

**Title: Functions of Unreported ‘Rocking-Embrace’ Gesture between Female Japanese Macaques
(*Macaca fuscata*) in Kinkazan Island, Japan**

Authors: Yukiko Shimooka¹⁾ and Naofumi Nakagawa²⁾ (corresponding author)

Authors’ affiliation:

¹⁾Faculty of Life and Environment Sciences, Teikyo University of Science, Yatsusawa 2525, Uenohara,
Yamanashi 409-0193, Japan. E-mail: shimooka@ntu.ac.jp

²⁾Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo, Kyoto, Kyoto
606-8502, Japan. E-mail: nakagawa@jinrui.zool.kyoto-u.ac.jp; Phone number: +81-75-753-4084; Fax
number: +81-75-753-4115

Running title: ‘Rocking-embrace’ Gesture in Female Japanese Macaques

Keywords Embrace; Japanese macaques; *Macaca fuscata*; Multimodal signals; Tension reduction; Tactile
signals; Visual signals

Abstract

Recently, research has focused on the effects of the concurrence of multimodal signals and their efficacy and meaning. We observed an unreported behaviour, a combination of a ventro-ventral ‘rocking-embrace’ gesture always accompanied by lip smacking as the facial expression and sometimes by a girney call in wild Japanese macaques (*Macaca fuscata*), living in Kinkazan Island, northern Japan. This study examined the form and contexts of the occurrence of such multimodal signals to reveal its functions. Eighty-eight cases of ‘rocking embrace’ were recorded during 183 h of observation over 22 d. Adult females were involved in all the cases. Of the 71 cases between adult females in which behaviours prior to the ‘rocking embrace’ could be identified, 13 cases were allogrooming interruptions, 11 cases of aggressions, and 42 cases of approaching, most of which occurred between non-kin grooming partners. The ‘rocking embrace’ was often followed by allogrooming. This suggested that ‘rocking embraces’ occurred under stressful conditions and might be appeared to function to reduce tensions. This conclusion was consistent with the contexts and functions of lip smacking and girneys shown in previous studies. In contrast with lip smacking and girneys, neither ‘rocking embrace’ nor ventro-ventral embrace (without rocking) between anoestrous adult females has been previously shown in Japanese macaques. In other macaque species, however, the latter gesture is often shown as an affiliative behaviour that immediately follows conflict, which functions to reconcile or as a greeting when it occurs immediately after an approach. ‘Rocking embraces’ among the Kinkazan macaques occurred in contexts similar to, and held a similar function as, the ancestral gesture of ventro-ventral embracing, which was hidden in Japanese macaques, and the ancestral display of lip smacking, which is still observed in Japanese macaques. The ventro-ventral embrace as a tactile signal might have been hidden since it was redundant with the visual signal of lip smacking in ancestral macaques.

(306 words)

Introduction

Signals are defined as any acts or structures that alter the behavior of other organisms (Maynard Smith and Hauser 2003). Animals communicate with each other by various modes of signals, such as odours, vocalisations, facial expressions, and gestures defined as body movements that can be used as visual, auditory and tactile signals, although there are differences in their relative importance among taxa (Hauser 1996). In addition, they often use several modes of signals simultaneously. Recently, studies have focused on the effects of the concurrence of signals and their efficacy and meaning (Rowe and Guilford 1996; Partan 2002; Bro-Jorgensen 2009; Slocombe et al. 2011; Stafstrom and Hebets 2013). Partan and Marler (1999) classified multimodal signals roughly into redundant signals and nonredundant signals. When presented separately, redundant signal components have equivalent effects on a receiver, whereas nonredundant components have different effects. Redundancies work as backup signals, whereas nonredundant components offer multiple messages.

Primates communicate by means of elaborate facial expressions (van Hooff 1967) and vocalisations (Hauser 1996). Recent experimental evidence has shown that they can integrate visual and auditory information during communication (Ghazanfar and Logothetis 2003; Izumi and Kojima 2004; Evans et al. 2005; Chandrasekaran et al. 2011). Such a multimodal perception may represent an evolutionary precursor to human speech, which is enhanced by a combination of visual and auditory signals (Ghazanfar and Logothetis 2003; Ghazanfar et al. 2013). To examine the hypothesis that human language evolved via gestural signals (Corballis 2002; Arbib 2005; Pollick and de Waal 2007), the study of links between manual gestures and vocalisations has been a focus of primatology (Call and Tomasello 2007).

Female Japanese macaques (*Macaca fuscata*) lip smack as a facial expression (van Hooff 1967) and utter coo or girney calls (*sensu* Green 1975) during or immediately before allogrooming (Mori 1975; Masataka 1989; Sakura 1989), similar to that by other macaque species (Shirek-Ellefson 1972 for review;

Rahaman and Parthasarathy 1968 for *M. radiata*; Holman and Goy 1980 for *M. mulatta*; Maestripieri and Wallen 1997 for *M. fascicularis*). Itani (1963) and Mori (1975) pointed out that girneys sometimes accompanied by lip smacks alleviated tension between the groomer and groomee in Japanese macaques because allogrooming necessitated body contact. Blount (1985) reported that lower-ranking Japanese macaque females emitted girneys when in the proximity of higher-ranking females. He suggested that girneys appeared to function as appeasement signals. Kutsukake and Castles (2001) showed that bi-directional lip smacking and reciprocal coo or girney call exchanges frequently occurred immediately after conflict and functioned to reduce post-conflict anxiety among Japanese macaques. Taken together, lip smacking, coos, and girneys serve the same function of tension reduction, although they do not necessarily occur concurrently.

