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Collective Arousal When Reuniting After Temporary Separation in Tonkean Macaques

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ABSTRACT Celebrations and bursts of communal joy can occur spontaneously in human communities based on mechanisms of emotional contagion. Some examples of similar collective excitement have been reported in animals when they reunite or anticipate rewards, but little is known about the processes and meaning of these multiple interactions. We experimentally studied such collective arousals in two captive groups of Tonkean macaques (*Macaca tonkeana*) within the context of reunions following the temporary separation of two subgroups. We compared the behaviors of individuals after separation periods of 2 and 48 h with a control period with no separation. This study showed that it is possible to reproducibly induce bursts of friendly interactions in which groupmates run around over a period of several minutes, embracing and grasping one another while displaying numerous affiliative vocalizations and facial expressions. The longer the period of separation, the higher and longer-lasting the rates of affiliative interactions were. Individuals affiliated more frequently with groupmates from a previously separated subgroup than with those having stayed in their own subgroup. Collective arousal was followed by a quieter period characterized by high rates of contact-sitting and social grooming. These results point at the role of collective arousals in social cohesion; they could resolve social tension and renew social relationships. We propose that the emotional state experienced by Tonkean macaques during such events represents a disposition similar to that giving rise to what we humans call "shared joy." Am J Phys Anthropol 146:457–464, 2011.

Collective celebration is common practice in human communities. Amongst various other social functions, it can be argued that it either has a role in social cohesiveness by renewing the bonds that hold society together, or that it provides individuals with occasional relief from hierarchies and social constraints (Ehrenreich, 2007). Whereas certain events such as dances, rituals, and ceremonies follow formalized rules and/or use techniques of ectasy, others occur as spontaneous bursts of excitement where groups appear united by communal joy and exaltation, all individuals experiencing a similar emotional state (Ehrenreich, 2007). In the second case, social interactions mainly rely on nonverbal communication; individuals synchronize and mimic each other through vocalizations, facial expressions, postures and movements conveying emotional contagion (Hatfield et al., 1994).

There is no need to resort to cognitive empathy to account for emotional contagion. The ability to react to the feelings of others appears early in life (Hoffman, 1975; Hatfield et al., 1994), and its neurobiological substrates have been documented (Decety and Jackson, 2004; Rizzolatti et al., 2007). Moreover, it is widely known that nonhuman primates react to communication signals expressing emotions (Seyfarth and Cheney, 2003; de Waal, 2008), and synchronize by mirroring the behaviors of conspecifics (Anderson and Bayart, 1985; Ferrari et al., 2006; Meunier et al., 2008). In view of these facts, we may ask to what extent collective excitement based on common positive emotional states can occur in nonhuman primates and other mammals.

In several mammals, individuals call in chorus (howls in wolves and other group-living canids: Gese and Ruff, 1998; Harrington and Asa, 2003; roars in lions: McComb et al., 1994; rumbles in elephants: Leighty et al., 2008; loud calls in howler monkeys: Kitchen, 2004; pant hoots in chimpanzees: Wilson et al., 2001). Once an individual starts vocalizing, others join in chorus. Whatever their function, these long-distance contact calls involve social contagion and coordination. It should however be noted that these signals are not addressed to members of the community present at the same location, contrary to the affiliative interactions observed in bursts of collective excitement in humans.

Greetings occurring between group members are another cause for mutual excitement. In many species individuals display intense affiliative interactions when meeting after a period of separation. In fission–fusion communities groups split and gather regularly, then

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Additional Supporting Information may be found in the online version of this article.

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individuals engage in acts of welcoming, touching each other, and exchanging affiliative behaviors, for example in African elephants (Moss, 1988), spotted hyenas (East et al., 1993), spider monkeys (Aureli and Schaffner, 2007), and chimpanzees (Goodall, 1986; Okamoto et al., 2001). Reunion events are potentially risky situations, and agonistic interactions sometimes occur (e.g., Goodall, 1986; Muller, 2002; Aureli and Schaffner, 2007). It is likely that greeting rituals allow partners to overcome social tension and reaffirm social bonds (Smuts and Watanabe, 1990; Kutsukake et al., 2006). The same may be said for individuals kept in captivity when they are reunited after temporary separation. In nonhuman primates in particular, individuals greet each other by displaying intimate body contacts and multiple affiliative signals (e.g., Thierry, 1984; de Waal, 1996; Matheson et al., 1996; Lynch Alfaro, 2008). Although these behaviors are mutual and intense, it must be emphasized that authors usually report observing them between single pairs of individuals; as such they do not qualify as cases of collective excitement.

Instances of intense affiliation simultaneously involving more than two individuals have been described in a small number of species. Greeting rituals in canids represent a first case. In wolves, pack members surround the leader either spontaneously or after grouping and display active submission and appeasement, using nose-pushing and licking his muzzle (Mech, 1970). African wild dogs address similar noisy behaviors to welcome back any member of the pack during reunions following separations (Rütten and Fleissner, 2004). The rubbing behavior observed in white-faced capuchins is another type of collective behavior. Several individuals simultaneously anoint themselves with pungent plants. Whether they are in physical contact or not, one or several will start rubbing their own fur, drawing the attention of other group members, who then mimic the same behavior (Meunier et al., 2008).

