

Capuchins recognize familiar faces



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Although growing neural evidence suggests that human and nonhuman primates share a similar face-processing mechanism, evidence from behavioural research has been mixed. If primates share a similar face-processing system, one would expect to observe similar behavioural effects in both human and nonhuman primates. A particularly robust effect observed in humans is the familiarity effect; humans are better able to recognize familiar as opposed to unfamiliar individuals. Here, we used a matching-to-sample paradigm to examine capuchin monkeys' ability to discriminate conspecific faces across three degrees of familiarity: individuals living in one's own social group ('in-group'), individuals living in one's neighbouring group ('out-group') and completely unfamiliar individuals ('unfamiliar'). We hypothesized that if capuchins utilize their knowledge of familiar individuals to help them discriminate photos of conspecific faces, then performance on the recognition task would increase with the familiarity of the individual. Capuchins were better able to individuate familiar in-group members and familiar out-group members compared to unfamiliar individuals, suggesting that familiarity affects capuchins' ability to discriminate conspecific faces, as it does that of humans and apes. However, there was no significant difference between in-group members and out-group members, suggesting that the concept of 'familiarity' may extend to individuals living in neighbouring groups that one interacts with regularly. This would be a fitness advantage for social species, like capuchins, which compete with neighbouring groups over access to food and mates. It may be an advantage for males in particular as they emigrate to neighbouring groups when they reach maturity.

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Like humans, most primates live in complex societies structured by kinship, dominance and reproductive status (Cheney & Seyfarth, 1990; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987), making it highly advantageous to recognize others individually and remember those with whom they have interacted. This is not limited to primates, either; a wide variety of species, including sheep, birds, fish and insects show individual recognition, and across these taxa, highly social species exhibit more complex forms of face recognition (reviewed in Leopold & Rhodes, 2010). Although individual recognition can take place through many modes, including olfaction (e.g. Johnston & Bullock, 2001) or audition (e.g. Kaplan, Winship-Ball, & Sim, 1978), most primates are highly reliant on vision (due to the shift from a nocturnal to a diurnal lifestyle; Strier, 2003) and, therefore, faces are expected to be particularly salient. For primates, both human and nonhuman,

faces provide valuable social information such as the sex of an individual, kinship, individual identity and the emotional state of others (Dasser, 1987, 1988; Ekman & Oster, 1979; Itakura, 1992; Parr, 2003, 2011; Parr & de Waal, 1999; Tranel, Damasio, & Damasio, 1988; de Waal & Pokorny, 2008). Thus, face recognition and its underlying neural mechanisms were likely under strong selective pressure throughout the course of primate, and therefore human, evolution. Evidence of similar face-processing abilities in nonhuman primates would suggest a common evolutionary route for this sociocognitive skill.

Several lines of evidence suggest that this may be the case. Recent studies have found several face-selective areas in the rhesus macaque, *Macaca mulatta*, brain that are similar in number and relative size to those in humans and that respond to a variety of human and monkey faces, changes in facial expressions, eye gaze and facial orientation, suggesting a common neural mechanism for face recognition in primates (see reviews in: Tovée & Cohen-Tovée, 1993; Tsao & Livingstone, 2008). Moreover, developmental studies have found that starting at a very early age, faces are highly salient social stimuli for both humans (Goren, Sarty, & Wu, 1975; Johnson,

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Dziurawiec, Ellis, & Morton, 1991) and nonhuman primates (Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004; Lutz, Lockard, Gunderson, & Grant, 1998; Myowa-Yamakoshi & Tomonaga, 2001). Human and nonhuman primate infants orient more towards face-like patterns (e.g. three dots arranged in a triangular fashion) compared to non-face-like patterns (humans: Goren et al., 1975; Johnson et al., 1991; Valenza, Simion, Cassia, & Umiltà, 1996; Japanese macaques, *Macaca fuscata*: Kuwahata et al., 2004; agile gibbon, *Hylobates agilis*: Myowa-Yamakoshi & Tomonaga, 2001), imitate facial gestures (humans: Meltzoff & Moore, 1977; chimpanzees, *Pan troglodytes*: Myowa, 1996; rhesus macaques: Ferrari et al., 2006), and they demonstrate a preference for human and monkey faces even when they have never before been exposed to faces (Sugita, 2008), suggesting an innate preference for the basic arrangement of faces (i.e. the eyes above the nose, which is above the mouth), or first-order configuration. Yet exposure to social stimuli both within and across species also appears to play a critical role in fine-tuning the primate face-processing system, as both human and nonhuman primates prefer to look at (Pascalis & Bachevalier, 1998) and selectively discriminate the species to which they are most frequently exposed (Pascalis, de Haan, & Nelson, 2002; Sugita, 2008), and this effect can be shaped by additional exposure to a particular species or race (humans: Malpass, Laviguer, & Weldon, 1973; Sangrigoli, Pallier, Argenti, Ventureyra, & De Schonen, 2005; see also Elliott, Wills, & Goldstein, 1973; Japanese macaques: Sugita, 2008; rhesus macaques: Humphrey, 1974; chimpanzees: Martin-Malivel & Okada, 2007).