We found an unreported behaviour, a combination of a ventro-ventral ‘rocking-embrace’ tactile gesture always accompanied by lip smacking and sometimes by girneys, in Japanese macaques. The ‘rocking embrace’ was defined as the behaviour of 2 individuals encircling each other ventro-ventrally, with their arms around each other, in a sitting position, and rocking their bodies back and forth rhythmically (Fig. 1; for details, see electronic supplementary material). The aim of this study was to examine the forms and contexts of the occurrence of such a multimodal signal and to reveal its functions. The phylogenetic and ontogenetic origins of this behaviour are also discussed.

Methods

Study Sites and Subjects

This study was conducted on the small island of Kinkazan (ca. 10 km²), in the northern part of Japan (38°8’N, 141°4’E). It has a mean annual rainfall of about 1500 mm and a mean annual temperature of 11°C. The island is mostly covered with natural cool temperate forests (for further details, Nakagawa 1997).

Japanese macaques (*Macaca fuscata*) form female philopatric multi-male/multi-female groups. There were approximately 250 individuals in 6 unprovisioned groups on the island at the time of observation (Izawa 2000). The age–sex composition of the target group (the A group) was as follows: 2 adult males (≥ 10 years old), 7 adolescent males (4.5–9 years), 15 adult females (≥ 6.5 years), 1 adolescent female (4.5–5.5 years), 12 juvenile males (1–3.5 years), 5 juvenile females (1–3.5 years), and 1 female infant (less than 12 months), totalling 43 individuals. All the adult and adolescent individuals were individually identified. There were 2 mother-daughter pairs, 2 sister pairs, and no grandmother-granddaughter pairs among adult females in the group, which are defined as kin with $r \geq 0.25$ in this study. Such a low degree of relatedness between females comes from a lower birth rate and higher infant mortality in the unprovisioned population than in the provisioned populations (Takahata et al. 1998; Fujita 2010).

Data Collections

Almost all the occurrences of the ‘rocking-embrace’ tactile gesture that Y.S. observed during 22 d (183 h) of following the A group in October 1997 were recorded, i.e. behaviour sampling (*sensu* Martin and Bateson 1980). Specifically, the onset and ending time of the behaviour, name of participants, and occurrence of agonistic interactions (e.g. threats, lunges, chases, and bites) within 1 minute (hereafter, immediately) before ‘rocking embrace’, were recorded. Because ‘rocking embrace’ often took place during grooming, grooming behaviours were also recorded via the sequence sampling method (Altmann 1974). Specifically, the onset and ending time of grooming, names of the groomer and groomee, and grooming solicitation were recorded.

Grooming solicitations included the following gestures: ‘lie down’, lying on the side or belly; ‘stand’, standing still on all fours and present the flank or buttocks; ‘head down’, drooping the head; ‘head up’, moving the head up; ‘touch’, touching another macaque’s body with a hand and then immediately

withdrawing it; and ‘bob’, moving the head up and down in rapid succession (Tsukahara 1990).

The study period coincided with the mating season (Fujita et al. 2004). Females’ oestrous status was checked every day by female facial redness and *a posteriori* faecal hormone profiles (Fujita et al. 2004). Once a female begins oestrous, she was considered to be in oestrous for the rest of the period. Eleven out of 16 adult/adolescent females began their oestrous during the study period.

Data Analyses

First, we completed a sociometric matrix to examine the age–sex distribution of the ‘rocking embrace’. As for the combinations of participating adult females, we compared the frequency of the ‘rocking embrace’ between kin dyads and between non-kin dyads by a Binomial test. Second, we counted the occurrence of the ‘rocking embrace’ in each context categorised by the behaviour immediately before the ‘rocking embrace’, such as approach, allogrooming, and aggression, and immediately after, such as allogrooming, in order to reveal the function of the ‘rocking embrace’. Third, we compared the grooming and grooming solicitation between immediately before and after ‘rocking embrace’ to scrutinise its function (see below for details).

Figure 2 schematises a series of typical grooming interactions in which the ‘rocking embrace’ between the same dyad of grooming interactions occurred. A grooming bout was defined as a continuous act of picking by an individual through the fur of another that was not interrupted by pauses of longer than 5 s. When interrupted by a pause of longer than 5 s, it was regarded as 2 different grooming bouts, which were separated by an interval in grooming. When the ‘rocking embrace’ occurred between 2 grooming bouts, the interval between the ‘rocking embrace’ and the following grooming (grooming+1) was named ‘interval+1’ and that between the ‘rocking embrace’ and the preceding grooming (grooming-1) was named ‘interval-1’ (for details of the naming of grooming bouts and grooming intervals, see Fig. 2). Grooming solicitations sometimes occurred during a grooming interval. We compared the

mean durations of grooming bouts, grooming intervals, and the frequency of grooming solicitations between immediately before and after a 'rocking embrace' with a Wilcoxon signed-rank test.

Results

General Characteristics of 'Rocking Embrace'

Eighty-eight cases of 'rocking embraces' were recorded during 183 h of observation over 22 d. In the cases where the duration was obtained, the mean was 17 s, ranging from 4 s to 46 s. Table 1 shows the number of cases of 'rocking embraces' in each dyad of participants. In all 88 cases, at least 1 of the 2 participants was an adult female. The 'rocking embrace' was observed in 78 cases between adult females: 21 cases between anoestrous females, 39 cases between anoestrous and oestrous females, and 18 cases between oestrous females. The 10 other cases included 3 between anoestrous adult females and anoestrous adolescents or juvenile females, 3 between oestrous adult females and adolescent females, 1 between an anoestrous adult female and a juvenile male, 2 between oestrous adult females and juvenile males, and 1 between an anoestrous adult female and an adolescent male. The case involving an adolescent male occurred between *Kb* and his elder sister. *Kb* is a relatively small 8-year-old male due to having been badly wounded at the age of 1 year and still remains in the natal group (Izawa 2002).

