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The Ontogeny of Social Comparisons in Rhesus Macaques (*Macaca mulatta*)

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Abstract

This longitudinal study investigated the development of social contrast-negative responses to inequitable rewards in rhesus macaques (*Macaca mulatta*). Although responses to inequity by humans appear universal, this is something that develops with age. Infants first recognize inequity when around 18 months old and respond to it only when they are around 3 years old. To date, however, there have been no studies of the ontogeny of the inequity response in any species other than humans. To address this, we used an exchange paradigm, in which 10 pairs of rhesus monkeys had to exchange inedible tokens with the experimenter to get food rewards that differed in quality depending on the condition. All subjects were tested first when they were an average of 17 months old and a subset, of four pairs, was tested again a year later. Subjects responded negatively to contrast-recognizing a disparity in expected, as compared to, received rewards based on both social and individual comparisons at the older age, but not at the younger age. Similar to humans, rhesus showed a developmental trajectory to social comparison, providing the first evidence for the ontogeny of this response in a non-human species.

Keywords: *Macaca mulatta*; Rhesus macaque; Social comparison; Inequity; Ontogeny; Social cognition

Introduction

For adult humans, the concept of fairness appears to be universal [1], but the ability to recognize or react to an unequal distribution (inequity) is something that develops with age [2-4]. An inequity response occurs if an individual refuses a poor-quality reward for completing the same task as their partner, who received a more desirable reward [5]. In humans, this behavioral response to inequity has been widely studied in both psychology [6, 7] and economics [8], and recently, there has been a surge of interest in how other species respond to inequitable outcomes and what this can tell us about the evolutionary origins of the human response. To date, however, there have been no studies of the ontogeny of the inequity response in any species other than humans.

Only certain (adult) nonhuman primate species compare their outcomes to those of others and respond to inequity (*Cebus apella* [9]; *Pan troglodytes* [10]; *Macaca fascicularis* [11]). The primary aim of this study, therefore, was to identify whether an, as yet, unstudied species (rhesus macaques, *M. mulatta*) responded to inequity and, if so, examine the ontogeny of this response. This would not only provide information specifically about rhesus macaques, but would also give insights into whether the developmental trajectory of this response in nonhuman primates mirrors that seen in human infants and children.

We selected rhesus macaques as our study species for a number of key reasons. Although no study of social contrast has been conducted with rhesus macaques, long-tailed macaques (*M. fascicularis*), which are typified by similar natural histories to rhesus macaques [12-15], have recently been shown to respond negatively to inequity [11]. Additionally, as a response to inequity, requires monitoring rewards gained by social peers, it is notable that *Macaca* species are able to follow conspecifics' gaze direction, which is essential for monitoring rewards received by social peers (*M. mulatta*, *M. arctoides*, *M. nemestrina* [16]; *M. nigra* [17]; *M. fascicularis* [18]). *Macaca* species are also able to

socially learn from conspecifics, leading to the emergence of behavioral traditions (*M. fuscata* [19,20]) and appear to recognize when they are being imitated (*M. nemestrina* [21]). Finally, they are known to be able to assess differences in quantities (*M. mulatta*, [22,23]). Given these findings, the rhesus macaque is a logical nonhuman primate species in which an investigation is to start regarding the ontogeny of inequity aversion in primates.

Longitudinal and microgenetic designs are often used with children to gain insight into the early developmental trajectory of cognitive processes or behavioral responses [e.g., 24,25]. Such an approach is key to understanding ontogeny; knowing how, and when, certain changes occur allows greater understanding of their interplay with other key developmental stages. Longitudinal designs, however, are less commonly possible with nonhuman primates (but see, for example, [26-28]). Taking a lead from the field of developmental psychology, we studied a single cohort of monkeys, born in the same year, at the same facility, over the course of a year. This enabled us to investigate ontogenetic changes whilst controlling for potential environmental confounds such as rearing histories, caging and husbandry types, and weather differences. Infant rhesus are weaned from their mother at approximately one year of age, when the next infant is typically born [29,30]. From weaning to sexual maturity (at around 36 months old), in addition to the typical changes in their behavioral repertoire [31],

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rhesus macaques show marked changes in their learning and problem solving abilities [32] and social cognition [33]. Perhaps such cognitive changes interplay with the development of social contrast effects. To answer this, we studied monkeys first after they had been weaned and again a year later when they were closer to sexual maturity.

