

Faces and Behinds: Chimpanzee Sex Perception

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Six adult chimpanzees (*Pan troglodytes*) trained on computerized matching-to-sample were shown a sample behind (anogenital region) of a chimpanzee and rewarded for selecting a corresponding facial image. If the two faces were of the same sex, and one belonged to the same individual as the behind, subjects made the correct association for familiar individuals, but not unfamiliar ones, suggesting whole-body knowledge of group mates. If the two faces were of opposite sex, subjects selected the same-sex face as the behind at first only for familiar individuals when face and behind belonged to the same individual. During subsequent exposures, however, they learned to associate the same-sex face with the behind even if the behind was “generic” male or female (i.e., unmatched to any known individual) provided the depicted individuals were familiar. This suggests that sex perception is aided by a “gender construct” derived from firsthand experience with group mates, and which construct is unavailable for unfamiliar individuals.

1. INTRODUCTION

Humans are adept at extracting sex-identity information from conspecific faces regardless of the presence or absence of additional visual cues such as hairstyle, facial hair, or clothing.¹ This suggests observable sex differences in the shape and proportions of male and female faces as reflected in distance measurements between facial features,² luminance of eye or mouth regions,³ as well as the interaction between two- or three-dimensional and textural information of the entire face.⁴ Perceivers are even able to consistently classify isolated facial features as being male or female.^{5–8} Thus, sex cues in human faces are reliably interpreted, making it possible for humans to quickly distinguish conspecifics according to their potential as mates, rivals, collaborators, and so on.

Nonhuman primates, too, live in complex societies that necessitate recognition of conspecifics as well as the ability to determine important attributes such as sex, kinship, and dominance. Little is known about how other primate species make these distinctions, and whether they mainly rely on olfactory, auditory, visual, or behavioral cues. Nonhuman primates have a sensitive visual system, and several species are able to visually discriminate facial images, indicating that the face is an important factor in individual recognition.⁹ In addition, chimpanzees (*Pan troglodytes*) have been found to spontaneously associate faces of unfamiliar females with those of their offspring, suggesting visual kin recognition through the detection of facial similarity.^{10, 11}

Thus far, no studies have measured physical differences between the faces of male and female nonhuman primates, and only one study has investigated the ability of nonhuman primates

to classify images of conspecifics by sex. Two Japanese monkeys (*Macaca fuscata*) were trained in a two-choice sex discrimination task in which a photograph appeared at the center of the screen and the subjects were to select a key on the left or on the right to indicate male or female, respectively.¹² The stimuli were full-body frontal images of unfamiliar adult conspecifics. After training, subjects successfully transferred to new stimuli, demonstrating an ability to categorize images of males and females. To examine which features of the images were most important, a follow-up experiment presented isolated parts of the images (e.g., face, chest, underbelly). Categorization remained accurate for faces alone. However, because the images in the follow-up study came from the earlier full-body set, subjects might have relied on prior learned categorizations. Hence it remains unclear to what degree faces alone contain sex-relevant information for nonhuman primates.

In the present study, we use an unusual paradigm to test facial sex perception in chimpanzees in a matching-to-sample task. The approach is to present a sample image of the most sex-specific body region, i.e., the behind, including genitals, which is then to be matched with either a male or female facial image. The correct response matches a behind with the same-sex face. This approach differs from the previously mentioned studies in that it is not based on categorization (classifying an image as being of one or the other sex), but rather on association (how does seeing the behind of one or the other sex subsequently bias the subject's choice between two opposite-sex faces?). Matching-to-sample training predisposes individuals to making visual associations, and all we are adding is sex as a dimension to affect these associations.

This paradigm permits investigation of the role of familiarity in sex recognition. For example, if both the sample image of the

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behind and the matching face derive from the same individual, subjects might associate the two by relying on whole-body integration of familiar individuals. They will not be able to do so with unfamiliar individuals. Whole-body integration applied to two-dimensional images has been reported once before in the primate literature,¹³ but because this study was conducted before the computer era, issues of experimental control remain. This study concerned macaques, but despite suggestions that these monkeys recognize two-dimensional depictions of conspecific faces,^{14,15} they seem better at learning visual patterns than at recognizing facial features. As opposed to humans and chimpanzees, which recognize faces at first exposure, macaques need hundreds of training trials before they achieve face discrimination.⁹ In the ensuing 20 years, this particular macaque study¹³ has never been successfully replicated.

