

# Human ability to detect kinship in strangers' faces: effects of the degree of relatedness

Gwenaël Kaminski<sup>1,2,\*</sup>, Slimane Dridi<sup>1</sup>, Christian Graff<sup>1</sup>  
and Edouard Gentaz<sup>2</sup>

<sup>1</sup>Centre de Biologie du Comportement, and <sup>2</sup>LPNC, CNRS, UMR 5105, Grenoble University 38040, Grenoble, France

The resemblance between human faces has been shown to be a possible cue in recognizing the relatedness between parents and children, and more recently, between siblings. However, the general inclusive fitness theory proposes that kin-selective behaviours are also relevant to more distant relatives, which requires the detection of larger kinship bonds. We conducted an experiment to explore the use of facial clues by 'strangers', i.e. evaluators from a different family, to associate humans of varying degrees of relatedness. We hypothesized that the visual capacity to detect relatedness should be weaker with lower degrees of relatedness. We showed that human adults are capable of (although not very efficient at) assessing the relatedness of unrelated individuals from photographs and that visible facial cues vary according to the degree of relatedness. This sensitivity exists even for kin pair members that are more than a generation apart and have never lived together. Collectively, our findings are in agreement with emerging knowledge on the role played by facial resemblance as a kinship cue. But we have progressed further to show how the capacity to distinguish between related and non-related pairs applies to situations relevant to indirect fitness.

**Keywords:** phenotypic matching; facial cues; kin recognition; indirect fitness

## 1. INTRODUCTION

In human fitness, the predominance of social components in the environment has selected abilities to infer conspecifics' intentions (Cosmides & Tooby 1992). Because social drive is strongly dependent on kinship, it is reasonable to infer that some ability to detect kin among strangers has developed in our species, in addition to the general ability to recognize one's own kin, which is shared with other animals (see Waldman 1988 for a review). Indeed, altruistic behaviour towards kin increases an individual's indirect fitness (Hamilton 1964) on the one hand, and excluding kin from mate selection avoids the negative effects of inbreeding (Charlesworth & Charlesworth 1987) on the other. Hence, kin discrimination is an important mechanism in maximizing inclusive fitness.

Human socioecology and population biology of hunter-gatherer societies suggest that our ancestors have been subject both to nepotism and inbreeding depression. Modern humans provide more assistance to kin than to non-kin and are more inclined to help close kin than more distant kin (Essock-Vitale & McGuire 1985; Burnstein *et al.* 1994; Kruger 2003; Lahdenpera *et al.* 2004; Laham *et al.* 2005; Michalski & Shackelford 2005; Jeon & Buss 2007; Stewart-Williams 2007). Moreover, consanguineous unions have a possible adverse effect on fertility through an increased rate of miscarriage, infant mortality and morbidity (Khoury *et al.* 1987; Ober *et al.* 1999, but see Helgason *et al.*'s 2008 study that examined the relationship between fertility and distant relatives).

The specific behaviours observed in these studies implicitly demonstrate the existence of kin recognition in humans, but its mechanisms (see Lieberman *et al.* 2007 for a recent theoretical model and Lieberman *et al.* 2008 for a functional framework) remain poorly documented. In general, kin recognition depends on the perception of specific phenotypic traits (made up of relevant cues). Cues may be mediated by any of the usual sensory modalities (i.e. vision, hearing, olfaction and touch) used in communication (Wells 1987; Porter 1991) and by kin terminology specific to human language (Jones 2003). In this regard, humans can recognize kin by learning through association with co-residents (family members often live together). In this way, childhood association serves as a relevant kinship cue (Lieberman *et al.* 2003, 2007; Fessler & Navarrete 2004) that regulates the development of sexual aversion (namely, the Westermarck effect). However, humans can also recognize kin directly by 'phenotypic matching'. This mechanism operates by comparing the phenotype (implicit evaluation) of potential social partners with mental representations of self or template kin members and by using the resulting information to make a decision (Sherman *et al.* 1997). The phenotypic matching and association mechanisms are not mutually exclusive.

People unquestionably pay attention to familial resemblance in appearance, making facial cues a likely candidate for phenotypic matching (DeBruine *et al.* 2008). Humans can both categorize their conspecifics by their faces (especially those of the same gender, age or ethnicity) and discriminate among kinship relationships via facial phenotype. The discrimination of relatedness is performed through an assessment of facial similarities between individuals, and humans correctly associate siblings with one another (Maloney & Dal Martello 2006;

\* Author for correspondence (gwenael.kaminski@upmf-grenoble.fr).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0677> or via <http://rspb.royalsocietypublishing.org>.

DeBruine *et al.* 2009), as well as parents with their offspring (Nesse *et al.* 1990; Christenfeld & Hill 1995; Brédart & French 1999; McLain *et al.* 2000; Bressan & Dal Martello 2002; Bressan & Grassi 2004; Oda *et al.* 2005; Alvergne *et al.* 2007). What are the advantages for individuals who can discriminate between people who are related to each other and those who are not? One can suggest two potential advantages to explain this ability. A primary interest, of course, is favouring discrimination in direct fitness (breeding behaviour, i.e. mate choice and parental care) and in indirect fitness (altruistic behaviour). In this way, it could reflect a by-product of the ability to recognize his or her own kin in the context of kin selection theories. In humans, facial resemblance exerts a positive effect on paternal investment (Burch & Gallup 2000) and cooperation (DeBruine 2002; Platak & Thompson 2007). Sexual attractiveness is also affected by self-resemblance and is strongly dependent on evaluator context (gender, hormonal state) (DeBruine 2004, 2005). A second possibility is that discrimination in kin relationships between other individuals, especially members of another group, is adaptive, as it may orient social behaviour. If strangers interact differently according to their degree of relatedness, it can be beneficial to know who is related to whom in order to better adapt one's behaviour. Being able to better predict other individuals' behaviour by knowing not only their needs, expectations, beliefs (theory of mind principle), but also their kinship relations can help to resolve or avoid problems and even modify one's behaviour. Anticipating hostile alliances, enlisting aid, pacifying conflicts among kin, forming coalitions, punishing people, obtaining sexual favours... or even trying to flatter someone may be indirectly achieved by addressing a related individual.