Behaviors quite similar to the collective excitement observed in human beings have been described in elephants and chimpanzees. In African elephants, subgroups that know each other perform an intense greeting ceremony when they meet. All group members run together, raising their heads, flapping their ears, rumbling, trumpeting, clinking their tusks together, and entwining their trunks (Moss, 1988). During similar reunion episodes, wild chimpanzees show collective behaviors named “celebration” or “carnival.” They display mass excitement with multiple social interactions including charging, loud hooting, kissing, and embracing (Reynolds and Reynolds, 1965; Goodall, 1986). In captive chimpanzees this type of celebration also occurs when animals await an oncoming distribution of food, and it could reduce social competition (de Waal, 1992, 1996).

It must be underlined, however, that we lack quantitative data which would allow a clear differentiation between collective events and the greeting interactions reported in other species at the dyadic level. Additionally, both kinds of events mostly involve intense body contacts and communication signals aiming to resolve social tension; they differ qualitatively from the calmer bouts of social grooming and contact-sitting commonly observed in groups at rest, the function of which is held in particular to reinforce social bonds (Dunbar, 1988; Aureli and Yates, 2010). It is worth adding that the latter contacts usually follow the occurrence of more intense behaviors (e.g., clasp, mount) in the context of reconciliation and at first meeting (see Kummer, 1975; Demaria and Thierry, 2001; Arnold et al., 2011).

Some anecdotal reports describe the occurrence of a group excitement called “collective arousal” in a few monkey species. This may happen after reunion, before food distribution, or after a conflict involving a large number of individuals (Tonkean macaques: Thierry et al., 1989, 2000; moor macaques: Matsumura, 1991; Petit and Thierry, 1992; stumptailed macaques: de Waal, 1996). On such occasions, all group members appear extremely excited, and display numerous affiliative signals and body contacts at the same time.

Studies about collective excitement in animals remain scarce, however, and little is known about the processes and meaning of these multiple interactions. The present study aims to investigate collective arousals in Tonkean macaques. These animals display a relaxed dominance style and a high level of social tolerance compared to other macaque species (Thierry, 2000, 2010). They show great propensity for appeasement and reconciliation of group members after conflict (Demaria and Thierry, 2001; Thierry et al., 2008). They are also characterized by complex polyadic interactions; when conflicts occur third parties can stop aggression by addressing appeasement signals to adversaries (Petit and Thierry, 1994), and groupmates uninvolved in a conflict are more likely to affiliate with one another after witnessing it (De Marco et al., 2010).

We experimentally tested the following predictions regarding collective arousals in two groups of Tonkean macaques: 1) if they are triggered by the reunion of individuals familiar to each other following separation, we should be able to induce this behavior in a reproducible way using a separation/reunion procedure; 2) if the length of separation increases the need to overcome its effects, the longer the period of separation, the more intense and long-lasting the collective arousal should be; 3) if affiliative interactions are primarily addressed to newcomers, they should occur more frequently between previously separated groupmates than between nonseparated ones; 4) it may be expected that, following the initial burst of communication signals characterizing collective arousal, calmer interactions occur at higher rates.

METHODS

Subjects

We studied two captive groups of Tonkean macaques, A and B, located at the *Parco Faunistico di Piano dell'Abatino* Rescue Centre in Rieti, Italy. Each group was housed in an outdoor enclosure ~1,000 m^2 and 5-m high, connected to an indoor enclosure of 25 m^2. Group A was founded 4 years before this study and consisted of 10 individuals originating from a group maintained at the Primatology Center of Strasbourg, France (Thierry et al., 1994): four adult males, three adult females, one juvenile male, one juvenile female, and one infant. Group B originated from the division 6 months earlier, for management reasons, of a larger group founded 20-years ago at the Orangerie Zoo of Strasbourg, France; it was also composed of 10 individuals: four adult males, three adult females, one juvenile male, and two juvenile females. Social relationships remained stable during the research period, while three infants were born in Group A, and three in Group B. Juveniles were defined as individuals

1–3 years of age, and adult individuals as those at least 4-years old. Enclosures were furnished with perches, slides, wooden structures, ropes, and platforms. Monkeys were fed every day with fresh fruit and vegetables outside observation hours. Water was available ad libitum.

Experimental procedures

We conducted experiments between 11:00 am and 13:00 pm from July 2007 to May 2008 in Group A, and from March to November 2008 in Group B. On average, experiments were carried out every 10–15 days. To induce a collective arousal we used the context of reunion following the temporary separation of groupmates in two subgroups (Fig. 1, Supporting Information Video). While one subgroup was kept in the home area, we attracted the other subgroup to a connected outdoor enclosure $\sim$ 600 m^2 and 5-m high. Subjects knew this area well, since the entire group had already been allowed to occupy it from time to time. Outdoor enclosures communicated through the indoor enclosure, composed of two compartments connected by a guillotine door. Both subgroups had visual and acoustic contact, but no tactile contact was possible between them.