In 2 out of 71 cases between identified adult females, the 'rocking embrace' occurred between maternal kin-related individuals. Compared to the number of kin dyads vs. non-kin dyads among adult females in the group, no significant difference was found in the frequency of 'rocking embraces' between kin and between non-kin (Binomial test, $n = 71$, $p = 0.489$). The lack of significant differences may be explained by the kin-biased tendency for allogrooming and proximity in female Japanese macaques (Nakamichi and Yamada 2010). Based on the result that allogrooming occurred in all kin dyads but in only 24% of non-kin dyads in this study group (Takahashi and Furuichi 1998), 24 out of non-kin

dyads and all 4 kin dyads were regarded as actual grooming partners and subject to reanalysis. Compared to the number of kin dyads vs. non-kin dyads among actual grooming partners, the frequency of 'rocking embraces' was significantly higher between non-kin than between kin (Binomial test, $n = 71$, $p = 0.001$).

Contexts of Occurrence of 'Rocking Embrace'

Table 2 shows the behaviours immediately before 'rocking-embrace' behaviours. Of the 66 cases between adult females in which behaviours prior to a 'rocking embrace' could be identified, there were 13 cases (20%) of allogrooming, 11 cases (17%) of aggressions, and 42 cases (64%) of approaching which were preceded by neither allogrooming nor aggressions. It should be noted that post-conflict 'rocking embraces' included those between the aggressee and a third party (2 cases) and between a pair of third parties (4 cases).

Cases of approaching which were not preceded by either allogrooming or aggressions occurred between kin dyads in only 1 out of 40 cases of identified adult females (see Table 1). No significant difference was found in the frequency of 'rocking embraces' between kin and non-kin after such approaches (Binomial test, $n = 40$, $p = 0.547$). Based on the result that allogrooming occurred in all kin dyads but in only 24% of non-kin dyads in this study group (Takahashi and Furuichi 1998), 24 out of non-kin 101 dyads and all 4 kin dyads as the actual grooming partners who were subject to reanalysis. When we compared the frequency of kin dyads with that of non-kin dyads among actual grooming partners, the frequency of 'rocking embraces' was significantly higher between non-kin than between kin, after such approaches (Binomial test, $n = 40$, $p = 0.016$).

Table 3 shows the behaviours immediately after 'rocking embraces'. Of the 77 cases between adult females in which behaviours following a 'rocking embrace' could be identified, there were 66 cases (86%) of allogrooming, 3 cases (4%) of 'rocking embraces', 5 cases (6%) of being driven away by a third

party, and 3 cases (4%) of leaving.

Details of ‘Rocking Embrace’ during Grooming Interaction

Figure 3 shows the mean duration of grooming bouts immediately before a ‘rocking embrace’ (grooming-1) and immediately after a ‘rocking embrace’ (grooming+1) (see Fig. 2). In 14 cases between adult females where the duration of both grooming-1 and grooming+1 were obtained, the grooming bout duration was significantly longer in grooming+1 than in grooming-1 (Wilcoxon signed-rank test, $T = 20$, $n = 14$, $p < 0.05$).

Figure 4 shows the mean duration of grooming intervals immediately before a ‘rocking embrace’ (interval-1) and immediately after a ‘rocking embrace’ (interval+1). In 14 cases between adult females where the duration of both interval-1 and interval+1 were obtained, the duration of the grooming interval was significantly longer in interval-1 than in interval+1 (Wilcoxon signed-rank test, $T = 0$, $n = 12$, $p < 0.01$).

The frequency of grooming solicitations was compared between intervals immediately before a ‘rocking embrace’ (interval-1) and those immediately after a ‘rocking embrace’ (interval+1). In 10 cases between adult females where the frequency of both interval-1 and interval+1 were obtained, the frequency of grooming solicitations was significantly higher in interval-1 than in interval+1 (Wilcoxon signed-rank test, $T = 0$, $n = 9$, $p < 0.01$).

Discussion

Functions of ‘Rocking Embrace’

Twenty-one percentage of ‘rocking embraces’ occurred immediately after the interruption of allogrooming. Grooming interactions immediately before ‘rocking embraces’ were shorter in bout duration, longer in intervals, and higher in frequency of grooming solicitation than for those immediately

after the ‘rocking embraces’. Although caution should be taken in drawing conclusions because of the small sample size, these characteristics may suggest that grooming interactions could become a stalemate immediately before ‘rocking embraces’. Although we do not have any data on self-directed behaviours (e.g. self-scratching and self-grooming), which are used as an indicator of stress or tension (Kutsukake and Castles 2001; Schino et al. 2007; Majolo et al. 2009 for *M. fuscata*; Arnold and Aureli 2007 for review), they often precede ‘rocking embraces’ during grooming interactions (N.N. pers. observ.). In long-tailed macaques, the rates of self-directed behaviours are known to be higher during the short interval following the end of allogrooming bouts (Schino et al. 1988). Given these observations, the monkeys are thought to experience a tense state during the grooming interval immediately before a ‘rocking embrace’.

Sixteen percentage of all ‘rocking embraces’ occurred immediately after the aggression. More or less, not only aggressees, but also aggressors (Schino et al. 2007) and even the bystanders of the aggression (De Marco et al. 2010), have been shown to be stressed based on the observation that they engage in more self-directed behaviour after aggression than during a control period.