Are visible facial cues limited to parents and siblings, or can they support inclusive fitness extended to other kin? There have been no studies on the role that visible facial cues play as a kinship signature for distant relatives ( $r < 0.5$ ), although attention has been paid to kin selection in distant relatives such as grandparents (Michalski & Shackelford 2005; Pollet *et al.* 2007), aunts/uncles (Gaulin *et al.* 1997) and cousins (Jeon & Buss 2007; Stewart-Williams 2007). We hypothesize that humans can use facial resemblance as a cue of relatedness to discriminate between kin and non-kin individuals, which facilitates kin selection. We conducted a study that explored the use of facial cues among individuals with different degrees of relatedness (close and distant relatives). One relevant objective was to investigate whether human adults possess perceptual abilities enabling them to discriminate between kin and non-kin. The second question is how potential distinct facial cues among related individuals fluctuate with the degree of kinship, and possibly with gender. An intuitive reading of inclusive fitness theory might suggest that an evaluator can competently discriminate among kin and non-kin and that facial cues should be weaker—but still exist—between two individuals related at a lower kinship degree.

## 2. MATERIAL AND METHODS

### (a) *Participants*

Fifty-nine undergraduate students from Grenoble University (54 women) participated in the study. The mean age of

participants was 21.6 years ( $\pm$ s.d. 3.3; range = 18–35). The students obtained partial credit in an introductory psychology course. The study was performed in accordance with the Declaration of Helsinki: it was conducted with the understanding and the written consent of each participant and was approved by local ethics boards (CNRS and Grenoble University).

### (b) *Database and stimuli*

The facial database includes 544 pictures of 219 Caucasian individuals belonging to 32 different families. For each individual, we have an average of 2.4 images ( $\pm$ s.d. 1.7; range = 1–10). The photos were gathered with the assistance of 32 students (out of 19 500 students attending the university), who were unknown to the participants and who brought us family photos of themselves, their siblings, parents and, ideally, of their grandparents, aunts/uncles and cousins. There was an average of seven individuals ( $\pm$ s.d. 3.5; range = 3–18) per family (ESM 1, electronic supplementary material). We told the 32 students that our study bore on cranial structure, but we did not tell them about other determinants of facial features visible on the pictures they provided. We also neglected to tell them how the features would be studied, though they knew the study was on psychology and kinship and gave consent for the anonymous use of their family pictures. We took these steps in order to avoid sampling bias (but a complete explanation of the present study was given after the experiment ended). Only high-quality photos with clearly visible frontal facial features were scanned. Full-face images, from chin to hair and including ears, were cut out in their entirety from the background scene. Pixel samples from participants' hair and skin were taken for colour evaluation, and the average luminosity of each cut-out face was calculated. The positions of the two inner corners of the eyes and the tip of the nose were recorded in order to estimate facial rotation and orientation. The geometric centre of the image was computed from the pixels' coordinates. The image was then rotated around this centre point so that the two corners of the eyes were horizontal. The image areas and luminosity were equalized, and the faces were pasted on a uniform grey background centred with reference to the centre of each face.

To construct the stimuli, two photos were placed side by side to make an image measuring 1160 by 580 pixels. We ended up with a stimulus set of 118 black-and-white image pairs, of which half showed two related individuals and half showed two unrelated individuals matched for age (ESM 2, electronic supplementary material). Our stimulus set was then further randomly divided into two sets of 60 and 58 stimuli (sets A and B, respectively). In order to keep the experiment from lasting more than 20 min, each participant saw only one set (there were 29 judges for set A and 30 for set B). Thus, the two experiment sets are duplications of each other. When we constructed the stimuli, double-blind photo matching was performed in two steps to avoid selection bias. First, each pair was selected solely on the basis of an anonymous code (i.e. without the experimenter seeing any photos) according to the degree of relatedness and the gender of the individuals who make up the pair. Second, because each individual's face might appear in several photos in the database, the photo of one individual making up a pair was randomly selected by one experimenter, and the second was independently and randomly selected by

the other experimenter. We were thus able to construct six different pair categories (ESM 2, electronic supplementary material) according to the degree of relatedness (the same individual was labelled 'Id', siblings were labelled 'Sb', grandparents/grandchildren 'Gp-child', aunt-uncle/nephews 'AU-child', cousins 'Cs' and the sixth category was made up of unrelated individuals). Control subsets were matched by pair-member genders (FF, FM, MM). The same individual appeared in both photos of Id pairs, but each individual only appeared once per set. Thus, we presented no individual more than once to each participant (ESM 2 and ESM 3, electronic supplementary material). Thus, for each of the five categories of relatedness degree, there was a corresponding control category of unrelated pairs (same age, same gender).

