Visual Kin Recognition and Family Resemblance in Chimpanzees (*Pan troglodytes*)

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The male-offspring biased visual kin recognition in chimpanzees (*Pan troglodytes*) reported by L. A. Parr and F. B. M. de Waal (1999) was replicated with human (*Homo sapiens*) participants and a principal components analysis (PCA) of pixel maps of the chimpanzee face photos. With the same original materials and methods, both humans and the PCA produced the same asymmetry in kin recognition as found with the chimpanzees. The PCA suggested that the asymmetry was a function of differences in the distribution of global characteristics associated with the framing of the faces in the son and daughter test sets. Eliminating potential framing biases, either by cropping the photos tightly to the faces or by rebalancing the recognition foils, eliminated the asymmetry but not human participants' ability to recognize chimpanzee kin.

For kin selection (Hamilton, 1964a, 1964b) to play the role posited by evolutionary biologists, there must be some mechanism for the discrimination of kin from nonkin. Suggested mechanisms have ranged from experiential familiarity with nest, troop, or clutch mates of nondispersing species to explicit genetic markers and shared tropisms in other species (e.g., Greenberg, 1979; Waldman & Adler, 1979; Wu, Holmes, Medina, & Sackett, 1980; reviewed in Rendall, 2004). Recently, Parr and de Waal (1999) reported an unusual example of visual kin recognition. In their study, 5 chimpanzee subjects matched facial photos of mothers and their male offspring at levels above chance when both were unre-

lated and unfamiliar to the subjects. However, they were not able to match photos of mothers to their female offspring.

This asymmetry in the chimpanzees' ability to match photos of mothers to their sons but not daughters was given a functional interpretation by Parr and de Waal (1999) as an adaptive response to the patrilineal structure of chimpanzee communities. In these communities, it is the males that form the stable core of related individuals, whereas adult females are unrelated, having immigrated in from other communities at sexual maturity. It is also the males that show high levels of social affiliation and cooperation, thereby potentially reaping the kin-selected fitness benefits associated with kin-biased social behavior (cf. Hamilton, 1964a, 1964b). According to Parr and de Waal, the fact, then, that these chimpanzees were better able to match the photos of faces of unfamiliar males as opposed to females to those of their mothers suggests that the patrilineally stratified nature of chimpanzee communities may have favored a specialized mechanism related to faces and face processing that facilitates efficient detection of male relatedness in this species.

Such a specialized face-recognition mechanism might arise in one of two ways. The first is the development of face-recognition routines in the perceiver that are specialized for the detection of preexisting differences in how the faces of sons and daughters resemble their mothers' faces. For example, developmental differences between sons and daughters may well result in differences in the extent to which certain facial characteristics resemble those of their mothers, some favoring sons and others favoring daughters (e.g., male development may exaggerate a trait of the mother's appearance—say, large ears—whereas female development may exaggerate a different trait of the mother's appearance—say, a flat nose). Given the characteristics of this species' social organization, selection might then favor the evolution of face-recognition routines specifically tuned to just those traits shared by mothers and

sons. Daughters' faces may also resemble their mothers' faces in some features, but the absence of selection pressure for mother–daughter recognition means that no analogous mechanism for the detection of these similarities has evolved.

An alternative possibility is that characteristics of the faces themselves—either structurally or, more plausibly in our view, through characteristic, identifying behaviors (e.g., pose, expression)—have been or through development are modified to bias preexisting recognition routines toward the detection of the facial similarity of mothers and their male offspring. Although we are not aware of any direct evidence for the latter, it is intuitively plausible that, for example, sons might tend to copy (perhaps unintentionally) the characteristic poses and facial expressions of their mothers precisely to encourage the detection of relatedness to her and, thereby, other male offspring. Because adult females disperse from kin at sexual maturity, there would be less requisite selective advantage for them to adopt the poses and expressions of their mothers or siblings.

In short, by one process, sons and daughters both resemble their mothers but in different ways, and selection has favored special recognition mechanisms in receivers that preferentially detect only mother–son resemblances. By the other process, recognition processes in receivers are unspecialized, and selection has instead favored either the expression of maternal facial characteristics in sons and not daughters or variable behavioral dispositions in sons and daughters to emulate their mother in ways that influence facial appearance.

