

Mimic Me While Playing! Social Tolerance and Rapid Facial Mimicry in Macaques (*Macaca tonkeana* and *Macaca fuscata*)

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Social play and tolerance are positively correlated and playful signals are more freely expressed in egalitarian than in despotic species. Macaque species are organized along a continuum from intolerant to tolerant social systems and, for this reason, they are good models to test some hypotheses about the possible linkage between communication and tolerance. We compared facial playful communication in 2 macaque species at opposite ends of the continuum: despotic Japanese macaques, *Macaca fuscata*, and tolerant Tonkean macaques, *Macaca tonkeana*. We predicted that tolerance has favored larger facial display repertoires and playful cooperative tendency. Moreover, we evaluated if tolerance could also reflect in the selection for emotional sharing expressed through rapid facial mimicry (RFM). RFM is an automatic, unconscious, and fast (<1 s) motor mirror response which favors emotional communication between subjects. Although *M. fuscata* and *M. tonkeana* performed play faces (PF) at comparable levels, only Tonkean macaques showed the phenomenon of RFM. The playful sessions characterized by RFM lasted longer than those characterized by the presence of playful signals perceived by a playmate but not followed by mimicry. Interestingly, the duration of playful sessions in Tonkean macaques overcame that of the sessions in Japanese macaques. It is likely that RFM improves communicative exchanges between the playmates and, at the same time, promotes behavioral coordination and cooperation in the sequence of actions. The tolerant nature of Tonkean macaques, also expressed in play, can foster RFM which, at the same time, positively enhances the propensity to cooperate in a sort of positive feedback.

Keywords: social play, facial mirroring response, emotional sharing, tolerance degree, genus *Macaca*

Tolerant species are characterized by a high variability of interactions which involve a large number of subjects who frequently act together under many different contexts, despite rank differences and kinship bonds. Therefore, tolerant species present complex and large social networks (Butovskaya, 2004; Freeberg, Dunbar, & Ord, 2012). The high degree of freedom characterizing the social relations of these species creates a high degree of uncertainty arising from such interactions (Butovskaya, 2004; Flack & de Waal, 2004). When social relations are uncertain, negotiable, and unpredictable, they are challenging to be managed. For this reason, a large and complex signal array and the capacity to read the signal in an appropriate way are needed to improve social

communication thus limiting misunderstanding (Freeberg et al., 2012; Maestripieri, 1995). As predicted by the social intelligence hypothesis (Byrne & Whiten, 1988; Humphrey, 1976), in more tolerant social systems individuals must rely on greater and more sophisticated communicative skills (Whiten & van Schaik, 2007).

The gradient of tolerance—from egalitarian to despotic—of a given species is strictly linked to the types of dominance relationships in animal societies (Vehrencamp, 1983) and to the way in which power (i.e., control of resources) is distributed in social communities (Flack & de Waal, 2004). In egalitarian societies, power is equally distributed and the relationship asymmetry is weaker (Butovskaya, 2004; Flack & de Waal, 2004; Preuschoft, 2004). On the contrary, in despotic societies, power is confined in the hands of few dominant individuals (Flack & de Waal, 2004; Preuschoft, Paul, & Kuester, 1998) which manage their interactions through formal displays, thus limiting communicative repertoire (Maestripieri, 1995). Hence, tolerance positively covaries with communicative complexity both in terms of redundancy and variety (Dobson, 2012). Such complexity allows a better efficiency in the management of changing social dynamics and in the negotiation of shifting and unpredictable relationships typical of tolerant species (Dobson, 2012).

Due to its plasticity and socially demanding nature, social play is one of the most complex behaviors based on nonverbal communication (Palagi, Burghardt, et al., 2015). Social play and tolerance are positively correlated. Comparative studies have shown that play is more frequent and freely expressed in egalitarian than in despotic species (Antonacci, Norscia, & Palagi, 2010; Ciani,

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Dall'Olio, Stanyon, & Palagi, 2012; Hare, Wobber, & Wrangham, 2012; Palagi, 2006; Palagi & Cordoni, 2012). During play, facial expressions are critical for the communication of emotions and intentions (Demuru, Ferrari, & Palagi, 2015; de Waal, 2003) and have an important role in managing the play session (de Waal, 2003; Mancini, Ferrari, & Palagi, 2013a; Palagi, 2008; Pellis & Pellis, 2009). In primates the specific facial expression of social play is the play face, which can vary in its performance as a function of the species-specific social features (Palagi & Mancini, 2011; Parr & Waller, 2007; Pellis, Pellis, Reinhart, & Thierry, 2011; Thierry, van Hooff, & Preuschoft, 2003; Waller & Micheletta, 2013).

