

Human and Chimpanzee Face Recognition in Chimpanzees (*Pan troglodytes*): Role of Exposure and Impact on Categorical Perception

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The respective influences of exposure and inborn neural networks on conspecific and nonconspecific face processing remain unclear. Although the importance of exposure in the development of object and face recognition in general is well documented, studies explicitly comparing face recognition across species showed a species-specific effect. For instance, laboratory monkeys exposed daily to human faces were better at discriminating monkeys than humans, suggesting that the role of exposure may not be the only factor affecting cross-species recognition. In the present study, the authors investigated conspecific and nonconspecific face recognition in chimpanzees (*Pan troglodytes*) from 2 primate centers that provided different exposure to chimpanzee and human faces. The authors showed that the chimpanzees from the center providing more exposure to human faces than to chimpanzee faces were better at discriminating human faces than they were at discriminating chimpanzee faces. The chimpanzees from the other center did not show the same effect. A computational simulation was developed to evaluate the average similarities among human pictures and among chimpanzee pictures. Both categories were comparable. Chimpanzees' scores were significantly correlated with the similarity coefficients. Overall, the results show that exposure is a critical determinant in conspecific and nonconspecific face recognition.

Keywords: exposure, cross-species face recognition, nonconspecifics, species-specific, other-species effects

Faces play a central role in social interactions among primates. The respective roles of exposure and of specialized inborn neural networks in face recognition remain unclear. Although there is evidence that face recognition in humans is the result of the development of expertise due to a high amount of exposure to faces, there is also evidence that it is the product of a highly specialized system that might be organized as such from birth. Because there is strong evolutionary pressure to discriminate individual conspecifics but not to discriminate individuals of other species, the evolution of such a specialized system might have favored the processing of conspecific faces. It remains unclear whether primates are genetically predisposed to process conspecific faces more efficiently than nonconspecific faces. This would be consistent with the finding that monkeys prefer to look at pictures of their own species than at pictures of other species (Fujita, 1987), even in monkeys reared without experience with individuals of their own species (Fujita, 1990, 1993). For instance, rhesus monkeys reared with Japanese monkeys still showed a

preference for pictures of their genetic species, rhesus monkeys (Fujita, 1990). Rhesus monkeys reared in isolation and with no other visual input than slides showed a preference for pictures of conspecific infants in comparison with other pictures and showed fear reactions to threat pictures (Sackett, 1966). Sackett (1970) has argued that monkeys have an innate predisposition to respond to the individual features of conspecifics, suggesting the possible existence of a *species-specific* recognition system.

However, there is also evidence that individuals reared by another species show a preference for their foster species. Chimpanzees reared in captivity showed a preference for human pictures over pictures of chimpanzees or other primates (Tanaka, 2003). Japanese monkeys reared with rhesus monkeys developed a preference for rhesus monkey pictures (Fujita, 1990). Similarly, sheep reared by goat foster mothers developed a preference for individuals of their fostered species (goats) rather than for individuals of their own genetic species (Kendrick, Hinton, Atkins, Haupt, & Skinner, 1998). Unfortunately, to our knowledge, there are no published data on the ability of these cross-fostered subjects to differentiate between individuals of their foster species and individuals of their genetic species.

Although there are studies showing that nonhuman primates are able to discriminate faces of either conspecifics (Boysen & Berntson, 1989; Parr & Heintz, 2006; Parr, Winslow, Hopkins, & de Waal, 2000) or humans (Boysen & Berntson, 1986; Keating & Keating, 1993; Martin-Malivel & Fagot, 2001), studies explicitly comparing the ability of primates to differentiate between individuals of their own species and between individuals of other species are scarce (Humphrey, 1974; Parr, Dove, & Hopkins, 1998; Parr, Heintz, & Akamagwuna, 2006; Pascalis & Bachevalier, 1998; Peirce, Leigh, daCosta, & Kendrick, 2001). Using a visual paired

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comparison procedure, Pascalis and Bachevalier (1998) showed that rhesus monkeys presented novelty preference for monkey faces but not for human faces, suggesting that the monkey subjects discriminated monkey faces more efficiently than they discriminated human faces. In contrast, human subjects showed a novelty preference for human faces but not for monkey faces, suggesting a better discrimination of human faces than monkey faces. Both humans and monkeys showed a clear species-specific effect, subjects showing better discrimination performance in recognizing faces from their own species than from another species. The difficulty for human subjects in recognizing monkey faces can be explained by a lack of practice and experience with monkeys. However, Pascalis and Bachevalier (1998) highlighted that this lack of practice and experience is not likely to explain the monkey subjects' results. These laboratory monkeys were raised by humans since birth and had been exposed to various exemplars of human faces during their lives. Pascalis and Bachevalier (1998) suggested that the role of exposure may not be the only factor affecting cross-species recognition.

Studies of face perception in animals investigating phenomena typically associated with configural processing provide indirect information on face processing of conspecifics and nonconspecifics. In chimpanzees, Parr et al. (1998) showed that, although no difference was found in scores with chimpanzee faces, human faces, capuchin faces, and cars, an inversion effect was found with human and chimpanzee pictures (species for which subjects had prior exposure), but no inversion effect was found with capuchin monkey (unfamiliar species) and automobile pictures. In another study looking at the composite effect in chimpanzees, Parr et al. (2006) showed configural processing for conspecific but not for human faces. Although some studies with chimpanzees showed an inversion effect with human faces (Parr et al., 1998; Tomonaga, 1999) and conspecifics (Parr et al., 1998; Parr & Heintz, 2006), another study showed no inversion effect with conspecifics (Tomonaga, Itakura, & Matsuzawa, 1993). A right-hemisphere advantage was found in chimpanzees for human faces (Morris & Hopkins, 1993). With monkeys, some studies showed no inversion effect for monkey faces (Bruce, 1982; Phelps & Roberts, 1994; Wright & Roberts, 1996) but showed an inversion effect with human faces (Phelps & Roberts, 1994; Wright & Roberts, 1996), and other studies showed an inversion effect with conspecific faces (Parr, Winslow, & Hopkins, 1999; Tomonaga, 1994) but not with human faces (Parr et al., 1999). In some studies, monkeys (Martin-Malivel & Fagot, 2001) and sheep (Peirce et al., 2001) did not use internal features to discriminate pictures of human faces. In contrast, sheep used internal features to discriminate sheep faces (Peirce, Leigh, & Kendrick, 2000). A right-hemisphere advantage was found in sheep with sheep faces but not with human faces (Peirce et al., 2000, 2001), although the sheep had a high amount of exposure to human faces. Peirce et al. (2001) concluded that different neural systems may be used for the recognition of sheep and human faces and that experience is probably not always sufficient, stating that "nurture may be unable to overcome the effects of nature in some forms of perception" (p. 25).

