DOTTORATO DI RICERCA IN ETOLOGIA, ECOLOGIA ANIMALE E ANTROPOLOGIA

(XXV° CICLO)

A MATTER OF STYLE.

How Tolerance affects Emotional contagion and Play in the genus *Macaca*

Tesi di

STEFANIA DALL’OLIO

Coordinatore Prof. Alberto Ugolini
Tutor interno Prof. Roscoe Stanyon
Tutor esterno Dott.ssa Elisabetta Palagi

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Ai macachi, che si sono lasciati osservare…

Dato che non penseremo mai nello stesso modo e vedremo la verità
per frammenti e da diversi angoli di visuale,
la regola della nostra condotta è la tolleranza reciproca.
La coscienza non è la stessa per tutti.
Quindi, mentre essa rappresenta una buona guida per la condotta individuale,
l'imposizione di questa condotta a tutti
sarebbe un'insopportabile interferenza nella libertà di coscienza di ognuno.

(Mohandas Karamchand Gandhi)

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ABSTRACT

Between-species or between-population variation in social tolerance can affect the development of social skills or social behaviours, especially in primate species that are often subjected to a great influence of inter-individual social relationships. The 20 macaque species are all organized in multi-male, multi-female groups but vary along a continuum from despotic/intolerant to egalitarian/tolerant social systems. These different social styles influence a wide range of behaviours including aggression and affiliation patterns, dominance relationships, and nepotism. In this thesis I tested hypotheses on how behaviours based on basic forms of empathic abilities (like consolation and rapid facial mimicry) and social activities like play should be modulated by the different social styles.

Hypotheses were tested by comparing play patterns and post-conflict management behaviours in two macaque societies at opposite ends of the continuum: despotic Japanese macaques, *Macaca fuscata*, and tolerant Tonkean macaques, *Macaca tonkeana*. The study revealed that these two species have striking differences in the distribution of social play according to the age and sex of the players. These findings strongly indicate that play, a highly plastic and versatile behaviour, is sensitive to the quality of inter-individual relationships of a species, thus reflecting the nature of the social network. The adult play propensity of Tonkean compared to Japanese macaques indicated that adult-adult play was a good predictor for the polarity of changes in aggressiveness between different groups separated either genetically (taxa) or culturally (human ethnies).

Play is also a fertile field for research on the role of facial expressions in modulating social relations. The ability to perform actions and facial expressions in the appropriate context was hypothesized to derive from a social play experience in which predicting the intentions of playmates is fundamental. The capacity to reproduce imitative responses (RFM) was present in both *Macaca fuscata* and *Macaca tonkeana.* It was then shown that communicative characteristics were indeed modulated by different play styles (competitive *vs* cooperative). The capacity to match the behaviour of other individuals could help synchronize activities with those of other group members and could also be useful in learning the context for an activity.

Hypotheses were also tested concerning social styles following agonistic encounters. Research has shown that the negative effects (costs) of aggression can be mitigated by conflict resolution through reconciliation and consolation. Reconciliation is widespread in primates. The use of bystander affiliation, a friendly, spontaneous contact received by the recipient of an aggression from a bystander not involved in the agonistic encounter was considered in primates to exist only in great apes and humans. It reduces victim's anxiety and is mostly directed towards friends. The research findings of my thesis revealed, that in

Tonkean macaques bystander affiliation is frequent and can be considered as a substitute of reconciliation. This is the first time that true consolation has been found in a monkey. The results also revealed striking differences between the two macaque species because it is absent in Japanese macaques. Moreover, it does not seem that bystander affiliation has any effect in reducing the likelihood of further attacks among group members whereas it reduces victims' probability to be re-attacked. Consolation is considered as one of the best candidates for evaluating the empathic potential in humans and apes, since it produces clear benefits to the receiver (e.g. anxiety reduction) and it is preferentially directed to kin and friends. Providing contact comfort to distressed others it is generally classified as an expression of empathic or sympathetic concern, that is the feeling of sorrow associated specifically with the suffering or need of another. Emotional contagion enables individuals to experience emotions of others. This important empathic phenomenon is closely linked to facial mimicry, where facial displays evoke the same facial expressions in social partners. The phenomenon of RFM seems to be linked to the presence of the "mirror neurons system", discovered in the macaque premotor and parietal cortex, composed by neurons that responded whenever a particular action was either observed or performed by the monkey. The behavioural synchrony that derived from facial matching behaviour seems to have a fundamental role in affective coordination and could have an important impact in the development of social competences and empathy.