Two different conditions were established for separation, corresponding to durations of 48 and 2 h. A condition without separation was a control period aimed to collect baseline rates of behaviors. All individuals present in each group served as focal subjects. Observational periods began the moment the two subgroups were reunited and at approximately the same time in the control condition. Four observers located at different viewpoints of the enclosure videotaped behaviors and interactions. Because collective arousal can continue for up to 10 min (Thierry et al., 2000), videotaping started immediately after the reunion of subgroups and lasted 10 min. In the control condition, videotaping started after all individuals were outside and the guillotine door of the indoor enclosure was closed. After the 10-min videotape corresponding to the arousal period, one observer followed the group over a postarousal period of 1 h, recording contact-sitting and social grooming at 2-min intervals using instantaneous scan sampling (Altmann, 1974).

Fig. 1. Example of multiple affiliative interactions between groupmates at the time of collective arousal.

The occurrence of collective arousals was subsequently identified from video analysis. To distinguish them from routine affiliation between groupmates, we considered a collective arousal to take place when at least 50% of adult and juvenile individuals were involved in an affiliative interaction within each 10-s interval of the 10-min observation. We arbitrarily defined the beginning to be the minute (i.e., six intervals) preceding the first interval involving at least 50% of individuals, and its end to be the last minute (i.e., six intervals) after the last interval involving at least 50% of individuals.

We submitted each group to 24 tests, i.e., 8 for each of the three experimental conditions (separation of 2 h, 48 h, and control). For each group we arranged subjects in two subgroups that were always composed of the same association of individuals (Table 1). These subgroups were balanced for age and sex as much as possible; for the most part we did not choose partners having particular relationships to constitute subgroups, but we did avoid some associations that could have favored the occurrence of social conflicts between adult males. For each condition we separated and reunited each group four times according to one combination of two subgroups, and four times according to the other combination of subgroups. Individuals were attracted into one enclosure or the other using incentives. For each group we ran tests in successive sequences composed of three tests corresponding to the three different conditions. The order of conditions was randomized within each sequence, whereas the two combinations of individuals alternated from one sequence to another (i.e., first combination three times in a sequence, second combination during the next sequence, etc.).

Data analysis

We quantified the behaviors occurring during arousal and control periods from video records. We measured the frequency per minute of brief behaviors for each individual: mount, clasp (an individual gently grasps another, passes one or both arms around her/his body, or embraces her/him), affiliative facial display (lip-smack, silent

TABLE 1. Composition of experimental subgroups in groups A and B

Group	Combination	Composition of the first subgroup	Composition of the second subgroup
A	First	3 adult males, 1 adult female	1 adult male, 2 adult females, 1 juvenile male, 1 juvenile female, 1 infant
	Second	3 adult males, 1 adult female, 1 juvenile female	1 adult male, 2 adult females, 1 juvenile male, 1 infant
B	First	2 adult males, 1 adult female, 1 juvenile female	2 adult males, 2 adult females, 1 juvenile male, 1 juvenile female
	Second	2 adult males, 1 adult female, 1 juvenile male, 2 juvenile females	2 adult males, 2 adult females

