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Animal behaviour

Identification of visual paternity cues in humans

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Understanding how individuals identify their relatives has implications for the evolution of social behaviour. Kinship cues might be based on familiarity, but in the face of paternity uncertainty and costly paternal investment, other mechanisms such as phenotypic matching may have evolved. In humans, paternal recognition of offspring and subsequent discriminative paternal investment have been linked to father–offspring facial phenotypic similarities. However, the extent to which paternity detection is impaired by environmentally induced facial information is unclear. We used 27 portraits of fathers and their adult sons to quantify the level of paternity detection according to experimental treatments that manipulate the location, type and quantity of visible facial information. We found that (i) the lower part of the face, that changes most with development, does not contain paternity cues, (ii) paternity can be detected even if relational information within the face is disrupted and (iii) the signal depends on the presence of specific information rather than their number. Taken together, the results support the view that environmental effects have little influence on the detection of paternity using facial similarities. This suggests that the cognitive dispositions enabling the facial detection of kinship relationships ignore genetic irrelevant facial information.

1. Introduction

The ability to identify kin, a prerequisite for the evolution of altruistic behaviour and inbreeding avoidance, has been documented in taxa as diverse as bacteria and primates [1]. At the proximate level, individuals use indirect environmental cues such as spatial proximity and shared life experience but in some circumstances, they might also use direct cues such as the assessment of phenotypic similarities [1]. When familiarity does not correlate with relatedness and detection errors are costly, e.g. when paternity is uncertain but males provide costly parental investment, the ability to detect phenotypic similarities with oneself or with others may be favoured. In humans, facial resemblance appears to be the most relevant cue for assessing kinship relationships [2] and for instance, father involvement in the care of offspring is not independent from real and perceived father–child facial similarities [3–6]. Although some degree of facial resemblance is expected as a by-product of the heritability of phenotypic traits, it does not guarantee that genetic paternity can accurately be detected as both facial phenotype and perceptual processes are shaped by the environment.

It has been argued that to be efficient, a kin recognition system inferring facial similarities should ignore those cues that do not inform on genetic relationships [7–9]. There is empirical evidence that the detection of kinship relationships is not influenced by either age and sex difference between the faces or the environmentally induced level of facial asymmetry ([8,9], but see [10]). In particular, the masking of the lower part of the face, otherwise

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highly sensitive to development, does not impair the detection of sibling relationships between children, while the masking of the upper part decreased substantially the detection rate [7]. Whether this effect still holds after development (i.e. with adult faces) is unknown.

Other studies show that kinship detection does not depend on cultural experience with faces [11]. This contrasts with facial identification, whereby individuals prove better at recognizing faces they have been exposed to during development [12,13]. This 'other race effect' is mainly attributable to configural processing [13], which uses information on the relationships between internal features within the face, as opposed to featural processing, which relies on featural information (e.g. the shape of the nose, eyes). The absence of an 'other race effect' for the facial detection of kinship relationships might indicate that configural similarities are ignored as they are modified by development [7,9] and the environmental pathogenesis [8]. However, the extent to which the impairment of the configural information in the face affects the detection of kinship relationships is unknown.

Here, we investigate where the paternity cues are in the adult face and which type of information is most potent for the accurate detection of paternity. We hypothesize that if paternity detection mainly results from information that is invariant with development, detection rates will be (i) lower when only the lower part of the face is presented and (ii) similar regardless of the alteration of configural information (achieved by disrupting the geometric relationships between internal features of the face or by masking the part that contains the majority of the elements that are involved in configural processing, the inner part [14]).

