analysis, the minimum models are indicated, as well as estimates, S.E.'s, and *p* values associated to each significant remaining variable. The ":" indicates an interaction effect between two variables.

[a] The variation of the effect of the second modality of *test* (father test) compared to the first one (mother test).

[b] The variation of the effect of the second modality of *child-sex* (girls) compared to the first one (boys).

* $p<.05$.

** $p<.01$.

*** $p<.001$.

resemblance was assessed by at least 51 judges. Altogether, 209 judges assessed the resemblance (120 men and 89 women) (Table 2). For all age classes, the global observed recognition rates (% Rec) of the judges were all significantly (exact binomial test, $p<.01$) greater than 1/3, indicating that a child resembles both his or her father and his or her mother (Table 3). The global resemblance of children to their parents tended to increase with the age of girls ($\chi^2=3.79$, $df=1$, $p=.05$) and, although not significant, with the age of boys ($\chi^2=1.49$, $df=1$, $p=.22$). Resemblance of children was ascribed by 52 mothers (for 28 girls and 24 boys) and by 53 fathers (for 28 girls and 25 boys). When all age classes are considered, mothers ascribe resemblance of children to their fathers in 67% of cases for boys and in 65% of cases for girls. Concerning fathers, they ascribe resemblance of children to themselves in 64% of cases for boys and in 61% of cases for girls. Thus, globally, mothers tend to ascribe resemblance of children more to their fathers (exact binomial test, $p<.05$) and fathers tend to ascribe resemblance of children more to themselves, while this is not significant (exact binomial test, $p=.09$). Sample size and percentage of ascription of resemblance by mothers and fathers for each age class and each child sex are indicated (Table 4).

3.2. Differential resemblance between mother and father

After simplification, the minimum model that explain resemblance contained, in particular, interaction terms with the variable *child-sex* ($\chi^2=12.54$, $df=1$, $p<.001$). Therefore, we built separate models for each sex (Table 5). For boys, the minimum model contained an interaction between *test* and *child-age*^{2} ($\chi^2=29.11$, $df=1$, $p<.0001$), *test* and *child-age* ($\chi^2=32.35$, $df=1$, $p<.0001$). Thus, differential resemblance varies according to age, with boys resembling their mother more when newborn and then resembling their father more when between 1 and 5 years old (Fig. 2A). For girls, the minimum model contained the effect of *test* ($\chi^2=29.02$, $df=1$, $p<.001$) and *child-age* ($\chi^2=3.81$, $df=1$, $p=.051$). Girls resemble their mothers more than their fathers, at all ages considered (Fig. 2B).

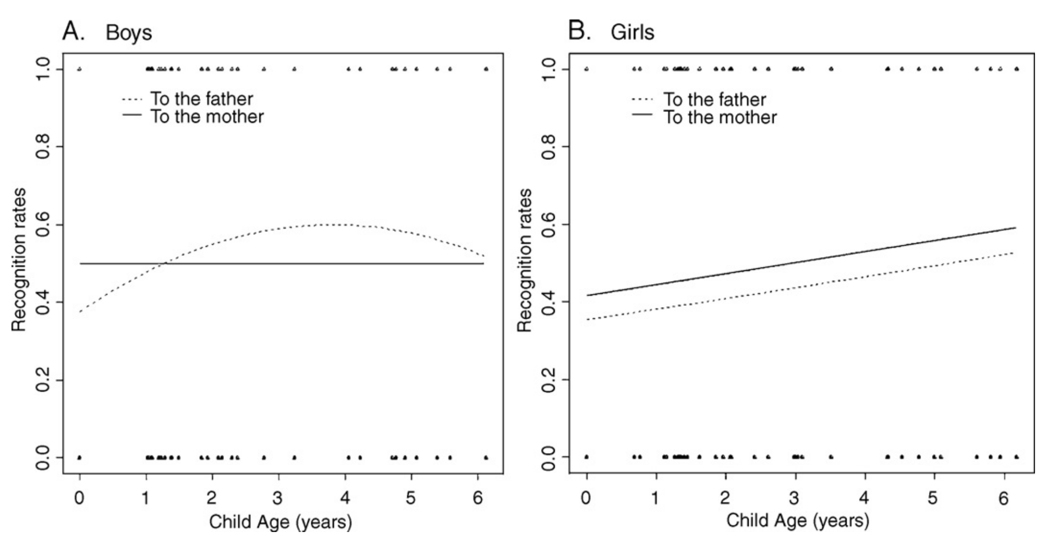

Fig. 2. Variation of differential facial resemblance for children according to their age (predicted values). (A) Boys. (B) Girls. No recognition (null hypothesis) is 0.33.

