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1 **Title: Functions of Unreported ‘Rocking-Embrace’ Gesture between Female Japanese Macaques**

2 **(*Macaca fuscata*) in Kinkazan Island, Japan**

3

4 **Authors:** Yukiko Shimooka<sup>1)</sup> and Naofumi Nakagawa<sup>2)</sup> (corresponding author)

5

6 **Authors’ affiliation:**

7 <sup>1)</sup>Faculty of Life and Environment Sciences, Teikyo University of Science, Yatsusawa 2525, Uenohara,

8 Yamanashi 409-0193, Japan. E-mail: [shimooka@ntu.ac.jp](mailto:shimooka@ntu.ac.jp)

9 <sup>2)</sup>Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo, Kyoto, Kyoto

10 606-8502, Japan. E-mail: [nakagawa@jinrui.zool.kyoto-u.ac.jp](mailto:nakagawa@jinrui.zool.kyoto-u.ac.jp); Phone number: +81-75-753-4084; Fax

11 number: +81-75-753-4115

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

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

24 signals; Visual signals

25 **Abstract**

26 Recently, research has focused on the effects of the concurrence of multimodal signals and their  
27 efficacy and meaning. We observed an unreported behaviour, a combination of a ventro-ventral  
28 ‘rocking-embrace’ gesture always accompanied by lip smacking as the facial expression and sometimes  
29 by a girney call in wild Japanese macaques (*Macaca fuscata*), living in Kinkazan Island, northern Japan.  
30 This study examined the form and contexts of the occurrence of such multimodal signals to reveal its  
31 functions. Eighty-eight cases of ‘rocking embrace’ were recorded during 183 h of observation over 22 d.  
32 Adult females were involved in all the cases. Of the 71 cases between adult females in which  
33 behaviours prior to the ‘rocking embrace’ could be identified, 13 cases were allogrooming interruptions,  
34 11 cases of aggressions, and 42 cases of approaching, most of which occurred between non-kin grooming  
35 partners. The ‘rocking embrace’ was often followed by allogrooming. This suggested that ‘rocking  
36 embraces’ occurred under stressful conditions and might be appeared to function to reduce tensions.  
37 This conclusion was consistent with the contexts and functions of lip smacking and girneys shown in  
38 previous studies. In contrast with lip smacking and girneys, neither ‘rocking embrace’ nor  
39 ventro-ventral embrace (without rocking) between anoestrous adult females has been previously shown in  
40 Japanese macaques. In other macaque species, however, the latter gesture is often shown as an  
41 affiliative behaviour that immediately follows conflict, which functions to reconcile or as a greeting when  
42 it occurs immediately after an approach. ‘Rocking embraces’ among the Kinkazan macaques occurred  
43 in contexts similar to, and held a similar function as, the ancestral gesture of ventro-ventral embracing,  
44 which was hidden in Japanese macaques, and the ancestral display of lip smacking, which is still  
45 observed in Japanese macaques. The ventro-ventral embrace as a tactile signal might have been hidden  
46 since it was redundant with the visual signal of lip smacking in ancestral macaques.

47

48 (306 words)

49 **Introduction**

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

61 Primates communicate by means of elaborate facial expressions (van Hooff 1967) and vocalisations  
62 (Hauser 1996). Recent experimental evidence has shown that they can integrate visual and auditory  
63 information during communication (Ghazanfar and Logothetis 2003; Izumi and Kojima 2004; Evans et al.  
64 2005; Chandrasekaran et al. 2011). Such a multimodal perception may represent an evolutionary  
65 precursor to human speech, which is enhanced by a combination of visual and auditory signals  
66 (Ghazanfar and Logothetis 2003; Ghazanfar et al. 2013). To examine the hypothesis that human  
67 language evolved via gestural signals (Corballis 2002; Arbib 2005; Pollick and de Waal 2007), the study  
68 of links between manual gestures and vocalisations has been a focus of primatology (Call and Tomasello  
69 2007).

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

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

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

90

## 91 **Methods**

### 92 **Study Sites and Subjects**

93 This study was conducted on the small island of Kinkazan (ca. 10 km<sup>2</sup>), in the northern part of Japan  
94 (38°8’N, 141°4’E). It has a mean annual rainfall of about 1500 mm and a mean annual temperature of  
95 11°C. The island is mostly covered with natural cool temperate forests (for further details, Nakagawa  
96 1997).