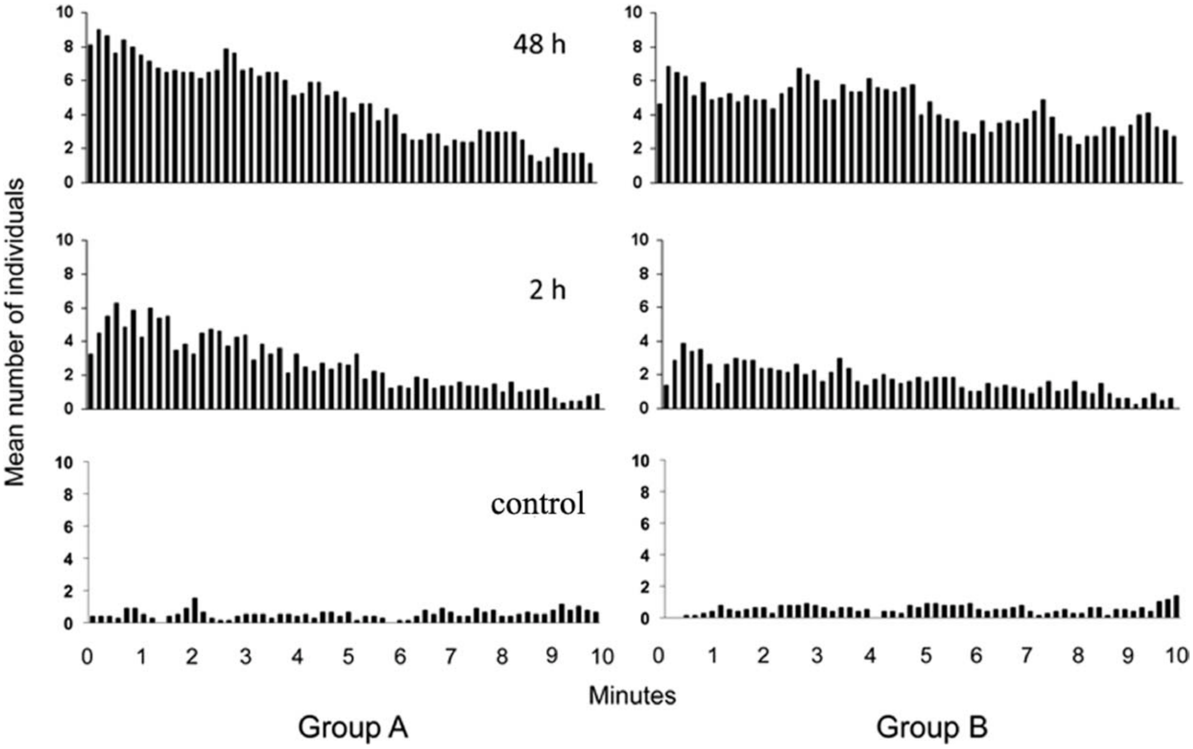

Fig. 2. Mean number of individuals involved in affiliative behaviors in each 10-s interval during the 10 min after reunions following separations of 48 and 2 h, and control periods in Groups A and B.

bared-teeth display), affiliative interference (an individual approaches partners exchanging clasps or mounts and directs affiliative behaviors toward them), conflict (agonistic interaction involving lunge, slap, grab, vocal, or facial threat), and behaviors indicating anxiety (scratch, yawn). When directed at the same partner, behaviors repeated at intervals of less than 5 s were considered as a single event. We also measured the mean durations of time for long-lasting behaviors: expressive run (an individual runs away from a partner while displaying affiliative vocalizations then often returns toward the partner), social play, social grooming, and contact-sitting (see Thierry et al., 2000, for further information about behavior patterns). Because it was not possible to reliably identify which individuals had uttered a vocalization, for this variable we counted the total duration of vocalizations regardless of the emitter. To calculate frequencies and percentages of time, we used the duration of collective arousals for the 48- and 2-h separation conditions, and the 10 min of the videotaped phase in the control condition.

We calculated the percentage of contact-sitting and social grooming over the total number of scans for each condition of arousal and postarousal periods. With respect to the analysis of partner preferences, however, the number of scans occurring during collective arousal remained limited, so we relied on the exact durations measured from videotape footage.

To compare different conditions, and arousal and postarousal periods, we applied the Kruskal–Wallis, Mann–Whitney, and Wilcoxon signed-rank tests, exact procedure (Siegel and Castellan, 1988) using the SPSS software version 16 (SPSS, Chicago, IL). All probabilities were two-tailed. The significance level was set at 0.05.

RESULTS

Duration of collective arousal

Collective arousal systematically occurred in both groups after a 48-h separation. It also occurred in all cases in Group A and in seven out of eight cases in Group B after a 2-hr separation. The number of individuals involved in affiliative interactions at each 10-s interval decreased during the 10-min recording period (see Fig. 2). No collective arousal was observed in the control period. Comparisons of the duration of collective arousal in the 48- and 2-h conditions showed that its mean duration was significantly longer following a 48-h separation both in Group A (Mann–Whitney test, $n_1 = 8$, $n_2 = 8$ $U = 11.0$, $P = 0.026$, 48 h: 8.5 min ± 1.6, 2 h: 6.3 ± 2.1) and Group B ($U = 10.5$, $n_1 = 8$, $n_2 = 8$, $P = 0.023$, 48 h: 8.0 ± 1.8, 2 h: 4.7 ± 3.2). It is worth noting that collective arousal periods usually began and ended quite abruptly (Supporting Information Fig. S1).

Social interactions occurring during collective arousal

We compared the mean rates per minute of behaviors between the three different conditions (Table 2). In both groups, rates significantly differed across conditions except for conflict and scratching in Group B, and yawning in both groups; affiliative behaviors appeared more frequent in the separation–reunion conditions. We additionally performed pairwise tests to compare the effects of 2- and 48-h separation conditions. This showed that the second condition yielded higher rates for several behavior patterns (Kruskal–Wallis test, $P < 0.05$): clasp, facial display, expressive run, social play, and conflict in

TABLE 2. Comparisons of behavioral rates after reunion across the separation and control conditions

