

The Evolution of Intergroup Bias: Perceptions and Attitudes in Rhesus Macaques

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Social psychologists have learned a great deal about the nature of intergroup conflict and the attitudinal and cognitive processes that enable it. Less is known about where these processes come from in the first place. In particular, do our strategies for dealing with other groups emerge in the absence of human-specific experiences? One profitable way to answer this question has involved administering tests that are conceptual equivalents of those used with adult humans in other species, thereby exploring the continuity or discontinuity of psychological processes. We examined intergroup preferences in a nonhuman species, the rhesus macaque (*Macaca mulatta*). We found the first evidence that a nonhuman species automatically distinguishes the faces of members of its own social group from those in other groups and displays greater vigilance toward outgroup members (Experiments 1–3). In addition, we observed that macaques spontaneously associate novel objects with specific social groups and display greater vigilance to objects associated with outgroup members (Experiments 4–5). Finally, we developed a looking time procedure—the Looking Time Implicit Association Test, which resembles the Implicit Association Test (Greenwald & Banaji, 1995)—and we discovered that macaques, like humans, automatically evaluate ingroup members positively and outgroup members negatively (Experiments 6–7). These field studies represent the first controlled experiments to examine the presence of intergroup attitudes in a nonhuman species. As such, these studies suggest that the architecture of the mind that enables the formation of these biases may be rooted in phylogenetically ancient mechanisms.

Keywords: intergroup bias, comparative cognition, rhesus monkeys

Innumerable conflicts around the world, now and in our history, involve groups demarcated along often-arbitrary social dimensions such as race/ethnicity, nationality, class, and religion. Although the political circumstances and putative causes of conflict vary, the

underlying processes that fuel prejudice, hatred, and even large-scale genocide are universal. For this reason, social psychologists have devoted much effort to understanding the roots of human intergroup conflict by studying the cognitive and affective processes that lead to such conflict. The emergence of intergroup preferences—specifically, a bias toward those within one's group and against those outside of one's group—has been singled out as an important aspect of understanding intergroup relations.

Over the past few decades, social psychologists have gained much insight into both the motivations and cognitive mechanisms that underlie intergroup biases in adults (see reviews in Brewer, 1991; Fiske, 1998; Miller & Prentice, 1999; Sidanius, 1993; Tajfel & Turner, 1979). By comparison, relatively little effort has been devoted to understanding *how* adult humans come to have these biases in the first place, both in terms of individual development and in terms of phylogeny (see Banaji & Heiphetz, 2010). Do intergroup biases emerge because of uniquely human cognitive capacities for noticing group differences, building stories around group differences, and rationalizing actions that promote ingroup benefits? Do they require human-specific motivational processes, such as a fear of death (Pyszczynski, Greenberg, & Solomon,

This article was published Online First January 31, 2011.

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The contents of this article are solely the responsibility of the authors and do not necessarily represent the official views of the National Center for Research Resources (NCRR) or the National Institutes of Health. The Cayo Santiago Field Station was supported by NCRR Grant CM-5 P40 RR003640-20. We thank Samuel Post, Jennifer Barnes, Riana Betzler, Marianne Horn, and Kelly Hughes for their help running these studies. We also thank Adaris Mas Rivera and James Ayala for their support at the Cayo Santiago Field Station.

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1997, 1999) or a need to justify the system (Jost & Banaji, 1994)? Do such biases require specific experiences that are a part of human development to emerge? Or do they demonstrate continuity across species, emerge early in development, and require minimal environmental input?

Although little work to date has addressed these questions empirically, claims about origins are implicit in a number of the major theoretical debates about the nature of intergroup preferences. Take, for example, recent theories that emphasize the role of motivations in promoting intergroup biases (e.g., system justification theory: Jost & Banaji, 1994; terror management theory: Pyszczynski et al., 1997, 1999; optimal distinctiveness theory: Brewer, 1991, 1999, 2001, 2003). Such theories emphasize that intergroup biases result from complex underlying motivations—ones that stem from anxieties about existential concerns (Jost & Banaji, 1994; Pyszczynski et al., 1997, 1999) or the competition between distinctiveness and assimilation motives (Brewer, 1991, 1999, 2001, 2003). Although these motivations are thought to work unconsciously, they necessarily rely on rather cognitively advanced capacities—a realization of death (e.g., Pyszczynski et al., 1997), the capacity to recognize uncertainty (e.g., Jost & Banaji, 1994), and a sense of self (Brewer, 1991; see also social identity theory; Abrams & Hogg, 2001; Hogg, 2000; Tajfel & Turner, 1979; Taylor & Moghaddam, 1994). In this way, a strong reading of these theories with motivational components (at least implicitly) predicts that for intergroup biases to emerge, it may be necessary for individuals to have gone through the development of processes such as a realization of death, a sense of self, and so forth. In addition, these biases should only be present in organisms sophisticated enough to understand these existential and self-relevant concerns. In contrast, other motivational accounts would predict that humans might not be unique in their intergroup biases. Social dominance theory (e.g., Pratto, Sidanius, Stallworth, & Malle, 1994; Sidanius, 1993; Sidanius & Pratto, 1993, 2001), for example, argues that intergroup biases stem from group-living motivations for survival, ones that promote hierarchy and competition. This view would predict that other group-living species with hierarchical dominance structures might share human-like intergroup biases.

Similar contrasting predictions emerge from different cognitive accounts of intergroup biases. Consider, for example, theories that emphasize the importance of essentialism in establishing the kinds of rigid social category boundaries that lead to prejudice and bias (e.g., Chao, Chen, Roisman, & Hong, 2007; Miller & Prentice, 1999; Prentice & Miller, 2006; Tate & Audette, 2001). Such essentialist accounts require that individuals attribute deep, non-obvious, and sometimes even unobservable properties to members of different social groups. By some accounts, this kind of essentialist reasoning should develop slowly over the human life course (e.g., Fodor, 1998), requiring other cognitive processes such as human language to bloom (e.g., Sperber, 1996; cf. Hirschfeld, 1996). Like motivational theories, these essentialist views would predict that intergroup biases should only develop in species that have a capacity for language and essentialist reasoning. Other cognitive accounts, in contrast, have emphasized the role of less sophisticated processes in the emergence of intergroup biases, such as the tendency to automatically categorize individuals in the absence of explicit awareness (e.g., Fiske, 1998, 2000, 2005). Because these accounts depend on reflexive and overgeneralized

processes, they would make different predictions about the emergence of intergroup biases, namely that such biases may emerge early in development and in creatures that lack language or advanced cognitive control capacities.

For these reasons, studying the origins of intergroup biases—both developmentally and evolutionarily—may provide an important way to arbitrate between different theoretical accounts of how these biases work. Unfortunately, the majority of empirical research on intergroup biases to date has used adult humans as its test population. To fully understand the origins of intergroup biases, researchers can turn to two subject populations—young human infants and children, who have not yet developed the sophisticated cognitive capacities of human adults, and nonhuman primates, who by nature will never develop such capacities.

By using such a combined comparative–developmental approach, social psychologists will be able to specifically test the extent to which different kinds of human experiences are necessary for the development of intergroup cognitive processes. In fact, studies employing comparative and developmental approaches have yielded new insight into social psychological processes in other domains, such as the development of prosocial behavior (see review in Brosnan, 2006; Warneken & Tomasello, 2009), the emergence of judgment and decision-making biases (Brosnan et al., 2007; Chen, Lakshminaryanan, & Santos, 2006; Lakshminaryanan, Chen, & Santos, 2008; Santos, 2008; Santos & Hughes, 2009; Santos & Lakshminaryanan, 2008), the origins of cognitive dissonance (Aronson & Carlsmith, 1963; Egan, Bloom, & Santos, 2010; Egan, Santos, & Bloom, 2007), the development of social evaluation (Hamlin, Wynn, & Bloom, 2007), the emergence of our belief in a just world (Olson, Dunham, Dweck, Spelke, & Banaji, 2008), and intergroup perception (Baron & Banaji, 2006).

We first review what researchers have learned to date about the origins of intergroup biases, most of which pursues this question from a developmental perspective. We then discuss the nature of grouping in nonhuman primate species and how investigating intergroup processes in nonhuman populations can provide specific insights for the nature of human intergroup cognition. Finally, we present the results of the present seven studies that directly test whether one primate species—the rhesus macaque (*Macaca mulatta*)—shares some of the intergroup processes that are found in humans.

Developmental Origins of Intergroup Cognition

Most work to date on the origins of intergroup cognition has focused on the ontogenetic development of these mechanisms (e.g., Aboud, 1998; Bar-Haim, Hodes, Lamy, & Ziv, 2006; Bigler, Brown, & Markell, 2001; Bigler, Jones, & Lobliner, 1997; Dunham, Baron, & Banaji, 2008; Huston, 1993; Kelly et al., 2005). This work converges on the perhaps surprising view that many aspects of implicit intergroup cognition emerge in the absence of experience with other social groups. First, there is a growing body of evidence that infants and children seem to divide others into groups and form a variety of social categories early in life (on the basis of race: Bar-Haim et al., 2006; Kelly et al., 2005; attractiveness: Langlois et al., 1987; native language spoken: Kinzler, Dupoux, & Spelke, 2007; dispositional attitudes: Hamlin et al., 2007).