However, behavioural evidence for a common face-processing system among primates has been mixed (reviewed in Parr, 2011). For instance, evidence for a similar face-scanning strategy in the eyes are of particular importance is clear (humans: Hainline, 1978; Roberts & Bruce, 1988; rhesus macaques: Gothard, Erickson, & Amaral, 2004; Keating & Keating, 1982, 1993; chimpanzees: Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Parr, Winslow, Hopkins, & de Waal, 2000), but it is still unclear to what degree nonhuman primates rely on second-order configural cues to discriminate individuals (e.g. Vonk & Hamilton, 2014). Second-order configuration refers to the relative arrangement of facial features and surface-based cues such as pigmentation and shading that provide the information necessary to individually discriminate faces (Diamond & Carey, 1986). Considering the studies that have employed methodologies that require direct responses from subjects, several nonhuman primate species have demonstrated the ability to individually discriminate conspecific faces, including chimpanzees (Parr et al., 2000, 2011), orang-utans (Hanazuka, Shimahara, Tokuda, & Midorikawa, 2013; Talbot, Mayo, Stoinski, & Brosnan, 2015; Vonk & Hamilton, 2014), rhesus macaques (Parr et al., 2000; Rosenfeld & van Hoesen, 1979; see also Bruce, 1982; Heywood, Cowey, & Rolls, 1992), crested macaques, *Macaca nigra* (Micheletta et al., 2015), and capuchin monkeys (Pokorny & de Waal, 2009a). Yet the mechanism by which these species make these discriminations remains unclear. For instance, in matching-to-sample tests in which subjects must match the same individual across viewpoints, subjects may use a simple rule, such as 'pick the image that looks most like the sample', rather than associating the images of conspecifics to the actual individuals (e.g. Vonk & Hamilton, 2014). Thus, it is difficult to determine the extent to which subjects rely on experience to individually discriminate conspecifics.

Sensitivity to configuration cues is greatly influenced by an individual's expertise with the type of stimulus. For instance, an interesting and robust behavioural effect observed in human face processing, the familiarity effect, manifests such that familiar face recognition is highly accurate even when the image is degraded,

whereas 'unfamiliar' face recognition is negatively affected by superficial image changes such as differences in lighting, facial expression or viewpoint of the facial stimuli (Bruce, 1982; Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001; Bruce, Valentine, & Baddeley, 1987; Burton, Wilson, Cowan, & Bruce, 1999; Hill & Bruce, 1996; Hill, Schyns, & Akamatsu, 1997). The detrimental effects that changes in viewpoint can have on the recognition of unfamiliar faces suggests that individuals may be relying on matching features of the photographs to discriminate them, whereas the robustness of familiar face recognition indicates that exposure aids the formation of viewpoint-independent representations of familiar faces. Recently, two species of great apes have also demonstrated the familiarity effect when matching the same individual across viewpoints: chimpanzees (Parr, Siebert, & Taubert, 2011) and orang-utans (Talbot et al., 2015). In contrast, no effect of familiarity was found in crested macaques (Micheletta et al., 2015). Thus, the ability to combine second-order information and real-life experience to individually discriminate faces may reflect one facet of face processing that is unique to humans and apes. However, studies of face recognition in monkeys, and in particular New World monkeys, are rare (but see Neiworth, Hassett, & Sylvester, 2007; Pokorny & de Waal, 2009a; Taubert, 2010) and those that objectively compare the face-processing skills for both familiar and unfamiliar individuals are even more so. The comparison of familiar and unfamiliar face recognition is essential to rule out the possibility that subjects are viewing photographs of conspecifics as artificial stimuli lacking any social significance (Zayan & Vauclair, 1998). Moreover, in most cases, familiarity is confounded with belonging to the same social group, which makes it difficult to say for certain that familiarity alone is the cause of the difference.

Thus, in this study, we examined the influence of familiarity on the face processing performance of brown capuchin monkeys, *Cebus apella*, a New World primate, across three degrees of familiarity: individuals living within their own social group ('in-group'), individuals living in their neighbouring group with whom they had visual and vocal access but did not physically interact ('out-group'), and completely unfamiliar individuals ('unfamiliar'). Specifically, we used a matching-to-sample paradigm, which is considered one of the most objective ways to evaluate face discrimination skills as it rules out the possibility that subjects are relying on irrelevant perceptual features (i.e. not facial features), such as symmetry or lighting, to match the stimuli, and it is generally accepted as evidence of individual recognition (Parr et al., 2000, 2011; Pokorny & de Waal, 2009a; Rosenfeld & van Hoesen, 1979). We hypothesized that capuchins would apply their real-life knowledge of familiar individuals, both in their own social group and in their neighbouring group, to successfully match photos of conspecific faces across different viewpoints. Therefore, we predicted that capuchins would better discriminate familiar individuals (both in-group and out-group) than unfamiliar individuals. Alternatively, if capuchins do not use familiarity to guide their decisions, we predicted that the capuchins would perform equally well across all three degrees of familiarity (in-group, out-group, unfamiliar).