The remaining 64% of the ‘rocking embraces’ occurred immediately after approaching that was preceded by neither allogrooming nor aggressions. Self-directed behaviour also suggested that proximity to dominant or unfamiliar individuals induced stressful conditions (Schino et al. 1990; Pavani et al. 1991; Manson and Perry 2000). ‘Rocking embraces’ more frequently occurred between the actual grooming partners in non-kin than those in kin in this context.

It follows from what has been said that ‘rocking embraces’ occurred under stressful conditions and that the ‘rocking embrace’ might be appeared to function to reduce such tensions. ‘Rocking embraces’ during allogrooming interactions may also facilitate the smooth progress of allogrooming, i.e. longer bout duration, shorter intervals, and lower frequency of grooming solicitation.

The ‘rocking embrace’ is always accompanied by lip smacking as a facial expression and sometimes

by girneys as a vocalisation. Our knowledge of the contexts and functions of lip smacking and girneys described in the Introduction suggest that they are consistent with those of the ‘rocking embrace’. As for the facilitation of the smooth progress of allogrooming, our results of ‘rocking embraces’ between grooming bouts agreed with Sakura’s (1989) result of coos and girneys in that in Japanese macaques, grooming bouts following coos and girneys lasted longer than those without such calls, regardless of whether the call was uttered by the groomer or groomee.

Phylogenetic and Ontogenetic Origins of ‘Rocking Embrace’

In contrast with lip smacking and girneys, neither the ‘rocking embrace’ nor the ventro-ventral embrace (without rocking) between anoestrous adult females has been previously reported in Japanese macaques, although the ventro-ventral embrace occurs between consort pairs (i.e. heterosexual: an adult male and an oestrous female; homosexual: two oestrous females) (Enomoto 1974; Vasey et al. 2008) or between a mother and infant pair (Negayama et al. 1986). Nakagawa et al. (2011) conducted a questionnaire survey of primatologists with 1 or more years of experience with field research at each study site and found no confirmed instances of ventro-ventral embrace between anoestrous adult female Japanese macaques at 3 well-known long-term study sites: Arashiyama, Katsuyama, and Takasakiyama. The ventro-ventral embrace has not even been included in lists of affiliative behaviours as candidates for reconciliatory behaviours (Kutsukake and Castles 2001; Majolo and Koyama 2006). To our knowledge, the present study is the first to show the ventro-ventral embrace with rocking, i.e. the ‘rocking embrace’ between anoestrous adult females. Judging from behaviours immediately before or after the ‘rocking embrace’, even the ‘rocking embrace’ involving oestrous adult females never occurred in a sexual context. In contrast with that observed among the Japanese macaques in Jigokudani (Enomoto 1974) and Arashiyama (Vasey et al. 2008), female–female mounting has rarely been observed in Kinkazan (Nakagawa et al. 2011). Moreover, the ‘rocking embrace’ has been observed during seasons other than

the mating seasons in Kinkazan (N.N. unpub), and therefore, considered to occur in an asexual context.

However, one cannot say that the ‘rocking embrace’s has nothing to do with the sexual condition of the females. The oestrous females are often more likely not only receive aggression from males (Enomoto 1978; Soltis et al, 1997) but also give aggression to females in macaques (Walker et al. 1983). Such an enhanced aggression may increase the frequency of ‘rocking-embraces’ between female opponents, between female aggressor and third party or between a pair of female third parties. Contrarily, the enhanced aggression may not lead to substantial increase of ‘rocking-embraces’ as might be the case with reconciliation in that conciliatory tendency is lower when one or both female opponents is in estrus than when they are not because the estrus female devotes herself to compete over male rather than to reconcile (Majolo and Koyama 2006).

In other macaque species, however, ventro-ventral embraces between adult females are known to occur in an asexual context, followed by allogrooming or huddling (for *M. mulatta*, *M. nemestrina*, *M. arctoides*; Maestripieri 1996, 2007) or accompanied by lip smacking (for *M. radiata*, Rahaman and Parthasarathy 1968; for *M. maurus*, *M. nigrescens*, *M. nigra*, *M. tonkeana*, Thierry et al. 2000). The behaviour is often depicted as an affiliative behaviour occurring immediately after conflict, with a reconciliatory function (for *M. arctoides*, Chevalier-Skolnikoff 1973; for *M. tonkeana*, see Thierry 1984; for *M. nemestrina*, Castles et al. 1996; for *M. fascicularis*, Das et al. 1998; for *M. assamensis*, Cooper et al. 2005; for *M. radiata*, Cooper et al. 2007) or as a greeting when it occurs immediately after an approach not preceded by an agonistic interaction (for *M. tonkeana*, Thierry 1984). Maestripieri (2007) compared gestural communication in 3 species of macaques (*M. mulatta*, *M. nemestrina*, and *M. arctoides*). He found that ventro-ventral embraces occurred with the least frequency in *M. mulatta* and concluded that it was a relatively ancestral gesture that had become very infrequent in *M. mulatta*. In females of Japanese macaques, which are phylogenetically closest to *M. mulatta* (Smith et al. 2007), the ventro-ventral embrace between anoestrous adult females might have been hidden and re-emerged in a

population in Kinkazan. Interestingly, when it re-emerged, it was accompanied by lip smacking, which is also an ancestral display (Preuschoft and van Hooff 1995) that had been kept in Japanese macaques. Lip smacking is also often followed by allogrooming (Rahaman and Parthasarathy 1968, Mori 1975, Holman and Goy 1980, Maestripieri and Wallen 1997) and functions as an affiliative signal (Maestripieri and Wallen 1997). It is also sometimes depicted as a reconciliatory behaviour when it occurs immediately after conflict (Kutsukake and Castles 2001). Since they are exhibited in similar contexts and considered to serve similar functions, ventro-ventral embrace as a tactile signal and lip smacking as a visual signal would have functioned as redundant signals in ancestral macaques. Therefore, lip smacking, which was still existent in Japanese macaques, might have been used as a backup signal (*sensu* Partan and Marler 1999) when ventro-ventral embrace was hidden in Japanese macaques