If the images of the sample behind and the same-sex face do not derive from the same individual, whole-body knowledge cannot play a role, not even for familiar individuals. If under this condition the sex association for familiar faces is stronger than for unfamiliar ones, this might indicate a “gender construct” based on whatever previous experience the subject has had with familiar individuals. The previous experience would provide extrinsic information (i.e., information not contained in the images) to facilitate decisions on sex identity.

In short, three different hypotheses might explain if and how chimpanzees will associate a sex-specific behind with a same-sex face. The hypotheses are given here with their predictions between parentheses:

- (1) *Facial sex cues*: facial sex characteristics are associated with a sex-specific behind (same for familiar and unfamiliar faces),
- (2) *Whole-body integration*: associating various isolated body parts belonging to the same individual based on knowledge of the whole individual (only for familiar individuals, provided the images of face and behind are identity-matched), or
- (3) *Gender construct*: reliance on extrinsic information not contained in the images, such as the real-life behavior of the depicted individual (only for familiar faces regardless of whether or not the images of face and behind derive from the same individual).

In humans, extrinsic information plays a role in sex recognition, as it has been shown that subjects classify faces as male or female faster if the face belongs to an individual familiar to the subject.^{16–19} In this case, familiarity refers to knowledge through the media, such as television and newspapers. The variation in sex recognition occurs in a graded fashion, such that latencies are shortest to highly familiar faces (celebrities), intermediate for learned faces, and slowest for completely unfamiliar faces when sex cues such as the hair and face shape are removed.¹⁶ When these cues are not available it takes longer to make a decision as to whether the face is male or female, to the point that personal information about known individuals is being retrieved to facilitate classification.

2. METHODS

2.1. Subjects and Procedures

The chimpanzees lived in two separate mixed-sex groups of 15 members each. Each group of chimpanzees at the field station of the Yerkes National Primate Research Center was kept in a large outdoor compound (respectively, 700 m² and 520 m²), with

heated indoor housing. The two groups could hear but not see each other; their enclosures were approximately 300 m apart, separated by a hill.

Upon being called by name, a chimpanzee would enter a testing facility with a computer set up. Some test subjects would come inside alone, others with a family member (e.g., an offspring or mother). The subject would remain behind glass or bars with a joystick protruding to its side, whereas the human experimenter, computer, and screen remained on the other side. The distance between the chimpanzee's face and the screen during tests was between 30 and 40 cm. The human experimenter sat behind the computer without seeing the images, hence without the ability to unconsciously cue the subject. Testing sessions lasted about half an hour, upon which the subject would rejoin its group.

Six adult (older than 12 years of age) subjects—three males and three females—had been trained to use a joystick to move a cursor across the screen. Training on matching-to-sample had been achieved previously on simple graphic images, such as clip art. Stimuli consisted of colored 8 × 8 cm digital images. First, the sample image would appear at random locations on the screen (i.e., centered at the bottom, top, left, or right). Upon being touched by the cursor, two additional images would come up simultaneously within a second on the opposite end of the screen. If the second image touched by the cursor matched the sample, a high sound would play and a reward given to the subject. Within a second the next trial would start. If the second image touched failed to match the sample, however, a low buzz would play, no reward would be given, and the interval to the next trial would be 5 sec. Rewards were given according to the subject's preference, typically small pieces of cantaloupe, apple, or banana.

2.2. Test Series

Three conditions, detailed below, were presented to each subject. The conditions presented a variable number of test series. A test series consisted of six sessions of 30 trials, typically presented over two separate days (i.e., three sessions, or 90 trials, per day) without other tests in between. All sessions within one test series used exactly the same stimulus set, but the trials were presented in variable, randomized order. Of the 30 trials per session, 10 concerned simple clip art, which the subjects had seen before. Subjects usually performed above 90% correct on the clip art; if they dropped under 70%, the entire session was considered invalid. This might be due to lack of attention and/or lack of motivation. The other 20 trials per test concerned facial stimuli, i.e., full frontal chimpanzee faces that looked directly at the camera. The faces were closely cropped to eliminate most background (Fig. 1). Facial stimuli were divided into those concerning chimpanzees with whom the subject lived (i.e., familiar faces) and those whom the subject had never met (i.e., unfamiliar faces). Most of the latter were photographed either at distant locations or at our own facility but concerning a group unknown to the subject.