Perceiving the feelings of another individual (empathy) and being able to perform the right behaviour for the specific context were features considered to be uniquely human until the arise of studies that found these abilities also in non-human primates. The findings of this thesis contribute to highlight the similarities between human and non-human primate's societies and the behavioural mechanisms required to face different social situations.

In order for cognitive and empathic capacities of a species to emerge through the expression of a behavioural mechanism, specific social conditions might be needed to favour such a mechanism. For this reason, investigating behavioural patterns driven by certain, even basic forms of empathy require the choice of appropriate species. In conclusion, we suggest that *M. tonkeana* and *M. fuscata* might be good models to investigate the evolution of social and empathic abilities in order to understand the full phylogenetic range of these intriguing phenomena.

1. INTRODUCTION

1.1. Aim of the work and hypotheses to be tested

The principal aim of this work is to analyze and compare social behaviours that can be influenced by social tolerance. Behaviours based on basic forms of empathic abilities (like consolation and rapid facial mimicry) and social activities like play can be modulated in different ways in relation to different social styles. For this reason we have chosen to study two species of the genus *Macaca* (*Macaca fuscata* and *Macaca tonkeana*) that have been classified as extremely different regarding temperament, aggression, affiliation patterns, dominance relationships, and nepotism (Thierry 1985a; 1990; de Waal and Luttrell 1989; Aureli et al. 1997; Petit et al. 1997).

Play is behaviour of great importance to manage social relations among group members. Information exchanged during play sessions can be helpful to enhance social competence (Byers and Walker, 1985; Brueggeman, 1978; Pellegrini et al., 2007), promote the creation and the development of social bonds (Palagi et al., 2004, 2006, 2007), and increase tolerance levels that in turn affect conflict management (Aureli and de Waal, 2000). This should mean that divergent social systems could show not only different play activity levels, but also different ways to perform play sessions. Then, play should be a good indicator of the quality of social bonds, especially if it is investigated on adult individuals that, in every community, are the most committed to managing social practices (Thierry et al. 1990; Schino et al. 2005). Because of there are no quantitative and standardized data on adult macaque play in the literature, we can consider this work as the first that tests some hypotheses on adult play distribution in relation to social style.

The two main hypotheses tested for play distribution are:

Hypothesis 1 - Adult and immature play frequency and distribution fluctuate according the degree of tolerance in a given species.

Hypothesis 2 - Play may have different roles as a function of the sex of the players.

Play is also an interesting behaviour for examining the role of signals in intentional communication systems (Palagi, 2008). In fact, the ability to perform actions and facial expressions in the appropriate context could derive from the social play experience in which foresee playmates' intentions is fundamental (Pellis and Pellis, 2009; Palagi, 2008). Rapid Facial Mimicry /RFM) is an involuntary, rapid, and automatic response, in which an individual mimic the facial expression of another individual. This phenomenon has to be distinguished by other voluntarily and cognitive forms of imitation (Dimberg et al., 2002; Iacoboni, 2009) because of the rapidity of the matched response. It has been recently investigated in an ape species (*Pongo pygmaeus*) (Davila-

Ross et al., 2008) and in a monkey species (*Theropithecus gelada*). In orangutans it has been demonstrated that subjects responded, within 1 sec, with a play face (typical play facial expression) to the same facial display performed by a playmate, thus suggesting that the positive emotional contagion and empathy, which in humans are linked to RFM, are homologous within the Hominoidea. If understanding instantly others' emotional states and fine-tuning its own motor sequences accordingly are adaptive, we expected to find the RFM phenomenon in both species due to the neurophysiological basis that they share (*Prediction 1*). Moreover, it was supposed that, for an effective communication during play, the frequencies of matching responses (PF-PF, FPF-FPF) should be higher than non-matching frequencies responses (PF-FPF, FPF-PF) for both species (*Prediction 2*). Finally, due to the more competitive connotation of Japanese macaques social play compared to Tonkean macaques play, it was hypothesized that in *Macaca fuscata* rapid responses (within 1 sec) levels should overtake delayed responses (from 1 to 5 sec) levels (*Prediction 3*).

