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DISCRIMINATION OF FACES, SEX, AND RELATIONSHIPS BY CAPUCHIN MONKEYS

by

CATHERINE F. TALBOT

Under the Direction of Sarah F. Brosnan, PhD

ABSTRACT

Whether attending a business function or moving to a new neighborhood, the ability to recognize, remember, and garner information about the social relationships of other individuals is critical for human survival. But to what degree is this unique to humans? Nonhuman primates provide us with the opportunity to study the evolutionary history and function of human socio-cognitive skills within a comparative framework. I tested capuchin monkeys on three computerized tasks that evaluated their ability to discriminate the faces, sexual identities and dominance relationships of conspecifics living in their own social group, a neighboring social group or completely unfamiliar individuals. This paradigm allowed for testing the effect of familiarity and parsed underlying mechanisms of these socio-cognitive skills, both of which help to elucidate how social knowledge emerges from the foundations of perception.

INDEX WORDS: Social knowledge, Face recognition, Capuchin monkey, Sex discrimination, Familiarity, Dominance

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by

CATHERINE F. TALBOT

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RECOGNITION OF PICTURES, CONSPECIFICS AND SOCIAL RELATIONSHIPS BY CAPUCHIN MONKEYS

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DEDICATION

First and foremost, I would like to thank my family for their continuous support. In particular, I would like to thank my parents for providing me with opportunities that they never had and the freedom to follow my wildest dreams. I would like to thank my Dad for encouraging me to think beyond my borders. I would like to thank my Mom for always listening and providing sound advice. Likewise, if it were not for the bravery of their grandparents leaving their native Ireland in the hope of a better life for themselves and their children, I would not be here.

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1 INTRODUCTION

The ability to recognize, remember, and garner information about other individuals and their social relationships is critical for navigating through human society. Humans recognize individuals, perceive their disposition and intentions, classify their relationships with others, and use these classifications to predict what others may do (Bruce & Young, 1986). Through the course of human evolution, these socio-cognitive skills were favored by natural selection. Moreover, social problems may have been the most cognitively complex problems our ancestors faced during the evolutionary critical period of brain expansion. Thus, a number of researchers have posited that large brains, which distinguish the human species from other primate species, and the cognitive capability I humans know as ‘intelligence’ evolved in conjunction with group living and the social complexities that arose with it (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966). This specialization for social cognition is thought to be possessed by other closely related primates as well (Brothers, 1990; Cheney & Seyfarth, 1990; Humphrey, 1976).

As in human societies, primate groups are structured by kinship, dominance, and reproductive status (Cheney and Seyfarth 1990; Smuts et al. 1987). Therefore, the ability to classify relations between others into abstract categories could allow individuals to quickly identify social information, which could increase their social and reproductive advantage over others, just as it does in humans. Thus, nonhuman primates (NHPs) provide us with the opportunity to study the evolutionary history and function of human socio-cognitive skills and visual perception within a comparative framework. Studying other NHP species can help elucidate which socio-cognitive skills are unique to humans, reflecting more recent advances in our evolutionary history, and which are shared, indicating a deep evolutionary history.

Unfortunately, despite the potential for gains in our understanding using this approach, our knowledge of NHPs' ability to recognize individuals and relationships between other individuals is limited, in part because it is difficult for us to determine what animals know about their environment and how that information is stored and organized in the mind.

1.1 Literature Review

1.1.1 Auditory Recognition

Previously, many researchers investigating social knowledge conducted studies in the auditory domain, primarily through playback experiments. In playback experiments, researchers record naturally occurring vocal stimuli. Then, in order to reproduce events that may occur naturally, or to present subjects with a novel situation, researchers play the pre-recorded stimuli back to subjects in very specific ecological or social situations in order to gauge the subjects' responses. This allows researchers to test hypotheses that would be difficult or otherwise impossible to address in a non-experimental setting. This paradigm has been used to examine individual discrimination (e.g., Gouzoules & Gouzoules, 1990), kin/non-kin discriminations (e.g., Rendall, Rodman, & Emond, 1996), recognition of relationships, such as mother-offspring relationships (e.g., Kaplan, Winship-Ball, & Sim, 1978), and recognition of third-party relationships (e.g., Cheney & Seyfarth, 1980). There is also evidence that vocal recognition may extend beyond the boundaries of the group (Cheney & Seyfarth, 1982; see Cheney & Seyfarth, 1990 and Tomasello & Call, 1997, for reviews; Waser, 1977).

Because individual recognition is a critical precursor to navigating and reasoning about the complex social world in which most primate species live (Cheney & Seyfarth, 1990), many of these studies claim to present evidence for individual vocal recognition. However, for individual recognition to take place, subjects must not only must recognize a call as familiar, but also perceive that it belongs to a specific individual (Beer, 1970). Although it is possible that individual recognition has occurred in these previous studies, there may be simpler alternative explanations. Rather than identifying each of these individuals specifically, subjects may have categorized the vocalizations at a more general level. For example, mother-offspring recognition may only involve discrimination between one's own offspring from all others. Similarly, when vervet monkeys react more strongly to the calls of individuals from a neighboring group when played from an inappropriate territory (Cheney & Seyfarth, 1982), this may simply reflect an association between a familiar neighbor's sound and its familiar location. Discrimination also could have been made based on family-specific acoustic cues, as evidence suggests is the case in pigtail macaques (Gouzoules & Gouzoules, 1990). Despite the large amount of evidence on vocal recognition, and many creative experiments, these issues have yet to be completely resolved.

1.1.2 Visual Recognition of Faces

Within the evolution of primates, the shift from a nocturnal to a diurnal lifestyle placed greater emphasis on visual communication, making most nonhuman primates (NHPs) heavily reliant on vision (Strier, 2003). NHPs must recognize the physical features of their environment, such as predators, and respond appropriately according to each stimulus. For example, studies from the wild and captivity have demonstrated that many NHPs are able to categorize predators based on where they encounter those predators in their environment (e.g., on the ground, in the air, etc.) and respond appropriately (flee to trees, move down into bushes; Cheney & Seyfarth, 1990; Kortland, 1994; Menzel, 1971; Zuberbühler, Noë, & Seyfarth, 1997).

Within the social domain, behaviors observed in the wild often seem to indicate impressive cognitive ability. However, controlled laboratory studies that manipulate the exposure to social information are necessary to rule out alternative hypotheses. This can be challenging in tightly controlled social cognition research, as it is difficult to present subjects with real individuals to whom they can respond. Thus, researchers frequently use two-dimensional images as experimental stimuli in place of real-life objects to assess human and nonhuman cognitive and neural processes. The use of photographic stimuli is more reliable than presenting real objects or individuals because it allows for repeated exposure of the same stimuli to all subjects. More importantly, the use of photographs provides controlled investigation of image qualities such a brightness, contrast, viewpoint, and so forth. Thus, not surprisingly, research in this area provides more conclusive results for individual recognition. In particular, much of the research has focused on the perception and recognition of faces.

Faces provide primates (including humans) with valuable social information such as the sex of an individual, kinship, individual identity and the emotional state of others (Dasser 1987, 1988; de Waal & Pokorny, 2008; Ekman & Oster 1979; Itakura, 1992; Parr, 2003, 2011; Parr & de Waal, 1999; Tranel, Damasio, & Damasio, 1988). Thus, face recognition and its underlying neural mechanisms were likely under strong selective pressure throughout the course of human evolution. Comparatively less is known about nonhuman primates' abilities to discriminate and process faces, and especially whether such discrimination is fundamentally different from the basic visual discrimination processes known to exist amongst primates. Evidence of similar face processing abilities in NHP would suggest a common evolutionary route for this socio-cognitive skill. Below, I discuss evidence from neurological, developmental, and behavioral research that support this hypothesis.

1.1.3 The Neurological Underpinnings of Face Perception

From a large body of behavioral and neurological data, I know that humans possess a specialized mechanism for face processing (Moscovitch, Winocur, Behrmann, 1997; Yin, 1969). Functional magnetic resonance imaging (fMRI) studies in humans have revealed a system of face-selective areas in the inferotemporal (IT) cortex that are involved in face recognition, including (but not necessarily limited to) the fusiform face area (FFA), the occipital face area (OFA), and an area of the superior temporal sulcus (STS-FA) (Kanwisher, McDermott, & Chun, 1997). These areas may be specialized for different functions. For example, the FFA is thought to be involved in processing identity (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Yovel & Kanwisher, 2005), whereas the OFA is involved in processing face parts (Pitcher, Walsh, Yovel, & Duchaine, 2007) and the STS-FA appears to respond selectively to emotional expression and eye gaze and therefore is thought to be involved in the processing of changeable aspects of the face (Allison, Puce, & McCarthy, 2000; Engell & Haxby, 2007; Hoffman & Haxby, 200l; see Tovée & Cohen-Tovée, 1993, for a review).

Growing evidence indicates that at least some species of NHPs possess a face processing system that shares similar neural underpinnings with humans. Electrophysiological studies in rhesus macaques have found such regions in the rhesus macaque brain. Neurons in the superior temporal sulcus of the temporal cortex respond specifically to face stimuli. These cells respond to a variety of human and monkey faces, changes in facial expressions, eye gaze, facial orientation, and they differentially respond to repeated exposures of faces (Desimone, 1991; Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, & Caan, 1982; Perrett et al., 1985, 1988; Rolls, 1984). These face-selective cortical areas or “face patches” include three regions in the IT cortex that are similar in relative size to humans (Tsao, Freiwald, Knutsen, Mandeville, & Tottell, 2003; Tsao, Moeller, Tootell, & Livingstone, 2006).

More recently, a comparative study in humans and macaques found two additional face patches in the anterior face region of the human brain, for a total of five face patches, and six face patches in the rhesus macaque brain, an overall comparable number (Tsao, Moeller, & Freiwald, 2008). Moreover, in both humans and rhesus macaques, fMRI studies have demonstrated increased blood flow in these cortical regions when subjects view images of faces compared to objects or other body parts (Kanwisher et al., 1997; Tsao et al., 2003). These findings suggest certain homologies between cortical areas in the human and monkey brain providing a common neural mechanism for face recognition in primates. Whereas this may be true for at least some primate species, it is not clear whether a common face-processing system exists for all primates that is a basic structure from which species specializations may have evolved.

1.1.4 The Development of Face Perception and the Role of Experience

The majority of developmental studies provide support for a similar face processing system among the primates. Numerous studies have found that faces are highly salient social stimuli for human (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991) and NHPs starting at a very early age (Lutz, Lockard, Gunderson, & Grant, 1998; Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004; Myowa-Yamakoshi & Tomonaga, 2001). Newborn babies and infant NHPs orient more towards face-like patterns compared to non-face-like patterns (*Homo sapiens*: Goren et al., 1975; Johnson et al., 1991; Valenza, Simion, Cassia, & Umilta, 2006; *Hylobates agilis*: Myowa-Yamakoshi & Tomonaga, 2001; *Macaca fuscata*:

Kuwahata et al., 2004). These “face-like patterns” can be as simple as three dots arranged in a triangular fashion, reflecting the basic arrangement of the eyes above the nose, which is above the mouth, and this is referred to as first-order configuration. First-order configural cues are important for identifying faces at the categorical level; that is, discriminating faces from non-faces (Diamond & Carey, 1986). The innate preference for first-order configural cues was further demonstrated by a study in which infant Japanese macaques raised in an enriched, but face-deprived environment for 6 to 24 months demonstrated a preference for both human and monkey faces over other complex visual stimuli (Sugita, 2008). Moreover, human, ape, and monkey infants imitate facial gestures (*Homo sapiens*: Meltzoff & Moore, 1977; *Macaca mulatta*: Ferrari, Visalberghi, Paukner, Fogassi, Ruggiero, & Suomi, 2006; *Pan troglodytes*: Myowa, 1996) and demonstrate a preference for their mother’s face when paired with the face another female (*Homo sapiens*: Bushneil, Sai, & Mullin, 1989; *Macaca mulatta*: Rosenblum & Alpert, 1974; *Pan troglodytes*: Tomonaga, Tanaka, Matsuzawa, Myowa-Yamakoshi, Kosugi, Mizuno, ... & Bard, 2004). Taken together, these studies seem to suggest that at least some aspects of the face-processing system may be innate and consistent across primate species.

However, other evidence suggests that early exposure to faces during a critical developmental period may fine-tune cortical networks to become specialized for the prototypical face to which an individual is exposed. For example, Sugita (2008) found that, following an early period of face deprivation, Japanese macaques preferred to look at and selectively discriminated the species that it was first exposed to (either human or conspecific faces). Likewise, de Haan, & Nelson (2002) showed that six-month old human babies were able to discriminate both human and monkey faces, but at nine-months of age, they only discriminated human faces. These results elucidate the role of experience in the development of the “other species effect” which has been likened to the “other race effect” in which it is easier to recognize members of one’s own ethic group or species (Meissner & Brigham, 2001; Pascalis & Bachevalier, 1998), or, perhaps more accurately given the evidence, to the prototypical face to which one is frequently exposed.

Other evidence supports the notion that these effects are influenced by experience or exposure as well. For example, children as young as three months old demonstrated the other-race effect, yet, short-term exposure to other-race stimuli may be sufficient to cancel this effect (Malpass, Lavigueur, & Weldon, 1973; Sangrigoli & Schonen, 2004). Additionally, Korean children reared exclusively with Koreans and later adopted by Caucasian families between the ages of three and nine, demonstrated the own-race effect for Caucasian faces as adults (the same that Caucasians exhibit), suggesting that this effect may be reversible with experience (Sangrigoli, Argenti, Ventureyra, & de Schonen, 2005; see also Elliot, Wills, & Goldstein, 1973; Malpass et al., 1973). Within nonhuman primates, rhesus macaques exhibited a species-specific effect in which they discriminated conspecifics, but not domestic animals, yet after several months of exposure to the domestic animals, the macaques could discriminate them as well (Humphrey, 1974). Similarly, chimpanzees with more exposure to human faces than to other chimpanzee faces were better at discriminating human faces than they were at discriminating chimpanzee faces (Martin-Malivel & Okada, 2007). Taken together, these studies suggest that experience plays a critical role in the processing of social stimuli within and across species and that there may be a critical period during early developmental during which the face processing system undergoes perceptual narrowing, but that with appropriate exposure this can be changed.

1.1.5 How similar is Face Perception Across Primates?

Behavioral evidence has provided mixed evidence of a common primate face-processing system. As stated above, the data support an innate preference for faces. Additionally, the eyes seem to be of special importance in face recognition. When chimpanzees and macaques were tested on which feature(s) were the most important in facial recognition, both species performed significantly worse when the eyes were masked (Parr, Winslow, Hopkins, & de Waal, 2000; see also Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010). This is true in other species as well (*Homo sapiens*: Hainline, 1978; *Macaca mulatta*: Gothard, Erickson, & Amaral, 2004; Keating & Keating, 1982), and it has recently been argued that all primates share a similar face-scanning strategy in which the eyes are of particular importance (Hirata et al., 2010).

Yet, it is unclear to what degree NHPs rely on second-order configuration, or the relative spatial arrangement of facial features unique to each individual, that are thought to provide the information necessary to individuate faces in humans (Diamond & Carey, 1986). Humans incorporate both first and second-order configuration cues into a single perceptual whole through a fast acting process referred to holistic processing. This is exemplified by the inversion effect, in which humans are slower and less accurate in recognizing faces (but not objects) when they are presented in an upside-down orientation compare to an upright orientation, due to the disruption of holistic processing (Yin, 1969; Valentine, 1988; see Parr, 2011, for a review on the parts-to-whole and composite task). Behavioral evidence of the inversion effect in NHPs is mixed. In chimpanzees, the inversion effect seems to be dependent on expertise, such that chimpanzees demonstrate the effect for human and chimpanzee faces, but not capuchin faces or cars (Parr, Dove, & Hopkins, 1998; but see Tomonaga, Itakura, & Matsuzawa, 1993). However, this does not seem to be the case for monkeys (see Parr, 2011, for a review). It is possible that these differences may reflect different adaptive specializations between the species, yet further comparative work is needed to rule out the possibility that differences in methodology contributed to inconsistent results.

Behavioral research also has focused on NHPs' ability to individuate conspecific faces. Results in this area of research have been more consistent. One of the most direct ways to evaluate NHPs' ability to individuate faces is to present them with a task in which they must match the same individual across different viewpoints. This task rules out the possibility that subjects are relying on irrelevant perceptual features specific to each photograph to match the stimuli and thus provides additional evidence for face recognition as an emergent property distinct from basic visual processing. Accordingly, positive results obtained from studies employing paradigms that require direct responses from subjects are generally accepted as evidence for individual recognition (Parr, Siebert, & Taubert, 2011; Parr et al., 2000; Pokorny & de Waal, 2009; Rosenfeld & Van Hoesen, 1979; but see Zayan & Vauclair, 1998). Using this type of methodology, all of the species tested thus far, including chimpanzees, orangutans, rhesus macaques and capuchin monkeys have demonstrated the ability to discriminate conspecific faces (*Cebus apella*: Pokorny & de Waal, 2009; Talbot, Leverett, & Brosnan, *in review*; *Pan troglodytes*: Parr et al., 2000; *Pongo spp*: Talbot, Mayo, Stoinski, & Brosnan, 2015; *Macaca spp.*: Micheletta, Whitehouse, Parr, Marshman, Engelhardt, & Waller, 2015; Parr et al., 2000; Rosenfeld & Van Hoesen, 1979).

