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Discrimination of Facial Expressions in Tufted Capuchin Monkeys (*Sapajus apella*)

By

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Master of Arts

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An abstract of a thesis submitted to the Faculty of the James T. Laney School of Graduate Studies of Emory University in partial fulfillment of the requirements for the degree of Master of Arts in Psychology 2012.

Abstract

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Facial expressions are important signals that facilitate primate social interactions. Tufted capuchins (*Sapajus apella*) readily discriminate conspecific faces and categorize them according to group membership. In three experiments, we examined whether this discrimination extends to facial expressions and how the discrimination is made. We tested whether tufted capuchins discriminate between neutral expressions and either affiliative eyebrow flash expressions or agonistic open-mouth threat expressions, whether the presence of salient facial features was sufficient for tufted capuchins to make such discriminations, and whether they demonstrated an inversion effect. Data were collected from nine adult and sub-adult monkeys using an oddity paradigm on touchscreen computers. Subjects discriminated between emotional and neutral expressions significantly above chance. Furthermore, they discriminated between open-mouth threats and neutral expressions with varying degrees of visible teeth and mouth opening significantly better than chance in all conditions and showed evidence of an inversion effect. These results suggest that discriminating emotional facial expressions is an important aspect of tufted capuchin communication and that like humans and chimpanzees, holistic, rather than feature-based processing is the dominant mechanism. By investigating the similarities in face processing between species, we gain a deeper understanding of the evolution of facial expressions as parts of communication systems.

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Table of Contents

List of Tables and Figures

Introduction

Face processing and recognition is widely regarded as a critical aspect of social cognition and communication. Living in a complex society demands that an individual be able to discriminate between conspecifics, interpret facial expressions, and respond with the appropriate behaviors given the context, individual, and expression (Leopold & Rhodes, 2010). Although the physical environment of non-human primates is ever-changing, the social environment not only changes more rapidly, but also more responsively to an individual's behavior (Adolphs, 2001). We define facial expressions as forms of social communication in which information about the motivational state of the sender is perceived by the receiver, resulting in a reduction of the uncertainty by the receiver as to the internal state of the sender (Seyfarth et al., 2010). Facial expressions convey critical information about the emotional state and possible intentions of the sender which should elicit appropriate responses from the receiver. A misunderstanding of this message can have dire consequences for the receiver, especially with regards to agonistic emotions (e.g., threat). Furthermore, at their most basic level, emotional contagion, empathy, and prosociality require that an individual be able to discriminate emotional cues, including facial expressions, and relate these emotions to states they have encountered themselves (Preston & de Waal, 2001).

Charles Darwin first put facial expressions into an evolutionary context with his 1872 book *The Expression of the Emotions in Man and Animals.* He categorized non-human facial expressions in the same way he categorized communicative signals such as vocalizations, thus putting forward the idea that facial expressions in non-human animals served a function. Further, he likened human facial expressions to facial expressions he observed in other animals, such as dogs, cats, and monkeys. As Schmidt and Cohn (2001) note, viewed in this light, facial expressions of both humans and non-human animals can be seen as behavioral phenotypes that are subject to environmental selective pressures. Furthermore, the authors state that facial expressions are low-cost signals that can easily be repeated in order to facilitate and maintain social stability as well as perhaps to promote affiliative interactions among social group members. In an evolutionary context, therefore, facial expressions can be seen as behavioral phenotypes subject to selection pressures that serve a communicative and facilitative function. As such, it’s reasonable to assume that homologies exist between human and non-human primate facial expressions. Preuschoft & Van Hooff (1995) assess the case for homology and investigate several similarities in facial expressions between related primate species, such as the muscle control of their production. The authors conclude that evidence suggests that many of the similarities between human and nonhuman primate facial expressions arise from homology.

Not surprisingly, there is increasing evidence that non-human primates process the information provided by faces in a similar fashion to humans. All primate species that have been tested for the capacity to individually discriminate conspecifics have demonstrated this ability (Leopold & Rhodes, 2010). In a match-to-sample paradigm, Parr et al (2000) presented chimpanzees (*Pan troglodytes*) with a black and white sample photograph of a conspecific face and then rewarded them for choosing an image of the same individual out of two subsequently-presented comparison images. In the first part of the experiment, the correct match was identical to the sample image and the chimpanzees chose the match above chance on the first presentation. To determine whether the chimpanzees were individually discriminating between conspecifics or discriminating between two complex grayscale images, Parr et al. (2000) then changed one of the comparison images to depict the same individual as the sample image but without being an identical photograph. After two presentations, the chimpanzees performed significantly above chance. Parr et al.'s (2000) results suggest that individual recognition is a relatively straightforward and easy task for chimpanzees that requires little to no training. In a continuation of this research, Parr et al. (2000) repeated this experiment with rhesus macaques (*Macaca mulatta*) and Although the monkeys required more trials to successfully match the sample, they, too, were able to individually discriminate.

Furthering the work of Parr et al. (2000), Pokorny & de Waal (2009a) used an oddity paradigm to probe the ability of tufted capuchins to individually recognize conspecifics. Three identical images of an individual were presented along with a fourth image of a different individual and monkeys were rewarded for choosing the "odd" image. Subsequently, the authors presented the monkeys with three *non*-identical images of the same individual along with a fourth image of a different individual in order to test the tufted capuchins' ability to generalize. Half of the trials utilized images from in-group individuals while half utilized images from out-group individuals in order to detect any effects of expertise. In humans, there is evidence for differential processing of known vs. unknown faces (Dubois et al., 1999). In the initial phase of this experiment, however, the tufted capuchins actually performed better in the out-group condition. The authors conclude that this difference might be accounted for by increased attention and viewing time for out-group faces.

Non-human primate identity recognition goes beyond discrimination and generalization. Parr & de Waal (1999) showed that chimpanzees could not only discriminate faces by identity, but could also detect similarity between faces based on familial traits. Furthermore, Pokorny and de Waal (2009b), using the same oddity paradigm as in their previous study, presented tufted capuchins with images of either three in-group and one out-group individuals or three out-group and one in-group individuals. Their results demonstrated that tufted capuchins can not only discriminate in-group and out-group individuals, but can also *categorize* them as such (Pokorny & de Waal, 2009b). The results of these two studies combined suggest that the chimpanzees and capuchins, respectively, were able to relate static images to real individuals. By making this connection, therefore, the non-human primates gathered *additional* information from the stimulus images. In a related study utilizing dynamic stimuli with rhesus macaques, Bovet & Washburn (2003) presented three monkeys with video clips of conspecifics and rewarded them for selecting the most dominant individual. Two of the three rhesus monkeys were able to generalize this discrimination to novel transfer videos suggesting that macaques can use features, including facial features, to infer identity and the traits that accompany that identity, such as dominance rank.

Although descriptive information can be gleaned from faces, it is important to also consider the mechanism by which humans and non-human primates gather and process this information. To compare the processing mechanisms of humans and rhesus macaques, Dahl et al (2009) compared the eye scan patterns of humans and monkeys while they were viewing human and macaque faces in upright, inverted, and blurred conditions. They assessed both viewing time and the locations on the stimuli (features) which were attended to most by the subjects. Their results suggested that both humans and macaques process the faces of conspecifics differently than those of other species. The authors conclude that conspecific faces tend to be processed *holistically* (or configurally) as opposed to feature by feature (parts-based processing) in both humans and macaques. The conclusion that both humans and macaques holistically process conspecific faces is further suggested by Dahl et al.'s (2009) investigation of the inversion effect. Although humans tend to process the faces of conspecifics holistically when the stimuli are upright, inverting the stimuli interrupts such processing (Young, Hellawell, & Hay, 1987). This finding was replicated by Dahl et al. (2009). Furthermore, it appears that non-human primates share this inversion effect (Dahl, et al., 2009; Leopold & Rhodes, 2010; Parr, Dove, & Hopkins, 1998; Pokorny & de Waal, 2009a; Tomonaga, 1994).

