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Grooming-at-a-distance by exchanging calls in nonhuman primates

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Abstract

The "social bonding hypothesis" predicts that, in large social groups, functions of gestural grooming should be partially transferred to vocal interactions. Hence, vocal exchanges would have evolved in primates to play the role of grooming-at-a-distance in order to facilitate the maintenance of social cohesion. However, there are few empirical studies testing this hypothesis. To address this point, we compared the rate of contact call exchanges between females in two captive groups of Japanese macaques as a function of female age, dominance rank, genetic relatedness and social affinity measured by spatial proximity and grooming interactions. We found a significant positive relationship between the time spent on grooming by two females and the frequency with which they exchanged calls. Our results conform to the predictions of the social bonding hypothesis, i.e. vocal exchanges can be interpreted as grooming-at-a-distance.

Keywords: call exchange, grooming, dominance rank, kinship, macaques

1. INTRODUCTION

The reasons why and how vocal communication became of prime importance in the course of primate evolution, potentially leading to human language, remains unclear. One of the non-mutually exclusive hypotheses relates to the need for spatial cohesion. This suggests that the habitat is crucial in determining the communicative modality [1]. Most primate species live in dense forested environments and vocal communication, in contrast to visual and gestural communication, has major advantages (e.g. long-distance 3D communication with several individuals). Another hypothesis related to the need for social cohesion suggests that language evolved with a social function to facilitate bonding between individuals in large groups [2]. This social bonding hypothesis implies that vocal exchange rates evolved together with group size in primates, in order to facilitate the maintenance of cohesion between allies and friends at a distance. Thus vocalizations replaced gestural grooming once it became impossible to allocate enough time to physically grooming all affiliated group members, as a form of "vocal grooming-at-a-distance" [3].

One of the socially important elements of vocal repertoires in nonhuman primates are contact calls, as they can encode acoustically individual [4], dyadic [5,6] and group [7] signatures, as well as information about the arousal state of callers [8]. They are the most acoustically varied calls in the vocal repertoire [9]. Importantly, contact calls are typically exchanged all day long between group members respecting so-called basic "conversational" rules (turn-taking, overlap avoidance, interlocutor selectivity) [10-13].

Japanese macaques, *Macaca fuscata*, are of special interest for studies on communication, as they live in large groups with complex social networks and stable bonds between females [14], and produce frequent flexible contact calls (named coos) [15]. Contact calls are produced by most members of a troop in a variety of contexts but always affiliative [15]. Previous studies on contact

calls of Japanese macaques have demonstrated individual recognition [16] as well as exchange rules [15], including turn-taking [17], acoustic matching between callers [18] and persistent waiting for a response [19].

Here, we tested the 'social bonding hypothesis' by studying vocal and non-vocal interactions in Japanese macaques. We compared the rate of contact call exchanges between females as a function of female age, dominance rank, genetic relatedness and social affinity measured by spatial proximity and grooming interactions. We predicted that preferences in grooming partner would reflect preferences in call exchange partners, independently of other social and genetic factors.

2. MATERIAL AND METHODS

Data were collected from February till August 2005 in the Primate Research Institute (Kyoto University, Japan). We studied two groups of Japanese macaques (Wakasa- WAK and Takahama- TAK). The WAK/TAK groups were composed of 10/18 adult males, 17/28 adult females and 4/8 offspring respectively. For this study, we sampled the behaviour of adult females (Table 1). Females were captive born and individually identified, with known ages and kin relationships.

Table 1. Characteristics of the adult females studied. Females with the same numeral in the "matriline" column are from the same matriline.

