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Social after-effects of fur rubbing in tufted capuchin monkeys (*Cebus apella*): increases in antagonism and decreases in affiliation

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Abstract

Fur rubbing is often thought to have a social bonding function in capuchin monkeys, yet a recent study found increased levels of aggression and decreased levels of affiliation after fur rubbing bouts in tufted capuchins. This observed decrease in group cohesion may be attributable to increased intragroup competition for fur rub material rather than being a direct effect of fur rubbing itself. To test this hypothesis, we separated individual tufted monkeys (*Cebus apella*) from their social group and provided them with fur rub material or control material, thereby avoiding intragroup competition. After engagement with materials, we released subjects back into their social group and observed their subsequent interactions with group members. We found that subjects were more likely to receive aggression and less likely to receive affiliation from others in the fur rub condition compared to the control condition. These results support the idea that fur rubbing carries social aftereffects for capuchin monkeys. The precise mechanisms of the observed effects remain to be clarified in future studies.

Keywords

capuchin monkey; fur rubbing; group cohesion; aggression; affiliation; olfactory communication

Introduction

Fur rubbing is a peculiar behavior that is most commonly observed in New World primate species (e.g. owl monkeys: Zito et al., 2003; spider monkeys: Campbell, 2000; lion tamarins: Guidorizzi and Raboy, 2009), but is perhaps best studied in capuchin monkeys (*Cebus* spp.). When fur rubbing, capuchin monkeys pick up a foreign substance (such as leaves, fruits, or insects) and rub it vigorously over their entire body with hands or feet. Substances used for fur rubbing typically contain insecticidal, antiseptic, and/or anti-inflammatory compounds (Huffman, 1997), which suggests that fur rubbing may improve fur condition and thereby serve a medicinal function (Baker, 1996).

However, not all capuchin monkeys fur rub in the same manner, and several differences in fur rub behavior have been noted between white-faced (*Cebus capucinus*) and tufted (*Cebus apella*) capuchins. For example, Lynch Alfaro et al. (2011) found that in the wild, white-faced capuchins are more likely to fur rub, particularly with plants and fruits, whereas tufted capuchins show a lower frequency of fur rubbing bouts and are more likely to fur rub with ants or other insects. These differences do not necessarily transfer to captive groups as

captive tufted capuchin monkeys are eager fur rubbers with materials such as onions, vinegar and tobacco (Ludes and Anderson, 1995), suggesting that selection of fur rub materials may be socially learned (Lynch Alfaro et al., 2011).

Researchers have been intrigued by the social aspects of fur rubbing. Capuchin monkeys have been observed to congregate during fur rubbing bouts by actively seeking out other individuals and sitting in close proximity to them (Leca et al., 2007; Paukner and Suomi, 2008). White-faced capuchins even perform a specific behavior, i.e. coiling their tail around other group members, which appears to motivate the other individual to join in with the fur rubbing behavior (Leca et al., 2007). In contrast, tufted capuchins have not been observed to perform this recruitment behavior, but show other differences in social behavior during fur rubbing. For example, tufted capuchins are more likely to fur rub with kin, with monkeys of similar dominance status, and with monkeys with which they share an affiliative relationship whereas white-faced capuchins are apparently less discriminatory about their fur rubbing partners. These observations led to the hypothesis that fur rubbing might serve to enhance social cohesion among white-faced, but not tufted capuchin monkeys (Leca et al., 2007).

Recently, this hypothesis has been tested in a captive group of tufted capuchin monkeys (Paukner and Suomi, 2008). Monkeys were provided with fur rub material (onions), and their social behavior was observed for 3 subsequent 15-minute intervals. Monkeys spent less time in social proximity to each other, were more frequently involved in aggressive interactions, and spent shorter amounts of time in affiliative interactions following provision of fur rub material compared to a control condition. Thus it appears that fur rubbing might actually have a negative effect on social relationships in tufted capuchin monkeys. However, it is presently unclear whether this observed effect was caused by fur rubbing itself, or whether it was the result of intra-group competition for fur rub material. In other words, these monkeys might have more aggressively competed for access to fur rub material rather than control material at the beginning of an observation, which may have resonated within the group in subsequent observation periods and made the effect dependent on provisioned material but independent of fur rubbing itself.

In the current study, we attempted to test this hypothesis by providing fur rub material or control material to individual subjects who were separated from their social group, thereby preventing the possibility of intragroup competition. Following interactions with materials, subjects were released back into their social group and were observed for two subsequent 15-minute intervals. We predicted that if aggressive interactions are caused by intragroup competition for fur rub material, we would not see any differences in social behavior between the fur rub condition and the control condition. Alternatively, if aggressive interactions are caused by fur rubbing, we predicted that we would see more aggressive and shorter affiliative interactions between each subject and its group members in the fur rub condition compared to the control condition. We also measured the directionality of interactions (initiated and received by the subject) in order to determine whether potential changes in social interactions originated from the subject or its group members.