Although previous studies typically examined this ability using unfamiliar faces, many of the more recent studies have included familiar facial stimuli as well. A number of these studies have found differences in performance based on familiarity, again suggesting that experience with, exposure to, and the familiarity of faces may play a critical role in influencing face recognition. For example, previous studies in humans have found that that changes in lighting, facial expression, or viewpoint of the facial stimuli impair the ability to recognize unfamiliar, but not familiar, faces (Bruce, 1982; Bruce, Valentine, & Baddeley, 1987; Bruce, Henderson, Greenwood, Hancock, Burton, & Miller 1999; Bruce, Henderson, Newman, & Burton, 2001; Hill & Bruce, 1996; Hill, Schyns, & Akamatsu, 1997). Likewise, chimpanzees performed better when individuating highly familiar conspecifics across viewpoints compared to moderately familiar conspecifics (those previously seen in a texting context), and worse when individuating completely unfamiliar conspecifics (Parr et al., 2011). More recently, orangutans also demonstrated a familiarity effect, discriminating familiar, but not unfamiliar, individuals (Talbot et al., 2015). However, the one study that has directly tested the effect of familiarity in a non-ape found that crested macaques discriminated the faces of familiar individuals living in their own social group and unfamiliar faces, but no advantages were found for familiar versus unfamiliar individuals (Micheletta et al., 2015). Thus, it is possible that the familiarity effect highlights a distinction in the face processing system of humans and apes compared to the rest of the primate order.

1.1.6 The Acquisition and Use of Social Information from Visual Stimuli

Primate societies are structured around kin relationships, dominance hierarchies, and reproductive status, suggesting that acquiring social information about others should be highly advantageous. The importance of acquiring social information is exemplified by studies that demonstrate that mere visual exposure to a conspecific is inherently rewarding to NHPs, more so than nonsocial stimuli and even food (e.g., Butler, 1954; see Anderson, 1998, for a review). It is possible that responsiveness to social stimuli may be influenced by the importance of the social context, and thus NHPs should prefer or value certain social information more than other information. For instance, male rhesus macaques are considered a despotic species (Thierry, 2000) in which the rank of males may change many times within their lives (Gachot-Neveu & Menard, 2004). Male behavior dramatically changes (e.g., increased male-male competition, visual inspections, and mating attempts) in the presence of females with swollen anogenital regions, which are an indicator that the female is sexually receptive (Nunn, 1999) and are therefore quite valuable for the reproductive success of male macaques. Consistent with this, males were willing to sacrifice preferred juice in order to have visual access to female genitalia or the faces of high-ranking monkeys, but they required payment of juice to view the faces of low ranking monkeys (Deaner, Khera, & Platt, 2005). Interestingly, however, males did not value the opportunity to view female faces over male faces.

Female macaques, however, may have different priorities. Unlike males, the dominance hierarchy of female rhesus macaques is stable and linear. Females remain in their natal groups and acquire the rank of their mothers (Gachot-Neveu & Menard, 2004). Therefore, they may not seek to gather social information on high-status females, as much of that information is relatively consistent throughout their lives. However, female rhesus macaques display active mate choice and prefer to mate with higher-status males (Sackett, 1990; Smuts, 1987). Presumably because of this, female rhesus macaques found the faces of dominant males to be more reinforcing than non-social controls (Watson, Ghodasra, Furlong, & Platt, 2012). Taken together, these findings suggest that NHPs differentially value social stimuli according to the adaptive value of those stimuli in guiding social interactions in the wild.

Evidence indicates that some NHPs respond in socially appropriate ways to visual stimuli even in experimental situations. Rhesus macaques display reactions such as fear, threat, or play when presented with colored slides of conspecifics engaging in social activities (Sacket, 1966). There is also evidence that suggests that NHPs are able to use social information garnered from visual stimuli. For example, chimpanzees were able to use the social information presented through televised images depicting a familiar caretaker hiding to facilitate the discovery of the individual in real life (Menzel, Premack, & Woodruff, 1978), which some have taken as evidence that at least some NHPs understand the representational context of two-dimensional visual stimuli. In a more ecologically relevant study, middle-ranking female pigtail macaques viewed videos of cage-mates displaying 'inappropriate' behavior for their rank, such as a dominant monkey displaying submissive behavior to lower ranking monkey. When the subject returned to her group after viewing such videos, she began to display higher levels of aggression as if she was attempting to rise in the hierarchy herself (Capitanio, 1987). This study, as well as those described above, provide evidence that monkeys perceive images of other individuals based on sex and social status (Deaner et al., 2005; Watson et al., 2012).

1.1.7 The Recognition of Dominance and Relationships

The ability to recognize the relations between others may allow individuals to more quickly (and safely) identify social information than through individual interactions alone. This could potentially increase social and reproductive advantage over others. Yet, knowledge of NHPs' ability to recognize relationships between other individuals (i.e., third-party relationships) is limited, in part because it is difficult for us to determine what animals know about their environment and how that information is stored and organized in the mind. Consequently, much of the evidence for the recognition of third-party relationships is tangential. For example, captive longtail macaques were first trained to choose pictures of one mother-offspring pair over pictures of two unrelated individuals. Later, both subjects transferred this skill to choose pictures of other familiar mother-offspring pairs over unrelated pairs and choose pictures of appropriate offspring when presented with a picture of its mother (Dasser, 1988). While this may be taken as evidence of the ability to recognize third-party relationships, it is also possible that the longtail macaques merely perceived some similarity between familiar mothers and their offspring. Supporting this, a follow up study on visual kin recognition in primates found that chimpanzees' ability to better match photos of mothers and sons than mothers and daughters (Parr & de Waal, 1999) indicated that this asymmetry was a function of similarities in global characteristics of the face such as pose, expression, and/or framing effects and that the perceptual mechanisms responsible for the detection of these features is shared with humans (Vokey, Rendall, Tangen, Parr, & de Waal, 2004).

Observational studies have provided much of the evidence of recognition of third-party relationships. For instance, monkeys selectively reconcile or aggress towards the kin of those involved in recent disputes (Aureli, Cozzolino, Cordischi, & Scucchi, 1992; Judge, 1982), and Japanese and bonnet macaques preferentially recruit individuals who are both higher-ranking than and unrelated to their opponents (Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999). Through the use of playback experiments conducted in the field, female baboons have demonstrated knowledge of the relative ranks of other females residing within their social group. Subjects responded more strongly when they heard a causally inconsistent sequence of calls in which a higher-ranking female responded submissively to a lower-ranking female's grunt as compared to casually consistent sequences, in which a lower-ranking female responded submissively to a higher-ranking female's grunt. Importantly, the novelty of the call sequences was controlled for by the inclusion of a series of control experiments that included a third female's vocalization to make a sequence casually consistent, thus ruling out the possibility that the subjects were merely reacting to the novelty of a particular sequence of calls (Cheney, Seyfarth, & Silk, 1995). In a similar experiment with free-ranging vervet monkeys, upon hearing the playback of an infant's scream, monkeys selectively looked at the infant's mother, often before the mother made any movement. The anticipatory behavior of the control females suggests that they recognized the relationship between the screaming juvenile and its mother (Cheney and Seyfarth, 1980).

Finally, experimental studies also provide strong evidence of primates' ability to garner information about the social relationships of unfamiliar conspecifics through observation alone. Bovet and Washburn (2003) demonstrated that two out of three rhesus macaques learned to choose the dominant individual from video clips of two unknown conspecifics and were able to generalize their performance to novel videos and also to novel social contexts. In a similar study, rhesus monkeys were presented with video clips comprising of artificial dominance interactions between unfamiliar conspecifics that were independent of their real-world rank. Subjects were able to select the dominant individual from the videos and transfer this judgment to novel videos (Paxton, Basile, Adachi, Suzuki, Wilson, & Hampton, 2010).

Taken as a whole, this research suggests that at least some species of NHPs have knowledge of third-party relationships within their own social group, and are able to learn these discriminations by observing the social interactions of others. It is less clear whether this also occurs across social groups. This would be a fitness advantage for species that regularly interact with neighboring groups, and in particular when these interactions are often aggressive or even lethal. However, there is little systematic evidence that demonstrates this ability in primates.

1.2 Overview of this Dissertation

This dissertation was designed to explore NHPs' social knowledge through the use of visual stimuli representing conspecific faces. In order to do this, I first had to verify that my study subjects, capuchin monkeys, could individually discriminate conspecific faces. Although several lines of evidence support the hypothesis that humans and NHPs share a similar face processing mechanism, behavioral evidence has been mixed. One particularly robust effect observed in humans is the familiarity effect, in which humans are better able to recognize familiar as opposed to unfamiliar faces, particularly across changes in viewpoint (Bruce, 1982; Bruce et al., 1987; 1999; 2001; Burton, Wilson, Cowan, & Bruce, 1999; Hill & Bruce, 1996; Hill et al., 1997). This effect has recently been observed in apes (Parr et al., 2011; Talbot et al., 2015), but not monkeys (Micheletta et al., 2015), suggesting a possible distinction in the perception of faces between humans and apes and the rest of the primate order. Other behavioral evidence also supports this notion (e.g., see discussion above on the inversion effect). Thus, the first study of this dissertation addressed whether the face discrimination skills of tufted capuchin monkeys, a highly social New World primate, vary as a function of familiarity. Using a matching-to-sample task, capuchins were tested on their ability to discriminate the conspecific faces of individuals living in their own social group (in-group), in a neighboring, and therefore familiar, social group (out-group), and in completely unfamiliar individuals (unfamiliar). This is the first study to examine face discrimination skills in familiar neighboring social groups and to directly test the effect of familiarity on face recognition in a New World primate.

In the second and third studies, I explored this species' knowledge of their social environment. Research on the classification of sexual identity by NHPs in the visual domain is limited. Moreover, the studies that have examined sex discrimination have produced mixed results (e.g., Ohshiba, 1995; Koba & Izuma, 2006). Therefore, in Study 2, I examined whether, like humans, capuchins obtained social information about the sex of conspecifics from faces alone and whether experience aided the discrimination of sex. I included three degrees of familiarity (in-group members, out-group members, and unfamiliar individuals). This allowed me to evaluate whether sex perception was aided by the additional cues that can be obtained when subjects are in close proximity (e.g., olfactory or tactile cues), which would be relevant for the ingroup vs familiar outgroup discrimination, or based on physical features, such a facial dimorphism (Weston et al., 2004), which might allow monkeys to discriminate male vs female even in unknown individuals.

Finally, much of the research on the recognition of third party relationships in NHPs is tangential. Well-controlled laboratory studies, however, provide more convincing evidence of NHPs ability to garner information about the dominance relations of others (Bovet & Washburn, 2003; Paxton et al., 2010). This has not been done in New World monkeys, and is important to do in order to determine whether they differ from Old World primates. In Study 3, I examine whether capuchins use social knowledge of dominance hierarchies to guide responses on a list-learning task employing conspecific faces as stimuli. Once again, performance was evaluated on lists of in-group members, out-group members with whom the subject monkey had visual and vocal access but did not physically interact, and unfamiliar individuals. The inclusion of unfamiliar individuals is important because recent evidence indicates that facial width to height ratio in both male and female capuchin monkeys is associated with alpha status (Lefevre, Wilson, Morton, F.B., Brosnan, S.F., Paukner, A., & Bates, 2014), indicating that it is at least possible that capuchin monkeys are able to deduce relative rank from facial features allowing alone.

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2 STUDY 1: DISCRIMINATION OF FAMILIAR AND UNFAMILIAR FACES IN CAPUCHIN MONKEYS

2.1 Introduction

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

Several lines of evidence suggest that this may be the case. First, the majority of developmental studies provide support for a similar face processing system among the primates. Numerous studies have found that faces are highly salient social stimuli for both humans (Goren, Sarty, & Wu, 1975; Johnson, Dziuraweic, Ellis, & Morton, 1991) and NHPs starting at a very early age (Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004; Lutz, Lockard, Gunderson, & Grant, 1998; Myowa-Yamakoshi & Tomonaga 2001). Human and NHP infants orient more towards face-like patterns (e.g., three dots arranged in a triangular fashion) compared to non-face-like patterns (*Homo sapiens*: Goren et al., 1975; Johnson et al., 1991; Valenza, Simion, Cassia, & Umilta, 1996; *Macaca fuscata*: Kuwahata et al., 2004; *Hylobates agilis*: Myowa-Yamakoshi & Tomonaga et al. 2001), imitate facial gestures (*Homo sapiens*: Meltzoff & Moore, 1977; *Pan troglodytes*: Myowa, 1996; *Macaca mulatta*: Ferrari et al., 2006), and demonstrate a preference for human and monkey faces even when they have never before been exposed to faces (Sugita, 2008), suggesting an innate specialized face-processing system within the primates. 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 humans and NHPs prefer to look at 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 (*Homo sapiens*: Malpass, Lavigueur, & Weldon, 1973; Sangrigoli, Pallier, Argenti, Ventureyra, & De Schonen, 2005; see also Elliot, Wills, & Goldstein, 1973; *Macaca fuscata*: Sugita, 2008; *Macaca mulatta*: Humphrey, 1974; *Pan troglodytes*: Martin-Malivel & Okada, 2007).

Second, recent studies have found several face-selective areas in the rhesus macaque brain that are similar in number and relative size to those in humans (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003; Tsao, Freiwald, Tootell, & Livingstone, 2006; Tsao, Moeller, & Freiwald, 2008; Yin, 1969) that respond to a variety of human and monkey faces, respond to changes in facial expressions, and respond to eye gaze and facial orientation (Engell & Haxby, 2007; Hoffman & Haxby, 2000; see Tovée & Cohen-Tovée, 1993 for a review). This suggests a common neural mechanism for face recognition in primates. Finally, if primates do share a similar face-processing system, one would expect to observe similar characteristics in human and NHP face processing, yet the behavioral evidence for a common face processing system among primates has been mixed (see Parr, 2011, for a review). For instance, evidence for a similar face-scanning strategy in which the eyes are of particular importance is clear (*Homo sapiens*: Hainline, 1978; Roberts & Bruce, 1988; *Macaca mulatta:* Gothard, Erickson, & Amaral, 2004; Keating & Keating, 1982; *Pan troglodytes*: Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Parr, Winslow, Hopkins, & de Waal, 2000), but it is still unclear whether NHPs process faces holistically, as a perceptual whole, as do humans (Parr, 2011; Maurer, Le Grand, & Mondloch, 2002). Comparatively, less is known about the social, cognitive and neural processes that influence face processing in NHPs than humans, so it is unclear whether these processes represent human specializations in the face processing system or whether they were also present in our common ancestor.

One interesting and robust behavioral effect observed in human face processing is known as the familiarity effect. This effect manifests such that *familiar* face recognition is highly accurate even when the image is degraded, whereas *unfamiliar* face recognition is negatively impacted by superficial image changes such as differences in lighting, facial expression, or viewpoint of the facial stimuli (Bruce, 1982; Bruce, Valentine, & Baddeley, 1987; Bruce, Henderson, Greenwood, Hancock, Burton, & Miller, 1999; Bruce, Henderson, Newman, & Burton, 2001; Burton, Wilson, Cowan, & Bruce, 1999; Hill & Bruce 1996; Hill, Schyns, & Akamatsu, 1997). The robustness of familiar face recognition indicates that exposure aids the formation of viewpoint-independent representations of *familiar* faces, whereas the detrimental effects that changes in viewpoint can have on the recognition of *unfamiliar* faces supports the notion that individuals are matching features of the photographs to discriminate them. Recently, two species of great apes have also demonstrated the familiarity effect when matching the same individual across viewpoints: chimpanzees (Parr, Siebert, & Traubert, 2011) and orangutans (Talbot, Mayo, Stoinski, & Brosnan, 2015). In contrast, no effect of familiarity has been observed in Old World primates (e.g., *Macaca nigra:* Micheletta, Whitehouse, Parr, Marshman, Engelhardt, & Waller, 2015). However, studies of face recognition in New World monkeys are rare and those that objectively compare the face-processing skills for familiar and unfamiliar individuals are even more so.

Thus, in this study, I examined the influence of familiarity on the face processing performance of 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 neighboring group with whom they have visual and vocal access but do not physically interact (out-group), and completely unfamiliar individuals (unfamiliar). Specifically, I 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 to match the stimuli and is generally accepted as evidence of individual recognition (Parr et al. 2000; 2011; Pokorny & de Waal, 2009a; Rosenfeld & Van Hoesen, 1979). That said, Zayan and Vauclair (1998) proposed that, in order to rule out the possibility that a species views pictures of conspecifics as artificial configurations with no social significance, discrimination tasks should compare performance between socially familiar and unfamiliar conspecifics with the expectation that performance should be higher on familiar as opposed to unfamiliar conspecifics. Accordingly, I hypothesized that capuchins would apply their real-life knowledge of familiar individuals, in their own social group and neighboring group, to successfully match photos of conspecific faces across different viewpoints. Therefore, I expect capuchins to discriminate familiar individuals (in-group and out-group) better than unfamiliar individuals. Alternatively, if capuchins do not use familiarity to guide their decisions, I would expect the capuchins to perform equally well across all three degrees of familiarity (in-group, out-group, and unfamiliar).

No other study on NHPs has compared face discrimination performance on familiar in-group members and members of a familiar neighboring group, making it impossible to make a prediction based on previous data. However, one experimental study indicated that capuchins differentiated between in-group members and out-group members (Pokorny & de Waal, 2009b). In addition, I know that in some species (e.g., hamsters) 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., behavioral or olfactory cues) that aid individual recognition in capuchin monkeys. Therefore, taken together with Zayan and Vauclair's (1998) hypothesis, I expect capuchins to better discriminate familiar in-group members as compared to familiar out-group members.

2.2 Materials and Methods

2.2.1 Subjects and Housing

Subjects were eight capuchin monkeys (three adult males, one subadult male, and four adult females) housed in two social groups (Group 1 and Group 2) at the Language Research Center (LRC) of Georgia State University. 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). At no time were the subjects deprived of food or water. All subjects 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. All subjects were mother-reared in captivity. 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 their own social group and the neighboring group. Indoors, each monkey had vocal access to all others and limited visual access to the neighboring 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.