Table 6
Minimum models for ascribed resemblance

Dependent variable	Predictor variables	Estimate (S.E.)	p value
Mother-ascription	Intercept	−2.41 (0.95)	*
	Child-sex[a]	2.43 (1.13)	*
	Child-age	0.06 (0.03)	*
	Child-sex[a]:child-age	−0.09 (0.03)	**
Father-ascription	Null model		

As the data were paired (resemblance was ascribed either by the father or by the mother for the same child), separate analyses were carried out for each parent. For each analysis, predictor variables are indicated with their associated estimates, S.E.'s, and p value. ":" indicates an interaction effect between two variables.

[a] The variation of the effect of the second modality of *child-sex* (girls) compared to the first one (boys).

* p <.05.

** p <.01.

3.3. Ascribed resemblance

3.3.1. Ascribed resemblance by the mother

The minimum model contained the interaction between *child-age* and *child-sex* (χ^2=8.20, df=1, p<.01) (explained deviance, 13.2%; Table 6). Ascribed resemblance by the mother to either herself or to the father varied according to the age and sex of child. At birth and until 1 year of age, mothers ascribed resemblance of boys to their fathers, and after that age more to themselves. The opposite pattern was obtained for girls, although this was less accentuated at birth, with mothers ascribing an intermediate resemblance (Fig. 3). We then conducted analysis to investigate the effect of actual resemblance toward mothers (resemblance assessed by judges, *mother-resemblance*) on ascription of resemblance by the mothers. The minimum model contains the effect of the interaction between *child-age* and *child-sex* (χ^2=6.2, df=1, p<.05), and the effect of *mother-resemblance* is not significant (χ^2=2, df=1, p=.1). One can however note that the actual resemblance toward the mother tends to be higher on average for children whose mothers ascribed resemblance to fathers (56.8%) than for children whose mothers ascribed resemblance to themselves (47.8%).

3.3.2. Ascribed resemblance by the father

The minimum model was the null model. There was no significant relation between the ascribed resemblance by fathers and the age or sex of children. The father tended to ascribe resemblance to themselves (mean ascription=0.62), although this was only slightly significant (exact binomial test, p=.049).

4. Discussion

4.1. On the basis of faces, do children resemble their parents?

For both parents, the recognition rates are significantly higher than those expected by chance for children of all ages (0–6 years) considered in this study. Therefore, children in the present data set do resemble their parents, that is, they are phenotypically closer to their parents than to random men or women from the general population. This has not always been found in studies of Caucasian families. For example, Christenfeld and Hill (1995) concluded that "children, in general do not look enough like their parents for resemblance to be detected, with the one exception that one-year-olds look like their fathers." However, although this last finding could not be replicated, Brédart and French (1999) found a significant resemblance between both parents and children at 1, 3, and 5 years. Another study reported that newborns resemble their mothers more than would be expected by chance (Porter, Cernoch, & Balogh, 1984), although no data on fathers were presented. Therefore, the general absence of a parent–child resemblance in the Christenfeld and Hill study is probably due to methodological problems. For example, each father and mother was associated with the same two men and women for all the judges, with no randomization of the false parents, precluding any direct conclusion on the parent/child resemblance.

4.2. Do children resemble one parent more than the other?

In various species, including primates, paternity uncertainty has shaped several social and psychological traits (Alberts, 1999; Van Schaik & Paul, 1997). In humans, parental resemblance is culturally assessed from the child's face, suggesting that paternity confidence is manipulable (Daly & Wilson, 1982). It is possible that a differential facial resemblance between two parents and their child could have evolved and, thus, a child's face could resemble one parent more than the other. This was

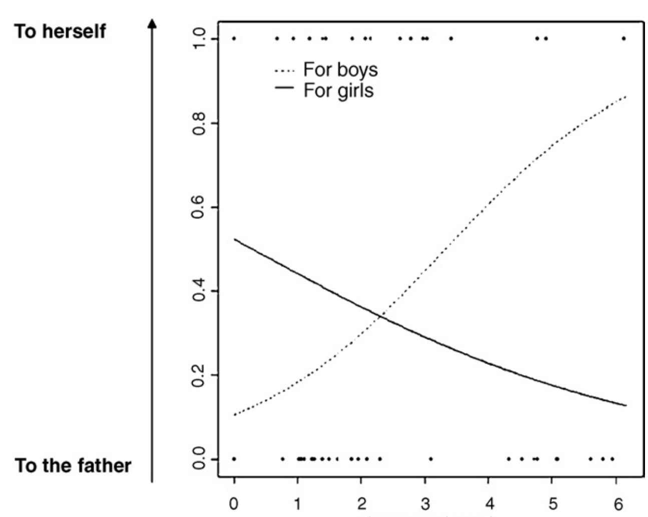

Fig. 3. Resemblance ascribed by mothers for both sexes according to age of the child. The y-axis is the ascribed resemblance by the mother (0 for 100% ascription to the father and 1 for 100% ascription to herself). The x-axis is the age of the child.

