

Face Recognition in Capuchin Monkeys (*Cebus apella*)

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Primates live in complex social groups that necessitate recognition of the individuals with whom they interact. In humans, faces provide a visual means by which to gain information such as identity, allowing us to distinguish between both familiar and unfamiliar individuals. The current study used a computerized oddity task to investigate whether a New World primate, *Cebus apella*, can discriminate the faces of In-group and Out-group conspecifics based on identity. The current study, improved on past methodologies, demonstrates that capuchins recognize the faces of both familiar and unfamiliar conspecifics. Once a performance criterion had been reached, subjects successfully transferred to a large number of novel images within the first 100 trials thus ruling out performance based on previous conditioning. Capuchins can be added to a growing list of primates that appear to recognize two-dimensional facial images of conspecifics.

Keywords: primates, cognition, oddity, visual discrimination

Humans rely on faces to quickly recognize individuals as well as to gain other information on sex, approximate age, and emotions or intentions of the other (Bruce & Young, 1986). Humans are able to organize their social world according to the information obtained, using the face as a visual label of identity and as a source of information on emotional state. Other primates are under similar pressures as humans to recognize individuals, as their social groups consist of individuals of different ages, sexes, ranks, and degrees of relatedness. Group life requires that individuals at the very least recognize each other individually and remember individuals with whom they have interacted.

There is evidence that in nonhuman primates faces are an important class of stimuli. Some of the first studies investigating the neurological components of face perception were conducted with nonhuman primates, specifically rhesus monkeys (*Macaca mulatta*). The rhesus monkey visual system in general is markedly similar to the human visual system (Tootell, Tsao, & Vanduffel, 2003). Neurons that are selectively responsive to faces and the

meaning extracted from faces have been found in several areas of the brain, including the inferior temporal gyrus, the superior temporal sulcus (STS), the frontal cortex, and the amygdala (Haxby, Hoffman, & Gobbini, 2002). Certain populations of neurons in the STS code recognize particular facial expressions; others are sensitive to gaze direction or different viewpoints of the face, and others are responsive to particular individuals irrespective of any facial expression or change in viewpoint (Perrett & Mistlin, 1990). This provides a neurological basis for the ability to discriminate between faces of different individuals while also generalizing across different viewpoints of the same individual. The neurological data provides evidence for specialized processing of faces in nonhuman primates and the ability to recognize a face across viewpoint changes. With the recent advancement of imaging technology in nonhuman primates, it appears that macaques may have a specialized face processing system similar to humans (for a review see Tsao & Livingstone, 2008). Behavioral findings, however, have been mixed as to whether nonhuman primates process faces in a configural manner—the specific way in which humans are thought to process faces (Diamond & Carey, 1986; Farah, Tanaka, & Drain, 1995; Farah, Wilson, Drain, & Tanaka, 1998; Freire, Lee, & Symons, 2000). The current study only addresses whether capuchins are able to discriminate and recognize conspecific faces, not whether they process the faces in a configural manner.

Even when conspecific faces are presented as two-dimensional images, the image provides important information for nonhuman primates. Several studies have noted macaques respond in socially appropriate, species-typical ways to images of conspecifics, by lip-smacking or threatening the image or by averting their gaze (Mendelson, Haith, & Goldman-Rakic, 1982; Overman & Doty, 1982; Plimpton, Swartz, & Rosenblum, 1981; Rosenfeld & van Hoesen, 1979; Sackett, 1965, 1966). Boysen and Bernston (1986, 1989) measured the heart rate of chimpanzees while they viewed images of either conspecifics or humans and found that their heart rate varied depending on the quality of the relationship the subject had with the individual depicted. They connected the two-

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dimensional images with actual individuals in their environment. This has been further demonstrated by chimpanzees being able to match the face of familiar conspecifics to an image of the corresponding behind (anogenital region) of that individual, suggesting whole-body knowledge of group mates (de Waal & Pokorny, 2008).

Using unfamiliar individuals as stimuli, nonhuman primates can also discriminate individuals within a species. For adult subjects, this may be limited to conspecifics or other species with whom the subject has had extensive experience. For instance, Humphrey (1974) used a habituation/dishabituation paradigm to present rhesus monkeys with images of conspecifics and other domestic animals. Subjects appeared to immediately discriminate conspecifics, but for other species, distinctions were made at the species level. However, after several months of exposure to images of the other domestic animals, rhesus monkeys were then able to discriminate them as individuals. It should be noted that in this study, the images were not confined to the face and did include full bodies, so it is not entirely clear that subjects were using the face to discriminate individuals. In a similar study that did confine images to the face, rhesus monkeys discriminated conspecifics but not dogs, birds, or marmosets (Dahl, Logothetis, & Hoffman, 2007), confirming the earlier study by Humphrey (1974).

Visual paired comparison (VPC) studies have provided evidence for discrimination of conspecifics. The VPC paradigm presents an image to a subject for a period of time to allow the subject to fully explore the image. The image is removed, and after a brief delay, two comparison images are presented, one of which is the image initially presented during the familiarization period and the other is a novel stimulus. Subjects typically spend more time looking at the novel stimulus. One study presented human and rhesus monkeys with images of objects, human faces, and rhesus monkey faces. Both humans and rhesus monkeys showed a novelty preference for conspecifics and objects but not for the other primate species (Pascalis & Bachevalier, 1998). A similar study replicated the species-specific effect for humans and extended the effect to Tonkean macaques (*M. tonkeana*) and brown capuchins using images of humans and six other nonhuman primate species (Dufour, Pascalis, & Petit, 2006). These studies suggest that individuals are only able to discriminate between faces of conspecifics, not other species. However, cotton-top tamarins (*Saguinus oedipus*), a new world monkey species, detected identity changes of conspecifics and humans (Neiworth, Hassett, & Sylvester, 2007), illustrating that experience can influence this ability.