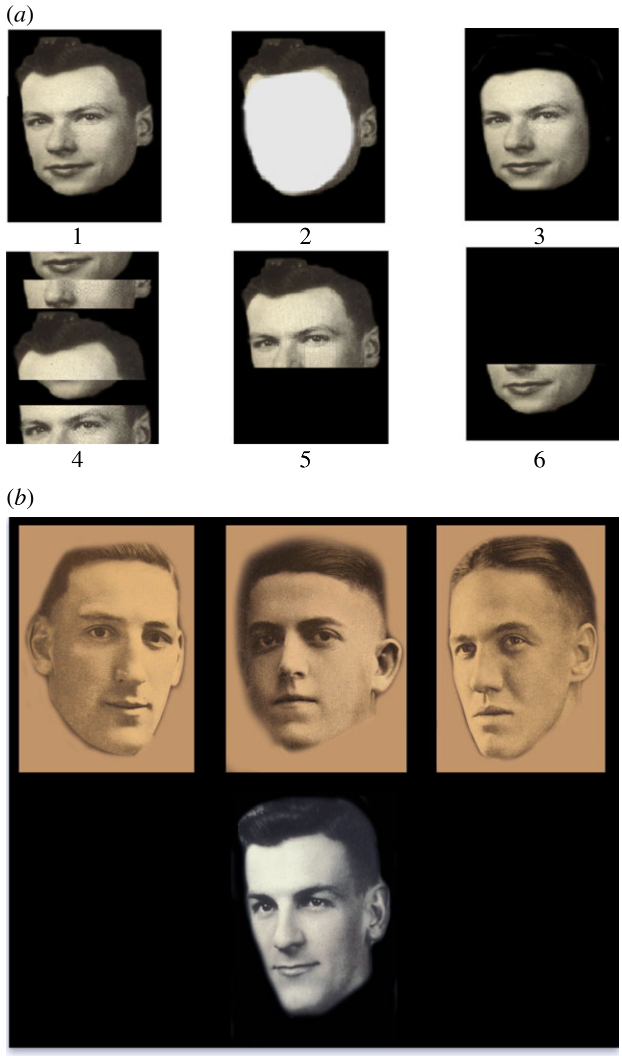

Figure 1. (*a*) Facial stimuli. 1, original face; 2, external features; 3, internal features; 4, mixed face; 5, upper part; 6, lower part. (*b*) Paternity detection using facial resemblance. Judges were asked to identify the father of the man displayed on the bottom line among three possible fathers (top line). The correct father is on the left. (Online version in colour.)

2. Material and methods

(a) Pictures

Black and white portraits of fathers and their sons were obtained from the West Point Academy (USA). The pictures were taken in the 1930s, 1950s and 1970s and depict adult faces. The age of individuals, fathers and sons, varies from 21 to 26 years old (mean $\pm$ s.d. $= 22.7 \pm 1.4$). Only pictures where individuals display a neutral face were included, leading to a total final sample of 27 pairs (14 pairs in which the individual photographed in 1950 is the son, and 13 pairs in which the individual photographed in 1950 is the father). All backgrounds were homogenized and six facial stimuli were created for each individual: the original face, the upper part the lower part the inner features, the external features and a mixed composite of the face (figure 1*a*). To create the upper and lower faces, methods from Dal Martello & Maloney [7] were used. To create mixed faces, horizontal parallel bands were cut and rearranged in the same order for all faces. Photograph manipulation was done using Adobe Photoshop 7.

(b) Assessment of facial similarities

Judges were presented with a computer screen and four facial stimuli depicting a son and three possible fathers (figure 1*b*). For each set of pictures, judges were asked to identify the correct father. A score of 0 was recorded for failure of detection, and 1 for success (the detection rate expected by chance is 1/3). Each judge saw each picture only once so that previous decisions did not influence later judgement [15]. Each part of the experiment was randomized (order of presentation of pictures, position of the real and false fathers and combination of false and real fathers) and results were recorded automatically using a computer program. For more details, see [3]. Judges were recruited from a cafeteria in London and were told that they were performing a test on the detection of familial resemblance. Judges were randomly assigned to one of four conditions: (1) original face; condition (2) upper and lower part of the face (random order); (3) inner and external part of the face with judges always seeing the external part of the face first and (4) mixed faces. For each judge, known confounding variables were recorded, such as age [16], sex [17] and birth order [18]. Data are available in the electronic supplementary material, S1.

(c) Statistical analysis

The measures are repeated (each pair was rated by several judges) and the dependent variable is binary so a mixed model with a binomial error structure was performed, including both the identity of the son and the identity of the judge as random effects. We added the type of treatment (six levels) and judges' variables as fixed effects. To investigate whether detection rates differ from chance (1/3), we compared the lower bound of the 95% confidence intervals (CIs) of the estimated rates to 1/3. Likelihood ratio tests were used to infer significance of variables. All analyses were carried out using R. v. 2.10.0 (The R development core team) and the packages lme4 [19].