formally investigated in three theoretical studies, in which two opposite results were obtained: when extrapair affairs increased, the preferential expression of a paternal gene was either selected against (with differential resemblance evolving toward the mother), leading to paternal anonymity (Bressan, 2002; Pagel, 1997), or selected for (with differential resemblance evolving toward the father), leading to adaptive paternal signaling (Johnstone, 1997). Thus, no consensus emerged from those formal approaches, probably because of various assumptions about the members of family who benefit from kin recognition. Indeed, either the interest of children only is taken into account (Pagel, 1997), or the interest of two members (father and children, Johnstone, 1997) or three members (mother, father, and children, Bressan, 2002) are considered. Moreover, the signaler strategy is modeled either as a discrete variable (Bressan, 2002; Pagel, 1997) or as a continuous one (Johnstone, 1997). Therefore, those theoretical approaches are currently quite difficult to compare and efforts should continue to improve this.

Both newborn boys and girls appear to significantly resemble their mother more than their father (Fig. 2A and B). This is the second study to show a mother–child differential resemblance in newborns (McLain et al., 2000). Thus, newborns have a relative facial paternal anonymity, which is consistent with other inheritable phenotypic traits not generally expressed in young children, such as eye color (blue for Caucasian babies) and, to a lesser extent, hair color (Stoppard, 1989).

Genomic imprinting may be a proximal cause of differential resemblance, resulting in the differential expression of a gene according to its parental origin (Haig, 2000). Several "imprinted" genes have been located in humans (25 are known, with at least 200 possible candidates Falls, Pulford, Wylie, & Jirtle, 1999), and they are involved in regulating the growth of both the placenta and the fetus (Bartolomei & Tilghman, 1997), or are involved in brain development, adult behavior, and genetic diseases (Falls et al., 1999). These imprinted genes are thought to be due to an "arms race" within the genome because of conflicts over parental investment between the mother and father (Haig, 1997). This arms race would result in paternal alleles evolving to get more of the limited maternal resources, whereas maternal alleles would evolve to reduce the expression of the paternal ones. Due to the conflict between parents over the certainty of the relationship, facial features being a cue for estimating relatedness could be subject to genomic imprinting.

Alternatively, these results may be explained by facial dimorphism between males and females. Men's faces have more accentuated features (a prominent chin or nose, a stronger jaw, etc.) than women's faces. Therefore, these exaggerated features make a man's face appear less like the child's face than to a woman's face, leading to a stronger facial resemblance between a child and his or her mother than his or her father. Whether, and how, does this affect the probability of matching the true parent among other same-sex adults is an open question. The ageing process also exacerbates these exaggerated features (Burt & Perrett, 1995), and fathers are generally older than mothers. In the present data set, this difference is 3.9 years and may further reduce resemblance of the child to the father. In our study, this age difference effect is probably minimal, as the variables describing the age of the father, or the difference in age between parents, did not have enough explanatory power to be retained during model selection. However, the facial sexual dimorphism effect could not be discarded, although it probably has a limited effect, as shown by the observed pattern of variation in differential facial resemblance according to the age and sex of children.

4.3. Variation in differential resemblance depends on both the age and sex of children

Variation in resemblance according to age of children is not new, and was first proposed by Christenfeld and Hill (1995) who found that only 1-year-old children resemble their father and not their mother. However, their study had several methodological problems (Table 1). Our study has shown that at 1 year of age there is either no differential resemblance (for boys) or a biased resemblance toward mothers (for girls).