2.2.2 Face Stimuli

All face stimuli consisted of high quality digital color photos taken from a variety of viewpoints. Photos included 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 only include the head, face and neck. The background of the photos was homogenized by filling in the area around the face with solid white. Brightness and contrast were standardized to control for differences in lighting. Presentation size of the photos was 16 cm by 16 cm with a resolution of 300 dots per inch.

Capuchins in Groups 1 and 2 were trained on face stimuli that represented a third social group of capuchin monkeys housed at the LRC (Group 3). Test stimuli represented a completely different set of monkeys never before seen by subjects in an experimental context. The individuals represented in the test stimuli varied based on familiarity to the subject: in-group, out-group and unfamiliar. 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 with whom they had close physical, visual and vocal access. Out-group stimuli included photos of individuals from the subjects' neighboring group with whom they had visual and vocal access, but no physical contact. Unfamiliar stimuli included photos of conspecifics whom the subjects had never before seen. These photos were obtained from St. Andrews University's Living Links Center in Edinburgh, Scotland.

2.2.3 Apparatus and General Procedure

Stimuli were presented on a 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 had 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 to a grey box in the center 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 centered on the screen and four choice stimuli randomly appeared in four of six possible locations. The location of the correct comparison stimulus was randomly chosen by the program. 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 (i.e., the same individual depicted in the sample photograph). Correct responses were automatically rewarded with a food reinforcer (a banana-flavored pellet) and a high-pitched tone was played followed by an inter-trial interval (ITI) of 1s, 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 20s. Subjects worked at their own pace completing a maximum of 1000 trials per day. Test sessions lasted approximately two hours. No experimenter was present throughout the test session. Subjects were tested multiple times per week until the completion of the study.

2.2.4 Clip Art

All subjects had extensive experience with the MTS procedure using clip art and previously performed at very high levels on this task (e.g., Perdue, Church, Smith, & Beran, 2015). However, to be consistent with previous research and to ensure that every subject was familiar with the testing paradigm, I first presented them with clip art trials in which samples and comparison images were randomly selected from a group of 500 clip art stimuli. For training, the performance criterion was set at 18 out of 25 trials correct (i.e., ≥ 72% correct) on two consecutive test sessions (analyzed in 25-trial blocks). Once performance criterion was met, subjects proceeded to the next phase of training.

2.2.5 Identical Photos

Once subjects met criterion on MTS paradigm with clip art images, facial stimuli were introduced. In the identical phase, subjects were required to match identical photos of conspecifics. Training stimuli represented the capuchins from Group 3 (N=10) at the LRC, a separate group of capuchin monkeys from the capuchins represented in the test stimuli. Training stimuli were randomly selected from a set of 100 portraits (10 views per individual). Stimulus sets were always composed of 4 different individuals (1 sample and 4 possible options). In the identical photos phase, one of the four options was the same exact photo as the sample. All other aspects of the testing (including criterion) were as described above for clip art images.

2.2.6 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 4 different individuals (1 sample and 4 options), but 5 different photos, because one of the options (the correct choice) 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. All other testing details were identical to the identical photos phase.

2.2.7 Individual Discrimination – Transfer Test

For the transfer test, the task was the same as the different photos training phase: subjects were required to match the same individual across viewpoints. However, during the transfer test, an entirely new set of face stimuli were presented that represented 15 individuals: 5 familiar in-group individuals, 5 familiar out-group individuals, and 5 unfamiliar individuals. No individuals represented in these test stimuli had ever been seen in a previous testing context. Subjects were never presented with images of themselves. Stimuli included 10 photos of each individual for a total of 150 images and each photograph was only presented once as a sample to each subject. Thus, there were 50 trials in each condition (in-group, out-group, and unfamiliar) and 150 total test trials. Test trials were randomly inserted among clip art 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 only presented 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 trials to guide their responses, only the familiarity of the individuals themselves.

2.2.8 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 (male/female). Therefore, I ran a two-way mixed design ANOVA with two independent variables: one within-subjects variable, *Familiarity*, with three levels (in-group, out-group, and unfamiliar), and one between-subjects factor, *Sex* with two levels (male and female). Binomial *z* scores were used to analyze individual performance. The number of training sessions needed to reach criteria was reported for each subject (Figure 2.1). Data were analyzed using SPSS version 21 statistical software.

2.3 Results

2.3.1 Training – Clip, 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) in 50 trials, which was the minimum required. On the identical photo-matching task, capuchins reached criterion in an average of 1,682 trials (range 50-3,370). On the different photo-matching task, the capuchins took an average of 10,192 trials (range 3,222-17,740; see Figure 2.1 for more detail).

2.3.2 Individual Discrimination – Transfer Test

Mauchly's test showed that sphericity was not violated ($p = 0.264$) and there was homogeneity of variance as assessed by the Levine's test for all levels of the repeated measures (in-group: $p = 0.577$; Out-group: $p = 0.660$, Unfamiliar: $p = 0.618$), I therefore ran a two-way mixed design ANOVA with planned difference contrasts. There was a significant main effect of familiarity (ANOVA: $F_{2,12} = 9.19$, $p = 0.004$). 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: $F_{1,6} = 23.459$, $p = 0.003$; Figure 2.3). There was no significant difference between in-group and out-group performance ($\mathrm{F}_{1,6} = 0.049$, $p = 0.832$). Binomial Z-scores were used to analyze 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 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 highest overall performance on the task (Nkima, Figure 2.3).

2.3.3 Sex Difference

There was no main effect of sex of the subjects (ANOVA: $F_{1,6} = 1.72$, $p = 0.238$). Although the interaction between sex of the subject and familiarity was not significant ($F_{2,12} = 3.43$, $p = 0.066$), it approached significance, suggesting that this is a trend worth considering in future research. Overall, males performed at a higher level on the face discrimination task than females (Mean percent correct: Males, χ + SE = 44.67 + 1.73; Females χ + SE = 38.5 + 1.52). In particular, males were better able to discriminate male faces whereas both males and females discriminated female faces equally well (Figure 2.4). Given this apparent difference, I decided to conduct a t-test to determine if this difference was significant. Although it was not significant (Independent *t* test: $t_6 = 2.14$, $p = 0.076$), it did approach significance suggesting that sex of the subjects as well as sex of the faces should be considered in future research.

2.3.4 Reaction Time

I examined the latency to respond on the computerized MTS task. There was no overall effect of response time across the three conditions (ANOVA: $F_{2,14} = 1.397$, $p = 0.280$; In-group, χ + SE = 2.363 + 0.211; Out-group, χ + SE = 2.474 + 0.306; Unfamiliar, χ + SE = 2.729 + 0.372).

2.4 Discussion

Capuchin monkeys spontaneously discriminated individuals depicted in photos across a range of viewpoints and conditions. Moreover, capuchins' ability to do so varied with the familiarity of individuals depicted in the photos. Capuchins were equally able to discriminate familiar individuals living in their own social group and those living in a neighboring group, with whom they had daily visual and vocal access, and did better on both of these categories as compared to unfamiliar individuals. These results indicate that familiarity plays a significant role in the discrimination of faces such that it aids recognition of familiar individuals.

In contrast to my prediction, however, there was no significant difference in performance when discriminating in-group members and out-group members (although see below for a discussion on potential sex differences). 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 neighboring 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 general categorization scheme rather than the recognition of specific individuals. For instance, one study found that mother squirrel monkey (*Saimiri sciureus*) vocalizations increased when hearing their own infant vocalize compared to a different infant, or no infant at all, suggesting that mothers were 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, neighbor 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 as many species are able to see far enough to recognize individuals in neighboring groups, but that does not necessarily mean that there has been an evolutionary or ecological pressure to evolve the ability to do so. These distinctions can shed light on the specializations that may have evolved more recently in our own evolutionary history.

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

Although sex had no significant effect on the results, the current data indicate that it may be important. Overall, males performed at a higher level on the face discrimination task than females. Males also were better able to recognize male faces, whereas there was no sex difference in the recognition of female faces. It is interesting to note that in humans the opposite effect has been observed: females perform at a higher level than males in the recognition of female faces, although no sex differences have been found in the recognition of male's faces. Although no conclusive explanation for this sex difference in face recognition performance in humans has been drawn, one suggestion is that females are demonstrating a familiarity effect as a result of increased exposure to female faces through advertising and elsewhere (Lewin & Herlitz, 2002). However, considering the data in this study, it is possible that the ability to recognize individuals residing in neighboring groups may be particularly advantageous for the sex that emigrates from their natal group once they reach maturity as they often join neighboring social groups. For instance, capuchin monkey society is thought to be matrilineal and group membership is relatively stable, with the exception of young males who emigrate from their natal groups (Janson, 1990). Thus, it may be particularly important for male capuchins to recognize their competition in neighboring groups. This hypothesis is worth examining in other species as well, especially those for whom females migrate to determine the degree to which this hypothesis generalizes.

Much like the cross-race effect in humans, the familiarity effect in the present study is robust and begs 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 dominant 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 the photos used as stimuli and the novelty of the individuals represented in those stimuli. I 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 unique photo of each individual was only presented as the sample once. Using only one trial with each photo allowed us to evaluate how capuchin monkeys spontaneously perform on the individual discrimination task. Thus, the results obtained from the current study represent emergent behavioral patterns that go beyond those employed in operant and respondent conditioning.

The results from this study are consistent with the hypothesis that humans and NHP 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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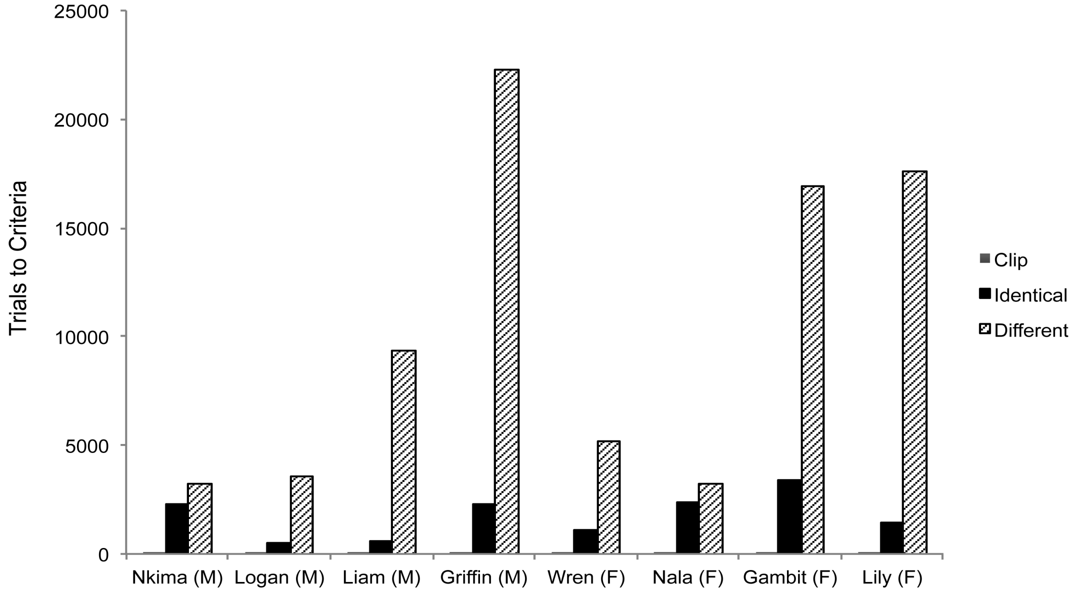
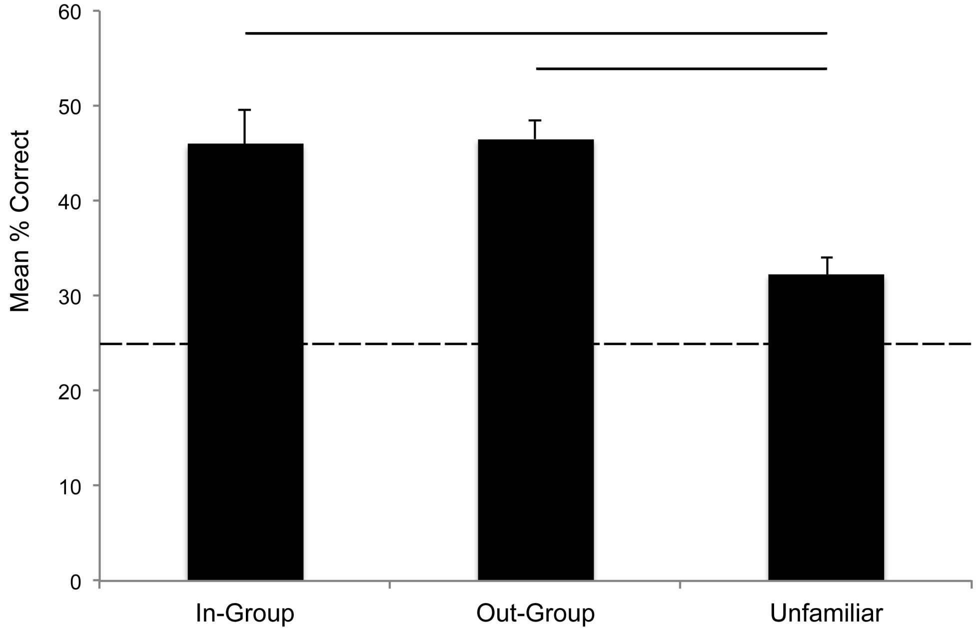
2.6 Figures

Figure 2.1. Training Results



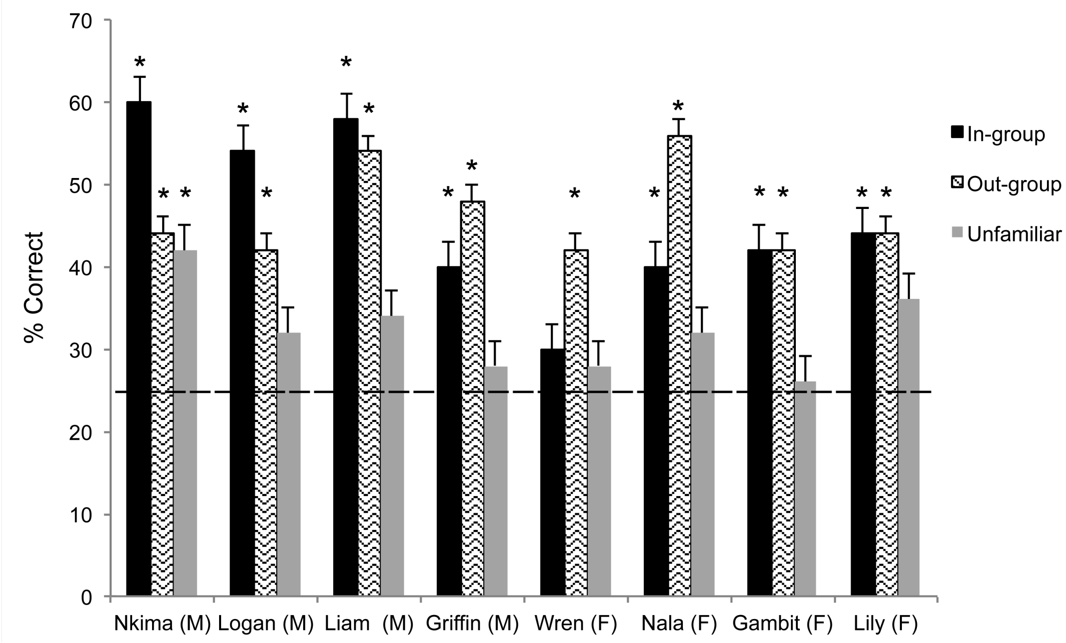
Number of trials it took subjects to reach criterion on each phase of training including *Clip* (grey), *Identical* (black) and *Different* (hatched). M and F after the monkey names indicate male or female sex of the individual.

Figure 2.2. Overall Performance on the Transfer Test



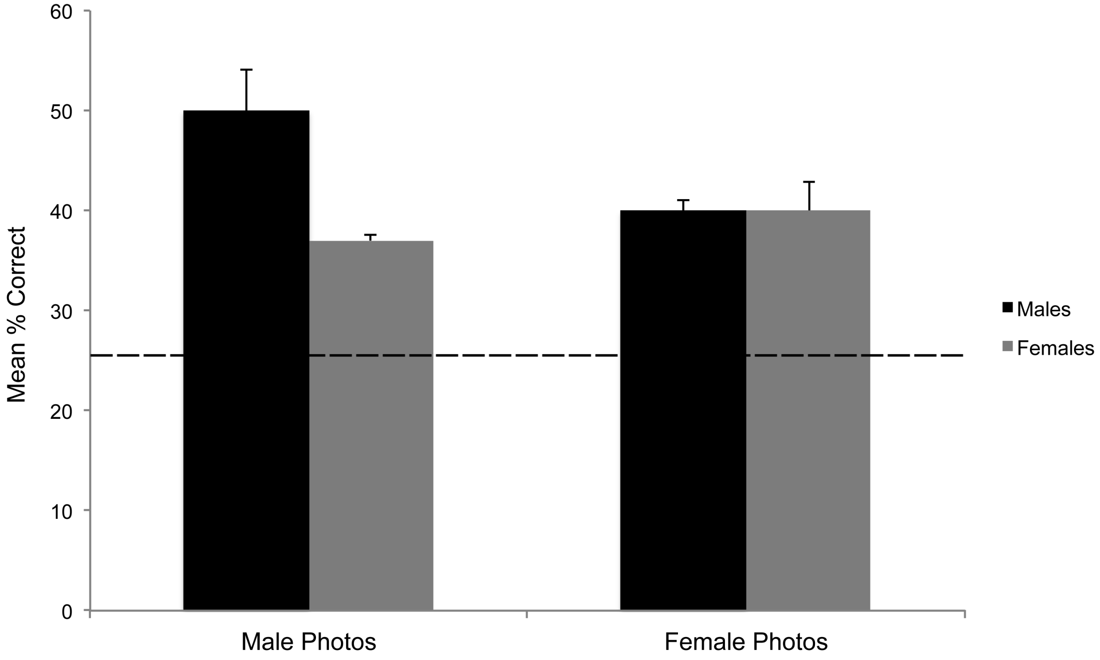
Black bars depict the mean percent correct on each of the three conditions (in-group, out-group, and unfamiliar). Horizontal dashed line represents chance level (25%), solid bars represent significance at the 0.05 level, and error bars reflect SEM. There was a significant main effect of familiarity. Capuchins performed significantly better on in-group and out-group members compared to unfamiliar individuals.