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Table 1. Detection rates across all conditions. Estimates, s.e., detection rates (logit(estimate)) and 95% CIs. Predicted rates are taken from mixed models that control for the non-independence of repeated measures. Paternity is detected in all conditions except when only the lower part of the face is visible (lower bound 95% CI < 1/3).

treatment	estimate	standard errors	paternity detection	95% CI
original face	−0.359	0.1826	0.46	[0.372; 0.545]
mixed face	−0.335	0.1815	0.42	[0.342; 0.506]
external features	−0.178	0.1877	0.42	[0.335; 0.505]
internal features	−0.346	0.1890	0.41	[0.333; 0.498]
lower part	−0.541	0.1857	0.37	[0.295; 0.456]
upper part	−0.186	0.1836	0.45	[0.372; 0.541]

3. Results

A total of 271 judges of Caucasian origin (125 women) participated in the experiment. Each treatment was performed by a minimum of 60 judges, leading to a total of 1627 observations. In the original face condition, the rate of paternity detection varies from 0.37 to 0.54 (mean = 0.46). The paternity is detected for 67% of the pairs. The sample may contain some level of non-paternity, which would decrease the overall rate of paternity detection. Nevertheless, paternity detection is observed in all conditions except when only the lower part of the face is presented (table 1 and figure 2). In the lower part condition, the detection rate is not different from the probability of identifying the correct father by chance (mean = 0.37; 95% CI [0.30; 0.46]). Surprisingly, paternity detection is achieved when only the external features are visible (mean = 0.42; 95% CI [0.34; 0.51]). This result is not due to similarities in facial orientation, as only 29.6% of father–sons pairs (eight out of 27) are oriented similarly in the sample, and the facial orientation of false fathers (right or left) is not different from that expected by chance (exact binomial test, $p = 0.60$). This suggests that judges used similarities in head, hair or ear shape. Across treatments, detection rates are not significantly different from each other ($\chi^2 = 5.04$; d.f. = 5; $p = 0.41$). None of the judges's characteristics is significant (all $p > 0.40$) and paternity detection does not increase over time, thus there is no effect of the number of pictures already seen on detection rates.

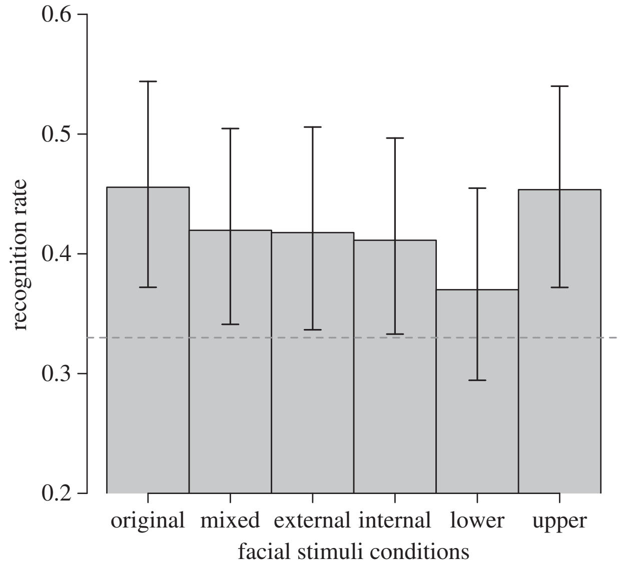

Figure 2. Predicted rates of paternity detection and 95% CIs in different experimental conditions. The grey shaded line indicates the rate expected by chance (1/3). Detection rate is higher than expected by chance (1/3) in all conditions except when only the lower part of the face is visible.

4. Discussion

We investigated the cues involved in the visual detection of paternity using portraits of fathers and their adult sons. The results show that paternity can be detected in adult faces. However, paternity detection cannot be achieved when only the lower part of the face is visible, which supports the idea according to which the lower part of the face contains fewer kinship signals as it undergoes major changes during development [7]. In addition, detection rates were not impaired if environmentally modified information (spatial relationships between internal features) was disrupted. This suggests that environmentally induced facial similarity is not an obstacle to the evolution of paternal detection in humans.

Surprisingly, detection is achieved even when only the external features are visible, which suggests that either the face shape, the ears and/or the hairline can be used as paternity cues in sons. Face shape may not be the most reliable cue as it skips generations and long faces often occur from round faces parents [20]. The ears may not be essential, as their masking does not impair recognition rates. Conversely, the hairline is visible in all cases where detection is achieved. The hairline changes through life in a predictable way [21] and given that fathers and sons are of similar age on the portraits, the hairline may have served as a reliable paternity cue in the context of this study. Conversely, cues may be used alternatively and the presence of one specific feature may not be mandatory (e.g. the eyes).

The results suggest that the cognitive mechanisms involved in the detection of paternity differ from that involved in facial identification: it mostly relies on featural rather than configural processing as paternity can be detected even if relational information are disrupted; the visibility of the eyes is not mandatory and the signal depends on the presence of specific cues rather than their number. Whichever system appeared first, the detection of facial similarities between kin might ignore the noise that would otherwise be introduced if all processes used in facial identification were involved.

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