### (c) Procedure

During the experiment, the participant was seated alone in a quiet room in front of a computer screen. Random series of stimuli appeared on the screen, using E-PRIME (v. 1.1 SP3; Psychology Software Tools, Pittsburgh, PA, USA). The participant's task was to judge whether or not the two individuals shown in the stimulus belonged to the same biological family. Response time for each stimulus was limited to 20 s, in accordance with Oda *et al.* (2005). The response was typed on a computer keyboard. If the judge responded before the 20 s elapsed, the stimulus displayed on the screen disappeared and was replaced by the following one. If the participant did not respond within 20 s, the stimulus was automatically replaced by the following one. Before each stimulus, a fixation point appeared in the centre of the screen for 1 s to attract the participant's attention. The participant started by looking at 10 training stimuli and was given visual feedback on the accuracy of his/her responses. During the training exercise, 5 of the 10 stimuli showed related individuals of varying degrees of kinship and the other five showed unrelated individuals. Then the experimental phase (set A or set B), during which there was no feedback, began. During this phase, half of the stimuli were of related individuals, while the other half were of unrelated individuals. For each stimulus, we recorded both response time and accuracy.

### (d) Statistical analysis

#### (i) Kin versus non-kin

Our task was analogous to a signal-detection problem (Green & Swets 1966). The participant was required to detect random signals (related individuals) embedded in background noise (unrelated individuals). This arrangement enabled search performance to be assessed in terms of detectability and bias measures. Signal-detection estimates of sensitivity  $d'$  and  $A'$ , as well as likelihood criteria  $C$  and  $B'_d$ , were used to find out if participants were able to differentiate between kin and non-kin individuals. In our experiment, the signal (whether absent or present) was the degree of kinship. The estimates of sensitivity were computed based on 'hits', defined here as the 'kin' response given to kin pairs, and 'false alarms', defined here as the kin response given to non-kin pairs. We considered the  $A'$  statistic (a non-parametric version of  $d'$ ) and its respective bias  $B'_d$  to be more appropriate than  $d'$  and  $C$  because data show some hit or false alarm rates of 1 or 0 (for comparison, all signal-detection metrics are shown in ESM 4, electronic

supplementary material). Likelihood criterion  $B'_d$  evaluates the judge's response strategy. Thus,  $B'_d$  was 0 when the participant had no particular strategy. When the participant adopted a 'risk' strategy, i.e. a tendency to respond that individuals in a pair are related (more false positives),  $B'_d$  was significantly less than 0. On the other hand, when the participant adopted a 'security' strategy (more omissions),  $B'_d$  was significantly higher than 0. We used the  $t$ -tests to compare criterion  $B'_d$  with its reference value (no bias,  $B'_d = 0$ ) in sets A and B, and then, more specifically, in the five categories of relatedness degree. We compared signal detection estimates of sensitivity for each of the five degree-of-relatedness categories with those of the matched unrelated control categories (same age, same gender), and significance was assessed with  $t$ -tests.

#### (ii) Degree of relatedness

The judge's choice for each stimulus was scored as 0 for inaccurate kin matching and 1 for accurate kin matching. We also recorded the response delay for each choice. Indeed, the time required to decide whether or not the two faces in the pair are related can show us the amount of difficulty caused by our experimental conditions. Longer response delays are interpreted as longer deliberation times and, therefore, as greater difficulty experienced by judges over the pair. We used logistic regression and GLM (general linear model) to test variations in the resemblance to related individuals according to the recorded variables. The dependent variable was *judge's choice* (binary variable) in logistic regression and *judge's delay* (quantitative variable) in GLM. Because response delays vary greatly from one participant to the next, we chose to take into account the response delay for each item divided by the average response delay of the participant (rather than response delay only). The independent variables dealing with individual pairs were the *degree of relatedness* (Id, Sb, Gp-child, AU-child and Cs, qualitative factor), *pair-gender* (female-female, female-male and male-male, qualitative factor), *pair-age* (age difference between the two individuals in each pair, quantitative factor). All variables are considered as fixed-effect variables, except for the judge variable, which is a random-effect variable. Pre-planned contrast analyses were performed to compare the different categories in each factor. Statistical analyses were conducted using SAS (SAS Institute Inc., release v.9.1, 2002-2003).

## 3. RESULTS

### (a) Kin versus non-kin

First, a general bias exists both in set A ( $B'_d = -0.4 \pm 0.4$ ;  $p < 0.001$ ) and set B ( $B'_d = -0.27 \pm 0.4$ ;  $p < 0.001$ ). Participants also responded 'related' more often than 'unrelated' and these biases, rated by  $B'_d$  metrics, were significant ( $p < 0.01$ ) in all degree-of-relatedness categories in each set (ESM 4, electronic supplementary material), except for Cs pairs. In sets A and B, the kinship pairs were detected significantly more ( $A'_{\min} = 0.65$ ,  $p < 0.001$ ) than unrelated pairs, no matter what the relatedness category (ESM 4, electronic supplementary material). Furthermore, response delays in sets A and B were not shorter in kinship pairs (mean for all kin =  $6.87 \pm 4.3$  s) than in non-kin pairs (mean for all non-kin =  $6.82 \pm 4.4$  s,  $p > 0.8$ ) across all relatedness categories.