In addition to differentiating between social categories, there is also evidence that *preferences* for those that belong to one's own

social category or group begin quite early. **Infants preferentially learn from individuals that speak the language of their ingroup versus individuals who speak an outgroup language** (Kinzler et al., 2007; Shutts, Kinzler, McKee, & Spelke, 2009), and by 3 years of age, children prefer to play with others of their same gender (Huston, 1983) and race (Aboud, 1988). A preference for one's ingroup is not the only early emerging social attitude; indeed, negative attitudes toward outgroup members also develop early in life. Children 3–5 years of age exhibit explicit verbal negative attitudes toward outgroups (for reviews, see Bigler & Liben, 2006; Hirschfeld, 1998) and are more likely to ascribe negative traits to children of other races (Aboud, 1988; Comer, 1989). **Bigler et al. (2001, 1997) observed that children preferred to associate with those even randomly assigned to the same group and believed their group to be superior to others.** Similar arbitrary distinctions can even lead children to treat those randomly assigned to a different group in a harmful manner (Sherif, Harvey, White, Hood, & Sherif, 1954/1961). By 6 years of age, children even demonstrate implicit attitudes nearly identical to those of adults (Baron & Banaji, 2006; Dunham, Baron, & Banaji, 2006; Rutland, Cameron, Milne, & McGeorge, 2005; Sinclair, Dunn, & Lowery, 2005; Skowronski & Lawrence, 2001). As one example, Baron and Banaji (2006) modified the traditional adult Implicit Association Test (IAT; Greenwald & Banaji, 1995) to be more accessible to children using both auditory stimuli and photos to represent social groups. Using this adapted child IAT, they found that the implicit race attitude of children at 6 years of age was identical in magnitude to that of 10-year-olds and adults. Finally, by 5 years of age, children hold essentialist-like beliefs about certain social categories (Diesendruck & haLevi, 2006; Hirschfeld, 1996), though both language and culture affect the emergence of such beliefs (Birnbbaum, Deeb, Segall, Ben-Eliyahu, & Diesendruck, 2010; Diesendruck & Haber, 2009; Rhodes & Gelman, 2009).

Taken together, this work suggests that many features of adult human intergroup cognition—social category knowledge and beliefs, group formation, ingroup preferences, and implicit intergroup attitudes—are present early in human ontogeny. However, the present work is silent on some aspects of how these intergroup processes develop. Specifically, it is still unclear whether these early emerging tendencies are due to human-specific cognitive capacities or cultural institutions. To really investigate the origins of intergroup processes, we also need to look at nonhuman species. Are humans unique in their intergroup categorization and ingroup biases? Or do the psychological mechanisms observed in humans also underlie the intergroup interactions of closely related primate species?

Investigating the Evolution of Intergroup Cognition

Humans are of course not the only species to live in social groups; in fact, species from ants to lions live in organized social structures. However, it is our closest living relatives, nonhuman primates, whose group structures bear the most striking resemblance to our own. Though there exists variation in group structures across different primate species, nearly all primates live in social groups (for a review, see Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987). Moreover, and critically for the present analysis, primate groups appear to share human-like levels of intergroup conflict and aggression. Contact between primate

groups often appears as specialized territorial defense behavior or competition for access to resources.

In addition, nonhuman primate groups, like human societies, organize themselves in terms of hierarchical structures. Social psychologists have long observed the subtle effects of status and hierarchy in humans, but such phenomena are not unique to our species. Although hierarchical structures vary across nonhuman primate species, most primates exhibit a relatively stable and enduring pattern of dominance by certain individuals or groups over others (e.g., Saunders & Hausfater, 1988). Such primate hierarchy differences mimic those observed in humans in which differential status between groups can influence everything from occupation to high school clique.

In spite of these similarities, there are a number of striking differences between human and nonhuman intergroup interactions. First, primates lack a number of higher level ways of establishing social categories such as linguistic labels and cultural institutions that separate groups. In addition, unlike humans, primates appear to have a limited set of social categories. Most primate categorizations are based on inherent biological traits relevant to reproduction (age, sex, kinship, estrous, etc.). Humans, on the other hand, seem to readily form categories based on just about any salient similarity—in addition to categorizing someone as male, young, and related, we might also label them as a Red Sox fan, croc shoe wearer, and Democrat. Currently there is no evidence that nonhuman primates will form novel categories based on nonbiologically relevant information. Indeed, this limitation on primate social categories is another reason that primates' intergroup processing might be interesting to study, as nonhumans may lack the flexibility of our own species with regard to forming new categories.

As seen above, primates share both important similarities and differences with those of our own species. Unfortunately, although much is known about primate intergroup interactions at the behavioral level, little is known about the *cognitive and affective processes* that govern these interactions. Although we know how intergroup cognition in this species manifests itself behaviorally, we do not have specific knowledge of the perceptual processes of categorization on which these behaviors rest. Understanding primate intergroup behavior at this process level will allow us to better determine whether behaviors that look similar on the surface are truly mediated by similar mechanisms across human and nonhuman primates.

Here, we present seven studies that represent the first research to explore systematically the nature of intergroup processing in a nonhuman primate species. On the basis of the richness of our own social categories, the flexibility with which we update our category knowledge and form novel categories, the complexity of our intergroup biases, and the salience of social category discourse in most human cultures, we might expect that language and other complex cognitive processes would play a foundational role in the formation of human intergroup processes, and we might not expect to find similar processes in other species. On the other hand, because of the striking similarities between group structures, dominance hierarchies, and modes of intergroup aggression, we might instead hypothesize that human-like intergroup processes are not unique to our species and instead may be shared with other primates.

To explore these issues, our studies focus on one model primate species—the rhesus macaque. As an Old World monkey species, rhesus monkeys diverged from our own ape evolutionary line between 25 and 30 million years ago. As such, rhesus macaques represent an evolutionarily ancient relative of humans. In addition, this species has served as the standard primate model for adult human cognition in a number of other domains (e.g., numerical cognition: Brannon, 2005; Feigenson, Dehaene, & Spelke, 2004; theory of mind: Flombaum & Santos, 2005; Hauser & Spelke, 2004; Santos, Nissen, & Ferrugia, 2006; imitation: Subiaul, Cantlon, Holloway, & Terrace, 2004; social preferences: Deaner, Khera, & Platt, 2005; decision making: Glimcher, 2003).

In addition, much is known about the group structure and intergroup interactions in this species. Rhesus macaques are a female philopatric species, meaning that social groups are based on female kinship lines, with one's status in the dominance hierarchy determined by the rank of one's mother. Female macaques are born into a particular social group and typically remain in that group throughout their life, whereas male macaques tend to leave their natal group around reproductive age to transfer to a new group (Rawlins & Kessler, 1987). This aspect of macaque group structure provided us with an important window into the flexibility of intergroup representations in this species—by studying a monkey species in which a subset of individuals switch their group affiliations, we could examine both the emergence and flexibility of primate intergroup representations.

Our specific macaque subjects came from a free-ranging population of approximately 1,000 rhesus macaques living on the island of Cayo Santiago (Rawlins & Kessler, 1987). The macaques living in the Cayo Santiago population have been studied extensively for almost six decades, and thus much is known about their intergroup behaviors and interactions. Macaques in this population naturally form social groups, with six different social groups currently in existence on the island. The macaques within these six social groups tend to travel as a coherent unit at least a couple of times a day, especially when venturing toward a feeding area (Boelkins & Wilson, 1972). Although none of the groups are confined to a particular area on the island (Carpenter, 1942), the groups tend to travel in distinct territorial areas that have some degree of overlap, usually around feeding areas. For this reason, most of the intergroup conflict in this population tends to take place at feeding areas (Kaufmann, 1967). Typically, such conflicts emerge when one group coming to eat displaces another that is finishing up its meal (Boelkins & Wilson, 1972). Although some of these displacements occur peacefully, most group displacements involve some degree of aggressive behavior, usually in the form of threatening communicative displays such as aggressive vocalizations and facial expressions (Loy, 1970; Vandenberg, 1968). Only rarely do such encounters escalate to physical violence; Boelkins and Wilson (1972), for example, observed that only around 9% of interactions between groups involved a physical fight between group members. Moreover, although these aggressive intergroup encounters can be initiated by members of both sexes, overt physical aggression generally occurs between male macaques, especially low-ranking subadult male macaques near the time in their life when intergroup transfers occur (Boelkins & Wilson, 1972).

Macaque Intergroup Cognition: The Present Studies

In the absence of existing procedures to test intergroup cognition in macaques (or any nonverbal primate species), the purpose of our present studies was manifold. First, we examined whether macaques spontaneously distinguished between ingroup and outgroup members. Although macaques may make such distinctions in their daily life, little work to date has actually measured the presence of such discrimination: how it happens, the magnitude of its occurrence, and whether it is even possible to bring this process under the necessary experimental control to develop a richer understanding of nonhuman intergroup cognition. To tackle this issue, Experiments 1–3 explored whether rhesus macaques spontaneously represent individuals as members of ingroups and outgroups. Second, we examined whether this species shared the human tendency to develop implicit and measurable preferences toward arbitrary stimuli associated with members of their own and other groups (Experiments 4–5). Third, we asked whether monkeys share a human tendency to automatically evaluate ingroup members positively and outgroup members negatively. To explore this issue, Experiments 6–7 developed a new procedure to measure intergroup attitudes in this species and to examine the nature of implicit intergroup attitudes.

Experiment 1

We first examined whether macaques spontaneously discriminated between other macaques as members of their own and other groups. Our measure of spontaneous discrimination involved a preferential looking method. Preferential looking methods were originally developed as way of measuring the preferences of preverbal infants (e.g., Baillargeon, 1987) but have also been adapted for use with nonhuman primates (e.g., Hauser & Spelke, 2004). In this method, subjects are presented with two images and are allowed to spontaneously allocate their attention across the two images for a set time period. The logic is that subjects should look reliably longer at the image that they find more interesting, relevant, or salient for any number of reasons. If subjects systematically attend more to one stimulus than another, then they must discriminate between the two images along some dimension. Here, we ask whether group membership can function as such a dimension.

In the preferential looking test used in Experiment 1, we presented adult macaques subjects with two static two-dimensional photographic images of other monkeys. One of these images depicted an ingroup member (a male monkey who had been part of the subject's group since birth), whereas the other image depicted an outgroup member (a male monkey of the same age who had never lived in the subject's group). Importantly, these photographs were presented without any additional context cues, such as other conspecifics or markers of the physical environment. If macaques spontaneously distinguish between ingroup and outgroup members based solely on visual images, then they should look longer at one of the two images presented. Specifically, on the basis of previous work showing that macaques in this population show vigilance increases toward dangerous individuals that they dislike (e.g., Hamlin, Cersonsky, & Santos, 2010), we hypothesized that macaques would look significantly longer at the outgroup member—the individual who should be considered most threatening and thus demand more attention.

