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Original Article

Is cooperativeness readable in static facial features? An inter-cultural approach

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ABSTRACT

There is evidence in the literature that non-verbal physical features are used as cues for a propensity to cooperate. However, further studies of the human ability to visually detect cooperativeness are required. In particular, the existence of static facial cues of altruism remains questionable. Moreover, an investigation of both sex differences and cross-cultural applicability with respect to altruism detection skills is crucial in the context of the evolution of human cooperation. In this study, we used both a public good game and a charitable contribution to assess the cooperativeness of 156 men and 172 women in rural Senegal and took facial photographs of these individuals. The second portion of the study was conducted in France. In total, 194 men and 171 women were asked to distinguish the most and least selfish individual from a series of 80 pairs of Senegalese facial photographs, each pair consisting of the highest and the lowest contributor from a group in the public good game. Using mixed modeling techniques, we controlled for facial masculinity, age and socio-economic status. For male pairs, both male and female French raters were able to identify more often than by chance which individual made the smallest contribution to the public good in each group; however, detection was not successful with female faces. These results suggest that sex-specific traits are involved and that only male facial traits indicating cooperative skills are, at least inter-culturally, readable. The specific facial traits involved are investigated. However, the charitable contribution was not correlated with the contribution to the public good, and further work is necessary to identify which specific altruistic traits are detectable and to assess the generality of these results.

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1. Introduction

A large body of experimental studies demonstrates that a substantial fraction of people behave cooperatively[1] with non-kin individuals even if they are given the opportunity to behave selfishly in anonymous interactions. This finding, observed in both industrialized (Andreoni & Miller, 1993; Cadsby, Hamaguchi, Kawagoe, Maynes, & Song, 2007; Cadsby & Maynes, 1998; Keser, 1996; Keser & Van Winden, 2000; Willinger & Ziegelmeyer, 1999) and small-scale societies (Fehr & Leibbrandt, 2011; Henrich, 2000; Henrich, 2004; Henrich et al., 2005; Lamba & Mace, 2011), remains a puzzle for evolutionary biologists (Alexander, 2006; Boyd & Richerson, 2009). Indeed, natural selection should, *a priori*, select selfish behaviors rather than cooperative ones because these selfish behaviors should be more competitive. Altruistic behavior with non-kin could be positively selected if cooperators receive direct benefits enhancing their fitness (West et al., 2007). Direct benefits can be gained by direct or indirect reciprocity when a cooperative behavior elicits a cooperative response by other individuals who observed the interaction, either directly or indirectly (Alexander, 1987; Fehr, 2004; Nowak & Sigmund, 1998; Trivers, 1971; for a review see: Nowak, 2006; West et al., 2007). If there is a choice to reciprocate toward more cooperative individuals because of the benefits they confer, then competition to be more cooperative than others can result (*competitive altruism hypothesis*: Noe & Hammerstein, 1995; Roberts, 1998). In addition, it has been suggested that more cooperative individuals are preferentially chosen as sexual partners, and thus cooperation can be sexually selected (Miller, 2007; Tognetti, Berticat, Raymond, & Faurie, 2012; Van Vugt & Iredale, 2013). Cooperation can therefore be used as a cue that other individuals can use to make social decisions, either to select partners to cooperate with or to select sexual partners. In addition, if cooperative behavior is socially and/or sexually selected, cues for the propensity to cooperate can evolve into signals. Cues are non-selected ways of transmitting and obtaining information, whereas a signal is defined as "any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Maynard-Smith & Harper, 2003). One of the main mechanisms hypothesized to ensure the honesty of a signal is condition-dependence; signals have to be costly so that only high-

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[1] Cooperative behavior is defined here as any behavior that provides a benefit to the recipient; it can only be selected for if it also provides direct or indirect benefits to the actor that suffered the costs. Note that this definition includes altruistic behavior but also mutually benefic behavior (West, El Mouden, & Gardner, 2011; West, Griffin, & Gardner, 2007).