Figure 2.3. Individual Performance on the Transfer Test



Bars depict the mean percent correct on each of the three conditions: In-group (black), out-group (hatched), and unfamiliar (grey). Horizontal dashed line represents chance level (25%) and error bars reflect SEM, * $p \leq 0.05$ (Binomial z-scores). M and F after the monkey names indicate male or female sex of the individual.

Figure 2.4. Performance as a Function of Sex



Bars represent mean percent correct by males (black bars) and females (grey bars) as a function of the sex of the individual depicted in photos (x-axis). Horizontal dashed line represents chance level (25%) and error bars reflect SEM.

3 STUDY 2: SEX DISCRIMINATION IN CAPUCHIN MONKEYS

3.1 Introduction

Human faces provide us with a plethora of social information including the relative age, sex, individual identity, and emotional state of others (Ekman & Oster, 1979; Tranel, Damasio, & Damasio, 1988). In particular, humans are incredibly accurate at making judgments about the sex of an individual for familiar and unfamiliar faces, even when characteristic features, such as facial hair, makeup and certain hairstyles are omitted (Bruce & Young, 1986). Previous research in humans suggests that the classification of sex is determined by cues from facial features as well as two-dimensional and three-dimensional textural information. For instance, the average male face is considered more distinctive than the average female face, in part, due to more prominent nose/ brow and chin/jaw areas, making these faces easier to discriminate even when degraded (Bruce, Burton, Hanna, Healey, Mason, Coombes,... & Linney, 1993).

Like humans, most nonhuman primates (NHPs) are gregarious, group-living species that are highly reliant on vision for communication, suggesting that acquiring visual information about conspecifics, such as identity, sex, social status, and reproductive quality, should be highly adaptive. Moreover, the correlation between neocortex size and social group size within the primate order supports the hypothesis that acquiring and using social information to guide behavior was likely an important selective force in the evolution of primate cognition (Dunbar, 1992). Although several species of NHPs are able to extract information about individual identity from faces alone (*Pan troglodytes*: Parr, Winslow, Hopkins, & de Waal, 2000; Parr, Siebert, & Taubert, 2011; *Pongo spp.*: Talbot, Mayo, Stoinski, & Brosnan, 2015; Vonk & Hamilton, 2014; *Macaca spp.*: Micheletta, Whitehouse, Parr, Marshman, Engelhardt, & Waller, 2015; Parr et al.

2000; Rosenfeld & van Hoesen, 1979; *Cebus apella*: Pokorny & de Waal, 2009; Talbot, Leverett, & Brosnan, *in review*), little is known about whether nonhuman primates extract other social information, such as the sex of the conspecific, which is fundamental to their reproductive success. In particular, the mode through which NHPs obtain information on the sexual identity of others is unclear. Do NHPs garner this information via auditory, olfactory, behavioral, or visual cues (as do humans)?

Sex differences in auditory communication are common in the animal world. Generally, visually restricted habitats and dispersed social organizations, which are relatively common in the primate order, promote greater vocal communication between individuals (e.g., Cheney & Seyfarth, 1996; Norcross & Newman, 1993). In some instances these differences manifest in distinctive patterns of calling by one sex, but not the other. This is the case in many species of songbirds; males, but not females, produce distinctive vocalizations during the breeding season (Hauser, 1996). In other instances, the acoustic structure of vocalizations differ due to variations in the anatomical features involved in the production of sound which, in turn, are due to differences in body size between the sexes, or sexual dimorphism. For example, loud calls produced by males and female chacma baboons vary in relation to age and sex, reflecting differences in body size (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001).

However, whether these differences in auditory cues are perceived and used in sex discrimination by conspecifics is another question. One common function of NHP long calls is to attract mates (Waser, 1982). Accordingly, some evidence suggests that certain species of NHPs discriminate sex from auditory cues alone. Acoustic analyses revealed that the temporal parameters of cottontop tamarins' long calls varied based on the sex of the caller, suggesting that tamarins could potentially use this as a cue to discriminate sex (Weiss Garibaldi, & Hauser, 2001). Moreover, male tamarins demonstrated a bias to approach the long calls of foreign females as compared to familiar ones, whereas females demonstrated the opposite effect for males, suggesting that tamarins are able to glean some information about the sex of the individual producing the long call (Miller, Miller, Gil-Da-Costa, & Hauser, 2001). Yet more direct evidence of the classification of sexual identity via auditory cues comes from baboons. Like cottontop tamarins, male and female baboon vocalizations differ in acoustic structure. Baboons that were trained to discriminate the grunt of one male from that of one female generalized this ability to new grunts from the same individuals, as well as completely novel males and females. Moreover, because these calls were from unfamiliar conspecifics, these discriminations could not be based on known acoustic cues of an individual's calls (Rendall Owren, Weerts, & Hienz, 2004) as has been suggested for other species (Gouzoules and Gouzoules, 1990). This parallels speech in humans as humans readily discriminate the voices of unfamiliar males and females (e.g., Whiteside, 1998).

To date, research on the classification of sexual identity in the visual domain is limited. One study demonstrated that a chimpanzee raised in an enculturated environment discriminated sex from full-body photographs of clothed humans in three orientations (front, back, and side), with greatest accuracy in the side orientation (Itakura, 1992). However, the four studies that investigated NHPs' ability to objectively classify *conspecifics* as either male or female produced mixed results. For example, Ohshiba (1995) trained three Japanese macaques to respond to pictures of conspecific faces (five male and five female) in sequence (i.e., first male and then female), yet only one monkey passed the training phase and this individual was unable to generalize performance to novel faces (three male and three female). Although it is possible that faces alone do not provide enough social information for Japanese macaques to discriminate sex, it seems more likely that these negative results were due to the limited number of stimuli used, given that a number of studies have demonstrated that the ability to form an identity concept increases with the number of training stimuli (Katz, Wright, & Bachevalier, 2002; Truppa, Garofoli, Castorina, Mortari, Natale, & Visalberghi, 2010).

More recently, Koba and Izuma (2006) trained two female Japanese monkeys (*Macaca fuscata*) on a two-choice sex categorization task employing a much larger number of full-body frontal pictures, with nipples and underbelly visible, of unfamiliar conspecifics (28 male and 28 female). Subjects learned to choose one of two keys either on the left or right for males and females, respectively. One of the two monkeys generalized its performance to novel pictures of males and females. In subsequent experiment, modified versions of the trained stimuli depicting the face, chest or underbelly were presented to evaluate which visual cues were important for the categorization of sex. The same monkey that previously showed evidence of sex discrimination was able to discriminate males and females from faces alone. However, because the images were modified images of those previously used in training, it is possible that the monkey could have been relying on previous associations with the stimuli (see Koba and Izuma, 2008 for sex discrimination using indirect measures).

Inoue, Hasegawa, Takara, Lukáts, Mizuno, & Aou (2008) examined three rhesus monkeys' (*Macaca mulatta*) ability to discriminate between male and females monkeys with different postures and appearances. After nine months of training, the monkeys were able to discriminate novel pictures with 80% accuracy. Importantly, performance was evaluated on novel pictures, with or without visible sexual features (e.g., male genitalia or female nipples), presented only once, ruling out the possibility that subjects were associating the images with previous reinforcement history. There was no difference in accuracy on pictures with or without visible sexual features, suggesting that subjects were able to discriminate gender without direct information on sexual features. These results indicate that NHPs may be able to discriminate sex from the face alone. Finally, using a matching-to-sample paradigm, de Waal and Pokorny (2008) demonstrated that chimpanzees (*Pan troglodytes*) were able to match pictures of the anogenital region of an individual to the corresponding conspecific face, but only if the individual was familiar, suggesting that sex perception may be aided by information obtained from real-life interactions and whole-body knowledge.

Taken together, these results suggest that NHPs may incorporate multiple visual cues to classify the sex of conspecifics and one's ability to discriminate sex may be aided by real-life interactions. More specifically, conspicuous sexual features, in addition to faces, may play an important role in the categorization of sex. Yet unlike the species previously tested on sex discrimination tasks (e.g., macaques and chimpanzees), many New World monkeys do not show conspicuous sexual features, such as chromatic or morphological variations in specialized "sexual skin," reflecting changes in estrogen or progestin levels (Dixson, 1983). Tufted capuchin monkeys (*Cebus apella*) are a particularly interesting species in this regard. In captivity, the morphology of the female clitoris is often confused with male morphology by humans, leading to inaccurate sexing (Fragaszy, Visalberghi, & Fedigan, 2004), and females lack sexual skin or any evident morphological changes during estrous (Dixson, 1983). In addition, female genitalia do not elicit male interest (Phillips, Bernstein, Dettmer, Devermann, & Powers, 1994). Thus, it is possible that capuchin monkeys use cues other than sex characteristics to discriminate sex visually.

One possibility is that certain species of primates are able to deduce the sex of an individual from facial morphology alone. Previous studies examining sex differences in face morphology across primate species have found that facial dimorphism is negatively correlated with canine morphology. That is, male primates with highly dimorphic canines (e.g., yellow baboons) have relatively longer faces, whereas males that have relatively the same size canines as females have proportionally broader, shorter faces compared to females (Weston, Friday, Johnstone, & Schrenk, 2004). The latter is the case for tufted capuchins. Male capuchins have relatively broader faces than females, partly due to the enlarged masticatory muscles, which cannot be explained by differences in diet (Masterson, 1997).

In this study, I examined whether tufted capuchin monkeys are able to categorize the sex of conspecifics from faces alone and whether experience aided the discrimination of sex. Specifically, I used a computerized dichotomous choice procedure that required a direct choice from subjects. Capuchins were presented with a sample image depicting either individuals living within their own social group (in-group), individuals living in their neighboring group with whom they have visual and vocal access but do not physically interact (out-group), or completely unfamiliar individuals (unfamiliar). Subjects were to choose one of two symbols that represented males and females, respectively.

In accordance with previous research that suggests that at least some primates may be able to discriminate sexual identity using faces alone and because tufted capuchins lack overt sexual characteristics, but display dimorphism in facial morphology (Weston et al., 2004), I predicted that capuchin monkeys would be able to discriminate the sex of conspecific faces. Although no other study has examined sex discrimination in capuchin monkeys, previous research with chimpanzees suggests that real-life interactions with the individuals depicted in the task may aide the concept of sexual identity (de Waal and Pokorny, 2008). Moreover, the capuchin monkeys tested in this study previously discriminated the faces of familiar in-group member and familiar out-group members (Talbot et al., *in review*). Therefore, I also predicted that capuchins monkeys would exhibit a familiarity effect in identifying the sex of conspecifics faces, such that they would perform better on familiar (in-group and out-group) as opposed to unfamiliar individuals. I did not have a specific prediction for the degree to which familiarity would influence choices; if sex perception is aided by additional cues obtained from close proximity, such as olfactory cues, one might observe a more graded familiarity effect such that capuchins best discriminate the sex of in-group members, are mediocre on out-group members, and are worst on unfamiliar individuals. Alternatively, if capuchin monkeys solely rely on cues from facial morphology such as the facial-height-to-width ratio described above, then one would expect the capuchins to perform equally well across all degrees of familiarity.

3.2 Methods

3.2.1 Subjects and Housing

Subjects included 14 capuchin monkeys (five males and nine females) housed in three social groups (Groups 1-3) at the LRC. All subjects were mother-reared in captivity. Group 1 consisted of 1 adult male and 4 adult females; Group 2 consisted of four adult males and two females; Group 3 consisted of two adult males and eight adult females. All three social groups had indoor/outdoor access and environmental enrichment (climbing structures, ropes, and other toys). From their outdoor areas, each monkey had vocal and visual access to members of at least one neighboring group. Indoors, each monkey could hear other groups, although could not see them.

At no time were subjects ever food or water deprived. All subjects had ad libitum access to water, including during cognitive and behavioral testing, and received a diet consisting of primate chow, fruits, and vegetables. Subjects' participation in this study was entirely voluntarily. All subjects had previous training with a variety of cognitive tasks using the computerized joystick testing apparatus (Evans et al., 2008) and seven of the 14 subjects had previously been tested on an individual discrimination task using the same facial stimuli as this study. 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).

3.2.2 Face Stimuli

All face stimuli consisted of high quality digital color photos taken from a variety of viewpoints. Photos included 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 only include the head, face and neck. Brightness and contrast were standardized to control for differences in lighting. Presentation size of the photos was 16 cm by 16 cm with a resolution of 300 dots per inch.

Face stimuli represented all of the capuchin monkeys housed at the LRC as well as photographs of unfamiliar capuchin monkeys obtained from various facilities housing capuchin monkeys. Photos of capuchin monkeys housed at Bucknell University in Lewisburg, PA, were used for training and photos of capuchins from the National Institute of Health (NIH) Animal Center in Poolesville, MD, were used for the generalization phase. During testing, subjects underwent three test conditions employing three different classes of face stimuli: 1) familiar individuals living in one's own social group with whom they had close physical, visual and vocal access (in-group), 2) familiar individuals, living in one's neighboring social group with whom they had visual and vocal access, but no physical contact (out-group), and 3) unfamiliar individuals, with whom subjects have never before interacted with (unfamiliar). Stimuli were used from each of the three LRC capuchin groups as both in-group and out-group facial stimuli, depending on the relationship between the test subject and the subject of the photograph. Unfamiliar test stimuli represented photos of capuchin monkeys residing at St. Andrews University's Living Links Center in Edinburgh, Scotland. There were no procedural differences between test conditions.

3.2.3 General Apparatus and Procedure

Face stimuli were presented on a computer that included a modified joystick and pellet dispenser mounted on a movable audiovisual cart that, at the beginning of the testing session, was placed approximately 30 cm in front of each individual testing chamber, with the monitor directly in front of the monkey. Testing chambers had a clear Lexan front panel for easy viewing of the computer monitor. Subjects were previously trained to manipulate a joystick that is inserted through an opening on the Lexan panel (Evans, Beran, Chan, Klein, & Menzel, 2008).

For each session, subjects voluntarily entered their individual testing chambers from their social groups to participate. A dichotomous choice procedure was used. Subjects initiated a trial by moving the cursor into contact with a colored grey square presented in the top center of the 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 moving the cursor into contact with it. The sample stimulus remained centered on the screen and two symbols appeared on the screen, one of which indicated that the sample was male (left) and the other female (right). The location for these symbols remained consistent throughout training and testing. The object of the task was to select the symbol that matched the sex of the individual presented as the sample.

Unless otherwise noted, correct responses were automatically rewarded with a food reinforcer (a banana-flavored pellet) and a high-pitched tone was played followed by an inter-trial interval (ITI) of 1s, 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 20s. Stimuli were presented in a pseudo-randomized order with all possible images presented one time within a block before any were re-presented.

No experimenter was present throughout the training and test sessions (except when setting up and taking down the computer apparatus). For each session, the software automatically recorded the subject, date, session number, trial number, type of trial (in-group, out-group, unfamiliar), names of the images presented, the stimulus that was selected to classify the sample as male or female, whether each trial was correct or incorrect, and whether feedback was provided. Each session lasted approximately four hours in duration. Subjects worked at their own pace completing as many trials and they chose each session. Subjects were tested multiple times per week until the completion of the study.

3.2.4 Training - Dichotomous Choice Procedure

I used a dichotomous choice procedure. Subjects were trained to pick the symbol that matched the sex of the sample face stimulus. On each trial, face stimuli were randomly selected from a stimulus set consisting of 4 females (5 views of each) and 2 males (10 views of each) for a total of 40 photos. Each individual was photographed from variety of perspectives. This way, subjects viewed multiple images of the same individual within a training or test session, reducing the chance that capuchins' performance was based on associations formed through reward or punishment to specific responses to specific stimuli. The performance criterion (≥ 88% on two consecutive 25-trial blocks, see Data Analysis for more info) had to be met for subjects to move on to the generalization phase.

3.2.5 Generalization Phase

In the generalization phase, photos of new individuals were inserted among the previously seen training trials. Twenty percent of trials were generalization trials. Facial stimuli for generalization trials were randomly selected from a stimulus set consisting of four females (five views of each) and four males (five views of each) from NIH, for a total of 40 portraits. During the generalization phase, non-differential reinforcement was provided on 50% of the generalization trials. The performance criterion (≥ 88% on two consecutive 25-trial blocks) had to be met for subjects to move on to the transfer test.

3.2.6 Sex Discrimination - Transfer Test

Once performance criterion was met on the generalization phase, subjects transferred to an entirely new set of five familiar in-group individuals, five familiar out-group individuals and five unfamiliar individuals (10 views per individual). Each photograph was only presented once to each subject, for a total of 50 trials per condition across 150 test trials. Test trials (20%) were interspersed among previously seen trials (training and generalization trials made up 80% of trials). Subjects were never presented with images of themselves. Only correct choices for training and generalization trials were rewarded according to correctness whereas test trials were randomly rewarded with a probability of 0.50. Therefore, the novelty of the photographs was controlled for such that subjects had never before seen these individuals' photos in training sessions. This allowed us to examine any potential differences in performance as a function of familiarity with the individuals from day-to-day life while controlling for any familiarity with the individuals *from training*. Note that this is the strongest possible test one can give for immediate, spontaneous sex discrimination of conspecific faces; each stimulus is presented only once so that subjects cannot learn to associate specific stimuli with specific responses.