Of course, the two paths could develop concurrently, and the functional result in any case would be the same, namely, that the faces of male as compared with female offspring would be perceived as more like those of their mothers. However, if the process underlying kin recognition were principally the former, then the recognition systems of other species (that are not specifically tuned to the different ways male and female offspring resemble their mothers in chimpanzees) should not preferentially match sons and not daughters to their mothers. That is, they might well be able to detect kin similarity, but not preferentially for sons over daughters. Conversely, if the process underlying kin recognition were primarily the latter, then other recognition systems should respond much as the chimpanzee subjects did, seeing sons' faces as more similar to their mothers' faces than are daughters' faces.

To investigate these possibilities, we undertook a series of experiments and a simulation designed to test both the species specificity of these potential biases in face processing or face production and to explore the potential structure of the underlying kin recognition mechanisms. In the first experiment, we replicated strictly the methods of Parr and de Waal (1999), using the same set of photos and the same match-to-sample procedures to test a group of human participants on their ability to match the mother–offspring pairs. The human participants had no special previous experience with chimpanzees or photos of them.

Experiment 1: Replicating the Recognition Asymmetry Observed in Chimpanzees With Human Participants

Objective and Rationale

The objective of this experiment was to replicate the original experiment conducted on chimpanzee subjects to test whether human participants, naive to chimpanzee faces, would show the same asymmetry in their ability to detect relatedness between mothers and their sons versus daughters. The outcome bears on the question of whether kin recognition processes involve species-specific perceptual mechanisms for detecting cues to kinship.

Method

Participants. Participants were 23 members (*Homo sapiens*) of the university communities of both the University of Lethbridge and McMaster University. All were naive to the purposes of the experiment.

Materials and design. The materials and basic structure of the experiment were identical to those of Parr and de Waal (1999). The materials consisted of 42 sets of gray-scale, head-and-shoulder photos of chimpanzees (*Pan troglodytes*), which were identical to those used by Parr and de Waal. Each set contained a *sample* photo, a *target* photo, and a *foil* photo. The sets were of four kinds: 12 individual recognition (IR) sets and 10 each of the mother–daughter (MD), mother–son (MS), and unrelated–control (UC) sets. IR sets consisted of two different photos of the same individual (5 females and 7 males), one serving as sample and the other as target, and a photo of an unrelated individual not explicitly matched for either age or sex that served as the foil. MD sets consisted of photos of mother–daughter pairs, the photo of the mother serving as the sample and the photo of the daughter as the target, and a photo of an unrelated female of roughly the same age as the target as the foil. MS sets consisted of photos of mother–son pairs, the photo of the mother serving as the sample and the photo of the son as the target, and a photo of an unrelated male of roughly the same age as the target as the foil. UC sets consisted of photos of 3 unrelated chimpanzees of the same sex, one serving as the sample, one arbitrarily (as originally selected by Parr & de Waal, 1999) serving as the target, and the third of a chimp that was the same sex and of roughly the same age as the target serving as the foil.

Procedure. Each participant received 42 trials consisting of the same random ordering of the 42 stimulus sets, presented via computer in a manner similar to the procedure with the chimpanzees in Parr and de Waal's (1999) article. On each trial, the sample photo for that trial was shown in the center of the computer display with a button labeled *ok* directly below it. Clicking the button replaced the display with the two test (i.e., target and foil) photos for that set, with the left–right positions of the test photos matching those of the corresponding test photos in Parr and de Waal's article.

Participants were instructed that they would be presented with photos of faces of chimps, one at a time, to study. They were told that clicking the *ok* button below the study photo would replace it with two other chimp face photos and that they were to select the one of them that they thought most closely resembled the chimp face photo they had studied. Clicking on either the left or right photo—which highlighted as the mouse cursor passed over it—indicated the participant's choice for that trial and initiated the next trial. On each trial, participants were free to study the sample photo as long as they wished and were unconstrained as to how long they took to decide between the two test photos.

Results and Discussion

The results are shown in the first line of Table 1, which shows the mean proportion of target test photos correctly selected as a function of test set type. The target photo for UC sets was the photo that Parr and de Waal (1999) had arbitrarily designated as the target. These data were subjected to an analysis of variance with set type crossing participants as the random variate. Effects were assessed for significance at the $\alpha = .05$ level.

