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Are parents' perceptions of offspring facial resemblance consistent with actual resemblance? Effects on parental investment

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Abstract

Human fathers face paternity uncertainty and are expected to use cues of relatedness to adjust their investment. So far, the main cue hypothesised to account for paternity assessment is facial phenotypic resemblance between a father and his child. However, previous studies showing a discriminative paternal investment either relied on fathers' perceptions of resemblance (which differs from actual resemblance, as perceived resemblance could be socially biased), or manipulated facial resemblance. In this study, we investigate in a real-life situation, whether (1) the perception of child facial resemblance and (2) the likelihood of parental investment were predicted by actual facial resemblance to self, for both parents. The actual facial resemblance of 79 French children was quantified by testing external judges. Data on ascription of resemblance and parental investment were collected in private for each parent. First, ascription of facial resemblance was found to be consistent between the two parents and to match actual resemblance to the father. Second, emotional closeness as reported by fathers, but not by mothers, was found to be predicted by actual facial resemblance to self. This suggests that paternity uncertainty has favored the use of facial phenotype matching in fathers.

Keywords: Human; Parental investment; Facial resemblance; Paternity uncertainty; Kin recognition; Ascription of resemblance

1. Introduction

In humans, the expression of paternal care influences survival or quality of offspring (e.g., Flouri & Buchanan, 2003, 2004; Hurtado & Hill, 1992; Sear & Mace, 2008). However, this important behaviour is costly for the father, particularly in terms of lost mating opportunities with other partners (Marlowe, 1999). In this context, evolutionary theory predicts that paternal investment will be conditional, based on the father's perception of paternity (Trivers, 1972). Cross-culturally, men invest more in their children in populations where paternity confidence is high (Gaulin & Schlegel, 1980). Furthermore, paternity confidence is not independent from actual paternity and men with low paternity confidence, voluntarily engaging in paternity testing, are more likely to discover non-paternity (median rate ~30.2%) than are men with high paternity confidence (median rate~1.9 %; Anderson, 2006). These results suggest that fathers should be able to use paternity cues to direct their parental investment. These cues may be indirect, for instance, using their perception of their mate's fidelity based on social cues (Flinn, 1988). Cues can also be more direct, using the phenotypic resemblance between himself and his offspring (phenotype matching: Hauber & Sherman, 2001; Lacy & Sherman, 1983). For instance, fathers may use perceived facial similarity with their children. Indeed, facial resemblance between individuals (assessed by unfamiliar judges) has been shown to be a good estimate of the probability that two individuals are close genetic relatives (Alvergne, Faurie, & Raymond, 2007; Alvergne, Faurie, & Raymond, 2009; DeBruine et al., 2009; Maloney & Dal Martello, 2006). If fathers do rely on facial phenotype matching to assess the likelihood that they are related to children, they are predicted both to perceive a socially unbiased (i.e., actual) level of child

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phenotypic resemblance to themselves, and to adjust their investment accordingly.

There is some evidence, in natural conditions, that fathers' perception of child facial resemblance predicts variation in paternal investment: when fathers who are no longer in a relationship with the mother of their children are asked about actual decisions of investment (how much they would invest on a 1-7 scale), perceived facial resemblance is a stronger predictor of investment than perceived fidelity (Apicella & Marlowe, 2004, 2007). If this is the case, however, one cannot rule out the alternative hypothesis that fathers' perception of their child's phenotype is socially influenced. For instance, in a study where children were aged 15 on average, fathers' perception of resemblance may have been modified by the long-term familiarity with the child's face (Apicella & Marlowe, 2004). Children may also come to resemble their fathers in traits other than static facial resemblance (including facial movements and expressions, voice, etc.) as a result of imitation mechanisms, which are at least partly independent of the biological status of the father. It is also likely that perception of resemblance by men is influenced by judgments from others. Indeed, men's own ratings of resemblance are highly correlated with what other people tell them, a phenomenon referred to as the "social mirror" effect (Burch & Gallup, 2000). Moreover, belief in genetic relatedness has been shown to increase perceived facial similarity between parents and children, and interestingly, this effect is more pronounced in men (Bressan & Dal Martello, 2002; Oda et al., 2005). In this context, the possibility that fathers' perception of facial similarities differs, at least partly, from actual resemblance is conceivable.