We also used photographs of chimpanzees taken from behind, again closely cropped, showing an individual's upper legs and anogenital region. The behinds were either from known individuals, hence could be coupled with the face of the same individual (“matched behinds”), or two freeze frames from video of wild chimpanzees collected at the Mahale Mountains in Tanzania: one male and one female behind. The latter two stimuli were used

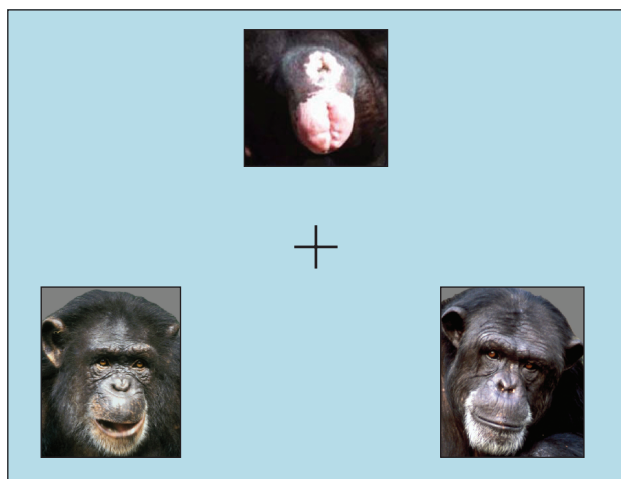


Fig. 1. Computer screen for the sex perception task. The top image shows a generic behind of a female. After this sample has been touched by the cursor, which is controlled by a joystick in the hands of the chimpanzee, the bottom two images of opposite sex faces appear, with a female face on the left and a male face on the right. For this trial, the correct choice is the left face.

over and over as “generic behinds” (Fig. 1). All female behinds showed slightly swollen genitals, never maximum tumescence. The following three conditions were completed, condition one first (one test series), then conditions two and three in alternation (each four test series):

1. *Within-Sex Face-to-Behind Matching*: The first condition, which presented one test series, explored if subjects could select the face of the same individual of which the behind was shown. Every trial presented a sample behind followed by two faces of the same sex as the behind. The correct choice was the face of the same individual as the behind. In half the trials, all stimuli (i.e., both faces and behinds) came from familiar individuals, and in the other half from unfamiliar individuals. Familiar and unfamiliar trials alternated in randomized order.

2. *Matched-Behind Sex Discrimination*: The second condition consisted of four test series of six sessions each. Each test series following the first had either entirely new stimuli or new combinations of faces and behinds. This condition presented a sample behind followed by two faces. One face was the same individual as the behind, whereas the other was an opposite-sex face. In half the trials, all stimuli came from familiar individuals, and in the other half from unfamiliar individuals. Familiar and unfamiliar trials alternated in randomized order. Equal numbers of male and female behinds were shown.

3. *Generic-Behind Sex Discrimination*: The third condition consisted of four test series of six sessions each, alternating with but separate from the second condition, and followed the same arrangement and included the same facial stimuli as the second condition, except that this time the behind samples were limited to “generic behinds.” The correct choice was the face that matched the generic behind’s sex.

2.3. Corrected Choice Measure

As found in human studies,^{18–22} chimpanzee subjects showed a small but systematic bias towards selecting male rather than female faces. No subject showed the reverse bias. For this reason, we used a Corrected Choice Measure (CCM), also known

as A' , i.e., a non-parametric measure of discrimination sensitivity derived by Grier²³ from signal detection theory, which controls for biased guessing. Here we follow the formula of Stanislaw and Todorov,²⁴ with CCM varying between 0 and 1, with 0.5 for chance performance.

3. RESULTS

3.1. Within-Sex Face-to-Behind Matching

Choosing between same-sex familiar faces, all six subjects performed above 50/50 chance on matching the facial identity to the behind’s identity (one-sample t -test, $t = 3.07$, $df = 5$, $P = 0.014$, one-tailed). As expected, subjects were unable to do the same with unfamiliar faces ($t = 0.62$, $df = 5$, NS).

3.2. Sex Discrimination Overall

Heterogeneity G -tests were performed for each individual subject on the number of correct versus false choices in the gender-discrimination tasks (matched-behind and generic-behind), first for all eight test series combined, and then for narrower categories, such as for matched behinds of familiar individuals. Five of the six subjects showed significantly more correct than false choices in either the overall data or any subcategory ($\alpha = 0.05$). One male subject who never did so was dropped from further analysis.