Set type was significant as a main effect, $F(3, 66) = 34.32$, $MSE = 0.02$. As can be seen in Table 1, on the basis of a Fisher's

Table 1
Mean Proportion of Targets Selected in Experiments 1–3 as a Function of Set Type

Experiment	IR	MD	MS	UC	uLSD (.05)
1	.84	.53	.68	.46	.083
2	.84	.56	.63	.46	.091
3	.87	.67	.65	.54	.089

Note. IR = individual recognition pairs; MD = mother–daughter pairs; MS = mother–son pairs; UC = unrelated–control pairs; uLSD (.05) = Fisher's unprotected least significant difference at the .05 level.

unprotected least significant difference (uLSD) at the .05 level of .083, the IR mean was significantly greater than each of the other three means, and the MS mean was significantly greater than both the MD and the UC means, which did not differ significantly from each other. Thus, the pattern of the results replicates the sex bias of the chimpanzees in Parr and de Waal's (1999) study that likewise matched IR photos best, followed by MS photos better than MD and UC photos, with no difference between MD and UC photos.

Given this outcome, it seems clear for both the chimpanzees of Parr and de Waal (1999) and our human participants that the IR test photos in this set are perceived as more similar to their corresponding samples than are the foils. Similarly, for both species, the photos of sons (MS photos) are more similar to the photos of their mothers than are the associated foils, but photos of daughters (MD photos) are not more similar to the photos of their mothers than are their associated foils. That the human participants replicated the mother–son recognition bias of the chimpanzee subjects suggests that the perceptual mechanism underlying this matching bias is not species specific and potentially also not evolutionarily specialized. Rather, the results suggest that the matching bias might reflect a more general perceptual mechanism that is common to both species. If so, then the evolutionary process responsible for the bias is more likely to follow the second of the two scenarios outlined earlier and, hence, should be tied to characteristics of the faces (or, more generally, the photos) themselves.

Principal Components Analysis (PCA) Network Simulation of Experiment 1

To investigate the latter possibility, we simulated Experiment 1 using a simple, autoassociative, artificial neural network. We used a technique that has proven effective in simulating the recognition of photos of human faces—the PCA of pixel maps of photos of faces (e.g., Abdi, Valentin, Edelman, & O'Toole, 1995; Hancock, Burton, & Bruce, 1996; Kirby & Sirovich, 1990; Turk & Pentland, 1991).

Each photo of a face is represented in terms of its pixel-map (i.e., point-by-point or pixel-by-pixel) covariation with every other face. One advantage of such low-level representations is that we are unlikely to miss similarities based on higher level featural representations; furthermore, using such low-level representations does not assume that similarity is necessarily a function of such high-level features as eyes, nose, or ears. This covariation matrix, $\mathbf{W}$, serves as the network's memory or "knowledge" of photos of faces. It is created as the cross-products matrix of the matrix of

pixel maps of individual photos (as individual columns in the matrix), $\mathbf{X}$, by (the transpose of) itself: $\mathbf{W} = \mathbf{X}\mathbf{X}^T$. Each photo is then coded as its projection into the eigenvector (or principal components) space of this cross-products matrix defined by all the photos of faces stored in the network. These projections (or *encodings* in terms of the eigenspace) may then be compared or correlated. In particular, the cosine of the angle between the vectors of the corresponding photos in this space indicates how similar one photo is to another in terms of this encoding. Cosines close to 1.0 mean the eigen projections (i.e., projection vectors) of the comparison photos lie in the same location in eigenspace and, hence, are similar; cosines close to 0 mean the corresponding vectors are nearly orthogonal and, hence, dissimilar. Thus, the cosines between the sample photo and each of the two test photos for a given trial as projected into the eigenspace defined by all of the photos are used to assess the similarity of each of the test photos to the sample photo (see, e.g., Abdi, Valentin, & Edelman, 1999, for further details on this technique).

Each photo was reproduced as a gray-scale pixel map, 150 × 150 pixels in size. As the original images differed in size and shape, they were scaled and centered with a white background in the 150 × 150 frame so that the longer dimension just filled the frame, producing a white border of varying thickness on the shorter dimension. Each row of the resulting image was then concatenated to the preceding row, and the result was then transposed to produce a column vector 22,500 (150 × 150) pixels in length. As there were 123 unique photos in Parr and de Waal's (1999) set, collecting the images into a single matrix resulted in a 22,500 × 123 input matrix, $\mathbf{X}$, and a resulting 22,500 × 22,500 cross-products matrix, $\mathbf{W}$. Each image for a given trial of the original experiment was then projected into the space defined by the eigenvectors of the cross-products matrix, and the cosine between the projected sample image and each of the two projected test images was computed. The test image with the higher cosine similarity was then "selected" as the two-alternative forced-choice response for that trial. These projected cosine similarities were computed as a function of eigenvector, ordered by variance accounted for (from most to least): first eigenvector alone, first and second eigenvectors, first three eigenvectors, and so on until the pattern for a typical participant of Experiment 1 was replicated. That goal was achieved with just the first three eigenvectors: 67% correct for IR trials, 40% for MD trials, 70% for MS trials, and 40% for UC trials.