Assessing whether fathers' perception of a child's resemblance to self differ from actual resemblance due to social influence is pivotal, as others do not necessarily share the reproductive interests of the father. For instance, while fathers benefit from adjusting their investment according to their perception of paternity, mothers always benefit from obtaining the maximum amount of paternal care for their children, independent of the biological status of the father. Interestingly, mothers' ascription of facial resemblance is not based on actual resemblance when recorded in the presence of the father: although newborns resemble their mothers more than their fathers, mothers are more likely to ascribe their newborn's resemblance to the social father (Alvergne et al., 2007; McLain, Setters, Moulton, & Pratt, 2000). A mother's tendency to preferentially ascribe a resemblance to the father when the child actually resembles his or her mother more (as determined by testing external judges) has also been observed with older children (Alvergne et al., 2007). It has been argued that mothers thus manipulate the social father's perception of paternity in order to increase the likelihood of substantial paternal investment and, in some cases, to avoid the costs of revealing an infidelity (Daly & Wilson, 1982; Regalski & Gaulin, 1993). Interestingly, when fathers are questioned about their newborn children in the presence of the mother, they tend to ascribe a resemblance to themselves, contradicting their actual resemblance to the child at that age (Alvergne et al., 2007). In previous studies, however, ascription of child resemblance was recorded while both parents were present, thus not controlling for possible familial influence, and thus inhibiting a conclusion on their true perception of resemblance. It is indeed not known whether a similar pattern (i.e., ascription of resemblance by parents not being predicted by actual resemblance) is obtained when ascription is recorded separately for both parents (i.e., true perception). When removing the social pressure, ascription of resemblance may possibly be closer to actual phenotypic resemblance, although this must be investigated further.

The evolution of a mechanism allowing fathers to discriminate among their children on the basis of direct cues (phenotype matching) not only implies that fathers' perception of resemblance reflects actual probability of relatedness but also that paternal behaviour is modified according to actual likelihood of paternity (approximated using actual father-child resemblance). There is indirect evidence that variation in father-child actual resemblance predicts variation in paternal investment: when men are asked about hypothetical adoption preferences, they pay special attention to self-perceived cues of facial resemblance, while mothers emphasise cuteness and health (Volk & Quinsey, 2002; Volk, 2007). Similarly, some studies suggest that when men are asked about hypothetical decisions of investment, they favour children whose faces have been morphed to resemble their own, while mothers do not (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003). This result has, however, not been replicated in other studies manipulating facial resemblance, and either both men and women (DeBruine, 2004) or women only (Bressan, Bertamini, Nalli, & Zanutto, 2008) were found to adjust their hypothetical decisions of parental investment on the basis of self facial resemblance. Note that previous experimental studies used different stimuli (e.g., concerning the degree of facial resemblance between children and participants, the manipulation of facial pictures) and various questionnaires to assess paternal investment, which makes these contrasting results difficult to interpret. Nevertheless, the use of facial phenotype matching as a response to paternity uncertainty is supported by neurocognitive studies, showing that men and women differ in the neural substrates that are activated when they see children who resemble themselves; in men, the activated area is potentially involved in the inhibition of negative responses (Platek et al., 2004; Platek, Keenan, & Mohameds, 2005). The previous empirical studies are intriguing, although this question can be better answered by investigating real-life conditions (true families), using objective and quantitative measures of father-child phenotypic similarities. A recent study in a rural polygynous population suggests that father-child resemblance, either through the face or through the body odour, is positively related to paternal investment

(Alvergne et al., 2009). The generality of this finding in different reproductive systems should thus be tested, along with an important control, i.e., how does mother resemblance affect mothers' decisions of investment. Indeed, mothers, as compared to fathers, are not expected to use self facial resemblance to adjust their decisions of investment, since they do not have the problem of uncertainty of relatedness with their children.

In the present study, we quantified the actual facial resemblance of French children to both their fathers and their mothers using unrelated and unfamiliar judges. Data were collected from each parent separately and included ascription of resemblance as well as paternal and maternal investment. Making the assumption that father-child resemblance is a cue used by fathers to assess their paternity and adjust their investment accordingly, we predict that (1) ascription of resemblance in the absence of the other parent should match actual resemblance (2) paternal investment, but not maternal investment, should be positively linked to actual resemblance to self. Furthermore, in an attempt to investigate some possible benefits of father facial resemblance for children, the possibility of an influence of paternal investment on children's body mass index was explored.

2. Methods

2.1. Study population

Families were recruited in summer, 2006 from visitors to an exhibition (entitled "Birth") located in a museum ("Musée de l'Homme") in Paris. All participants were Caucasian. Only biological children were included in the sample. Thirty-seven families participated in the study (each having from 1 to 5 children), leading to a total sample of 79 children (39 boys and 40 girls) aged between 3 months and 22 years (mean±S.D.=6.6±5.1). The protocols used for recruitment and data collection have received the agreement of the French National Committee of Information and Liberty, and informed consent was obtained from all the subjects.