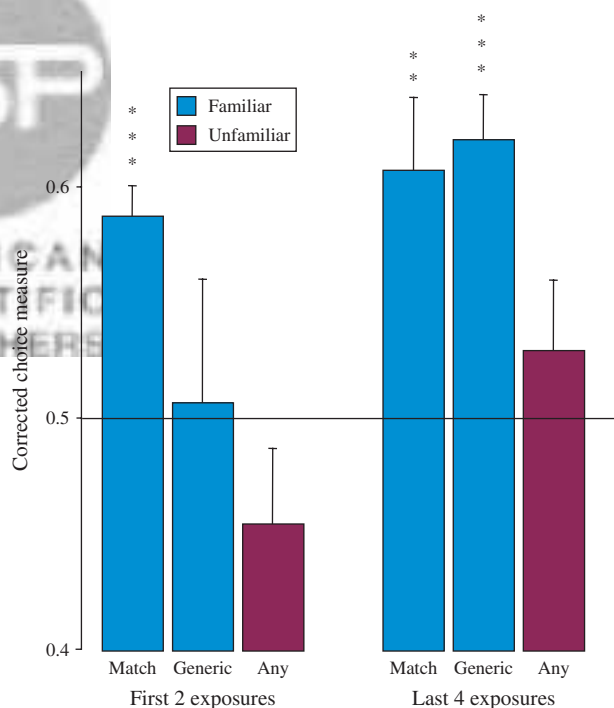


Fig. 2. The corrected choice measure (CCM) is 0.50 in case of random choice, and ranges between 0 and 1. This measure, which corrects for biased choosing, shows that during the very first two exposures (left bars) familiar faces were correctly associated with the same-sex matched behind, but not with generic (i.e., unmatched) behinds. For unfamiliar faces, there was no significant association. During later exposures (right bars), familiar faces were correctly associated with the same-sex behind regardless of whether the behind was identity-matched or generic. This level of performance was never achieved for unfamiliar faces. Asterisks indicate performance significantly above chance: *** $P < 0.001$, and ** $P < 0.01$.

Within each test series of six sessions, stimuli remained the same even though their order varied. As expected, performance on the first exposures of the same stimuli differed from performance on subsequent exposures, hence in the following analyses a distinction is made between the first two exposures within a test series and the last four exposures.

The data were inspected for trends in performance across the eight test series (generic-behind and matched-behind sex discrimination), but no significant trends, up or down, were found. Therefore, data on test series of each kind (i.e., matched vs. generic behinds) were combined. As expected, performance on unfamiliar faces was unaffected by whether the sample behind was identity-matched or generic, which is why these results have been combined under the category “any behind.”

3.3. Immediate Association: Familiar versus Unfamiliar Faces

For the first two exposures within each test series, it was found that the CCM rose significantly above 0.50 for familiar faces if one face was identity-matched to the sample behind (one-sample t -test, $t = 7.62$, $df = 4$, $P = 0.001$, two-tailed), but not for familiar faces with a generic sample behind ($t = 0.15$, NS). Unfamiliar faces with any behind showed no significant difference from chance ($t = -1.56$, NS). Results are presented in Figure 2.

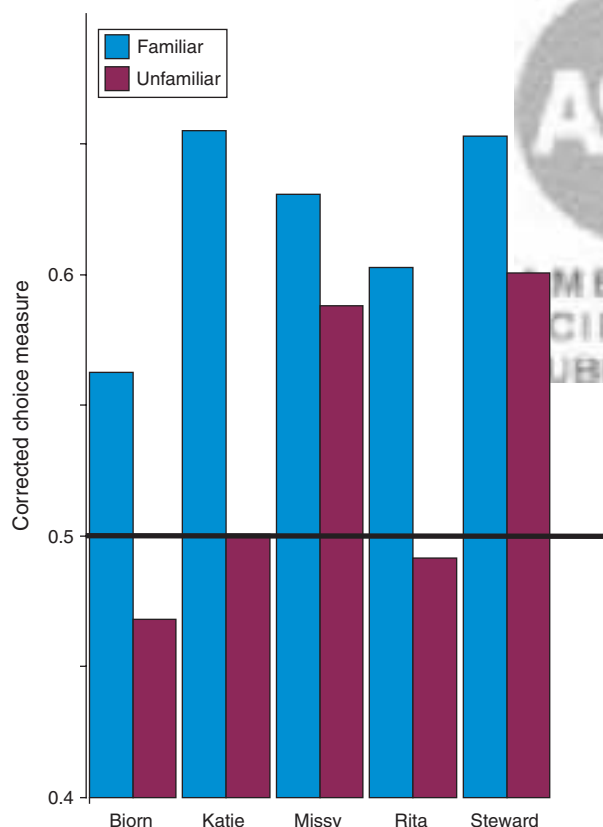


Fig. 3. Data by subject on later stimulus exposures (i.e., four through six per test series), hence, after familiarization. This data is limited to arrangements in which knowledge of the bodies of the depicted individuals is irrelevant, i.e., familiar faces paired with a generic behind and unfamiliar faces paired with any behind. All five subjects performed better with the familiar faces, and the overall result was significant (see text).