In humans, a positive feedback loop sets up during play when seeing an emotional face causes a congruent facial expression in the observer's face (RFM; Dimberg, 1982, 1990; Dimberg & Thunberg, 1998). RFM is also present in nonhuman primates (orangutans; Davila Ross, Menzler, & Zimmermann, 2008; chimpanzees; Davila Ross, Allcock, Thomas, & Bard, 2011; geladas; Mancini et al., 2013a) and dogs (Palagi, Nicotra, & Cordoni, 2015). RFM is a phenomenon that appears as an automatic, unconscious, and fast (<1 s) motor response (Dezecache, Jacob, & Grèzes, 2015; Duffy & Chartrand, 2015). The same face-same emotion mechanism is an adaptive phenomenon (Dezecache et al., 2015) that is based on the perception-action coupling mechanism mediated by the mirror neuron system (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Ferrari, Bonini, & Fogassi, 2009; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Preston & de Waal, 2002). Mirroring the facial display of a partner creates an emotional sharing and liking by communicating attention and motivation, thus limiting misunderstanding which represents the highest risk of play, especially in tolerant species (Hess & Fischer, 2013; Lakin, Jefferis, Cheng, & Chartrand, 2003). Moreover, mimicry regulates dyadic relations and might favor the formation of strong, enduring social bonds, which, in turn, enhance reproductive success (Hess & Fischer, 2013).

In this work we postulate that playful facial expressions and their mimicry can covariate with the levels of tolerance and social complexity. We selected two species belonging to the genus *Macaca*: a tolerant, *Macaca tonkeana*, and a despotic species, *Macaca fuscata* (Thierry, 2000). Thierry (2000) proposed to arrange macaque species along a 4-grade tolerance scale, from the most despotic (Grade 1, e.g., *Macaca mulatta* and *Macaca fuscata*) to the most tolerant species (Grade 4, e.g., *Macaca tonkeana*, *Macaca nigra*, *Macaca maura*, all living in Sulawesi Island). Despite their similarities, there is a substantial interspecific variation in macaque social styles (Thierry, 1985a, 2000, 2007). High



Figure 1. Shots illustrating facial expressions in *M. fuscata*. (a) Playful session involving two juvenile subjects, one performing play faces (PF) in direct visual contact; (b) playful session involving two adult males, both performing PF in direct visual contact; and (c) an adult female performing a bared teeth display (BT) while playing.

levels of reconciliation (Demaria & Thierry, 2001), bidirectional aggression and counterattacks (Ciani et al., 2012; Thierry, 1985b, 2000), and affiliative contacts characterize the macaques belonging to Grade 4 (Adams et al., 2015; de Waal & Luttrell, 1989; Matsumura, 1998; Neumann, Agil, Widdig, & Engelhardt, 2013).

As for play, *M. fuscata* is competitive with little physical contact and low risky strategies (Petit, Bertrand, & Thierry, 2008; Reinhart et al., 2010); on the contrary, play in *M. tonkeana* appears to be less defensive, more cooperative (Reinhart et al., 2010), and less age- and gender-biased (Ciani et al., 2012) than in *M. fuscata*. Possibly due to the degree of freedom characterizing social interactions in Tonkean macaques, a redundancy and complexity of signals have evolved in this species (Maestripieri, 1999; Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013; Preuschoft, 2004). PF in *M. fuscata* is a relaxed, open-mouth (ROM) expression with lower teeth, and occasionally upper teeth, exposed (Figure 1a and 1b; Table 1); in *M. tonkeana*, during PF animals open their mouth and simultaneously bare their teeth (open mouth expression + teeth-baring; see Table 1; Figure 2a and 2b).