No other study on nonhuman primates has compared face discrimination performance on both familiar in-group members and members of a familiar neighbouring group, making it difficult to make a prediction based on previous data. However, one experimental study indicates that capuchins are able to differentiate between in-group members and out-group members (Pokorny & de Waal, 2009b). In addition, we know that in some species physical contact is necessary to discriminate between other individuals (Johnston & Bullock, 2001; Wilkinson, Specht, & Huber, 2010). Thus, it is possible that physical exposure to individuals provides important additional cues (e.g. behavioural or olfactory) that aid individual recognition in capuchin monkeys. Therefore, our last prediction

was that capuchins would better discriminate familiar in-group members than they would familiar out-group members.

METHODS

Subjects and Housing

Subjects included eight capuchin monkeys (three adult males, one subadult male, four adult females) housed in two social groups (Group 1 and Group 2) at the Language Research Center (LRC), Georgia State University. All subjects were mother-reared in captivity. The two groups were formed in 2006 when a single social group was split, but subjects had not lived together for almost a decade at the time of the study and three monkeys, one of which was a subject (Nkima), were born after the group was split. Subjects were housed in social groups with indoor/outdoor access and environmental enrichment (climbing structures, ropes and other toys). Outdoors, each monkey had vocal and visual access to members of its own social group and the neighbouring group. Indoors, each monkey had vocal access to all others and limited visual access to the neighbouring group. All subjects had previous training with a variety of cognitive tasks using a computerized joystick-testing apparatus and a matching-to-sample (MTS) paradigm (Evans, Beran, Chan, Klein, & Menzel, 2008). No subject had any previous experience with computerized social stimuli, such as faces, prior to these studies.

Group 1 consisted of two adult males and four adult females. Group 2 consisted of three adult males, one subadult male and two females. A third group of LRC capuchins, Group 3, was photographed for training stimuli. Group 3 consisted of two adult males and eight adult females. Groups 1 and 2 were stable social groups housed together and next to each other since 2006. At the time of training and testing, Groups 1 and 2 did not have visual access to Group 3.

All capuchins had ad libitum access to water, including during testing, and received a daily diet consisting of primate chow, fruits and vegetables, regardless of the day's testing schedule. The LRC is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care. All procedures for this study were approved by the Institutional Animal Care and Use Committee of Georgia State University (IACUC approval number: A13022) and were in accordance with the Association for the Study of Animal Behaviour/Animal Behavior Society's guidelines for the use of animals in research. At no time were the subjects ever deprived of food or water.

Face Stimuli

All face stimuli consisted of high-quality digital colour photos of males and females of all ages displaying different head positions and gaze orientations with a neutral facial expression (i.e. relaxed mouth and no bared-teeth display). Photos were cropped to include only the face and head. The background of the photos was homogenized by filling in the area around the face with solid white. Photos of the LRC capuchins were taken within 1 year prior to the start of the study using a digital single-lens reflex (SLR) camera. Brightness and contrast were standardized using the auto tone and brightness software tools to control for differences in lighting. Presentation size of the photos was 16×16 cm, with a resolution of 300 dots per inch.

Capuchins in Groups 1 and 2 were trained on face stimuli of monkeys in a third social group of capuchin monkeys housed at the LRC (Group 3). Test stimuli were drawn from a different set of monkeys (Groups 1 and 2 and an unfamiliar group from Scotland; see details below) that varied based on familiarity to the subject. This included five in-group members, five out-group members and five unfamiliar individuals (from Scotland). Ten photos of each individual, taken from a variety of viewpoints (see details of photos,

above), were presented during testing. Both the in-group and out-group stimuli represented capuchins from Groups 1 and 2 housed at the LRC. In-group stimuli included photos of individuals within the subjects' own social group. Out-group stimuli included photos of individuals from the subjects' neighbouring group with whom they had visual and vocal access, but had not had physical contact for a decade (see above for details). Subjects had never before seen photos of either their in-group or the out-group members. Subjects were never presented with images of themselves. Unfamiliar stimuli included photos of conspecifics obtained from St Andrews University's Living Links Centre in Edinburgh, Scotland, whom subjects had never before seen.

Apparatus and General Procedure

Stimuli were presented on a PC-compatible computer that included a modified joystick and pellet dispenser mounted on a movable audiovisual cart. All subjects were previously trained to manipulate the joystick to make selections on the computer monitor. At the beginning of each session, computers were placed approximately 30 cm in front of each individual testing chamber, with the monitor directly in front of the monkey. Testing chambers have a clear Lexan front panel for easy viewing of the computer monitor (Evans et al., 2008).

For each session, subjects were called into their individual testing chambers from their social groups to participate. All participation was entirely voluntary. The experiments were conducted using a MTS procedure with which the monkeys were familiar. Subjects initiated a trial by moving the cursor into to a grey box in the centre of the computer screen, following which a sample stimulus appeared in its place. To ensure that subjects were attentive to and viewed the sample, they were again required to orient to the sample, by touching the cursor to it. The sample stimulus remained centred on the screen and four choice stimuli randomly appeared in four of six possible locations (Fig. 1). The location of the correct comparison stimulus was randomized. Stimulus sets were presented in randomized order with all sample stimuli presented one time within a block before any were re-presented as the sample stimulus (although they could appear as a match in a different trial).