Conflict can generate further conflicts (Watts et al. 2000; Palagi and Cordoni, 2009; Barash and Lipton, 2011) and/or can affect the affinitive interactions among all group members (de Waal, 2000; De Marco et al. 2010; Ellemers, 2012). This implies that, at the end of a conflict, some forms of post-conflict management should occur. The first spontaneous post-conflict affinitive contact directed by a third party to the victim, as documented for humans and great apes, was coined as consolation (de Waal and van Roosmaleen, 1979; Palagi et al., 2008; Fraser et al., 2009; Romero et al., 2010). The terms "consolation" or "comfort" include a hypothesis about the function of the post-conflict mechanism as distress alleviation, that up to now has been demonstrated only for humans and great apes (Wittig and Boesch 2003, 2010; Kutsukake and Castles 2004; Palagi et al. 2006; Koski and Sterck 2007; Fraser and Aureli 2008; Fraser et al. 2008; Romero and de Waal, 2010; Cordoni et al. 2006; Mallavarapu et al. 2006; Palagi et al. 2004b; Fujisawa et al. 2006; Burleson 1983; Eisenberg 1992). Due to the high levels of social tolerance characterizing Tonkean macaques, we expected to find third-party affiliation (term coined to describe these types of contact in monkeys, Call et al., 2002) in *Macaca tonkeana*, but not in *Macaca fuscata* (*Prediction 1*). Moreover, it was supposed that third-party affiliation to victims functions as a substitute of reconciliation when it fails to occur (*Prediction 2*). It was also expected that it should be primarily received from friends (i.e. individuals frequently exchanging grooming) (*Prediction 3*) and it should have a role in reducing the victim's anxiety (*Prediction 4*). Moreover, it was tested if third-party affiliation protects the victim against further conflicts (Victim Protection Hypothesis) (*Prediction 5*) and/or if it has a role in reducing the spreading of aggression to the whole group (Tension Reduction Hypothesis) (*Prediction 6*).

1.2. Play

When you see someone playing, you do not find any difficulties to say that he/she/it is playing. But when you ask someone to give you a definition of "play" (ethologically speaking), then it starts to be a difficult matter. Compared to the so-called "serious" behaviours, whose modalities and functions are easier to detect and understand, play remains an intriguing challenge for researchers interested in the study of this ephemeral and controversial phenomenon.

Figure 1.1 – Play behaviour in *Macaca tonkeana*

Burghardt (2005) listed five criteria to define play:

1) Play is a behaviour that is not completely functional in the form or context in which it is performed because it does not seem to contribute to current survival.
2) Play is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic ("done for its own sake").
3) Compared to other ethotypic behaviours, play is incomplete, exaggerated, awkward, or precocious and it generally involves patterns modified in their form, sequencing, or targeting.
4) During a play session, the behavioural pattern performance is repeated in a not rigidly stereotyped way.
5) Play generally occurs when animals are free from environmental and social stressors.

Play has probably many benefits but they are not easily detectable. Some authors attempted to define mammalian play as a functionless behaviour, but this interpretation implies a very subjective view by the observer (Martin and Caro, 1985). Another important feature of play is that it borrows behavioural patterns usually showed in different contexts (e.g. agonistic, antipredatory, and mating behaviour). This means that what can help the observer to distinguish "play" from "non play" contexts, are not the type of behavioural patterns but the way they are performed (Martin and Caro, 1985; Pellis and Pellis 1996).

Beyond its definition, among all social activities, play stands out for its versatility, plasticity, and unpredictability (Fagen, 1993; Burghardt, 2005, 2011; Špinka et al., 2001; Palagi et al., 2007). Moreover, play is a multifunctional behaviour, which can have many different functions, according to factors such as species, sex, age, relationship quality between playmates, and group-membership (Cordoni, 2009; Dolhinow, 1999; Pellegrini et al., 2007).