In the human literature, however, there is evidence that exposure has an important influence on our ability to discriminate human faces. Although infants have a natural tendency to look at face-like stimuli at a very early age (Johnson, Dziurawiec, Ellis, & Morton, 1991), face recognition processes

in human infants develop as a result of prolonged exposure to faces (de Schonen & Mathivet, 1989). Another line showing the role of exposure is provided by the study of the so-called *other-race* effect. Human subjects more easily discriminated faces of their own ethnic group than faces of other ethnic groups (O'Toole, Deffenbacher, Valentin, & Abdi, 1994). This effect is reversible with experience. For instance, Korean children adopted after 3 years of age by Caucasian families became experts with Caucasian faces, identifying Caucasian faces better than the Asian ones (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005). Furthermore, intensive training with other-race faces can extinguish the other-race effect in adults who initially demonstrated the effect (Goldstein & Chance, 1985).

It is important to differentiate between the *other-race* effect, in which faces belong to the same species (humans), and the *other-species* effect, in which faces belong to different species (e.g., human and chimpanzee faces). Although the other-race effect is explained by exposure to specific types of faces and has no genetic components, the other-species effect could possibly have a genetic component in which primate face recognition systems would be specifically tuned for the recognition of conspecific faces. However, in the hypothesis that exposure is also the critical factor affecting the other-species effect, it is likely that the two effects have common mechanisms.

Another phenomenon providing information on the way facial categories are encoded is the categorical perception (CP) effect. CP arises when a physical continuum is perceived in terms of relatively discrete categories. CP occurs when physical differences of equal size are not psychologically perceived as being equal in size (Harnad, 1987). Recent studies in human subjects showed that CP could be demonstrated with faces by use of morphing techniques to create a physical continuum between individual faces of humans (Beale & Keil, 1995; Stevenage, 1998) and between faces of different species (Campbell, Pascalis, Coleman, Wallace, & Benson, 1997). CP has been demonstrated in animals in the auditory domain, for instance (Ehret, 1987). In the present study, we tested the existence of a CP effect between chimpanzee faces and between human faces and a potential link between exposure and the emergence of such an effect.

In addition to species and procedural differences, the discrepancies observed among studies in animals might be partially due to the differences in subjects' exposure to the categories tested and to differences in the stimuli sets used (in terms of similarity among the members of each category and spatial frequency content, among other items). In the present study, we evaluated face recognition performance with conspecific and nonconspecific faces and used a computational simulation both to control the stimuli and to model the subjects' performance. Two groups of chimpanzees having different exposure to human and conspecific faces were compared. A computational simulation was developed to evaluate the similarity among the human pictures and among the chimpanzee pictures, providing an assessment of the task difficulty for chimpanzee pictures and for human pictures. The purpose of the study was to (a) evaluate the chimpanzees' recognition skills with conspecific and human faces, (b) assess the correlation between the subjects' scores and the computational simulation similarity rating, and (c) investigate a potential link between face recognition performance and the emergence of a CP effect. The experiments were

in compliance with American Psychological Association ethical standards in the treatment of the animals and were approved by the Institutional Animal Care and Use Committee of Emory University.

Method

Subjects

Eight chimpanzees (*Pan troglodytes*) from two different primate research centers were tested: Four chimpanzees from the Language Research Center (LRC; Georgia State University, Atlanta, GA) and 4 chimpanzees from the Yerkes National Primate Research Center (Emory University, Atlanta, GA). These two groups of chimpanzees have different backgrounds and histories of interaction with other chimpanzees and with humans. The chimpanzees from the Yerkes National Primate Research Center (1 female and 3 male chimpanzees: Katrina, Scott, Lamar, and Jarred, 16 years old at the time of the study) were born in captivity and raised by humans in a group of baby chimpanzees. They moved into social groups (of 2 to 5 chimpanzees) with older chimpanzees at 4 years of age. After that age, the Yerkes chimpanzees had social interactions with some other chimpanzees and exposure to neighbors with whom they shared auditory contact and occasional physical contact through mesh. The subjects were pair-housed and therefore had physical interaction only with one conspecific. Although it was difficult to evaluate the number of chimpanzees that these subjects had been exposed to, we assumed that the number of conspecifics with which they had direct social interaction was somewhat limited in comparison with what they would encounter in the wild. Although the Yerkes population was quite large, therefore offering its chimpanzees repeated opportunities to be in visual contact with chimpanzees at a distance, the number of conspecifics they had direct social interaction with was limited. Concerning humans, the number of humans with whom the chimpanzees had direct interaction (e.g., caretakers, veterinary staff, maintenance staff, research staff, and visitors) was high, but after reaching 4 years of age, the chimpanzees' exposure to humans was limited to partially occluded faces. Humans at the Yerkes center wore personal protection equipment, including a mask, a face shield, and a hair net, as shown in Figure 1.