The ontogenetic origins of clasping behaviour, such as ventro-ventral embraces, lateral embraces, and hugs, are considered to be the infant behaviour of clinging to the mother (Thierry 1984), which was, of course, found in Japanese macaques (Negayama et al. 1986). Lip smacking is also considered to originate from the infant behaviour of nursing or non-nutritive sucking movement (Redican 1975). Therefore, ontogenetically, 'rocking embraces' may date back to infant behaviour. N.N. observed 'rocking embraces' between sex-unknown infants (N.N. pers. obs.). On the other hand, adult and adolescent males rarely exhibited 'rocking embraces' in this study. Adult and adolescent males exhibit lip smack toward oestrus females during hind-quarters display and embrace oestrous females during the mounting series or just before or after the mounting series (Enomoto 1974). Thierry (1984) mentioned that mounting between adult males serves similar social functions to clasping behaviour in Tonkean macaques. This might be the case with male Japanese macaques (Mori 1975; Mizuhara 1981). Further research is needed to reveal the ontogenetic development of the 'rocking embrace', especially its sex difference and the acquisition of the rocking movement.

Acknowledgements

We would like to express our thanks to emeritus Prof. Y. Sugiyama, Kyoto University, for his guidance during the study. We are also grateful to emeritus Prof. K. Izawa, Miyagi University of Education for providing invaluable information and help. We extend special thanks to Dr. M. Nakamura and an anonymous reviewer for providing comments and constructive criticism. Drs. H. Sugiura, Kyoto University, and S. Fujita, Kagoshima University, were kind enough to permit us to offer valuable video footage of a ‘rocking embrace’ as an electronic supplemental material, and data on females’ status of oestrus, respectively.

This study was financed by the Cooperative Research Fund of the Primate Research Institute, Kyoto University, to Y.S. and a grant from the Japan Society for the Promotion of Science (#23370099) to N.N.

References

- Altmann J (1974) Observation study of behavior: sampling methods. *Behaviour* 49: 227–267
- Arbib M (2005) The Mirror System Hypothesis: how did protolanguage evolve? In: Tallerman M (ed) *Language Origins: Perspectives on Evolution*. Oxford University Press, New York, pp 21–47
- Arnold K, Aureli F (2007) Postconflict reconciliation. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) *Primates in Perspective*. Oxford University Press, Oxford, pp 592–608
- Blount BG (1985) “Girney” vocalization among Japanese macaque females: context and function. *Primates* 26: 424–435
- Bro-Jorgensen J (2009) Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends Ecol Evol* 25: 292–300
- Call J, Tomasello M (eds) (2007) *The Gestural Communications in Apes and Monkeys*. Lawrence Erlbaum Associates, New Jersey

336 Castles DL, Aureli F, de Waal FBM (1996) Variation in conciliatory tendency and relationship quality
 337 across groups of pigtail macaques. *Anim Behav* 52: 389–403
 338 Chandrasekaran C, Lemus L, Trubanova A, Gondan M, Ghazanfar AA (2011) Monkeys and humans
 339 share a common ‘Computation for face/voice integration’. *PLoS One* 7: e1002165
 340 Chevalier-Skolnikoff S (1973) Visual and tactile communication in *Macaca arctoides* and its ontogenetic
 341 development. *Am J Phys Anthropol* 38: 515–518
 342 Cooper MA, Bernstein IS, Hemelrijk CK (2005) Reconciliation and relationship quality in
 343 Assamese macaques (*Macaca assamensis*). *Am J Primatol* 65: 269–282
 344 Cooper MA, Aureli F, Singh M (2007) Sex Differences in Reconciliation and post-conflict anxiety
 345 in Bonnet macaques. *Ethology* 113: 26–38
 346 Corballis MC (2002) *From Hand to Mouth: The Origins of Language*. Princeton University Press,
 347 Princeton
 348 Das M, Penke Z, van Hooff JARAM (1998) Postconflict affiliation and stress-related behavior of
 349 long-tailed macaque aggressors. *Int J Primatol* 19: 53–71
 350 Enomoto T (1974) The sexual behavior of Japanese monkeys. *J Hum Evol* 3: 351–372
 351 Enomoto T (1978) On the social preference in sexual behavior of Japanese monkeys (*Macaca fuscata*). *J*
 352 *Hum Evol* 7: 283–293
 353 Evans TA, Howell S, Westergaard GC (2005) Auditory-visual cross-modal perception of communicative
 354 stimuli in tufted capuchin monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process* 31: 399–406
 355 Fujita S (2010) Interaction between male and female mating strategies and factors affecting reproductive
 356 outcome. In: Nakagawa N, Nakamichi M, Sugiura H (eds) *The Japanese Macaques*. Springer, Tokyo, pp
 357 221–239
 358 Fujita S, Sugiura H, Mitsunaga, F, Shimizu K (2004) Hormonal profiles and reproductive characteristics
 359 in wild female Japanese macaques (*Macaca fuscata*). *Am J Primatol* 64: 367–375

360 Ghazanfar AA, Logothetis NK (2003) Facial expressions linked to monkey calls. *Nature* 423: 937–938

361 Ghazanfar AA, Morrill RJ, Kayser C (2013) Monkeys are perceptually tuned to facial expressions that

362 exhibit a theta-like rhythm *Proc Natl Acad Sci USA* 110: 1959–1963

363 Green S (1975) Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*):

364 a field study. In: Rosenblum LA (ed) *Primate Behavior*, vol 4, Academic Press, New York, pp 1–102