Female	Group	Age	Matriline	Rank
Hasi	WAK	10	I	1
Mina	WAK	4	I	2
Mini	WAK	6	I	3
Nira	WAK	6	I	4
Rumi	WAK	17	II	5
Mila	WAK	9	II	6
Reka	WAK	14	II	7
Beli	WAK	5	III	8
Lara	WAK	5	III	9
Jesi	WAK	7	IV	10
Rani	WAK	20	IV	11
Soma	WAK	18	IV	12
Sara	WAK	8	IV	13
Tsuyu	TAK	21	I	1
Kin	TAK	15	I	2
Yuki	TAK	21	I	3
Shinju	TAK	10	II	4
Umi	TAK	19	II	5
Yama	TAK	13	III	6
Kame	TAK	5	IV	7
Mori	TAK	22	IV	8
Shima	TAK	8	V	9
Take	TAK	17	VI	10
Iwa	TAK	11	VI	11
Kaki	TAK	8	VII	12
Tani	TAK	24	VIII	13
Ume	TAK	8	VIII	14
Ame	TAK	25	IX	15
Kuri	TAK	9	X	16

The two groups occupied different outdoor enclosures. The WAK group was housed in a larger (4600 m^2), visually dense (forested) enclosure, while the TAK group was housed in a smaller (960 m^2) and visually open enclosure.

- Behavioural observations and analysis of social bonds

The two groups were observed twice a day (morning and afternoon), for 90 minutes each session, during which 10-min focal samples were performed on adult females in a random order. Focal sampling consisted in recording the duration of allogrooming interactions and spatial proximities (defined as less than 1 m), the number of agonistic interactions (i.e. chases, approach avoids, supplants, bites, pushes, facial threats) as well as the number of contact call exchanges between females (defined as two, or more, individuals calling in a row with their respecting coos trailing each other with intervals of less than 2 s) [18]. At the time of a vocal interaction, we also

noted whether the exchanging callers were close (< 5m) or distant (> 5m apart). We conducted a total of 1047 focal observations with a mean ± SD = 36.1± 6.7 focals per female.

Based on affiliative data, directional dyadic grooming rate were calculated for each of 198 intra-group pairs of adult females (i.e. A->B: total duration of A grooming B during A and B focals divided by number of focals of A+B). Proximity (bidirectional) was measured as a total time females A and B stayed within 1 m from each other during A and B focals divided by number of focals of A+B.

Based on vocal exchange data (N=281 vocal interactions), we counted the number of times the first two callers only interacted with each other in a given order (i.e. A->B exchange rate: number of times B responds to A in A and B focals divided by number of A+B focals) focusing on the individual who responded (and thus created the exchange). When more than two callers (e.g. ABC) were involved (8.9%), the others were discarded because it was not possible to decide whom they were responding to. When more than two calls were involved from the same two callers (e.g. ABA), all combinations were counted (i.e. A->B and B->A).

Based on the 825 dyadic agonistic interactions recorded, we constructed dominance matrices for each group, with rank order determined by minimizing the number of reversals against the hierarchy (i.e., interactions below the diagonal). The Landau indices in Wakasa and Takahama groups were respectively h'=0.57 ($p=0.002$) and h'=0.53 ($p<0.001$), which indicates a linear dominance hierarchy in both groups (see ranks in Table 1).

- Statistical analysis

We performed all analyses using the statistical software R (R Development Core Team 2011). We used Generalized linear mixed models (GLMM) with Poisson log function, run with the lme4 package [20] to test for the impact of social and genetic factors on vocal interactions. We tested the influence of kinship, age and dominance rank differences, aggression, group, grooming

duration and spatial proximity rates (per focal) (independent variables) on call exchange rates (dependent variable) with the initiator and responder identities (as random factors), and focal time as a model offset. One data point represented the directional relationship of A to B.

For grooming and call exchanges, we calculated the degree of reciprocity within each female dyad by dividing the lower directional rate by the higher rate. Reciprocity indices varied from 0 to 1. To investigate the potential relation between grooming and calling reciprocity indices, we ran another GLMM. The same analysis was then done to test for a potential relation between call reciprocity and call rates, as well as between grooming reciprocity and grooming rates.

3. RESULTS

While degree of kin relatedness, age and rank differences, frequency of aggression, spatial proximity and group did not influence significantly contact call exchange rates between two given females, grooming duration did (Table 2). Hence, the longer a given female is being groomed by another one, the more often she responds to her contact call (Fig. 1).