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quality individuals can support the cost of exhibiting them (Grafen, 1990; Zahavi, 1977). Altruistic acts represent costly and risky behavior (Clutton-Brock et al., 1998; Heinsohn & Legge, 1999). They could therefore signal the propensity to cooperate and also the individual's quality (*theory of costly signaling*: Gintis, Smith, & Bowles, 2001; Roberts, 1998; Zahavi, 1995); such a signal can be used, for example, in mate choice.

All of the current theories that attempt to explain the evolution of altruism among non-kin, e.g., indirect reciprocity, costly signaling, competitive altruism and sexual selection, are therefore based on the assumption that altruists can be distinguished from egoists by potential partners, thereby allowing the assortment of individuals by cooperative altruistic behavior (Wilson & Dugatkin, 1997). Preferences for a similarly cooperative partner can lead to the evolution of cooperation altruism if the advantages of selfish individuals are out-competed by the benefits of mutual cooperation between altruists. Thus, there is likely to be selection for an ability to use visual cues to quickly detect whether an individual is altruistic.

Several studies have suggested that humans are able to estimate another individual's propensity to cooperate, thereby allowing assortment based on cooperativeness. For instance, a study performed in secondary school classes revealed that students were able to predict the decisions of their classmates in a dictator game more accurately than chance alone would have predicted and that altruists were friends with more altruistic students than were egoists (Pradel, Euler, & Fetchenhauer, 2009). At the university level, altruist students tend to choose other altruist students to play at an economic game (Sheldon, Sheldon, & Osbaldiston, 2000).

Nevertheless, altruistic acts may not be the only traits conveying information about the individual's cooperativeness. Every behavioral or physical trait correlated with the individual's cooperativeness could also be used by potential partners as cues to distinguish altruists from egoists. In humans, several experimental studies demonstrate that facial traits could be involved in this detection. For example, several studies used facial photographs obtained while individuals were playing an economic game (Verplaetse, Vanneste, & Braeckman, 2007) or silent video clips of individuals' faces while they were talking about themselves (Brown, Palameta, & Moore, 2003; Fetchenhauer, Groothuis, & Pradel, 2010; Oda, Naganawa, Yamauchi, Yamagata, & Matsumoto-Oda, 2009a; Oda, Yamagata, Yabiku, & Matsumoto-Oda, 2009b) to demonstrate that non-verbal facial cues are implicated in the detection of altruism; the participants in these studies were able to either differentiate cooperators from non-cooperators or to predict the cooperativeness of a target individual more accurately than chance alone would dictate.

Facial emotional expressivity is likely to be among the non-verbal traits that serve as cues of cooperativeness. Previously published studies have provided evidence that cooperators exhibit greater numbers of emotional expressions (positive or negative) than do non-cooperators (Mehu, Grammer, & Dunbar, 2007a; Mehu, Little, & Dunbar, 2007b; Schug, Matsumoto, Horita, Yamagishi, & Bonnet, 2010). Moreover, cooperators exhibit more expressions that are under involuntary control, such as the felt smile, which is characterized by the activity of the orbicularis oculi muscle (Brown et al., 2003; Oda et al., 2009b).

However, little empirical research has investigated the role of traits other than expressions and movements (i.e., static traits) in the detection of cooperativeness, although there is evidence that individuals' decisions regarding whom to trust are biased by static traits, such as facial attractiveness (Wilson & Eckel, 2006) and similarity to kin (DeBruine, 2002). Moreover, an experimental study based on economic games demonstrated that the facial width-to-height ratio of males, a sexually dimorphic and testosterone-linked facial trait, could be used as a cue of trustworthiness; men with greater facial widths were more likely to exploit the trust of others and that other players, particularly females, were less likely to trust males with wide faces (Stirrat & Perrett, 2010). These results emphasize the existence of static traits that indicate altruism, at least in males; the previously established findings also suggest that the ability to detect cooperativeness may be dependent on the sex of the rater and the sex of the target. Therefore, the first aim of this study was to evaluate the existence of static facial cues of cooperativeness and to examine whether their detection was sex-specific.