The object of the task was to select the comparison image that matched the sample based on the predetermined rule. For instance, in the 'identical photos phase', the correct match was a copy of the same photograph as the sample, whereas in the 'different photos phase', the correct match was a different photograph of the same individual. Correct responses were automatically rewarded with a food reinforcer (a banana-flavoured pellet) and a high-pitched tone was played followed by an intertrial interval (ITI) of 1 s, during which the screen remained white. Incorrect responses were not rewarded, were accompanied by a low-pitched tone, and were followed by an ITI of 20 s. Subjects worked at their own pace and completed a maximum of 1000 trials per day. Test sessions lasted approximately 2 h. No experimenter was present throughout the test session. Subjects were tested multiple times per week until the completion of the study, but they were never tested more than once per day on this study.

Clip Art

All subjects had extensive experience with the MTS procedure using clip art and previously performed at very high levels on this task (Perdue, Church, Smith, & Beran, 2015), however, to be consistent with previous research and to ensure that every subject was familiar with the testing paradigm and met the same criterion for performance on the MTS procedure, we first presented them

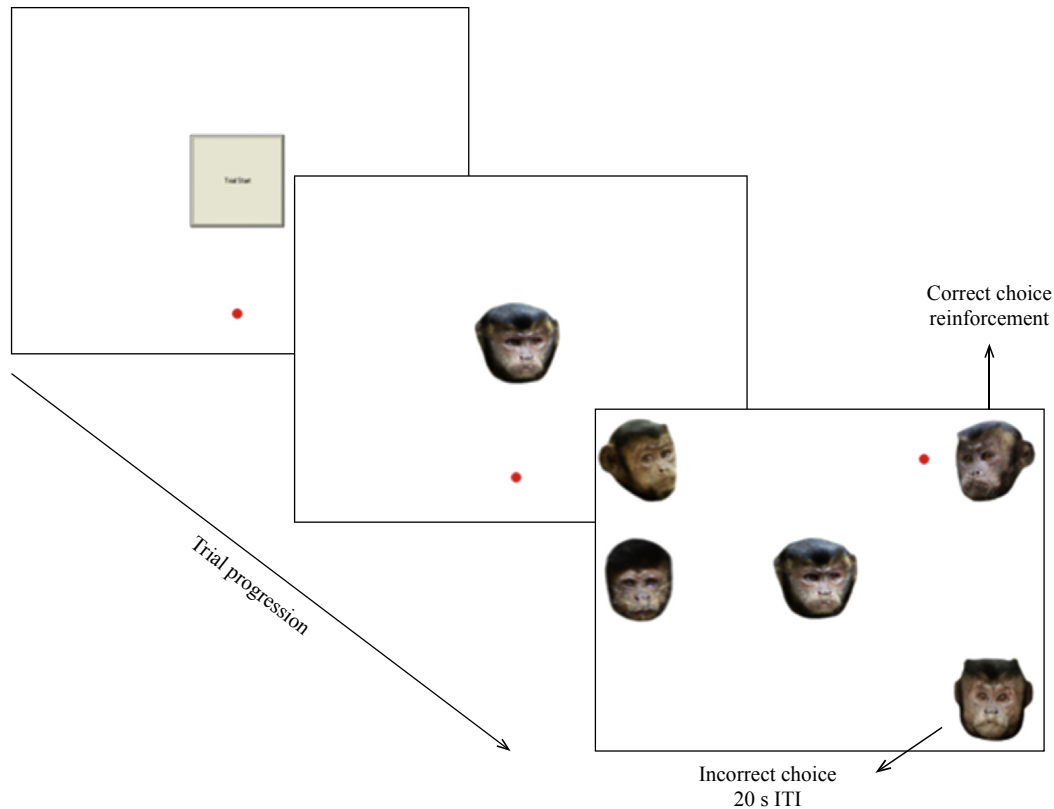


Figure 1. Progression of test trial. Monkeys started a trial by moving the cursor into contact with a grey box in the centre of the screen, following which a sample stimulus appeared in its place. Once the monkeys moved the cursor into contact with sample, four additional stimuli appeared on the screen, randomized into four of six possible locations. The monkeys could earn food by selecting the individual that matched the sample. ITI: intertrial interval.

with clip art trials. Samples and comparison images were randomly selected from a group of 500 clip art stimuli. For all phases of training, the performance criterion was set at 18 out of 25 (i.e. $\geq 72\%$ correct, or $P \leq 0.000001$) on two consecutive test sessions (analysed in 25-trial blocks). This criterion was chosen because the level of performance exceeded that required to reach significance in a two-tailed binomial test (11 out of 25 choices, i.e. $\geq 44\%$, or $P \leq 0.049$). Once performance criterion was met, subjects proceeded to the next phase of training.

Identical Photos

Once subjects met criterion on the MTS paradigm with clip art images, facial stimuli were introduced. In the identical photos phase, subjects were required to match identical photos of conspecifics. Training stimuli represented the capuchins from Group 3 ($N = 10$) at the LRC, a completely separate group of capuchin monkeys whose images were never used in testing (just in this phase and the subsequent training phases). Training stimuli were randomly selected from a set of 100 portraits (10 views for each of the 10 individuals in this group). Stimulus sets were always composed of four different individuals (one sample and four possible options). In the identical photos phase, one of the four options was the same photo as the sample.