While all of these studies indicate that nonhuman primates are able to discriminate within the class of conspecific, and possibly highly familiar faces, they do not test for recognition of individuals generally. Conspecific faces may be a stimulus class that subjects can detect small changes between individuals, but they may not recognize those faces as individuals with a specific identity, conserving identity across visual changes in the stimulus. Thus, discrimination does not indicate recognition. For the above studies to demonstrate recognition, subjects must generalize the identity of the individual across different viewpoints or lighting conditions. In the Dahl et al. study (2007), subjects did exhibit greater adaptation to a change in identity than to a rotation change of the same individual. However, the change was rotation of the two-dimensional image, not a rotation of the face of the individual, that is, a viewpoint change. In the VPC studies noted above, the

comparison image was identical to the familiarization image. A test of recognition would be to present a conspecific face as the sample, then the comparison images would be (1) the same individual but from another viewpoint and (2) a novel individual. This would test whether subjects generalize across identity and recognize that the two images are the same individual.

A few studies have examined individual face recognition using tasks that require an explicit behavioral response from the subject, such as a discrimination task or matching images of faces. An early study presented rhesus monkeys with images of unfamiliar conspecifics in a simultaneous discrimination task (Rosenfeld & van Hoesen, 1979). In the task, a subject was presented with two images, one of which was the positive stimulus, the stimulus they were to select, while the other was the negative stimulus, or the incorrect image. Once subjects acquired the task using full-face images, they were transferred to images taken from other viewpoints and reached the performance criterion set by the researchers in less time than the initial acquisition of the full-face images. Bruce (1982a) also utilized a discrimination task with long-tailed macaques, requiring a 90% performance criterion on one trial before transferring to new images of same individuals depicted in training trials, but varying the lighting conditions, size or facial expression presented. Results from the first session of 100 trials suggest that subjects performed well, performing between 67% and 90% (one case 43%).

Heywood and Cowey (1992) trained rhesus monkeys to perform various tasks (e.g., oddity, delayed nonmatching to sample, visual discrimination, familiarity judgments, visual identification) with images of human and "monkey" faces (the species of monkey remained unspecified). The visual discrimination task was quite similar to the task used by Rosenfeld & van Hoesen (1979) in that initial training used two images of individuals and then after acquisition, presented the discrimination task using images taken from three different viewpoints and also added two new individuals into the stimulus set. Subjects performed relatively well on this task, making approximately 76 errors before reaching a performance criterion of 90% correct. In the oddity task, also using images taken from different viewpoints, subjects were performing at nearly 80% correct in the first 1000 trials.

More recently, chimpanzees and rhesus macaques were both tested on their ability to match unfamiliar conspecific faces when the images were taken of different views (Parr, Winslow, Hopkins, & de Waal, 2000). Chimpanzees quickly generalized performance from matching identical photos to photos taken from a different view, requiring only two exposures with 14 novel trials to perform significantly above chance. Rhesus monkeys, on the other hand, required 200–400 trials on 15 unique trials before performing above chance. Ten novel trials were added to assess transfer to new images for the monkeys. Subjects then performed above chance after completing between 2–14 exposures to the novel trials. The study allowed for the direct comparison of two different species on the ability to perform the same task, and it appeared that chimpanzees were more successful in generalizing across viewpoints when matching on individual identity, though some rhesus subjects did transfer to novel stimuli rather well after acquiring the individual recognition task.

One issue that may have affected performance in the aforementioned studies requiring an explicit behavioral response is that many used very small stimulus sets, resulting in only 2–15 unique

trials for the subjects (Bruce, 1982a; Heywood & Cowey, 1992; Parr, Winslow, Hopkins, & de Waal, 2000; Rosenfeld & van Hoesen, 1979). Several studies have previously demonstrated that pigeons and rhesus monkeys who are trained on small set sizes fail to generalize their knowledge of a task to new stimuli (e.g., Katz, Wright, & Bachevalier, 2002; Wright & Katz, 2006). For that reason it may be that prior studies report subjects needing many exposures (e.g., 16–400) to the same few trials before they performed significantly above chance or reached performance criterion. While subjects needed less exposures to these novel trials than to the training trials, they were essentially relearning the task with new stimuli. Ideally, one would want to see positive transfer on novel trials during the first exposure. The current study took this into account and introduced stimulus sets that ranged from 50 to 108 images, resulting in over 200 possible unique trials, significantly reducing the likelihood that subjects would learn only trial-specific rules and not transfer to novel stimuli. We wanted to assess performance immediately after transfer with novel, unique trials not repeated exposures, which strengthens the conclusion that subjects are generalizing performance across tasks.

Another aspect that may affected performance in the prior studies is that the stimuli presented were often of unfamiliar conspecifics. Several human studies have found decreased performance on tasks when subjects are to recognize unfamiliar individuals when there has been a change from the trained stimulus in (1) viewpoint (Bruce, Henderson, Newman, & Burton, 2001; Burton, Wilson, Cowan, & Bruce, 1999; Hill, Schyns, & Akamatsu, 1997; Longmore, Liu, & Young, 2008; Newell, Chiroro, & Valentine, 1999; O'Toole, Edelman, & Bulthoff, 1998), (2) lighting (Hill & Bruce, 1996), or (3) expression (Bruce, 1982b; Bruce et al., 1999). This decrement is not found when familiar individuals are presented in the tasks with the same visual manipulations. Many of the nonhuman primate studies introduced novel images of unfamiliar conspecifics, and it is possible that because there was a change, typically in viewpoint, this change hindered subjects in generalizing more readily to the new stimuli, again needing numerous exposures to novel trials. Aside from physical differences from the training stimuli, one model of face recognition poses that one of the primary differences in recognizing familiar and unfamiliar faces is that seeing a familiar face involves evoking not only biographical information about the person, but also generating an affective response (Breen, Caine, & Coltheart, 2000). If subjects are presented with facial stimuli representing only unfamiliar conspecifics, it is possible that they do not see the stimulus as a face, per se, but just as another complex visual stimulus. Presenting familiar conspecifics may generate an affective response in subjects, making it more likely that they connect the facial image to a particular known individual, which may aid in interpreting the faces of unfamiliar conspecifics as individuals as well.