In macaques nonspecific signals used during play vary consistently along the 4-grade scale (Thierry, 2000). In particular, the *bared-teeth* display (BT; for description see Table 1) expresses submission in macaques of Grade 1 (de Waal & Luttrell, 1985; Maestripieri, 1996; Preuschoft, 1995a), whereas in grade-4 species it no longer communicates social status. BT display conveys, instead, a message of peaceful intentions and serves to initiate affiliative interactions (Petit & Thierry, 1992; Preuschoft, 1995b; Samson & Waller, 2010; Thierry, Demaria, Preuschoft, & Desportes, 1989). Moreover, BT display can be combined together with other facial expressions such as lip smacking (LS), in order to produce multicomponent communicative signals which are more effective in inducing a positive response in the receiver (Micheletta et al., 2013). Indeed, the LS display (for description see

Table 1

Descriptions of Facial Expressions Collected During Playful Interactions in *Macaca fuscata* and *Macaca tonkeana*

Facial expression	Description
Play face (PF)	<i>M. fuscata</i> : relaxed, open-mouth expression with lower teeth, and occasionally upper teeth, exposed (Figure 1a and 1b). <i>M. tonkeana</i> : open mouth expression co-occurring with the bared-teeth display (teeth-baring) (Pellis et al., 2011). Both the upper and lower teeth are exposed (Figure 2a and 2b).
Scalp retraction (SR)	The scalp is retracted, ears may be flattened against the head while the individual looks at a partner.
Bared-teeth (BT)	The upper lip or both lips are retracted, often exposing the teeth. Contrary to the PF, the corners of the mouth are drawn back. It could be associated with SR (Figure 1c for <i>M. fuscata</i> ; Figure 2c for <i>M. tonkeana</i>).
Lip-smacking (LS)	The lips are pursed and the lower jaw is moved up and down rapidly and rhythmically. The lips often produce an audible sound. The scalp may be retracted and the ears flattened.



Figure 2. Shots illustrating facial expressions in *M. tonkeana*. (a) Playful session involving an adult and an immature subject both performing PF in direct visual contact, (b) playful session involving an adult male (right side) and an adult female (left side) both performing PF in direct visual contact, and (c) an adult male performing a BT display while playing with an adult (not present in the shot).

Table 1) manifests the motivation to pacifically and playfully interact in several macaque species (Maestripieri & Wallen, 1997; Matsumara, 1994, 1997; Preuschoft, 1992, 1995a; Thierry, 1984, 1985a, 1986).

In some Old World monkeys, such as *M. tonkeana* and *Theropithecus gelada*, the silent BT appears to be an expression of friendly attraction that can be added to the relaxed open ROM as an invitation to play. The outcome of this *morphological* convergence between the two displays is named open mouth bared teeth display (OMBT). In other less tolerant Old World monkeys, such as *M. fuscata*, the ROM display indicates a playful propensity in the emitter. Due to the *functional* convergence of OMBT display (typical of *M. tonkeana*) and ROM display (typical of *M. fuscata*; Preuschoft, 2004) in signaling play, here we decided to refer to both expressions as PF. The expressions of both species are shown in Figures 1 and 2.

The *scalp-retraction* display (SR; for description see Table 1) is performed exclusively in aggressive contexts in *M. fuscata* (Maestripieri, 1997). On the contrary, in Tonkean macaques the same display can be used as an invitation to play (Thierry et al., 2000).

Since Tonkean macaque play is characterized by higher levels of unpredictability compared to Japanese macaque play (Ciani et al., 2012; Reinhart et al., 2010) we expect to find a redundancy in PF in *M. tonkeana* (Prediction 1a). Moreover, due to the affiliative and positive nature of nonspecific facial expressions (BT, LS, SR) in Tonkean macaques, we predict that these signals can be recruited to punctuate play sessions in this species (Prediction 1b).

The motor and emotional resonance occurring during RFM could help individuals to better catch another's emotions and synchronize motor actions (Dezecache et al., 2015), thus reducing the uncertainty characterizing the playful sessions of tolerant species (Mancini, Ferrari, & Palagi, 2013b). Hence, the larger facial display repertoires of tolerant species (Dobson, 2012) and their cooperative tendency during play (Reinhart et al., 2010) may be reflected in the selection for emotional sharing expressed through RFM. Therefore, if RFM is positively sensitive to tolerance, we expect the phenomenon to be more likely expressed in *Macaca tonkeana* compared to *Macaca fuscata* (Prediction 2a). RFM has proved to be predictive of the cooperative success of playful interactions by prolonging them over time (*Theropithecus gelada*, Mancini et al., 2013b; *Pan troglodytes*, Davila Ross et al., 2011; *Canis lupus familiaris*, Palagi Nicotra, et al., 2015). Since Tonkean macaques show more cooperative and longer play sessions than Japanese macaques (Burghardt, 2013; Ciani et al., 2012; Reinhart et al., 2010), we predict that the presence of RFM in Tonkean

macaques is responsible of such prolonged play sessions (Prediction 2b).