		Group A				Group B			
Behavior	Condition	Mean[a]	SD	X^2	P	Mean[a]	SD	X^2	P
Clasp[b]	48 h	0.54	0.14	17.4	<0.001	0.71	0.25	16.9	<0.001
	2 h	0.29	0.23			0.24	0.12		
	control	0.01	0.01			0.01	0.01		
Mount[b]	48 h	0.06	0.02	13.3	<0.001	0.03	0.02	10.2	0.003
	2 h	0.02	0.02			0.03	0.04		
	control	0	0.01			0	0		
Interference[b]	48 h	0.25	0.08	17.2	<0.001	0.34	0.19	15.3	<0.001
	2 h	0.08	0.11			0.13	0.11		
	control	0	0			0	0		
Facial display[b]	48 h	3.5	0.8	15.9	<0.001	3.1	1	17.7	<0.001
	2 h	3	1.4			1.39	0.63		
	control	0.17	0.09			0.09	0.07		
Scratch[b]	48 h	0.06	0.04	11.1	0.002	0.09	0.08	2.0	0.379
	2 h	0.11	0.07			0.11	0.08		
	control	0.24	0.13			0.11	0.02		
Yawn[b]	48 h	0.1	0.07	2.5	0.290	0.02	0.01	1.5	0.481
	2 h	0.07	0.09			0.01	0.01		
	control	0.06	0.06			0.01	0.02		
Conflict[b]	48 h	0.20	0.13	13.9	<0.001	0.11	0.13	3.0	0.202
	2 h	0	0			0.01	0.04		
	control	0.04	0.07			0.04	0.05		
Vocalization[c]	48 h	40.2	9.9	16.2	<0.001	48.4	6.2	16.1	<0.001
	2 h	34.2	14.2			30.4	17.3		
	control	0.31	0.83			0	0		
Expressive run[c]	48 h	7.6	1.8	18.0	<0.001	4.9	2	18.2	<0.001
	2 h	3.5	2.7			1.3	0.88		
	control	0.05	0.04			0.03	0.05		
Social play[c]	48 h	2.52	1.77	9.3	0.010	2.8	1.8	6.2	0.039
	2 h	2.52	0.98			0.86	1.37		
	control	0.86	1.35			1.61	1.3		

Kruskal-Wallis test, $n_1 = 8$, $n_2 = 8$, $n_3 = 8$, d.f. = 2.

[a] Means are given per test and per individual (except for conflicts and vocalizations which are given per group).

[b] Frequency per minute.

[c] Duration in seconds per minute.

Group A, and mount and interference in Group B; other differences were not statistically significant.

Partner preferences during collective arousal and postcollective arousal

We compared the mean rates per minute of affiliative interactions occurring during collective arousal in individuals belonging to previously separated subgroups and individuals remaining in the same subgroup (Table 3). After a 48-h separation, both groups showed higher rates of all behaviors between partners from different subgroups. After a 2-h separation, we found similar trends but differences were statistically significant only for clasps, mounts, and contact-sitting in Group B, and for clasps and social grooming in Group A. No significant partner preferences appeared in control periods.

We compared partner preferences during the postarousal period from the percentages of scans of social grooming and contact-sitting (Table 3). We did not find statistically significant preferences for contact-sitting between partners regardless of their subgroup membership, whereas individuals in both groups exchanged significantly more grooming with partners from which they had been separated for 48 h. The difference was also significant after a 2-h separation for Group B but not Group A. The comparison of partner preferences in the control period did not yield significant differences.

Contact behaviors occurring during arousal vs. postarousal periods

We compared the percentage scans of social grooming and contact-sitting which occurred during arousal and the hour following the 10-min videotaped period in the 48- and 2-h separation conditions (Table 4). In both groups, contact-sitting increased significantly during the postarousal period for the 48- and 2-h conditions. Levels of social grooming also rose during the postarousal period, except for the 48-h condition in Group A.

DISCUSSION

This is the first experimental study demonstrating that it is possible to reproducibly induce bursts of affiliative interactions in a monkey species, as stated in our first prediction. After a period of separation, Tonkean macaques welcome each other through collective arousal; all individuals run around, embrace or grasp one another, while displaying many affiliative facial expressions and uttering noisy vocalizations. Based on the proportion of group members engaged in affiliation per time unit, the event lasted between a few and ten minutes. Collective arousal should not however be reduced to this operational definition; for instance, it is also characterized by the occurrence of simultaneous affiliative interactions, including polyadic ones (see Supporting Information Video).

TABLE 3. Comparisons of behaviors during arousal and post-arousal periods according to partner preferences in the different experimental conditions

Behavior	Condition	Subgroup membership	Group A				Group B			
			Mean[a]	SD	*T*	*P*	Mean[a]	SD	*T*	*P*
Clasp[b]	48 h	same	0.006	0.003	0	0.002	0.009	0.006	0	0.002
		different	0.02	0.006			0.025	0.013		
	2 h	same	0.004	0.003	1	0.004	0.003	0.001	0	0.002
		different	0.009	0.003			0.01	0.005		
	control	same	0.0001	0.0003	7	0.563	0	0	4	0.109
		different	0.0003	0.0003			0	0		
Mount[b]	48 h	same	0.006	0.005	0	0.002	0.007	0.005	0	0.004
		different	0.018	0.015			0.018	0.011		
	2 h	same	0.005	0.004	18.5	0.389	0.001	0.002	0	0.016
		different	0.007	0.005			0.005	0.004		
	control	same	0.002	0.003	0	0.250	0.003	0.003	6	0.219
		different	0.002	0.002			0.002	0.002		
Social play[c]	48 h	same	2.31	1.96	0	0.002	3.6	3.3	0	0.004
		different	7.3	7.2			10	7.1		
	2 h	same	2.51	2.82	16	0.275	0.79	1.26	3	0.078
		different	4.1	3.6			2.42	2.91		
	control	same	0.24	0.32	0	0.250	2.49	3.32	6	0.219
		different	0.18	0.23			2.12	2.23		
Contact-sitting[c]	48 h	same	5.0	4.2	5	0.020	2.74	2.82	3	0.010
		different	10.0	7.5			5.4	4.3		
	2 h	same	3.4	3.4	9	0.064	3.6	5.2	3	0.010
		different	14.4	16.7			11.1	10.1		
	control	same	20.0	8.4	20	0.820	12.1	10.3	19	0.734
		different	21.8	14.9			13.8	13.4		
Social grooming[c]	48 h	same	0.05	0.07	0	0.004	0	0	0	0.008
		different	10.0	11.1			2.50	3.62		
	2 h	same	0	0	0	0.008	0.08	0.16	2	0.094
		different	2.23	3.09			0.38	0.5		
	control	same	5.6	4.9	17	0.945	3.1	2.9	13	0.547
		different	5.6	4.7			3.3	2.8		
Contact-sitting[d]	48 h	same	4.54	1.75	20	0.479	2.66	1.19	8	0.098
		different	4.88	1.99			3.64	2.61		
	2 h	same	6.73	2.33	20	0.492	3.43	1.38	18	0.652
		different	5.92	2.58			3.98	1.73		
	control	same	5.76	2.73	13	0.160	3.22	1.80	10.5	0.184
		different	4.18	2.12			2.54	1.39		
Social grooming[d]	48 h	same	1.36	0.89	4.5	0.016	0.53	0.55	2	0.006
		different	3.17	1.76			2.01	1.53		
	2 h	same	1.76	0.61	19	0.432	0.53	0.54	4	0.047
		different	2.39	1.59			1.37	1.24		
	control	same	1.28	0.82	11.5	0.398	0.82	0.64	10	0.156
		different	1.10	0.83			0.58	0.42		