Thus far, almost all studies of face recognition using explicit behavioral tasks have focused on Old World primates. The goal of the present study was to investigate face recognition abilities in a New World species of primate marked by a relatively large brain to body ratio (Rilling & Insel, 1999; Roth & Dicke, 2005) and complex sociality (Fragaszy, Visalberghi, & Fedigan, 2004). While capuchins are highly encephalized, they do have smaller and less gyrified temporal lobes than expected for their brain size while rhesus monkeys' temporal lobes are larger (Rilling & Seilgman, 2002). Considering that the majority of comparative neurological

work concerning face processing has been conducted in the temporal lobe of rhesus monkeys, there may be behavioral differences in face recognition abilities of a primate whose temporal lobes are smaller than expected. Incorporating information from a greater variety of primate species helps to identify which processes are similar as well as aid in determining where along the evolutionary split these abilities originated. One can gain a better understanding of face recognition and whether this is a skill that arose recently and is limited to humans and Old World Primates or is found in all primates, particularly given that the visual modality is prominent among the primates (Napier & Napier, 1996).

In this study, we sought to expand on the nonhuman primate face recognition research by taking into account some of the issues found in previous studies, such as small stimulus set sizes, only a few individuals represented in the stimuli, and a lack of transfer data. Compared to the majority of previous studies, this study used a large stimulus set, and included two transfer tests with both novel combinations of stimuli and entirely novel stimuli, improving upon the methodology of those prior studies. Seeing as the human literature finds differences when asking people to recognize familiar and unfamiliar human faces, our second objective was to explore any differences between presenting familiar and unfamiliar conspecifics as prior studies with nonhuman primates typically used only unfamiliar conspecifics.

Method

Subjects and Housing

Subjects were five adult brown capuchin monkeys from two separately housed social groups, the Group 1 and Group 2, at the Yerkes National Primate Research Center. Training began in November 2005 at which time the groups consisted of 15 individuals in Group 1 and 13 individuals in Group 2. Training and testing lasted until September 2006 for three subjects while two subjects continued testing until February 2008. During this time, two infants were born into Group 2, bringing the total number of individuals to 15. Subjects were two females from Group 1 (named "Wilma" aged 8, and "Winnie" aged 21), as well as one male ("Mason" aged 7) and two females ("Bias" aged 18, and "Georgia" aged 20) from Group 2. Ages of the subjects are given for when they began training. Bias and Georgia both had dependent offspring present during a portion of training and testing, but this did not appear to interfere with their performance. One other subject was initially trained on the oddity task but was dropped before the present study because he became alpha in his group while training with clip art images and refused to test any longer.

The two groups were housed in the same facility, with differently sized indoor/outdoor areas (25 m² and 31 m² respectively), which were separated by an opaque screen. The monkeys had free access to indoor and outdoor areas unless inclement weather required closing off the outdoor area. Monkey chow and water were available ad libitum, with supplemental food trays containing fresh fruits, vegetables, bread, and protein solution provided in the late afternoon, after testing sessions were completed. Tests were conducted once a day between 12:00 and 18:00 hours, approximately 5 days per week.

Apparatus

Testing took place in a mobile test chamber, which was located in the same facility that the capuchins were housed in and was positioned in front of their group's indoor enclosure, facing away from the enclosure. Subjects were removed from the group, and transferred to the test chamber by the use of a trained procedure. The test chamber measured 155 × 64 × 58 cm and was divided into two separate sections using an opaque partition, which blocked visual contact between subjects. This allowed for simultaneous testing of two subjects. The front of the test chamber was made of clear Lexan[®] with multiple armholes cut out so that an individual could stick a hand out to perform the task.

A cart, upon which a touch-sensitive monitor (43 cm Elo En-tuitive Touchmonitor, IntelliTouch technology) connected to a desktop PC, was situated and was positioned directly in front of the test chamber. The cart also had an automatic pellet dispenser containing either Kix[®] cereal or Bio-Serv Precision Pellets as a reward. Visual Basic 6.0 controlled the display presentation, reward delivery, playback of appropriate sound response, and data collection.

Stimuli

Stimuli used for training and as baseline in facial tasks were two-dimensional and three-dimensional clip art images sized 84 × 84 mm. The stimuli used in facial tasks were digital color photographs taken of all adult and subadult individuals (>6 years of age) in both groups. These served as both the In-group and Out-group facial stimuli for each subject. Hereafter, "In-group" refers to conspecifics living in the same social group as the subject whereas "Out-group" refers to conspecifics living in the other social group. The two groups had no visual contact with each other, though four of the older adult females had been housed together more than 14 years ago. The terms "In-group" and "Out-group" are used to specify that while subjects may have been familiar at one point with an individual from the other social group, they are not a member of the current In-group, which has been formed since 1991.

All photos were taken using a Konica Minolta Maxxum 7D digital camera and edited on a computer with Adobe Photoshop 6.0. Photos were cropped to only include the head, face and neck and were sized to 8.4 cm² with a resolution of 300 pixels per inch. Images included various viewpoints of each face as well as different gaze orientations. Background information was removed by filling in the area around the face with solid gray. Brightness and contrast were standardized to control for differences in lighting conditions.