The eigenvectors may be reproduced as images, or "eigenfaces." The eigenfaces resulting from the first three eigenvectors are shown in Figure 1. The first eigenface represents, roughly, the "average" or prototypical photo of the faces. The second and third eigenfaces depict the two most important (orthogonal) differences in covariation in this set of photos from the first eigenface. As illustrated, the principal differences appear to be in the framing of the faces. The second eigenface is characterized by light lateral borders and dark borders on top and bottom, whereas the third eigenvector shows the opposite pattern. These borders are the result of the aforementioned process of reproducing the photos as square, 150 × 150 pixel maps and reflect the original differences in shape among the photos. These shape differences are a function of the fact that the photos of the chimp faces in Parr and de Waal's (1999) set generally were cut or cropped from photos that originally depicted more of the chimps' bodies and surrounding envi-
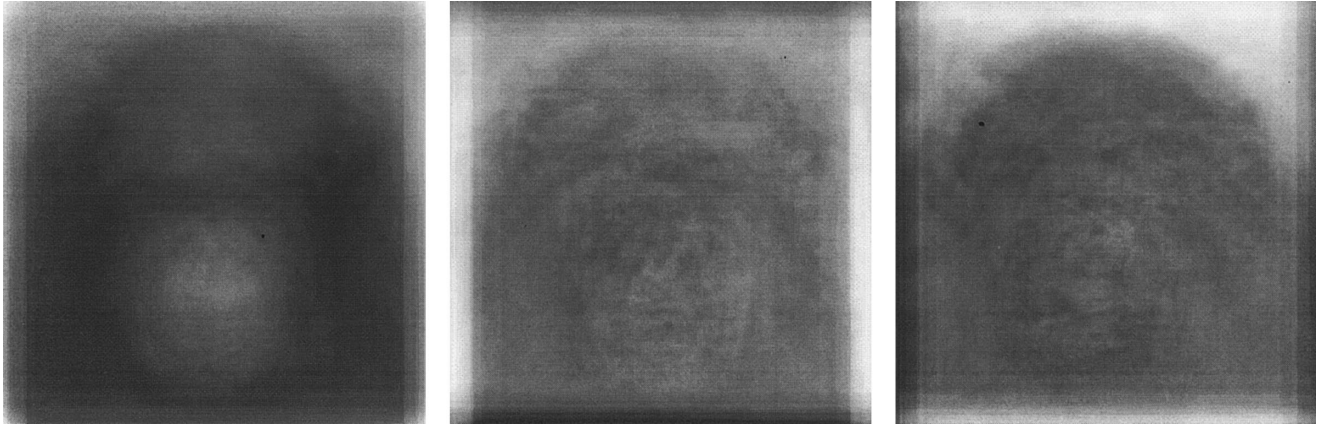
Figure 1. Depiction of the first three eigenvectors of the cross-products matrix of the images used in Experiment 1.

ronment. One consequence of this cropping of the photos to center on the faces was that characteristics of the face such as pose and gaze (e.g., three-quarters profile vs. frontal), expression (e.g., mouth wide open vs. closed), and face type (e.g., long and narrow vs. broad) were inadvertently reflected in the framing of the resulting image. Furthermore, some of the cropped photos were head-and-shoulder shots (generally wider than taller), whereas others were strictly of the face (generally taller than wider)—differences again that were reflected in the framing of the images.

The correlation of these differences in pose and so on and their resulting influences on the framing of the photos are not obvious in the static depictions of the eigenfaces in Figure 1. Indeed, they are not apparent in a casual inspection of the photos; nor were they mentioned by any of the participants in Experiment 1. However, the correlations are apparent if the eigenfaces are animated to reflect the variation in the weight of that particular eigenvector over the photos in the set.[1] As the individual weights of these eigenfaces in reconstructing the photos were sufficient to reproduce the preferential matching of both IR and MS photos, the results suggest that these global aspects or "macrofeatures" of the photos may have played a critical role in the recognition choices of both the chimpanzees of Parr and de Waal (1999) and our human participants in Experiment 1. We tested this possibility in Experiment 2.