2.2. Questionnaires: parental investment and ascription of facial resemblance

Both parents were asked to report the age, sex and birth order of each child present during the interview and, if measured during the last 2 months, the child's height and weight. Although the validity of height and weight reported by parents has not been assessed in this study, self-reported and measured height and weight have previously been found to be highly correlated, suggesting that the present data are valid (Elgar et al., 2005). Each parent was then given a questionnaire and asked to provide answers without any oral communication with the other parent. There was no opportunity for one parent to look at the other's questionnaire; this procedure was controlled by A. A. Each parent was asked to give his or her birth date, monthly income (divided into nine classes from less than 760 euros to more than 3618 euros), number of children, and number of working hours per week. To assess parental investment, each parent was asked to report, for a non-working day, the number of hours spent with each child (focusing on the children present during the questionnaire). Additionally, for families of more than one child, each parent was asked to report the name of the child to whom he or she feels emotionally closest, among all the children. Then, each parent was asked to report whom each child present resembles the most (0: the mother; 1: the father, 2: other). Because of the low sample size for the category "other" (2% from fathers, 0% from mothers), only the categories "the mother" and "the father" were analysed. Body mass index (BMI) was calculated [weight/(height)^2 × 10 000] and then subtracted from the optimal BMI-by-age obtained from the French National Institute of Prevention and Education for Health (http://www.inpes.sante.fr/) to create a new variable describing deviation from optimal BMI. The variable describing the birth order of children contained two levels (first-born and later-born).

2.3. Quantification of facial resemblance between children and parents

Participants were photographed in a frontal view from a distance of approximately 1 m. All images were taken in the same location, using the same digital camera (Canon EOS 20D) with the same general settings. Participants were asked to look directly at the camera with a neutral expression. Glasses, if worn, were removed before photographs were taken. All photographs were processed using Adobe Photoshop 7 to normalise contrast and luminosity and to turn all backgrounds black.

To assess father-child facial similarities, we used the general procedure described in Alvergne et al. (2007). Resemblance was assessed by asking judges to identify the true parent among a set of three adults of the same sex. The other two adults presented in addition to the true parent were randomly selected among parents of children not tested by a given judge. For each child, the resemblance to the father and to the mother was evaluated independently by the same judges. The judges were volunteers recruited in public places in Montpellier, to prevent recognition of people in the photographs (taken in Paris). We recorded the judges' sex, age, number of children, and birth order. Judges were unaware of the purpose of the study when assessing resemblance. A computer program (written in Delphi, version 7) was used to randomise and to assist each part of the test. Each picture was seen by a given judge only once, except those displaying children (viewed twice: in the mothers' test and in the fathers' test). For each child, in a given test, the judge's recognition score was recorded as 0 for failure or 1 for success. The expected proportion of correct matches from all judges for one child varies between 1/3 (no resemblance) and 1 (perfect resemblance).

2.4. Statistical analysis

(a) Facial resemblance: to compare recognition rates to those expected by chance for each parent, a general linear mixed model (GLMM) was built to take into account the structure of the data (Crawley, 2007). The response variable (each judge's recognition score, for each child) was modelled as binary. The 95% CIs around the predicted value of the mean were then compared to the rate expected by chance. The variables characterising the judge and the child, as well as the type of test (resemblance to mother or father) and all the meaningful interactions, were entered in the model as fixed effects. The identities of the judges and children were fitted as cross random effects to take into account the fact that one judge assessed several children, and that one child was evaluated by several judges. Models were not reduced to avoid the number of false positives (Whittingham, Stephens, Bradbury, & Freckleton, 2006). Following Bates & Sarkar (2007), *p* values, and 95% CIs were calculated using a sample generated after 10,000 simulations from the posterior distribution of the parameters of the fitted model using Markov Chain Monte Carlo (MCMC) methods (P_{MCMC}).

(b) Parental ascription and actual facial resemblance: Parental ascription of resemblance was fitted as a binary response variable (resemblance to either the mother or the father) and mixed effects models were used to take into account the presence of several children per family. First, all variables describing father and child characteristics were entered into a model as fixed effects to control for potential sources of variation, but were not found to be significant predictors of either maternal or paternal ascription of resemblance. Secondly, a new model with a similar random effects structure was built and included the effects of interest, namely the actual resemblance towards the mother and actual resemblance towards the father, quantified as described in (a). This procedure was used to maximise, given the sample size, the available degrees of freedom when testing the significance of the effects of interest. Actual resemblance variables were both entered concomitantly in the same model to control for potential facial assortative mating between parents. At each step of the procedure, as in (a), models were not reduced to avoid the number of false positives (Whittingham et al., 2006), and the significance of the terms was determined using MCMC methods (Bates & Sarkar, 2007).