Further investigating the similarities between the mechanisms of human and non-human primate face processing, Dufour, Pascalis, & Petit (2006) examined how Tonkean macaques (*Macaca tonkeana*), tufted capuchins, and humans process the faces of either conspecifics or phylogenetically close or distant species. Human subjects were shown a sample image of either a human face, a Tonkean macaque face, or a rhesus macaque face for three seconds. After a three second delay, the human subjects were then shown two images of the same species as the sample image, one of which was novel and the other of which was identical to the sample image and the subject's viewing time of each image was assessed. Tonkean macaques and tufted capuchins were tested in the same way as humans except that they were shown three non-conspecific species instead of two (stumptailed macaques (*Macaca arctoides*), rhesus macaques, and humans for the

Tonkean macaques and white-faced capuchins (*Cebus capucinus*), longtailed macaques (*Macaca fascicularis*), and humans for the tufted capuchins. All three species demonstrated a conspecific-bias for face recognition suggesting similarities in the way all three primate species individuate faces.

Just as there are many similarities between the mechanisms by which humans and non-human primates process faces, there are also many parallels between the neural substrates thought to influence face processing in various primate species. Face-selective circuits have been identified in the human fusiform gyrus or fusiform face area (FFA) (Johnston & Edmonds, 2009). In contrast, neurons selective for facial emotion have been identified in the superior temporal sulcus (STS). These observations have led to the idea that there are separate pathways involved in face recognition and facial expression processing (but see Calder & Young, 2005). Face-selective and emotion-selective neurons have also been identified in similar neural substrates in non-human primates, which may suggest a homology (Adolphs, 2001; Ghazanfar & Santos, 2004; Leopold & Rhodes, 2010).

Parr et al. (1998) used a match to sample paradigm to probe the ability of chimpanzees to discriminate amongst common conspecific facial expressions (reviewed in Parr, 2003). The authors presented each subject with a sample photograph of an individual depicting one of five facial expressions and then presented the subject with two comparison images, one of which was a photograph of a different individual making the same expression as the sample image, and one of a different individual with a neutral facial expression. The chimpanzees discriminated three of the five expressions (bared-teeth display, play face, and scream) from the neutral expression above chance in the first session, while one expression (relaxed-lip face) was never discriminated above chance. To further explore how chimpanzees process facial expressions, Parr et al (1998) then scored each of the five expressions based on their characteristic features (e.g. open mouth, visible teeth) and paired each expression with every other expression using the same paradigm as before to determine if chimpanzees would discriminate two highly distinct expressions (as determined by their categorical ratings) more easily than highly similar expressions. Although, as would be predicted by feature-based processing, the chimpanzees did discriminate more distinct images with more success, certain expression, such as the scream, were discriminated from each of the other expressions well, regardless of the degree of similarity. Parr et al (1998) therefore conclude that something in addition to feature-based processing must be aiding discrimination. A later study by Parr et al (2008) confirmed these findings while using standardized computer images of chimpanzee expressions instead of photographs.

Although they tend to display more discrete rather than graded facial expressions than chimpanzees or humans, tufted capuchins are still able to display a large range of expressions (Weigel, 1979). Two of the most common capuchin expressions are the open-mouth threat expression and the eyebrow flash (Fragaszy, Visalberghi, & Fedigan, 2004). The open-mouth threat features a large degree of mouth opening and many visible teeth—both of which are salient facial features. The eyebrow flash, by contrast, is affiliative and usually occurs during sexual courtship. It is part of the repertoire of a female capuchin’s receptive display. Male capuchins also display the eyebrow flash when responding to a female in estrus, or a state of sexual receptivity. It features an increased forehead length and an increased degree of eye opening due to a lifting of the eyebrows.

Although tufted capuchins have been shown to discriminate the identities of conspecifics as well as categorize individuals as either in-group or out-group, to date there is no research about facial expression recognition in tufted capuchins or about emotional information conveyance by facial expressions (Dufour, et al., 2006; Pokorny & de Waal, 2009a, 2009b). The vast majority of comparative research in the area of face and emotion processing has focused on chimpanzees and rhesus macaques (Ghazanfar & Santos, 2004; Kano, Tanaka, & Tomonaga, 2008; L. A. Parr & Heintz, 2009; Parr, et al., 2008). Only a few studies have broadened their research to include New World species such as tufted capuchins (Dufour, et al., 2006; Evans, Howell, & Westergaard, 2005; Hook-Costigan & Rogers, 1998; Pokorny & de Waal, 2009a, 2009b). Focusing comparative studies on primates that are phylogenetically close to humans provides an incomplete picture of the evolution of these abilities. It is also important to research species that differ from Old World monkeys, apes, and humans in order to determine which aspects of facial emotion processing are evolutionarily conserved and which arose separately as a result of convergent evolution. How different species solve the same challenges, including social challenges, as a function of their morphology, phylogeny, and environment is one of the fundamental questions of the biological sciences.

Hypotheses & Predictions

Experiment 1. The current study aimed to determine whether or not captive tufted capuchins discriminate between neutral facial expressions and emotional facial expressions using a computerized oddity task. In Experiment 1, subjects were presented with three non-identical images of neutral facial expressions and one image of either an affiliative expression (eyebrow flash) or an agonistic expression (open-mouth threat) and were required to choose the odd image.

Hypothesis 1, Expression discrimination, posits that like their human and non-human primate counterparts, subjects will be able to complete this task for both emotional expressions. *Hypothesis 2, Differential discrimination,* further posits that like chimpanzees, subjects will discriminate the open-mouth threat from neutral more readily than the eyebrow flash. This difference would be predicted due to either the more salient nature of the facial cues associated with open-mouth threats (i.e., a large mouth opening and visible teeth) or the greater fitness consequences that might accompany an open-mouth threat as compared to an eyebrow flash.

Experiment 2. This study further aimed to determine the degree to which different facial features, namely the degree of mouth opening and visible teeth, affected the ability of subjects to discriminate open-mouth threats from neutral expressions. In Experiment 2, subjects were presented with images of neutral expressions with varying degrees of two salient features: mouth opening and visible teeth. *Hypothesis 3a, Rule-based discrimination,* posits that capuchins use a rule-based mechanism to discriminate expression. In this case, the presence of one specific facial feature automatically links the expression to a behavioral response. This idea is concurrent with the possibility that capuchins use feature-based processing as opposed to holistic processing. This mechanism predicts that they will fail to discriminate the odd emotional expression from neutral when the degree of mouth opening or visible teeth in the neutral expression images is close to that of the emotional expression itself. Alternately, *Hypothesis 3b, Template discrimination*, posits that capuchins discriminate expressions using a complex template of facial feature arrangements. Unlike rule-based discrimination, template discrimination predicts that the arrangement of the entire face area is responsible for signal discrimination, indicating holistic, rather than feature-based processing. This idea predicts that capuchins will discriminate open-mouth threats from neutral expressions above chance in both mouth opening and visible teeth experimental conditions.

Experiment 3. In order to further investigate whether capuchins use holistic or feature-based processing with facial expressions, Experiment 3 presented inverted emotional images alongside inverted neutral images. If capuchins demonstrated the inversion effect in which upright faces are discriminated more successfully than are inverted faces, it would provide evidence that they process faces holistically. *Hypothesis 4, Inversion effect*, posits that, like humans and the other non-human primates that have been tested, capuchins will discriminate upright emotional images (from Experiment 1) with greater success than inverted emotional images.