Procedure

The experiments were conducted using an oddity paradigm. Training on the oddity paradigm was achieved over a 9-month period using colored two-dimensional clip art images. Trials began with a colored square located at the center of the screen. Upon contact, the square disappeared and four images appeared simultaneously on the screen in either a diamond or square layout. Three of the images were identical, or related, and one was different, or "odd," that is, the correct choice. The location of the odd stimulus

was randomly chosen on each trial. When the correct image was touched, all images disappeared, a high tone was played, and a food reward was delivered automatically via the pellet dispenser controlled by the computer. For incorrect selections, all images disappeared, a low tone was played, no reward was delivered, and an additional penalty of 4 sec was added to the intertrial interval. Subjects had 30 sec to make their selection, or the trial ended and was recorded as aborted. Aborted trials were not included in data analysis. We employed a correction procedure such that when an incorrect selection was made, the trial was repeated four times or until the subject selected the correct response, which ever occurred first. Data analysis only included the first presentation, not repeated trials.

During trials, an experimenter sat behind the apparatus such that he or she was unable to see the stimuli and the choices made. The experimenter was there to monitor the attention and behavior of the subjects and to abort testing if the subject appeared overly distracted or stopped performing.

Clip Art Oddity Training

All subjects were trained to perform the oddity task using images of clip art. Starting with a set of 560 images, 20 were initially selected to be the "same" image while the odd image was selected from the remaining 540 images. Over several sessions, the set of "same" grew to be 50 images from the entire set while the odd image was from the remaining 510 images. At this point, the odd image was switched to be one of the 50 images initially presented as "same" while the remaining 510 images were now the "same." After this switch, several sessions were presented in which the odd was any of the 560 images while the same was a group of 100 from the 560, adding in groups of 100 stimuli every couple of sessions. The final stage was randomly selecting the odd and same image from the group of 560. Later, additional clip art images were added, bringing the total number of stimuli to 680.

Face Training

Following training of the oddity paradigm using clip art, subjects were presented with digital images of conspecifics. A trial consisted of three identical images of a conspecific and one image of a different conspecific. Within a trial, the individuals presented were either both In-group members or both Out-group members in relation to the subject. Each session was comprised of 25 trials of In-group individuals, 25 trials of Out-group individuals, and 25 trials of clip art. The previously trained clip art trials served as a baseline measure of subject's attention level and motivation. If performance on clip art trials fell below 60% correct in one session, the data for the entire session was discarded due to inattention of the subject. This resulted in the removal of 8% of data (Bias = 4 out of 46; Georgia = 11 out of 65; Mason = 0 out of 23; Winnie = 2 out of 70; Wilma = 0 out of 18), the majority being removed from Georgia's data. Stimuli were randomly selected from a set of 101 portraits, 60 from Group 1 and 41 from Group 2.

Individual Recognition Task

Following training and familiarization with images of conspecifics, subjects were presented with trials in which three stimuli

were portraits of the same individual but from different views, and the odd (i.e., correct) stimulus, was a portrait of a different individual (see Figure 1). Again, all individuals presented in each trial were either both members of the In-group or both members of the Out-group in relation to the subject. Sessions consisted of 25 trials of In-group individuals, 25 trials of Out-group individuals, and 25 trials of three-dimensional clip art. The clip art set consisted of three different views of 70 different three-dimensional clip art images for a total of 210 images. If performance on clip art fell below 60% correct, the entire session for that subject was discarded. This led to the removal of one session for Bias. On each trial, facial stimuli were randomly selected from a stimulus set consisting of three different views of eight individuals from Group 1 and nine individuals from Group 2, for a total of 51 images. Subjects never were presented with images of themselves.

Transfer tests. Once performance had reached a criterion of 60% correct on both the In-group and Out-group conditions, subjects were transferred to a new set (Transfer 1) of three pictures per individual (this time a total of 10 different individuals from Group 2). A final transfer phase (Transfer 2) consisted of combining the original set of stimuli with those used in Transfer 1, thus randomly presenting any of the six pictures of each individual. This final set consisted of a total of 108 pictures, 54 from each group.

Data Collection and Analysis

All data collection was recorded via the computer controlling stimulus presentation. Information recorded per trial included: subject, experimenter, date, type of test, trial condition (In-group/

Out-group), trial number, the names of the image files presented at each location, the location of the odd stimulus, the latency to start the trial as well as the latency to make a response (in msec), the image and location that was selected by the subject, and whether the trial was correct, incorrect or aborted (no response from subject). Data were analyzed using SPSS 15.0. The primary dependent variable of interest was the response (correct/incorrect) and the independent variable was the type of condition, In-group or Out-group. The latency, the time from starting a trial to selecting a response, was also used in analyses as a dependent variable. The data were typically analyzed using a hierarchical logistic regression analysis which allowed us to examine multiple independent variables, such as performance over time and condition type (In-group/Out-group). In addition, the hierarchical technique permitted statistical control of the subject factor, since this was a repeated design. Two-way chi-square contingency tests using the Yates correction (Siegel & Castellan, 1988) were used to compare performance on a task prior to transfer and after transfer as well as to assess differences between In-group and Out-group trial types. These analyses compared the last 50 trials for each subject prior to transfer (“pretransfer”) to the first 50 trials of transfer (“transfer”) for all subjects, analyzing In-group and Out-group separately. To evaluate performance above chance level (25%), Heterogeneity G-tests were conducted. Heterogeneity G-tests compare performance with random chance, similar to a chi-square, but the G-test takes into account individual contributions.