The results of this previous study also provide an indirect indication that men with low testosterone levels (i.e., less masculinized men) behave more cooperatively and are considered to be more cooperative; this conjecture is supported by the finding that based on a self-report personality scale, cooperativeness is negatively correlated with testosterone level (Harris, Rushton, Hampson, & Jackson, 1996). In addition, men with high testosterone levels are more likely to reject low-ultimatum game offers (Burnham, 2007). Male facial width, which is linked to testosterone level (Verdonck, Gaethofs, Carels, & de Zegher, 1999), could be one of several traits that are involved in the indication of cooperativeness. Every testosterone-linked facial trait (e.g., larger jawbones, more prominent cheekbones, and thinner cheeks) grouped under the concept of facial masculinity is a likely candidate with respect to the indication of cooperativeness. The second aim of this study was thus to examine whether facial masculinity is linked with an individual's propensity to cooperate and whether it is used as a cue of cooperativeness, at least in men.

For this purpose, we initially assessed cooperativeness in a sample of men and women in rural Senegal and obtained facial photographs of the sampled individuals. We used two measures. The first measure is a public good game, which is more similar to natural situations (such as food sharing, collective hunting and collective building) than dyadic games (used in Stirrat & Perrett, 2010; Verplaetse et al., 2007) or self-reports (used in Fetchenhauer et al., 2010; Oda et al., 2009a; Oda et al., 2009b). The second measure involves a charitable contribution; at the end of the public good game, participants could donate part of their gain from the game to the village school. The second part of the study was conducted in France; for each combination of raters' and players' sex, raters were asked to distinguish the most and the least selfish from a series of paired photographs of Senegalese players, while controlling for players' age, socio-economic status and facial masculinity.

2. Methods

2.1. A measurement of cooperativeness

The experimental measurements of cooperativeness were obtained in five rural villages that are located in the Sine Saloum area of Senegal (which is close to the west coast of Africa). The participants were recruited on a voluntary basis. The protocols that were used to recruit the study's participants and collect data were approved by the French National Commission on Informatics and Liberties (CNIL declaration #1321739). Written informed consent was obtained from all of the adult subjects and from a parent of each subject who was younger than 18 years of age ($n = 3$). The rules of the public good game and the donation were completely explained to the participants in their local language.

2.1.1. The public good game

Groups of four same-sex individuals (four men or four women), who were not close kin, were formed. In total, 39 groups of men and 43 groups of women were recruited. These individuals were between 16 and 78 years of age (the mean age $\pm$ s.d. was 39 $\pm$ 16 years for men and 38 $\pm$ 14 years for women). We repeated the game for five periods (a sequential game), which allowed the players to modify their strategies on the basis of how other members of their group played the game; this repetition allowed reciprocity aspects to be included in our evaluations of cooperative behavior. At the beginning

of each period, each of the four players received 200 grams of rice. We used rice rather than coins to obtain continuous rather than incremental data; rice was also used because most participants were illiterate, and this factor would have caused monetary calculations and conversions to be problematic. The players individually entered a van. The players were instructed to allocate, once inside the van, their endowment of rice between a private good and a public good. At the end of each period, the players were informed of the total amount of rice that had been invested by the group during the period, but the quantity of rice that each player had allocated to a private good was secretly weighed (the accuracy of the scale was 1 grams). At the end of the game, the total quantity of rice that each group had invested in the public good was first doubled and then divided into four equal portions that were paid out to the four players of the group. The rice that each player had allocated to their private good was then added to their payoff. These payoffs were placed in opaque bags to ensure the secrecy of the amounts that had been won and were provided to each player in private.

2.1.2. The donation

When the participants received their final payoff in the van, they were informed about the possibility of donating part of it to the school canteen of the village. It was specified that this donation was optional and that any amount of rice would be accepted. At the end, each player received an opaque bag containing the payoff won during the public good game minus the donation to school, if any. The amount of rice donated to the school was weighed at the end of the experiment.