In the present study, differential facial resemblance varies according to both age and sex of children. In particular, the facial resemblance inverts for boys, but not for girls (Fig. 2A and B). The effect of the interaction between age and sex of children for preferential resemblance needs to be interpreted carefully, as the sample size is not sufficient for detecting small effects. Thus, the absence of an interaction effect between differential resemblance and age for girls should not be interpreted as definitive, whereas positive findings are likely to be strong. In any case, the interesting interaction effect between age and sex of children needs replication by further studies. Moreover, we are currently unable to explain this pattern clearly because a formal modeling of the situation has not been properly carried out, leaving only verbal arguments to explain this complex familial situation. Some limitations of the published models are mentioned above, and for the most elaborate model (Bressan, 2002; Johnstone, 1997), we can mention a discrete decision (rejection or acceptance of children) as a simplistic paternal investment strategy, with no cost for the production of a phenotypic paternal signal (Johnstone, 1997). Important variables, such as paternal investment and its variation with the age of children, should be measured precisely.

In some specific situations, such as the presence of a stepfather, children are particularly at risk between birth and 1 year of age (Daly, 1994). This suggests that very early in childhood the cost of discrimination is maximal, possibly explaining the relative paternal anonymity during the first year of life. In addition, between birth and 1 year of age, the mother's investment in child growth, through breast-feeding, strongly affects child fitness (van den Bogaard, van den Hoogen, Huygen, & van Weel, 1991). Although a mother is always certain of being related to the child, the levels of her investment can vary due to conflicts between the mother and child regarding investment, with optimal investment systematically differing (Trivers, 1974). Breast-feeding is documented in humans as a source of conflict (Fouts et al., 2005), an example being the duration of breast-feeding, which is involved in the neural, psychomotor, and cognitive development of children (Horwood, Darlow, & Mogridge, 2001; Vestergaard, Obel, Henriksen, Sorensen, & Skaiaa, 1999). Facial resemblance may therefore be a mechanism selected in newborns to manipulate investment from the mother. As a result, we would expect from birth until 1 year of age that the costs associated with revealing paternity are too high, thus selecting relative paternal anonymity, and/or that facial resemblance to the mother is linked to the extent of investment provided by her, thus selecting relative maternal resemblance.

The preferential facial resemblance of boys toward father, peaking between 2 and 3 years old, is intriguing. However, giving the small Age × Sexes groups, this new finding needs to be replicated by further studies before speculating about it. One can however note that, at this age, stepfather studies have suggested that the cost of discrimination is lower, perhaps leading to an evolutionary stable strategy of preferential signaling of paternal genes. Why this is restricted to boys requires further studies. It may be due to the higher investment required by boys than by girls (Mace, 1996; Trivers & Willard, 1973). For instance, it has been reported that sons are more physiologically demanding to produce than daughters (Hoffman, Stark, Lundin, & Ashbrook, 1974; Mace & Sear, 1997; Marsál et al., 1996), and that they have a detrimental effect on mother longevity (Helle, Lummaa, & Jokela, 2002). At the same time, males are characterized by a higher variance in their reproductive success (Bateman, 1948; Low, 2001). Thus, the combination of these two effects will increase the cost for fathers to make a mistake in the decision of either discrimination in cases of true paternity or investment in cases of nonpaternity. Other variables, such as paternal and maternal investment for various ages of both boys and girls, as well as probability of paternity need to be precisely measured to understand this better. Indeed, the probability of paternity is known to vary between 0% and 30% across human populations (Bellis, Hughes, Hughes, & Ashton, 2005) and could thus influence the results of the present study: in the first case (0%), there would be no mismatch, whereas in the second case (30%), a third of the fathers would be "wrong" implying that the actual biased resemblance toward the father would be stronger than observed. Also, the probability of paternity was found to vary between social classes in a rural society (Cerda-Flores, Barton, Marty-Gonzalez, Rivas, & Chakraborty, 1999), which may lead to a concomitant variation of paternal investment and thus of facial resemblance according to socioeconomic status. We found no effect of socioeconomic status in this study, although this may be due to upper-class families being overrepresented relatively to middle and lower classes (exact binomial test, $p = .01$), thus reducing the variance. However, it is not known whether the probability of paternity varies according to socioeconomic status in modern societies, and this requires further study.