Since the latencies were typically skewed, we followed a set procedure to determine whether to transform the data or not. First,

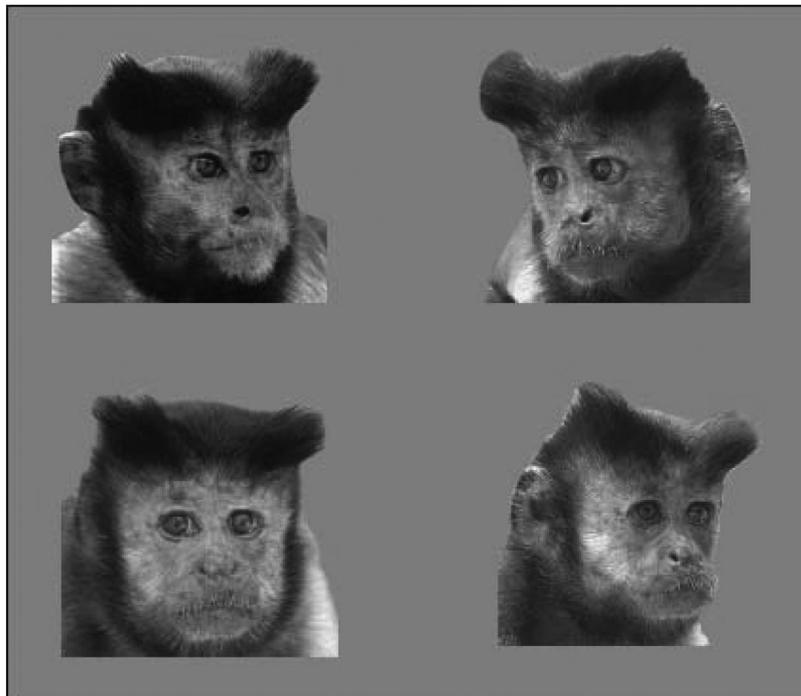


Figure 1. An example of a single Individual Recognition trial. The same individual is depicted in the top right, bottom left and bottom right positions. The odd individual, and correct response, is the top left position. Both individuals are adult females from Group 2. The images were presented in color during the experiment.

a Kolmogorov–Smirnov (K-S) test ($\alpha = .05$) was conducted on the latencies of each subject to determine if the distribution deviated from a normal distribution. If found to be significantly deviant, the latencies were transformed via a natural log transformation. The K-S test was conducted again on the transformed data, and if still significant, then an inverse transformation was applied to the original latencies and again tested for deviation from a normal distribution with the K-S test.

Results

Face Training

Face training consisted of presenting three identical faces and one different face, both from the In-group or from the Out-group in relation to the subject, and was used to familiarize subjects with facial stimuli. Data were analyzed in 25-trial blocks. The criterion for significantly above chance (i.e., 25%) performance for each session of 25 trials was 44%, based on a binomial test for 25 trials. The subjects reached this level for two consecutive sessions on In-group trials after an average of 22 sessions (Bias: 26, Georgia: 30, Mason: 16, Winnie: 32, Wilma: 6) and on Out-group trials after an average of 16 sessions (Bias: 16, Georgia: 24, Mason: 14, Winnie: 14, Wilma: 11). Final performance criterion was arbitrarily set at 60% correct for two consecutive sessions and was achieved in an average of 38 sessions for In-group trials (Bias: 42, Georgia: 54, Mason: 23, Winnie: 64, Wilma: 9) and on Out-group trials after an average of 27 sessions (Bias: 30, Georgia: 43, Mason: 17, Wilma: 18). After criterion was reached, subjects continued performing several training sessions to demonstrate that they were maintaining consistent performance above 60% on In-group and Out-group trials. Winnie never officially reached criterion on Out-group trials, but maintained high performance on In-group trials, so began the Individual Recognition task after completing 70 training sessions. In the instance of Georgia, her performance varied between 40% and 55% for many sessions after technically reaching criterion, resulting in her performing over 100 training sessions before starting the Individual Recognition task.

A hierarchical logistic regression analysis was conducted to assess learning over all sessions performed by all subjects and to determine if In-group and Out-group faces were learned at different rates. First, performance (correct or incorrect) was regressed against subject, to determine if all subjects performed, or learned, in the same manner. This was found to be significant ($R^2 = .001$, $Wald = 14.224$, $p < .001$, $Exp(B) = 0.95$, $CI_{.95} = 0.93, 0.98$), indicating that there were subject differences. This is likely because some subjects ended up performing 40 sessions whereas a subject such as Georgia performed over 100. The second step examined performance over time, regressing performance against consecutive trials (time), and was significant ($R^2 = .069$, $Wald = 783.085$, $p < .001$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$), demonstrating that the performance of subjects improved over time. The condition type, In-group or Out-group, was entered into the model to determine if there was a difference between In-group and Out-group trials. Results showed that controlling for time, there was an effect of condition type ($R^2 = .070$, $Wald = 10.747$, $p = .001$, $Exp(B) = 1.11$, $CI_{.95} = 1.04, 1.18$), such that subjects performed better overall on Out-group trials ($M = .54$, $SD = .50$) compared to In-group trials ($M = .51$, $SD = .50$). Finally, to

determine whether learning rates differed between In-group and Out-group conditions, the interaction between time and condition type was added to the regression analysis and not found to be significant ($R^2 = .070$, $Wald = 1.929$, $p > .05$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$).