Method

Ethics Statement

This study was approved by University of Pisa (Animal Care and Use Board). Since the study was purely observational the committee waived the need for a permit. The study was conducted with no manipulation of animals.

Subjects and Data Collection

Behavioral data were video recorded on one group of *M. fuscata* (143 hr) and one group of *M. tonkeana* (151 hr) by three observers (including the first author; Table 2). During the training phase (the trainer was Stefania Dall'Olio) that lasted 1 month, the observers learned to identify the animals. To recognize playful activity, the same focal animal was followed by the observers simultaneously and the data were then compared. Interobserver reliability was tested and the Cohen's kappa values obtained for play were always >0.90.

The colony of *M. fuscata* was housed in the Olomouc Zoo (Olomouc, Czech Republic). During data collection (2 months,

Table 2

List of the Animals of both Species Included in the Analyses

Animal initials	Species	Sex class	Age class
BE	<i>M. tonkeana</i>	Male	Adult
CN	<i>M. tonkeana</i>	Male	Adult
DA	<i>M. tonkeana</i>	Male	Adult
EL	<i>M. tonkeana</i>	Male	Adult
HS	<i>M. tonkeana</i>	Male	Adult
LK	<i>M. tonkeana</i>	Male	Adult
MB	<i>M. tonkeana</i>	Male	Adult
PE	<i>M. tonkeana</i>	Male	Adult
SK	<i>M. tonkeana</i>	Male	Adult
LB	<i>M. tonkeana</i>	Female	Adult
FR	<i>M. tonkeana</i>	Female	Juvenile
CY	<i>M. tonkeana</i>	Male	Juvenile
IN	<i>M. tonkeana</i>	Female	Juvenile
MC	<i>M. tonkeana</i>	Male	Juvenile
PAN	<i>M. tonkeana</i>	Male	Juvenile
RG	<i>M. tonkeana</i>	Male	Juvenile
SN	<i>M. tonkeana</i>	Male	Juvenile
JK	<i>M. fuscata</i>	Male	Adult
CS	<i>M. fuscata</i>	Male	Adult
GS	<i>M. fuscata</i>	Male	Adult
IN	<i>M. fuscata</i>	Male	Adult
KR	<i>M. fuscata</i>	Male	Adult
BEA	<i>M. fuscata</i>	Female	Adult
HE	<i>M. fuscata</i>	Female	Adult
BA	<i>M. fuscata</i>	Male	Adult
GA	<i>M. fuscata</i>	Male	Juvenile
CL	<i>M. fuscata</i>	Female	Juvenile
RB	<i>M. fuscata</i>	Male	Juvenile
FI	<i>M. fuscata</i>	Male	Juvenile
GU	<i>M. fuscata</i>	Male	Juvenile
PI	<i>M. fuscata</i>	Male	Juvenile
AB	<i>M. fuscata</i>	Male	Juvenile
DR	<i>M. fuscata</i>	Male	Juvenile
AD	<i>M. fuscata</i>	Male	Juvenile

June–July 2010) the colony was composed of five adult males, eight adult females, and 12 immature subjects (1–4 years of age). Animals were housed in a large enclosure, about 1 ha of pine tree forest enriched with ropes, wooden structures, shelters, and a natural stream. Food was distributed twice a day at 08:30 and 14:30 hours and water was available ad libitum. The group of *M. tonkeana* was housed in the Parc Zoologique de Thoiry (Thoiry, France). During data collection (about 3 months, August–October 2011) the colony was composed of 30 adult males, 31 adult females, and 10 immature subjects (1–4 years of age). The animals were housed in an enclosure with both indoor and outdoor facilities (about 200 m² and 5,000 m², respectively). The large outdoor grass area was equipped with pools, rope structures, trees, and bushes. Food was distributed twice a day at 11:45 and 18:00 hours. Water was available ad libitum.

Due to the presence of visual obstacles (e.g., ropes, wooden structures, shelters) it was not possible to record play sessions by all occurrences sampling. Play was collected ad libitum. The observers videotaped the playful sessions each time they were completely visible for their entire duration (101 playful sessions for Tonkean macaques and 235 for Japanese macaques). Animals were videotaped daily from 8:00 a.m. until 5:00 p.m. A play session began when one partner directed a playful pattern toward a conspecific who responded with another playful pattern. A session ended when playmates ceased their activities, one of them moved away, or when a third individual interfered, thus interrupting the interaction. If another play session began after a delay of 10 s, that session was counted as new. For each play session video-analyzed we recorded: (a) identities of the subjects (i.e., name, sex, age), (b) playful motor patterns and facial expressions in their exact sequence, and (c) length (s) of interaction. Only the subjects who showed at least four play sessions (completely visible to the observer) were included in the analysis (see Table 2).