Method

Subjects

Subjects for Experiments 1-3 were 7 adult (1 male, 6 females) and 2 sub-adult (1 male, 1 female) tufted capuchin monkeys (*Sapajus apella*). Subjects ranged in age from 4-36 years old (*Mdn* = 9, *SD* = 11.36) at the time that each began Experiment 1. Training began in November of 2010 and testing was conducted from March-July of 2011. All ages reflect the age of the subject at the time the individual began testing. Two subjects (Winnie and Bias) had been previously trained and tested on face recognition (Pokorny & de Waal, 2009a). Five subjects (Luther, Bailey, Benny, Gonzo, and Star) had been previously trained on various oddity paradigms using the touchscreen computers in the same procedure described above, but had never been subjects in any tests. Finally, two subjects (Lance and Lark) had no previous experience using the touchscreen computers before November of 2010.

Subjects were housed at Yerkes National Primate Research Center in Atlanta, Georgia as members of one of two naturalistic social groups. Yerkes National Primate Research Center is fully accredited by the American Association for Accreditation for Laboratory Animal Care. A detailed description of the enclosures can be found in Pokorny & de Waal (2009a). During training and testing, group 1 was composed of 11 individuals (3 males, 8 females) including 2 sub-adults and 9 adults at the beginning of testing and 8 adults at the conclusion of testing, as 1 adult male individual was removed as a result of a failed bid for the alpha male position. Group 2 was composed of 15 individuals (6 males, 9 females) including 2 juveniles, 1 sub-adult, and 12 adults throughout the duration of testing. Five test subjects were members of Group 1 (Star, Bias, Benny, Bailey, and Gonzo) and four test subjects were members of Group 2 (Winnie, Luther, Lark, and Lance). Three test subjects came to the Yerkes National Primate Research Center from the Wisconsin Primate Center in 1989 (Winnie, Star, and Bias) and the other six test subjects were born into the respective social groups in which they lived during the time of testing.

Three test subjects from group 1 were categorized as low-ranking (Gonzo, Bailey, and Bias), one as middle-ranking (Benny), and one as high-ranking (Star). Two test subjects from group 2 were categorized as low-ranking (Lark and Lance), one as middle-ranking (Luther), and one as high-ranking (Winnie). All rank assignments were made before testing commenced and were re-assessed for accuracy at the conclusion of testing.

No changes to the original categorizations were made. See *Table 1* for information about each test subject.

Water and Purina monkey chow biscuits were available *ad libitum* throughout the day and a mixture of fresh produce, bread, and a protein solution was fed to each group each afternoon after all testing for the day had concluded. All testing procedures were approved by the Institutional Animal Care and Use Committee of Emory University (application 136-2008Y).

Table 1

Subject characteristics

Individual	**Rank**	**Group**	**Sex**	**Date of Birth**	**First Test Date**	**Age**
Winnie	High	2	F	1/1/1984*	3/1/2011	27
Lance	Low	2	F	3/13/2002	5/18/2011	9
Lark	Low	2	F	6/23/2002	5/20/2011	8
Luther	Middle	2	M	1/17/2005	3/4/2011	6
Star	High	1	F	1/1/1975*	5/19/2011	36
Bias	Low	1	F	1/1/1987*	3/27/2011	24
Bailey	Low	1	F	11/9/1999	6/10/2011	11
Benny	Middle	1	M	12/9/2003	6/10/2011	7
Gonzo	Low	1	F	12/22/2005	3/27/2011	4

Note. All ages reflect the age of the individual at the first test date.
* denotes estimated birth dates

Apparatus

See Pokorny & de Waal (2009a) for a detailed description of the testing chamber and touchscreen computers. Subjects were moved into a mobile testing chamber from their enclosure. The testing chamber was divided into two halves by an opaque screen so two subjects could be tested simultaneously. One of two touchscreen computer monitors on top of a cart was moved in front of the testing chamber (both were Elo Entuitive Touchmonitors; one was 22.87 x 36.56 cm and the other 23.11 x 30.71 cm). The front of the testing chamber was made out of transparent Lexan® panels and had armholes positioned such that the subject could reach out and make a selection on the touchscreen. If a subject answered a trial correctly, automated feeders attached to the touchscreen computers were triggered to release either one piece of Kix® cereal or one flavored Bio-Serv Primate Precision Pellet. All displays, auditory signals, reward dispensation, and data collection were controlled via a computer.

Design & Procedure

This study utilized a computerized touchscreen oddity task. All subjects completed the training requirements laid out by Pokorny & de Waal (2009a) before beginning the testing phase. All subjects were then put through a training phase specifically designed for the current study. Each training session for Experiments 1 & 2 was comprised of 75 trials: 30 in-group test trials, 30 out-group test trials, and 15 clip art control trials. Three non-identical stimulus images were presented depicting the same facial expression along with one stimulus image that depicted a different facial expression. The location of the images was randomized and they were presented either in a diamond or square configuration. In order to control for attention, clip art trials with three identical clip art images and one different clip art image were included. The order that trials were presented were randomized.

Once a test subject reached a criterion of 60% success on all trial types (chance was 25%) for each experiment in two sessions in a row, the subject was given two sessions of a transfer test which was composed of exactly the same number and type of images present during the training phase, but which were completely novel. Training sessions were designed to ensure that test subjects understood the task and transfer sessions tested their knowledge without the possibility that subjects were memorizing stimuli. All analyses were performed using the results of the two transfer test sessions instead of the training sessions as learning assessment was not part of the study's aims.

Test sessions for Experiment 3 were comprised of 158 trials: 60 in-group trials and 60 out-group trials which were identical to those used in the testing phase of Experiments 1 & 2, 30 clip art control trials, 4 out-group probe trials, and 4 in-group probe trials. Each subject completed two sessions for each experiment. No training was given for Experiment 3 because the aim of probe trials is to assess what the test subjects know without any reinforcement (all answers were rewarded) or prior learning.

All subjects were tested for 20 minutes or until the session was completed, whichever occurred first. In alignment with previous studies, a start square was presented between each trial. Once a subject touched the start square, the trial images were presented. A correct answer was accompanied by an auditory signal, a food reward (see above), and a 2 second inter-trial interval. An incorrect answer was accompanied by a different auditory signal, no food reward, and a 5 second inter-trial interval. A trial was repeated up to four times until the subject answered correctly. Only trials which were answered correctly on the first presentation were considered for analysis. If a subject did not touch the screen at all for 10 seconds during presentation of either the start square or the trial images themselves, the trial was aborted and a new trial started. Aborted trials were not considered for analysis. All possible answers for probe trials were accompanied by the auditory signal and inter-trial interval which corresponded with a correct answer and were followed by the dispensation of a food reward.

Stimuli. All stimuli were digital photographs edited using Adobe Photoshop Elements 9.0®. Images were cropped such that only the face was visible and were sized to fit within a 300 x 300 pixel square. Furthermore, all images were edited to control for luminosity. All gaze and head directions were included but were not randomized throughout testing. No trial presented three images that were similar along another obvious dimension, such as identity, to avoid confusion as to which image should be considered "odd." Photographs were converted to grayscale and were presented on a solid black background, both to highlight the photograph itself and to differentiate these experiments from previous experiments involving conspecific faces.

Photographs for test stimuli were taken by the authors between October 2010 and May 2011. All images for in-group trials depicted individuals currently in Group 1 or Group 2, whichever group to which the test subject belonged. However, test subjects never viewed images of themselves. Most images for out-group trials also depicted individuals currently in Group 1 or Group 2, whichever group to which the test subject did not belong, but a few images were also used of wild tufted capuchins from Puerto Iguazú National Park in Puerto Iguazú, Argentina taken between August 2008 and November 2009. There were no trials that presented both in-group and out-group images simultaneously.

Experiment 1. Three of the trial images depicted a neutral expression. These images were randomly selected from a pool of 60 images (30 in-group, 30 out-group). No two identical images were presented simultaneously within a trial. The odd image depicted either an eyebrow-flash or an open-mouth threat and was randomly selected from a pool of 20 images (10 in-group, 10 out-group). See *Appendix A* for an example layout of an Experiment 1 trial with an eyebrow flash and *Appendix B* for an example layout of an Experiment 1 trial with an open-mouth threat.