365 Hauser MD (1996) *The Evolution of Communication*. MIT Press, Cambridge

366 Holman SD, Goy RW (1980) Behavioral and mammary responses of adult female rhesus to strange

367 infants. *Horm Behav* 14: 348–357

368 Itani J (1963) Vocal communication of the wild Japanese monkeys. *Primates* 4: 11–66

369 Izawa K (2000) The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi

370 Prefecture on the population change 1995–2000. *Bull Miyagi Univ Educ* 35: 329–337 (in Japanese with

371 English summary)

372 Izawa K (2002) Tracing the history of two male Japanese macaques in Kinkazan. *Japanese Monkeys in*

373 *Miyagi Prefecture* 12: 20–29 (in Japanese)

374 Izumi A, Kojima S (2004) Matching vocalizations to vocalizing faces in a chimpanzee (*Pan troglodytes*).

375 *Anim Cogn* 7: 179–184

376 Kutsukake N, Castles DL (2001) Reconciliation and variation in post-conflict stress in Japanese macaques

377 (*Macaca fuscata fuscata*): testing the integrated hypothesis. *Anim Cogn* 4: 259–268

378 Maestripieri D (1996) Gestural communication and its cognitive implications in pigtail macaques

379 (*Macaca nemestrina*). *Behaviour* 133: 997–1022

380 Maestripieri D (2007) Gestural communication in three species of macaques (*Macaca mulatta*, *M.*

381 *nemestrina*, *M. arctoides*). Use of signals in relation to dominance and social context. In: Liebal K,

382 Muller C, Pika S (eds) *Gestural Communication in Nonhuman and Human Primates*. John Benjamins

383 Publishing Company, Amsterdam/Philadelphia, pp 51–66

384 Maestripeiri D, Wallen K (1997) Affiliative and submissive communication in rhesus macaques. *Primates*
 385 38: 127–138
 386 Majolo B, Koyama N (2006) Seasonal effects on reconciliation in *Macaca fuscata yakui*. *Int J Primatol*
 387 27: 1383–1397
 388 Majolo B, Ventura R, Koyama N (2009) Anxiety level predicts post-conflict behavior in wild Japanese
 389 macaques (*Macaca fuscata yakui*). *Ethology* 115: 986–995
 390 Manson JH, Perry S (2000) Correlates of self-directed behaviour in wild white-faced capuchins. *Ethology*
 391 106: 301–317
 392 De Marco A, Cozzolino R, Dessi-Fulgheri F, Thierry B (2010) Conflicts induce affiliative interactions
 393 among bystanders in a tolerant species of macaque (*Macaca tonkeana*). *Anim Behav* 80: 197–203
 394 Martin P, Bateson P (1990) *Measuring Behavior*, Cambridge University Press, Cambridge
 395 Maynard Smith J, Harper D (2003) *Animal Signals*. Oxford University Press, Oxford
 396 Mori A (1975) Signals found in the grooming interactions of wild Japanese monkeys of the Koshima
 397 troop. *Primates* 16: 107–140
 398 Masataka N (1989) Motivational referents of contact calls in Japanese monkeys. *Ethology* 80: 265–273
 399 Mizuhara H (1981) *Notes on Behavior in Japanese Macaques*. Dobutsusha Tokyo (in Japanese)
 400 Nakagawa N (1997) Determinants of the dramatic seasonal changes in the intake of energy and protein by
 401 Japanese monkeys in a cool temperate forest. *Am J Primatol* 41: 267–288
 402 Nakagawa N, Nakamichi M, Yamada K (2011) Report on the questionnaire for infrequently observed
 403 behaviors in Japanese macaques. *Primate Res* 27: 111–125 (in Japanese with English summary)
 404 Nakamichi M, Yamada K (2010) Lifetime social development in female Japanese macaques. In:
 405 Nakagawa N, Nakamichi M, Sugiura H (eds) *The Japanese Macaques*. Springer, Tokyo, pp 241–270
 406 Negayama K, Negayama T, Kondo K (1986) Behavior of Japanese monkeys (*Macaca fuscata*) mothers
 407 and neonates at parturition. *Int J Primatol* 7: 365–378

408 Partan SR (2002) Single and multichannel signal composition: facial expressions and vocalizations of
 409 rhesus macaques (*Macaca mulatta*). Behaviour 139: 993–1027
 410 Partan S, Marler P (1999) Communication goes multimodal. Science 283: 1272–1273
 411 Pavani S, Maestripieri D, Schino G, Turillazzi PG, Scucchi S (1991) Factors influencing scratching
 412 behavior in long-tailed macaques (*Macaca fascicularis*). Folia Primatol 57: 34–38
 413 Pollick AS, de Waal FBM (2007) Ape gesture and language evolution. Proc Natl Acad Sci USA. 104:
 414 8184–8189
 415 Preuschoft S, van Hooff JARAM (1995) Homologizing primate facial displays: a critical review of
 416 methods. Folia Primatol 65: 121–137
 417 Rahaman H, Parthasarathy MD (1968) The expressive movements of the bonnet macaques. Primates 9:
 418 259–272
 419 Redican WK (1975) Facial expressions in nonhuman primates. In: Rosenblum LA (ed) Primate Behavior:
 420 Development in Field and Laboratory Research, vol. 4. Academic Press, New York, pp 103–194
 421 Rowe C, Guilford T (1996) Hidden colour aversions in domestic chicks triggered by pyrazine odours of
 422 insect warning displays. Nature 383: 520–522
 423 Sakura O (1989) Variability in contact calls between troops of Japanese macaques: a possible case of
 424 neutral evolution of animal culture. Anim Behav 38: 900–902
 425 Schino G, Maestripieri D, Scucchi S, Turillazzi PG (1988) Allogrooming as a tension-reduction
 426 mechanism: A behavioral approach. Am J Primatol 16: 43–50
 427 Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1990) Social tension in familiar and unfamiliar pairs
 428 of long-tailed macaques. Behaviour 113: 264–272
 429 Schino G, Rosati L, Geminiani S, Aureli F (2007) Post-conflict anxiety in Japanese macaques (*Macaca*
 430 *fuscata*): aggressor's and victim's perspectives. Ethology 113: 1081–1088
 431 Shirek-Ellefson J (1972) Social communication in some old world monkeys and gibbons. In: Dolhinow P