Data Analysis, Operational Definitions, and Statistics

Video analysis was conducted by C. S. using Kinovea v. 0.7.10 software with one-frame accuracy (1 frame/4 csec). Interobserver reliability was tested by C. S. and E. P. and the Cohen's kappa values obtained for the facial expressions (see Table 1) were always >0.85.

The frequency of specific (PF) and nonspecific facial expressions (other expressions [OE]: BT, LS, and SR; see Table 1) was calculated as the number of facial expressions performed on the total duration of play each animal engaged in. Then, due to the nonnormal distribution of data the frequency of facial expressions was compared between the two species by Mann–Whitney *U* test.

To examine the presence of RFM, defined as the mirror facial response given by the observer within 1 s from the perception of the stimulus (Mancini et al., 2013a), we focused on the specific playful signal PF (see Table 1). We measured the facial expression of one individual (the observer, hereafter) to see whether it varied as a function of the signal displayed by the playmate (the trigger, hereafter) within a 1 s time window. The trigger was defined as the first playmate who emitted the stimulus (PF). To reliably assess that the response produced by the observer was actually elicited by the stimulus emitted by the trigger, we considered only those interactions in which the observer looked at the trigger and did not show PF in the 1 s prior to the emission of the stimulus by the

trigger. The RFM latencies were measured frame-by-frame starting from the onset of the trigger stimulus and ending with the onset of the observer's facial response with 4 csec accuracy. We measured the attentional state of the receiver by considering the head orientation (Figure 3). When the trigger was in front of the receiver (i.e., within the range of its stereoscopic view, direct visual contact condition, see Figures 1a, 1b, 2a, and 2b), we considered facial expressions as perceived. When the receiver was facing away from the trigger (without direct visual contact condition), we considered facial expressions as not perceived. All the doubtful cases linked to lateral views were discarded from the analyses (see Figure 3). In addition we also introduced a further control to ascertain that the congruent response was actually linked to the specific stimulus ($PF_{\text{observer}}/PF_{\text{trigger}}$) and it was not due to the arousal experienced by animals during the perception of other facial stimuli (OE, Table 1; $PF_{\text{observer}}/OE_{\text{trigger}}$). We compared the frequency of the congruent response ($PF_{\text{observer}}/PF_{\text{trigger}}$) between the "direct visual contact condition" and the "without visual contact condition" (paired sample *t* test due to the normal distribution). We performed the same analysis for incongruent response ($PF_{\text{observer}}/OE_{\text{trigger}}$; exact Wilcoxon's paired sample test due to the nonnormal distribution).

In order to verify, if the presence of RFM was linked to the duration of the play session, we categorized the play interactions into two clusters. The first cluster included those sessions punctuated by at least one event of RFM. The second cluster comprised those interactions characterized by the presence of at least two signals performed independently by the two players and that were not linked by an event of RFM. Due to the normality of the data distribution (Kolmogorov–Smirnov test; $p > .05$), we compared the duration of the play sessions belonging to the two different clusters by paired-sample *t* test.

Finally, via the independent-sample *t* test we compared the duration of the play sessions between the two species, *M. fuscata* and *M. tonkeana*.

Results

During playful interactions, specific facial expressions did not differ between the two species (PF; Mann–Whitney $U = 102.00$, $n_{M.\text{tonkeana}} = 17$, $n_{M.\text{fuscata}} = 17$, $p = .143$; mean $\pm$ $SE_{M.\text{tonkeana}} 0.214 \pm 0.067$; mean $\pm$ $SE_{M.\text{fuscata}} 0.084 \pm 0.012$). On the contrary, in playful contexts LS and BT expressions were more frequent in Tonkean macaques than in Japanese macaques (LS,

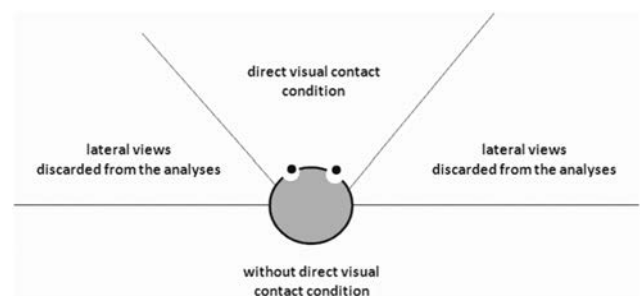


Figure 3. Scheme illustrating the criteria used to evaluate the attentional state of the observer in relation to the perception of facial expressions. Only when the observer was in front of the trigger (direct visual condition) we considered the stimulus as perceived.