Method

Subjects. We tested 37 adult rhesus macaques in the two largest groups on the island (R and F). Additional monkeys ($n = 21$) were approached but were excluded because of interference (e.g., another monkey approached the display and frightened our subject during testing), disinterest (e.g., the subject turned or walked away from the testing area during testing), or experimental error (e.g., problems with the apparatus moving because of wind, picture placement errors, or camera malfunction). This number of excluded trials is common for studies in this population because animals range freely throughout the island (see Cheries, Newman, Santos, & Scholl, 2006; Flombaum & Santos, 2005; Santos et al., 2006). Importantly, in this and all other experiments, the decision to exclude a trial was made by an experimenter who was blind to condition.

For this experiment, 21 female subjects and 16 male subjects were tested. In this and all future experiments, we tested only subjects who were at least 2 years of age.

Apparatus. Stimuli were presented on a white foamcore stage (152 cm long \times 28 cm high \times 10 cm deep), the front of which had two red screens (24 cm \times 27 cm) velcroed at either end (see Figure 1). The screens occluded two 20 cm \times 20 cm headshot color photographs of forward-facing adult male monkeys: one (Monkey 44T) who had been born in and was currently a member of Group R, and one (Monkey 43P) who had been born in and was currently a member of Group F. Thus, the Group R face would be the “ingroup” face for members of Group R and the “outgroup” face for members of Group F (and vice versa). The two monkeys chosen as target photographs were matched as well as possible for age, size, and distinctiveness (no obvious facial scars, etc.). The locations of these two faces could be swapped, such that both the location of the individual faces and the face’s ingroup or outgroup status could be counterbalanced across side. All sessions were filmed with a Sony video camera.

Procedure. Two experimenters conducted the experiment: one as the presenter, and the other as the cameraperson. After

locating a subject, the presenter positioned the stage 2–4 m from the subject. The cameraperson stood directly behind the presenter and filmed the subject’s looking. The presenter first drew the subject’s attention to each of the occluders. The session began when the presenter removed the occluders (thus revealing the two hidden photos to the monkeys) and said “now” to initiate the beginning of the 30-s trial. To remove experimenter bias, the presenter remained blind to which face was positioned where; faces were swapped randomly before each trial by the cameraperson, who was unaware of which face belonged to which group. The presenter could therefore decide which trials should be aborted while remaining blind to the test condition.

Coding. Trials were digitized onto a Macbook computer and then analyzed using Quicktime software. A single coder who was blind to the experimental condition analyzed looking to the left and right photo in each trial, thus coding for every subject the length of time that subject spent looking at each photo. A second blind coder analyzed 10 sessions to establish reliability ($r = .75$).

Results

We analyzed subjects’ duration of looking using a repeated measures analysis of variance (ANOVA) with group of face (ingroup/outgroup) as a within-subject factor and subject sex (male/female) and group (F/R) as between-subjects factors. Although we observed no significant main effects of sex, $F(1, 33) = 0.15$, $p = .70$, or group, $F(1, 33) = 2.31$, $p = .14$, we did find a significant main effect of the face stimulus, $F(1, 33) = 9.35$, $p = .004$. Specifically, monkeys looked reliably longer at the outgroup face ($M = 10.83$ s) than the ingroup face ($M = 6.58$ s; see Figure 2). Moreover, we observed no interaction between the subject’s group and our face effect, $F(1, 33) = 0.22$, $p = .64$; monkeys in both group F and group R were vigilant toward whichever face was outgroup for them, regardless of their own group membership. We also observed no interactions between sex and face stimulus, $F(1, 33) = 0.01$, $p = .95$, suggesting that male and female subjects displayed the effect of face equally.

Discussion

This pattern of performance demonstrates three important features of macaques’ intergroup processing. **First, our results show that monkeys spontaneously discriminate ingroup and outgroup faces.** Like humans, monkeys appear to extract an individual’s group membership spontaneously, suggesting that this factor is a salient aspect of how monkeys represent other conspecifics. Second, these results suggest that monkeys are able to extract grouping information even from static photographs of faces presented without any contextual or environmental cues. In this way, monkeys—like humans—spontaneously extract an individual’s group identity from minimal input, in this case, a single static photograph. **Finally, in addition to discriminating between ingroup and outgroup members, our results suggest that monkeys appear to devote more vigilance toward outgroup individuals than ingroup members, suggesting that macaques also find outgroup members threatening** and thus may differentially devote attentional resources to outgroup stimuli (e.g., Allport, 1954/1979, Brewer & Kramer, 1985; Kurzban, Tooby, & Cosmides, 2001; Payne, 2001).



Figure 1. A photo of the experimental set-up used in Experiments 1–3. The experimenter simultaneously lifted two occluders to reveal an ingroup monkey face and an outgroup monkey face.

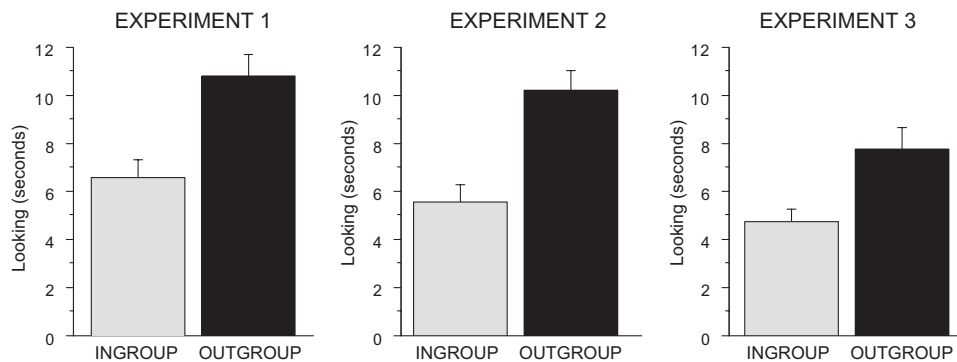


Figure 2. Monkeys' duration of looking at ingroup and outgroup faces in Experiments 1–3. Across both studies, monkeys reliably looked longer at the outgroup face. Error bars represent standard errors.

Although we interpret the results of Experiment 1 as evidence that monkeys look reliably longer at outgroup members because of vigilance, the present results are also consistent with a simple alternative explanation: macaques may look longer at the outgroup member because this face is more novel than the ingroup face. Under this account, monkeys increase their vigilance toward outgroup faces not because these faces are outgroup per se but because they are unfamiliar. Experiment 2 attempted to address this alternative explanation by controlling for the novelty of the two faces.

Specifically, Experiment 2 presented monkeys with a different set of ingroup and outgroup faces that were more closely matched on overall familiarity. Normally this would be a near impossible task, but it was possible here because of the nature of rhesus macaque social groupings and because the Cayo Santiago Field Station maintains a database that tracks the movements of male monkeys between groups. We therefore knew the history of each male's familiarity with various outgroup individuals. Specifically, we were able to pair the face of a male who had remained in the subject's social group since birth (ingroup) with the face of a male who had originally been born in the subject's group but had recently transferred to another social group (outgroup). If subjects were merely looking longer at the outgroup face because it was an unfamiliar monkey who had never been a member of their group, we should not see the effect obtained in Experiment 1 or should see a much weakened version of it. If, on the other hand, the effects seen in Experiment 1 were not due to mere unfamiliarity but a genuine vigilance for outgroup members, we would expect to see the same pattern as observed in Experiment 1.

Experiment 2

Method

Subjects. We tested 39 monkeys (18 female monkeys and 21 male monkeys) from Groups R and F who had not participated in Experiment 1. Additional monkeys ($n = 21$) were approached but were excluded because of interference, disinterest, or experimental error.

Procedure. We used the same procedure and apparatus as in Experiment 1, except that two additional photos were used: one of a male monkey (Monkey 290) who had been born in Group R but

was at the time of testing in Group F (RF face), and one of a male monkey (Monkey 48L) who had been born in Group F but was at the time of testing in Group R (FR face). For subjects in Group F, the photo of the FR face (outgroup) was paired with the photo from Experiment 1 of a male who had been born in Group F and remained there throughout his life (FF face—ingroup). Similarly, for subjects in Group R, the photo of the RF face (outgroup) was paired with the photo from Experiment 1 of a male monkey who had been born in and had remained in Group R (RR face—ingroup). Again, the monkeys used in these photos were matched as closely as possible for age, size, and distinctiveness. Sides were counterbalanced across subjects. Coding was done in the same manner as in Experiment 1.

Results

We again performed a repeated measures ANOVA with group of face (ingroup/outgroup) as a within-subject factor and subject sex (male/female) and group (F/R) as between-subjects factors. As in Experiment 1, we observed a significant main effect based on the group status of the faces, $F(1, 35) = 19.69, p < .0001$. Although both target faces were equally familiar to the monkeys, subjects looked longer at the face of an outgroup than ingroup monkey (mean outgroup = 10.20 s vs. mean ingroup = 5.59 s; see Figure 2). Again, the effect held equally strongly for both subjects in Group R and subjects in Group F, $F(1, 35) = 0.72, p = .40$, and for male and female subjects, $F(1, 35) = 0.83, p = .37$.

Discussion

In Experiment 2, we replicated the pattern observed in Experiment 1. Even though both faces used in Experiment 2 were familiar to the monkeys, subjects continued to look significantly longer at the outgroup face than at the ingroup face. In fact, the difference in looking times across the two experiments was quite similar. We interpret these data as evidence that monkeys look longer at outgroup faces not merely because such faces are unfamiliar but instead because such faces represent individuals who are not members of the subjects' ingroup.

Although this experiment controls for the possibility that unfamiliarity was the driving factor behind the increased vigilance found in Experiment 1, a strict interpretation leaves open the

possibility that macaques could be looking longer at the outgroup face not because it is unfamiliar but because it is *less familiar* than the ingroup face. Although both faces are familiar to each of the subjects, the ingroup face is slightly more familiar because of being in the group for the additional short period of time since the outgroup monkey had left. Additionally, in all cases here, the monkey who transferred at adolescence was the outgroup face, and the monkey who did not was the ingroup face. It is also possible that there is something more inherently interesting about faces of monkeys who transferred than faces of monkeys who did not (or something more attention-grabbing about the RF and FR faces compared with the FF and RR ones).