4.4. Ascription of resemblance

At birth, facial resemblance of a child ascribed by mothers is clearly biased toward the father. This is consistent with previous studies on newborns (Daly & Wilson, 1982; McLain et al., 2000; Regalski, J., & Gaulin, S., 1993) and with the hypothesis that women evolved a psychological mechanism to comfort fathers in their paternity by claiming paternal resemblance. The evolution of this psychological mechanism in women that allows them to eliminate subtle signals of deceit is supported by the observed contradiction between what mothers claim about resemblance (biased toward fathers) and actual resemblance assessed by external judges (biased toward mothers), which has previously been shown for newborns (McLain et al., 2000). In this way, unfaithful mothers can avoid the costs of infidelity and faithful mothers can increase probability of fathers investing in children (Daly & Wilson, 1982; McLain et al., 2000; Regalski, J., & Gaulin, S., 1993). Given the divergent selection pressures on fathers and mothers due to paternity uncertainty, if mothers are expected to claim paternal resemblance of offspring, fathers are expected to be skeptical about these claims (Regalski, J., & Gaulin, S., 1993). Facial resemblance of newborns claimed by fathers have been found to be similar to that assessed by judges (McLain et al., 2000), showing that fathers ascribe actual resemblance. However, we did not observe this in our study, as fathers assigned resemblance of newborns to themselves in 83% of cases (observed values), being opposite to that assigned by nonrelated judges. We can identify several types of bias. First, fathers or mothers were always interviewed in the presence of the other parent, thus reducing the possible skepticism signal of fathers. Second, the sample size for newborns ($n = 21$) was small compared to other studies ($n = 190$, Regalski, J.M., & Gaulin, S.J.C., 1993). Nevertheless, although this result should be interpreted with care, we cannot exclude that the biased ascription of fathers toward themselves may account for the efficiency of mothers' psychological mechanism that misleads fathers about phenotypic resemblance. This could be investigated by comparing ascription of facial resemblance by fathers before and after the mother had answered.

If we consider all age classes (Fig. 3), from birth to 6 years old, ascription of facial resemblance by mothers is different for both sex and age of offspring. For boys, mothers ascribed facial resemblance increasing toward themselves as the age of the child increased, whereas actual resemblance was increasingly biased toward the father. By contrast, mothers increasingly ascribed facial resemblance of girls to fathers, whereas actual resemblance of girls was increasingly biased toward the mother. However, if mothers considered together tend to ascribe the opposite of reality, the same tendency found for individual mothers is not significant, which precludes any general conclusion. We believe that this study is the first to consider different ages in ascribing facial resemblance. Our observations are possibly a response to variation of paternal investment when considering the age and sex of children. However, the effect of the interaction between age and sex of children concerns a small sample size and the interpretation of this effect should be done carefully. A possible hypothesis is that the patterns of ascription are linked to the actual probability of paternity in a given population, with the expectation that the lower the probability of paternity is, the more the mothers will ascribe resemblance toward the fathers. Therefore, more data need to be collected to improve our understanding. Nevertheless, we suggest that if the level of investment of the father positively correlates with facial resemblance, ascribed resemblance by the mothers, which is globally opposite to actual resemblance, may be a mechanism for mothers to equalize the amount of investment obtained by all her children.

5. Conclusion

Facial appearance is a cue for genetic similarity as we found that children resemble both their parents more than other adults of the same sex. However, there is differential resemblance between the two parents, depending on age and sex of the child, suggesting that the facial phenotype may be biased in response to costs and benefits of paternal investment. We found that mothers claim a paternal resemblance at birth that does not correspond to the actual resemblance, suggesting possible manipulation of the perception of facial resemblance to increase confidence of paternity. The hypothesis that fathers use the facial phenotype of their children to assess paternity is well supported. It could be argued that fathers have not always used their own phenotype as a self-referent to evaluate relatedness because mirrors are a recent innovation. However, reflections in water as an indicator of a person's own phenotype is probably an old feature (e.g., the Greek legend of Narcissus) and fathers may use a "social mirror" (Burch & Gallup, 2000), such as the advice of external judges on facial resemblance, to be sure of their paternity. Interestingly, there is suggestive evidence that perception of resemblance generates the appropriate neural mechanisms that induce the appropriate adaptive paternal-investment behaviors (Platek et al., 2002, 2004, 2005). Thus, facial resemblance is an interesting way to study certain family conflicts over parental investment, particularly for paternity uncertainty.

Acknowledgments

We thank D. Caillaud, A. Courtiol, and E. Huchard for comments; the families from Montpellier, Hyères, and Grenoble participating in the study; P. Labbé for help in programming; A. Courtiol, M. Houzet, P. Callabro, E. Benfardjallah, E. Kerinec, N. Guyot, V. Metz, and Y. Diouf, for help in testing; J. David and D. Caillaud for statistical suggestions; V. Durand for bibliographic help; and two anonymous reviewers for their helpful comments. This study was supported financially by the ANR "BIOEVOLHUM" project (NT05-1_43865); contribution 2006.062 of the Institut des Sciences de l'Evolution de Montpellier (UMR CNRS 5554).

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