Mann–Whitney $U = 93.50$, $n_{M.tonkeana} = 17$, $n_{M.fuscata} = 17$, $p = .008$; BT, Mann–Whitney $U = 28.5$, $n_{M.tonkeana} = 17$, $n_{M.fuscata} = 17$, $p = .0001$). SR did not differ between the two species (SR, Mann–Whitney $U = 102.00$, $n_{M.tonkeana} = 17$, $n_{M.fuscata} = 17$, $p = .107$). Only the subjects performing at least four playful sessions and one facial expression (both specific and nonspecific) were included in the following analysis. The rate of facial expressions was obtained by dividing the number of facial expressions per the total duration of play (s).

In *Macaca fuscata*, the level of PF performed in absence of direct visual contact with the playmate (no perception of the PF emitted by the trigger, control condition) was comparable with the level of PF performed in presence of direct visual contact with the playmate (perception of the PF emitted by the trigger, experimental condition) (paired-sample t test; $t_{\text{congruent response}} = 0.854$, $df = 11$, $p = .411$). Only subjects that perceived at least two PF stimuli were included in this analysis. The RFM phenomenon does not seem to be present in Japanese macaques.

In *Macaca tonkeana* the level of PF performed in presence of direct visual contact with the playmate was significantly higher if compared with the level of PF performed when the stimulus emitted by the trigger was not visually perceived by the receiver (paired-sample t test; $t_{\text{congruent response}} = 5.580$, $df = 11$, $p = .0001$; Figure 4). Only subjects that perceived at least two PF stimuli were included in this analysis. In Tonkean macaques, the

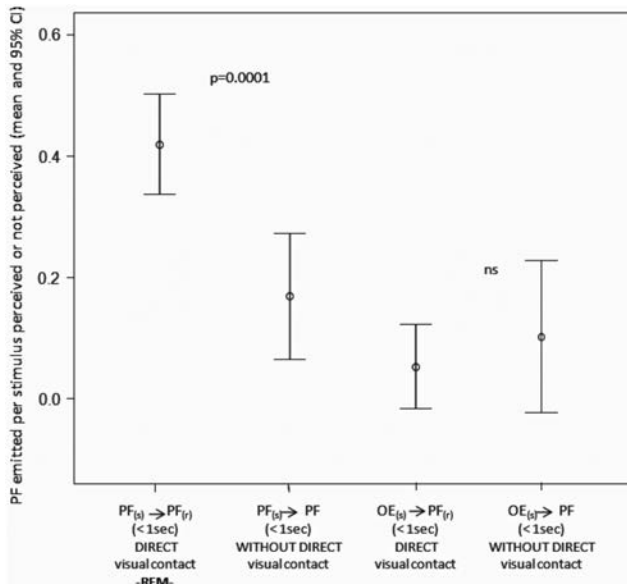


Figure 4. Mean and 95% CIs of PF emitted ($PF_{(r)} = PF$ response) after the perception of the stimulus ($PF_{(s)} = PF$ stimulus) in direct visual contact within 1 s (experimental condition, RFM, congruent response), were compared with PF performed when the stimulus emitted by the trigger ($PF_{(s)}$) was not visually perceived by the receiver (without direct visual contact, control condition) in *Macaca tonkeana*. Mean and 95% CIs of PF emitted ($PF_{(r)} = PF$ response) after the perception of other expressions ($OE_{(s)} = \text{lip smacking} + \text{scalp retraction} + \text{bared teeth}$) in direct visual contact within 1 s (experimental condition, noncongruent response) were compared with PF performed when the stimulus emitted by the trigger ($OE_{(s)}$) was not visually perceived by the receiver (without direct visual contact, control condition) in *Macaca tonkeana*.