432 (ed) Primate Patterns Holt Rinehart and Winston, New York, pp 297–311
 433 Slocombe K, Waller BM, Liebal K (2011) The language void: the need for multimodality in primates.
 434 Anim Behav 81: 915–924
 435 Smith DG, McDonough JM, George DA (2007) Mitochondrial DNA variation within and among regional
 436 populations of longtail macaques (*Macaca fascicularis*) in relation to other species of the *fascicularis*
 437 group of macaques. Am J Primatol 69 182–198
 438 Soltis J, Mitsunaga F, Shimizu K, Yanagihara Y, Nozaki M (1997) Sexual selection in Japanese macaques
 439 I: female mate choice or male sexual coercion? Anim Behav 54: 725–736
 440 Stafstrom J, Hebets E (2013) Female mate choice for multimodal courtship and the importance of the
 441 signaling background for selection on male ornamentation. Curr Zool 59: 200–209
 442 Takahashi H, Furuichi T (1998) Comparative study of grooming relationships among wild Japanese
 443 macaques in Kinkazan A troop and Yakushima M troop. Primates 39: 365–374
 444 Takahata Y, Suzuki S, Agetsuma N, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Furuichi
 445 T, Hill DA, Maruhashi T, Saito C, Sato S, Sprague DS (1998) Reproduction of wild Japanese macaque
 446 females of Yakushima and Kinkazan Islands: a preliminary report. Primates 39: 339–349
 447 Thierry B (1984) Clasping behavior in *Macaca tonkeana*. Behaviour 89: 1–28
 448 Thierry B, Bynum EL, Baker S, Kinnaird MF, Matsumura S, Muroyama Y, O’Brien TG, Petit O,
 449 Watanabe K (2000) The social repertoire of Sulawesi macaques. Primate Res 16: 203–226
 450 Tsukahara T (1990) Initiation and solicitation in male-female grooming in a wild Japanese macaque troop
 451 on Yakushima Island. Primates 31: 147–156
 452 van Hooff JARAM (1967) The facial displays of the catarrhine monkeys and apes. In: Morris D (ed)
 453 Primate Ethology, Weidenfeld and Nicolson, London, pp 7–68
 454 Vasey PL, Rains D, VanderLaan DP, Duckworth N, Kovacovsky SD (2008) Courtship behaviour in
 455 Japanese macaques during heterosexual and homosexual consortships. Behav Processes 78: 401–407

- 456 Walker ML, Wilson ME, Gordon TP (1983) Female rhesus monkey aggression during the menstrual cycle.
- 457 Anim Behav 31: 1047-1054

458 Table 1 Distribution of ‘rocking-embrace’ behaviours. The total number of cases of ‘rocking embrace’ in each dyad of participants is shown; those between anoestrous adult
459 females are parentheses. Above and to the right of the diagonal line: entire data set and below and to the left of the diagonal line: subset where ‘rocking embrace’ occurred
460 immediately after approaching. ¹UN: Unidentified; ²Adu: adults; Ado: adolescents; Juv: juveniles. ³M: males; F: females. Grey rectangles: kin-related ($r \geq 0.25$)
461 individuals.

Name ¹⁾	Age ²⁾	Sex ³⁾	<i>Kb</i>	<i>At</i>	<i>Sr</i>	<i>Kr</i>	<i>Ku</i>	<i>Be</i>	<i>Sf</i>	<i>Kk</i>	<i>Er</i>	<i>Ha</i>	<i>Mm</i>	<i>Mg</i>	<i>Fr</i>	<i>So</i>	<i>Ok</i>	<i>Ml</i>	<i>Mr</i>	<i>Mi</i>	<i>Ms</i>	<i>Hr</i>	UN1	UN2
<i>Kb</i>	Ado	M			1																			
<i>At</i>	Adu	F			1	2																		
<i>Sr</i>	Adu	F				1		1				1	1				1							
<i>Kr</i>	Adu	F		1	1					1														
<i>Ku</i>	Juv	M								1														
<i>Be</i>	Adu	F			1							4	4				1		1					
<i>Sf</i>	Adu	F											1						2					
<i>Kk</i>	Adu	F				1																		
<i>Er</i>	Adu	F									2	11 (4)											2	
<i>Ha</i>	Adu	F						1		1		13 (6)			1	2 (2)	1		4(1)				3	
<i>Mm</i>	Adu	F			1			3	1	7	9				1	1	1		4(1)				2	1
<i>Mq</i>	Adu	F																						
<i>Fr</i>	Adu	F											1						2					
<i>So</i>	Adu	F										1												
<i>Ok</i>	Adu	F											1						6(2)					
<i>Ml</i>	Ado	F																	3(3)					
<i>Mr</i>	Adu	F						1				3	3		1		1	1	1		2(2)			
<i>Mi</i>	Juv	F																						
<i>Ms</i>	Juv	M																						
<i>Hr</i>	Adu	F																	1	1				
UN1	Adu	F								1			2											
UN2	Ado/Juv	F																						

462 Table 2 Behaviours immediately before ‘rocking embraces’. The number of cases of ‘rocking embrace’
 463 between adult females is shown. The total number of cases is shown in parentheses.