3.2.7 Data Analysis

I assessed individual performances by means of binomial tests. For the training and generalization phases, the subjects' training should lead to them choosing the correct stimulus classification stimulus (male or female) more often than the incorrect classification stimulus, so one-tailed binomial tests were used to evaluate training and generalization phases. For both phases, performance criterion was set at 22 out of 25 trials correct (≥ 88% correct or $p \leq 0.002$) on two consecutive 25-trial blocks. Because there were no directional predictions or expectations based on previous training, only two-tailed binomial tests were used to evaluate the subjects' performance on the transfer test. A two-way Mixed Design ANOVA was used to evaluate performance across conditions (in-group, out-group, unfamiliar) and sex (male and female).

3.3 Results

3.3.1 Training and Generalization

Capuchins met criterion (≥ 88% correct on two consecutive 25 trial blocks) in an average of 2,468 trials (range: 10-674). On the generalization trials, subjects met criterion in average of 2,914 trials (range: 35-328; see Figure 3.1 for more detail).

3.3.2 Sex Discrimination – Transfer Test

I assessed overall performance using a mixed design ANOVA with familiarity as the within-subjects variable and sex as the between-subject variable. Mauchly's test showed that sphericity was not violated ($p = 0.052$) and there was homogeneity of variance as assessed by the Levine's test for all levels of the repeated measures (in-group: $p = 0.612$; out-group: $p = 0.388$, unfamiliar: $p = 0.559$). There was no main effect of familiarity (ANOVA: $F_{2,24} = 0.435$, $p = 0.562$; Figure 3.2). Binomial Z-scores were used to analyze individual performance. Liam performed above chance (72%) on discriminating the sex of in-group members. Nala, Nkima, and Bias performed significantly above chance (66%, 66%, and 68%, respectively) on discriminating the sex of familiar out-group members (Figure 3.3). No other monkeys performed significantly above chance in any of the conditions.

3.3.3 Sex Difference

Overall, males and females performed equally well (or equally poorly) on the sex discrimination task (Mean percent correct: Males, χ + SE = 56.8 + 2.68; Females χ + SE = 55.96 + 1.48). There was no main effect of sex (ANOVA: $F_{1,12} = 0.090$, $p = 0.769$), however, the interaction between sex of the subject and familiarity approached significance ($F_{2,24} = 3.346$, $p = 0.052$). This effect appears to have been driven by the difference in performance on discrimination of in-group members. Males were better able to identify the sex of in-group members compared to females (Independent *t* test: $t_{12} = 2.186$, $p = 0.049$; Figure 3.4).

3.3.4 Reaction Time

I examined the latency to respond on the computerized MTS task. There was no overall effect of response time across the three conditions (ANOVA: $F_{1,12} = 0.903$, $p = 0.361$; In-group, χ + SE = 1.083 + 0.106; Out-group, χ + SE = 1.102 + 0.086; Unfamiliar, χ + SE = 1.282 + 0.209).

3.4 Discussion

The aim of the present study was to determine whether capuchin monkeys could discriminate the biologically relevant feature of sexual identity by categorizing two-dimensional stimuli of conspecifics' faces as either male or female. Additionally, I examined whether experience with individuals aided the monkeys' ability to discriminate sex. Overall, the capuchins in this study did not perform above chance on the sex discrimination task and no effect of familiarity was observed. Yet, on this individual level, four of the 14 subjects did perform above chance on discriminating the sex of familiar (either in-group or out-group) individuals. This is in line with previous research on chimpanzees that suggests that real-life exposure to individuals aids sex perception (de Waal and Pokorny, 2008).

Previous research suggests that larger sets of training exemplars are useful for the formation of identity concepts (Katz et al., 2002; Truppa et al., 2010). Although I trained the capuchins monkeys in this study on a total of 80 photographs of 14 different individuals (8 females and 6 males), a much larger training set than those employed in previous studies of sex discrimination, one limitation of the current study that I cannot ignore is that this is still a limited number of individuals for the training stimuli. Although researchers tend to focus on the number of novel photographs in these designs, I argue that number of individuals represented in those photographs is an important factor that should be considered in future studies.

Nonetheless, the current findings may be interpreted in several ways. First, it is possible that faces do not provide monkeys with enough information to discriminate the sexual identity of conspecifics. However, the distinctive facial dimorphism in *Cebus apella,* in which males have broader, shorter faces compared to females (Weston et al., 2004), indicates that faces do provide capuchins with enough information to visually discriminate sex. The positive results from four of the capuchins in this study also supports this possibility, as does previous research with rhesus macaques (Inoue et al., 2008). Of course, this does not imply that capuchins are actually paying attention to these visual cues.

Second, it is possible that capuchins may preferentially discriminate sex through alternative modes of communication. I know, for example, that in a related species, *Cebus capucinus*, food-associated calls differ between the sexes (Grois-Louis, 2006). However, direct evidence of the discrimination of these calls from playback experiments is lacking. Another mode of communication worth consideration is olfaction. Although the effects of sexual steroids on female odors have been demonstrated in NHPs and other mammals (Dixson, 1998), how conspecifics use olfactory cues to aid in sex determination is less clear. For capuchins in particular, there is no evidence that scent-marking behavior plays a role in reproductive communication. Although capuchins do urine wash (a behavior that consists of urinating onto the palms of the hands and the soles of feet and subsequently rubbing them together), there is no evidence that females perform this behavior more often when trying to attract males (i.e., when they are in estrous). In fact, some data show the opposite trend (Carosi, Heistermann, & Visalberghi, 1999), and the current data on urine washing in capuchin monkeys supports a thermoregulatory function (Fragaszy et al., 2004).

For capuchins, as with many primates, one of the most obvious signs of female receptivity is the female's behavior. Females use a varied behavioral repertoire to initiate and solicit sexual interactions from males (usually the alpha male of the group), including following the male, grimacing, raising the eyebrows, and displaying submissive-like postures usually accompanied by distinctive vocalizations (Janson, 1984). Thus, it is likely that behavior may provide important cues that aide the discrimination of sex, perhaps in concert with visual, vocal, or olfactory cues. This highlights a key point; none of these alternatives are mutually exclusive, and in fact, it is likely that capuchins incorporate multiple cues to classify the sex of conspecifics. One possible avenue for future research is to take a top-down approach to determine whether subjects can classify sex using multi-modal cues before systematically eliminating particular cues to evaluate each cue's role in the discrimination of sex.

3.5 References

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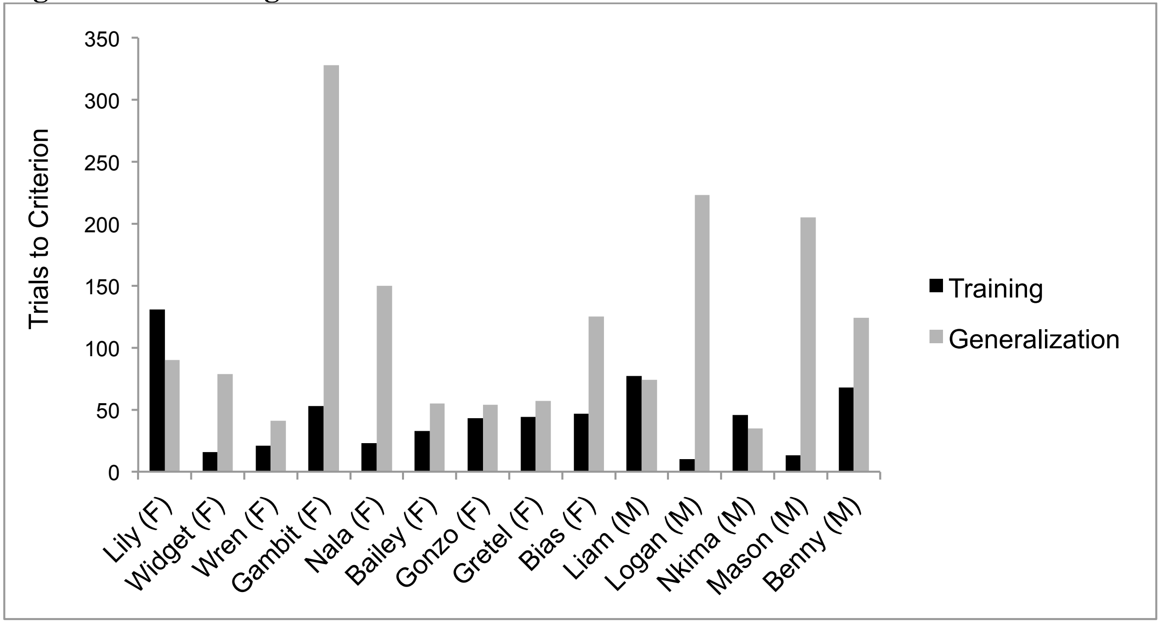
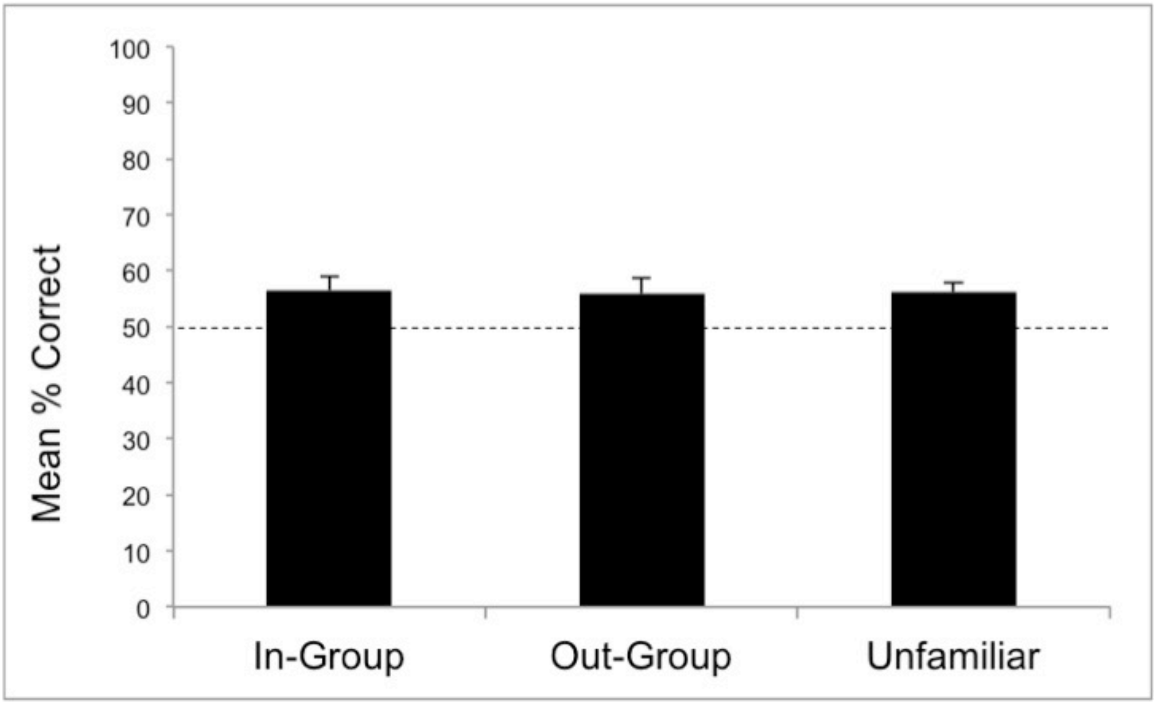
3.6 Figures

Figure 3.1. Training and Generalization Results



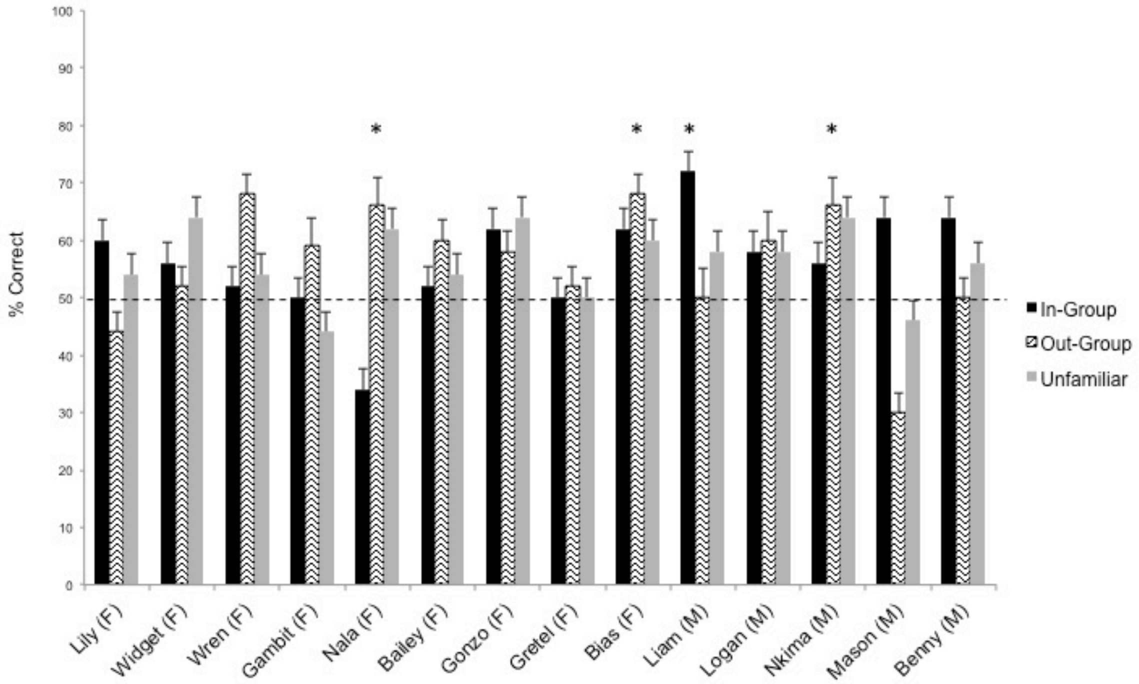
Number of trials it took subjects to reach criterion in *Training* (black) and *Generalization phase* (black). M and F after the monkey names indicate male or female sex of the individual.

Figure 3.2. Overall Performance on the Transfer Test



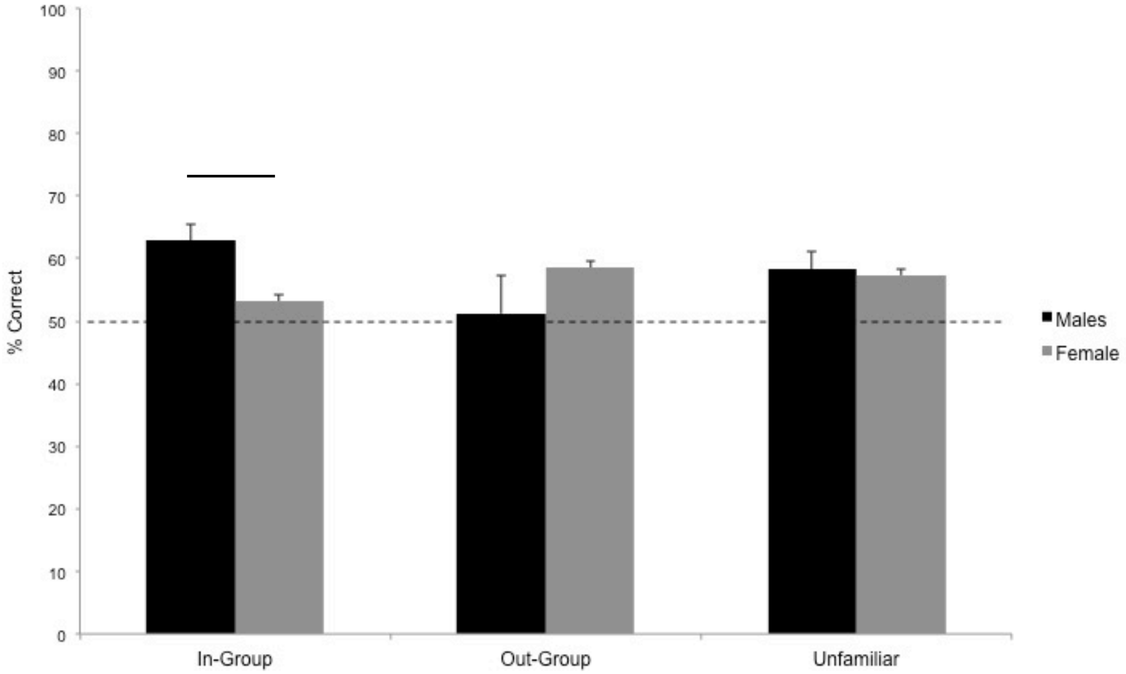
Black bars depict the mean percent correct on each of the three conditions (in-group, out-group, and unfamiliar). Horizontal dashed line represents chance level (50%) and error bars reflect SEM. There was no significant main effect of familiarity or sex of the subject.

Figure 3.3. Individual Performance on the Transfer Test



Bars depict the mean percent correct on each of the three conditions: In-group (black), out-group (hatched), and unfamiliar (grey). Horizontal dashed line represents chance level (50%) and error bars reflect SEM, * $p \leq 0.05$ (Binomial z-scores). M and F after the monkey names indicate male or female sex of the individual.

Figure 3.4. The Interaction Between Sex and Familiarity



Bars depict the mean percent correct on each of the three conditions for male subjects (black) and female subjects (grey). Horizontal dashed line represents chance level (50%) and error bars reflect SEM. Although there was no main effect of sex, the interaction between sex of the subject and familiarity approached significance ($F_{2,24} = 3.346$, $P = 0.052$). Males were better able to identify the sex of in-group members compared to females (Independent *t* test: $t_{12} = 2.186$, $P = 0.049$).