Wilcoxon test, $n = 10$.

[a] Means are given per test and per individual.

[b] Frequency per minute.

[c] Duration in seconds per minute.

[d] Percentage scans per partner.

TABLE 4. Comparisons of contact behaviors (mean percentage scans per individual and per test) during arousal and post-arousal periods in the two separation conditions

Behavior	Condition	Period	Group A				Group B			
			Mean	SD	*T*	*P*	Mean	SD	*T*	*P*
Contact-sitting	48 h	arousal	6.1	4.5	0	0.008	6.5	4.8	2	0.023
		post arousal	42.5	22.8			28.7	12.2		
	2 h	arousal	7.5	7.6	0	0.008	3.8	5.5	0	0.008
		post arousal	57.3	29.2			33.9	22.8		
Social grooming	48 h	arousal	5.8	6.3	9	0.250	0.9	1.3	0	0.008
		post arousal	10.7	5.6			5.9	3.1		
	2 h	arousal	1.1	2.4	0	0.008	0	0	0	0.008
		post arousal	9.5	4.0			4.5	2.3		

Wilcoxon test, $n = 8$.

A single observation in the field testifies that wild Tonkean macaques experience collective arousals; a group was prevented from crossing a road for over an hour due to the presence of an observer unknown to the animals, then an episode of collective arousal followed once they had crossed the road (Thierry et al., 2000). The only other event closely related to this behavior is the collective excitement described in chimpanzees and elephants (Goodall, 1986; Moss, 1988; de Waal, 1992). Such episodes differed in length and intensity from the greetings observed at a dyadic level in other species (see Introduction), but are nonetheless reminiscent of the friendly interactions involving several group members in white-faced capuchins (Meunier et al., 2008) and canids (Mech, 1970; Rütten and Fleissner, 2004).

Our second prediction, namely that the intensity and duration of the collective arousals would be related to the length of the separation period, proved to be correct. When two subgroups of groupmates had not been in contact with one another for 2 days, not only did subgroups reunite using numerous friendly interactions that were not observed in a control situation, but several behaviors were seen to last longer or to be more frequent than when the separation lasted two hours. Similarly, Moss (1988) noted that greeting ceremonies in elephants were longer and more intense when the separation had lasted for a few days rather than a number of hours. It is known that the longer an individual has been removed from its home group, the more difficult its return will be (Watts and Meder, 1996). Meeting after separation being a potentially risky situation, it is understandable that uncertainty or social tension can be heightened. The study of nonhuman primates in captivity has shown that introducing individuals into an established group represents a stressful event which incurs significant risks of injury, even when reunited individuals are known to each other (Bernstein et al., 1974; Gust et al., 1993; Brent et al., 1997). In Tonkean macaques rates of scratching differed between separation conditions in Group A but not in Group B, and no significant effect was observed for yawning. These results could be related to the fact that challenges occurred between the two higher-ranking males of Group A before and during the study period (De Marco, unpublished data). Conflicts were also more likely to occur after 48-h separation compared to 2-h separation in this group, although their frequency remained quite low in all experimental conditions—on average no more than one conflict per 10 min during collective arousals in both groups. Collective arousals could serve to overcome tension and potential hostility, and/or to renew social relationships. This explanation is in agreement with the fact that in Tonkean macaques collective arousals can occur, albeit very rarely, after conflicts having involved many group members (Thierry et al., 2000). Emotional contagion can help individuals attain the same emotional state, as suggested by the collective arousals observed in the context of an oncoming food distribution.