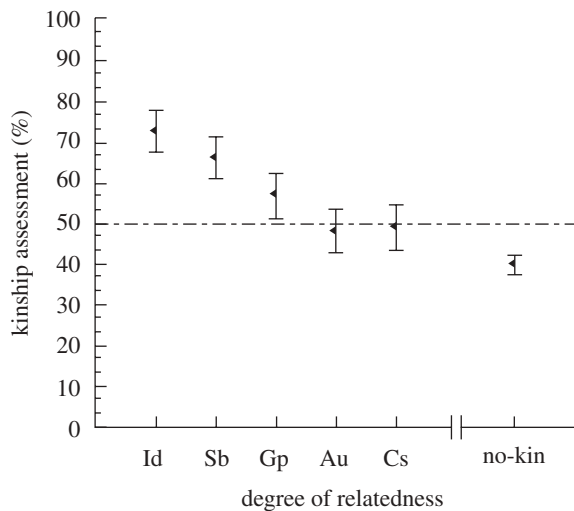


Figure 1. Kinship assessment based on the resemblance between two faces varies according to the degree of relatedness. Id, Sb and Gp were assessed as kin more often than by random choices ( $p < 0.05$ ); Au and Cs were not ( $p > 0.7$ ), but they were rated differently from non-kin pair ( $p < 0.001$ ). Non-kin pairs were significantly detected to be unrelated ( $p < 0.001$ ). For each degree of relatedness, mean observed values with 95 per cent confidence intervals are shown. The dashed line corresponds to random choices. Id, the same individual; Sb, siblings; Gp, grandparents/grandchildren; AU, aunt-uncle/nephews; Cs, cousins.

#### (b) Degree of relatedness

Second, we assessed the effects of degree of relatedness, pair-gender and pair-age on judges' choices by multiple logistic regressions with judge as random effect (*Proc Glimmix*). The general facial resemblance of two kin individuals tended to increase with the degree of relatedness (figure 1). The comparison between Id and all of the other categories of kinship degree shows that judges more easily recognize pairs that show the same individual at different ages than those of any other related individuals (table 1). Contrast comparisons showed that, in general, participants detect kinship differently depending on the degree of relatedness (table 1). Analyses conducted on pair-age revealed no effect on judges' choices, but the one conducted on pair-gender showed a significant main effect (table 1). For the Id pair, the analysis detected a marginally significant difference ( $\chi^2 = 3.61$ , d.f. = 1,  $p = 0.057$ ) between the 'MM' pairs (correct choice 76.8% of the time) and the 'FF' pairs (correct choice 67.8% of the time). For the other kinship degree, when the pair includes a woman, it is easier to judge whether the individuals are related than in MM pairs. The discrimination rate is not higher in same-gender pairs than in opposite-gender pairs (table 1).

Finally, we examined the relationship between pair-age and judges' response delay using linear regression ( $r^2 = 0.01$ ,  $F_{1,1732} = 18.02$ ,  $p < 0.001$ ). Thus, our measure of judges' response delay was the standardized residual of this linear regression. We assessed the effects of kinship degree, pair-gender and judge's choice on judges' response delay by using GLM with judge as random effect (*Proc Mixed*). Judges' response delay was only influenced by interaction between the degree of relatedness and judges' responses (table 1). Response delay also tends to be shorter for close kin pairs ( $r = 1$  or  $0.5$ ) and

for correct responses. However, among distant kin (Gp-Child, AU-Child and Cs) pairs, our analysis did not show any difference in judges' response delay, no matter what their responses.

#### 4. DISCUSSION

Humans have been shown to possess visual perceptive abilities to help them discriminate between kin and non-kin in situations relevant to direct fitness (parent-offspring only, see Nesse *et al.* 1990; Christenfeld & Hill 1995; Brédart & French 1999; McLain *et al.* 2000; Bressan & Dal Martello 2002; Bressan & Grassi 2004; Oda *et al.* 2005; Alvergne *et al.* 2007). However, our results go further in showing how the capacity to distinguish between related and non-related pairs applies to situations relevant to indirect fitness when the degree of relatedness is lower than 1/2. They show how kinship discrimination varies with the type or degree of relatedness. Kinship discrimination also applies to kinship between strangers (i.e. among pairs that are not related to the observer), an important criterion for anticipating people's reactions, a basis of the theory of mind.

Our categorization task (related versus unrelated) required long processing delays (approx. 7 s), when compared with other facial judgments (e.g. facial recognition, gender discrimination, facial signs of emotions (Hoss *et al.* 2005; Jacques & Rossion 2006)) that require rapid cognitive processing (approx. 1 s). We can interpret this as being caused by the greater complexity involved in determining whether two faces belong to related individuals.

Among the degrees of relatedness investigated in our study, two of them, Id and Sb pairs, have already been studied (Christenfeld & Hill 1995; Maloney & Dal Martello 2006; DeBruine *et al.* 2009). Our results are generally in line with the three previous studies, indicating that for a kinship degree greater than or equal to 0.5, it is easy to see that the pairs are related. As the research by Maloney & Dal Martello (2006), and to a lesser degree DeBruine *et al.*'s (2009) study showed, our participants adopted a 'risk' strategy by responding related more often than unrelated. However, in contrast to the other studies, our participants had lower success rates. We can hypothesize that success rates are lower because of our sampling procedure. Indeed, we asked the student population to gather family photos, which we scanned and normalized. Therefore, the quality of the photos varied, as did the age of individuals in each photo (ESM 2, electronic supplementary material). A more thorough standardization may improve the judges' ability to discriminate between related and non-related individuals. However, the age variations of our samples are surely closer to ecological conditions. Surprisingly, our analyses failed to detect a possible influence of age-pair on judges' choices. Age difference has a slight influence on participant response delays but not on their ability to detect whether the two individuals within the pair are related or not. This may reflect the fact that facial features useful for assessing kinship (i) become more difficult to perceive when the age difference between two related individuals increases, but (ii) that these facial cues, though they evolve with age, are still present throughout the individual's lifetime.