2.2. Facial photographs

Facial photographs of all of the players were obtained from a frontal perspective at a distance of approximately 1 m using a digital camera (Canon EOS 20D) with a 50-mm focal length. The subjects were asked to express a neutral face (without a smile) and look at the camera. The photographs were all cropped to identical dimensions, and Adobe Photoshop CS2 (version 9.0.2) was used to change all of the photograph backgrounds to white.

2.3. The detection of altruism

The test was implemented in France using facial photographs from Senegal. In total, 194 men and 171 women, 18–69 years old (mean age ± s.d.: 27 ± 7 years for men and 27 ± 11 years for women), were recruited on a voluntary basis in various areas of Montpellier (in the south of France) in the summer of 2011; in particular, this recruitment occurred at the university, in two research laboratories, and at a public location (the zoo). The participants were shown pairs of facial photographs and were asked to choose the more selfish individual from each pictured pair of Senegalese game players. The protocols that were used to recruit the participants and collect the data were approved by the French National Commission on Informatics and Liberties (CNIL declaration #1321739). Written informed consent was obtained from all of the subjects.

The pairs of photographs contained players from the same group in the public good game to control for any potential group effects. Moreover, to maximize the amplitude of the difference in cooperativeness, the highest and lowest contributors from each group were used to constitute a pair. The first period of the game was used as the criterion because (1) this period produced the greatest inter-individual variance in the contribution amounts compared to the following periods or to the amount donated, and (2) a high proportion of individuals did not make any donation (~35%), making the selection of the most selfish individuals based on the donation impossible for many groups (~40% of groups contained at least two non-donators).

The choices were presented using a computer program that was written in Delphi (version 7). For each of the 80 pairs of face photographs (two pairs were excluded from the initial sample of 82 pairs; one of these exclusions occurred because a mistake in the weight measurements of the private good allocations prevented an accurate distinction between the highest and lowest contributors of a group, whereas the second excluded pair was omitted from the sample because a woman in that pair had only one eye), the raters had to click on the individual whom they considered to be more selfish. The raters were provided with an unlimited amount of time to answer for each pair. To examine whether the detection of the cooperativeness of men and women was sex-specific, two series of pairs were used: one series of male players (39 pairs) and one series of female players (41 pairs). The order of appearance of the pairs and the relative location of each photograph (left or right) were randomized. The score for each comparison was recorded as either 0 for failure or 1 for success (i.e., the identification of the lower contributor as the more selfish individual).

2.4. Masculinity assessments

Fourteen points of interest were positioned on the photographs composing the pairs used in the test (Bovet, Barthes, Durand, Raymond, & Alvergne, 2012; Little et al., 2008; Penton-Voak et al., 2001). Nine distances were then computed between these points (Bovet et al., 2012). A linear discriminant analysis (LDA) according to sex was performed, providing a synthetic variable corresponding to a femininity/masculinity axis. The coordinate of each participant along this axis represents the individual masculinity value used in the following models. All morphological measurements were performed using ImageJ software, version 1.43.

2.5. Statistical analysis

To investigate whether the raters were able to determine the lowest contributor in the pairs significantly more often than chance would dictate, the success rate of these determinations was calculated for each rater. A proportion test (the *prop.test* function in R) was used to compare the success rates with the null hypothesis of no detection (50%) for each combination of the sex of the raters and the sex of the players.