Although it was likely that rhesus macaques would respond to inequity given that long-tailed macaques did so [11], given their relatively more despotic nature (which may lead to a lack of expectancy for equity [33]), we did not know whether they would be more likely to respond to inequity [10] or to frustration, as has been seen in other monkey species (e.g., *Saimiri* spp. [34]).

Methods

Subjects and testing environment

The test subjects for this study were 20 rhesus macaques (*M. mulatta*), housed at the Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, USA (KCCMR). KCCMR is fully accredited by the American Association for the Assessment and Accreditation of Laboratory Animal Care-International (AAALAC-I). Approval for this study was gained from the Institutional Animal Care and Use Committee (IACUC approval number: 06-88-04488) of the University of Texas MD Anderson Cancer Center.

To assess whether the rhesus macaques' response to inequity changed with age, monkeys were assessed using a longitudinal design. 20 monkeys (12 females, 8 males) were tested initially, when their average age was 17 months (range: 12-19 months). The following year, a subset of these (N=8, 6 females, 2 males) were tested again when their average age was 27 months. Unfortunately due to circumstances beyond our control, we were unable to test 12 of the 20 monkeys at the second time of testing, but did test all those that were available.

At KCCMR, rhesus macaques are mother-reared in harem groups and thus have experienced species-typical social interactions; such social competence is critical when testing social behavior and cognition. At approximately seven months of age, the monkeys are weaned and moved to mixed-sex peer groups. Thus, all the monkeys in this study had had a minimum of six months to adjust to their new housing conditions, prior to the beginning of the study, making it extremely unlikely that their responses in the test conditions were due to social stressors resulting from the weaning process.

Due to the fact that it was difficult to separate a pair from their larger 'home' group (comprised of approximately 15 individuals) for testing, the monkeys were temporarily housed in pairs in highly enriched indoor/outdoor enclosures (2.7 m×3 m×3.5 m). All the pairs of monkeys were comprised of individuals from the same home group, so they were familiar with their partners prior to testing. Each pair was given one week to adjust to their pair housing prior to the testing phase. During this pre-test week, for familiarization purposes, the experimenter visited the monkeys once a day, everyday, to ensure that all the monkeys were comfortable coming up to the front of the caging, exchanging tokens with the experimenter, and taking food from the experimenter. During this week, the experimenter rewarded the monkeys with peanuts and dried banana chips, both highly desirable foods that were not used as rewards during the test period. Following this and the testing period, which took approximately one month in total, all monkeys were returned to their original home groups. Both when the monkeys were group housed in their home cages, and whilst pair housed for testing, water and commercial monkey chow were

available *ad libitum*. Furthermore, the monkeys continued to receive their two daily meals of fresh produce (a variety of fruits and vegetables) irrespective of the training or testing schedule.

Procedure

To test the potential ontogeny of inequity responses in rhesus, we employed an exchange paradigm, which has been used successfully in cognitive experiments with other macaque species (e.g., *M. tonkeana* [35]) and in many tests of inequity with other primate species [36]. In an exchange paradigm, monkeys are required to exchange inedible rewards with the experimenter to gain food rewards. Within each test session, pairs of monkeys would take turns exchanging tokens with the experimenter until each had been given 20 opportunities to exchange. For every successful token exchange, the monkey was offered a food reward by the experimenter. Depending on the condition, the foodstuff would either be a highly preferred item, or one that was less preferred by the monkeys within each pair. Refusals to such 'unfair' payments indicate dissatisfaction [9]; a response that is also shown by humans in comparable test settings [5].

The specific exchange behavior required of the monkeys was an adaptation of that used successfully with New World monkeys to identify contrast effects [9,34]. To gain a reward, each monkey had to exchange a plastic token (a PVC tube 15 cm long and 2 cm in diameter) with the experimenter. The experimenter held the token flat and passed it through the bars toward the monkey whilst maintaining a hold on the end still protruding out of the cage. For a successful exchange, the monkey had to push the end of the token into their cage, up and out, and then back toward the experimenter so that the tip passed through a 180 degree arc. Training for the exchange procedure, which was conducted by the experimenter using shaping and positive reinforcement was begun while the monkeys were group housed in their home cages and continued during the first week, the monkeys were pair housed prior to testing to ensure that all monkeys could exchange. A monkey was considered 'trained' when he or she would make 20 consecutive exchanges in one session. As stated above, the foods used for this training were distinct from those identified as the HR and MR and included dried banana chips, peanuts and dried papaya. Training lasted from two days to two weeks for each monkey.