Behaviours		<i>n</i>
Approach		42 (44)
Grooming	spontaneous break of allogrooming	8 (10)
	intervention of allogrooming by third party	5 (5)
Aggression	between participants involved in ‘rocking embrace’	5 (5)
	between 1 of the 2 participants involved in ‘rocking embrace’ and a third party	2 (2)
	between a pair of third parties	4 (4)
Lactating		0 (1)
Unknown		12 (17)
Total		78 (88)

464

465 Table 3 Behaviours immediately after ‘rocking embraces’. The number of cases of ‘rocking embrace’ between
466 adult females is shown. The total number of cases is shown in parentheses.

Behaviours	<i>n</i>
Allogrooming	66 (73)
‘Rocking embrace’	3 (3)
Being driven away by a third party	5 (5)
Leaving	3 (4)
Just sitting aside	0 (1)
Unknown	1 (2)
Total	78 (88)

467

Figure Legends

Fig. 1 A typical context in which ‘rocking embraces’ occur, i.e. post conflict. (a) A pair consisting of an alpha-female and her adolescent daughter poses a threat (b) against a low-ranking adult female, who emits a scream. (c) Immediately after the end of the aggressive interaction, a ‘rocking embrace’ between the aggressor adolescent daughter (right) and the aggressee occurred (left), (d) ending with an exchange of grooming (Photo by N.N. on 1 December 1986).

Fig. 2 Schematic flowchart of allogrooming interactions in which the ‘rocking embrace’ was observed to occur between the same dyad in which a grooming interaction had occurred.

Fig. 3 Comparisons of the mean duration of grooming bouts immediately before ‘rocking embraces’ (grooming-1) and immediately after ‘rocking embraces’ (grooming+1). Upper whisker: maximum; upper box range: 75th percentile; lower box range: 25th percentile; lower whisker: minimum.

Fig. 4 Comparisons of the mean duration of grooming intervals immediately before ‘rocking embraces’ (interval-1) and immediately after ‘rocking embraces’ (interval+1). Upper whisker: maximum; upper box range: 75th percentile; lower box range: 25th percentile; lower whisker: minimum.

Electronic supplemental material

Another typical context in which the ‘rocking embrace’ occurs, i.e. an interruption of grooming interactions. (Video by Dr. H. Sugiura on 21 May 1998).

Fig. 1

a



b



c



d



Fig. 2

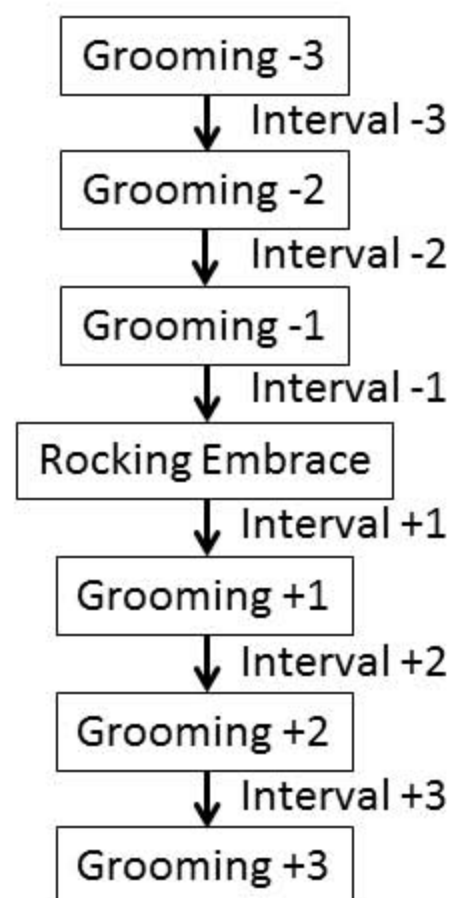


Fig. 3

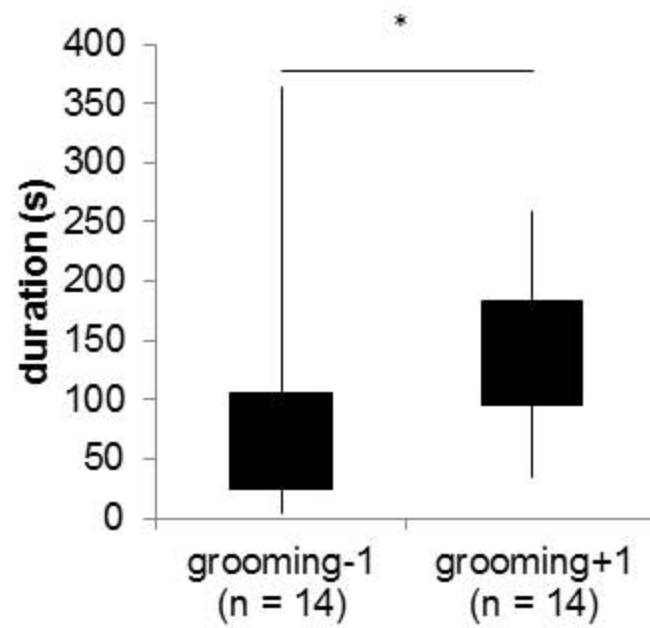


Fig. 4