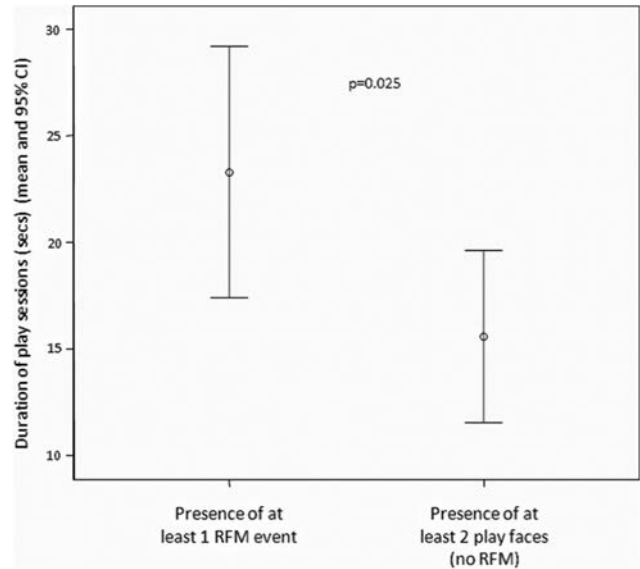


Figure 5. Duration lengths (s) of *M. tonkeana* play sessions characterized by at least one RFM event were compared with the sessions characterized by the presence of at least two PF without RFM.

perception (direct visual contact condition) of OE (BT, SR, and LS) did not elicit in the receiver a rapid incongruent response (OE-PF; exact Wilcoxon signed-ranks test $T_{\text{incongruent response}} = 5.00$; ties = 7; $n = 12$; $p = .563$; Figure 4). We never recorded a congruent rapid response to BT, SR, and LS in case of their perception. These results revealed that the presence of RFM in *Macaca tonkeana* is strictly linked to the specific playful expression (PF) and the possibility for the receiver to perceive it. Moreover, in this species play interactions punctuated by at least one RFM event lasted significantly more than sessions punctuated by at least two PF signals performed by different subjects not followed by RFM (paired-sample t test; $t = 2.586$, $df = 11$, $p = .025$; Figure 5).

The play sessions of *M. tonkeana* were significantly longer than those of *M. fuscata* (mean calculated per individual which showed at least four play sessions; independent-sample t test; $t = 2.726$, $df = 32$, $n_{M.tonkeana} = 17$, $n_{M.fuscata} = 17$, $p = .010$; Figure 6).

Discussion

Here, we provided data about the frequency and the use of playful facial signals in two species of macaques characterized by different levels of social tolerance. While we did not find any difference during social play between the performance of specific facial displays (PF) (Prediction 1a not supported), we detected a difference in the use of nonspecific facial expressions (OE). In particular, the BT display and LS were performed more frequently by Tonkean than Japanese macaques (Prediction 1b supported). The comparable levels of PF recorded in the two macaque species may be explained by the highly functional conservative nature of this facial expression in primates and other nonprimate mammals (Palagi, Norscia, & Spada, 2014; Palagi, Burghardt, et al., 2015; Provine, 1996, 2004). It is therefore reasonable that this facial display does not differ in the use between phylogenetically close

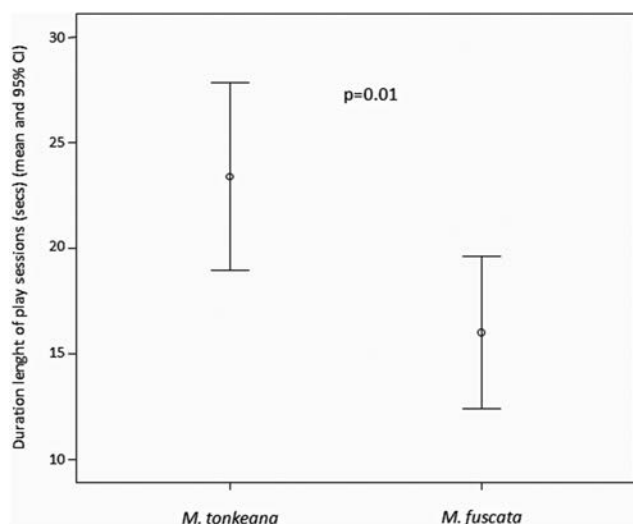


Figure 6. Duration of playful sessions in the two *Macaca* species.

species. Moreover, differently from OE, which acquire different meanings as a function of the context and the species in which they occur (Bout & Thierry, 2005; Palagi & Mancini, 2011; Pellis et al., 2011; Preuschoft & van Hooff, 1995; Thierry et al., 1989), PF is exclusively part of playful interactions in primates. Due to its idiosyncrasy, the PF is considered to be mainly driven by the spontaneous expression of specific emotional internal states of the sender more than by the strategic transfer of actual information to the receiver, even though emotions and intentions may be considered as two dimensions of the same phenomenon (Darwin, 1872; Demuru et al., 2015; Duffy & Chartrand, 2015; Mancini et al., 2013b).