General Linear Mixed Models (GLMMs) were then implemented for each player's sex to test whether the probability that a player was picked as the most selfish was influenced by the cooperative behavior of the two players in the pair. For this purpose, GLMMs with a binomial error structure were used (*lmer* function of the *lme4* package in R); the identities of the raters and the player pairs were included as random-effect variables, and the response was a binary variable (1 if the picture on the left of the screen was chosen as the most selfish, 0 otherwise). Two explanatory variables were simultaneously included: (1) a binary variable concerning the contribution to the public good (1 if the individual on the left was the most selfish, 0 otherwise) and (2) a three-category variable concerning the donation to the school (1 if the individual on the left was the most selfish, −1 if the individual on the left was the least selfish and 0 when both individuals made the same donation). Our model included the following as potential confounding effects: the raters' sex and the difference in age and socio-economic status between the player on the left and the player on the right. Because the amount allocated to the public good and to the school were not correlated (Spearman rank correlation: $\rho = -0.01$; $p = 0.85$) and because the players' age and socio-economic status were also not correlated (Spearman rank correlation: $\rho = -0.07$; $p = 0.22$), these variables were included in the same model. The data were analyzed by multimodel inference (Burnham & White, 2002; Symonds & Moussalli, 2011). From a global binomial generalized linear mixed model,

the fits of all possible models were compared using AIC, allowing their Akaike weights to be calculated (*dredge* function of the *MuMIn* package in R). Model averaging (*model.avg* function of the *MuMIn* package in R) was performed on all models, weighting the contribution of each model according to its Akaike weight (Hegyi & Garamszegi, 2011). The relative importance of each variable (the sum of the Akaike weights of the models in which the variable appears) and the averages of the estimates (weighted by Akaike weights) were calculated (Anderson, Link, Johnson, & Burnham, 2001; Symonds & Moussalli, 2011).

To assess whether facial masculinity was linked with the players' behavior in the first period of the public good game and in the donation, non-parametric Spearman correlation tests were performed (*cor.test* function in R) for each players' sex. Then, to examine whether the masculinity of the players influenced the raters' choices, a binary variable (1 if the individual on the left was more masculinized, 0 otherwise) was added to the previous GLMM. The data were analyzed by multimodel inference.

All of the statistical analyses were performed using R software, version 2.15.1 (R Development Core Team, 2010).

3. Results

3.1. Cooperativeness in the public good game and the donation

Globally, Senegalese participants allocated slightly more than half of their initial endowment to the public good both during the initial period (mean ± s.d.: 104 ± 58 grams of rice) and as an average over the course of all five periods of the game (mean ± s.d.: 109 ± 52 grams). From their final gain, they donated 111 ± 122 grams of rice, with 1/3 of participants not making any donation (108 out of 318 participants, after removing the 10 participants whose data were missing). Wilcoxon non-parametric tests indicated that the men's contributions did not significantly differ from the women's contributions either during the initial period of the game (men: 102 ± 57 grams, women: 106 ± 60 grams, $W = 13761$, $p = 0.43$), over the course of all five periods (men: 108 ± 53 grams, women: 109 ± 50 grams, $W = 327277$, $p = 0.83$), or in the donation to the school (men: 117 ± 127 grams, women: 106 ± 118 grams, $W = 13404.5$, $p = 0.32$). We did not observe a correlation between the contribution to the public good (either for the first period or as an average over the course of all five periods) and the donation to the school (Spearman rank correlation: $\rho = -0.01$; $p = 0.85$ for the first period; $\rho = -0.04$; $p = 0.51$ for the average of all periods). This suggests that our two measures do not represent the same component of cooperative behavior. Furthermore, no correlation was found between the contributions to the public good (either for the first period or as an average over the course of all five periods) or the amount donated to the school and the players' age or socio-economic status (Spearman rank correlation: ρ coefficients ranging from −0.08 to 0.10; $0.07 < p < 0.55$).

3.2. Detection of altruism

The male and female series of player pairs were assessed by 101 and 93 male raters, respectively, and by 83 and 88 female raters, respectively.

The raters of both sexes were able to distinguish the highest and the lowest contributor to the public good among the male pairs; the observed detection rates were significantly higher than 50% for the male players (male raters: 57 %, $X^2 = 163$, df = 101, $p < 0.0001$; female raters: 58 %, $X^2 = 158$, df = 83, $p < 0.0001$). However, significant detection was not observed for the female players (male raters: 49 %, $X^2 = 70$, df = 76, $p = 0.96$; female raters: 50 %, $X^2 = 77$, df = 88, $p = 0.79$).