The subjects from the LRC were born in captivity and raised with extensive contact with humans. Lana, Sherman, Panzee, and Mercury (2 female and 2 male chimpanzees) were 33, 30, 18, and 17 years old, respectively, at the time of the study. Because they were part of a research project on language training in chimpanzees, the chimpanzee subjects had been involved in numerous training sessions requiring extensive direct interaction with humans since they were babies. The chimpanzees had met numerous humans (e.g., caretakers, veterinary staff, experimenters, and visitors, among others). Because humans at the LRC did not wear personal protection equipment, such as facial masks, their faces were freely visible. The LRC chimpanzees had extensive interaction with humans as social partners, and their exposure to human faces was very high. In contrast, the LRC chimpanzees had little exposure to chimpanzee faces. LRC chimpanzees lived together and therefore encountered only 3 other chimpanzees in their daily lives. Lana and Sherman had lived in a group of 3 chimpanzees since 1985 (the 3rd chimpanzee, Austin, died in 1996). Mercury



Figure 1. Human face visibility. Humans encountered by the Yerkes chimpanzees wore the personal protection equipment illustrated (mask, face shield, and hair net). Faces of the humans encountered by the Language Research Center chimpanzees were freely visible.

was Lana's son and had lived in the group since birth. Panzee joined them in early age. Duane Rumbaugh estimated that the chimpanzees probably encountered a maximum of 12 different chimpanzees in their lifetimes, on rare occasions and for short periods of time.

Procedure

The chimpanzees from the two research centers had extensive training with joysticks and computerized video tasks such as the matching-to-sample task used in this study (Morris & Hopkins, 1993; Parr & de Waal, 1999; Parr et al., 2000). The chimpanzees were tested in their home cages with a similar wheeled computerized testing system. Grayscale pictures (180 × 180 pixels) were presented on a 14-in. screen. The human pictures were taken from the FERET database (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips, Wechsler, Huang, & Rauss, 1998) and modified to present the faces on a uniform black background. The experiment in both centers was controlled with the same custom-made Visual Basic (Version 6.0) program. To initiate a trial, the subject had to manipulate the joystick in order to place the cursor on the fixation point. A single image (model) was then presented for 3 s. When the model disappeared, two images were presented (comparison stimuli), and the subject had to select with the cursor which one was identical to the model image. Feedback was given by two different sounds for correct and incorrect answers and by food reward for every correct answer.

Human faces were matched only with human faces (eight unknown individuals; four male and four female humans; the human condition), and chimpanzee faces were matched only with chimpanzee faces (eight unknown individuals; four male and four female chimpanzees; the chimpanzee condition). Two types of trials were presented: baseline trials (in which normal images were used) and CP trials (in which morphed images were used). The

baseline trials were used for evaluating the expertise levels of the subjects with human and chimpanzee faces (Figure 2a). We used the CP trials for evaluating the categorical perception effect. Morphed images were created by preparing a continuum between individuals of the same species (four humans or four chimpanzees) using a morphing program called NovaFx. One continuum for each species is illustrated in Figure 2b. For each continuum, six images were selected, from one end point to the other, with a step of 20% difference between adjacent images. Each of the four human images was morphed with the images of three other humans, resulting in six possible continua of human morphed images. The same rule applied to the chimpanzee pictures.

A CP trial consisted of the presentation of one of the morphed images as model, followed by two comparison samples: one being identical to the model, the other being an adjacent image (which was 20% different from the model). Therefore, each sample pair was one of the five possible pairs represented in Figure 2b (P1, P2, P3, P4, P5), from one of the 12 possible continua (6 human and 6 chimp continua). Two continua were used in each session (one human and one chimp continuum). Each session consisted of 48 baseline trials [2 species(4 images × 3 combinations × 2 sides)] and 40 CP trials (2 continua × 5 pairs × 2 presentations × 2 sides). Six sessions were needed to present the 12 possible con-

tinua, and each session was repeated twice. Therefore, each subject received 12 sessions of 88 trials each, for a total of 1,056 trials per subject. The original images were presented both in the baseline trials and in the Pairs 1 and 5 of the CP trials. Because these images were presented considerably more often than the morphed images, these pairs were excluded from the CP analyses in order to avoid an anchor effect. For both baseline and CP trials, trials for which response times exceeded 10 s were considered as null. Scores and response times were the dependent variables.

Results

Performance With Human and Chimpanzee Pictures

Figure 3 shows the performance and response times of the LRC and Yerkes chimpanzees for the first session. Mixed factorial analyses of variance (ANOVAs) with center (LRC vs. Yerkes chimpanzees) as the between-subjects factor and species (human vs. chimpanzee pictures) as the within-subjects factor were used to test the study hypotheses. Subjects were used as a random factor in the following analyses. In addition, Levene's tests for equality of variances across independent groups were computed and showed equality of variances for all analyses. The ANOVA on response