Food preference tests

To determine the test rewards, the experimenter conducted food preference tests with each pair prior to testing. To be chosen as an High-value Reward (HR), in a dichotomous preference test [37], the monkey had to select that food over the other food item 80 percent of the time on two tests of 10 trials each, run on two separate days. Furthermore, each monkey had to eat 10 pieces of the Medium-value Reward (MR) in a separate session when it was the only food offered to the monkeys (as well as being the only food visible or available for that session). For all pairs in year 1, the HR was a mini-marshmallow and the MR was a raisin. These food preference tests were repeated prior to testing in year 2, and for three of the four pairs, the food rewards remained the same, but for one pair, the HR used was a mini-marshmallow and the MR was a piece of Cheerios® breakfast cereal.

Experimental conditions

All testing took place in the large indoor/outdoor enclosures (2.7 m×3 m×3.5 m) in which the pairs of monkeys were housed during the test period. Following Brosnan et al. [10], the subject and partner were tested as a pair in the same cage with no screen or divider between them. During the week prior to testing, the monkeys were trained to

come to the front of the cage and sit on a perch to exchange the tokens with the experimenter. From this position, the monkeys could clearly see whether their partner exchanged, which food they were offered and whether they accepted it. All testing occurred in the early afternoon, midway between the monkeys' two meals of primate chow and in the midst of multiple daily produce enrichment periods.

Each pair of monkeys was tested in a condition designed to test their response to inequity, the Social Contrast condition (SCC). Two control conditions were also included. The first was an Individual Contrast Condition (ICC), while the second was an Equity Control (EC). In the SCC, the subject received an MR for each successful token exchange while their partner received a more preferred HR for all exchanges. In the ICC, prior to each exchange opportunity the experimenter showed the monkey an HR, but once the monkey had exchanged the token successfully, they were offered an MR. This procedure controlled for frustration effects potentially elicited by seeing, but not being able to obtain, the HR irrespective of whether their partner received it [39,40]. Finally, the EC, in which both the subject and the partner received MRs for each exchange ensured that both monkeys were willing to work for the MR when no other reward was offered to them. During each test, both food rewards were held in cups in plain sight of both monkeys regardless of the condition (e.g., HRs was present and visible even in the equity control, when no monkey received an HR). Each monkey in every pair was tested twice as the subject in all three conditions and all pairs were tested in the conditions following a randomized schedule. Tests were run on separate days such that no monkey participated as either a subject or a partner more often than one time per day.

Subjects could return the token (coded as accept) or refuse to do so [10]. A refusal of the token was classed as either not approaching or touching the token within 10 seconds, pulling the token into the cage and not returning it to the experimenter within 30 seconds, or taking the token and giving it to their partner (note that during testing the monkeys never gave their token to their test partner). Similarly, for every successful exchange, monkeys were offered a food reward which they could either accept or refuse. Food refusals were coded as the monkey not taking the food item from the experimenter within 10 seconds, taking the food but pushing it back out of the cage uneaten, accepting the food item but not eating it within 30 seconds, or giving the food item to their partner. No monkey ever refused a food item, thus all analyses relate to refusals of tokens only.

Coding and analysis

All test sessions were coded by the experimenter onto datasheets in real-time during each test session; she noted each monkey's response before commencing the token exchange with the next monkey in the pair. This took roughly 5 seconds. Additionally, all test sessions were videotaped using a Canon ZR950 camcorder and miniDV tapes. After the completion of all test sessions, a random selection of 5% of the trials were blind-coded from the tapes by a Senior Animal Technician from the rhesus colony at KCCMR who is familiar with rhesus behavior, but was unaware of the conditions of this particular experiment. Inter-observer reliability results showed high agreement (Cohen's Kappa, $k=0.83$).

Due to the small sample sizes, nonparametric tests were used throughout. To determine whether rhesus behavior varied between conditions, we conducted nonparametric Wilcoxon signed-ranks tests for related samples (where n = number of pairs and N =number of pairs for which $y_1=y_2$). Specifically, we were interested to learn whether the monkeys refused more in response to inequity or frustration and

so their refusals in the SCC and ICC conditions were compared to those in the EC. Comparisons between males and females were done using nonparametric Mann-Whitney U-tests for unrelated samples. Comparisons of variances in different years were done using Levene's test. We also used McNemar's test to compare the monkeys' responses from their first test session of a particular condition to their second session (within the same age group). All tests were two tailed.