(c) Parental investment and facial resemblance: The investment of time spent with each child by either mother or father was fitted as a continuous response variable in a mixed effects model (GLMM taking into account the presence of siblings in the sample). The same procedure as described in (b) was used to investigate the effects of explanatory variables (actual resemblance towards each parent). Significance of terms was evaluated using *F* tests.

(d) Parental closeness and facial resemblance: Parental closeness, for each child, was fitted as a binary response variable (0: the closest, 1: not the closest). Binary mixed-effects models (GLMM taking into account the presence of siblings in the sample) were used, and two models were built, explaining either paternal closeness or maternal closeness. The same procedure as described in (b) was used and the significance of the terms was determined using MCMC methods.

(e) Deviation from optimal BMI and parental closeness: Body Mass Index was fitted as a continuous response variable, and a linear mixed effect model was used. The same procedure as described in (b) was used and the significance of terms was evaluated using *F* tests.

All statistical analyses were carried out with *R* software (R.2.4.1, 2006).

3. Results

3.1. Facial resemblance

A total of 359 judges (120 men; 239 women), 14–79 years old, performed the test of facial recognition. Each child was assessed by 45±12 judges (mean±SD). The detection rates of father-child pairs (0.44) and mother-child pairs (0.49) are significantly (P_{MCMC} <0.001) above the rate expected by chance (0.33). At a general level, the recognition score is not influenced by the type of test (i.e., resemblance to mother or father) (P_{MCMC}=0.54) or by the sex of the judge (P_{MCMC}=0.21). It is also not associated with the judge's number of children (P_{MCMC}=0.39), the judge's birth order (P_{MCMC}=0.27) or the child's sex (P_{MCMC}=0.69). However, recognition scores decreased as the judge's age increased (P_{MCMC} <0.01). Scores also increased with the age of the children, although this effect was marginally significant (P_{MCMC}=0.08). Finally, the interaction between the type of test (resemblance to mother or father) and the sex of the child was not significant (P_{MCMC}=0.63), nor was the interaction between the sex of the judge and the sex of the child (P_{MCMC}=0.84). However, the recognition rate of women judges was higher than that of men judges when they assessed a child's resemblance to the mother (predicted means are 0.50 for women judges and 0.46 for men judges; P_{MCMC}=0.02). Using the recognition scores obtained from all judges, the mean levels of paternal and maternal resemblance were attributed to each child. For a given child, the levels of paternal and maternal resemblance were positively and significantly correlated (Kendall correlation: τ=0.12 p=.05).

3.2. Ascription and facial resemblance

Mothers and fathers were consistent in their ascription of facial resemblance [Pearson's Chi-squared test of independence with Yates' continuity correction χ^2=18, df=1, p<.001; Phi coefficient (the degree of association between two binary variables) φ=0.59]. Ascription of children's resemblance by the father (to either the mother or himself) did not vary with the child's age (P_{MCMC}=0.87), the child's sex (P_{MCMC}=0.79), the interaction between sex and age (P_{MCMC}=0.68), the child's birth order (P_{MCMC}=0.50), the father's age (P_{MCMC}=0.40), or the father's income (P_{MCMC}=0.98). It was significantly predicted by the level of paternal resemblance as perceived by the judges (P_{MCMC}=0.02), but not by the level of maternal resemblance (P_{MCMC}=0.86). Similarly, maternal ascription of resemblance (to either herself or the father) did not vary with the child's age (P_{MCMC}=0.21), the child's sex (P_{MCMC}=0.14), the interaction between sex and age (P_{MCMC}=0.16), the child's birth order (P_{MCMC}=0.58), the mother's age (P_{MCMC}=0.97), or the mother's income (P_{MCMC}=0.20). It was marginally predicted by the level of paternal resemblance as perceived by the judges (P_{MCMC}=0.06), but not by the level of maternal resemblance (P_{MCMC}=0.27) (Table 1; Fig. 1). Ascription of facial resemblance, either by the mother or by the father, was predicted by actual facial resemblance to the father as assessed by independent judges. However, it was not predicted by facial resemblance to the mother.