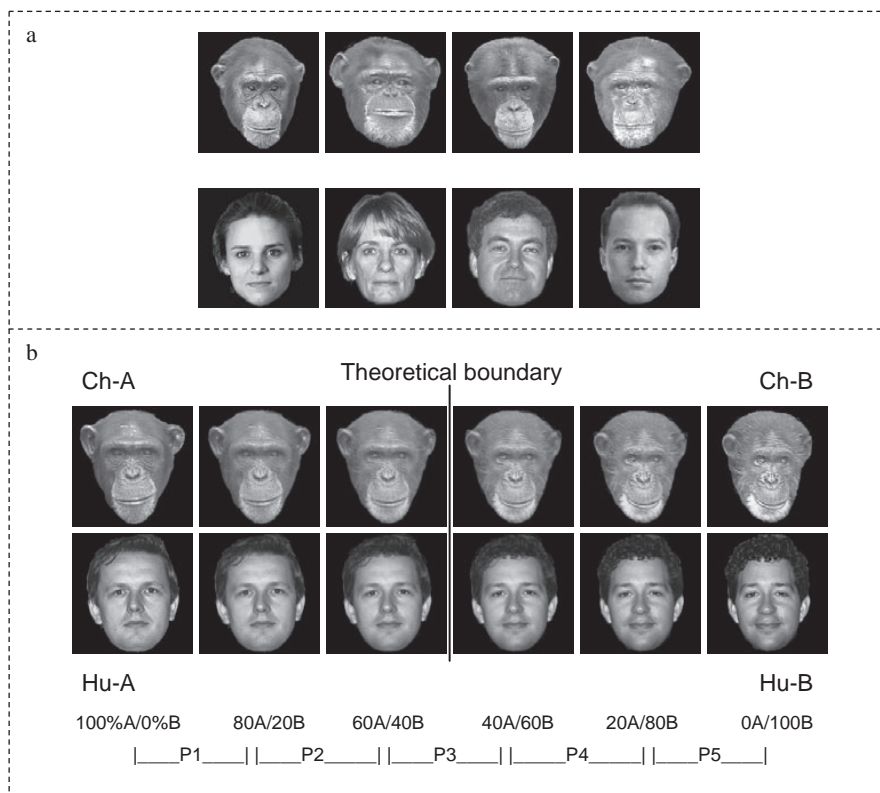


Figure 2. Stimuli used. a: Example of human and chimpanzee pictures used for baseline trials (images of 2 female and 2 male models for each species). b: Example of a chimpanzee continuum and a human continuum created by morphing (creating a step of 20% difference between each image) for categorical perception (CP) trials. For each CP trial, one image was used as model, followed by two comparison samples: the same image and an adjacent image. When CP occurred, subjects more easily discriminated the stimuli of Pair 3 (cross-categories) than they discriminated the stimuli of the other pairs (within-category). Ch = chimpanzee; Hu = human.

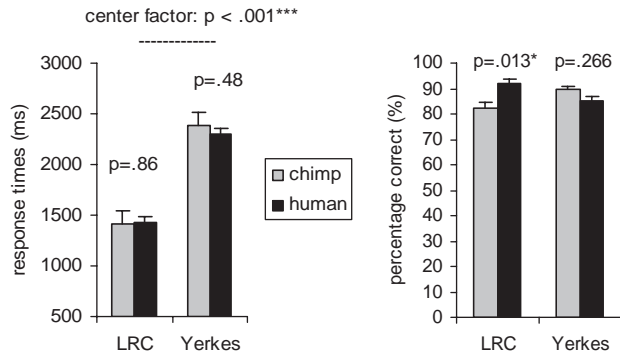


Figure 3. Performance on baseline trials, first session. Average response times (left) and percentage correct (right) on the baseline trials (normal images, first session) for subjects of each center (the Language Research Center and the Yerkes National Primate Research Center) and for each tested category (chimpanzee and human pictures). Vertical bars represent standard errors.

times showed a significant effect of the center factor, $F(1, 6) = 55.950$, $p < .001$. The LRC chimpanzees responded faster ($M = 1,421$ ms) than the Yerkes chimpanzees ($M = 2,340$ ms). The main effect of species was not statistically significant, $F(1, 6) = 0.309$, $p > .05$. The Center \times Species interaction was not significant, $F(1, 6) = 0.59$, $p > .05$. A second analysis taking into account the 12 test sessions replicated these findings. The LRC chimpanzees responded significantly faster than the Yerkes subjects, $F(1, 6) = 33.194$, $p = .001$. No other effect was significant.

The ANOVA on scores showed no significant effect of center, $F(1, 6) = 0.00$, $p > .05$, or species, $F(1, 6) = 1.742$, $p > .05$, factors. However, the Center \times Species interaction was significant, $F(1, 6) = 13.886$, $p = .01$. To determine the nature of the interaction, tests of species effects were conducted separately for the LRC and Yerkes chimpanzees. For the LRC chimpanzees, the species effect was significant, $F(1, 3) = 29.007$, $p = .013$. The LRC chimpanzees discriminated the human pictures more easily than they did the chimpanzee pictures. For the Yerkes chimpanzees, the species effect was not significant, $F(1, 3) = 1.855$, $p > .05$. These findings were replicated when considering the 12 test sessions. The species effect was significant for the LRC chimpanzees, $F(1, 3) = 14.581$, $p = .032$, showing that they discriminated human faces more easily than they did chimpanzee faces. In contrast, there was no effect of the species factor for the Yerkes chimpanzees, $F(1, 3) = 0.034$, $p > .05$.

The LRC chimpanzees responded significantly faster than the Yerkes chimpanzees (900 ms faster; 1.6 times quicker). Moreover, the analyses of performance showed a significant interaction between the center and species factors, showing that the chimpanzees from the two centers were not processing the human and chimpanzee faces the same way. Considering these results and the fact that the chimpanzees from the two centers had different backgrounds and exposure to human and chimpanzee faces, scores are hereinafter analyzed separately.

Computational Simulation

Could a machine also discriminate the human pictures more easily than the chimpanzee pictures? We can indeed hypothesize

that the fact that the LRC chimpanzees discriminated human faces more easily than they discriminated chimpanzee faces could be an artifact due to a bias in the set of pictures used in this experiment. It is possible that the random choice of a small stimuli set (eight different individuals for each species) resulted in chimpanzee pictures that were more similar to each other than the human pictures and therefore more difficult to discriminate. It is also possible that, at the population level, human faces are more different from each other than are chimpanzee faces. There are no data, to our knowledge, on the amount of variability among chimpanzee faces in comparison with the amount of variability among human faces.

We developed a computational simulation in order to evaluate the similarity among human pictures and among chimpanzee pictures. This simulation is based on a model developed by Okada et al. (1998) in the context of artificial face recognition and has been successfully used in the past (Nederhouser, Mangini, Biederman, & Okada, 2002, 2003). The simulation was inspired by a theoretical face recognition model proposed by Biederman and Kalocsa (1997). In the simulation, similarity coefficients are computed for pairs of human or chimpanzee pictures. For each pair, a grid representing a regular lattice with 11×11 nodes is placed on both images, as illustrated in Figure 4. It computes local descriptors (Gabor jets) at each of the 100 corresponding nodes (details are presented in Okada et al., 1998). One image (see Figure 4A) is taken as a reference, and the grid is translated on the second image (see Figure 4B), looking for the best match location. This method is used to achieve approximate pixel correspondence between the two images, the nodes being more likely to point at the same physical locations across images than when no translation is used. If the locations of faces are different across images, the translation corrects for alignment. A similarity coefficient is computed for each pair. Two series of similarity coefficients are obtained: one for the human set, one for the chimpanzee set. To compare the human and the chimpanzee sets, both the similarity averages (human vs. chimpanzee) and the variances around these averages were important to consider. A Levene's test for equality of variances showed that the variances were equal across groups (human set and chimpanzee set), $F(1, 22) = 0.089$, $p = .769$. Figure 4