Consistent with our third prediction, subjects affiliated more often with groupmates from the previously separated subgroup than with those who had remained in their own subgroup. Moreover, they continued to exchange most of their grooming interactions with members of the joining subgroup in the hour following collective arousal. Similar results have been found in chimpanzees (Okamoto et al., 2001). Such specific greetings again point at the role of collective arousals in renewing social relationships. As previously mentioned, and in accordance with our fourth expectation, the quiet period following collective arousal was characterized by high rates of contact-sitting and social grooming. While the exceptional frequency of interactions particular to the "hot" period had ended, the phenomenon was then prolonged by a "cooler" period of affiliative contacts. An emotional contagion leading individuals to high levels of excitement therefore appears as a main feature of the first period. Some authors have used the word "joy" and "euphoria" to describe such excitement (Moss, 1988; de Waal, 1996). As noted by Ehrenreich (2007) for humans, the thrill of a group united in joy and exaltation is difficult to objectivize. This is all the more so for nonhumans. However, it remains certain that the mutual and exuberant affiliative behaviors displayed by Tonkean macaques are underpinned by the internal states of individuals. The emotional state experienced by them during collective arousals could be a disposition similar to that giving rise to what we humans call "shared joy." At this stage, however, we can only ask whether such emotional states have arisen independently through the evolutionary process as an outcome of certain kinds of sociality, or whether such mechanisms are the same in primates and elephants for instance, thus arguing for mammalian homology and raising the question of why they have not been reported in more taxa. The occurrence of collective arousals in Tonkean macaques may be promoted by the remarkably tolerant social relationships and the numerous conciliatory contacts which characterize them (Thierry et al., 1994; Thierry, 2007, 2010). Some macaque species display similar behaviors, and there are hints that they also display collective arousals (Sulawesi macaques: Thierry et al., 2000; stumptailed macaques: de Waal, 1996). It would be worthwhile to compare different macaque species to establish whether there is a relation between the species-specific social style and the proneness of individuals to take part in collective arousals.

Transmitting emotion through positive behaviors enables individuals to quickly adapt to social situations. Collective arousal appears to enhance social cohesion this way. Future research should investigate whether the conclusions drawn from two captive groups are applicable to animals in the wild, and specify which factors are liable to promote the occurrence of collective arousals.

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LITERATURE CITED

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior 49:227–265.

Anderson JR, Bayart F. 1985. Les effets du miroir sur le comportement de macaques: habituation, évitement et facilitation sociale. Biol Behav 10:159–167.

Aureli F, Schaffner CM. 2007. Aggression and conflict management at fusion in spider monkeys. Biol Lett 3:147–149.

Aureli F, Yates K. 2010. Distress prevention by grooming others in crested black macaques. Biol Lett 6:27–29.

Bernstein IS, Gordon TP, Rose RM. 1974. Factors influencing the expression of aggression during introductions to rhesus monkey groups. In: Holloway RL, editor. Primate aggression, territoriality, and xenophobia. New York, NY: Academic Press. p 211–240.

Brent L, Kessel AL, Barrera H. 1997. Evaluation of introduction procedures in captive chimpanzees. Zoo Biol 16:335–342.

De Marco A, Cozzolino R, Dessì-Fulgheri F, Thierry B. 2010. Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (*Macaca tonkeana*). Anim Behav 80:197–203.

de Waal FBM. 1992. Appeasement, celebration and food sharing in the two *Pan* species. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors. Topics in primatology, Vol. 1: Human origins. Tokyo: University of Tokyo Press. p 37–50.

de Waal FBM. 1996. Good natured: the origins of right and wrong in humans and other animals. Cambridge, MA: Harvard University Press.

de Waal FBM. 2008. Putting the altruism back into altruism: the evolution of empathy. Ann Rev Psychol 59:279–300.

Decety J, Jackson PL. 2004. The functional architecture of human empathy. Behav Cogn Neurosci Rev 3:71–100.

Demaria C, Thierry B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. Behavior 138:397–410.

Dunbar RIM. 1988. Primate social systems. London: Croom Helm.

East ML, Hofer G, Wickler W. 1993. The erect "penis" is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. Behav Ecol Sociobiol 33:355–370.

Ehrenreich B. 2007. Dancing in the streets: a history of collective joy. London: Granta Books.

Ferrari PF, Visalberghi E, Paukner A, Fogassi L, Ruggiero A, Suomi SJ. 2006. Neonatal imitation in rhesus macaques. PLoS Biol 4:e302.

Gese EM, Ruff RL. 1998. Howling by coyotes (*Canis latrans*): variation among social classes, seasons, and pack sizes. Can J Zool 76:1037–1043.

Goodall J. 1986. The chimpanzees of Gombe. Cambridge, MA: Harvard University Press.

Gust DA, Gordon TP, Hambright MK. 1993. Response to removal from and return to a social group in adult male rhesus monkeys. Physiol Behav 53:599–602.

Harrington FH, Asa CS. 2003. Wolf communication. In: Mech LD, Boitani L, editors. Wolves: behavior, ecology, and conservation. Chicago: University of Chicago Press. p 66–103.

Hatfield E, Cacioppo JT, Rapson RL. 1994. Emotional contagion. Cambridge: Cambridge University Press.