Different Photos

In the different photos training phase, subjects were required to match two different photos of the same individual. Therefore, a trial consisted of four different individuals (one sample and four options) but five different photos, because one of the options was a

different photo of the sample individual. Again, facial stimuli were randomly selected from a stimulus set consisting of 100 portraits (10 views per individual, $N = 10$) of capuchins from Group 3.

Individual Discrimination: Transfer Test

During the transfer test, test trials were randomly inserted among clip art trials. Within a session, trials from each of the three conditions (in-group, out-group, unfamiliar) were inserted in a randomized order. The task was the same as the different photos training phase: subjects were required to match the same individual across viewpoints (Fig. 1). However, in this transfer test, an entirely new set of face stimuli were presented that represented 15 individuals: five familiar in-group individuals, five familiar out-group individuals and five unfamiliar individuals. There were 10 photos of each individual for a total of 150 images, and each photograph was presented only once as a sample to each subject. Thus, there were 50 trials in each condition (in-group, out-group, unfamiliar) and 150 total test trials. Note that this is the strongest possible test one can give for immediate, spontaneous matching of monkey identity where stimulus identity no longer exists as a cue, because each stimulus is presented only once so that learning cannot occur with regards to associating specific stimuli with specific responses. Thus, subjects were not able to use the familiarity with the stimuli from previous exposure to guide their responses, only the familiarity of the individuals themselves.

Data Analysis

For each test session, the computer software automatically recorded the subject, date, trial number, condition (training, in-

group, out-group or unfamiliar), names of the images presented, the image that was selected by the subject, response time and whether each trial was correct or incorrect. The primary dependent variable of interest was the response (correct/incorrect) and the independent variables were the condition (in-group/out-group/unfamiliar) and sex of the subject (male/female). Therefore, we ran a two-way mixed design ANOVA with two independent variables: one within-subjects variable (familiarity) with three levels (in-group, out-group, unfamiliar) and one between-subjects factor (subject sex) with two levels (male, female). We used binomial Z scores to analyse individual performance. The number of training sessions needed to reach criteria was reported for each subject. Data were analysed using SPSS v.21 statistical software (IBM, Armonk, NY, U.S.A.).

RESULTS

Training: Clip Art, Identical, Different

Not surprisingly, given their previous experience with the clip art MTS task, all subjects met criterion (72% on two consecutive sessions of 25 trials each) within 50 trials, which was the minimum required. On the identical photo-matching task, capuchins reached criterion in an average of 1682 trials (range 50–3370). On the different photo-matching task, the capuchins took an average of 10 192 trials (range 3222–17 740; see Fig. 2 for more detail).

Individual Discrimination: Transfer Test

Mauchly's test showed that sphericity was not violated ($P = 0.264$), and a Levine's test confirmed homogeneity of variance for all levels of the repeated measures (in-group: $P = 0.577$; out-group: $P = 0.660$; unfamiliar: $P = 0.618$). Therefore, we ran a two-way mixed design ANOVA. There was a significant main effect of familiarity (ANOVA: $F_{2,12} = 9.19$, $P = 0.004$, $\eta^2 = 0.605$). Because we hypothesized that performance would differ based on familiarity, we

used planned difference contrasts to compare performance on unfamiliar versus familiar individuals (the mean effect of both in-group and out-group performance) as well as to compare out-group versus in-group performance. Capuchins performed significantly better on both the in-group and out-group individuals compared to the unfamiliar individuals (comparing the mean effect of in-group and out-group combined to unfamiliar: $F_{1,6} = 23.459$, $P = 0.003$, $\eta^2 = 0.796$; Fig. 3). There was no significant difference between in-group and out-group performance ($F_{1,6} = 0.049$, $P = 0.832$, $\eta^2 = 0.008$).

There was no main effect of sex (ANOVA: $F_{1,6} = 1.72$, $P = 0.238$, $\eta^2 = 0.222$). Although the interaction between sex of the subject and familiarity was not significant ($F_{2,12} = 3.43$, $P = 0.066$, $\eta^2 = 0.364$), it approached significance, so we explored it further. Overall, males performed at a higher level on the face discrimination task than females, but again, this difference was not significant. Males were better able to discriminate male faces whereas both males and females discriminated female faces equally well (mean \pm SE percentage correct: males: 44.67 ± 1.73 ; females: 38.5 ± 1.52 ; independent t test: $t_6 = 2.14$, $P = 0.076$; Fig. 4, see [Supplementary Material](#) for additional discussion of the same analysis excluding individuals who required more extensive training).

We used binomial Z scores to analyse individual performance. Overall, analyses on the individual level were consistent with the results from the ANOVA. All but one monkey performed significantly above chance when discriminating in-group members, and all monkeys performed significantly above chance when discriminating out-group members. In contrast, only one monkey performed above chance when discriminating unfamiliar individuals. This individual also demonstrated the best overall performance on the task (Nkima, Fig. 5).

Response Time

We examined the latency to respond on the computerized MTS task. There was no overall effect of response time across the three conditions (ANOVA: $F_{2,14} = 1.397$, $P = 0.280$).