To explore this issue, Experiment 3 pitted the variable of familiarity against that of group status as best we possibly could given the constraints of macaque grouping structure: We engineered the target faces such that the outgroup face was *more familiar* to the subject than the ingroup face, allowing the effect to reverse if it reflects novelty. Specifically, Experiment 3 paired the face of a male who had been born in another social group but had transferred to the subject's group within the past 4 months (ingroup) with a face of a monkey who had been in the subject's social group since birth but had, within the 4 months of testing, transferred to another group (outgroup). In this case, subjects would have had years more exposure to the outgroup face, so if familiarity were at all driving the effects in Experiments 1 and 2, we would expect subjects to look longer at the less familiar (ingroup) face. If on the other hand, longer looking time reflected a contextually sensitive outgroup vigilance effect, we would expect subjects to look longer at the more familiar but now outgroup face. Further, Experiment 3 allowed us to control for the fact that the outgroup monkey in previous studies had recently transferred. In Experiment 3, we used faces of male monkeys who had *both* transferred groups recently, and thus subjects cannot use transfer alone as a cue to distinguish the faces.

Experiment 3

Method

Subjects. We tested 40 monkeys (23 female monkeys and 17 male monkeys) from two groups on the island: KK and R. Additional monkeys ($n = 8$) were approached but were excluded because of interference, disinterest, or experimental error. We switched to Group KK instead of Group F here because of our need to match exact transfer times for the monkeys we were using as our stimuli faces. Because no male monkeys in Group F had recently transferred from Group R, we were unable to use this group in our sample. However, we were able to find such an individual from a smaller group: KK. We were thus able to use a pair of monkeys in Group R and Group KK that were matched for age and had switched groups at the same time; these monkeys were used in our photos for Experiment 3.

Procedure. We used the same procedure and apparatus as in Experiments 1 and 2, except for the specific photos used. In this study, we used new male monkey photos: one of an adult male who had spent the majority of his life in Group R but had in the past 4 months transferred to Group KK (Monkey 36V), and one of an adult male who had spent the majority of his life in Group KK but had in the past 4 months transferred to Group R (Monkey 58R).

In that way, the current "outgroup" face was actually more familiar to subjects than was the current "ingroup" face. Monkeys chosen as targets were matched as well as possible for age, size, and distinctiveness. Side of photo was counterbalanced between subjects. Data coding was conducted in the same manner as in Experiments 1 and 2.

Results

We analyzed monkeys' duration of looking using a repeated measures ANOVA with stimulus face (ingroup/outgroup face) as a within-subject factor and subject's sex (male/female) and group (KK/R) as between-subjects factors. We observed no effect of sex, $F(1, 36) = 2.90, p = .10$, or group, $F(1, 36) = 0.20, p = .65$, but we did find a significant effect of stimulus face, $F(1, 36) = 17.06, p = .0002$. As in Experiments 1 and 2, monkeys looked longer at outgroup faces ($M = 7.78$ s) than at ingroup faces ($M = 4.72$ s; see Figure 2). There was no interaction between group and this face effect, $F(1, 36) = 0.05, p = .81$, suggesting that both KK and R monkeys showed this effect equally. We also observed no interaction of sex, $F(1, 36) = 0.43, p = .52$, suggesting that male and female subjects displayed this effect equally.

Discussion

The aim of Experiment 3 was to test whether monkeys' performance in Experiments 1 and 2 was merely driven by a familiarity effect. To investigate this issue, we pitted familiarity against group membership. Even when the outgroup member was more familiar than the ingroup member, monkeys still looked reliably longer at the outgroup face than the ingroup face. Again, the difference in looking time was similar to that found in the previous two experiments. This pattern of performance suggests that familiarity alone was not driving the effects observed in our earlier experiments. Moreover, the results of Experiment 3 provide even more evidence for our original outgroup-vigilance interpretation. Indeed, we observed increased looking toward the outgroup faces across three separate experiments and several different macaque groups.

Taken together, the results of the first three experiments demonstrate that rhesus macaques spontaneously categorize other monkeys as members of an ingroup or outgroup and, like humans (Allport, 1954/1979; Brewer & Kramer, 1985; Kurzban et al., 2001; Sherif, 1954/1961), are more attentive to outgroup than ingroup members. Moreover, these new results suggest that rhesus macaques can quickly and robustly learn to treat former ingroup members as outgroup individuals. Like humans (Kurzban et al., 2001), macaques are flexibly able to update an individual's current grouping status on the basis of new group membership information.

Having established that rhesus macaques can spontaneously discriminate images of conspecific faces on the basis of their ingroup/outgroup status and display more vigilance toward outgroup members, we next sought to explore the consequences of this discrimination and vigilance. That is, given that monkeys, like humans, distinguish those who belong to their group from those who do not and respond appropriately to them, what are the consequences of these distinctions? Do they also readily evaluate and respond to ingroup and outgroup members and stimuli associated with them differently?

As members of the human species, our evaluation of ingroup or outgroup members goes beyond simply establishing a preference for the grouped individual. Humans also quickly associate ingroup and outgroup members with novel stimuli or symbols. Indeed, human history provides numerous examples in which an arbitrary symbol comes to be imbued with information related to the social group with which it is associated. This is true both when a symbol is specifically adopted to represent a group (such as a swastika representing the Nazi Party) and also for everyday objects with learned associations with social groups. This phenomenon is especially strong when objects or ideas are uniquely associated with a group. As a result, chopsticks can remind us of East Asians, plaid kilts of the Scottish, and the World Trade Center of New Yorkers.

Once an association has been created or “learned,” objects and symbols can arouse strong emotions in us, even when they do not appear conjointly with the group they are associated with. In many cases, preferences for particular items can be viewed as markers of group membership: Objects associated with one’s ingroup are objects one “should” like, and an object associated with a disliked person “should” also be disliked.

In Experiment 4, we focus on the question of whether macaques, like humans, will automatically tag arbitrary novel objects with group membership after minimal association between the object and a particular group member. Specifically, do monkeys readily learn an association between a novel object and an ingroup monkey or an outgroup monkey? If so, will the learned association lead them to be more vigilant to objects associated with outgroup member? Such second-order vigilance will provide stronger evidence of the depth and breadth of group-based perception and learning that may serve as the basis of intergroup preferences.

To deal with this issue, Experiment 4 presented monkeys with a short single-trial event aimed at establishing an association between a group member (either ingroup or outgroup) and an arbitrary novel object. Specifically, we showed monkeys a single event in which a picture of an ingroup or outgroup face looked at a novel object. If macaques, like humans, readily learn the unique associations between the novel objects and the social groups with which they are paired, then subjects should distinguish and respond to these objects appropriately even in the absence of any visual indicators of the social groups. In particular, we predicted that monkeys should treat these novel objects like the social groups with which they were associated, exhibiting more vigilance (and thus longer looking) toward objects associated with outgroup members than those associated with ingroup members.

Experiment 4

Method

Subjects. We tested 79 macaques (41 female macaques and 38 male macaques) from Groups F and R. Additional monkeys ($n = 90$) were approached but were excluded because of interference, disinterest, or experimental error.

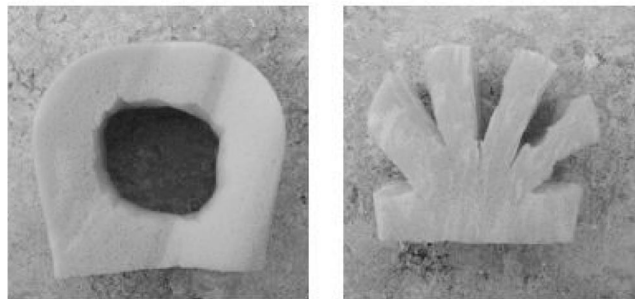
Apparatus. The same apparatus as in Experiments 1–3 was used, with a few minor modifications. We added two raised red platforms (28 cm long \times 8 cm high \times 10 cm deep) to the sides of the framed photos (one toward each outer edge of the apparatus). We also placed a piece of Velcro in the center of each platform, such that a foam object could easily be attached and removed from

that spot. Additionally, four novel foam objects were used: two donut-shaped objects (round) and two coral-shaped (spiky) objects (see Figure 3). One object of each shape was constructed of bright orange foam, and the other was constructed of bright green foam. Finally, in addition to the forward-facing headshots of monkeys in Groups F and R, we also had high-resolution photos of side-facing shots of these same monkeys, for reasons that will become obvious shortly.

Procedure. The procedure began as in Experiments 1–3. After locating a subject and positioning the stage 2–4 m from the subject, the presenter first drew the subject’s attention to one of the occluders and removed it to reveal one of the forward-facing photos (see Figure 4). Once the monkey saw this photo, she replaced the occluder and placed one of the four novel foam objects on the platform adjacent to this photo. Next, she lifted the occluder again to reveal a side-facing shot of the same monkey such that it now appeared that this monkey was looking at the novel foam object. After giving the subject approximately 2 s to view the association between the face and the object, she removed the foam object and replaced the occluder, thus hiding both the face and object from view. Next, she repeated the process with the face on the other side of the apparatus with a second novel foam object that was both a different color and a different shape from the first object.

After both occluders were back in place and both objects were out of view, she simultaneously placed both objects back on their platforms and got the subject’s attention, calling “now” to initiate the beginning of a 10-s trial (trials were shorter than in Experiments 1–3 because of the length of the display—no subjects

Objects Used in Experiment 4



Objects Used in Experiment 5

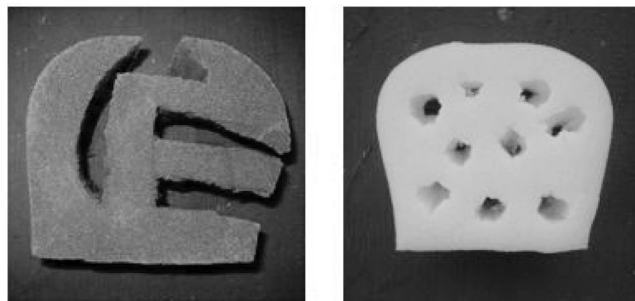


Figure 3. A photograph of the stimulus objects used in Experiments 4 and 5.