97 Japanese macaques (*Macaca fuscata*) form female philopatric multi-male/multi-female groups.  
98 There were approximately 250 individuals in 6 unprovisioned groups on the island at the time of  
99 observation (Izawa 2000). The age–sex composition of the target group (the A group) was as follows: 2  
100 adult males ( $\geq 10$  years old), 7 adolescent males (4.5–9 years), 15 adult females ( $\geq 6.5$  years), 1 adolescent  
101 female (4.5–5.5 years), 12 juvenile males (1–3.5 years), 5 juvenile females (1–3.5 years), and 1 female  
102 infant (less than 12 months), totalling 43 individuals. All the adult and adolescent individuals were  
103 individually identified. There were 2 mother-daughter pairs, 2 sister pairs, and no  
104 grandmother-granddaughter pairs among adult females in the group, which are defined as kin with  $r \geq$   
105 0.25 in this study. Such a low degree of relatedness between females comes from a lower birth rate and  
106 higher infant mortality in the unprovisioned population than in the provisioned populations (Takahata et  
107 al. 1998; Fujita 2010).

108

### 109 **Data Collections**

110 Almost all the occurrences of the ‘rocking-embrace’ tactile gesture that Y.S. observed during 22 d (183 h)  
111 of following the A group in October 1997 were recorded, i.e. behaviour sampling (*sensu* Martin and  
112 Bateson 1980). Specifically, the onset and ending time of the behaviour, name of participants, and  
113 occurrence of agonistic interactions (e.g. threats, lunges, chases, and bites) within 1 minute (hereafter,  
114 immediately) before ‘rocking embrace’, were recorded. Because ‘rocking embrace’ often took place  
115 during grooming, grooming behaviours were also recorded via the sequence sampling method (Altmann  
116 1974). Specifically, the onset and ending time of grooming, names of the groomer and groomee, and  
117 grooming solicitation were recorded.

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

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

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

126

## 127 **Data Analyses**

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

136           Figure 2 schematises a series of typical grooming interactions in which the ‘rocking embrace’  
137 between the same dyad of grooming interactions occurred. A grooming bout was defined as a  
138 continuous act of picking by an individual through the fur of another that was not interrupted by pauses of  
139 longer than 5 s. When interrupted by a pause of longer than 5 s, it was regarded as 2 different grooming  
140 bouts, which were separated by an interval in grooming. When the ‘rocking embrace’ occurred between  
141 2 grooming bouts, the interval between the ‘rocking embrace’ and the following grooming (grooming+1)  
142 was named ‘interval+1’ and that between the ‘rocking embrace’ and the preceding grooming  
143 (grooming-1) was named ‘interval-1’ (for details of the naming of grooming bouts and grooming intervals,  
144 see Fig. 2). Grooming solicitations sometimes occurred during a grooming interval. We compared the

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

147

## 148 **Results**

### 149 **General Characteristics of 'Rocking Embrace'**

150 Eighty-eight cases of 'rocking embraces' were recorded during 183 h of observation over 22 d. In the 36  
151 cases where the duration was obtained, the mean was 17 s, ranging from 4 s to 46 s. Table 1 shows the  
152 number of cases of 'rocking embraces' in each dyad of participants. In all 88 cases, at least 1 of the 2  
153 participants was an adult female. The 'rocking embrace' was observed in 78 cases between adult  
154 females: 21 cases between anoestrous females, 39 cases between anoestrous and oestrous females, and 18  
155 cases between oestrous females. The 10 other cases included 3 between anoestrous adult females and  
156 anoestrous adolescents or juvenile females, 3 between oestrous adult females and adolescent females, 1  
157 between an anoestrous adult female and a juvenile male, 2 between oestrous adult females and juvenile  
158 males, and 1 between an anoestrous adult female and an adolescent male. The case involving an  
159 adolescent male occurred between *Kb* and his elder sister. *Kb* is a relatively small 8-year-old male due  
160 to having been badly wounded at the age of 1 year and still remains in the natal group (Izawa 2002).