3.3. Paternal care and facial resemblance to the father

3.3.1. Time spent with each child on a week-end day

In the first model, paternal investment in time spent with the child was negatively linked to the father's age ($F_{1,35}$=5.71, p=.02), while it was positively correlated to maternal time investment ($F_{1,22}$=19.45, p<.001). However, neither the father's income ($F_{1,35}$=2.75, p=.10), number of children ($F_{1,35}$=0.57, p=.45), number of working hours ($F_{1,35}$=2.95, p<.09), the child's age ($F_{1,22}$=1.38, p=.25), sex ($F_{1,22}$=0.49, p=.49) nor birth order ($F_{1,22}$=0.56, p=.45) predicted the time that fathers report spending with their children. In the second model controlling for significant effects (i.e., father's age and maternal time investment) and for facial resemblance to the mother, facial resemblance to the father did not predict variations in paternal time investment ($F_{1,23}$=1.77, p=.19) (Table 2).

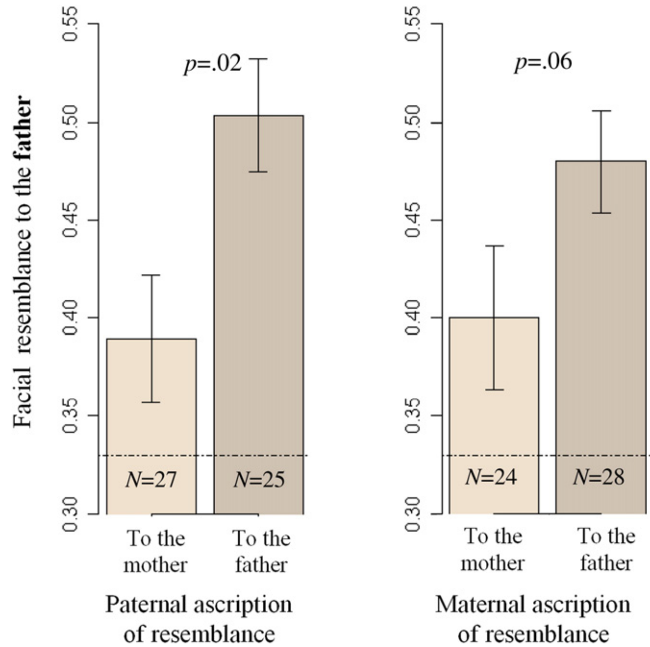

Fig. 1. Ascription of resemblance by parents and level of facial resemblance to the father as detected by external judges. (A) Paternal ascription. (B) Maternal ascription. Sample sizes and error bars (standard errors of the mean) are indicated. The dashed line indicates the rate of parent-child pair detection expected by chance (0.33). Both parents preferentially ascribe their child's resemblance to the father when the child actually expresses a high level of facial resemblance to the father.

3.3.2. Closeness

In the first model, emotional closeness between father and child, as reported by fathers, was negatively related to

Table 1
Final models explaining ascriptions of resemblance (binary variable: 0 = to the mother; 1 = to the father) by either mother (maternal ascription) or father (paternal ascription) as a function of actual facial resemblance assessed by external judges (explanatory variables)

	Estimate	Lower 95% CI	Upper 95% CI	P_{MCMC}
Paternal Ascription				
Intercept	−1.7353	−3.7143	0.0228	
Resemblance to father	3.7220	0.7835	7.2415	<0.05
Resemblance to mother	0.2351	−3.0266	2.6346	0.87
Maternal ascription				
Intercept	−0.2241	−2.0051	1.5461	
Resemblance to father	2.8890	0.3043	6.589	0.06
Resemblance to mother	−1.7539	−4.790	0.7970	0.20

Estimates and 95% CIs are indicated.

Table 2
Final models explaining either paternal or maternal time investment as a function of paternal and maternal resemblance

	Estimate	S.E.	t value	Pr (>|t|)
Paternal investment of time				
Intercept	11.81	4.35	2.71	
Maternal investment of time	0.46	0.09	5.14	<0.001
Father's age	−0.14	0.10	−1.44	0.16
Resemblance to father	−1.36	1.18	−1.15	0.26
Resemblance to mother	−1.73	1.49	−1.15	0.26
Maternal investment of time				
Intercept	2.19	2.13	1.03	
Child's age	−0.21	0.03	−6.56	<.001
Child's birth order	−0.56	0.23	−2.40	0.06
Paternal investment of time	0.51	0.08	6.16	<.001
Resemblance to father	0.89	0.68	1.34	0.20
Resemblance to mother	−0.90	0.84	−1.06	0.30

closeness between mother and child, as reported by mothers (P_{MCMC}=0.03). Then, father-child closeness was not explained by the child's age (P_{MCMC}=0.80), the child's sex (P_{MCMC}=0.30), the father's age (P_{MCMC}=0.08), or the father's income (P_{MCMC}=0.59). In the second model controlling for previously significant effects (i.e., maternal closeness) and facial resemblance to the mother, facial resemblance to the father predicted variations in closeness (P_{MCMC}=0.04). Levels of emotional closeness were higher for children who resemble their fathers the most (Table 3; Fig. 2).