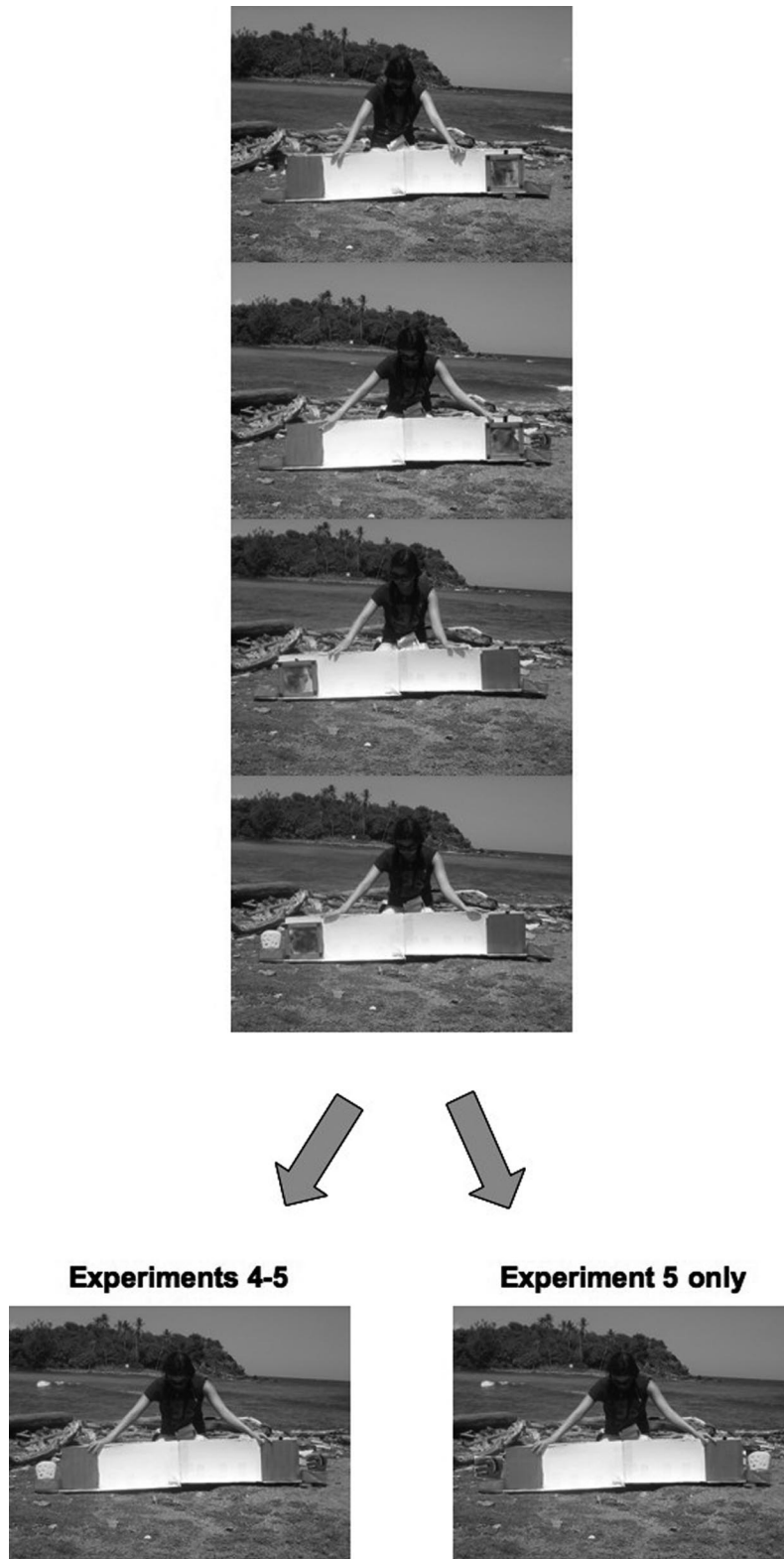


Figure 4. A photo of the experimental set-up used in Experiments 4 and 5. The experimenter showed subjects an ingroup monkey face looking at one object and an outgroup monkey face looking at a second object, after which the faces were occluded, and only the objects remained.

watched past the 10-s mark). Again, to reduce bias, the presenter remained blind to which face was positioned where; faces were swapped randomly before each trial by the cameraperson. The presenter could therefore decide which trials should be aborted while remaining blind to the test condition. Coding was the same as in previous studies.

Results

We analyzed monkeys' duration of looking using a repeated measures ANOVA with object (ingroup/outgroup) as a within-subject factor and sex (male/female) and group (R/F) as between-subject factors. Again, we observed no main effect of sex, $F(1, 75) = 0.19, p = .66$, or group, $F(1, 75) = 0.55, p = .46$, but we did find a main effect of object, $F(1, 75) = 45.71, p < .0001$. Monkeys looked reliably longer at the object associated with the outgroup face ($M = 3.32$ s) than at the object associated with the ingroup face ($M = 1.60$ s; see Figure 5), indicating that monkeys may show the same sort of increased vigilance toward an object that has come to be associated with an outgroup than toward an ingroup. We also observed no interaction of sex and object, $F(1, 75) = 0.02, p = .90$, suggesting that male and female subjects displayed this effect equally.

Discussion

After a brief exposure that paired a face with an object, rhesus macaques tagged these objects with the group membership of the face they had been associated with. **Particularly striking is that the increased vigilance toward a novel arbitrary object occurred after a single, 2-s exposure to an outgroup member looking at that particular object. These results are consistent with the data from humans showing rapid processing of intergroup information (e.g., Fiske, 1998) and that minimal information seems to be sufficient to associate objects and symbols with particular groups and to respond to these symbols as proxies for the group.**

Although we interpret these results as evidence that macaques rapidly pair objects with the groups to which they were associated, at least one critical alternative interpretation remains. Though subjects looked reliably longer at the object associated with the outgroup face, the objects remained spatially close to the two faces that had been exposed only moments earlier. It is possible that

rather than looking at the objects at all, subjects were merely more attentive to the side of the apparatus that had come to represent the outgroup side. That is, perhaps monkeys increased vigilance to the area associated with the outgroup monkey in anticipation that his picture might return. In this way, monkeys' increased looking time in Experiment 4 may have reflected their anticipation of a specific picture rather than an increased vigilance for the object associated with the outgroup monkey.

Before interpreting the data further, we decided to control for this potential artifact in Experiment 5. Specifically, Experiment 5 used the same procedure as Experiment 4 but reversed the sides on which the two objects were presented during the final event. In doing so, each object was on the side of the apparatus closer to the face that it had *not* been previously paired with. In other words, if an object had been paired with the ingroup face, it was now presented on the side of the apparatus where the outgroup face had been, and if an object had been paired with the outgroup face, it was now presented on the side of the apparatus where the ingroup face had been.

This procedural change allowed us to assess the hypothesis that if the prior presence of the outgroup face was causing the increased vigilance in Experiment 4, we would expect subjects to look longer at the side of the apparatus where the outgroup face had been (in other words, look longer at the ingroup object). If on the other hand, macaques had more deeply associated the meaning of the object with social group membership, they should look longer at the outgroup object even though it is presented closer to the position where the ingroup monkey had appeared.

Experiment 5

Method

Subjects. We tested 155 macaques (73 female macaques, 82 male macaques) from Groups F, R, HH, and KK. Additional monkeys ($n = 128$) were approached but were excluded because of interference, disinterest, or experimental error. One additional monkey was tested completely but was excluded from our final analysis because this monkey walked away before his sex or identity could be recorded.

Apparatus. The same apparatus and materials as in Experiment 4 were used, with a couple of minor changes. Four photos were used, each one a forward-facing headshot of a monkey in one of the four groups tested. Two novel foam objects were used: one a yellow foam rounded square with small holes dotted throughout its interior, and the other a blue foam symbol resembling an inverted "E" (see Figure 3).

Procedure. The procedure for half the subjects was identical to that of Experiment 4. The procedure for the other half of subjects was identical except that prior to the final trial in which vigilance was measured, the presenter switched the sides of the objects such that the object paired with the ingroup face was now adjacent to where the outgroup face had been, and the object paired with the outgroup face was now adjacent to where the ingroup face had been. Coding procedures were the same as in Experiment 4.

Results

We performed a repeated measures ANOVA with object grouping (ingroup vs. outgroup) as a within-subject factor and side

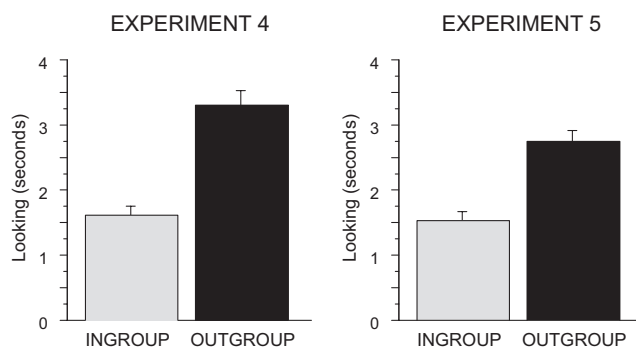


Figure 5. Monkeys' duration of looking at ingroup and outgroup objects in Experiments 4 and 5. Across both studies, monkeys reliably looked longer at the outgroup object. Error bars represent standard errors.

(same side or switched), sex (male/female), and group (HH, F, KK, and R) as between-subjects factors. We found no effect of sex, $F(1, 139) = 0.15, p = .70$, or side, $F(1, 139) = 0.66, p = .42$. We did however observe an effect of group, $F(3, 139) = 3.96, p < .01$; across all trials, Group HH appeared to look longer at our stimuli than the other groups. Most importantly, however, we observed a significant main effect of object grouping, $F(1, 139) = 35.62, p < .0001$. As in Experiment 4, monkeys looked longer at the object associated with the outgroup (2.76 s) than the object associated with the ingroup (1.53 s; see Figure 4). Critically, we observed no interaction between side and object grouping, $F(1, 139) = 0.13, p = .72$; monkeys showed the ingroup versus outgroup effect equally across same side and different side trials. Finally, we observed an interaction between group and object grouping, $F(3, 139) = 7.67, p < .0001$. Although all groups exhibited the effect overall ($p < .0001$), some groups (particularly Groups HH and F) showed the effect more strongly than others. Finally, we observed no interaction between sex and object grouping, $F(1, 139) = 0.43, p = .51$, suggesting that male and female subjects showed this effect equally.