Table 2. Relationship between socio-genetic characteristics of female callers and contact call exchange rates in Japanese macaques (P values: likelihood ratio tests; N=396).

Factors	Estimate	SE	P
Kinship	-0.44	0.28	0.12
Age difference	-0.07	0.02	0.051
Rank difference	0.03	0.02	0.25
Aggression	0.02	0.01	0.18
Grooming duration	0.35	0.06	<0.001
Spatial proximity	0.003	0.002	0.32
Group	-0.8	0.43	0.08

Moreover, reciprocity indices in grooming and call exchange responsiveness were positively related (GLMM: N= 198, F=61.5, P<0.001), i.e. reciprocity in grooming interactions was reflected in reciprocity in responding to the calls of the other. Then, we found a significant positive relationship between vocal response reciprocity and vocal response rate (GLMM: N=198, F=60.2, P<0.001), and between grooming reciprocity and grooming rate (GLMM: N=198, F=95.1, P=0.02).

Finally, we observed that 98.2% of call exchanges between two given females were produced when they were not grooming each other. Also, in 90% of the call exchanges, the two exchanging partners were spatially distant from each other (i.e. > 5 meters apart).

4. DISCUSSION

As predicted by the social bonding hypothesis, contact call exchange among female Japanese macaques can be seen as grooming-at-distance behaviour. The key finding here is that the only social or genetic factor explaining contact call rates between two given females is the time they also spend on grooming each other.

Previous studies in apes have shown that audience composition, and notably the number of affiliated individuals around, impacts individual call rates for calls with a referential function aiming at transmitting a message to the friend (food or predator presence [21, 22]. Here, we show that even non-referential (contact) calls of non-ape species are impacted by affiliation between individuals in the form of vocal interactions. Our findings support previous studies which found that individuals involved in a positive relationship are more likely to exchange calls (e.g. pygmy marmosets *Cebuella pygmaea* [23], squirrel monkeys *Saimiri sciureus* [24] and bonobos *Pan paniscus* [13]). Here, we found that this effect is particularly strong for preferred grooming partners. Moreover, we also found that females that groomed each other more reciprocally, also responded to

each others' calls more reciprocally. This suggests that their affiliation was based on equal, voluntary social involvement of both parties and not based on kinship ties, a relationship typically termed 'friendship' [25]. Interestingly, we found that reciprocity was a good indicator of friendship (defined by frequent interactions) for call exchanges and for grooming.

The fact that contact call exchanges typically did not occur during a grooming event or between females close to each other, supports the idea that call exchange may function in strengthening and/or advertising friendships when grooming is not an option or when low-cost bonding behaviours are preferred. In chimpanzees, male dyads were more likely to be involved in affiliative behaviours, such as reciprocal grooming, joint non-vocal displays and coalitions, on days when they chorused together, compared to days when they did not [26]. It was also found that primate species with more grooming interactions have larger vocal repertoires regardless of habitat conditions [27]. All this support the social bonding hypothesis.

To conclude, we showed that vocal exchanges can be interpreted as a form of grooming-at-the-distance to enhance the bond strength between affiliated individuals. Future studies now need to focus on contextual analysis to understand when and why friends decide to opt for physical or distant (vocal) grooming. Also, in the framework of the ongoing debate about Human language evolution, more comparative studies with socially varied primates are needed to understand how social pressures guided the evolution of vocal usage flexibility.

Ethical statement

All animal care and data collection protocols are consistent with the Guide for the Care and Use of Laboratory Primates and were approved by the Institutional Animal Care and Use Committee of the Primate Research Institute, Kyoto University (JSPS ID P04803).

Competing interests

We declare we have no competing interests.

Authors' contributions

The study was designed by A.L., R.J. and N.M.; the data were collected by A.L. and R.J. and analysed by M.A. and A.L.; all authors wrote the manuscript, provided intellectual input, edited/approved the final version and agree to be held accountable for the work performed.

Data accessibility

Data is available on request to AL.

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References

1.Partan SR, Marlan P. 2005 Issues in the classification of multimodal communication signals. Am. Natural. **166,** 231-245.