Therefore, the following analyses were performed only for male players. Several variables demonstrated a significant probability to be in the best approximating model; within each pair of players, the most selfish player in the game ($\beta = 0.66$; $I > 0.99$), the oldest player ($\beta = 0.09$; $I = 0.99$), and the poorest player ($\beta = -0.30$; $I > 0.99$) were more likely to be considered selfish by the raters, independently of the raters' sex ($\beta = -0.01$; $I = 0.27$). Having donated more or less to the school did not exhibit a significant probability of being in the best approximating model ($I = 0.24$).

The masculinity index varied from −1.70 to 3.53 for male players and from −3.10 to 1.12 for female players. We did not observe a correlation between players' behavior and their facial masculinity for either male players (Spearman rank correlation: $\rho = -0.11$; $p = 0.32$ for the contribution to the public good; $\rho = -0.15$; $p = 0.20$ for the amount donated to the school) or female players (Spearman rank correlation: $\rho = 0.09$; $p = 0.39$ for the contribution to the public good; $\rho = 0.20$; $p = 0.07$ for the amount donated to the school).

The multimodel inference on the GLMM demonstrated that more masculinized male players were more likely to be considered selfish ($\beta = 0.11$; $I = 0.69$). Nevertheless, even when controlling for masculinization, the contribution to the public good continued to exhibit a high probability of being in the best approximating model, with men contributing less being more likely to be considered as selfish ($\beta = 0.67$; $I > 0.99$). Older ($\beta = 0.09$; $I = 0.99$), and poorer ($\beta = -0.30$; $I > 0.99$) men also being more likely to be considered selfish. The raters' sex ($I = 0.27$) and the amount donated ($I = 0.44$) did not exhibit a significant probability of being in the best approximating model.

4. Discussion

The main aim of this study was to examine whether individuals are able to discriminate cooperators from non-cooperators on the basis of static facial cues. Facial traits, including static characteristics, are known to represent a component of attractiveness (through averageness, symmetry and secondary sexual traits); indicate phenotypic quality, genetic quality and developmental health (Little, Apicella, & Marlowe, 2007; Little & Hancock, 2002; Scheib, Gangestad, & Thornhill, 1999; Thornhill & Gangestad, 1993; Thornhill & Gangestad, 1999); reveal fertile windows (Manning, Scutt, Whitehouse, Leinster, & Walton, 1996; Scutt & Manning, 1996); provide information about an individual's diet (Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012); and demonstrate the relatedness of individuals (Alvergne, Faurie, & Raymond, 2007; Dal Martello & Maloney, 2006; Maloney & Dal Martello, 2006).

Non-static facial traits are known to provide cues for cooperativeness, such as facial emotional expressivity (e.g., Brown et al., 2003; Oda et al., 2009b). However, until now it was unclear whether static facial features also convey this type of information (Verplaetse et al., 2007). In this study, both male and female raters were able to detect, from facial photographs, which one of two men was the lowest contributor to the public good, at rates that were superior to the probabilities predicted by chance. We used face photographs with a neutral expression; therefore, only static facial cues were used to detect cooperativeness. Because the photographs represented Senegalese faces and the raters were French, at least some facial cues of cooperativeness appear to be inter-culturally readable. To our knowledge, this is the first evidence of the existence of such cues for social behavior in static faces that are shared across cultures.

However, the contribution to the public good was not correlated with the charitable contribution to the school canteen, and being pointed out as the most selfish was not significantly linked with being the smallest donator. This raises some question on what public good contributions in games represent, as compared to the charitable contributions, which could be thought *a priori* as a more realistic measure. Nevertheless, in this study, a high proportion of individuals

did not make any donation (~35%), so that many pairs of photographs did not differ in their donation, preventing the use of this measure.