Results

In year 1 (average subject age=17 months), the monkeys neither respond to inequity, nor did they respond to the frustration created in the ICC; there was no difference in the number of refusals that the monkeys made in the ICC compared to the EC (Wilcoxon's signed-ranks test, $T=4$, $n=19$, $N=7$, $P=0.41$) nor was there a significant difference in the number of refusals made by monkeys tested in the SCC compared to the EC ($T=7$, $n=19$, $N=11$, $P=0.66$).

A year later, however, when the monkeys' average age was 26.7 months, the animals in the subset that was studied did appear to make social contrasts and responded to the inequity created in the SCC condition. The monkeys refused more in the SCC compared to the EC ($T=6$, $n=4$, $N=4$, $P=0.048$). No differences were found between the number of refusals made in the ICC compared to the EC ($T=20$, $n=4$, $N=5$, $P=0.242$) suggesting that their refusals in the SCC condition were unlikely to be elicited by frustration effects. Unfortunately, we were only able to test two males at this older age, we were unable to run any meaningful analysis on whether there were sex differences in the monkeys' responses to inequity (as has been reported for chimpanzees [10], and squirrel monkeys [34]).

Discussion

We provide evidence that rhesus macaques (*M. mulatta*) respond to social contrast and show that this sensitivity develops with age. Our results provide the first insight into the development of such a behavioral response and indicate that macaques only become sensitive to inequity (or show a behavioral response to it) at around two years of age. Importantly, the monkeys increased refusals in the SCC condition which appeared to be driven by a response to inequity [9], rather than by frustration at seeing, but not receiving, the more-preferred HRs [39,40]. Perhaps then, it is only with age and experience that a sense of inequity develops universally for rhesus macaques, as has been shown for human infants [41]. This maturation may also relate to physical development of the ventromedial prefrontal cortex which has been shown to develop late in rhesus macaques [42,43], and in humans, it is known to be involved in responses to unfairness [44]. It is known that not every primate species responds to inequity [34], but until comparable tests are run with adult rhesus macaques, we cannot say whether this failure to respond is indicative of the species in general, or rather an age-dependent effect. It will be interesting to determine the degree to which other primate species reveal changes in their responses with age. These results beg for more ontogenetic research into the development of inequity responses. Even for human children, we are only beginning to scratch the surface of the topic [3,41].

While at this stage, we might only be able to infer that both rhesus macaques and human infants show parallel directions in the emergence of inequity aversion, it is interesting to note that they share other common developmental stages [45,46]. Neonatal imitation, for example, is apparent in the first day of life for both human infants [47] and rhesus macaques [48]. Furthermore, rhesus infants show many of the 'Machiavellian' tactics shown by human infants to

increase parental investment and attention, and show these at similar developmental stages [49]. That human infants and rhesus macaques also appear to start responding to social comparisons around the same developmental stage is therefore not surprising. However, despite the seemingly comparable ontogenetic origin of this response in humans, we cannot make direct comparison to our own results because our measures differed (e.g., our procedure measures responses to inequity, not recognition of inequity, as in the studies with very young human infants). It will be interesting to see if future research can untangle recognition versus response in species other than humans, using similar techniques as are used in human infant studies (i.e., measuring looking times [50]).

Like human infants, we note that, perhaps at this young age, the monkeys were 'unable' to resist taking food, irrespective of its quality. The monkeys never refused the food rewards which may indicate that such self-restraint only emerges later during development, as is seen in human infants and children [51], but we note that (adult) squirrel monkeys tested with the same paradigm also showed fewer food, than token, refusals [34]. Perhaps then, although the monkeys' responses reveal a response to the inequity, the food rewards, if offered, may represent potent stimuli that they cannot resist. Using looking times, rather than a behavioral response like 'refusals' may therefore prove to be a more sensitive method to use with young monkeys. Looking times have been used successfully in a number of studies with adult rhesus macaques [52], indicating that it may be a viable measure for infant macaques in tests comparable to those used with human infants [41]. Given that humans and rhesus share other common developmental stages, like neonatal imitation [48], it might be anticipated that young macaques may, like human infants, show recognition of inequity, even if they do not respond to it behaviorally.

We are only just gaining an understanding of the development of this inequity response in human infants and children [3,41]. Without a thorough knowledge of the development of responses of both human children and the juveniles of other species, we will neither be able to fully explain how social comparison develops in relation to other behaviors nor will we understand the evolutionary development of the behavior. This combined ontogenetic and phylogenetic approach is extremely powerful for a full understanding of any behavior, and seems particularly critical here, given the relatively late onset of the inequity response.

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