Methods

Subjects

Subjects came from a captive breeding group of tufted capuchin monkeys (*Cebus apella*), which comprised 17 adults (9 female and 8 male, aged 4–27 years), 5 juveniles (2 female and 3 male, aged 1–2 years) and 5 infants (all male, aged 0–1 years). All monkeys were captive born, mother-reared, and housed in the LCE primate facilities at the NIH Animal Center near Poolesville, MD. We used 15 adult animals as subjects (8 female and 7 male); two additional adult animals were dropped from the study as they showed elevated stress

responses to social separation. All adult and juvenile animals were included in proximity and interaction measurements; infants were disregarded throughout.

Monkeys were housed in three indoor runs (6.9 × 4.1 × 2.1m each) which were connected via sliding doors. The middle run contained a series of 3 connected cages (50 × 50 × 55 cm LHW each) which allowed separation of individual animals via sliding panels. Subjects were not food deprived for this study, and they received daily nutritional supplements of seeds and fresh fruit or nuts. Commercial monkey biscuits and water were available *ad libitum*. The IACUC of NICHD approved all research performed in this study.

Procedure

Each subject was separated from the social group by allowing it to enter the series of cages in the middle run; the rest of the social group was temporarily restricted to the outer two runs only. Whilst in these cages, subjects maintained visual and auditory contact with group members, but were not able to physically touch or interact with them. We ran 2 conditions with each subject: a *fur rub condition*, in which subjects were given half a yellow onion (*Allium cepa*) separated into its layers; and a *control condition*, in which subjects were given half an apple cut into slices so as to resemble the size and shape of the onion pieces. We let each subject interact with the onion or the apple for 15 minutes, during which we scored the total duration of fur rub behaviors or other interactions with the material using the Pocket Observer (PDA HP iPAQ Pocket PC hx2190 and The Observer 5.0, Noldus). We then removed all traces of material from the cages, released the subject into the middle run, and reunited the subject with the group by opening the sliding doors to the outer runs. Immediately upon opening the doors, we scored the subject's behavior for 2 additional 15 minute intervals. Each monkey was tested three times in each condition in random order with only one test session per day conducted for the whole group.

Data analysis

We measured the frequency of all aggressive interactions (supplant, threat, chase, attack); the duration of all affiliative interactions (groom, mount/clasp, play); and the duration spent in proximity to other animals (ca. 30cm or within arm's reach) in each observation period. In addition, we distinguished whether subjects initiated or received aggressive or affiliative interactions with others. For analysis, we created average aggression, affiliation, and proximity scores from all three test sessions in each condition for each individual, and compared the average aggression, affiliation, and social proximity scores between fur rub and control conditions using paired-sample t-tests. One monkey failed to interact with materials in two test sessions (once in the fur rub condition and once in the control condition); these sessions were dropped and averages from only 2 sessions were computed for this monkey. Due to non-normal distribution, we performed square-root transformations on all data prior to analysis.

Results

Interactions with apples and onions

In the fur rub condition, monkeys spent on average 6 min interacting with the onion, including 2 min 2 sec fur rubbing and 3 min 58 sec interacting with the onion in other ways (manipulating, eating, sniffing etc). In the control condition, monkeys spent on average 4 min 46 sec interacting with/eating the apple.

First observation interval

Following exposure to the different materials, we found no difference in social proximity to others during the first observation interval ($t(14) = -0.43$, $p > 0.05$), and no differences in

initiating aggression ($t(14)=-0.24$, $p>0.05$) or initiating affiliation ($t(14)=-0.54$, $p>0.05$; Table 1). However, subjects were significantly more likely to receive aggression from group member in the fur rub condition ($t(14)=2.47$, $p=0.027$; Table 1) compared to the control condition. Generally, aggression was only mild; the overall breakdown was in the fur rub condition: supplant = 52%, threaten = 3%, and chase = 6%, and in the control condition: supplant = 32%, threaten = 2%, and chase = 5% of all received aggressive interactions. No subject was attacked in this phase. Monkeys were also significantly less likely to receive affiliation in the fur rub condition ($t(14)=-2.25$, $p=0.041$; Table 1) compared to the control condition. Here, the breakdown was groom = 14%, mount/clasp = 1%, and play = 1% in the fur rub condition, and in the control condition groom = 77%, mount/clasp = 2%, and play = 5% of all received affiliative interactions in this phase.

In addition, we tested possible associations between interactions with materials and received aggressive and affiliative interactions. Spearman's correlations showed that the frequency of received aggression correlated positively with the combined amount of time spent manipulating and fur rubbing with onions ($N=44$, Spearman's $\rho = 0.354$, $p=0.018$); when broken down into manipulating and fur rubbing separately, both associations remained positive, but failed to reach significance (both $p>0.05$). For received affiliation, the association with combined amount of time spent manipulating and fur rubbing with onions was negative, but failed to reach significance ($N=44$, Spearman's $\rho = -0.152$, $p>0.05$).

Second observation interval

We found no differences in behavior between the two conditions during the second observation interval (all $p>0.05$).