3.4. Learned Association: Familiar versus Unfamiliar Faces

After the first two exposures, there were four more sessions using the same stimulus set within each test series. These later choices were expected to show learning effects. A significantly above-chance CCM was found for all familiar faces, both with a matching behind ($t = 3.85$, $P = 0.009$) and a generic behind ($t = 6.97$, $P = 0.001$). No significant result was found, however, for unfamiliar faces with any behind ($t = 1.11$, NS).

Comparing performance on the first two versus the last four exposures within each test series failed to show improvement for tests with matched behinds and familiar faces (paired t -test, $t = 0.62$, $df = 4$, NS). Improvement did occur, however, for generic behinds and familiar faces ($t = 2.73$, $P = 0.026$, one-tailed). Unfamiliar faces with any behind also showed significant improvement ($t = 2.29$, $P = 0.042$), though performance never rose significantly above chance.

Figure 2 illustrates performance during the last four exposures, and how a significant difference between familiar and unfamiliar faces remained even if matching could play no role, such as between familiar faces with generic behinds and unfamiliar faces with any behind ($t = 4.48$, $df = 4$, $P = 0.011$, two-tailed). The latter difference is illustrated per individual subject in Figure 3, which shows that it applied to all five subjects, and that some subjects achieved a CCM on familiar faces with generic behinds of 0.65.

4. DISCUSSION

Presented with a choice between two faces of the same sex, subjects associated the correct face with the corresponding behind, providing the first conclusive proof of whole-body integration in a nonhuman primate. This result requires that the chimpanzees (a) recognize photographs as representations of known individuals, and (b) have a mental representation of the whole body of familiar conspecifics. Subjects were unable to do the same with unfamiliar individuals, thus ruling out matching based on visual cues. Whole-body integration also might explain the correct choice between familiar faces of opposite sex in relation to a matching behind of either sex.

The final condition, presenting a generic behind, tested whether subjects could match a face to a representative image of a male or female behind. Initial performance was at-chance for familiar faces, but did improve to above-chance in later sessions. This trend was not seen for unfamiliar faces, i.e., performance remained at chance levels. Overall, the level of performance on these tasks was not nearly as high as typical of human recognition and categorization, which might be explained by the fact that our subjects were not trained on a strict classification of stimuli, but were presented with stimuli of different kinds between which they needed to make associations. Their performance was typical of other nonhuman primate studies using a matching-to-sample design.^{10, 25, 26}

Although ideally the presented task was designed to ask whether chimpanzees could assign a sex to a face, it is not clear that this is what they were actually doing. Assuming that chimpanzee faces, like those of humans^{2, 4} and macaques,^{12, 27} contain sex cues, there are two ways to explain association of familiar faces with generic behinds. One is generalization between the generic behind and the depicted individual's actual behind. The



Fig. 4. We humans, find it easy to recognize differences between male and female chimpanzees (i.e., male on left, female on right). The present study, however, presented close-up portraits cropped to the same size, so that differences could have been less obvious. It appears that chimpanzees are greatly helped by extrinsic information on familiar individuals (such as their behavior in the group), because they prove better at associating familiar faces with sex-specific behaviors even if those behaviors are not identity-matched. Photograph by Frans de Waal.

second is that subjects did interpret the task as sex classification, and learned the correct answer only for familiar faces because of extrinsic information that they had available for familiar but not for unfamiliar individuals (Fig. 4).

More testing is needed to distinguish between these two alternatives, but the possible use of extrinsic information is most intriguing because it would fit human research. Human subjects discriminate gender faster if the face belongs to a familiar individual (see Section 1). Possibly, our chimpanzees operate with a “gender construct,” i.e., retrieve information based on real-life interactions with the depicted individuals, which helps them decide to which sex they belong. For unfamiliar individuals they do not have such a construct to assist them.

Acknowledgments: We thank Rebecca Singer, Jennifer Rybak, and Marietta Dindo for technical assistance. Research

was supported by private donations to Living Links and a National Institutes of Health grant to the Yerkes National Primate Research Center (RR-00165). We would like to thank the animal care and veterinary staff at the Yerkes Primate Center for their support and assistance. The Yerkes Center is fully accredited by the American Association for Accreditation for Laboratory Animal Care.

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Received: 5 October 2007. Accepted: 15 October 2007.