This hypothesis is in agreement with Pellis et al. (2011). The authors found that PFs were scored at all possible bodily orientations, including when facing the partner's rump. PFs were equally likely to occur in *Macaca fuscata* and *Macaca tonkeana*, irrespective of the line of sight of the recipient. This finding strongly supports the central function of the PF to regulate the performer's emotional state in both species. Therefore, emotion is probably one

of the crucial components in the production of playful facial expressions in primates (Waller & Cherry, 2012). Hence, it is not surprising that RFM involves the highly context-specific PF more than the "totipotent," eclectic OE (Dobson, 2012; Duboscq et al., 2013; Maestriperi, 1999; Mancini et al., 2013b; Micheletta et al., 2013). We demonstrated the presence of RFM in Tonkean but not in Japanese macaques (Prediction 2a supported). In the former, RFM occurred only in response to a PF with OE that did not elicit any congruent response in the observers. If certain signals occur more often than others the possibility that they can produce a higher level of congruence exists; however, the comparable levels of PF performed by *M. tonkeana* and *M. fuscata* rule out this possibility. In humans it has been demonstrated that mimicry is not the mere consequence of the linkage between perception and behavior, but rather a behavior which is unconsciously activated and motivated by social affiliation (Chartrand, Maddux, & Lakin, 2005; Duffy & Chartrand, 2015). Human facial mimicry is strongly affected by the balance between cooperation and competition that characterize the social interactions of the emitter and the observer (Lanzetta & Englis, 1989; Weyers, Mühlberger, Kund, Hess, & Pauli, 2009). Cooperative contexts and affiliative intent between human subjects increase their probability of mimicry response; on the contrary, competitive contexts stimulate a behavioral response that leads subjects to react to others more than with others (Hess & Fischer, 2013). Therefore, RFM in macaques could be linked to the different attitude to cooperate during play shown by species characterized by different levels of tolerance. The tolerant nature of play in Tonkean macaques (Ciani et al., 2012; Reinhart et al., 2010) can foster RFM which, at the same time, positively enhances the propensity to cooperate in a sort of positive feedback (Figure 7). Our data on RFM indicate that this phenomenon has a role in prolonging the sessions. In Tonkean macaques the playful sessions characterized by RFM lasted longer than those characterized by the presence of playful signals perceived by a playmate but not followed by mimicry (Prediction 2b supported). Finally, Tonkean macaques engage in longer playful sessions compared to Japanese macaques (Reinhart et al., 2010; present study). It is likely that RFM improves communicative exchanges between the playmates and, at the same time, promotes the behavioral coordination and cooperation in the sequence of actions (see

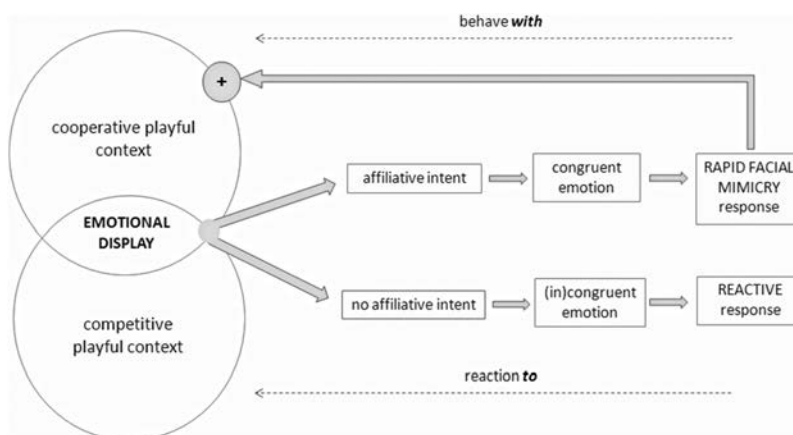


Figure 7. The model of RFM in playful contexts. See the text for the explanation.

Figure 7). The more the coordination, the more the duration of social interactions.

The high level of unpredictability characterizing the playful interactions in the tolerant Tonkean macaque could have favored not only the recruitment of OE from other behavioral contexts to reinforce the playful message, but also a positive selection toward those communicative mechanisms that increase coordination between play partners, such as RFM. Being involved in prolonged interactions is particularly advantageous for the playmates of tolerant societies because these subjects can increase the opportunity to assess their reciprocal ability and to test their social relationships which, due to their uncertainty, need to be continuously renegotiated.

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