Discussion

Subjects who saw each object near the face it had previously been paired with performed identically to those who saw each object near the opposite face, suggesting that the effect seen in Experiment 4 could not have been due to increased vigilance toward the spatial location associated with the outgroup member. These results provide the first evidence that a nonhuman species reveals the same core human tendency to automatically associate arbitrary information with ingroup and outgroup.

Moreover, the results of Experiments 4 and 5 provide new insight for interpreting the results of Experiments 1–3. Note that in Experiments 4 and 5, our monkey subjects increased their vigilance toward objects associated with outgroup members even when pictures of these group members were absent. These results suggest that the results we observed in Experiments 1–3 cannot be due to any idiosyncratic aspects of the specific photographic images used as test stimuli in these studies. Indeed, monkeys in Experiments 4–5 showed essentially the same outgroup vigilance pattern even when monkey photographs were absent on test trials. The results of Experiments 4 and 5 thus provide further evidence that our results are due to processing—and representing—group information as opposed to subtle low-level aspects of the photographs used.

Though we now know that a nonhuman primate species will readily respond to ambiguous stimuli as though it belongs to the group it is associated with, as humans we do more than just display appropriate behavior toward those in and out of our group. Humans not only recognize, distinguish, and respond to ingroup and outgroup members differently but also *evaluate* these individuals differently, holding negative attitudes toward those in outgroups (Heider, 1958). The most compelling case for intergroup processes being similar between human and nonhuman primates would be if nonhuman primates showed similarly valenced attitudes toward ingroup and outgroup members.

The aim of the next set of studies was to explore whether macaques automatically evaluate ingroup members positively and outgroup members negatively. To do so, we developed a task that

mimicked human methods, such as the IAT (Greenwald & Banaji, 1995), that have been used to measure the associative strength among concepts. Such IAT methods have revealed that humans have significantly more positive implicit attitudes toward those in our own group than toward those who belong to other groups in a variety of different domains: race (e.g., Gawronski, Ehrenberg, Banse, Zukova, & Klauer, 2003; Greenwald, McGhee, & Schwartz, 1998; Powell & Williams, 2000), sexual orientation (e.g., Banse, Seise, & Zerbes, 2001), religion (e.g., Vargas, von Hippel, & Petty, 2004), political orientation (e.g., Knutson, Wood, Spampinato, & Grafman, 2006), and food preference (e.g., Karpinski & Hilton, 2001), among others.

Unfortunately, we were unable to test our free-ranging macaque subjects on a standard IAT for obvious reasons. As such, we had to modify the procedure significantly for use with this population. Importantly, our new method uses the same logic as the human IAT: The more two categories are conceptually linked, the more quickly these two categories should be processed when presented together. One method that has been used to look at processing speed in nonverbal populations is the habituation paradigm. In this procedure, subjects are shown a stimulus repeatedly until they “habituate” or begin to get bored and stop paying attention.

As this method is used to determine how nonverbal subjects group and process the events they see, we used a modified habituation paradigm to look at macaques’ associations between two different sets of objects: ingroup/outgroup faces and positive/negative natural stimuli. We hypothesized that monkeys should habituate more quickly to sequences that involve consistently valenced information (e.g., a sequence of two kinds of good images or a sequence of two kinds of bad images) than to sequences that are inconsistent in valence (e.g., a sequence alternating between good and bad images). In this way, we were able to use differences in habituation rates to explore the extent to which macaques link ingroup faces to positive stimuli and outgroup faces to negative stimuli.

Experiment 6

Method

Subjects. We tested 78 macaques from Groups F, R, HH, and KK. Additional monkeys ($n = 57$) were approached but were excluded because of interference, disinterest, or experimental error.

Apparatus. We used a black foamcore box (61 cm long \times 31 cm high \times 20 cm deep) with a window on the front covered by a white foamcore occluder. When the occluder was removed, a 20 cm \times 20 cm photo could be seen through the window. The photos used in this experiment were 12 headshots of adult male monkeys, three each from Groups F, R, HH, and KK (matched for age between groups), three images of positive objects (fruits), and three images of negative objects (spiders). To counterbalance specific photographs used in this study, we tested F and R group subjects with the F and R monkey photographs, and the HH and KK group subjects with the HH and KK photographs. This design allowed us to ensure that an individual target face photo would be used both as an ingroup and outgroup face depending on the group of the subject being tested. Our fruit and spider images involved high-resolution images of fruits and spiders

taken from the Internet. The monkeys in this population are familiar with both spiders (several species are native to the island) and fruits (which are typically brought on the island by human experimenters). However, to balance the novelty of the object stimuli used, all the target images presented involved photographs of fruits and spider species that (at least to our knowledge) are nonnative to the island.

Procedure. We developed a new measure of implicit attitudes, the Looking Time Implicit Association Test (LT-IAT), on the basis of its resemblance to the IAT, used extensively with adult and young humans (Baron & Banaji, 2006; Dovidio, Gaertner, Kawakami, & Hodson, 2002; Fazio & Olson, 2003; Greenwald & Banaji, 1995). In the LT-IAT, subjects were shown a six-trial habituation sequence (see Figure 6) consisting of three photos of male monkey faces (either all *ingroup* members or all *outgroup* members) alternating with three pictures of objects (either all positive *fruit* images or all negative *spider* images).

This led to four different possible sequences: ingroup/fruit, ingroup/spider, outgroup/fruit, and outgroup/spider. Note that two of these sequences—ingroup/fruit and outgroup/spider—involved categories of presumed *consistent* valence, whereas the other conditions—ingroup/spider and outgroup/fruit—involved categories of presumed *inconsistent* valence. That is, if monkeys attach a positive valence to ingroup members, then they should habituate, or lose interest more rapidly, when viewing such consistent sequences in which ingroup members were paired with positive fruit images than when viewing inconsistent sequences in which those ingroup members were paired with negative spider images.

Similarly, if monkeys attach negative valence to outgroup members, then subjects should habituate more quickly to consistent sequences involving outgroup members and spiders than to inconsistent sequences pairing those outgroup members with fruit. In turn, if monkeys do not evaluate ingroup members positively and outgroup members negatively, then there should be no difference in the habituation rates between the so-called “consistent” and “inconsistent” sequences.

Sessions in Experiment 6 consisted of six 10-s trials. As in Experiments 1–5, the presenter and cameraperson would set up 2–4 m from a solitary subject. Each trial began when the presenter removed the occluder and called “now.” After 10 s had elapsed, the cameraperson would call “stop,” and the presenter would replace the occluder, hiding the photo from view. The presenter would then switch photos before the next trial.

To reduce bias, the cameraperson remained blind to the test condition and thus was able to decide whether trials should be aborted. In addition, the condition presented to each monkey (ingroup/food, ingroup/spider, outgroup/food, or outgroup/spider) was determined randomly using a spinner after each subject was chosen.

Coding. A single coder blind to the experimental condition analyzed looking for each trial. Unlike Experiments 1–5, in Experiment 6, the coder merely coded looking toward the display (as opposed to looking away from the display) for each of the six 10-s trials. A second blind coder analyzed 10 sessions (60 trials) to establish reliability ($r = .88$).

Results

We first explored whether monkeys showed different patterns of habituation across the consistent and inconsistent sequences. Specifically, we predicted that monkeys would reduce their looking over the course of the six trials in the consistent sequences but not in the inconsistent sequences. To test this prediction, we analyzed subjects’ duration of looking on each trial using a repeated measures ANOVA with trial (one to six) as a within-subject factor and sex (male or female) and condition (consistent or inconsistent sequences) as between-subjects factors. On the whole, monkeys showed the expected pattern of performance, looking longer overall at inconsistent sequences than at consistent trials, $F(1, 74) = 6.05$, $p = .016$. Interestingly, however, this pattern of performance did not seem to hold across our entire subject population (see Figure 7). Indeed, we observed a significant interaction between sex and

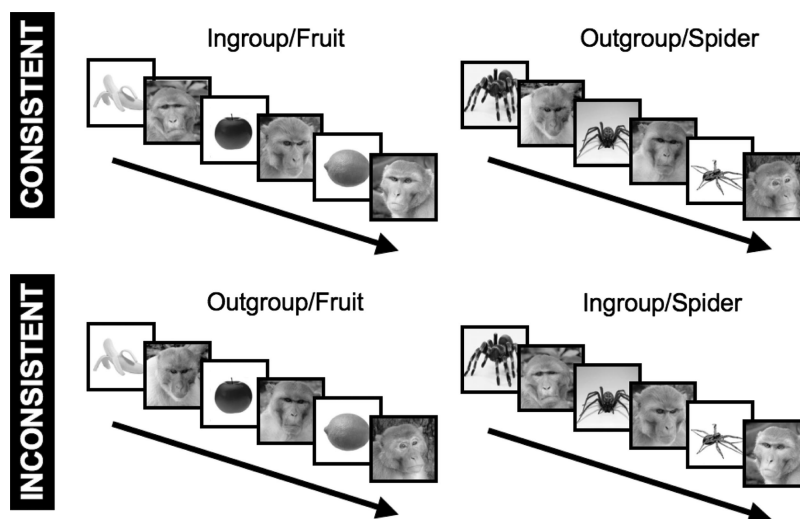


Figure 6. A depiction of the habituation sequences used in Experiment 3. Monkeys were either habituated to a consistent sequence (ingroup/fruit or outgroup/spider) or an inconsistent sequence (outgroup/fruit or ingroup/spider), each involving six different images.