Hoffman ML. 1975. Developmental synthesis of affect and cognition and its implications for altruistic motivation. Dev Psychol 11:607–622.

Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behavior and reproductive investment. Anim Behav 67:125–139.

Kummer H. 1975. Rules of dyad and group formation among captive gelada baboons (*Theropithecus gelada*). In: Kondo S, Kawai M, Ehara A, Kawamura S, editors. Proceedings of the fifth congress of the international primatological society. Tokyo: Japan Science Press. p 129–159.

Kutsukake N, Suetsugu N, Hasagawa T. 2006. Pattern, distribution, and function of greeting behavior among black-and-white colobus. Int J Primatol 27:1271–1291.

Leighty KA, Soltis J, Leong K, Savage A. 2007. Antiphonal exchanges in African elephants (*Loxodonta africana*): collective response to a shared stimulus, social facilitation, or true communicative event? Behavior 145:297–312.

Lynch Alfaro J. 2008. Scream-embrace displays in wild black-horned capuchin monkeys. Am J Primatol 70:551–559.

Matheson MD, Johnson JS, Feuerstein J. 1996. Male reunion displays in tufted capuchin monkeys (*Cebus apella*). Am J Primatol 40:183–188.

Matsumura S. 1991. A preliminary report on the ecology and social behavior of moor macaques (*Macaca maurus*) in Sulawesi, Indonesia. Kyoto Univ Overseas Res Rep Stud Asian Non-Hum Primates 8:27–41.

McComb K, Packer C, Pusey A. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Anim Behav 47:379–387.

Mech LD. 1970. The wolf: the ecology and behavior of an endangered species. Minneapolis: University of Minnesota Press.

Meunier H, Petit O, Deneubourg JL. 2008. Social facilitation of fur rubbing behavior in white-faced capuchins. Am J Primatol 70:161–168.

Moss C. 1988. Elephant memories: thirteen years in the life of an elephant family. New York: Fawcett Columbine.

Muller MN. 2002. Agonistic relations among Kanyawara chimpanzees. In: Boesch C, Hohmann G, Marchant LF, editors. Behavioral diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press. p 112–123.

Okamoto K, Agetsuma N, Kojima S. 2001. Greeting behavior during party encounters in captive chimpanzees. Primates 42:161–165.

Petit O, Thierry B. 1992. Affiliative function of the silent bared-teeth display in moor macaques (*Macaca maurus*): further evidence for the particular status of Sulawesi macaques. Int J Primatol 13:97–105.

Petit O, Thierry B. 1994. Aggressive and peaceful interventions in conflicts in Tonkean macaques. Anim Behav 48:1427–1436.

Reynolds V, Reynolds F. 1965. Chimpanzees of the Budongo forest. In: DeVore I, editor. Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart & Winston. p 368–424.

Rizzolati G, Sinigaglia C, Anderson F. 2007. Mirrors in the brain: how our minds share actions, emotions, and experience. Oxford: Oxford University Press.

Rütten S, Fleissner G. 2004. On the function of the greeting ceremony in social canids—exemplified by African wild dogs *Lycaon pictus*. Canid News 7.3 [online].

Seyfarth RM, Cheney DL. 2003. Meaning and emotion in animal vocalizations. Ann N Y Acad Sci 1000:32–55.

Siegel S, Castellan NJ. 1988. Nonparametric statistics for the behavioral sciences, 2nd ed. New York: McGraw-Hill.

Smuts BB, Watanabe JM. 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). Int J Primatol 11:147–172.

Thierry B. 1984. Clasping behaviour in *Macaca tonkeana*. Behavior 89:1–28.

Thierry B. 2000. Covariation of conflict management patterns across macaque species. In: Aureli F, de Waal FBM, editors. Natural conflict resolution. Berkeley: University of California Press. p 106–128.

Thierry B. 2007. Unity in diversity: lessons from macaque societies. Evol Anthropol 16:224–238.

Thierry B. 2010. The macaques: a double-layered social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective, 2nd ed. New York: Oxford University Press. p 229–241.

Thierry B, Anderson JR, Demaria C, Desportes C, Petit O. 1994. Tonkean macaque behavior from the perspective of the evolution of Sulawesi macaques. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N, editors. Current primatology, Vol. 2. Strasbourg: Université Louis Pasteur. p 103–117.

Thierry B, Aureli F, Nunn CL, Petit O, Abegg C, de Waal FBM. 2008. A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. Anim Behav 75:847–860.

Thierry B, Bynum EL, Baker S, Kinnaird MF, Matsumura S, Muroyama Y, O'Brien TG, Petit O, Watanabe K. 2000. The social repertoire of Sulawesi macaques. Prim Res 16:203–226.

Thierry B, Demaria C, Preuschoft S, Desportes C. 1989. Structural convergence between silent bared-teeth display and relaxed open-mouth display in Tonkean macaque (*Macaca tonkeana*). Folia Primatol 52:178–184.

Watts E, Meder A. 1996. Introduction and socialization techniques for primates. In: Thompson KW, Lumpkin L, Harris H, editors. Wild mammals in captivity: principles and techniques. Chicago: University of Chicago Press. p 67–77.

Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Anim Behav 61:1203–1216.