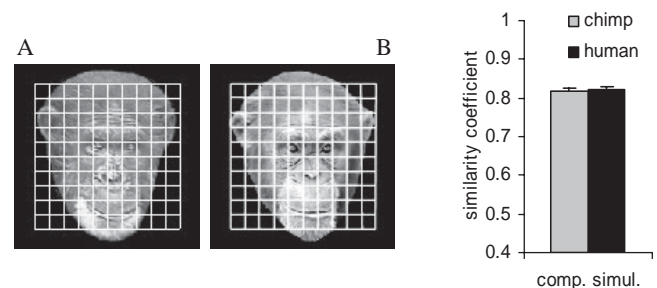


Figure 4. Computational (comp.) simulation (simul.). Similarity coefficients were computed for each pair of pictures. A grid representing a regular lattice with 11×11 nodes was placed on both images. Local descriptors (Gabor Jets) were computed at each of the 100 corresponding nodes. One image was taken as a reference (A) and the grid was translated on the second image (B) to look for the best match location. The graph illustrates the average similarity coefficients obtained for the human and the chimpanzee pictures. Vertical bars represent standard errors.

shows the average similarity index for each set. An ANOVA showed that there was no difference between the average similarity coefficients of human pictures and chimpanzee pictures, $F(1, 22) = 0.185, p > .05$. This computational simulation showed that, for the stimuli used in this experiment, chimpanzee pictures were not more similar than human pictures and should therefore not have been more difficult to discriminate than human pictures.

Correlation Between Computational Simulation and Chimpanzees' Scores

Separate correlations controlling for species were computed to investigate whether there was a link between the computational simulation ratings (similarity coefficients for each pair) and the chimpanzees' performance (average scores for each pair). For both the LRC and Yerkes chimpanzees, the similarity coefficients and the scores were significantly correlated: first testing session for LRC chimpanzees, $r(21) = -.466, p = .025$; first testing session for Yerkes chimpanzees, $r(21) = -.758, p < .001$. The same results were found when considering the 12 test sessions: LRC chimpanzees, $r(21) = -.627, p = .001$; Yerkes chimpanzees, $r(21) = -.817, p < .001$. Figure 5 illustrates the correlations between scores (12 sessions) and similarity coefficients. Subjects' scores were lower for high similarity coefficients (pairs in which pictures were the most similar and therefore more difficult to discriminate) than for low similarity coefficients (pairs in which pictures were the most different).

Effect of the Species Factor After Adjusting for Similarity

Scores were analyzed again using the computational simulation similarity rating as a covariate. For both centers, the results strengthen the previous findings. For the LRC chimpanzees, consistent with the correlation findings, an analysis of covariance (ANCOVA) with picture pairs as random factors showed that the impact of the similarity covariate on performance was significant, $F(1, 20) = 5.37, p = .03$. The similarity factor accounted for

21.2% of the variance in performance. The Species \times Similarity interaction was not significant, $F(1, 20) = 0.056, p > .05$, showing that the similarity covariate had a parallel impact for both species conditions. Figure 6 represents the scores adjusted for the similarity covariate. An ANCOVA on the scores from the first session showed that, when the similarity coefficients were taken into account, the species effect was significant, $F(1, 21) = 8.377, p = .009$, for the LRC chimpanzees. This finding reinforces the conclusion that the LRC chimpanzees discriminated human faces more easily than they discriminated chimpanzee faces. These findings were replicated when considering the 12 test sessions. The similarity covariate was statistically significant, $F(1, 20) = 12.723, p = .002$, and accounts for 38.9% of the variance in scores. No Species \times Similarity interaction was found. After adjusting for similarity, the species effect was statistically significant, $F(1, 21) = 8.657, p = .008$, with discrimination for human faces greater than for chimpanzee faces.

Similarly, for the Yerkes subjects, the ANCOVA showed a significant effect of the similarity covariate on scores, $F(1, 20) = 27.876, p < .001$. The similarity factor accounted for 58.2% of the variance in performance. The Species \times Similarity interaction was not statistically significant, $F(1, 20) = 2.096, p > .05$, showing that the similarity covariate had a parallel impact on both species conditions. The ANCOVA on the scores adjusted for similarity showed no significant effect of the species factor, $F(1, 21) = 2.136, p > .05$. Analyses on the 12 test sessions replicated these findings. Similarity had a significant effect on scores, $F(1, 20) = 39.631, p < .001$, accounting for 66.5% of the variance in performance. There was no Species \times Similarity interaction ($p > .05$) and no statistically significant species effect after adjusting for similarity, $F(1, 21) = 0.018, p > .05$.

Categorical Perception

Figure 7 shows the results on the CP trials. For the LRC chimpanzees, an ANOVA of scores showed a significant effect of