Table 1. Effects of the degree of relatedness, pair-gender and pair-age on judges' choices and delays. Id, the same individual; Sb, siblings; Gp, grandparents/grandchildren; AU, aunt–uncle/nephews; Cs, cousins. Odds ratio (OR) is a measure of effect size.  $OR > 1$ , effect more likely in the first category (kin or gender);  $OR < 1$ , effect less likely in the first category;  $OR = 1$ , effect equally likely in both category.

model	effects	statistics			
		<i>F</i>	d.f.	<i>p</i> -value	OR
judges' choice (Glimmix)	degree of relatedness	15.27	4,1674	<0.0001	
	Id versus other kin	31.42	1,1674	<0.0001	
	Id versus Sb	3.56	1,1674	0.059	1.37
	Sb versus Gp	6.27	1,1674	0.012	1.48
	Gp versus Au	5.18	1,1674	0.023	1.43
	Au versus Cs	0.10	1,1674	0.751	1.05
	pair-gender	11.03	2,1674	<0.0001	
	FF versus MM <sup>a</sup>	9.76	1,939	0.001	1.65
	FF versus FM <sup>a</sup>	5.57	1,939	0.018	1.44
	MM versus FM <sup>a</sup>	0.72	1,939	0.39	0.87
	FF+MM versus FM <sup>a</sup>	0.78	1,939	0.37	1.26
	pair-age	2.83	1,1674	0.09	
	judges' delay (mixed)	degree of relatedness (DR)	1.12	4,1720	0.34
pair-gender		0.13	2,1720	0.87	
judges' choice (JC)		3.33	1,1720	0.068	
DR × JC		4.01	4,1720	0.003	

<sup>a</sup>Because the Id pair increases the likelihood of answering related more than other pairs do, it is quite possible that the pair is biasing the pair-gender comparisons. We therefore conducted a new logistic regression, by eliminating the Id pair, to perform contrast analyses. In the new analysis, pair-gender still had a significant influence on judges' choices ( $F_{2,939} = 5.25$ ,  $p = 0.005$ ).

#### (a) Ability among kin

Our study is the first to examine the general progress of facial cues with kinship degree and shows that humans can detect relatedness between siblings ( $r = 1/2$ ), and even between grandparents and grandchildren ( $r = 1/4$ ), i.e. between individuals who are related but two generations apart. The task, however, appears difficult for relatives who are no less distant ( $r = 1/4$ ), but who are less directly linked (uncles or aunts with nephews and nieces: an explanation is provided in the following) or those who are more genetically distant (cousins;  $r = 1/8$ ). Nevertheless, two observations can be made. First, Cs and AU–child pairs were treated differently from non-kin pairs. Indeed, while Cs and AU–child pair responses were not found to differ significantly from random choices, non-kin pairs were largely found to be unrelated (figure 1). Moreover, when we compare a category of aunt–uncle/nephew pairs or cousin pairs with unrelated individual pairs sharing the same characteristics (same age, same gender), participants are able to identify the kinship pair (ESM 4, electronic supplementary material). Second, this study is built on an experimental paradigm using static, two-dimensional facial images, and we can therefore assume that the capacity to perceive that individuals are related should be even greater under more ecological conditions (moving faces, various facial expressions). Furthermore, from the judges' point of view, the facial images were all of strangers (i.e. non-kin) and of people with whom they could not have interacted, aside from the 20 s of exposure during the experiment.

#### (b) Facial resemblance plasticity

Facial features are to a large degree the result of the interaction between genetic and environmental factors. The plasticity of facial resemblance among related individuals

may therefore depend on these different cues. At birth, the greatest amount of facial resemblance can be attributed to innate, genetic signals, which increase the likelihood that neonates will be associated with their parents (Porter *et al.* 1984; Mclain *et al.* 2000; Alvergne *et al.* 2007). Later on, when individuals share the same environment, an additional explanation can also be weighed. Consider, for instance, that two siblings eating carotenoids and living in the same surroundings for a set period of time will easily be identified as being related, because they share the same complexion, and not necessarily based solely on genetic kinship cues. Such a phenomenon of 'phenotypic convergence' of facial features among cohabiting individuals was demonstrated between humans in the same couple (Zajonc *et al.* 1987). Thus, as time passes after birth, the genetic and phenotypic convergence mechanisms mix and combine to develop facial resemblance between two individuals. The differences between judges' assessments of Gp–child, AU–child and Cs stimulus pairs and those of non-kin pairs highlights the possibility of associating individuals who have not necessarily lived together. In Sb pairs, the high score of kinship attribution may be due to both factors. If we look at the Id category, in which only the environment changes during the individual's lifetime, we can see that the pairs are not systematically recognized (figure 1) and that there is a difference in kinship assessment between male (77%) and female pairs (68%). The result contrasts with that of other kinship categories, in which kinship assessment is easier when the pair includes at least one woman (FF > FM > MM). One can suggest two hypotheses to explain kinship assessment made according to gender. One possible explanation would be that human males' facial features are more affected by their environment (permanent scars, for example). Such phenotypic individual features

are more abundant and distinct in males and therefore allow judges to associate faces in the Id<sub>M</sub> pairs and to differentiate faces in other MM pairs. Women's facial features, conversely, would be less affected by their environment (or be less visible in day-to-day life thanks to facial-care products), which means that they may better reveal genetic kinship signatures (less 'epigenetic noise'). Thus, women are more easily associated with related individuals, no matter what the qualitative kinship degree. The data are in line with previous studies, which show that children's faces generally resemble their mothers' more than their fathers' (McLain *et al.* 2000; Oda *et al.* 2005), with a differential resemblance with one or the other parent depending on the age and gender of the child (Alvergne *et al.* 2007). It is of course speculative to say that men's facial features are in general more affected by their environment than women's; the reasons behind and the workings of differing kinship assessment of male, female and opposite-gender pairs are matters for future research. The second explanation is own-sex bias (Lewin & Herlitz 2002), combined with our study population (92% female participants). Women seem to better identify, recognize and categorize female faces (Slone *et al.* 2000; Lewin & Herlitz 2002). The skills required for these tasks could be applied in our paradigm and may help to explain the better FF kin detection.