161 In 2 out of 71 cases between identified adult females, the 'rocking embrace' occurred between  
162 maternal kin-related individuals. Compared to the number of kin dyads vs. non-kin dyads among adult  
163 females in the group, no significant difference was found in the frequency of 'rocking embraces' between  
164 kin and between non-kin (Binomial test,  $n = 71$ ,  $p = 0.489$ ). The lack of significant differences may be  
165 explained by the kin-biased tendency for allogrooming and proximity in female Japanese macaques  
166 (Nakamichi and Yamada 2010). Based on the result that allogrooming occurred in all kin dyads but in  
167 only 24% of non-kin dyads in this study group (Takahashi and Furuichi 1998), 24 out of non-kin 101



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

172

### 173 **Contexts of Occurrence of 'Rocking Embrace'**

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

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

189 Table 3 shows the behaviours immediately after 'rocking embraces'. Of the 77 cases between adult  
190 females in which behaviours following a 'rocking embrace' could be identified, there were 66 cases  
191 (86%) of allogrooming, 3 cases (4%) of 'rocking embraces', 5 cases (6%) of being driven away by a third

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

193

#### 194 **Details of ‘Rocking Embrace’ during Grooming Interaction**

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

200 Figure 4 shows the mean duration of grooming intervals immediately before a ‘rocking embrace’  
201 (interval-1) and immediately after a ‘rocking embrace’ (interval+1). In 14 cases between adult females  
202 where the duration of both interval-1 and interval+1 were obtained, the duration of the grooming interval  
203 was significantly longer in interval-1 than in interval+1 (Wilcoxon signed-rank test,  $T = 0$ ,  $n = 12$ ,  $p <$   
204  $0.01$ ).

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

210

#### 211 **Discussion**

##### 212 **Functions of ‘Rocking Embrace’**

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

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

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

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

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

239 The 'rocking embrace' is always accompanied by lip smacking as a facial expression and sometimes

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

246

#### 247 **Phylogenetic and Ontogenetic Origins of ‘Rocking Embrace’**

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

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

265 However, one cannot say that the 'rocking embrace's has nothing to do with the sexual condition of  
266 the females. The oestrous females are often more likely not only receive aggression from males (Enomoto  
267 1978; Soltis et al, 1997) but also give aggression to females in macaques (Walker et al. 1983). Such an  
268 enhanced aggression may increase the frequency of 'rocking-embraces' between female opponents,  
269 between female aggresse and third party or between a pair of female third parties. Contrarily, the  
270 enhanced aggression may not lead to substantial increase of 'rocking-embraces' as might be the case with  
271 reconciliation in that conciliatory tendency is lower when one or both female opponents is in estrus than  
272 when they are not because the estrus female devotes herself to compete over male rather than to reconcile  
273 (Majolo and Koyama 2006).

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

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

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

311

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323

324 **References**

- 325 Altmann J (1974) Observation study of behavior: sampling methods. *Behaviour* 49: 227–267
- 326 Arbib M (2005) The Mirror System Hypothesis: how did protolanguage evolve? In: Tallerman M (ed)  
327 *Language Origins: Perspectives on Evolution*. Oxford University Press, New York, pp 21–47
- 328 Arnold K, Aureli F (2007) Postconflict reconciliation. In: Campbell CJ, Fuentes A, MacKinnon KC,  
329 Panger M, Bearder SK (eds) *Primates in Perspective*. Oxford University Press, Oxford, pp 592–608
- 330 Blount BG (1985) “Girney” vocalization among Japanese macaque females: context and function.  
331 *Primates* 26: 424–435
- 332 Bro-Jorgensen J (2009) Dynamics of multiple signalling systems: animal communication in a world in  
333 flux. *Trends Ecol Evol* 25: 292–300
- 334 Call J, Tomasello M (eds) (2007) *The Gestural Communications in Apes and Monkeys*. Lawrence  
335 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* 29: 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 Maestripietri D (1996) Gestural communication and its cognitive implications in pigtail macaques  
379 (*Macaca nemestrina*). *Behaviour* 133: 997–1022

380 Maestripietri 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, Maestriperi 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, Maestriperi 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, Maestriperi 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) Clasp 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. <sup>1</sup>UN: Unidentified; <sup>2</sup>Adu: adults; Ado: adolescents; Juv: juveniles. <sup>3</sup>M: males; F: females. Grey rectangles: kin-related ( $r \geq 0.25$ )  
 461 individuals.