Experiment 2. Three of the trial images depicted a neutral expression with varying degrees of mouth opening or visible teeth. Small mouth opening trials presented three neutral photographs of capuchins with less than 33% of maximum mouth opening, medium mouth opening trials with 33-65% maximum mouth opening, and large mouth opening trials with greater than or equal to 66% maximum mouth opening. See *Appendix C* for examples of each type of neutral mouth opening trial image. Few visible teeth trials presented three neutral photographs of capuchins with fewer than 50% of teeth visible and high visible teeth trials with greater than or equal to 50% of teeth visible. Visible teeth trials only included photographs with less than 33% mouth opening in order to control for a possible interaction between the two different salient features. See *Appendix D* for examples of both types of visible teeth trial images. Images for all trial types were randomly selected from one of five pools (one for each trial type) with 24 images each (12 in-group, 12 out-group). The odd image for all Experiment 2 trials depicted an open-mouth threat and was an image not presented in any previous experiments. It was randomly selected from a pool of 20 images (10 in-group, 10 out-group).

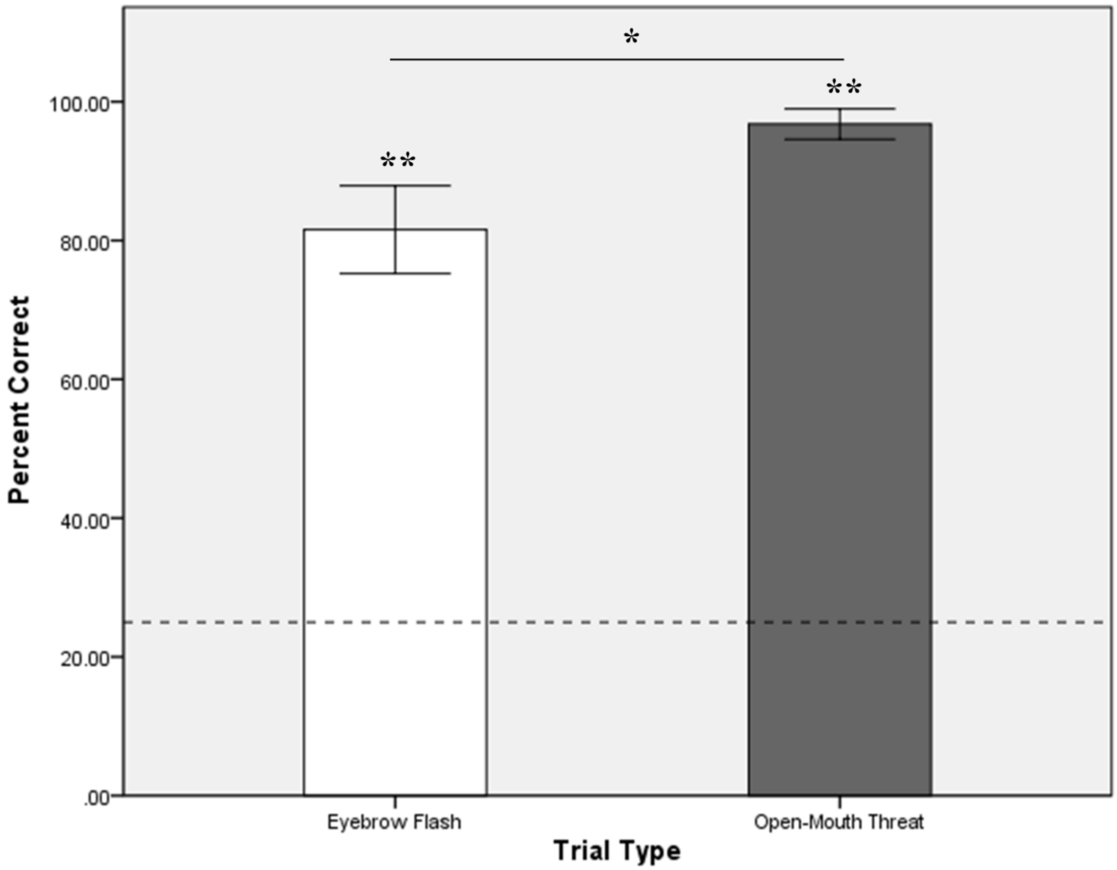
Experiment 3. Three of the trial images depicted an inverted neutral expression that had not been used in any previous experiment and were randomly selected from a pool of 20 images (10 in-group, 10 out-group). The odd image depicted an inverted eyebrow flash that had not been used in any previous experiment. It was randomly selected from a pool of 8 images (4 in-group, 4 out-group), but once it was selected for a probe trial, it was not re-selected for any subsequent probe trials so that all odd probe images were viewed only once by each test subject.

Results

All statistical analyses were conducted using IBM$^{®}$ SPSS$^{®}$ version 19.0 (SPSS, Inc., Chicago IL). Further, all analyses are two-tailed.

Experiment 1

Experiment 1 tested the ability of tufted capuchins to discriminate between neutral facial expressions and either affiliative or agonistic emotional facial expressions. A one-sample t-test revealed that subjects successfully chose the odd image significantly above 25% chance, $t(8) = 38.77$, $p < .001$. Furthermore, a paired-samples t-test revealed that subjects were more successful when the trials were composed of out-group individuals than when they were composed of in-group individuals, $t(8) = -3.27$, $p = .01$. Subjects discriminated agonistic from neutral expressions with greater success than they did affiliative from neutral expressions $t(8) = -4.53$, $p = .002$ (see Figure 1).