Our results show a differential assessment of kinship between Gp-child and AU-child categories, although the degrees of kinship of grandparents/grandchildren on the one hand, aunts and uncles/nephews and nieces on the other hand, are both 0.25, on average. In most societies (both hunter-gatherer and modern), it seems that more care is given to children by their grandparents than by their aunts and uncles (see Sear & Mace 2008 for a review). The care leads to more time spent together and therefore to more visual contact in Gp-child pairs than in AU-child pairs. For this reason, if phenotypic convergence exists (through ordinary environmental influence or imitation), it is more likely to be in Gp-child pairs than in AU-child pairs. The effect may be enhanced by imprinting-mate choice (Berezkei *et al.* 2002, 2004, 2008): when a woman or man chooses a mate who resembles her father or his mother, their children are more likely to look like the parent (and therefore the grandparent) than the siblings (and therefore the aunt/uncle).

However, another hypothesis rests on three genetic principles that lead us to conclude that Gp-child and AU-child pairs do not possess the same 'qualitative' degree of kinship. The first principle arises when calculating the kinship degree 'forward' from parent to offspring and reflects the random nature of meiotic segregation. Because there are two generational steps between individuals in Gp-child pairs and three in AU-child pairs, the latter are more subjected to genetic drift. The second principle arises when calculating 'backward' from offspring to parent and reflects uncertainty about whether a randomly chosen allele entered a zygote in an egg or sperm (Haig 2000). The classical theory of inclusive fitness implicitly assumes that a gene's expression is unaffected by its parental origin, but this assumption is now known to be violated in cases of genomic imprinting (Efstratiadis 1994). By applying the principle of kinship theory of genomic imprinting to our research, a

paternal grandmother (GMp) has a kinship degree of 0.25 ( $r_{GMp} = \frac{1}{2} * \frac{1}{2}$ ) with her grandchild and a paternal uncle (Up) has a kinship degree of 0.25 ( $r_{Up} = (1/2 * 1/2 * 1/2)_{GMp} + (1/2 * 1/2 * 1/2)_{GPp}$ , with GPp representing the link via the paternal grandfather), but the two kinship degrees are certainly not equivalent from a qualitative point of view. Fragmentation in the combined pools of genes is more likely to break up a 'Gestalt' of familiarity in faces. The third principle arises when we consider the paternity certainty hypothesis (Smith 1988). Because the vertical links through fathers are less certain than the links through mothers, the number of uncertain links between distant kin members should also be affected. From this point of view, if  $p_c$  stands for paternity certainty, GMp will have a kinship degree of  $r_{GMp} = 1/4p_c$  with her grandchild, whereas Up will have a kinship degree of  $r_{Up} = 1/8 + 1/8p_c^3$  with his niece or nephew. Thus, the effects of environmental and genetic factors can help to explain the differential kinship assessment of facial resemblance in Gp-child and AU-child pairs observed in our findings. Differentiating the impact of each of these two hypotheses (an environmental hypothesis and a genetic hypothesis with three principles) on facial resemblance remains an area for further study.

In conclusion, this experiment confirms the workings of the important mechanisms required for human inclusive fitness theory and included in the theory of mind. We show that humans are capable of determining whether or not two strangers are indirectly related. The findings are in agreement with emerging knowledge on the role played by facial features as a kinship cue. Furthermore, this research highlights the dependence of facial cue assessment on various kinship degrees and gender. The study is the first to show that humans are capable of identifying which individuals are related, even in cases when they are more than a generation apart and have presumably not lived together.

We would like to thank all the families who offered their photos and the judges who participated in the experiment. We would also like to thank Benjamin de Vulpillières and three anonymous reviewers for their constructive discussions and comments about the manuscript.

*Author contributions.* G.K. proposed the project. G.K. and S.D. designed and conducted the experiments and performed the statistical analyses. All authors wrote, discussed the results and commented on the manuscript.

*Funding.* This research was financed by the French CNRS and a grant from the French National Research Agency (ANR Family'Air to E.G.).

*Competing interests.* The authors have declared that no competing interests exist.

## REFERENCES

- Alvergne, A., Faurie, C. & Raymond, M. 2007 Differential facial resemblance of young children to their parents: who do children look like more? *Evol. Hum. Behav.* **28**, 135–144. (doi:10.1016/j.evolhumbehav.2006.08.008)
- Berezkei, T., Gyuris, P., Koves, P. & Bernath, L. 2002 Homogamy, genetic similarity, and imprinting; parental influence on mate choice preferences. *Pers. Individ. Differ.* **33**, 677–690. (doi:10.1016/S0191-8869(01)00182-9)