Name <sup>1)</sup>	Age <sup>2)</sup>	Sex <sup>3)</sup>	<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												
<i>Ku</i>	Juv	M										1												
<i>Be</i>	Adu	F			1																			
<i>Sf</i>	Adu	F																						
<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>Mg</i>	Adu	F																						
<i>Fr</i>	Adu	F											1											
<i>So</i>	Adu	F										1												
<i>Ok</i>	Adu	F											1											
<i>Ml</i>	Ado	F																						
<i>Mr</i>	Adu	F						1				3	3		1		1		1	1		1		
<i>Mi</i>	Juv	F																						
<i>Ms</i>	Juv	M																						
<i>Hr</i>	Adu	F																						
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



468 **Figure Legends**

469

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

475

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

478

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

482

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

486

487 **Electronic supplemental material**

488 Another typical context in which the ‘rocking embrace’ occurs, i.e. an interruption of grooming interactions.

489 (Video by Dr. H. Sugiura on 21 May 1998).

Fig. 1

a



b



c



d



Fig. 2

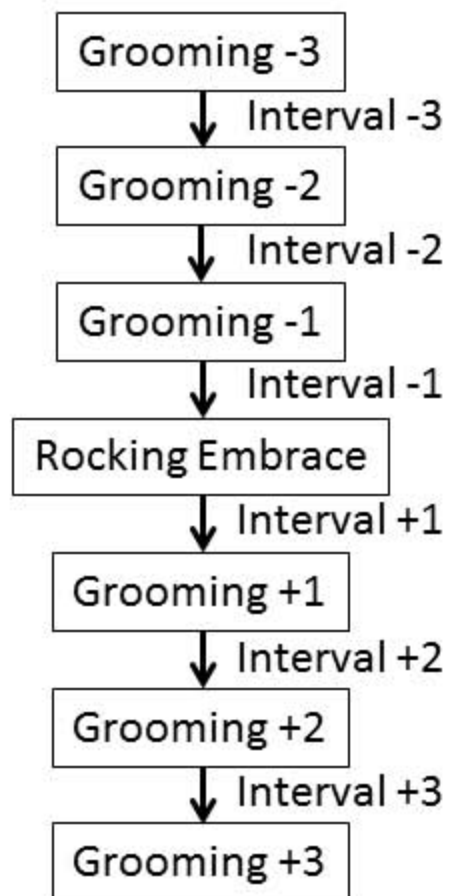


Fig. 3

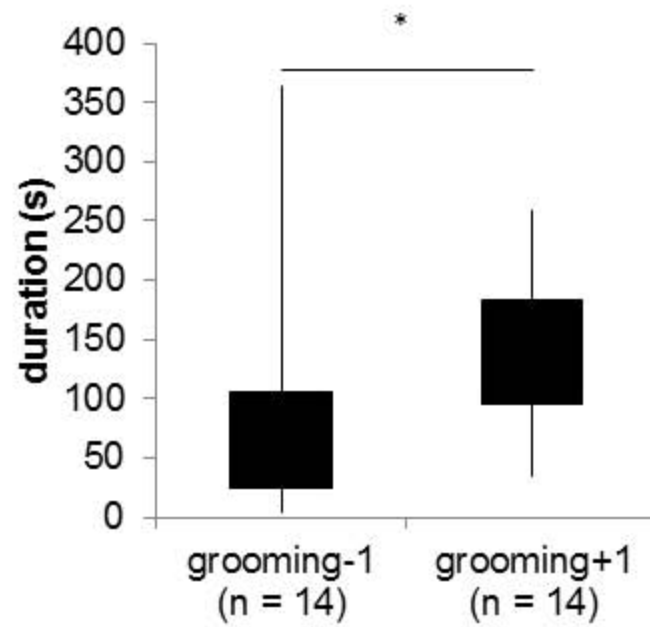


Fig. 4