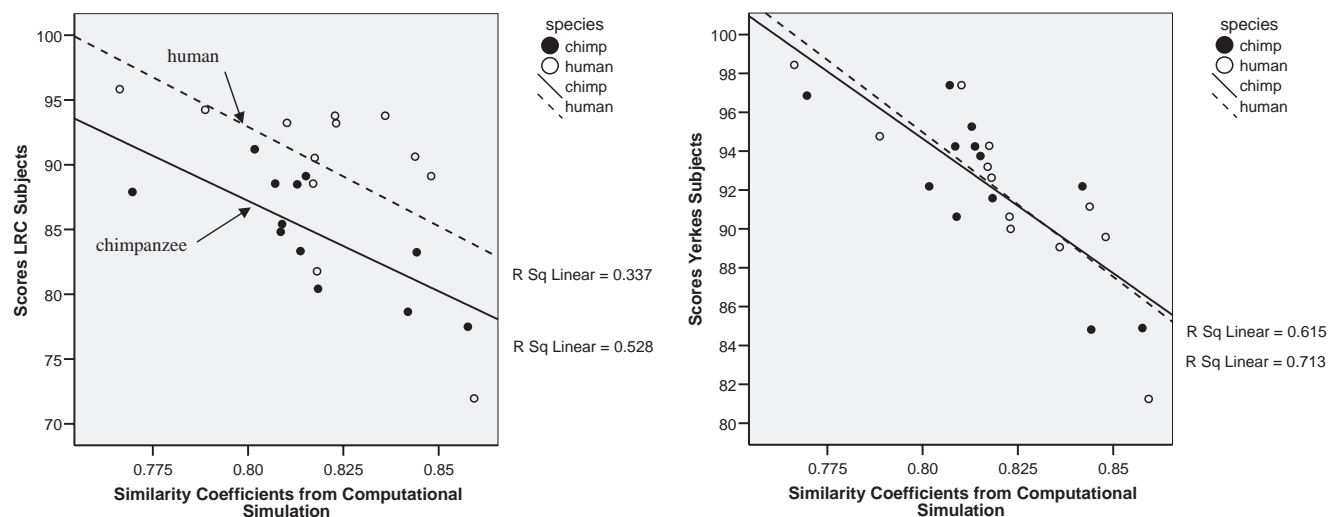


Figure 5. Correlation between subjects' performance and computational simulation. The graph represents the average chimpanzees' scores for each pair plotted against the similarity coefficient obtained from the computational simulation. R Sq = root square; LRC = Language Research Center.

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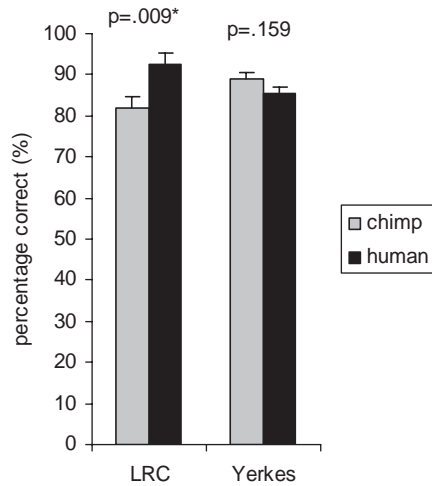


Figure 6. Average chimpanzees' scores adjusted for the similarity covariate for subjects of each center (the Language Research Center and the Yerkes National Primate Research Center) and for each category tested (human and chimpanzee pictures). Vertical bars represent standard errors.

categorical perception for human faces, $F(1, 3) = 16.11, p = .028$. Scores were higher in the cross-category condition (stimuli crossing the theoretical boundary) than in the within-category condition (stimuli on the same side of the boundary). In contrast, there was no significant effect of categorical perception with chimpanzee faces, $F(1, 3) = 0.178, p > .05$. For the Yerkes chimpanzees, there was no significant effect of categorical perception for either human faces, $F(1, 3) = 5.069, p > .05$, or chimpanzee faces, $F(1, 3) = 0.32, p > .05$.

Discussion

In the present study, the LRC chimpanzees discriminated human pictorial faces more easily than they discriminated chimpanzee pictorial faces and showed a categorical perception effect only with human pictures. The computational simulation showed that the average similarity among the human pictures was equivalent to the average similarity among the chimpanzee pictures. The performance difference for the LRC chimpanzees between human and chimpanzee pictures is therefore unlikely to be the consequence of differences in task difficulty due to stimuli sets. A hypothesis to

explain the difference in performance is that the nature of the human faces per se is different than the nature of the chimpanzee faces. For instance, it is possible that human faces are more homogeneous than are nonhuman primate faces, eliciting different processes such as configural processing, as suggested by Wright and Roberts (1996). This would be consistent with the finding that monkeys showed an inversion effect with human faces but not with faces of other primate species (Phelps & Roberts, 1994; Wright & Roberts, 1996). However, evidence for configural processing was also found with conspecific faces (Parr et al., 1999, 2006; Tomonaga, 1994) but not with human faces (Parr et al., 1999, 2006) in both monkeys and chimpanzees. Further investigations are needed to evaluate the relative complexity of faces of different species and the impact of this complexity on face processing.

An alternative hypothesis to explain the highest performance with human pictures is that the LRC chimpanzees might have developed better recognition skills for human faces than for conspecific faces through exposure. The LRC chimpanzees had been exposed to a greater number of humans than chimpanzees. As explained in the Method section, LRC chimpanzees lived together and therefore had encountered only three other chimpanzees in their daily lives. It is estimated that they had had only brief contact with as many as 12 other chimpanzees in their lives. In contrast, the LRC chimpanzees continually encountered a greater number of humans, with freely visible faces. Although the hypothesis of a role of exposure in better discrimination of nonconspecifics (humans) than conspecifics is not consistent with the species-specific effect previously demonstrated both in face recognition (Pascalis & Bachevalier, 1998) and in social interest (Fujita, 1990) in monkeys, it is consistent with the literature on the role of exposure in visual perception in general. In the human literature, there is evidence that exposure has an important influence on humans' ability to discriminate faces and objects. In the domain of nonface stimuli, Diamond and Carey (1986) showed an inversion effect for dog pictures in dog experts equivalent to the inversion effect found with faces. Similarly, human subjects can be trained to become experts in "Greebles," novel objects sharing a common spatial configuration (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). Furthermore, some studies have shown that areas of the brain normally associated with face recognition are activated in expert subjects discriminating Greebles (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). In contrast, other studies have

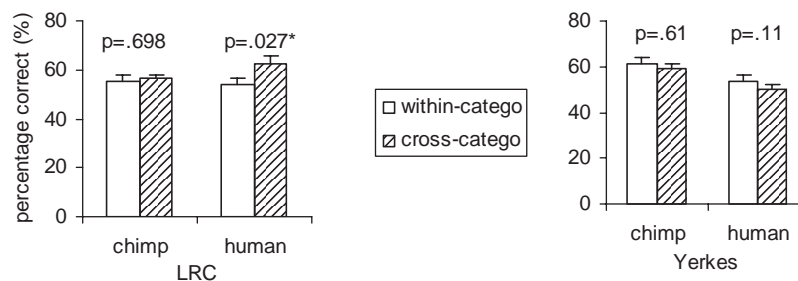


Figure 7. Average chimpanzees' scores for the categorical perception trials for each species (human and chimpanzee pictures) and each condition (within-category and cross-categories). Vertical bars represent standard errors. category = category.