Individual Recognition—Initial Performance

The Individual Recognition task presented three different portraits of a single individual and one portrait of another individual, both individuals being either In-group members or Out-group members relative to the subject. Subjects performed significantly above chance (criterion of 44% correct for 25 trials based on a binomial test) on two consecutive sessions after an average of 4 sessions for the In-group condition (Bias: 2, Georgia: 4, Mason: 4, Winnie: 3, Wilma: 6) and after an average of 7 sessions for the Out-group condition (Bias: 2, Georgia: 2, Mason: 2, Winnie: 24, Wilma: 5). A performance criterion of 60% correct for two consecutive sessions was attained in an average of 13 sessions for the In-group condition (Bias: 2, Georgia: 10, Mason: 19, Winnie: 22, Wilma: 10) and the Out-group condition (Bias: 3, Georgia: 5, Mason: 2, Winnie: 36, Wilma: 20). Once performance criterion was attained, subjects were exposed to several more sessions (15–30 sessions) using the same initial stimulus set to guarantee consistent performance. Georgia was removed from the group for social reasons and transferred to another facility so no further data are available for her.

To determine whether there were differences in the rates of learning for In-group and Out-group trials, a hierarchical logistic regression analysis was conducted over all sessions performed for the four subjects who completed this task (Bias, Mason, Winnie, and Wilma). First, performance was regressed against subject and was significant ($R^2 = .003$, $Wald = 19.224$, $p < .001$, $Exp(B) = 0.89$, $CI_{.95} = 0.85, 0.94$), indicating that there were differences between individuals' performance. Performance was then regressed against consecutive trials to determine learning over time, which was significant ($R^2 = .019$, $Wald = 108.862$, $p < .001$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$). This demonstrated that subjects continued to improve on the task over time. Next, the effect of condition (In-group/Out-group) was examined by adding condition type to the regression. The result was nonsignificant ($R^2 = .019$, $Wald = 3.148$, $p > .05$, $Exp(B) = 0.93$, $CI_{.95} = 0.85, 1.01$). Lastly, the interaction between time and condition type was added to determine if there were differences in the learning rates of the two conditions. Here, the interaction was significant ($R^2 = .020$, $Wald = 5.967$, $p < .05$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$). To investigate this interaction, we conducted separate hierarchical logistic regression analyses for In-group trials and for Out-group trials. The analysis revealed that for Out-group trials, there was a subject effect ($R^2 = .009$, $Wald = 29.396$, $p < .05$, $Exp(B) = 0.82$, $CI_{.95} = 0.77, 0.88$) that was not significant for In-group trials ($R^2 = .000$, $Wald = 0.560$, $p > .05$, $Exp(B) = 0.97$, $CI_{.95} = 0.91, 1.04$). Both trial types demonstrated learning effects (Out-group: $R^2 = .020$, $Wald = 37.918$, $p < .001$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$; In-group: $R^2 = .022$, $Wald = 73.902$, $p < .001$, $Exp(B) = 1.00$, $CI_{.95} = 1.00, 1.00$).

We wanted to assess whether beginning performance on the Individual Recognition task was similar to the ending performance of the Face Training task. To do so, we compared the last 50

In-group trials of all subjects on the Face Training task to the first 50 In-group trials of all subjects on the Individual Recognition task, and likewise for Out-group trials, using a two-way chi-square contingency test using the Yates correction, for the group as a whole (Siegel & Castellan, 1988), and was significant for both In-group, $\chi^2(1) = 25.48, p < .001$, odds ratio = 2.62, $CI_{.95} = 1.81, 3.80$, and Out-group, $\chi^2(1) = 18.08, p < .001$, odds ratio = 2.62, $CI_{.95} = 1.56, 3.28$, conditions. This result indicates that initial performance on the Individual Recognition task was below prior performance on the Face Training task. Despite this drop, a Heterogeneity G-test on the first 50 trials did find that both In-group and Out-group performance was significantly above chance (In-group: $G_h = 9.28, df = 4, p = .054, G_p = 71.92, df = 1, p < .001$; Out-group: $G_h = 10.77, df = 4, p < .05, G_p = 90.52, df = 1, p < .001$). The significant G_h value, indicating that departures from expectation may not be in a consistent direction, is due to one subject in each condition performing above chance but at, or below, 40%. Performance differences between In-group and Out-group trials in these first 50 trials for the group as a whole was assessed with a two-way chi-square contingency test using the Yates' correction (Siegel & Castellan, 1988) and was not significant, $\chi^2(1) = 0.40, p > .05$, odds ratio = 0.88, $CI_{.95} = 0.62, 1.25$. No further data are available for Winnie as she did not complete this task.

Individual Recognition—Transfer 1

Subjects attained a performance criterion of 60% correct for two consecutive sessions on Transfer 1 in an average of 7 sessions for In-group trials (Bias: 9, Mason: 9, Wilma: 2) and 5 sessions for Out-group trials (Bias: 4, Mason: 3, Wilma: 7). All subjects completed 8 to 10 sessions. We performed a hierarchical logistic regression analysis to assess the group's performance over time, which was not found to be significant ($R^2 = .000, Wald = .044, p > .05, Exp(B) = 0.99, CI_{.95} = 0.86, 1.13$), indicating that subjects performed in a similar manner. Again, subjects showed improved performance over time ($R^2 = .005, Wald = 5.022, p < .05, Exp(B) = 1.00, CI_{.95} = 1.00, 1.00$). Adding condition type (In-group/Out-group) to the regression was not significant ($R^2 = .006, Wald = 0.420, p > .05, Exp(B) = 1.08, CI_{.95} = 0.86, 1.34$), indicating that there was no difference in performance between the two condition types. Lastly, the interaction between condition type and time was added and was not significant ($R^2 = .006, Wald = 0.502, p > .05, Exp(B) = 1.00, CI_{.95} = 0.99, 1.00$).