3.4. Maternal care and facial resemblance to the mother

3.4.1. Time

In the first model, maternal time investment was positively linked with paternal time investment ($F_{1,17}$=20.00, p<.001) and negatively correlated with the child's age ($F_{1,17}$=25.60, p<.001). Moreover, maternal investment of time was lower for later-born than for first-born children ($F_{1,17=}$4.53, p=.05). However, it was not correlated to the child's sex ($F_{1,17}$=0.09, p=.77), the mother's age ($F_{1,21}$=0.60, p=.44), the mother's income ($F_{1,21}$=1.60, p=.21), the number of children ($F_{1,21}$=0.00, p=.99) or the mother's number of working hours ($F_{1,21}$=2.23, p=.15). In the second model controlling for significant effects (paternal time investment, child's age and birth-order category) and resemblance to the father ($F_{1,21}$=1.69, p=.20), resemblance to the mother did not predict maternal time investment ($F_{1,21}$=1.12, p=.30) (Table 2).

3.4.2. Closeness

In the first model, emotional closeness between mother and child, as reported by mothers, was not linked to either the child's age (P_{MCMC}=0.10) or the child's sex (P_{MCMC}=0.12), but it was negatively correlated with paternal closeness (P_{MCMC}=0.04). In the second model controlling for this effect and for resemblance to the father (P_{MCMC}=0.59), facial resemblance to the mother did not predict variations in maternal closeness (P_{MCMC}=0.46) (Table 3).

Table 3
Final mixed models explaining either paternal or maternal emotional closeness (binary variables) as a function of both paternal and maternal facial resemblance

	Estimate	Lower 95% CI	Upper 95% CI	P_{MCMC}
Paternal closeness				
Intercept	−9.9912	−37.9548	−5.9227	
Resemblance to father	14.946	12.7194	46.4272	**<0.05**
Resemblance to mother	7.9015	−3.5108	48.8652	0.41
Maternal closeness	−5.2649	−20.4944	−4.7508	0.14
Maternal closeness				
Intercept	−1.4675	−8.0095	1.7202	
Resemblance to father	2.1431	−7.992	10.3231	0.60
Resemblance to mother	2.1621	−3.5013	8.7846	0.47
Paternal closeness	−3.1514	−8.3980	−0.0611	0.08

95% CI and p values and are indicated.

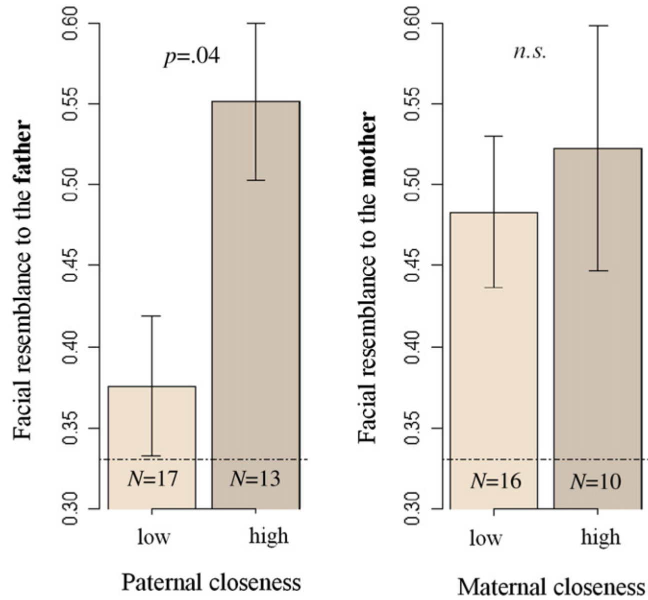

Fig. 2. Parental emotional closeness and facial resemblance of children. (A) Paternal closeness and resemblance to the father. (B) Maternal closeness and resemblance to the mother. Sample sizes and error bars (standard errors of the mean) are indicated. The dashed line indicates the rate of parent-child pair detection expected by chance (0.33). "High" closeness means that the child is the parent's preferred child among his/her offspring, and "low" closeness means that the child is not the parent's preferred child. Facial resemblance to the father, as assessed by external judges, predicts paternal closeness while facial resemblance to the mother is not related to maternal closeness. *n.s.*, nonsignificant (p>.05).