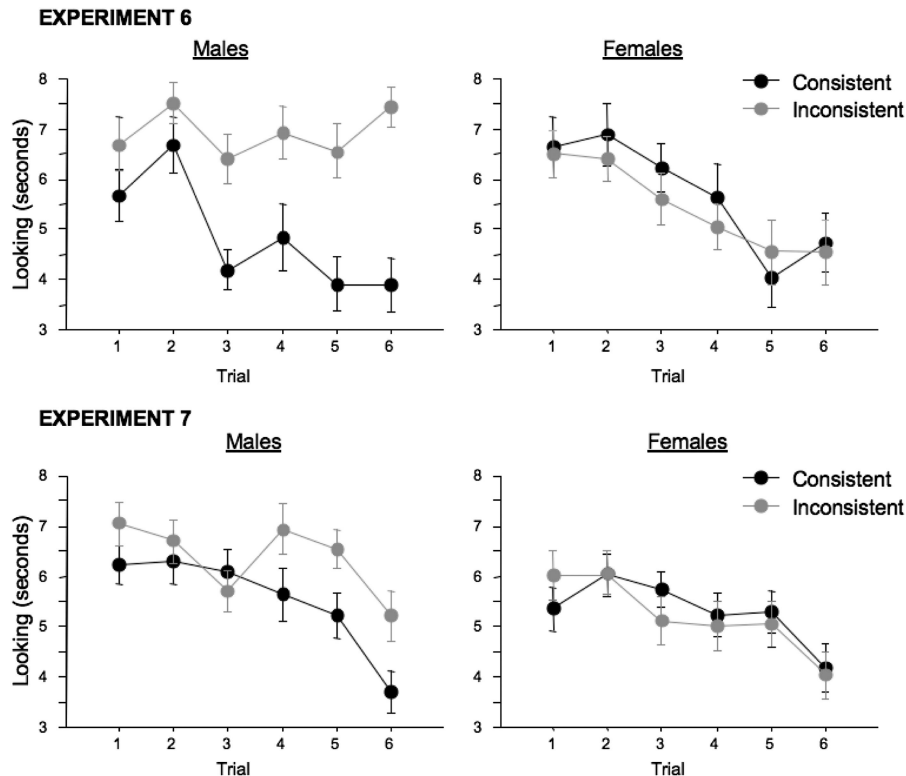


Figure 7. Monkeys' duration of looking across trials for consistent and inconsistent sequences in Experiments 3 and 4. Male, but not female, monkeys took longer to habituate to inconsistent than to consistent sequences. Error bars represent standard errors.

condition, $F(1, 74) = 9.88, p = .0024$. To explore this issue, we split our data across sex, and we reanalyzed subjects performance using trial (one to six) as a within-subject factor and condition (consistent or inconsistent sequences) as a between-subjects factor. In male monkeys, we observed a significant interaction between trial number and condition; male monkeys habituated more quickly to consistent sequences than to inconsistent sequences, $F(5, 185) = 3.06, p = .011$. We also observed a main effect of condition in male monkeys; male monkeys showed overall longer looking to inconsistent than to consistent sequences, $F(1, 37) = 17.26, p = .0002$. Female monkeys, in contrast, failed to show either an overall difference between consistent and inconsistent sequences—main effect of condition, $F(1, 37) = 0.22, p = .65$ —or a difference in habituation to the two sequences: interaction between condition and trial, $F(5, 185) = 0.46, p = .81$.

Discussion

Overall, monkeys who saw ingroup faces paired with fruit images or outgroup faces paired with spider images (consistent sequences) habituated more quickly than those subjects who saw ingroup faces paired with spider images or outgroup faces paired with fruit images (inconsistent sequences). Interestingly, however, this pattern was not observed across all subjects; male monkeys, but not female monkeys, showed differential habituation rates across consistent and inconsistent sequences.

This pattern suggests that male macaques valence ingroup members positively (i.e., more like fruit images) and outgroup members negatively (i.e., more like spider images). Importantly, we saw no differences between either of the consistent sequences or either of the inconsistent sequences, suggesting that monkeys associate ingroup members and positive items equally strongly as outgroup members and negative items. This represents the first work to show human-like evaluations of ingroup and outgroup members in a nonhuman species, suggesting that group processing mechanisms in these primates may be more qualitatively similar to those of humans than previously thought.

One puzzling aspect of these results, however, is the sex difference we observed in the habituation studies. When we began this research, we were not expecting to see a sex difference and the first several studies supported this expectation. This leaves us with the observed result that whereas male macaques responded differently to inconsistent and consistent sequences, female macaques failed to show any discrimination between the two kinds of sequences. Further, as we observed in Experiments 1–5, both male and female macaques are equally adept at discriminating and displaying vigilance appropriately toward ingroup and outgroup members. As such, the sex difference we observe cannot reflect female subjects' failure to discriminate ingroup and outgroup members but rather seems to reflect a sex difference in the degree to which monkeys *valence* ingroups and outgroups.

One alternative possibility, however, is that the sex difference observed in Experiment 6 resulted from our use of male faces as stimuli. Although subjects of both sexes were able to distinguish the male faces presented in Experiments 1–5, it is possible that monkeys are better at evaluating group members positively or negatively when viewing faces of their own sex. To address this issue, Experiment 7 replicated Experiment 6 but used female instead of male faces as stimuli.

Experiment 7

Method

Subjects. We tested 141 rhesus macaques from Groups F, R, HH, KK, V, and S. Additional monkeys ($n = 167$) were approached but were excluded because of interference, disinterest, or experimental error.

Procedure. The procedure was identical to Experiment 6, and the apparatus used was the same, except that we used 18 headshots of adult female macaques, three each from Groups F, R, HH, KK, V, and S (matched for age between groups). To counterbalance the specific photographs used in this study, we tested F and V group subjects with the F and V monkey photographs, HH and KK group subjects with the HH and KK photographs, and R and S group subjects with the R and S photographs.

Results

We analyzed male and female subjects' duration of looking using a repeated measures ANOVA with trial (one to six) as a within-subject factor and condition (consistent or inconsistent) as a between-subjects factor. This study revealed the same pattern of performance as Experiment 6: Male subjects, $F(5, 330) = 2.44$, $p = .035$, but not female subjects, $F(5, 350) = 0.85$, $p = .51$, showed a significant interaction between condition and trial number. This pattern suggests that male, but not female, subjects differentially habituated to inconsistent and consistent sequences (see Figure 7).

Discussion

As in Experiment 6, male macaques showed differential habituation patterns to consistent and inconsistent sequences, losing interest more quickly when viewing the former. When shown sequences of ingroup faces paired with positive images or outgroup faces paired with negative images, male monkeys (but not female monkeys) decreased their looking over time more quickly than when shown either of the reverse pairings. These data suggest that the effects we observed in Experiment 6 were not related to processing same-sex faces differently from opposite-sex faces but instead are in some way because of the sex of the subject, with only male monkeys reliably evaluating ingroup faces positively and outgroup faces negatively. The results of Experiment 7 therefore replicate those of Experiment 6, suggesting male macaques automatically evaluate ingroup and outgroup members differently, and provide further suggestion that male and female macaques may differ in the extent to which they valence members of their own and other groups.

One way to explain the sex difference in performance we observed is to consider more specifically the roles that male and female primates play in intergroup aggression. Intergroup hostilities in primates often involve male primates more so than female primates (Carpenter, 1972; Cheney, 1987; Wilson & Wrangham, 2003). Even in female philopatric species, such as macaques, males tend to play a more active role than females in aggression and intergroup conflict (e.g., Boelkins & Wilson, 1972). Such a pattern of increased male involvement in intergroup activities has caused some researchers (e.g., Wrangham & Peterson, 1998) to argue that male primates are specialized for intergroup interactions.

Indeed, some researchers have used this pattern in primates to argue that a similar sex difference may be observed in human intergroup cognition studies as well (Baumeister & Sommer, 1997; Schaller & Neuberg, 2008; Sidanius & Pratto, 2001). Such a hypothesis is borne out in numerous empirical studies. On explicit measures, men consistently show more prejudice than women (e.g., Akrami, Ekehammar, & Araya, 2000; Altemeyer, 1998; Ekehammar & Sidanius, 1982; Hoxter & Lester, 1994; Moore, Hauck, & Denne, 1984; Sidanius & Pratto, 1999; Whitley, 1999). Similar patterns are also observed on more implicit measures of prejudice; although men and women both show similar patterns of grouping on IAT tasks, in some cases men show stronger intergroup biases than women (Nosek et al., 2007).

One difference between the results of Experiment 6 and those of Experiment 7 is that we did not find a main effect of consistent versus inconsistent sequences on the rate of subjects' habituation when female stimuli were used. For female stimuli, the differential rate of habituation across consistent and inconsistent sequences occurred only in the latter half of trials. This pattern makes sense, as the sequences grow increasingly more consistent or inconsistent after more exemplars are presented over trials. Nevertheless, it is not clear why we observed a difference in the monkeys' speed of detecting such consistency across Experiments 6 and 7. One possibility is that our monkey subjects may treat male stimuli as more representative of the group than female stimuli, which could increase the speed with which subjects processed the consistency of sequences in Experiment 6 relative to Experiment 7. In spite of this difference across the two experiments, both Experiments 6 and 7 showed a robust effect of condition across trials, suggesting that our general IAT effect does obtain for both male and female stimuli.

Because this is the first demonstration of an IAT result in nonhuman primates, we do not know the full range of intergroup effects that will emerge in the future. From these first studies, however, we can conclude that the intergroup preference observed with the LT-IAT and using these stimuli and groups holds for male monkeys. It is possible that our looking time test of intergroup preference is subtle enough that it detects a gender different that will vanish when we construct tests that are more powerful detectors of intergroup behavior. Especially if that is the case, then these studies will be particularly important as a test with a sufficiently low threshold for detection of intergroup preference to demonstrate a sex difference.

General Discussion

The seven experiments reported here represent the first test of intergroup processing in a nonhuman species. Taken together, our results demonstrate that one nonhuman species—the rhesus macaque—shares several critical features of human intergroup cog-

nition. First, rhesus monkeys spontaneously distinguish members of their social group from members of other social groups. Most impressively, rhesus monkeys seem to identify ingroup and outgroup members from stimuli that are contextually quite impoverished; our subjects recognize an individual monkey as an ingroup or outgroup member from a single photograph presented in the absence of any other information.

Further, this grouping distinction is not based on a simple recognition of familiarity. Indeed, even when familiarity is pitted against current group membership, monkeys correctly recognize which faces are ingroup and which are outgroup. Macaques also flexibly update their group representations on the basis of information about past and current group membership. Monkeys show a clear sense of the current ingroup even for ingroup members who have joined their group in the past few months. Additionally, macaques appear to tag arbitrary objects with group membership on the basis of a brief (2-s) association between a novel object and a member of a particular group. Once tagged with grouping information, monkeys respond to these novel objects with the same increased vigilance as they devote to the group members themselves. Finally, male monkeys show positive attitudes toward those in their ingroup and negative attitudes toward those in their outgroup: They habituate more quickly to sequences that consistently link positive images and ingroup members or negative images and outgroup members than to sequences that contain the opposite, more inconsistent pairings.