- Bereczkei, T., Gyuris, P. & Weisfeld, G. E. 2004 Sexual imprinting in human mate choice. *Proc. R. Soc. Lond. B* **271**, 1129–1134. (doi:10.1098/rspb.2003.2672)
- Bereczkei, T., Hegedus, G. & Hajnal, G. 2008 Facialmetric similarities mediate mate choice: sexual imprinting on opposite-sex parents. *Proc. R. Soc. B* **276**, 91–98. (doi:10.1098/rspb.2008.1021)
- Brédart, S. & French, R. M. 1999 Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld & Hill (1995). *Evol. Hum. Behav.* **20**, 129–135. (doi:10.1016/S1090-5138(98)00047-6)
- Bressan, P. & Dal Martello, M. F. 2002 Talis pater, talis filius: perceived resemblance and the belief in genetic relatedness. *Psychol. Sci.* **13**, 213–219. (doi:10.1111/1467-9280.00440)
- Bressan, P. & Grassi, M. 2004 Parental resemblance in 1-year-olds and the Gaussian curve. *Evol. Hum. Behav.* **25**, 133–141. (doi:10.1016/j.evolhumbehav.2004.03.001)
- Burch, R. L. & Gallup Jr, G. G. 2000 Perceptions of paternal resemblance predict family violence. *Evol. Hum. Behav.* **21**, 429–435. (doi:10.1016/S1090-5138(00)00056-8)
- Burnstein, E., Crandall, C. & Kitayama, S. 1994 Some neo-Darwinian decision rules for altruism: Weighing cues for inclusive fitness as a function of the biological importance of the decision. *J. Pers. Soc. Psychol.* **67**, 773–789. (doi:10.1037/0022-3514.67.5.773)
- Charlesworth, D. & Charlesworth, B. 1987 Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. Syst.* **18**, 237–268. (doi:10.1146/annurev.es.18.110187.001321)
- Christenfeld, N. J. S. & Hill, E. A. 1995 Whose baby are you? *Nature* **378**, 669. (doi:10.1038/378669a0)
- Cosmides, L. & Tooby, J. 1992 Cognitive adaptations for social exchange. In *The adapted mind* (eds J. Barkow, L. Cosmides & J. Tooby). New York, NY: Oxford University Press.
- DeBruine, L. M. 2002 Facial resemblance enhances trust. *Proc. R. Soc. Lond. B* **269**, 1307–1312. (doi:10.1098/rspb.2002.2034)
- DeBruine, L. M. 2004 Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proc. R. Soc. Lond. B* **271**, 2085–2090. (doi:10.1098/rspb.2004.2824)
- DeBruine, L. M. 2005 Trustworthy but not lust-worthy: context-specific effects of facial resemblance. *Proc. R. Soc. B* **272**, 919–922. (doi:10.1098/rspb.2004.3003)
- DeBruine, L. M., Jones, B. C., Little, A. C. & Perrett, D. I. 2008 Social perception of facial resemblance in humans. *Arch. Sex. Behav.* **37**, 64–77. (doi:10.1007/s10508-007-9266-0)
- DeBruine, L. M., Smith, F. G., Jones, B. C., Roberts, S. C., Petrie, M. & Spector, T. D. 2009 Kin recognition signals in adult faces. *Vis. Res.* **49**, 38–43. (doi:10.1016/j.visres.2008.09.025)
- Efstratiadis, A. 1994 Parental imprinting of autosomal mammalian genes. *Curr. Opin. Genet. Dev.* **4**, 265–280. (doi:10.1016/S0959-437X(05)80054-1)
- Essock-Vitale, S. M. & McGuire, M. T. 1985 Women's lives viewed from an evolutionary perspective. I. Sexual histories, reproductive success, and demographic characteristics of a random sample of American women. *Ethol. Sociobiol.* **6**, 155–173.
- Fessler, D. M. T. & Navarrete, C. D. 2004 Third-party attitudes toward sibling incest: Evidence for Westermarck's hypotheses. *Evol. Hum. Behav.* **25**, 277–294. (doi:10.1016/j.evolhumbehav.2004.05.004)
- Gaulin, S. J. C., McBurney, D. & BrakemanWartell, S. 1997 Matrilateral biases in the investment of aunts and uncles: A consequence and measure of paternity uncertainty. *Hum. Nat.* **8**, 139–151. (doi:10.1007/s12110-997-1008-4)
- Green, D. N. & Swets, J. A. 1966 *Signal detection theory and psychophysics*. New York, NY: Wiley.
- Haig, D. 2000 The kinship theory of genomic imprinting. *Annu. Rev. Ecol. Syst.* **31**, 9–32. (doi:10.1146/annurev.ecolsys.31.1.9)
- Hamilton, W. D. 1964 The genetic evolution of social behavior. Part I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)
- Helgason, A., Pálsson, S., Guðbjartsson, D. F., Kristjánsson, O. & Stefánsson, K. 2008 An association between the kinship and fertility of human couples. *Science* **319**, 813–816. (doi:10.1126/science.1150232)
- Hoss, R. A., Ramsey, J. L., Griffin, A. M. & Langlois, J. H. 2005 The role of facial attractiveness and facial masculinity/femininity in sex classification of faces. *Perception* **34**, 1459–1474. (doi:10.1068/p5154)
- Jacques, C. & Rossion, B. 2006 The speed of individual face categorization. *Psychol. Sci.* **17**, 485–492. (doi:10.1111/j.1467-9280.2006.01733.x)
- Jeon, J. & Buss, D. M. 2007 Altruism towards cousins. *Proc. R. Soc. B* **274**, 1181–1187. (doi:10.1098/rspb.2006.0366)
- Jones, D. 2003 The generative psychology of kinship Part 1. Cognitive universals and evolutionary psychology. *Evol. Hum. Behav.* **24**, 303–319. (doi:10.1016/S1090-5138(03)00038-2)
- Khoury, M. J., Cohen, B. H., Diamond, E. L., Chase, G. A. & McKusick, V. A. 1987 Inbreeding and prereproductive mortality in the Old Order Amish. I. Genealogic epidemiology of inbreeding. *Am. J. Epidemiol.* **125**, 453–461.
- Kruger, D. J. 2003 Evolution and altruism: combining psychological mediators with naturally selected tendencies. *Evol. Hum. Behav.* **24**, 118–125. (doi:10.1016/S1090-5138(02)00156-3)
- Laham, S. M., Gonsalkorale, K. & von Hippel, W. 2005 Darwinian grandparenting: preferential investment in more certain kin. *Pers. Soc. Psychol. Bull.* **31**, 63–72. (doi:10.1177/0146167204271318)
- Lahdenpera, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. 2004 Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* **428**, 178–181. (doi:10.1038/nature02367)
- Lewin, C. & Herlitz, A. 2002 Sex differences in face recognition—women's faces make the difference. *Brain Cogn.* **50**, 121–128. (doi:10.1016/S0278-2626(02)00016-7)
- Lieberman, D., Tooby, J. & Cosmides, L. 2003 Does morality have a biological basis? An empirical test of the factors governing moral sentiments relating to incest. *Proc. R. Soc. Lond. B* **270**, 819–826. (doi:10.1098/rspb.2002.2290)
- Lieberman, D., Tooby, J. & Cosmides, L. 2007 The architecture of human kin detection. *Nature* **445**, 727–731. (doi:10.1038/nature05510)
- Lieberman, D., Oum, R. E. & Kurzban, R. 2008 Does the family of fundamental social categories include kinship? *Eur. J. Soc. Psychol.* **38**, 998–1012. (doi:10.1002/ejsp.528)
- Maloney, L. T. & Dal Martello, M. F. 2006 Kin recognition and the perceived facial similarity of children. *J. Vis.* **6**, 1047–1056. (doi:10.1167/6.10.4)
- McLain, D. K., Setters, D., Moulton, M. P. & Pratt, A. E. 2000 Ascription of resemblance of newborns by parents and nonrelatives. *Evol. Hum. Behav.* **21**, 11–23. (doi:10.1016/S1090-5138(99)00029-x)
- Michalski, R. L. & Shackelford, T. K. 2005 Grandparental investment as a function of relational uncertainty and emotional closeness with parents. *Hum. Nat.* **16**, 292–304. (doi:10.1007/s12110-005-1012-5)
- Nesse, R. M., Silverman, A. & Bortz, A. 1990 Sex differences in ability to recognize family resemblance. *Ethol. Sociobiol.* **11**, 11–21. (doi:10.1016/0162-3095(90)90003-O)