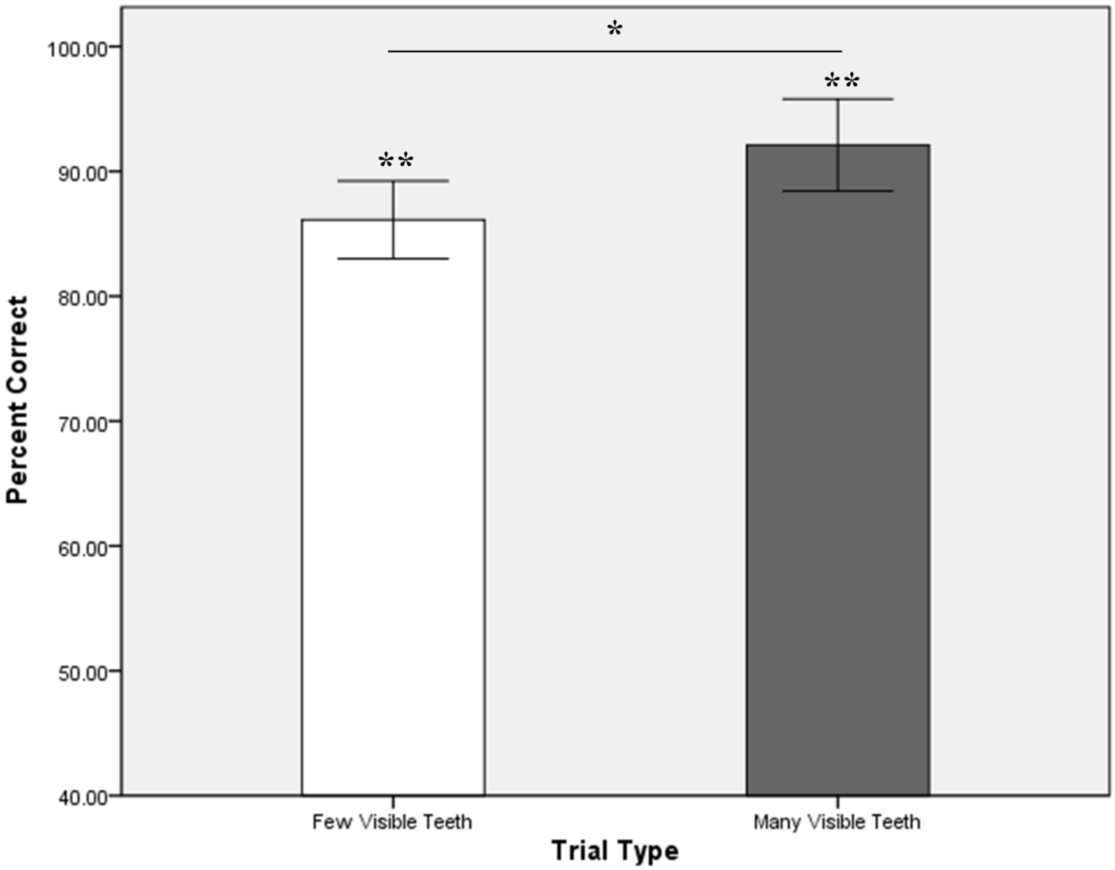


* p = .002, ** p < .001

Figure 1. Percent correct choice of the emotional expression (either eyebrow flash or open-mouth threat) over neutral expressions in an oddity task. White bar represents trials in which eyebrow flash images were odd. Grey bar represents trials in which open-mouth threat images were odd. The horizontal dotted line indicates chance level (25%) and error bars denote the SEM. Subjects performed significantly above chance in both experimental conditions, but performed significantly more successfully on trials in which open-mouth threat images were odd.

Experiment 2

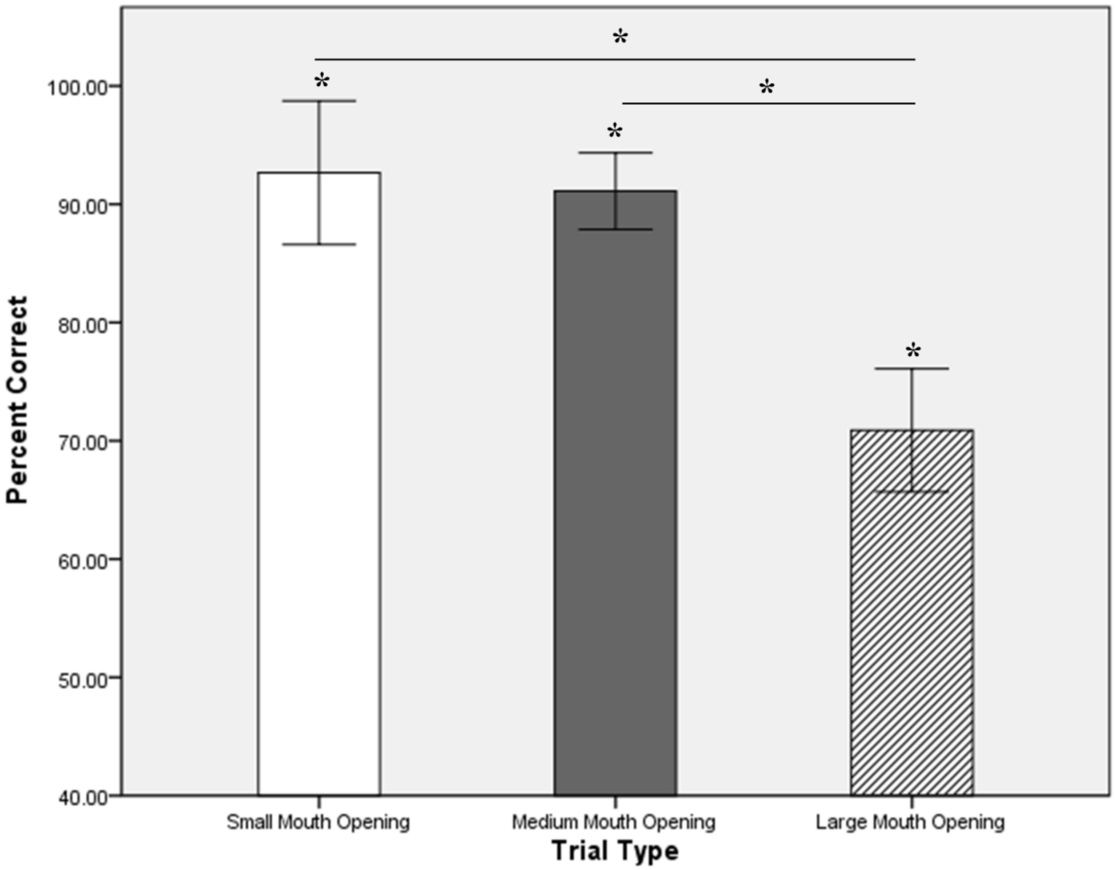
Experiment 2 investigated whether tufted capuchins discriminated open-mouth threats from neutral expressions when the neutral expressions depicted different degrees of mouth opening or visible teeth. A one-sample t-test revealed that when the neutral images had a low degree of teeth visible (<50%), subjects discriminated the open-mouth threat from neutral expression significantly above chance, $t(8) = 39.21$, $p < .001$. When neutral images had a high degree of teeth visible, they still discriminated open-mouth threats (≥50%), $t(8) = 36.39$, $p < .001$. Furthermore, subjects chose the odd agonistic expression with greater success when the neutral images had a higher degree of visible teeth than when they had a lower degree, $t(8) = -3.29$, $p = .01$ (see *Figure 2*).



* p = .01, ** p < .001

Figure 2. Percent correct choice of the open-mouth threat expression over neutral expressions with different degrees of visible teeth (few or many) in an oddity task. White bar represents trials in which the neutral images had few (<50%) of teeth visible. Grey bar represents trials in which the neutral images had many (≥50%) of teeth visible. Error bars denote the SEM. Subjects performed significantly above chance in both experimental conditions, but performed significantly more successfully on trials in which many teeth were visible.

A one-sample t-tests revealed that subjects discriminated the open-mouth threat image from neutral significantly above chance for all degrees of mouth opening, $t(8) = 22.28$, $p < .001$ for low trials; $t(8) = 40.82$, $p < .001$ for medium trials; $t(8) = 17.65$, $p < .001$ for high trials. A 3 x 2 one-way within-subjects ANOVA revealed that there was a significant effect of trial type on subject success, $F(2,16) = 35.99$, $p < .001$, partial $\eta^2 = .82$ (see *Figure 3*).