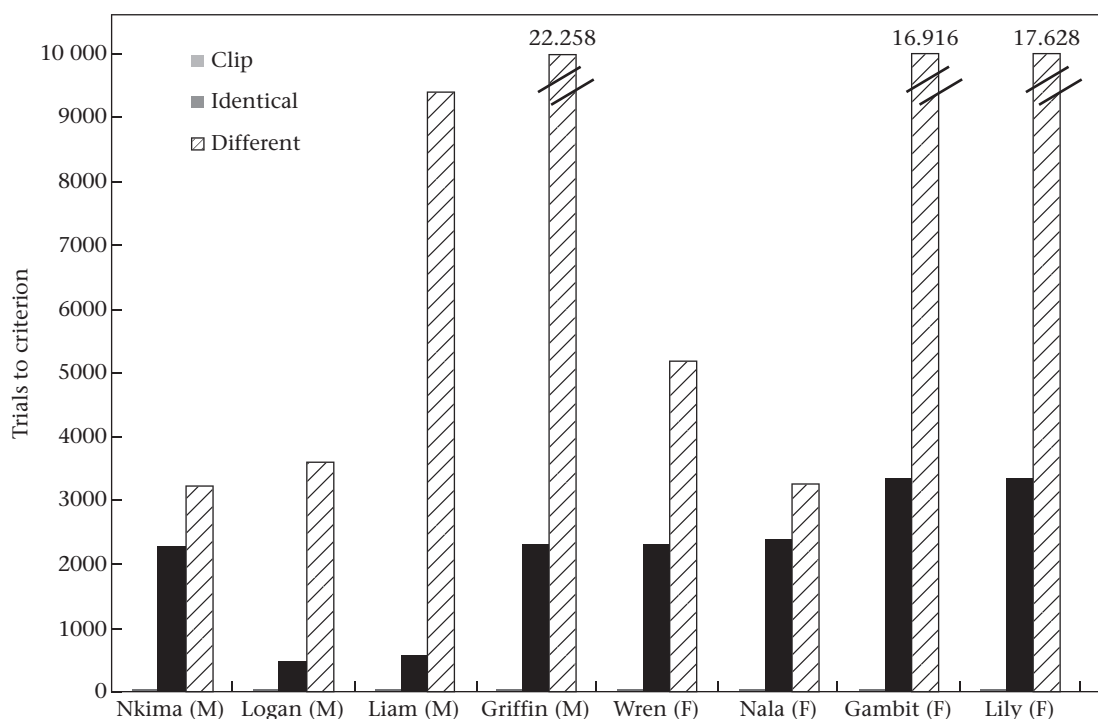


Figure 2. Number of trials it took subjects to reach criterion on each phase of training, including clip art, identical photos and different photos. (M): male; (F): female.

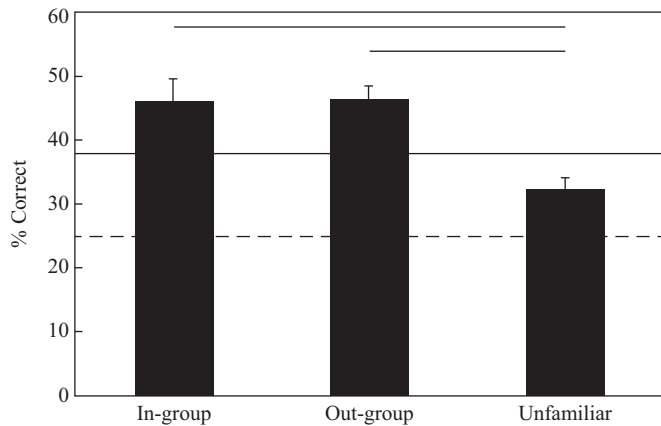


Figure 3. Overall performance on the transfer test. Black bars depict the mean percentage correct on each of the three conditions (in-group, out-group, and unfamiliar). The solid black horizontal line represents performance significantly above chance (38%) when $P \leq 0.05$; the horizontal dashed line represents chance (25%). Error bars reflect SEM.

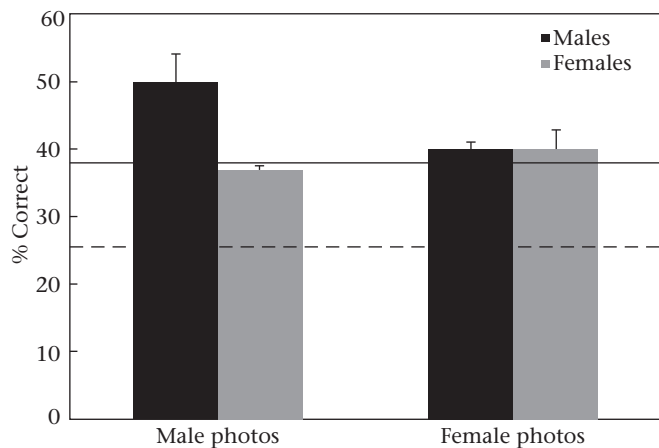


Figure 4. Performance as a function of sex. Bars represent the mean percentage correct by males and females as a function of the sex of the individual depicted in photos (X axis). The solid black horizontal line represents performance significantly above chance (38%) when $P \leq 0.05$; the horizontal dashed line represents chance (25%). Error bars reflect SEM.