- Ober, C., Hyslop, T. & Hauck, W. W. 1999 Inbreeding effects on fertility in humans: evidence for reproductive compensation. *Am. J. Hum. Genet.* **64**, 225–231. (doi:10.1086/302198)
- Oda, R., Matsumoto-Oda, A. & Kurashima, O. 2005 Effects of belief in genetic relatedness on resemblance judgments by Japanese raters. *Evol. Hum. Behav.* **26**, 441–450. (doi:10.1016/j.evolhumbehav.2005.04.002)
- Platek, S. & Thomson, J. W. 2007 Facial resemblance exaggerates sex-specific jealousy-based decisions. *Evol. Psychol.* **5**, 223–231.
- Pollet, T. V., Nettle, D. & Nelissen, M. 2007 Maternal grandmothers do go the extra mile: factoring distance and lineage into differential investment in grandchildren. *Evol. Psychol.* **5**, 832–843.
- Porter, R. H. 1991 Mutual mother–infant recognition in humans. In *Kin recognition* (ed. P. G. Hepper), pp. 413–432. Cambridge, UK: Cambridge University Press.
- Porter, R. H., Cernoch, J. M. & Balogh, R. D. 1984 Recognition of neonates by facial-visual characteristics. *Pediatrics* **74**, 501–505.
- Sear, R. & Mace, R. 2008 Who keeps children alive? A review of the effects of kin on child survival. *Evol. Hum. Behav.* **29**, 1–18. (doi:10.1016/j.evolhumbehav.2007.10.001)
- Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997 Recognition systems. In *Behavioural ecology: an evolutionary approach* (eds R. Krebs & N. B. Davies), pp. 69–96. Oxford, UK: Blackwell Scientific.
- Slone, A. E., Brigham, J. C. & Meissner, C. A. 2000 Social and cognitive factors affecting the own-race bias in Whites. *Basic Appl. Soc. Psychol.* **22**, 71–84.
- Smith, M. S. 1988 Research in developmental sociobiology: Parenting and family behavior. In *Sociobiological perspectives on human development* (ed. K. B. MacDonald), pp. 271–292. New York, NY: Springer-Verlag.
- Stewart-Williams, S. 2007 Altruism among kin vs. nonkin: effects of cost of help and reciprocal exchange. *Evol. Hum. Behav.* **28**, 193–198. (doi:10.1016/j.evolhumbehav.2007.01.002)
- Waldman, B. 1988 The ecology of kin recognition. *Ann. Rev. Ecol. Syst.* **19**, 543–571. (doi:10.1146/annurev.es.19.110188.002551)
- Wells, P. A. 1987 Kin recognition in humans. In *Kin recognition in animals* (eds D. J. C. Fletcher & C. D. Michener), pp. 395–415. New York, NY: Wiley.
- Zajonc, R. B., Adelman, P. K., Murphy, S. T. & Niedenthal, P. M. 1987 Convergence in the physical appearance of spouses. *Motiv. Emot.* **4**, 335–346. (doi:10.1007/BF00992848)