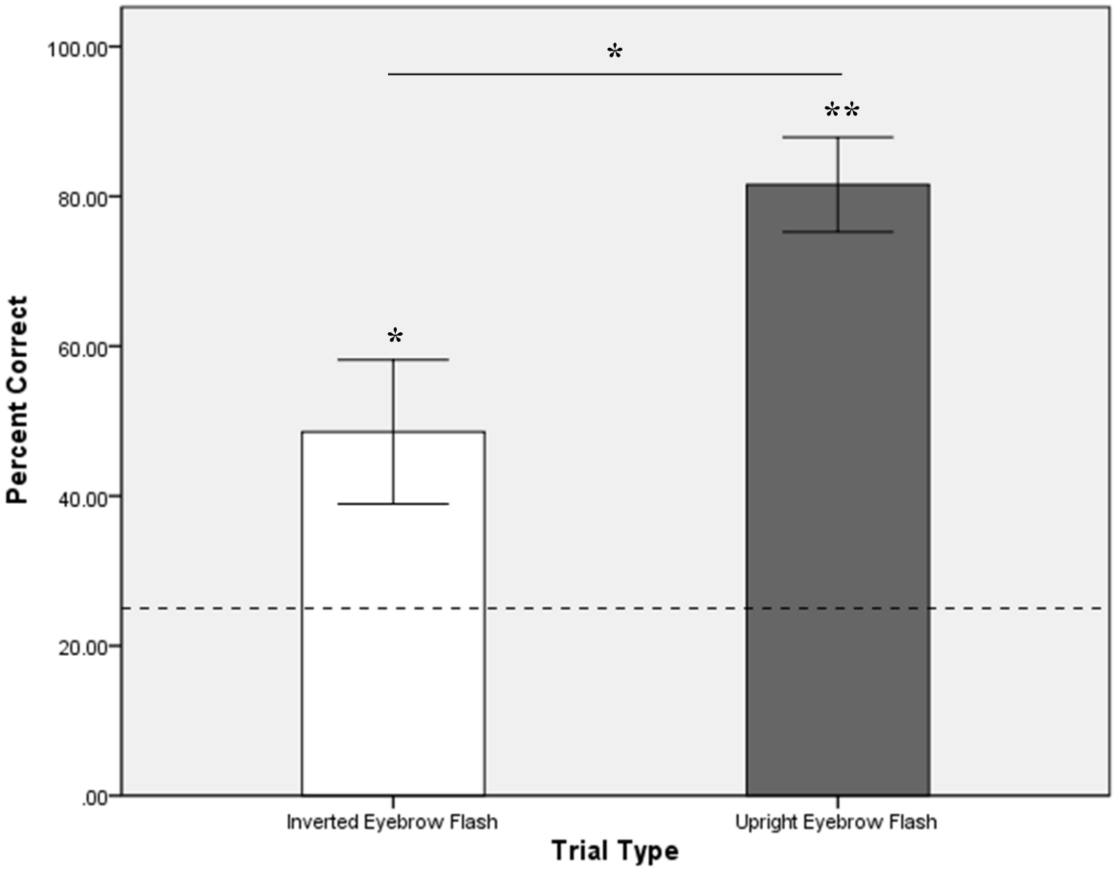


* p < .001

Figure 3. Percent correct choice of the open-mouth threat expression over neutral expressions with different degrees of mouth opening (small, medium, or large) in an oddity task. White bar represents trials in which the neutral images had small mouth openings (<33%). Grey bar represents trials in which the neutral images had medium mouth openings (≥33%, <66%). Striped bar represents trials in which the neutral images had large mouth openings (≥66%). Error bars denote the SEM. Subjects performed significantly above chance in all experimental conditions, but performed significantly more successfully on trials with small compared to large mouth openings, and on trials with medium compared to large mouth openings.

Experiment 3

Experiment 3 consisted of probe trials designed to determine whether or not capuchins exhibited an inversion effect when discriminating eyebrow flashes from neutral expressions. A paired-samples Student's t-test revealed that subjects performed significantly better on the upright trials, in which the odd image was an eyebrow flash from Experiment 1, than on the inverted probe trials, $t(8) = -5.29$, $p = .001$, revealing an inversion effect (see *Figure 4*). Nevertheless, a one-sample Student's t-test revealed that subjects discriminated the affiliative expression from neutral significantly above chance, $t(8) = 4.90$, $p = .001$.



* p = .001, ** p < .001

Figure 4. Percent correct choice of the eyebrow flash expression in both upright and inverted experimental conditions. White bar represents success on trials in which both the neutral images and the emotional (eyebrow flash) images were inverted. Grey bar represents success on trials in which both the neutral images and the emotional images were upright. Data for the inverted eyebrow flash trials were collected during probe trials in which all answers were rewarded (16 trials total randomly presented in between 300 non-probe trials from Experiments 1&2). Data for the upright eyebrow flash trials were collected during Experiment 1 non-probe trials (60 trials total). The horizontal dotted line indicates chance level (25%) and error bars denote the SEM. Subjects performed significantly above chance in both experimental conditions, but performed significantly more successfully on upright than inverted trials, revealing an inversion effect.

Age, Rank, and Sex Analyses

Additional analyses were performed to determine whether subject sex, age, or rank moderated subject success in all experimental conditions. See *Table 2* for a summary of results.

Table 2

Effects of sex, age, and rank

Experiment	Trial Type	Statistic	df within	df between	*p*
Sex		**t**			
1		-1.479	7		0.183
2	*Few teeth*	0.527	7		0.614
	Many teeth	2.437	7		0.045*
	Low mouth opening	-0.474	7		0.65
	Medium mouth opening	0.189	7		0.855
	High mouth opening	1.851	7		0.107
3		2.52	7		0.04*
Age		**t**			
1		1.683	7		0.136
2	*Few teeth*	0.479	7		0.646
	Many teeth	-0.321	7		0.757
	Low mouth opening	3.837	7		0.006**
	Medium mouth opening	0.755	7		0.475
	High mouth opening	-0.733	7		0.487
3		0.122	7		0.906
Rank		**F**			
1		2.066	6	2	0.208
2	*Few teeth*	5.636	6	2	0.042*
	Many teeth	1.194	6	2	0.366
	Low mouth opening	0.388	6	2	0.694
	Medium mouth opening	0.831	6	2	0.48
	High mouth opening	1.454	6	2	0.305
3		0.369	6	2	0.706

Note. All p-values presented are two-tailed. All t-statistics presented are independent-samples Student's t statistics. All F-statistics presented were obtained via a 3x2 one-way ANOVA. Age was categorized as young (<20 years) or old (≥20 years). Rank was categorized as low, medium, or high.

* $p < .05$, ** $p < .01$

Discussion

The results of this study support the idea that tufted capuchins discriminate emotional facial expressions, both affiliative and agonistic, from neutral ones. **Hypothesis 1, Expression** discrimination, which predicted that capuchins could discriminate between facial expressions, was strongly confirmed. That subject age, sex, and rank were not significant predictors of overall success rate is probably indicative of the fact that this task was relatively easy for all subjects and that facial expression discrimination is something that all tufted capuchins are able to do. The high degree of success displayed by the subjects in Experiment 1 further highlights the ease with which they appear to make this discrimination.

Furthermore, **Hypothesis 2, Differential discrimination**, which predicted that agonistic expressions would be more discriminable than would affiliative expressions was also confirmed. Capuchins discriminated open-mouth threats more readily from neutral expressions than they did eyebrow flashes from neutral expressions. Like the chimpanzees in Parr et al.'s (1998) study, the capuchins discriminated the agonistic expression (an open-mouth threat instead of a scream, in this case) from neutral with greater success than the affiliative expression. This finding indicates either that the features displayed in open-mouth threat expressions are more salient or that recognizing agonistic expressions is of greater importance or urgency than recognizing affiliative expressions. It is important to note that these are *not* mutually exclusive ideas. It is plausible that open-mouth threat expressions evolved to display very salient facial features because of their adaptive importance.

Experiment 1 confirmed that tufted capuchins readily discriminate between facial expressions, but did not indicate anything about how they do so. For this reason, Experiment 2 tested the means by which capuchins discriminate between expressions by manipulating the appearance of two salient facial features: an open mouth and visible teeth. In both mouth opening and visible teeth experimental conditions, subjects were able to discriminate open-mouth threat expressions from neutral expressions. Therefore, the results of Experiment 2 do not support **Hypothesis 3a, Rule-based discrimination**, which predicted that capuchins would fail to discriminate the odd emotional expression from neutral when the degree of mouth opening or visible teeth in the neutral expression images was close to that of the emotional expression itself. Rule-based discrimination posited that the mechanism of expression discrimination is such that discriminations are made according to the appearance of a specific facial feature as opposed to the larger arrangement of the face. A rule-based mechanism is in accordance with the idea of feature-based processing which identifies expressions based on single features (Carey & Diamond, 1977). Although this hypothesis was not supported, an interesting finding was that in large mouth opening trials, capuchins were not able to discriminate the emotional expression with the same success as when the neutral expressions featured a small or medium degree of mouth opening. This suggests that Although a single feature does not provide enough information to discriminate expressions, an open mouth is enough of a salient facial feature to *distract* an individual from discriminating successfully.