DISCUSSION

Corroborating previous findings, capuchin monkeys spontaneously discriminated individuals depicted in photos across a range of viewpoints and conditions (Pokorný & de Waal, 2009a). Importantly, however, we found that, capuchins' ability to do so varied with the familiarity of individuals depicted in the photos, providing evidence of the familiarity effect in a New World primate species. Capuchins were equally able to discriminate familiar individuals living in their own social group and those living in a neighbouring group, with whom they had daily visual and vocal access, and they discriminated both of these categories better than they did unfamiliar individuals. These results indicate that familiarity plays a significant role in the discrimination of faces by aiding recognition of familiar individuals. Moreover, since subjects saw each photograph used in the transfer test only once, these findings suggest that capuchins applied their real-life knowledge of individuals to a computerized task. Thus, we would argue that capuchins, to some degree, are able to connect the individuals depicted in two-dimensional photographs to their three-dimensional counterparts.

Fagot, Martin-Malivel, and Dépy (2000) proposed three modes by which animals may process pictures. The first is the independence mode. In this context, pictures are processed as a combination of features or patterns. Thus, the picture and the representational content of the picture are completely disparate. The observed familiarity effect in this study suggests that the capuchins were not processing the stimuli in the independence mode, as a combination of features or patterns, without any connection to the representational content of the pictures. If this were the case, they would have performed equally well, or equally poorly, across all three degrees of familiarity.

In the second mode, the confusion mode, pictures and objects are processed in exactly the same way and are not distinguishable from each other. Rhesus macaques, for instance, display reactions such as fear, threat or play when presented with coloured slides of conspecifics engaging in social activities (Sackett, 1966; but see Judge, Kurdziel, Wright, & Bohrman, 2012), suggesting that they equate the photos with actual conspecifics. However, this behaviour was not observed in the current study and, to our knowledge, has never been observed in capuchin monkeys, whose behavioural reactions to photographs are not the same as their reactions to the actual individuals depicted in a photo (Morton et al., 2016).

The third and final mode is the equivalence mode. In this mode, the animal is able to associate the picture with its three-dimensional counterpart, while also being aware that they are different entities. Leighty, Menzel, and Frigaszy (2008) proposed two submodes of the equivalence mode: featural equivalence processing and complex equivalence processing. In the featural equivalence processing submode, local features are used such that observed features in one dimension are matched to the features in the other dimension. In the complex equivalence processing submode, knowledge of the object's three-dimensional global form is gained from the two-dimensional picture. Thus, one recognizes the relational elements of the object across dimensions. It is possible that capuchins process photos in the complex equivalence processing submode, demonstrating global knowledge of the three-dimensional form, what some researchers refer to as 'representational insight' (e.g. Aust & Huber, 2010). This is essentially understanding that the photos represent actual individuals, much like humans do. However, it seems more plausible that capuchins were operating in the featural equivalence processing submode, in which they were able to detect facial features in one viewpoint and match them to features displayed in different viewpoints. Thus, the effect of familiarity in the study indicates that exposure aids the formation of viewpoint-independent representations of familiar faces.

Our second prediction was that we would find a significant difference in performance when discriminating in-group members and out-group members. In contrast to this prediction, however, there was no such difference, with individuals discriminating both classes of familiar individuals equally well (although see [Supplementary Material](#) for a discussion on potential sex differences that should be explored in future work). This result has several implications for the nature of the recognition process and the knowledge that individuals have of one another. First, it suggests that information obtained from close physical proximity (e.g. tactile, chemical and/or olfactory cues) is not necessary to form representations of other individuals in capuchin monkeys. Rather, capuchins appear to be highly reliant on visual information to discriminate individuals, and faces alone are sufficient for such recognition.

Second, this implies that capuchin monkeys are actually paying attention to the individual members of neighbouring groups, rather than simply discriminating between their own social group and all other monkeys. One major criticism of previous work on visual and vocal recognition is that results can often be explained by a more