2.Dunbar RIM. 1993 Coevolution of neocortical size, group size and language in humans. Behav. Brain Sci. **16**, 681-694.

3. Dunbar RIM. 2003 The origin and subsequent evolution of language. In MH Christiansen, S Kirby (Eds.) *Language evolution*. Oxford: Oxford University Press, pp.219-234.

4. Rendall D, Owren MJ. 2002 Animal vocal communication: Say what? In M Bekoff, C Allen, GM Burghardt (Eds.) *The cognitive animal.* pp. 307–313.Cambridge, MA: The MIT Press.

5.Lemasson A, Ouattara,K, Petit EJ, Zuberbűhler K. 2011 Social learning of vocal structure in a nonhuman primate? BMC Evol. Biol. **11**, 362-369.

6. Snowdon CT, Elowson AM. 1999 Pygmy marmosets modify call structure when paired. Ethol. **105**, 893–908.

7.Crockford C, Herbinger I, Vigilant L, Boesch C. 2004 Wild chimpanzees produce group-specific calls: a case for vocal learning. Ethol. **110**, 221-243.

8. Lemasson A, Remeuf K, Rossard A, Zimmermann E. 2012 Cross-taxa similarities in affect-induced changes of vocal behavior and voice in arboreal monkeys. PLOS One 7(9): e45106.

9. Bouchet H, Blois-Heulin C, Lemasson A. 2013 Social complexity parallels vocal complexity: a comparison of three nonhuman primate species. Front. Psychol. **4**, 390.

10.Hauser MD. 1992 A mechanism guiding conversational turn-taking in vervet monkeys and rhesus macaques. In T Nishida, FBM de Waal, W McGrew, P Marler, M Pickford (Eds) *Topics of primatology*. vol. 1. Human origins. pp. 235–248. Tokyo, Japan: Tokyo University Press.

11. Lemasson A, Gandon E, Hausberger M. 2010 Attention to elders' voice in nonhuman primates. Biol. Lett. **6**, 325-328.

12. Lemasson A, Glas L, Barbu S, Lacroix A, Guilloux M, Remeuf K, Koda H. 2011 Youngsters do not pay attention to conversational rules: is this so for nonhuman primates? Sci. Rep. **1,** 22**.**

13. Touitou S, Lemasson A, Frédet J, Nairaud B, Guéry J-P, Levréro F. (under revision) Social bonding drives vocal plasticity in bonobos. Sci. Rep.

14. Sueur C, Petit O, Jacobs AT, Watanabe K, Thierry B. 2011 A comparative network analysis of social style in macaques. Anim. Behav. **82**, 845-852.

15. Sugiura H. 1993 Temporal and acoustic correlates in vocal exchange of coo calls in Japanese macaques. Behav. **124**, 207-225.

16. Mitani M. 1986 Voice print identification and its application to sociological studies of wild Japanese monkeys (*Macaca fuscata yakui*). Primates **27**, 397-412.

17. Lemasson A, Guilloux M, Rizaldi, Barbu S, Lacroix A, Koda H. 2013 Age- and sex-dependent contact call usage in Japanese macaques. Primates **54**, 283–291.

18. Sugiura H. 1998 Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. Anim. Behav. **55**, 673–687.

19. Koda H. 2004 Flexibility and context-sensitivity during the vocal exchange of coo calls in wild Japanese macaques (*Macaca fuscata yakui*). Behav. **14**, 1279-1296.

20. Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-41/r1341.

21. Schel AM, Machanda Z, Townsend SW, Zuberbühler K, Slocombe KE. 2013 Chimpanzee food calls are directed at specific individuals. Anim. Behav. **86**, 955-965.

22. Schel AM, Townsend SW, Machanda Z, Zuberbühler K, Slocombe KE. Chimpanzee alarm call production meets key criteria for intentionality. PLOS One 8:e76674

23. Snowdon CT, Cleaveland J. 1984 'Conversations' among pygmy marmosets. Am. J. Primatol.

7, 15-20.