3.5. Child physical condition and parental closeness

In the first model, deviations from optimal BMI are not predicted by either the father's income ($F_{1,23}$=2.23, p=.14), the mother's income ($F_{1,23}$=01.07, p=.31), the child's age ($F_{1,11}$=1.20, p=.30), the child sex ($F_{1,11}$=0.24, p=.63) or the interaction between age and sex ($F_{1,11}$=1.21, p=.29). In the second model testing the effects of interest, the deviation from the optimal BMI was not found to be predicted by parental closeness, whether it is reported by the father ($F_{1,7}$=2.64, p=.15) or the mother ($F_{1,7}$=0.14, p=.71).

4. Discussion

4.1. Ascription of resemblance and true resemblance

As actual facial similarities between father and child are predicted to influence paternal investment, a father's perception of resemblance is expected to match actual resemblance, unless there is some manipulation by the mother.

Interestingly, both parents are consistent in their ascription of resemblance, whatever the child's age or sex. This result is in accordance with previous studies on newborns wherein the ascription of resemblance was made, as in the present study, independently by both parents (McLain et al., 2000). Indeed, a contradiction between the mother's ascription of resemblance towards the father and actual resemblance to the father was only observed when the mother's ascription was made in the presence of the father (Alvergne et al., 2007; McLain et al., 2000). Therefore, the hypothesis that mothers ascribe the resemblance of their children to the father to promote assurance of paternity was not disproven by the present study, in which parents ascribed resemblance separately.

Our study shows that, when the ascription of one parent cannot be heard by the other, actual paternal resemblance is a better predictor of both parents' ascriptions than actual maternal resemblance. In other words, the more a child resembles his/her father, the more the parents are likely to state that he/she is more similar to the father than to the mother. On the opposite, when the child's resemblance to his/her father is weak, parents tend to state that he/she resembles the mother the most. It is therefore the expression of paternal traits that plays the largest role in determining how both parents (separately) perceive global phenotypic similarity. These results indicate that father-child phenotypic similarities are of particular concern for both parents, while mother-child similarities are less important. They suggest that paternity uncertainty has acted as a selection pressure favouring a bias in the detection of facial similarities towards better detecting similarities with the father.

4.2. Child resemblance and parental investment

Different selective pressures act on maternal and paternal investment as a result of paternity uncertainty: fathers are expected to be sensitive to paternity cues and to preferentially direct their investment towards genetically related children, while mothers' strategies of investment are predicted to be insensitive to such cues. In this study, we investigated whether time investment and emotional closeness to the child were predicted by the level of facial resemblance to self, for both parents.

We first found that fathers are more likely to feel the highest emotional proximity to a child expressing a higher degree of resemblance to self. Such a link was not observed for mothers, a result which was expected since phenotype matching is not associated with reproductive benefits from a mother's point of view (i.e., mothers do not face the problem of uncertainty of relatedness). These results are thus consistent with the view that paternity uncertainty has acted as a selective pressure on fathers favouring the use of direct phenotypic cues (e.g., father-child facial similarities) to assess their probability of paternity, and subsequently adjust their resource allocation among their children. The observed link between father-child resemblance and paternal emotional closeness could also be interpreted in the opposite direction, i.e., as a result of an influence of paternal closeness on resemblance. This may occur through the process of imitation of facial expressions, which could increase when father-child interactions are more frequent. Such a mechanism is, however, unlikely to explain our results, as facial resemblance was assessed on neutral, static facial images. Rather, our findings provide the first evidence in western settings and in real families that paternal investment is discriminative on the basis of actual facial resemblance (see Alvergne et al., 2009 for a similar finding in a non-western polygynous population).

Secondly, we found that time investment, another proxy of parental investment, was not related to facial resemblance for mothers or fathers. It could be that time investment as reported by parents does not reflect actual individual investment. Indeed, paternal and maternal time investments are positively correlated, suggesting that this measure reflects more the time spent "in family" than the time spent by each parent with each child. It is also possible that parents try (ideally or in reality) to provide equal time to each child, independently of the emotional closeness that they feel. Indeed, emotional closeness does not predict variation in time investment for the father [analysis of variance (ANOVA), $F_{1,33}$=0.08, p=.77] or the mother (ANOVA, $F_{1,32}$=0.17, 32, p=.68).