shown that face-like holistic processing does not emerge for objects of expertise (Robbins & McKone, 2007; see McKone, Kanwisher, & Duchaine, 2007, for a review). For example, Robbins and McKone (2007) failed to replicate Diamond and Carey's (1986) results with dog experts. The debate between the expertise hypothesis and the domain-specific hypothesis has generated a heated discussion (Gauthier & Bukach, 2007; McKone & Robbins, 2007; Robbins & McKone, 2007). However, the literature seems to agree on the fact that experience plays a role in object and face processing in general. In the experience-expectant innate template model proposed by McKone et al. (2007), the authors suggested the existence of an innate template that would code the basic structure of a face (eye blobs above nose blob above mouth blob) and would necessitate appropriate input during infancy to develop holistic processing coded by specific neural structures. They also proposed that the coding of face structure must remain general enough to enable holistic processing to be applied to initially nonexperienced subtypes of faces after practice (e.g., other-race faces). Our findings are not contradictory with either the expertise hypothesis or McKone et al.'s (2007) proposition. Within this latter framework, our results imply that if an innate template exists, it must be general enough to allow the development of holistic processing with nonspecific faces if sufficient exposure is provided. This hypothesis is consistent with the developmental work.

Studying the other-species effect in humans, Pascalis, de Haan, and Nelson (2002) tested the ability of 6-month-olds, 9-month-olds, and adults to discriminate human and monkey faces. Although the youngest humans showed discrimination among human and among monkey faces, older infants and adults showed evidence of discrimination of human faces only. This result parallels the finding that human infants' ability to discriminate among foreign speech sounds decreases between 6 and 10 months of age (Kuhl, Tsao, & Liu, 2003). This general narrowing of perceptual abilities was also found at the intersensory level (Lewkowicz & Ghazanfar, 2006). Lewkowicz and Ghazanfar (2006) showed that young human infants (4–6 months of age) were able to match specific monkey vocalizations with the video of a monkey producing the corresponding vocalization, while older infants (8–10 months of age) were not able to match the vocalizations with the faces. The authors proposed that the youngest babies (4–6 months of age) were able to detect basic low-level features (such as the synchrony of the video of the facial expression and its corresponding vocalization), but the oldest babies (8–10 months of age) did not pay attention to these low-level elements anymore and were looking for higher level features to integrate auditory and visual information. The existence of such a broad perceptual window at an early age would be adaptive in that it accommodates diverse forms of sensory information, including those from a different primate species.

Investigating the role of early exposure in human babies, Pascalis et al. (2005) demonstrated that exposure to monkey faces between 6 and 9 months of age facilitates the discrimination of monkey faces. The 9-month-olds that received exposure were still able to discriminate monkey faces, an ability that is otherwise lost at around that age. In the case of the LRC chimpanzees, it is possible that early exposure to numerous human faces (and reduced exposure to chimpanzee faces) explains the ability to discriminate human faces more efficiently than chimpanzee faces.

However, it is difficult to draw a conclusion about the effect of early exposure versus that of later exposure, as these chimpanzees had exposure to human faces their entire lives. It would be interesting to have the possibility to compare populations of primates with long-lasting exposure, only early exposure, and only late exposure. It is likely that, in contrast with late exposure, early exposure significantly facilitates the development of expertise. However, it is possible that early experience is not sufficient and that expertise would be lost in the absence of further exposure (Parr et al., 2006).

The literature on CP suggests a link between expertise level and the emergence of CP. In human subjects, Levin and Beale (2000) showed that CP can occur with unfamiliar human faces belonging to both familiar (same-race) and unfamiliar (other-race) ethnic groups, although the effect was smaller for the other-race faces. Levin and Beale argued that these CP effects reflect the rapid acquisition of the new faces as new perceptual classes. The CP effect magnitude varied systematically with the difficulty of representing the end points: for faces difficult to memorize (other-race faces), the CP effect was weaker than that for same-race faces. It was more difficult for subjects to rapidly encode good visual representations of the new faces for faces for which they had a lower expertise. According to Levin and Beale (2000), CP reflects a quick parse of new perceptual categories into equivalence classes and is correlated with expertise level. The finding that the LRC chimpanzees showed CP for the species for which they had the highest performance is consistent with Levin and Beale's conclusion.

In Levin and Beale's (2000) study, CP was found even for novel continua between novel other-race faces, a category for which subjects have a low level of expertise. We believe that the fact that we did not show a CP effect for the categories for which the subjects had the lowest performance does not conflict with this finding. Although subjects in human studies had a lower level of expertise for the other-race category, it is likely that they have some degree of expertise through exposure and generalization from the same-race category. Both other-race and same-race faces belong to the "human" category and share important similarities. In contrast, even if they share a common general configuration, human and chimpanzee faces are quite different. We believe that, for the categories for which they did not have high recognition skills, our subjects were not able to rapidly learn new faces as new perceptual classes and therefore did not show CP.

Some elements in favor of the role of exposure in nonconscious recognition are found in the literature on the neural basis of visual recognition. In a study on the onset latencies of inferotemporal neuronal responses to various types of objects and faces in rhesus monkeys, Kiani, Esteky, and Tanaka (2005) found that inferotemporal neurons responding specifically to faces responded faster to faces of primates than to faces of animals other than primates. This finding seems consistent with the finding that, in human subjects, human faces evoked potentials earlier than did animal faces (McCarthy, Puce, Belger, & Allison, 1999; Rousselet, Macé, & Fabre-Thorpe, 2004). Kiani et al. (2005) also found that face-responding cells responded with similar onset latencies to macaque and human faces. Kiani et al. (2005) noted the inconsistency between their finding and the species advantage shown by Pascalis and Bachevalier (1998). However, as underlined by Kiani et al. (2005), the neural activity was recorded in laboratory mon-

keys for which human faces are likely to be as salient as monkey faces, due to their extensive exposure to human faces. The onset latencies observed might be correlated with the recognition skills of the studied monkeys. This would be consistent with the finding that responses of inferotemporal cells are influenced by visual experience (Kobatake, Wang, & Tanaka, 1998; Logothetis, Pauls, & Poggio, 1995) and that, as the stimulus becomes more effective, the magnitude of response increases and its latency decreases (Koch, 1999).