24. Biben M, Symmes D, Masataka N. 1986 Temporal and structural analysis of affiliative vocal exchanges in squirrel monkeys (*Saimiri sciureus*). Behav. **98,** 259-273.

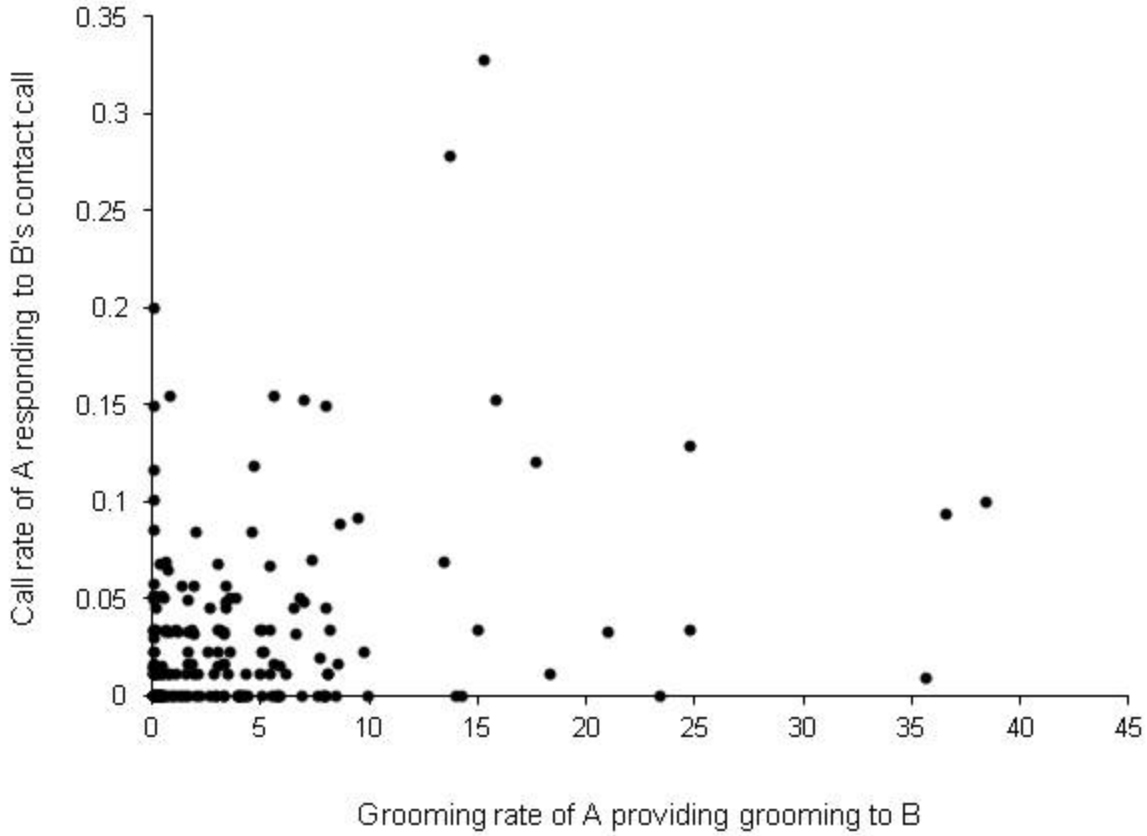
25. Silk JB. 2002 Using the 'F' –word in primatology. Behav. **139**, 421-446.

26. Fedurek P, Machanda ZP, Schel AM, Slocombe KE. 2013 Pant hoot chorusing and social bonds in male chimpanzees. Anim. Behav, **86**, 189-196

27. McComb K, Semple S. 2005 Coevolution of vocal communication and sociality in primates. Biol. Lett. **1**, 381–385.

Figures

Fig.1 The relation between exchange rate and grooming rate (per focal) in females of Japanese macaques. Each dot represents the directional relationship of female A to female B within a dyad (N=396).


Call rate of A responding to B's contact call
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
5
10
15
20
25
30
35
40
45
Grooming rate of A providing grooming to B