To assess generalization of the Individual Recognition task, subjects were transferred to an entirely new stimulus set. As there were 270 possible random stimulus combinations from Group 1 and 216 from Group 2, only the first 50 Familiar and 50 Unfamiliar trials were selected to analyze transfer performance; the probability of image combinations being repeated during this time frame was low, therefore eliminating, or significantly reducing, the possible role for reinforcement history. The three subjects as a whole performed above chance on the first 50 In-group trials and the first 50 Out-group trials (In-group: $G_h = 5.39, df = 2, p > .05, G_p = 45.38, df = 1, p < .001$; Out-group: $G_h = 3.08, df = 2, p > .05, G_p = 65.09, df = 1, p < .001$), indicating a positive transfer to the new images. Comparing pretransfer performance to transfer 1 for In-group and Out-group trials of the group did reveal a significant difference in the Out-group condition, $\chi^2(1) = 5.72, p < .05$, odds

ratio = 1.83, $CI_{.95} = 1.14, 2.95$, and a trend toward differential performance for the In-group condition, $\chi^2(1) = 3.47, p = .06$, odds ratio = 1.59, $CI_{.95} = 1.00, 2.51$ (Figure 2a). There was no difference between In-group and Out-group facial stimuli in the first 50 trials of transfer, $\chi^2(1) = 0.66, p > .05$, odds ratio = 0.81, $CI_{.95} = 0.51, 1.27$.

Another measure that may be sensitive to differences in cognitive processing between trial types is the latency to make a response, which was recorded in milliseconds (ms). To examine this, we conducted paired t tests on the first 50 trials of In-group and 50 Out-group trials for each subject. Only one subject, Mason, showed a significant difference in the latency to respond to In-group (3266.66 ± 301.26) and Out-group (2682.90 ± 234.05) conditions, $t(49) = 2.07, p < .05$, two-tailed, $CI_{.95} = -1323.86, 156.34$, reacting more rapidly with Out-group faces.

Individual Recognition—Transfer 2

After reaching the performance criterion of 60% correct for two sessions, subjects were transferred to the final stimulus set, consisting of the previous two stimulus sets randomly combined, for a total of 108 images, 54 from each group. Performance correct on the first 50 In-group and 50 Out-group trials for this second transfer was significantly above chance (In-group: $G_h = 2.03, df = 2, p > .05, G_p = 44.80, df = 1, p < .001$; Out-group: $G_h = 1.15, df = 2, p > .05, G_p = 73.38, df = 1, p < .001$). Furthermore, there was no difference between In-group and Out-group conditions in these early trials, $\chi^2(1) = 1.63, p > .05$, odds ratio = 0.72, $CI_{.95} = 0.46, 1.14$. Transfer 2 performance did not differ from pretransfer performance in the Out-group condition, $\chi^2(1) = 0.90, p > .05$, odds ratio = 1.29, $CI_{.95} = 0.81, 2.05$, but did in the In-group condition, $\chi^2(1) = 4.90, p < .05$, odds ratio = 1.73, $CI_{.95} = 1.09, 2.74$ (Figure 2b). We again looked at the latency to select a response in both the In-group and Out-group conditions in these first 100 trials, and no subject demonstrated a significant difference in response times to In-group versus Out-group faces.

Discussion

Before assessing whether capuchin monkeys were able to recognize conspecific faces and generalize the identity of an individual across multiple views, we examined capuchins' ability to discriminate faces in the Face Training Task. This familiarized subjects with conspecific faces in the oddity task, which presented three identical images of one individual and one image of a different individual. Subjects needed to perform many sessions before reaching our performance criterion of 60% (In-group: 38 sessions, 950 trials; Out-group: 27 session, 675 trials). While it may have taken several sessions to acquire the task, the fact that they are able to discriminate conspecific faces is consistent with the studies presented earlier (e.g., Dahl, Logothetis, & Hoffman, 2007; Dufour, Pascalis, & Petit, 2006; Parr, Winslow, Hopkins, & de Waal, 2000; Pascalis & Bachevalier, 1998).

After subjects demonstrated successful discrimination of conspecific faces, we determined whether they were able to generalize the identity of the individual depicted in the image across multiple viewpoints. This is something that has not been tested in face recognition studies that utilize implicit tasks, such as the VPC paradigm (e.g., Dahl, Logothetis, & Hoffman, 2007; Dufour, Pas-

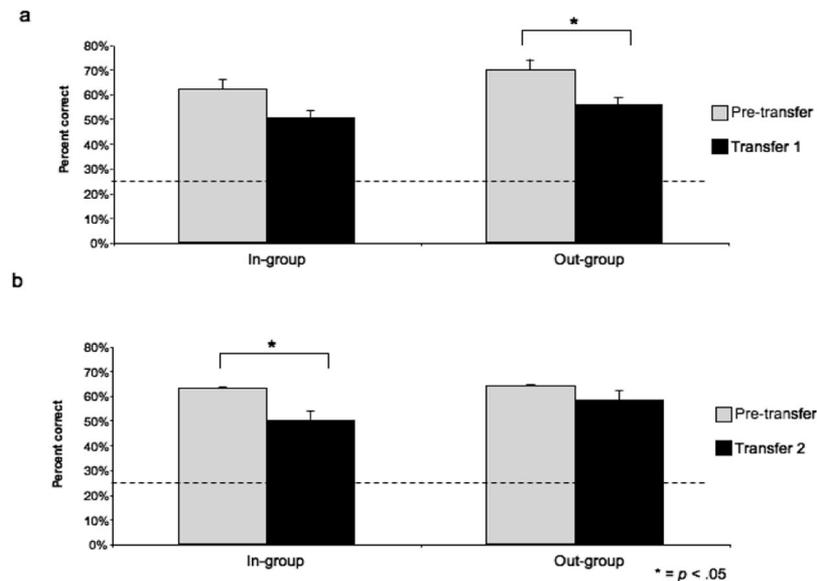


Figure 2. Comparing the group's performance prior to transfer and after transfer in the Individual Recognition task, (a) Transfer 1 and (b) Transfer 2. Gray bars represent the last 50 trials of all subjects (i.e., 150 trials total) prior to transfer and the black bars represent the first 50 trials of all subjects (i.e., 150 trials total) of transfer, for both the In-group and Out-group conditions. Horizontal dotted line indicates the chance level (25%) and error bars reflect the SEM. For Transfer 1, there was a significant decrease in performance after transfer in the Out-group condition, while on Transfer 2 there was a significant decrease in performance after transfer in the In-group condition.