An alternate hypothesis, **Hypothesis 3b, Template discrimination**, which predicted that capuchins will discriminate open-mouth threats from neutral expressions above chance in both mouth opening and visible teeth experimental conditions, was confirmed. A template discrimination mechanism is in accordance with the idea of holistic processing which implies that individuals are using the relationship *between* facial features to discriminate different expressions. A related hypothesis is **Hypothesis 4, Inversion effect**, which predicted that capuchins will discriminate upright emotional images with greater success than inverted emotional images, implying that upright expressions are processed holistically (Young, Hellawell, & Hay, 1987). Although there were fewer inverted trials than there were upright trials, due to the fact that inverted trials were presented as probes, the strength of the statistic and the large effect size (d = -3.74) indicate that the inversion effect is not simply a result of this difference in trial number. Furthermore, although there was a demonstrable inversion effect, subjects were still able to discriminate the emotional expression from neutral in inverted probe trials.

Females discriminated inverted emotional expressions with greater success than males. This difference could be accounted for in a couple of different ways. There were seven female subjects and only two male subjects which could explain this finding. Another possibility is that females may be better at discriminating subtle, feature-based cues than males. There is evidence that this is the case for humans, beginning early in childhood (McClure, 2000). The feature that distinguishes eyebrow flash expressions from neutral expressions is primarily the raised eyebrows and subsequent increase in forehead length. This difference is probably more subtle and more difficult to detect than the more obvious cues available in an open-mouth threat, as indicated by the results of Experiment 1.

The confirmation of **Hypotheses 3b & 4** is consistent with the idea that tufted capuchins process facial expressions holistically, lending further credence to the idea of homology not only in the production of facial expressions, but also in their perception

(Preuschoft & Van Hooff, 1995).

Conclusion

Complex sociality is a hallmark of the primate lineage. An important aspect of primate communication and social cognition is the processing of conspecific facial expressions. The findings of this study suggest that tufted capuchins share many features of facial emotion expression processing with humans, apes, and Old World Monkeys. By expanding research of facial expression processing to include a broader range of primate species, we may gain a deeper understanding of the evolution of facial expressions as parts of a social signaling system and therefore better understand what happens when this system breaks down, as in the case of human psychological disorders with social impairments. What's more, by investigating the fundamental requirements for empathy and theory of mind we can explore the possibilities of how and when these traits evolved.

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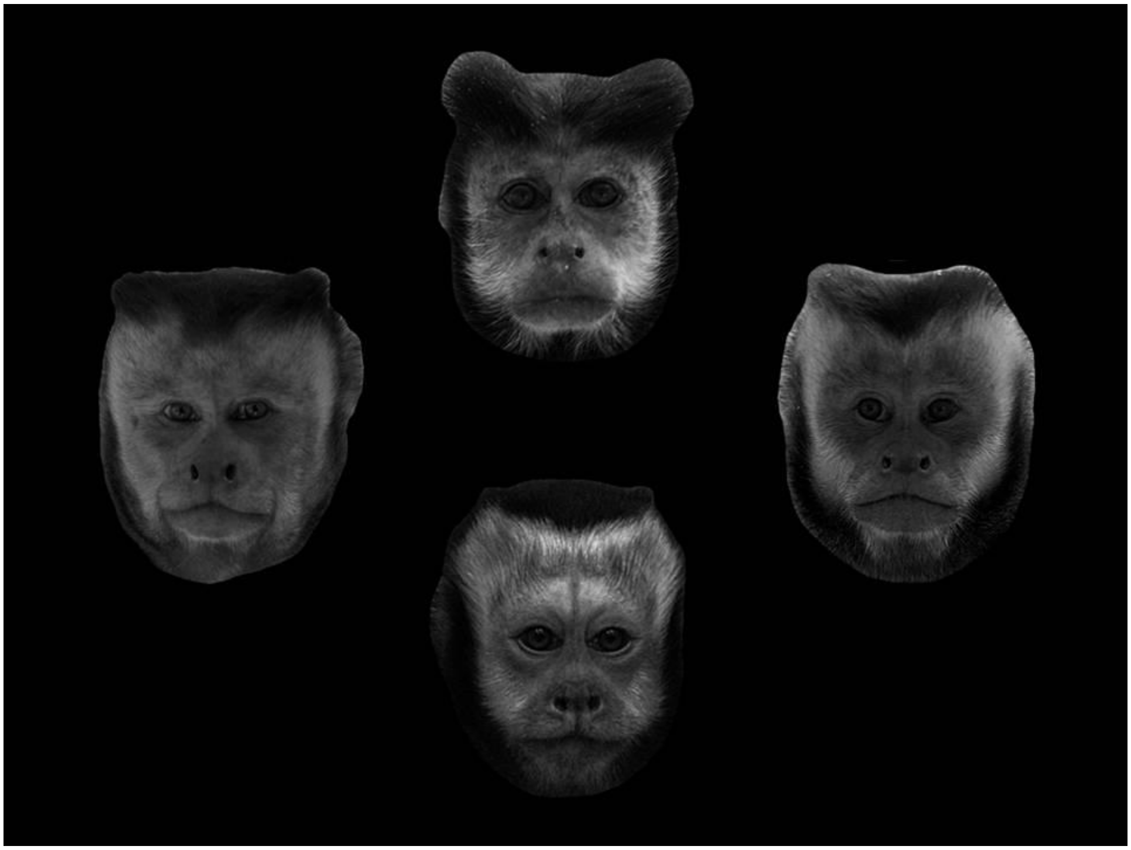
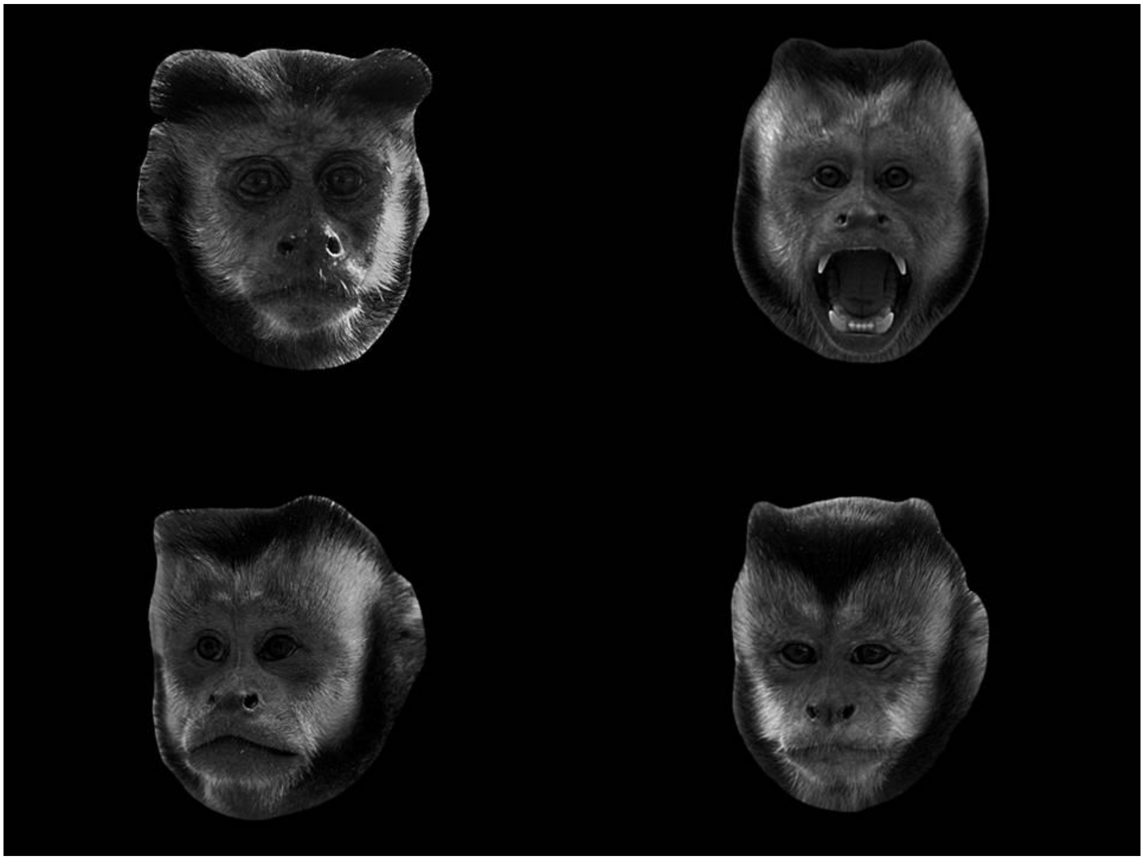
Appendix A