These studies provide the first evidence that several cognitive and affective processes—particularly a tendency to view the outgroup as a negative entity—are not unique to human intergroup processing. Although the primatological record suggests many reasons to suspect that intergroup interactions might not be unique to humans, our studies provide the first systematic evidence that such interactions are likely to be subserved by *nearly identical cognitive mechanisms* in human and nonhuman primates. Indeed, these results hint that human intergroup processing may resemble that of our evolutionary ancestors more than we imagined.

Further, in studying the nature of these mechanisms in a primate species, we have learned more about how such biases operate in humans. In particular, our findings present some potential constraints on the kinds of mechanisms that are likely to operate in humans. For example, the observation that macaques—who lack rich motivational processes—share human-like intergroup attitudes poses a challenge for strong versions of motivational theories of intergroup biases. Macaques almost surely lack rich existential concerns, assimilation motives, and a human-like sense of self, yet they still exhibit a bias toward their ingroup in the IAT task we presented in Experiments 6 and 7. This finding presents a problem for any motivational account that requires such rich processes to explain all aspects of human ingroup biases (e.g., Abrams & Hogg, 2001; Brewer, 1991; Hogg, 2000; Jost & Banaji, 1994; Pyszczynski et al., 1997, 1999; Tajfel & Turner, 1979; Taylor & Moghaddam, 1994). Although it is clearly possible that these motivations exaggerate intergroup biases in humans, our macaque results suggest that such motivations cannot be *necessary* for these biases to emerge (at least in their most rudimentary form). Instead, our results hint that other less rich—but perhaps evolutionarily older—motivations (e.g., a drive for hierarchical dominance; e.g., Sidanius, 1993; Sidanius & Pratto, 1993) may be more critical for the initial emergence of these biases than previously suspected.

Our results also provide some hints about the kinds of cognitive processes that may govern intergroup biases in humans. Some researchers have posited that human intergroup biases result from fast, encapsulated, and automatic mechanisms that require little in the way of controlled processes (e.g., Fiske, 1998). Because monkeys clearly possess the same kinds of automatic processes as humans, our findings fit nicely with accounts that explain human intergroup bias in terms of these automatic mechanisms.

In addition to discriminating between specific theoretical accounts in humans, the present results also provide broader hints about the cognitive processes that are and are not required for the development of intergroup biases. Our results suggest that at least some aspects of intergroup biases are not solely dependent on human language. Some psychologists have hypothesized that linguistic labeling, such as the use of collective pronouns (e.g., Perdue, Dovidio, Gurtman, & Tyler, 1990), is likely to play a significant role in shaping and maintaining prejudice (see also Fishman, 1956). Indeed, even Allport (1954/1979) famously argued that noun labels “cut slices” in way that leads us to form classifications and biases.

In contrast to these predictions, the results of the present study suggest that organisms who lack linguistic labels can also “cut slices” in their social world. Specifically, our macaques results demonstrate that nonlinguistic creatures also divide the world into distinct ingroups and outgroups, associate and categorize novel stimuli associated with these groups, and valence these groups as “good” or “bad”—all in the absence of language. Such findings hint that language may not be as necessary in human social categorization as some social psychologists have previously thought. Although it is possible that language can (and surely does) redirect intergroup biases toward arbitrarily constructed social groups, the biases themselves appear to predate language. The challenge now is to determine which aspects of human intergroup biases require linguistic shaping and which aspects of the biases can instead emerge in the absence of linguistic processing at all.

Beyond their implications for social psychological theories about the nature of human intergroup processing, our findings also have important implications for the field of primatology as well. Although primatologists have long known that macaques behave differently with ingroup and outgroup individuals (e.g., Boelkins & Wilson, 1972; Rawlins & Kessler, 1987), little work to date has examined the proximate mechanisms that subserve these behaviors. Our present results provide new insight in this regard, suggesting that primate intergroup behavior may be subserved by the same proximate mechanisms as those underlying the intergroup behavior of our own species. The current studies therefore suggest that primatologists may gain new insight into the nature of primate intergroup behaviors by turning to intergroup cognition in our own species.

Our findings provide new evidence that human-like grouping mechanisms are likely to be evolutionarily quite ancient, possibly even present in the macaque–human common ancestor that lived 25 million years ago. This long evolutionary history suggests that intergroup processes may map onto adaptive problems that have long faced our primate ancestors. Such new insights provide increased clarity on recent debates regarding how and why humans find some groups—such as race—to be so cognitively salient. Kurzban et al. (2001), for example, have argued that race could not have been a relevant social category throughout human evolution, and thus our human mind was not designed to encode race as a special salient category. Instead, these researchers have hypothe-

sized that race is salient in modern times only because it maps onto other categories that were crucial for early humans' survival, such as coalitional alliances. Finding intergroup biases in macaques—who lack groupings like race or ethnicity—lends credence to this theory as well as to the possible adaptive nature of these processes.

Our results suggest that primate biases are rooted in categorical structures much older than the prevalent modern day social categories such as race and religion. Indeed, our results suggest that social psychologists would be well-served to think of even *more* ancient adaptive problems when trying to explore the reasons underlying the evolutionary development of human intergroup biases.

These results also raise new questions about the extent to which human intergroup biases are likely malleable over human development. Cognitive processes old enough to be shared by macaque species are often thought to be modular, informationally encapsulated, and thus more difficult to override (e.g., Chen et al., 2006; Santos, 2004). In contrast, we already know that there exists a great deal of flexibility in human intergroup cognition and that biases, stereotypes, and prejudiced beliefs *can* be mitigated. We are now poised to ask the question of whether the same flexibility affects primate group processing as well. As one example, Olsson, Ebert, Banaji, and Phelps (2005) demonstrated that humans can more readily be conditioned to fear other-race members than same-race members but that this bias in fear conditioning can be diminished with interracial romantic relationships. Might the same be true in rhesus macaques, a species in which female macaques sometimes mate with outgroup males? Our studies suggest that a similar degree of flexibility may be observed in monkeys and in humans, and we are now in position to directly test such questions empirically. On the other hand, humans appear to essentialize their social categories, treating them as stable and inductively relevant. It is likely that macaques—who probably lack essentialist reasoning—do not treat categories with this level of stability. In this way, macaques may exhibit more flexibility than humans when categorizing and evaluating some social groups. Indeed, future work should explore in detail the flexibility with which macaques categorize and valence novel social groups.

Importantly for any future studies, the present experiments provide a new methodology by which these and other questions of human social psychological phenomena can be explored in greater detail in nonverbal populations—both evolutionarily and developmentally. The present vigilance (Experiments 1–5) and LT-IAT measures (Experiments 6–7) are well-equipped to explore social categories and group preferences in human populations much younger than the ones previously tested in any intergroup studies to date. Indeed, our LT-IAT method was designed from habituation measures that have been used with even newborn infants. Having a method to test ingroup biases and preferences in such experience-free infant populations is particularly significant: Having this new pipeline will mean that developmental researchers no longer have to focus solely on older children, who necessarily have many of the same kinds of cognitive skills and motivations as adults. As such, our method can be adapted to truly determine the role of these influences in the development of human intergroup cognition by testing even younger developmental populations.

Our findings do, however, raise some new questions about the nature of intergroup cognition across human and nonhuman primates. For example, Experiments 6 and 7 both found unexpected sex differences, whereby male subjects evaluated ingroup mem-

bers positively and outgroup members negatively, and female subjects failed to do so altogether. Although similar sex effects exist in humans in that men sometimes show stronger biases than women, in all cases women still *do* show the same types of biases as men, just to a lesser extent. As we do not see any sex differences in Experiments 1–5, it seems that male and female subjects are equally able to distinguish ingroup and outgroup members, readily ascribe group status to ambiguous stimuli, and respond to each with appropriate vigilance; the difference is that female primates do not seem to valence the social categories they form in the same way as male primates, evaluating ingroups positively and outgroups negatively. Interestingly, human sex differences in intergroup tasks also appear to be most robust in cases of automatic evaluations, ones that involve a valencing of ingroup and outgroup members (Nosek et al., 2007). This similarity hints that more work may be needed to explore individual and sex differences in the nature of group preferences in humans.

Our results also raise the question of *why* such a sex difference might emerge in monkeys (and also humans). We see a couple of possible answers. First, there are a number of salient differences in the evolutionary life histories of males and females that predict differences in intergroup interactions; sex differences in behaviors as diverse as parental investment, mate choice, or level of aggression may cause patterns of grouping to be especially salient to males in a variety of primate species, including humans. Another possibility is that the robust nature of the sex difference we observed is the result of studying only one particular nonhuman species. It is largely possible that the differences we observe in the present studies are due to the specific grouping pattern of rhesus macaques. Put differently, perhaps the results we observed are *rhesus*-specific rather than male-specific, caused in a large part by the female philopatric rhesus grouping structure. One way to tease apart these explanations would be to run similar comparative studies on species with different grouping patterns. For example, chimpanzees live in a male philopatric society in which female chimpanzees are the ones to transfer groups at adolescence. It is possible that testing this species on our LT-IAT task would reveal the reverse sex difference, with female subjects showing IAT effects more robustly than male subjects. Future studies could therefore profit from applying these tests to other comparative populations to determine the roots of the sex difference we have observed. Testing different primate species will also help us understand the extent to which particular social systems, levels of stratification, and group structures might influence intergroup processing.

In summary, the present results provide strong evidence that adult human intergroup attitudes are not simply the result of cultural training and experience; instead, our findings suggest that such attitudes reflect evolved tendencies that are shared broadly across the primate order. The very affective and cognitive mechanisms observed in our own species may underlie the often-aggressive intergroup interactions seen in other primates. The human tendency to divide the world into “us” and “them” may thus be the result of mechanisms that were cognitively and affectively adaptive early in our evolutionary ancestry to promote coalitional relations and to facilitate processing of and success in hostile intergroup interactions (Cosmides, Tooby, & Kurzban, 2003; Sidanius & Pratto, 2001; Singer et al., 2006).

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Received March 4, 2010

Revision received June 14, 2010

Accepted June 17, 2010 ■