Previous studies on discriminative paternal investment relied only on fathers' perceptions of resemblance (Apicella & Marlowe, 2004, 2007), which is potentially influenced by social manipulation or self-deception in real life interactions (Bressan & Dal Martello, 2002; Daly & Wilson, 1982). Conversely, experimental studies based on photographic morphing excluded any social manipulation of the perception of resemblance, potentially restricting the application of their results to real familial situations (Platek et al., 2002, 2003, 2004). However, an obvious limitation of the present study is the use of reports by fathers for measures of paternal investment (both time spent with the child and emotional closeness). Social desirability or social norms may thus introduce a bias directed toward increasing the quantity of reported investment and reducing the reported inequality among children. However, this potential bias cannot account for the significant associations between reported paternal closeness and actual paternal resemblance, as assessed by external judges.

Another potential concern is whether or not the judges' estimates of similarity can be treated as comparable to the fathers' estimates. More than half (66%) of the judges were parents themselves. Additionally, when men are confronted with self-facial resemblance tasks, activation of specific regions of the brain involved in such tasks is observed even in non-fathers, suggesting that sensitivity to facial resemblance is already present men, regardless of whether they are fathers or not (Platek et al., 2004, 2005). However, if external judges are nonetheless inferior detectors relative to true fathers, using such judges to assess resemblance makes these results conservative. One remaining question is the means by which fathers become aware of their own facial phenotypes, as mirrors are a recent innovation in human societies. It is possible that a water reflection of the face is sufficient for such learning. It is also possible that fathers rely on what other kin tell them about actual resemblance ("social mirror" Burch & Gallup, 2000) or that they use the phenotype of unambiguous relatives as "kin templates" (Hauber & Sherman, 2001).

4.3. Paternal closeness and children's physical condition

For a child, facial resemblance to his or her father strengthens paternal investment, at least as estimated by emotional closeness that the father feels towards the child. Does this translate into a better physical condition for the child? We used the deviation from the optimum body mass index by age as an indicator of a child's physical condition and found no significant results. Additionally, the time invested in a child by the mother or the father also does not predict variations in the child's physical condition. It is possible that, in industrialised societies, mothers can compensate for a loss of paternal investment as they have independent access to food resources (95% of women in our sample are working), thus buffering some aspects of the effect of paternal investment on child condition. Interestingly, we found that maternal closeness was negatively correlated with paternal closeness, suggesting that mothers compensate for decreases in paternal investment. This agrees with parental-investment theory for biparental species, which generally predicts an inverse relationship between the level of parental care provided by each parent and compensation by one parent in response to reduced parental care by the other (Trivers, 1972). There is now some evidence that such a mechanism has evolved in birds (reviewed in Sanz et al., 2001). However, to our knowledge, the occurrence of maternal compensation has not been documented in humans and deserves further study. Indeed, maternal compensation may explain how costs associated with a low paternal closeness could be reduced. Most importantly, the absence of a link between paternal investment and deviation from optimum BMI could also result from a limited impact of paternal investment on child growth in industrialised societies. In such societies, as alimentary resources are generally not a common limiting factor, it is likely that parental investment is not a crucial factor in children's ability to attain an optimal BMI. A similar study, conducted in rural Senegal where access to nutritional resources is limited, showed a significant impact of father investment on both BMI and another measure of child nutritional status (Alvergne et al., 2009).

Fathers, however, are still likely to play a role in other aspects of child development in industrialised societies. It is worth noting that the absence of a father is associated with changes in children's social and reproductive development (Alvergne, Faurie & Raymond, 2008; Ellis, 2003; Pfiffner, McBurnett, & Rathouz, 2001). The level of paternal involvement predicts educational achievement (Flouri & Buchanan, 2004), mental health in later life (Flouri & Buchanan, 2003) and the level of respect for social norms (Flouri & Buchanan, 2002). Therefore, through both their presence and involvement, fathers have an important impact on several aspects of child development. The effect of facial resemblance to the father on such traits, particularly on social traits, remains to be investigated.

4.4. Conclusion

Overall, this study indicates that the perception of paternity by fathers, through father-child similarities, is consistent with actual resemblance. Furthermore, phenotypic similarities influence paternal emotional closeness, but not maternal closeness. These results support the hypothesis that paternity uncertainty has favoured the evolution of paternal recognition mechanisms through phenotype matching in humans. In turn, this implies that resemblance to the father should be advantageous for children. This intriguing possibility, though not confirmed for one physical measure (BMI), deserves further studies, particularly on traits that are susceptible to substantial influence by the father in a given society.

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