Experiment 2: Testing the Recognition Asymmetry in Human Participants Using Photos With Matched Frames

In this experiment, we tested whether the global differences among the photos revealed through the neural network simulation were responsible for the mother–son recognition asymmetry in Experiment 1 (and, possibly, that of Parr & de Waal, 1999). We did so by the simple expedient of recropping the original photos, centered on the faces, to the same shape to eliminate potential framing differences and then rerunning Experiment 1 with all other details the same.

Method

Participants. Participants were 23 members of the university community of the University of Lethbridge. All were naive to the purposes of the experiment.

Materials, design, and procedure. The materials were the same as those used in Experiment 1, except that each photo was recropped to a standard shape (a square) to eliminate any differences in framing. Recropping consisted of centering a square on the face in each photo from Parr and de Waal's (1999) set, adjusted in size to capture the whole face. All other differences between the photos (size, pose, scaling, lighting, etc.) were retained. Thus, the correlations between pose and so on and framing revealed in Eigenfaces 2 and 3 were eliminated. The procedure was otherwise the same as Experiment 1.

Results and Discussion

The data were analyzed as in Experiment 1, and the results are shown in the second line of Table 1. Notably, the IR and UC means remained unchanged, whereas the MS mean dropped and the MD mean increased. As in Experiment 1, set type was significant as a main effect, $F(3, 66) = 25.31$, $MSE = 0.02$. Once again, on the basis of a Fisher's uLSD at the .05 level of .091, the IR mean was significantly greater than each of the other three means. However, although the differences in the means from the results of Experiment 1 were not large, the MS and MD means no longer differed significantly from each other, and both the MS and MD means were now significantly greater than the UC mean.

Thus, removing the framing information from the photos was sufficient to eliminate the original kin recognition bias (the preferential matching of MS photos) found in Experiment 1 and in Parr and de Waal's (1999) article but left individual recognition and kin recognition intact. Recropping the photos, then, had no effect on participants' ability to recognize individuals but did influence their ability to match kin. These results suggest that the original matching asymmetry did not involve a specialized perceptual mechanism tuned only to similarities shared by mothers and sons but rather appears to have been a function of global characteristics of the photos themselves, possibly reflecting original differences in pose, expression, and face type.

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[1] Animations or "eigenmovies" of Eigenvectors 2–5 of Parr and de Waal's (1999) photo set may be viewed on the Web at http://people .uleth.ca/~vokey/movies.

Experiment 3: Reexamining the Original Recognition Asymmetry

Another way to examine the nature of the perceptual information in the photos of the chimpanzee faces underlying the recognition asymmetry in Experiment 1 (and potentially also in Parr & de Waal, 1999) is to analyze the nature of the relationship between foils and targets in each of the photo-set types. The results of Experiment 2 suggest that global characteristics of the original daughter but not son foils rendered the foils in the MD set more likely to be selected. If so, assigning new foils to each of the targets might be expected to eliminate any such bias in global characteristics and, hence, eliminate the recognition asymmetry in much the same way as recropping the photos did in Experiment 2. To investigate this possibility, we randomly reassigned the foils across the entire corpus of test sets. Thus, the foils for the targets of every test type were now not specifically matched to the foils in any way, and any potential bias in global characteristics between targets and foils was distributed randomly across all of the set types.

Method

Participants. Participants were 20 members of the broader university community of the University of Lethbridge. All were naive to the purposes of the experiment.

Materials, design, and procedure. The materials were identical to those used in Experiment 1. The procedure was the same as Experiment 1, with one exception. This time, rather than using the foils as assigned by Parr and de Waal (1999) and in our Experiments 1 and 2, we assigned foils at random uniquely for each participant from the entire set of 42 possible foils.

Results and Discussion

The data were analyzed as in Experiment 1, and the results are shown in the third line of Table 1. Set type was significant as a main effect, $F(3, 57) = 19.04$, $MSE = 0.02$. As can be seen in Table 1, on the basis of a Fisher's uLSD at the .05 level of .089, the IR mean was significantly greater than each of the other three means, the MS and MD means were both significantly greater than the UC mean, and the MS and MD means did not differ significantly from each other. Thus, as in Experiment 2, the asymmetry in recognition of the mothers and sons versus daughters was eliminated, in this case through the random assignment of the foils.