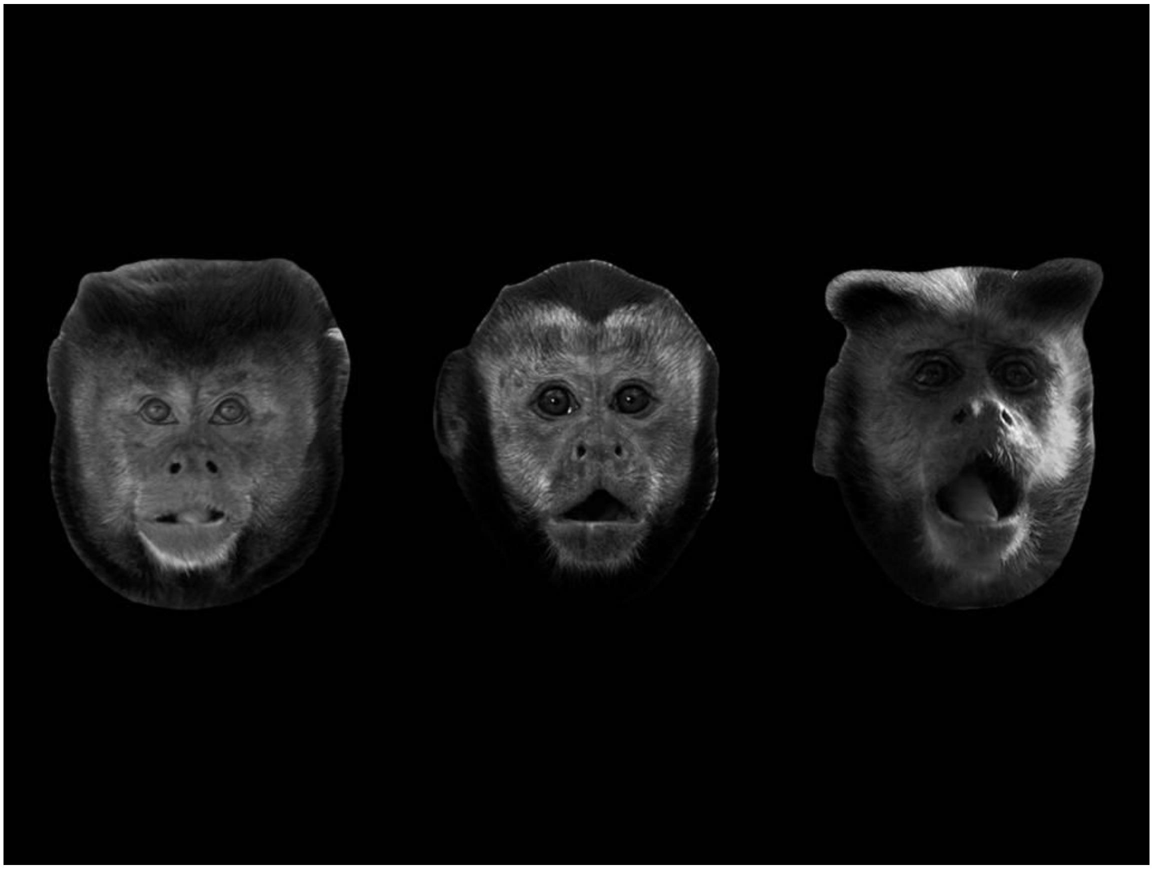
The layout of a trial in Experiment 1 with an eyebrow flash expression. The correct answer is the bottommost image.

Appendix B



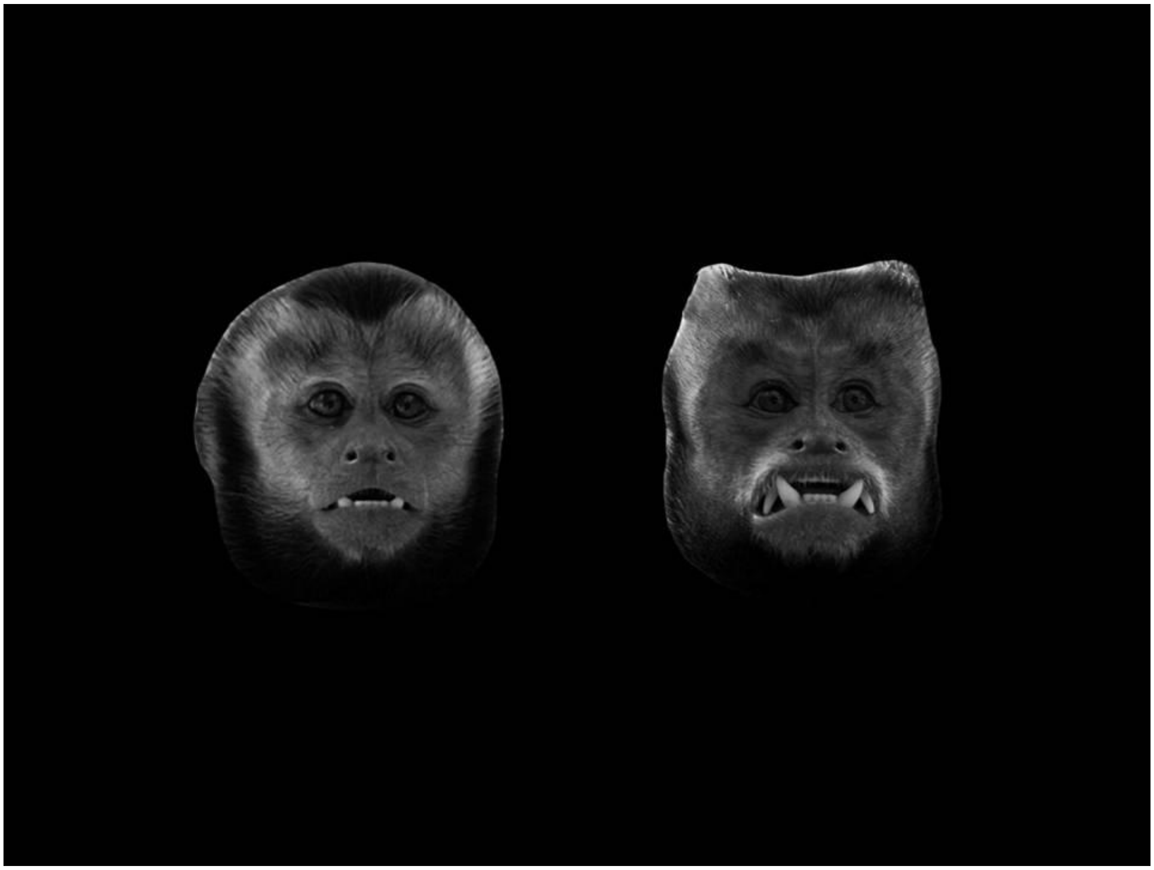
The layout of a trial in Experiment 1 with an open-mouth threat expression. The correct answer is the image in the upper right corner.

Appendix C



Examples of neutral expressions in Experiment 2 with differing degrees of mouth opening. From left to right: small mouth opening, medium mouth opening, large mouth opening.

Appendix D



Examples of neutral expressions in Experiment 2 with differing degrees of visible teeth. The image on the left depicts few visible teeth and the image on the right depicts many visible teeth.