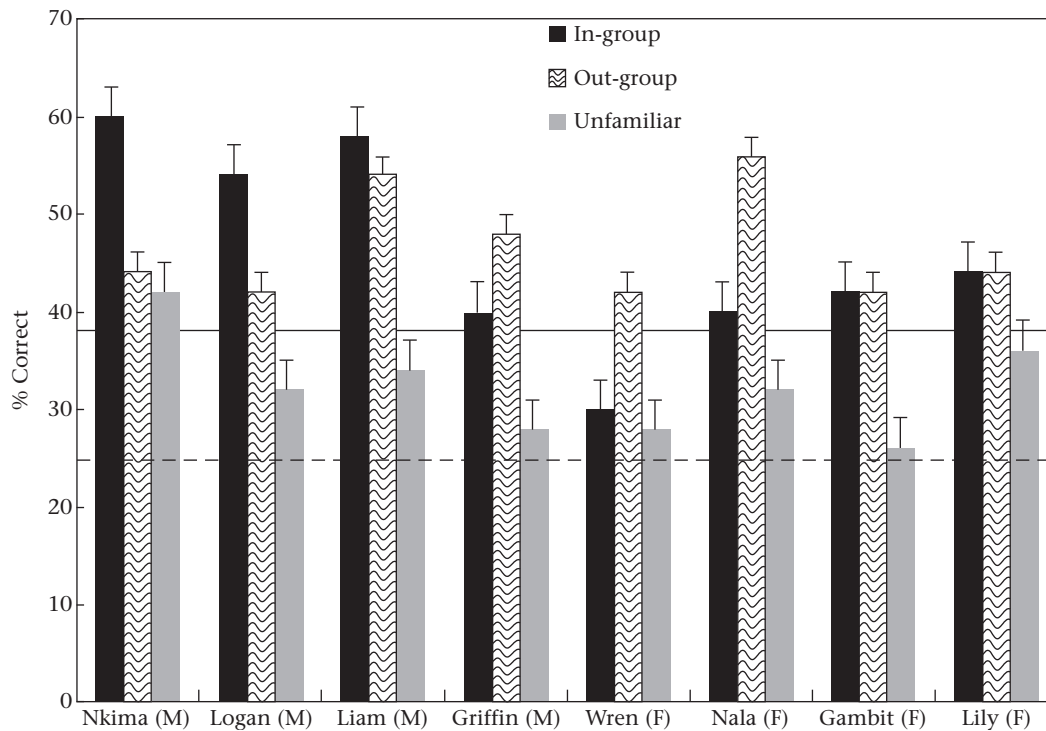


Figure 5. Individual performance on the transfer test. Bars depict the mean percentage correct on each of the three conditions: in-group, out-group and unfamiliar. The solid black horizontal line represents performance significantly above chance (38% when $P \leq 0.05$); the horizontal dashed line represents chance (25%). Error bars reflect SEM. (M): male; (F): female.

general categorization scheme rather than the recognition of specific individuals. For instance, one study found that mother squirrel monkeys, *Saimiri sciureus*, make more vocalizations when they hear their own infant vocalize compared to a different infant, or no infant at all, suggesting that mothers are able to recognize their infant based on auditory cues alone (Kaplan et al., 1978). However, mother–offspring recognition may only involve the discrimination of one's own offspring from all others. Likewise, neighbour recognition (e.g. Cheney & Seyfarth, 1982) may simply involve the discrimination of familiar versus unfamiliar individuals rather than individual recognition per se. The distinction between more cognitively complex skills such as face recognition and more general heuristic rules is important to explore. Many species are able to see far enough to recognize individuals in neighbouring groups, but that does not necessarily mean that there has been evolutionary or ecological pressure to evolve the ability to do so. These distinctions can shed light on when and in what contexts such specializations may have evolved.

The fact that visual recognition extended beyond the boundaries of one's own social group in our study may not be surprising when you consider the ecology of capuchin monkeys. In the wild, capuchins live in social groups of approximately 14–17 individuals and regularly come into visual and physical contact with neighbouring groups (Defler, 1982; Spironello, 2001). Like most group-living animals, capuchins alter their behaviour depending on whom they are interacting with. Although intergroup encounters are often aggressive both in captivity and in the wild, they can also be relatively peaceful (Defler, 1982; Di Bitetti, 2001). When regularly interacting with neighbouring groups, the ability to quickly and accurately recognize individuals may aid in determining the level of threat that they pose, ultimately leading to decreased frequency of unnecessary fights and increased fitness.

The familiarity effect in the present study is robust and, in combination with evidence that other species also show familiarity effects (i.e. the cross-race effect in humans; see Introduction for a discussion of familiarity across species) raises the question, 'What makes a face familiar?' Clearly, exposure is an important factor in strengthening familiarity. One hypothesis is that, as an individual becomes more familiar, the internal features of a face (e.g. eyes, eyebrows, nose, cheekbones) come to dominate the recognition process and strengthen view-invariant representations (Ellis, Shepherd, & Davies, 1979; Young, Hay, McWeeny, Flude, & Ellis, 1985; see also Johnston & Edmonds, 2009). Evidence also suggests that, at least in humans, familiar and unfamiliar faces may be processed in the brain differently (De Haan & van Kollenburg, 2005). Although this study cannot shed light on this debate, it would be productive to examine the influence that particular features, such as internal versus external features, have on the recognition of individuals across varying degrees of familiarity.

In contrast to previous studies, the current study controlled for possible novelty effects on both the photos used as stimuli and the individuals represented in those stimuli. We did this by training the monkeys on one set of individuals and then introducing an entirely new set of individuals for testing. Moreover, the test trials were presented under extinctive conditions: each individual was only presented as the sample once. Using stimuli only once allowed us to evaluate how capuchin monkeys spontaneously performed on the individual discrimination task. Thus, the results obtained from the current study represent emergent behavioural patterns that go beyond those employed in operant and respondent conditioning.

The results from this study are consistent with the hypothesis that humans and nonhuman primates share similar face-processing mechanisms. Like humans (Bruce, 1982; Bruce et al., 2001; Hill et al., 1997) and apes (Parr et al., 2011; Talbot et al., 2015),

capuchins' ability to recognize conspecific faces varies as a function of familiarity such that they better recognize familiar individuals, whether in-group members or out-group members, as compared to unfamiliar individuals. Although the specific mechanism(s) by which face recognition occurs is still unknown, growing evidence suggests that familiarity may be of fundamental importance for future researchers to parse social and cognitive mechanisms underlying face processing.

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Supplementary Material

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