4 STUDY 3: DISCRIMINATION OF RANK BY CAPUCHIN MONKEYS

4.1 Introduction

The ability to classify relations between others into abstract categories allows individuals to more quickly identify social information, saving time and avoiding potentially dangerous interactions with higher-ranking group members. In particular, individuals may use this information to predict what others may do in social interactions, such as alliance formation and aggressive encounters, which gives them an edge during quickly-changing events. Thus, this socio-cognitive skill was likely advantageous in the evolution of group living species. Yet, knowledge of nonhuman primates' (NHPs) ability to recognize relationships between other individuals (i.e., third-party relationships) is limited, in part because it is difficult for us to determine what animals know about their environment and how that information is stored and organized in the mind.

Although there have been numerous studies looking at third-party relationships, much of the evidence in NHPs is indirect, and alternate explanations are difficult to rule out. For example, captive longtail macaques trained to choose pictures of one mother-offspring pair over pictures of two unrelated individuals later transferred this skill to choose novel mother-offspring pairs and pictures of the appropriate offspring when presented with a picture of its mother (Dasser, 1988). Although this may be considered evidence of recognition of third-party relationships, it is possible that the monkeys were able to perceive some visual similarity between the mother and its offspring and use this information, instead of knowledge of the relationship, to guide their responses. Likewise, a playback experiment on free-ranging vervet monkeys found that when monkeys heard the playback of an infant's scream, they selectively looked toward the infant's mother, often without any behavioral cues from the mother (Cheney & Seyfarth, 1980). Again, however, one cannot rule out the possibility that the monkeys merely perceived acoustic similarities between the calls of the mother and offspring, such as family specific acoustic cues acoustic cues, which have been reported in other species (Gouzoules & Gouzoules, 1990).

Other studies have provided evidence for a specific type of third party interaction, that is, the recognition of dominance relationships between others. Playback experiments show that female baboons have knowledge of the relative ranks of other females residing within their social group. Subjects responded more strongly when they heard a causally inconsistent sequence of calls, in which a higher-ranking female responded submissively to a lower-ranking female's grunt, as compared to casually consistent sequences (Cheney, Seyfarth, & Silk, 1995). Moreover, when dominant female baboons hear a playback of a relative in a dispute with another individual, they are more likely to displace a relative of their own relative's conflict partner (Cheney & Seyfarth, 1999). Observational studies have found that Japanese and bonnet macaques preferentially recruit opponents that are higher-ranking than both themselves and their opponent (Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999) and selectively aggress or reconcile towards the kin of individuals involved in aggressive interactions (Aureli, Cozzolino, Cordischi, & Scucchi, 1992; Judge, 1982). Likewise, white-faced capuchin monkeys preferentially solicit coalitionary partners that are dominant to their opponents and that they have better relationships with compared to their opponents (Perry, Barrett, & Manson, 2004).

Although the preponderance of evidence from the aforementioned studies strongly implies that these animals have the ability to recognize dominance relationships, it is difficult to rule out that these patterns are due to associative learning of each individual relationship drawn from their life-long experience with these individuals. Therefore, controlled experimental laboratory studies are needed to provide stronger evidence of primates' ability to garner information about the dominance relationships of unfamiliar conspecifics, a situation in which associative learning based on previous experience can be ruled out. Some studies do show that NHPs can learn these relationships through observation alone. Bovet and Washburn (2003) demonstrated that two rhesus macaques were able to choose the dominant individual from video clips of two unknown conspecifics. Crucially, the monkeys were able to generalize their performance not only to novel videos but also to novel social contexts. In a similar study, rhesus monkeys were presented with video clips comprised of artificial dominance interactions between unfamiliar conspecifics that were independent of their real-world rank, ruling out the possibility that physical differences that co-vary with rank (e.g., size or health) guided responses. Subjects were able to select the dominant individual from the videos and transfer this judgment to novel videos (Paxton, Basile, Adachi, Suzuki, Wilson, & Hampton, 2010). However, to my knowledge there are as yet no such data on New World monkeys. Understanding how this group behaves in relation to Old World monkeys is needed to understand the evolutionary trajectory of the behavior.

One area that has not been well studied is whether knowledge of such third–party relationships extends beyond the boundaries of the group. The research discussed above supports the notion that NHPs have knowledge of third-party relationships within their own social group and are able to learn these discriminations by through social observation. While it is clear that the recognition of relationships within one's own social group might benefit individuals, in some cases the ability to recognize relationships in neighboring groups might also be a fitness advantage. Capuchin monkeys, for instance, compete for food and mates with neighboring groups and regularly interact with neighbors during inter-group encounters, so it should be in individuals' best interests to recognize relationships (e.g., dominance rank or coalitionary support networks) amongst individuals encountered in these often violent, and potentially lethal, interactions (Defler, 1982; Di Bitetti, 2001). Unfortunately experimental evidence of this is lacking in NHPs, in part because most captive NHPs are isolated from other social groups, and controlled studies of this type are difficult or impossible in wild-living primates.

Therefore, in this study, I examined whether capuchin monkeys demonstrated social knowledge of the relative ranks of individuals residing in not only their own social group (in-group), but also individuals residing in a neighboring group with whom they had visual and vocal access but did not physically interact (out-group) and completely unfamiliar individuals (unfamiliar). This latter category is important because particular physical traits may be related to behavioral traits, allowing for the possibility that animals attend to these physical cues in order to garner social information that may help predict what others may do. For instance, among primates within the same age class, body size has been linked to social rank (Cowlishaw & Dunbar, 1991). Moreover, recent evidence indicates that facial width to height ratio in both male and female capuchin monkeys is associated with alpha status and the personality dimension 'Assertiveness' (Lefevre, Wilson, Morton, Brosnan, Paukner, & Bates, 2014), indicating that it is at least possible that capuchin monkeys are able to deduce relative rank due entirely to anatomical features. If so, they should be able to identify relative rank from unfamiliar, as well as familiar, faces.

Using a unique approach to the study of dominance recognition, I employed a serial chaining task (Terrace, 1983) to examine whether monkeys were better able to learn 3-items lists in which the order of the visual stimuli was either congruent with the dominance hierarchy of the group of monkeys being tested or incongruent with the dominance hierarchy. These visual stimuli included conspecific faces of in-group members, out-group members, and unfamiliar individuals. Capuchins can identify faces (Talbot, Leverett, & Brosnan, *in review*), so this paradigm should allow them to display their recognition of dominance if they do indeed have it. Given the previous observational evidence supporting the recognition of dominance in the genus, *Cebus* (Perry et al., 2004), I hypothesized that capuchin monkeys have knowledge of the relative ranks of other individuals. Specifically, I predicted that capuchins would perform better at sequencing lists in which the order was consistent with the dominance hierarchy (*congruent* condition) than when it was inconsistent with the hierarchy (*incongruent* condition). I did not have specific predictions for the influence of familiarity on their performance. If monkeys demonstrate knowledge of the relative social rank of conspecifics, then I expect that a familiarity effect could manifest in one of three ways in the *congruent* condition. If direct individual interactions (i.e., tactile or olfactory) aid the formation of a dominance concept, then the monkeys should perform better on the in-group category than either of the other two categories. If less direct individual interactions (i.e., visual or vocal) are more important, the monkeys should perform better on the familiar categories (in-group and out-group) than the unfamiliar category. If both are required, the monkeys should exhibit a graded effect in which they perform best in on their in-group members, less well on individuals living in their neighboring group (with whom they are able to observe but do not physically interact) and poorly on completely unfamiliar monkeys. Finally, if monkeys rely on facial features to deduce relative social rank, then they will perform similarly well for all three conditions (in-group, out-group, and unfamiliar).

4.2 Methods

4.2.1 Subjects and Housing

Subjects included eight mother-reared capuchin monkeys (3 adult males, 5 adult females) housed in three social groups (Groups 1, 2, and 3) at the Language Research Center (LRC), Georgia State University. The capuchins housed at the LRC are an excellent population for this study because there are multiple long term, mixed sex social groups that have both visual and vocal access with at least one other social group. Thus, they are socially competent monkeys living in species appropriate conditions that have at least the possibility of being aware of social relationships outside of their own group. Group 1 consisted of 1 adult male and 4 adult females; Group 2 consisted of 4 adult males and 2 females; Group 3 consisted of 2 adult males and 8 adult females. Two males, Liam and Logan, in Group 2 had recently been separated from their group to minimize fighting among the four similarly aged males, but still had mesh contact with the rest of Group 2 and still had some direct interactions with the females. These two monkeys were also tested but due to this change in their social context, were considered separately.

All three social groups had indoor/outdoor access and environmental enrichment (climbing structures, ropes, and other toys). From their outdoor areas, each monkey has vocal and visual access to members of at least one neighboring group. Indoors, each monkey can hear other groups, although cannot see them. At no time were subjects deprived of food or water. All subjects had ad libitum access to water, including during cognitive and behavioral testing, and received a diet consisting of primate chow, fruits, and vegetables. Subjects' participation in this study was entirely voluntarily and there were no negative consequences for declining to do so at any time. All subjects had previous training with a variety of cognitive tasks using the computerized joystick testing apparatus including those that employed face stimuli. 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).

4.2.2 Stimuli

In the pilot study, arbitrary stimuli were used. I chose three categories of images that the subjects have been exposed to in their environment: birds, cars, and flowers. Three images of each of these categories were presented, for a total of nine images. Testing included face stimuli, which consisted of high quality digital color photos taken from a variety of viewpoints. Photos included 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 only include the head, face and neck. The background of the photos was homogenized by filling in the area around the face with solid white. Brightness and contrast were standardized to control for differences in lighting. Presentation size of the photos was 16 cm by 16 cm with a resolution of 300 dots per inch.

The individuals represented in the face stimuli varied based on how familiar they were to the subject: in-group, out-group and unfamiliar. The in-group and out-group stimuli represented capuchins from Groups 1, 2, and 3 housed at the LRC. In-group stimuli included photos of individuals within the subjects' own social group with whom they had close physical, visual and vocal access. Out-group stimuli included photos of individuals from the subjects' neighboring group with whom they had visual and vocal access, but no physical contact. Unfamiliar stimuli included photos of conspecifics that subjects had never before seen. These photos were obtained from St. Andrews University's Living Links Center in Edinburgh, Scotland.

4.2.3 Apparatus

Stimuli were presented on a computer that included a modified joystick and pellet dispenser mounted on a movable audiovisual cart that, at the beginning of the testing session, was placed approximately 30 cm in front of each individual testing chamber, with the monitor directly in front of the monkey. No experimenter was present throughout the training and test sessions (except when setting up and taking down the computer apparatus). Testing chambers had a clear Lexan front panel for easy viewing of the computer monitor. Subjects were previously trained to manipulate a joystick that is inserted through an opening on the Lexan panel (Evans, Beran, Chan, Klein, & Menzel, 2008).

4.2.4 Simultaneous Chaining Paradigm

The paradigm I used, the simultaneous chaining paradigm (SCP), was developed in previous research on serial learning in nonverbal organisms (Terrace, 1983). SCP is based on chaining theory, which assumes that animals learn sequences based on particular stimuli becoming associated with particular responses (Ebbinghaus, 1885). Specifically, the idea is that complex cognitive behaviors can be broken down into simpler, discrete units, each of which represents on stimulus-response association. Therefore, by studying these discrete units, one can more carefully study the complex behavior with an understanding of what features are important in its manifestation in the animal. Although SCP has traditionally been useful in exploring human serial memory (e.g., Chase & Ericsson, 1981; Ebbinghaus, 1885; Eichenbaum, 1999), the experiments employing SCP have provided opportunities for investigating a wide range of serially organized cognitive phenomena in both humans and animals that are beyond the scope of traditional chaining theory, including numerical quantities (Brannon & Terrace, 2002), timing (Church, 2002), short term memory (Wright, 2002), concept formation (Wasserman, Fagot, & Young, 2001) and ordinal position of list items (Chen, Swartz, & Terrace, 1997; Terrace, Son, & Brannon, 2003).

The SCP differs from traditional chaining paradigms by presenting *n* list items simultaneously. Additionally, the spatial location of the list items changes randomly from trial to trial so that the subject cannot learn responses as a fixed sequence of motor responses. The subject's task is to respond to each items in the sequence defined by the experimenter, yet the subject is not given any differential feedback concerning the correctness of the sequence it produces until it completes the entire sequence. Thus, this paradigm has great potential in examining social information or images that may be encoded analogically (Kosslyn, 1980; Lashley, 1951) or spatially (Gallistel, 1992), such as a monkey's ability to judge the relative social rank of other monkeys in their group (Harcourt & de Waal, 1992). To my knowledge, however, this study is the first to do so.

4.2.5 Procedure

For each session, subjects were called in from their social groups to participate voluntarily. To ensure that subjects were attentive to and viewed the trial, each trial was initiated by moving the cursor into contact with a colored grey square presented in the center of the screen, following which the grey box disappeared. Subsequently, three face stimuli appeared in 3 out of 9 randomly selected locations. Thus, there were 60,480 [9!/ (9-3)!] possible configurations of list items on each trial. Once the monkey moved its cursor into contact with one of the three stimuli, it disappeared. Feedback was provided only after all three stimuli had been selected. In this way, subjects learned the correct order of the three-item list by trial and error. Subjects had a 1 out 3 chance of correctly choosing the correct first stimulus, 1 out of 2 chance of choosing the second, and 1 out 1 chance of choosing the third. Therefore, subjects had a (1/3)*(1/2)*(1/1), or 1/6 (~17%) chance of getting any one trial correct. Correct responses were automatically rewarded with a food reinforcer (3 banana-flavored pellets) and followed by an inter-trial interval (ITI) of 1 s. Incorrect responses were not rewarded and were followed by an ITI of 5 s. During the ITI, the screen remained white. There was no time limit for each trial. Subjects worked at their own pace during 4-hour sessions until they reached training criterion (≥ 80% correct on two consecutive 25-trial blocks) or completed up to 10,000 trials.

4.2.6 Assessing Rank

Dominance relationships were primarily measured by caretaker/researcher ratings. It is extremely difficult to rank some individuals, particularly in the middle of the hierarchy, due to the shallowness of the hierarchy (Fragaszy et al., 2004; Parr et al., 2004), so rather than linear rank I used categories. Monkeys from both research facilities were classified into rank categories as “high” “medium” or “low”.

4.2.7 Pilot Training: Clip Art

During training, 3 lists of arbitrary images were used in order to determine how many trials these monkeys typically required to learn the task when the stimuli have no inferred order. Each list consisted of three images from one of the following categories: birds, cars, and flowers. Within each list, the category of images remained consistent. All three lists (*Clip1*, *Clip2*, and *Clip3*) were tested on their own until subjects met criterion, which was set at 20 out of 25 trials correct (≥ 80% correct) on two consecutive 25-trials blocks. The order in which the lists were presented to each group was counterbalanced such that Group 1 was presented with birds, cars, and then flowers; Group 2 was presented with car, flowers and then birds; Group 3 was presented with flowers, birds, and then cars. Once monkeys achieved criterion on each list independently, they were tested on all three lists concurrently (*All Clip*) and the presentations of the lists were randomized. Once subjects passed criterion (≥ 80% correct on two consecutive 25-trial blocks) on all three lists concurrently, they moved onto the Transfer Test. I used the pilot data to determine approximately how many trials the subjects took to acquire the task with arbitrary stimuli. I then used this approximation to determine the number of trials to run on each condition during testing.

4.2.8 Transfer Test

Testing consisted of two conditions: congruent and incongruent. In each condition, subjects were presented with three lists, each of which included three individuals who were either in their own social group (in-group), neighboring social group (out-group), or were unfamiliar to the subjects (unfamiliar). Subjects completed 10,000 trials of each condition. In the congruent condition, the order of the faces was consistent with the dominance hierarchy of each group. In the incongruent condition, the order of the faces was inconsistent with the dominance hierarchy of each group. Trials within a session were intermixed with in-group, out-group, and unfamiliar, but I never mixed different groups within the same trial. The order in which subjects experienced the conditions was counterbalanced across subjects. Subjects were tested multiple times per week until they finished 10,000 trials.

4.2.9 Data Analysis

For each session, the software automatically recorded the subject, date, trial number, names of each stimulus that was presented, the order in which stimuli were selected, and whether the order in which each stimulus was selected was correct/incorrect. The primary dependent variable of interest was the response (correct/incorrect) and the independent variables were the *Condition* and *Group*. I first evaluated performance on the two conditions (*congruent* and *incongruent*) collapsed across *Group* using a Mann-Whitney test. Next, I ran a two-way mixed design ANOVA with one within-subjects variable, *Group* (in-group, out-group, and unfamiliar), and one between-subjects variable, *Condition* (congruent and incongruent). To control for the number of trials in each category, I only analyzed the first 3,000 trials on each list (in-group, out-group, and unfamiliar), in each condition (congruent/incongruent). Secondly, because three of the subjects completed both conditions, I ran a factorial-repeated measures ANOVA on the first 3,000 trials on each list (in-group, out-group, and unfamiliar), in each condition (congruent/incongruent) for the three subjects who completed both conditions.

4.3 Results

4.3.1 Pilot Training

All eight capuchins met criterion (≥ 80% correct on two consecutive 25-trial blocks) in pilot training in an average of 6,803 trials. Subjects met criterion on the first list in an average of 3, 654 trials (range: 1,485-7,144), the second list in an average of 2,272 trials (range: 531-3,749), the third in an average of 667 trials (range: 99-2,028) and all three lists in an average of 210 trials (range: 44-618; see Figure 4.1 for more detail). To examine acquisition speed across the four training phases (*Clip1*, *Clip2*, *Clip3*, and *All Clip*), I used repeated measures ANOVA.