General Discussion

We began by asking whether the asymmetry found by Parr and de Waal (1999) in chimpanzees' ability to match photos of mothers to their sons but not daughters could provide evidence for the underlying perceptual mechanisms of kin recognition in chimpanzees—possibly related functionally to the patrilineal structure of chimpanzee societies. At issue is whether such biased kin recognition reflects a specialized perceptual process in the perceiver for detecting only the similarities that sons share with their mothers or one that relies on a more general perceptual mechanism, possibly shared widely among other species, that is responsive to the greater real similarity between mothers and sons. If the former, then one would not expect other primate species (e.g., humans) lacking that

perceptual specialization to evince the same recognition asymmetry. Conversely, if it were a general perceptual mechanism common to many species, then the asymmetrical results for chimpanzees of Parr and de Waal (1999) should also be found with humans asked to evaluate the similarity of chimpanzee faces.

In Experiment 1, human participants were presented with the same photos in the same match-to-sample design as the chimpanzee subjects of Parr and de Waal (1999). Human participants replicated the results obtained with the chimpanzee subjects, including the preferential matching of photos of mothers and sons. That human participants showed the same recognition asymmetry as the chimpanzee subjects suggests that the mechanism underlying the asymmetry does not involve a species-specific perceptual mechanism of chimpanzees specialized to detect only the similarities that exist between sons and their mothers and not those that exist between daughters and their mothers. Rather, it suggests the operation of a more general perceptual mechanism shared between at least chimpanzees and humans that is similarly responsive to characteristics manifest in the photos of the chimpanzee faces.

On the basis of this result, subsequent experiments investigated the relevant perceptual characteristics of the chimpanzee faces as they appeared in the photos. First, we simulated the results of Experiment 1 using a simple, autoassociative neural network and showed that a similar pattern of results could be obtained using only the first three eigenvectors that summarized dimensions of variation in detailed pixel maps of the photos of Parr and de Waal (1999). Visual inspection of the eigenfaces depicting the first three eigenvectors suggested that the source of the recognition asymmetry could be traced to variation in the global characteristics of the photos, specifically differences in how the photos of the chimpanzee faces were framed. Such differences in framing could be a simple artifact of the construction of the photo set itself. Alternatively, they could reflect genetic relatedness through biases induced by, for example, pose, expression, or even face shape shared by mothers and sons (but not daughters) on the framing of the photos.

Second, in Experiment 2, we repeated Experiment 1, but with the framing information removed from the chimpanzee photos. Under these circumstances, human participants still showed both individual recognition and kin recognition, but the asymmetry in their ability to match photos of mothers to their sons but not daughters was eliminated. Thus, they were now also able to match equally well the photos of daughters and sons to those of their mothers. These results suggest that, in fact, the photos of faces of sons and daughters both resemble their mothers, although not necessarily in the same specific ways.

As an additional test of the extent to which the original recognition asymmetry hinged on global characteristics of the photos, in Experiment 3, we used the original photos but randomly reassigned the foils associated with the targets to remove any potential bias in the matching based on shared framing characteristics. In this case, again, the human participants showed both individual recognition and kin recognition, but there was no asymmetry in their ability to match photos of mothers to sons and daughters. These results support and extend those of Experiment 2 and indicate that when these global characteristics of the photos are controlled for (either by recropping the photos to a consistent shape or by balancing the global characteristics through random

assignment of foils to targets), the photos of faces of sons and daughters both resemble the photos of their mothers.

In summary, the results of the three experiments suggest that (a) humans are sensitive to the same characteristics of the photos of chimpanzee faces as were chimpanzee subjects in the original experiment by Parr and de Waal (1999); (b) the preferential matching of MS photographs (both in Experiment 1 and in Parr & de Waal, 1999) was a function of the photographic materials and their presentation, specifically global characteristics of the photographs and differences in them between targets and foils in certain set types, to which both humans and chimpanzees were sensitive; and (c) in fact, the photos of faces of sons and daughters both resemble the photos of the faces of their mothers. Our results do not allow us to say which features of the photos of sons and daughters are similar to their mothers or even whether they are the same features between the sexes. We also cannot say whether the features are ones that are structurally inherent (e.g., nose size or ear shape) or perhaps emerge epigenetically through shared behavioral dispositions that produce similar postures or expressions that influence the way the faces are captured in photographs. These are clearly important issues to be explored in future research.

However, our results do clearly indicate that the perceptual mechanisms responsible for the detection of these features in receivers are not specialized, species-specific routines unique to chimpanzees but rather are more general ones shared at least between chimpanzees and humans and perhaps more widely. The next major step in this research, then, would be to test several other primate species (including chimpanzees) with the revised methodologies used here to explore the extent to which the recognition mechanisms underlying the detection of family resemblance are indeed shared quite widely. Additional research might profitably explore the nature of the features that are perceptually similar among kin.

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