Note that in addition, our experiment suggested that cooperative skills are also detected within the Senegalese population. Indeed, small groups of local raters of each sex were recruited and were asked to estimate, before the game, the players' propensity to contribute to the public good and to donate to the school on the basis of a short observation (including both verbal and non-verbal cues). These Senegalese men ($n = 3$) were able to evaluate both men's and women's cooperativeness in the public good game (Spearman rank correlation: for the male players: $\rho = 0.45$, $p = 0.006$; for the female players: $\rho = 0.43$, $p = 0.009$ game) and in the donation (Spearman rank correlation: for the male players: $\rho = 0.55$, $p = 0.006$; for the female players: $\rho = 0.42$, $p = 0.008$). The ability to detect cooperativeness is thus also present within the Senegalese population, although the specific verbal or non-verbal cues that were involved remain unidentified. This result extends the findings of previous studies, which had been restricted to examinations of industrialized cultures (Brown et al., 2003; Fetchenhauer et al., 2010; Oda et al., 2009a; Oda et al., 2009b; Verplaetse et al., 2007), suggesting that the ability to detect cooperativeness may be shared across cultures. However, Senegalese women did not appear to be able to detect cues of cooperativeness. It is notable that because of field conditions, only one group of three male raters and one group of three female raters were involved in this study; this limited number of raters precludes any generalization and study of the inter-rater variations that were observed.

The ability to accurately estimate cooperativeness among unfamiliar individuals through facial features, which are easily visible individual characteristics, is likely to play an important role in the choice of a social partner or mate. Indeed, this choice is pivotal for the outcome of an interaction. The use of both static and dynamic facial cues probably facilitates the detection of altruists. Altruists can therefore choose other altruists not only on the basis of past interactions but also from cues that are obtained during an initial encounter. The assortment of individuals by altruistic tendencies has been observed both in experimental studies and in real life, and altruistic participants are frequently preferred as partners for cooperative interactions (Barclay & Willer, 2007; Chiang, 2010; Pradel et al., 2009; Sheldon et al., 2000; Sylwester & Roberts, 2010). Moreover, this type of assortment also occurs with respect to mate choice; assortative mating according to cooperativeness has been observed in several countries (Buss, 1984; Guttman & Zohar, 1987; Luo & Klohnen, 2005; Price & Vandenberg, 1980). Preferences for a cooperatively similar mate can allow the evolution of altruism if the selfish advantage of egoistic individuals is out-competed by the benefits of mutual cooperation between altruists.

However, the specific facial traits that are involved in detecting cooperation remain unidentified. Notably, the French raters were unable to detect cooperativeness in the female Senegalese faces, which suggests that sex-specific traits are involved, at least interculturally. One of these traits could be facial masculinity. However, we did not find a link between male cooperativeness and facial masculinity or facial width-to-height ratios (results available upon request) as opposed to Stirrat and Perrett (2010). Nevertheless, further investigations suggested that male contributions to the public good were related to the distance between the external sides of the eyes (Spearman rank correlation: $\rho = -0.26$; $p = 0.02$ for the first period; $\rho = -0.24$; $p = 0.04$ as an average over the course of all five periods of the game). Experimental studies using artificial faces for which this distance can be manipulated are needed to confirm that this trait is a cue of cooperativeness.

In contrast to men, women's static traits do not appear to provide cues of cooperativeness, at least in this inter-cultural context. However, our small sample of Senegalese male raters was able to evaluate women's contributions. The female facial traits that are involved could therefore be culture-dependent. Another possible scenario is that women indicate their propensity to cooperate only via either dynamic facial traits (e.g., expressivity) or non-facial traits (e.g., gesture and language) that were available to the Senegalese raters but not to the French raters. A study using the identical photographs with Senegalese raters is necessary to discriminate between these hypotheses.

Static facial features are likely to represent honest signals and could therefore be crucial in the detection of cooperativeness. By contrast, although certain dynamic facial traits, such as the felt smile (characterized by orbicularis oculi muscle activity), are reliable, many dynamic traits can be falsified. Previous studies have indicated the presence of dynamic altruistic facial traits, such as emotional expressivity, but did not examine the detection components that are contributed by static traits. An investigation of the relative importance of static and dynamic traits should provide significant insights into the understanding of altruism detection.

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