Mauchly's test indicated that the assumption of sphericity was met ($p = 0.136$). There was a significant difference in acquisition speed between the four training phases (ANOVA, ME of phase: $F_{3,21} = 19.333, p < 0.001$). Capuchins performed significantly better on the second list introduced compared to the first (comparing *Clip1* vs. *Clip2*: $F_{1,7} = 6.222, p = 0.041$), the third list compared to the second (comparing *Clip2* vs. *Clip3*: $F_{1,7} = 14.068, p = 0.007$), and the fourth compared to the third (comparing *Clip3* vs. *All Clip*: $F_{1,7} = 3.823, p = 0.091$). These results were consistent at the individual level as well (Figure 4.1).

4.3.2 Transfer Test

Six of the eight capuchins that passed the pilot training completed the first condition. The condition that subjects first experienced was counterbalanced across subjects. Therefore, three subjects completed the *congruent* condition and three subjects completed the *incongruent* condition. To test my prediction that capuchins would perform better on lists in which the order was consistent with the dominance hierarchy (*congruent* condition) compared to when it was inconsistent with the hierarchy (*incongruent* condition), I used a Mann-Whitney test to compare performance on the two conditions. Performance on the *congruent* condition did not significantly differ from the *incongruent* condition ($U = 4$, $z = -0.218$ $P = 1.0$; Figure 4.2).

To examine performance as function of *Condition* and *Group*, I ran a mixed-design ANOVA with *Condition* as the between-subjects factor and *Group* as the within-subjects factor. Mauchly's test showed that sphericity was not violated ($P = 0.996$) and there was homogeneity of variance as assessed by the Levine's test for all levels of the repeated measures (in-group: $p = 0.806$; out-group: $p = 0.243$, unfamiliar: $p = 0.093$). There was no main effect of condition (ANOVA: $F_{1,4} = 0.001, p = 0.980$) or group (ANOVA: $F_{1,4} = 2.340, p = 0.352$; see Figure 4.3

for individual data). Finally, there was no interaction between the condition and group (ANOVA: $F_{2,8} = 1.183$, $p = 0.355$).

Due to the apparent individual differences in performance on the task, I decided to examine the data as a within-subjects design for those individuals who completed both conditions (N = 3). Mauchly's test indicated that the assumption of sphericity was violated for the main effect of condition ($p < 0.001$), but not group ($p = 0.487$) or the interaction between group and condition ($p = 0.509$). Therefore, I report the Greenhouse-Geisser corrected degrees of freedom for the main effect of condition. There was no main effect of *Condition* (ANOVA: $F_{1,2} = 1.155$, $p = 0.395$) or *Group* (ANOVA: $F_{2,4} = 0.091$, $p = 0.915$), nor was there an interaction between the two (ANOVA: $F_{2,4} = 0.780$, $p = 0.517$; see Figure 4.4 for individual data).

4.4 Discussion

The aim of the present study was to determine whether capuchin monkeys could apply a social concept of dominance to a list-learning task utilizing photos of conspecifics faces in which the order of the list was either congruent or incongruent with the dominance hierarchy. Furthermore, to examine what type of experience or interactions may be necessary to acquire knowledge about the relative rank of others, I examined capuchins' performance on the list learning task using photos of individuals living in one's own social group with whom they directly interacted, individuals living in a neighboring group with whom they were able to observe but did not physically interact, and completely unfamiliar individuals.

In contract to my prediction, capuchins did not perform better on the *congruent* condition, in which the order of the list was consistent, as opposed to the *incongruent* condition, in which the order of the list was inconsistent with the dominance hierarchy. Moreover, regardless of whether a between-subjects design (M=6) or a within-subjects design (N=3) was used, there was no main effect of either *Condition* or *Group*. Still, all of the eight monkeys who completed pilot training improved their performance on arbitrary lists of stimuli over the course of training (Figure 4.1), showing evidence of learning the object of the task.

These results may be interpreted in a number of ways. First, despite the potential of the SCP to examine concept formation in the social domain, the design may simply be too complicated for monkeys without extensive experience with this type of task. The subjects required approximately 4,000 trials to reach criterion on the task employing arbitrary stimuli the first time that they experienced the task (they improved on later stimulus sets, but still required 600+ trials to learn the new order). Thus, the lack of expertise in the monkeys may have inhibited their ability to apply real-world knowledge to such an unfamiliar task. Another potential flaw in the design of this study was that the subjects had no training on social stimuli within the context of this task (all training trials involved images of birds, cards, and flowers), and previous research indicates that the ability to form an identity concept increases with the number of training stimuli used (Katz et al., 2002; Truppa et al., 2010). However, increasing the number of training exemplars of social stimuli would have been logistically extremely difficult. Our social groups are very small (five to 10 individuals) so that it was not possible to train them on one set of stimuli and then test them on another (that requires, at minimum seven individuals, and assumes that it is possible to create two stimulus sets of high-medium-low ranked individuals from those six individual, which is highly unlikely). Nonetheless, future research should take this into consideration. For example, it may be possible to acquire multiple stimulus sets from animals that live in larger social groups or have moved among different groups.

Alternately, it may be possible to train them on stimuli from unfamiliar individuals, which at least exposes them to social stimuli, albeit not familiar ones.

The other obvious possibility is that capuchin monkeys do not understand rank at the conceptual level. I believe, however, that this is less likely. In the wild, capuchin monkeys preferentially solicit coalitionary partners that are dominant to their opponents and that they have better relationships with compared to their opponents (Perry et al., 2004), suggesting knowledge of third-party dominance relations. Moreover, from experimental work, I know that capuchins are capable of forming concepts in the physical domain (e.g., Spinozzi, Lubrano, & Truppa 2004) and, within the social domain, research indicates that are able to form concepts on identity (Talbot et al., *in review*) and group membership (Pokorny & de Waal, 2009). Therefore while it is possible that they lack an understanding of the concept of dominance, I find it unlikely.

Our data show that performance on the simultaneous chaining task varied widely across individuals. I hope to further examine individual performances using a within-subjects design, and are currently in the process of testing all of the subjects on the alternate condition (i.e., the one that they have not already completed). As in humans, I expect to observe a wide range of individual variation in the socio-cognitive skills of NHPs. If this is not successful, however, I recommend (at least) two future courses of action. First, future studies should explore the dominance concept in capuchins using an alternate methodology that may be simpler for the animals to understand. This would not be the first time in which animals perform very differently when the same question is asked in different ways (Horner, Carter, Suchak, & de Waal, 2011; Jenson, Call, & Tomasello, 2007; Proctor, Williamson, de Waal, & Brosnan, 2013; Silk, Brosnan, Vonk, Henrich, Povinelli, Richardson, … & Schapiro, 2005). Second, future work should consider examining individual variation and other socio-behavioral traits that may covary with these skills, such as the personality or social status of the individual. Although I have analyzed the data from six individuals, which is larger than the sample used in other studies of social cognition, it is still quite a small number from which to draw firm conclusions.

4.5 References

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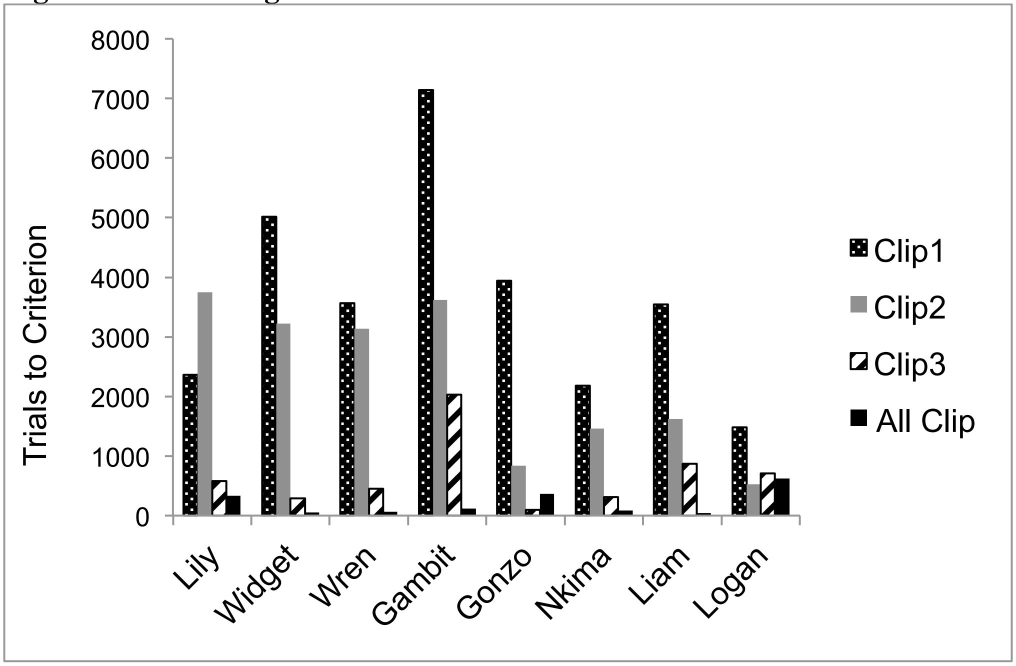
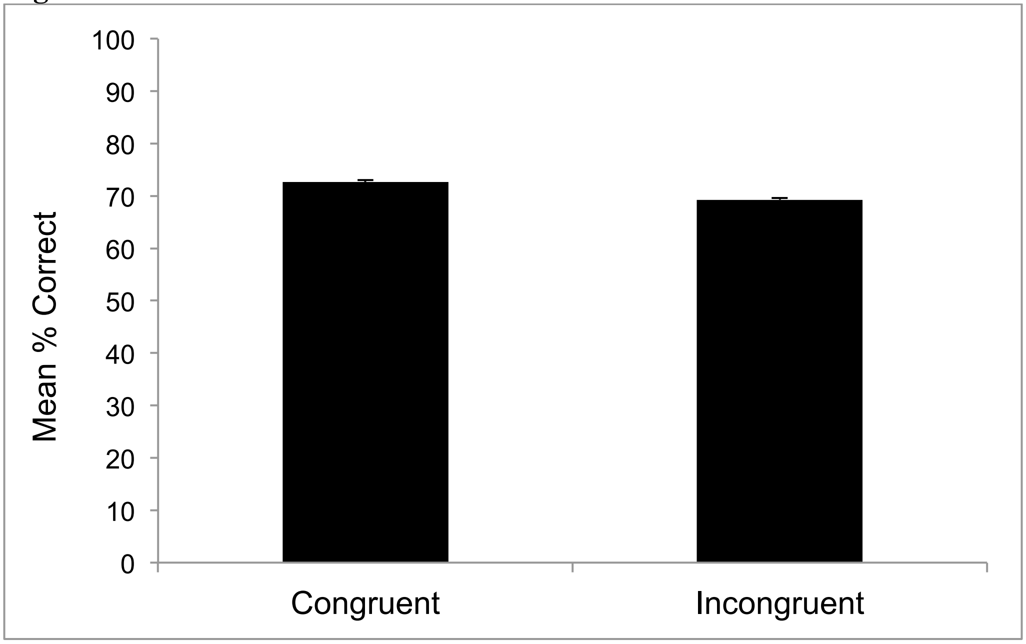
4.6 Figures

Figure 4.1. Training Results



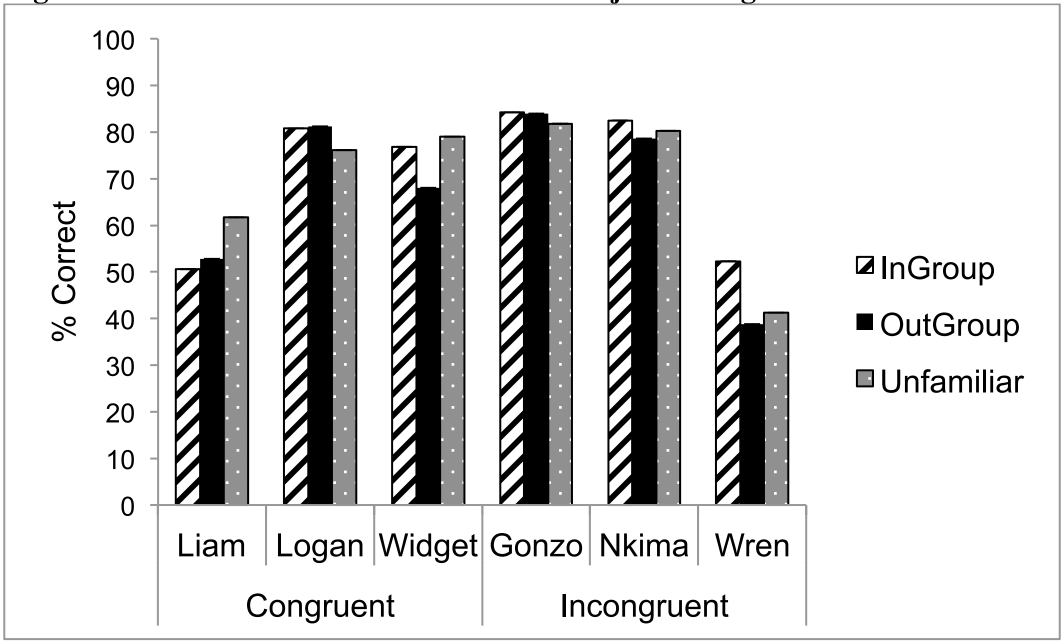
Number of trials it took subjects to reach criterion in each phase of training including the first list of arbitrary stimuli introduced, *Clip1* (black with white dots), the second list, *Clip2* (grey), the third list, *Clip3* (black stripes), and all three lists combined, *All Clip* (black).

Figure 4.2. Overall Performance Across Conditions



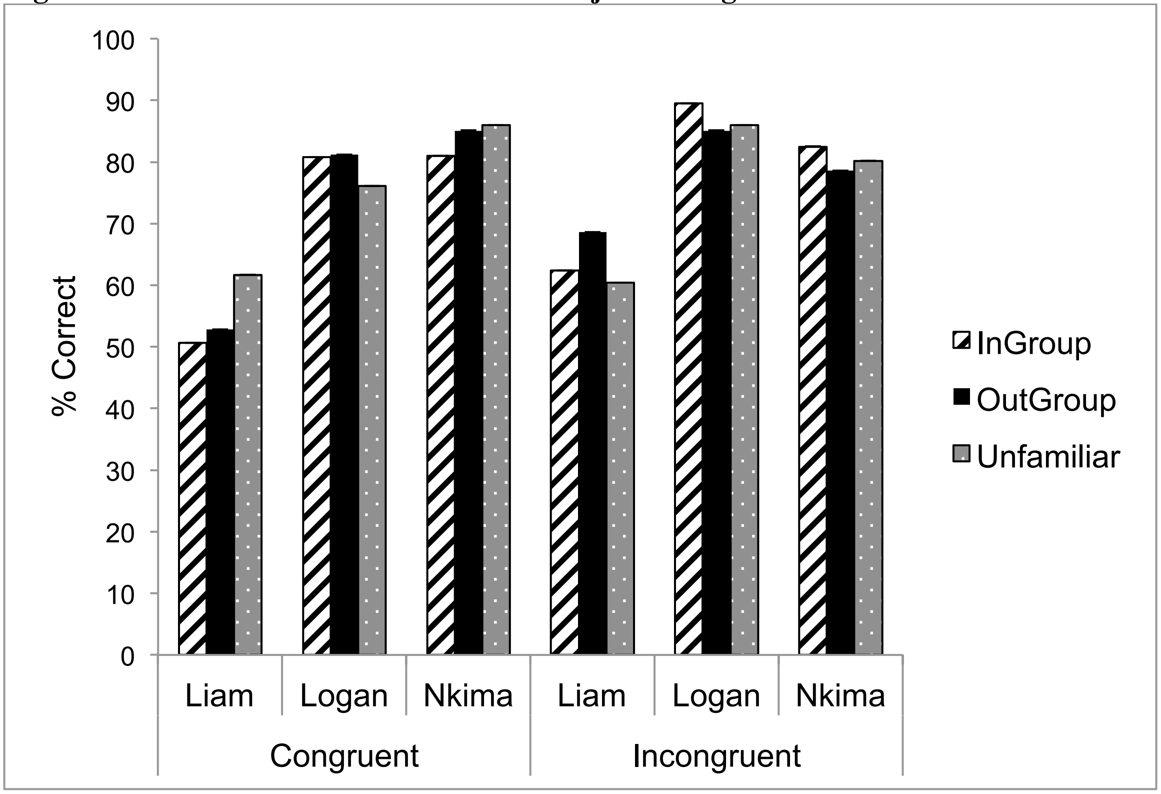
Black bars depict the mean percent correct on each of the two conditions, *congruent* and *incongruent*. Performance on the *congruent* condition did not significantly differ from the *incongruent* condition ($U = 4$, $z = -0.218$ $P = 1.0$). Error bars reflect SEM.

Figure 4.3. Individual Data for Between-Subjects Design



Bars represent percent correct for each of the six individuals for each of the Groups, in-group (hatched), out-group (black), and unfamiliar (grey polka dots). Condition (*congruent*/*incongruent*) is indicated along the x-axis.

Figure 4.4. Individual Data for Within-Subjects Design



Three subjects completed both conditions. *Condition* and *subject* are indicated along the x-axis. Bars represent percent correct for each of the groups, in-group (hatched), out-group (black), and unfamiliar (grey polka dots).

5 CONCLUSIONS

5.1 Summary of results

A key defining characteristic of the human species is that, compared to almost all other animals, human brains are much larger as a percentage of our body weight. Thus, one of the most pressing questions regarding the evolutionary history of the human species is what were the selective forces that lead to the evolution of our large brains? Several scientists have hypothesized that large brains and human ‘intelligence’ arose in response to the increased cognitive demands of social life (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966). This hypothesis suggests that as social group size increases, the complexity of social relationships and the problems that arise in tandem with this also increase, which may have placed important selective forces, particularly in the social domain, on the evolution of primate cognition. Studying the behavioral capabilities of extant nonhuman primates (NHPs) allows us to study the evolutionary function of human intelligence within a comparative framework.