calis, & Petit, 2006; Neiworth, Hassett, & Sylvester, 2007). To this end, we presented three images of a single individual taken from different perspectives along with an image of a different individual. Subjects readily transferred to this task, evidenced by the fact that they performed significantly above chance within the first 50 novel trials, though this performance level was not as high as the ending performance on the Face Training Task. That subjects performed significantly above chance on novel trials demonstrates that capuchins not only can detect differences between images of conspecific faces, but that they can recognize individuals, extracting the identity of the individual represented even when presented from different viewpoints. Subjects continued to perform above chance when they were presented with novel stimuli and novel combinations of stimuli in Transfer 1 and Transfer 2.

Many of the previous studies did not report what the initial performance of subjects were on the first exposure of novel trials, instead reporting how long before subjects reached a given performance criteria. This makes comparisons between the current and prior studies difficult. However, the rhesus macaques in the Parr et al. (2000) study required 200–400 trials with 15 unique trials before performing above chance in the initial face recognition task. Several other studies had similar results, with subjects receiving many exposures to only a few unique trials before performing above chance (e.g., Heywood & Cowey, 1992; Rosenfeld & van Hoesen, 1979). It would be premature to conclude that capuchins more readily recognize conspecific faces from multiple viewpoints when presented as a two-dimensional image when there are many methodological differences between the current and previous studies. A strength of the current study was that subjects were presented with a larger stimulus set, allowing for

many unique trials, making it less likely that subjects were relying on item-specific associations (Katz, Wright, & Bachevalier, 2002; Wright & Katz, 2006). Including more than one transfer test also reinforced our conclusion that capuchin monkeys can identify conspecific faces across viewpoint changes as subjects repeatedly performed above chance in the first 50 novel trials on these transfer tests. While we cannot conclude that this ability is confined to conspecific faces, given the design of the study, future studies will look at subjects' ability to discriminate other species' faces.

In-Group Versus Out-Group Performance

While it appears that several species can discriminate between conspecifics, even those that are unfamiliar, Zayan and Vaclair (1998) advise that individuals should perform better (more accurately) with familiar as opposed to unfamiliar conspecifics, as was our initial hypothesis based on human studies (Breen, Caine, & Coltheart, 2000; Bruce, Henderson, Newman, & Burton, 2001; Burton, Wilson, Cowan, & Bruce, 1999; Hill, Schyns, & Akamatsu, 1997; Newell, Chiroro, & Valentine, 1999; O'Toole, Edelman, & Bulthoff, 1998). Differences were found in the initial Face Training Task, but not in the direction we had predicted. Instead, subjects performed better on Out-group trials than on In-group trials. As subjects were from both groups, this result could not be due to possible differences in the stimuli presented, as what was considered In-group for one subject was the Out-group for another subject. Rather, it is possible that greater attention was given to out-group conspecifics, which allowed for better discrimination of those individuals. Both individually housed (Andrews & Rosenblum,

2001) and group-housed (Brannon, Andrews, & Rosenblum, 2004) bonnet macaques prefer to view videos of out-groups as opposed to familiar conspecifics, possibly for the novelty or that unfamiliar individuals may provide additional information that cannot be gained from familiar conspecifics. The novelty of out-group portraits may have attracted more attention by our subjects.

In subsequent tasks, no accuracy differences were found for in-group and out-group faces when looking at either (1) the first 50 trials or (2) over all sessions performed. While this was contrary to our hypothesis given the human findings, the differences found in human studies are typically more pronounced when profile views are used and when there is a large rotation away from the trained view (see Longmore, Liu, & Young, 2008). The images used in the current study included only a couple of profile views (approximately 10%), and probably none that would be considered a full profile. While the images were taken from different viewpoints and rotations, we did not systematically manipulate the degree of change from the initial stimuli, which may be why there were not more striking differences in performance between In-group and Out-group trial types. Also, subjects were presented with different pictures of each individual from the beginning and thus may have been able to more readily generalize across additional viewpoints since they had at least three stored images to compare the novel image to as opposed to only one image which is how many of the human studies are designed.

It is possible that past living situations may have reduced our ability to detect differences between In-group and Out-group. Three subjects (Winnie, Bias, and Georgia) did come from the same colony 14 years prior and therefore were “familiar” with one another though they were separated into two groups that had no visual contact. For those subjects, a couple of the individuals presented, and analyzed, as Out-group may have been “familiar.” These images were not removed because we did not want to reduce the number of individuals represented in the stimuli as this was one of our concerns with other studies. The photos used were acquired just prior to testing and it is unknown how, and if, capuchins recognize individuals when taken from different time points across their life span. However, it is possible that including these images for certain subjects did lessen our ability to find a difference between In-group and Out-group trials.

The current study did allow for comparisons not only of accuracy, but also of response latencies, between In-group and Out-group conditions. An analysis of the latencies found that only Mason responded at a different speed to these conditions in the first transfer. However, in this case his latencies were shorter to Out-group conspecifics. Again, Out-group faces may have roused Mason due to the novelty factor, resulting in shorter response times to those faces. He was also the beta male of the group and sexually mature during the time of testing. In the wild, he would be preparing to leave his natal group and seek out another group. Most of the images in the stimulus sets were of adolescent and adult females. It is quite possible that his mature status made Mason more attentive to Out-group conspecifics.

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