Discussion

In the current study, capuchin monkeys exhibited significant differences in behavior towards subjects who had engaged in fur rubbing bouts when compared to a control condition. In particular, subjects in the fur rub condition were significantly more likely to receive aggression, and significantly less likely to receive affiliation from group members. These results cannot be explained by intragroup competition for fur rub material as subjects were separated from the group when materials were available. Furthermore, it appears that the behavior of group members towards subjects, rather than subjects' behavior towards group members, was altered in the fur rub condition: differences were only observed for behaviors that subjects received, but not initiated by themselves. However, attributing the effect solely to (non-fur rubbing) group members may be premature: it can be difficult to discern when and how social interactions begin. For example, following fur rubbing bouts subjects might have displayed altered body postures, spatial position within the enclosure, gaze behavior towards conspecifics, or any other subtle social cue which we did not explicitly measure but which may have prompted the observed changes in social behavior by group members. Nonetheless, the observed pattern suggests that group members reacted to subjects in a more negative way in the fur rub condition.

Since intragroup competition for fur rub materials cannot account for this result, other hypotheses must be considered. It has previously been suggested that fur rubbing with pungent materials might have a disruptive effect on olfactory communication within capuchin groups (Paukner and Suomi, 2008). Although little is known about olfactory communication, there are several indicators that capuchins rely on it in their daily lives. For example, capuchins engage in hand sniffing, urine-washing, and genital inspections of new infants and adult males, which suggests that they might be sensitive to pheromones (Fragaszy et al., 2004). Urine washing in particular has been linked to social situations, especially in the context of submission (Miller et al., 2007), although other functions have

also been proposed (e.g. Roeder and Anderson, 1991; Campos et al., 2007; Schino et al., 2011). Interference with subjects' scent is consistent with the current results: group members reacted to potentially missing indicators of social status by displaying their own dominance status towards subjects and, not necessarily independently, refrained from reaffirming social bonds through affiliative displays. It is also consistent with the fact that we only observed these effects during the first observation interval when odor from the fur rub material most likely was more prominent. Although we did not measure incidents of urine washing by subjects, it is possible that subjects were able to re-balance their own scent by the second observation interval and thereby restore levels of social interactions to normal levels. In addition, fur rubbing might also have affected more than just scent in subjects. Observations of capuchin monkeys' fur rubbing generally highlight these monkeys' enthusiasm and apparent enjoyment of the activity (Baker, 1996; Fragaszy et al., 2004), suggesting that monkeys might also react emotionally to fur rubbing. It is possible that fur rubbing led to changes in subjects' levels of arousal and thereby affected noticeable differences in subsequent behavior as discussed above. These ideas could be explored experimentally in future studies.

Several differences to our previous study (Paukner and Suomi, 2008) should also be noted. For example, previously observed differences in proximity to group members were not replicated, and as mentioned above, effects appeared to be less pronounced in the current study since they were only found during the first observation interval. These differences suggest that while effects in the current study may be attributable to fur rubbing, some effects in our previous study may indeed have been the result of intragroup competition for fur rub material.

The social aspects of fur rubbing remain an intriguing area of investigation for future studies. In particular, the causes of differences in fur rub behavior between white-faced and tufted capuchin monkeys remain largely unexplored. Leca et al. (2007) suggested that differences in fur rub behavior between these two species might be related to differences in social organization (such as different levels of social tolerance and gregariousness), and that communal fur rubbing in white-faced, but not tufted capuchins, might be a way to test and reinforce social bonds. If so, white-faced capuchins might actually benefit from a loss of olfactory indicators of social status during fur rubbing bouts as it could facilitate social bonding; the more dominance-sensitive tufted capuchins on the other hand would experience a decline in social tolerance as observed in the present study. We believe that direct tests of olfactory components that may play a role in both white-faced and tufted capuchin monkeys' social behavior hold significant potential for future investigations.

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Table 1

Average behavioral scores per individual in each condition and each interval (standard deviations given in parentheses). Proximity and affiliation scores as durations in seconds, aggression scores as frequency of occurrence.

Behavioral Category	Condition	Interval1	Interval 2
Proximity	<i>Fur rub</i>	237.69 (143.72)	281.42 (136.73)
	Control	247.24 (125.27)	245.15 (131.68)
Initiate Aggression	<i>Fur rub</i>	0.89 (0.92)	0.68 (0.78)
	Control	1.19 (1.97)	1.50 (1.86)
Receive Aggression	<i>Fur rub</i>	1.67 (1.87)*	0.96 (1.01)
	Control	1.04 (1.41)*	1.16 (1.88)
Initiate Affiliation	<i>Fur rub</i>	14.53 (30.85)	31.14 (44.49)
	Control	17.08 (26.15)	32.58 (45.52)
Receive Affiliation	<i>Fur rub</i>	4.98 (7.26)*	27.26 (33.01)
	Control	29.56 (66.22)*	21.42 (28.60)

* denotes significance difference between conditions with $p < 0.05$.