Although many of the problems confronting NHPs under natural conditions derive from social interactions with conspecifics, NHP intelligence has traditionally been examined using biologically arbitrary objects or images. As a result, comparatively little is known about the knowledge that primates acquire from social interactions. Moreover, the majority of what I do know about NHP social knowledge comes from behaviors observed in the wild (e.g., Cheney & Seyfarth, 1990). Yet animals routinely exhibit seemingly complex behavior without actually using complex cognition to carry out those behaviors. For example, when an ant removes the dead carcasses of conspecifics from its nest, it functions to rid the nest of bacteria. But ants do not recognize the relation between dead carcasses and bacteria, they simply respond to the oleic acid they perceive emanating from the dead carcasses (Wilson, 1971). Therefore, while ethological studies are important to the study of primate social intelligence, especially to help identify situations in which complex cognition might play a role, controlled laboratory studies that manipulate the exposure to stimuli are essential to studying what NHPs know about conspecifics and how they acquire such information. In particular I need studies that systematically evaluate NHPs' performance using social stimuli, like photos of familiar conspecifics.

Thus, in this dissertation, I explored NHP social knowledge through controlled experimental studies employing photographic social stimuli. First, and perhaps most importantly, group living requires that primates must recognize individual groupmates. Along with general cognitive processes of learning and memory, this skill enables individuals to remember those with whom they have interacted and, over time, form relationships with them. Faces, in particular, are a highly salient class of social stimuli (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991), and several species of NHP are able to use visual cues present in the face to discriminate individuals from photographs, indicating that they actually recognize the individuals. However, much of the experimental research has focused on limited number of species, mainly chimpanzees and macaques, and typically employed stimuli representing unfamiliar individuals (Parr, 2011). Thus, one aim of Study 1 was to investigate the face discrimination skills in a less well-studied species, the capuchin monkey. Because previous studies in humans and apes have found differences in performance based on familiarity such that performance increases with familiarity, a second aim of Study 1 was to objectively examine the effect of familiarity on face discriminations in this species. Using a matching-to-sample procedure, I tested capuchins' ability to match photos of conspecifics faces of familiar individual living in one's own social group (in-group), familiar individuals living in a neighboring group (out-group), and completely unfamiliar individuals (unfamiliar). I hypothesized that if capuchins utilized their knowledge of familiar individuals to help them discriminate photos, then performance on the task would increase with the familiarity of the individual. Capuchins were indeed better able to individuate familiar in-group members and out-group members compared to unfamiliar individuals, suggesting that familiarity impacts capuchins' ability to discriminate conspecific faces, as it does 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 neighboring groups that one interacts with regularly. This would be a fitness advantage for social species, like capuchins, which compete with neighboring groups over access to food and mates. It may be an advantage for males in particular, as they emigrate to neighboring groups when they reach maturity.

Beyond individual identity, acquiring visual information about conspecifics, such as sex, or reproductive status should be highly adaptive. However, little is known about whether NHPs extract other social information from faces, such as the individual's sex, which is fundamental to reproductive success. Previous research indicates that conspicuous sexual features may play an important role in the categorization of sex in NHPs (i.e., genital swellings in female chimpanzees). Yet unlike previously tested species (i.e., macaques and chimpanzees), many New World monkeys, including capuchin monkeys, do not show conspicuous sexual features, such as chromatic or morphological variations in specialized "sexual skin." Nonetheless, capuchins display facial dimorphism (Weston, Friday, Johnstone, & Schrenk, 2004), suggesting that they could at least in principle deduce the sex of an individual from facial morphology alone.

Therefore, in Study 2, I used a computerized dichotomous choice procedure to examine whether capuchin monkeys were able to categorize the sex of conspecific faces, and whether experience with or exposure to individuals aided their ability to do so. Overall, capuchins were not successful on the task and no effect of familiarity was observed; however, on the individual level, four of the subjects performed above chance when discriminating the sex of familiar (either in-group or out-group) individuals. Thus, although some individuals may be able to perceive sex from faces alone, it is likely that capuchins may naturally classify sex by incorporating multiple cues, not only involving physical features (i.e., odor or vocalizations), but also including secondary cues such as female's receptivity behavior.

One form that social complexity can take in primate society is that of triadic social interactions, or the relations between two other individuals. The ability to recognize relations between others (i.e., third-party relationships) enables individuals to quickly and safely identify social information, potentially increasing their social and reproductive advantage over others. However, much of the evidence for the recognition of third-party relationships in NHPs is indirect, and alternate explanations are difficult to rule out. In Study 3, I evaluated capuchins' ability to recognize a specific type of third party interaction, dominance relationships, using a list learning task (Terrace, 1983) in which the order of the visual stimuli was either congruent or incongruent with the dominance hierarchy of the group. Again, visual stimuli depicted the faces of in-group members, out-group members, and unfamiliar individuals. I expected that capuchins would demonstrate their knowledge of rank and perform better on *congruent* lists, in which the order of the list was consistent with the dominance hierarchy, as opposed to the *incongruent* lists. However, neither condition nor the degree of familiarity affected the overall performance of the capuchin monkeys. Because I observed a wide range of individual differences in my results, I hope to further examine individual performances using a within-subjects design with a larger sample.

5.2 **Implications**

5.2.1 Capuchins Recognize Familiar Faces

The results from Study 1 corroborate previous findings that capuchin monkeys are able to discriminate the faces of conspecifics (Pokorny & de Waal, 2009). These data further provide evidence of a familiarity effect on face perception in a New World primate species. The familiarity effect observed in this study suggests that capuchins were able to apply their real-life knowledge of individuals to an abstract computerized task. This hints at the possibility that capuchins may actually be connecting the individuals depicted in two-dimensional photographs with their three-dimensional counterparts. Despite the fact that many researchers frequently use two-dimensional images as experimental stimuli in place of real life objects to assess human and animal cognitive processes, surprisingly few studies have addressed the question of whether animals actually interpret the two-dimensional photographs as representations of real life three-dimensional objects (Morton, Brosnan, Prétôt, Buchanan-Smith, O'Sullivan, Stocker, D'Mello, & Wilson, 2016). Although the current study cannot discriminate the mode by which capuchins process pictures, I will nonetheless consider my results within this context.

Fagot, Martin-Malivel, & 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. In the second mode, termed the *confusion* mode, pictures and objects are processed in exactly the same way and are not distinguishable from each other. 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 Fragaszy (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.

The observed familiarity effect 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 they had, I would have expected the monkeys to perform equally well, or equally poorly, across all three degrees of familiarity. The *confusion* mode in which pictures and objects are processed in exactly the same way and are not distinguishable from each other has been observed in other primate species. For example, rhesus macaques display reactions such as fear, threat, or play when presented with colored slides of conspecifics engaging in social activities (Sacket, 1966), suggesting that they equivocate the photos with actual conspecifics. It is possible that capuchins process photos in the *complex equivalence processing* submode, demonstrating global knowledge of the three-dimensional form, what some researcher's refer to as "representational insight" (e.g., Aust and Huber, 2006, 2010), 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 view-point independent representations of familiar faces.

Considering a broader comparative perspective, previous studies found evidence of a familiarity effect in the perception of faces in apes (*Homo sapiens*: Bruce, Henderson, Greenwood, Hancock, Burton, & Miller, 1999; Bruce, Henderson, Newman, & Burton, 2001; Hill & Bruce 1996; *Pan troglodytes*: Parr, Siebert, & Traubert, 2011; *Pongo spp.*: Talbot, Mayo, Stoinski, & Brosnan, 2015) but not crested macaques (Micheletta, Whitehouse, Parr, Marshman, Engelhardt, & Waller, 2015), an Old World primate, which implied that this effect reflected a derived trait of the face processing system, shared among humans and apes, but not the rest of the primate order. However, given the current results, this is unlikely. The lineages of Hominoids (humans and apes) and Old World monkeys diverged approximately 25 and 30 million years ago, whereas New World monkeys diverged about 35 million years ago. Thus, the fact that this effect has been observed in New World monkeys, but not Old World monkeys, suggests one of three possibilities. Through natural selection, traits tend to be preserved in all of the descendants of a common ancestor, unless there were strong selective forces working against the trait. Thus, the first possibility is that this trait was present in the common ancestor of Hominoids and New World primates, but was subsequently selected against in Old World primates. However, this seems unlikely given the presumed benefit of this ability. A second possibility is that the familiarity effect is a convergent trait of the face processing system, affected by social organization, with species that live in larger, more complex, social groups exhibiting greater nuances in face perception. However, social group size cannot account for this as crested macaques live in large multi-male, multi-female groups of up to 100 individuals (Kinnaird & O'Brien, 2000), whereas tufted capuchins groups are significantly smaller, ranging in the teens to low twenties in size (Defler, 1982). Moreover, orangutans, a primarily solitary species, also exhibit the effect (Talbot et al., 2015).

A third possibility is that differences in methodology may have impacted results. For instance, in Micheletta et al. (2015), macaques were presented with a different number of familiar (N=24) and unfamiliar individuals (N=4), and tested with novel photos of the same individuals observed in training. In contrast, the current study controlled for the number of individuals in each category of familiarity and used different individuals in training than in testing. By training monkeys on a different set of individuals, I controlled for novelty effects on both the photos used as stimuli and the novelty of the individuals represented in those stimuli.

Second, in Micheletta et al. (2015), ‘novel’ test photos were repeatedly presented until subjects reached criterion (75%, chance = 50%) or refused continued participation in the task. Only one out of the three subjects reached criterion with familiar and unfamiliar trials. Our set of test photos, of novel individuals, was presented under extinctive conditions: each individual was only presented as the sample once. 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, and where learning cannot occur with regards to associating specific stimuli with specific responses. This allowed us to examine any potential differences in spontaneous discriminations as a function of familiarity with the *individuals*, not test stimuli. Thus, the results obtained from the current study represent emergent behavioral patterns that go beyond those employed in operant and respondent conditioning. Overall, my results support the hypothesis that the face processing abilities in nonhuman primates (NHP) and humans share a common evolutionary route.

5.2.2 Social Inferences in Capuchins

Despite the evidence that capuchins individually discriminated the faces of conspecifics in Study 1, the results from Studies 2 and 3 seem to suggest that capuchins are not using the visual information present in facial stimuli to make social inferences.

Despite the fact that tufted capuchin monkeys do not display conspicuous sexual features, such as chromatic or morphological variations in specialized "sexual skin" that may aide the recognition of conspecific sex, they do exhibit facial dimorphism (Weston et al., 2004). Therefore, it is plausible that they may be able to deduce the sex of conspecifics from facial morphology alone. Additionally, and not mutually exclusively, experience with or exposure to individuals during their daily interactions provides additional information (e.g., olfactory, tactile or behavioral) that aids sex perception (e.g., de Waal & Pokorny, 2008). Neither of these possibilities was supported by the data in the study as the capuchins, overall, did not perform above chance on the sex discrimination task, and no effect familiarity was observed.

One possible explanation for these results is that the test of sexual discrimination I used in this study was not appropriate. However, I think this is unlikely for several reasons. First, the same monkeys were able to individually discriminate photos of conspecific faces and did so better with familiar in-group and familiar out-group members, suggesting that the monkeys were able to extract some social information about conspecifics from visual cues present in the stimuli. Second, previous studies employing similar paradigms (even some with smaller training sets), have found positive results, albeit with some individual differences (Koba & Izuma, 2006; Ohshiba, 1995). Likewise, at the individual level, four of the monkeys in the study did show evidence of discriminating the sex of either in-group members or out-group members, with whom they were familiar. This is congruent with previous evidence in chimpanzees that indicates that real-life exposure to individuals aids sex perception (de Waal and Pokorny, 2008).

More likely is the possibility that capuchins discriminate sex through alternative, or multiple, modes of communication. Although there is no evidence that scent-marking behavior plays a role in reproductive communication in capuchins, the female's behavioral repertoire during receptivity may be a particularly conspicuous cue in this species that has a direct connection to reproductive fitness. Thus, future research should consider examining sex discrimination through the use of social stimuli that provide multiple cues, such as video recordings in which full-bodied images and behavior are displayed, before examining the role of individual cues in the discrimination of sex. I found no evidence that capuchin monkeys applied their knowledge of the dominance relations between in-group or out-group members to solve this task, nor was there evidence from unfamiliar individuals, which could have indicated that they were extracting this information from cues in the monkeys' faces rather than their previous knowledge of their relationships. However, the fact that there was no difference between the congruent and incongruent condition suggests that this was not the case. The lack of significant results may mean that capuchins cannot make these judgments about the dominance relationship between other individuals. In the wild, however, capuchin monkeys preferentially solicit coalitionary partners that are dominant to their opponents and with whom they have better relationships compared to their opponents (Perry, Barrett, & Manson, 2004). Furthermore, experimental works suggest capuchins are capable of forming concepts in the physical domain (e.g., Spinozzi, Lubrano, & Truppa, 2004), and possibly the social domain (Pokorny & de Waal, 2009; Talbot, Leverett, & Brosnan, *in review*). Thus, while it is possible capuchins are unable to recognize the dominance relations between others, I consider this unlikely.

Alternatively, these results may imply that the simultaneous chaining paradigm was too complicated for monkeys without extensive experience with this type of task. Because the capuchins tested in this study were largely naïve to this type of task, their ability to apply real-world knowledge to the task may have been limited. In particular, the fact that the subjects had no training on social stimuli within the context of this task may have also contributed to their performance on this task. Although increasing the number of training exemplars of social stimuli would have been logistically difficult, future studies should consider acquiring multiple stimulus sets from animals that live in larger social groups to utilize in training.

5.3 Future Directions

There are several extensions to this research that I am interested in pursing. Although many researchers use two-dimensional images as experimental stimuli (in place of real life objects) to assess human and animal cognitive and neural processes, surprisingly few studies have addressed the question of whether animals actually interpret the two-dimensional photographs as representations of real life three-dimensional objects and to what degree. Moreover, studies that examined object-picture correspondence have produced mixed results (e.g., Davenport & Rogers, 1971; Winner & Ettlinger, 1979). Although the question of picture-object correspondence has typically been approached through cross-modal matching (Malone, Tolan, & Rogers, 1980; Tolan, Rogers, & Malone, 1981) or categorization tasks (Itakura, 1994; Savage-Rumbaugh, Rumbaugh, Smith, & Lawson, 1980; Vauclair, 2002), Aust and Huber (2006, 2010) recently employed a paradigm, known as the *complementary information procedure* (CIP), to study this ability in pigeons. This paradigm has the potential to rule out transfer based on perceptual feature matching of stimuli. The underlying idea of this approach uses similar logic as Dasser's (1987) classic study in which rhesus macaques matched pictures of *different* body parts of the same familiar group members (see also de Waal & Pokorny, 2008). In this way, the sample image and the matching image do not contain the same perceptual information, but rather are complementary to one another. Thus, transfer cannot be based on any simple feature matching, but can only occur if the subject associates the individual parts of the real object. Studies examining picture-object correspondence and the underlying modes by which animals process pictures are necessary to validate the use of both social and non-social two-dimensional stimuli (Fagot et al., 2000).

The effect of familiarity on face discriminations in capuchin monkeys, taken with other evidence from the human literature, bolsters the notion that there may be qualitative differences in the face processing mechanisms of familiar versus unfamiliar faces. Whereas there are factors that have reliably shown to impair the recognition of both familiar and unfamiliar faces, such as lighting, negation and inversion (*Inversion*: Yarmey, 1971; Scapinello & Yarmey, 1970; *Composite*: Young, Hellawell, & Hay, 1987; Hole, 1994; Collishaw & Hole, 2000; *Lighting*: Hill and Bruce, 1996; *Negation*: Galper, 1970; Phillips, 1972), and improve the recognition of both classes (*Distinctiveness*: Light, Kayra-Stuart, & Hollander, 1979; Valentine, 1991; Valentine & Bruce 1986), other factors differentially affect the recognition of familiar and unfamiliar faces. Certain factors appear to *improve* one's ability to recognize *familiar* faces but do not affect the recognition of unfamiliar faces. For example, early research indicated that humans are better able to recognize famous faces from their internal features (e.g., eyes, eyebrows, nose, cheekbones) than from the external features (e.g., forehead, hairline, ears, chin), whereas unfamiliar faces are equally recognized from both internal and external features (Ellis, Shepherd, & Davies, 1979; see also Young, Hay, McWeeny, Flude, & Ellis, 1985). This reliance on internal features in the recognition of familiar faces suggests that internal features may be important for the construction of view-invariant representations. Therefore, in the future I hope to explore what makes a face familiar, within a comparative framework.

Finally, I am interested in examining how the nature and quality of social information affects the attention to or preference for social stimuli and whether such social variables (e.g., dominance, kinship, and friendship) may affect the way in which stimuli are encoded, possibly affecting memory retrieval. For instance, a recent study on face discriminations in rhesus macaques found that the performance of all three subjects was affected by social characteristics of the familiar individuals represented in the photos, such that subjects were more accurate when responding to higher-ranking individuals. Additionally, the macaques showed a trend towards slower responses when evaluating high-ranking unfamiliar individuals, suggesting that they may have perceived the dominance of unfamiliar individuals through facial features alone. Although primates may be predisposed to attend to social stimuli, studies demonstrating that primates exhibit different (or better) cognitive abilities within the social domain as opposed to the nonsocial or physical domain are lacking. Moreover, even within species, there is a great amount of individual variation in the level of social expertise that an individual may exhibit. Therefore, one avenue of research I am interesting in pursing is the comparison of cognition between social and nonsocial contexts at the individual level.

5.4 References

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