In the present study, in contrast with the LRC chimpanzees, the Yerkes chimpanzees showed equivalent performances with human and chimpanzee faces. This result is consistent with the findings of Parr et al. (1998), in which the same subjects were tested. The subjects showed similar performances for human faces, chimpanzee faces, capuchin faces, and cars (only scores for humans were significantly higher than scores for cars) but showed an inversion effect only for human and chimpanzee faces, species for which they had exposure. The results from Parr et al. (1998) suggest that these chimpanzees developed some expertise with both human and chimpanzee faces and that their recognition skills are equivalent for both species, which is consistent with our results. However, the findings from Parr et al. (1998) and from our study are partly in contradiction with the findings of Parr et al. (2006), in which the same chimpanzees showed configural processing for chimpanzee faces but not for human faces, suggesting higher recognition skills with chimpanzee faces than with human faces. A potential explanation is that the recognition skills might have evolved over time. Although these subjects had a significant exposure to freely visible human faces before the age of 4 years, most of the humans they encountered wore personal protection equipment, particularly after the chimpanzees were 4 years of age. It is possible that the subjects lost part of their expertise with human faces between the ages of 8–9 years (Parr et al., 1998) and 18 years (Parr et al., 2006) due to a lack of exposure to freely visible faces. This would be consistent with the observation that these chimpanzees appeared to primarily use the top part of human faces to discriminate pictures (Parr et al., 2006). The hypothesis of a decrease of expertise over time is consistent with the findings of Sangrigoli et al. (2005), which showed that Korean children adopted when they were between the ages of 3 and 9 years by Caucasian families later showed reduced recognition for Korean faces in comparison with control Korean children living in Korea. Our study was run prior to Parr et al.'s (2006) study, so it is possible that the chimpanzees still had equivalent recognition skills with human and chimpanzee faces at the time of our study. However, the subjects were already 16 years old (in contrast with being 18 years old in the Parr et al., 2006, study). Although we cannot rule it out, 2 years seems a short lapse of time to explain the drop of performance observed between the two studies. Procedural differences (e.g., variation in sample display time) or stimuli sets could also potentially explain the discrepancy.

Although the recognition skills of our subjects might have evolved over time, it can, however, be considered that they have some form of expertise with both species (at least if “expertise” is understood as the ability to individuate exemplars of a category), as it is likely that they are able to individuate the humans and the chimpanzees with whom they interact. Why the Yerkes chimpanzees did not show a CP effect in our study is unclear. It might be that a higher level of expertise is required for the emergence of a

CP effect. The exposure level of the Yerkes chimpanzees with humans and chimpanzees is more difficult to evaluate than the exposure level of the LRC chimpanzees with humans and chimpanzees. Yerkes chimpanzees encountered numerous humans but saw them with personal protection equipment masking part of the face (particularly when the chimpanzees were older than 4 years of age). Yerkes chimpanzees also encountered multiple chimpanzees, but their daily physical interaction was primarily limited to one conspecific over a period of many years. Because of the differences in the subjects' backgrounds, it is difficult to compare the LRC and Yerkes subjects. It is possible, however, that the Yerkes chimpanzees developed some expertise level for both humans and chimpanzees, but not one as fine-tuned as that of the LRC chimpanzees. This would be consistent with the finding that their response times were slower than those of the LRC chimpanzees (920 ms slower; $p < .001$) and explain why Yerkes chimpanzees did not show a CP effect. Future studies should investigate the possibility that humans and nonhuman primates can have different levels of expertise depending on their level of exposure to non-conspecifics. For example, casual observations suggest that humans with no experience with chimpanzees find it difficult to identify them. After a relatively short period of time, humans are able to individuate the animals, but initially by using simple cues (i.e., “the chimpanzee with the spot on the cheek”), and the recognition seems to become more holistic over time, and recognition skills appear to increase with experience, over the years. Empirical studies with both nonhuman primates and humans having different amounts of exposure are needed to evaluate the possibility that observers can develop different levels of face recognition skills depending on their exposure.

An alternative hypothesis to explain the results of the present study is that CP is more likely to emerge with human faces than with chimpanzee faces, consistent with a potential difference in nature eliciting different types of processes. Within that framework, both the Yerkes and LRC chimpanzees would not show CP for chimpanzee faces; the LRC chimpanzees would show CP for human faces because they are fully processing the faces, whereas the Yerkes chimpanzees would not show CP because they do not process the human faces in a configural way, as demonstrated by Parr et al. (2006).

It is also possible that language training influenced the emergence of CP for the LRC chimpanzees by eliciting a particular way of processing categories. It is interesting to note that one of the subjects, Mercury, served as a control in the language studies and was never explicitly language trained. The observation that this subject presented a CP pattern comparable to those of the 3 other subjects does not support the hypothesis that language training influenced the emergence of CP, but because the present study was not designed to assess this aspect, and because studies on CP in animals are scarce, it is not possible to conclude on this point, and it merits further investigation.

Overall, we propose that the results of the present study suggest that exposure plays a critical role in the encoding and recognition of conspecific and nonconspecific faces. Chimpanzees exposed to a greater number of human than conspecific faces can become more efficient at recognizing human faces than conspecific faces. A high level of recognition skills might be necessary for the emergence of a CP effect with faces, suggesting that fine-tuned face processing does not occur only on the basis of innate percep-

tual programming. Although the present study does not rule out the existence of an inborn neural network specifically tuned to conspecific faces (Sackett, 1970), it does support the hypothesis that exposure is a critical determinant. If a species-specific predisposition exists, we suggest that exposure can supersede the genetic predisposition.

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