Nonetheless, social play does follow rules, which if violated can lead to serious aggression (Pellis and Pellis, 1998; Pellis et al., 2010). While rules are followed in both free play, such as in play fighting, and structured games, such as in rugby matches, the nature of the rules differ (Power, 2000, Burghardt, 2005). Structured games, unlike free play, are built on *a priori* and written rules and the participants have to follow such pre-set rules if they do not want to be penalized in some form. Animal and children "free play" is a ground in which rules exist but they are not formalized and fixed (Pellegrini et al., 2007). Each new play session is a new item on the agenda on which new rules have to be redefined and written every time. The formulation and application of such *hic et nunc* codes depend on a vast arrays of variables which can change continuously. Indeed, the rules are rearranged and re-discussed as a function of the players involved (gender, ranking position, age, size, kin) and the kind of play performed (tickling, locomotor-rotational activities, fighting). As a matter of fact, different from structured games, the "true rule" of animal (and children) play is "no rule" or, at least, different and less rigid rules more similar to "guidelines" than to formal codes. Therefore, managing new playful interactions requires sophisticated and complex communicative skills, which have to change flexibly when it is necessary. Since a new session means a new situation to cope with, the capacity to ad-lib and the communicative effort required to play may be more *mentally* demanding than to engage in many other non-aggressive contexts (Palagi et al., 2006; Palagi, 2008; Pellegrini et al., 2007, Flack et al., 2004).

Play, in those species characterized by prolonged immaturity and extended parental care, (Fagen, 1993), starts in infancy, peaks in juvenility, and decreases at puberty (rodents: Pellis and Pellis, 2009; lemurs: Palagi et al., 2002; chimpanzees/humans: Cordoni and Palagi, 2011; humans: Pellegrini, 2009). However, in many species social play continues into adulthood (ungulates: Aldis, 1975; rodents: Pellis, 2002; canids: Bauer and Smuts, 2007; non-human primates: Pellis and Iwaniuk, 2000; humans: Power, 2000), thus suggesting that this behaviour can provide benefits throughout life (Palagi et al., 2006; Antonacci et al., 2010). Therefore, variability in play often reflects important social system parameters in both animal and human societies such as cooperation, parental behaviour, tolerance and affiliation (Norbeck, 1974; Thierry et al., 2000; Gosso et al., 2005; Palagi, 2011). More relaxed social organizations and less fixed dominance relationships help to maintain high levels of play between adults. For example, despite their phylogenetic closeness and similar social structure (*fission-fusion* society), bonobos and chimpanzees have striking differences. Bonobos have more egalitarian and tolerant social relationships (Hare et al., 2012), and are much more playful than chimpanzees (Palagi, 2006).

Due to all these considerations, play between adult and unrelated immature subjects (both in human and nonhuman primates) could represent a sort of “social bridge” mechanism, which favours adult social networks (Palagi, 2011). In fact, play serves to test the strength of inter-individual social bonds and cooperation (geladas: Mancini and Palagi, 2009; chimpanzees: Palagi et al., 2004a). For the present purpose, we suggest that it is also the reason for why social play is an ideal context to deepen the differences in inter-individual relationships that characterize *Macaca fuscata* and *Macaca tonkeana*.

1.3. Facial expressions and Rapid Facial Mimicry

Charles Darwin, in *The expression of emotions in man and animals* (1872) was the first to provide accurate descriptions and detailed analyses of human facial expressions. Darwin underlined that human facial expressions have strong similarities with those of other animals. Such similarity represents a shared heritage of our species, which supports the evolutionary continuity between humans and other mammals. According to some, the origin of human facial expressions, such as smiling, dates back to an ancestral non-human primate (de Waal, 2003; van Hooff and Preuschoft, 2003). Due to the highly stereotypical and conservative nature of primate facial expressions, researchers have identified specific facial displays in related species (e.g., macaques, *Macaca* spp.; geladas, *Theropithecus gelada*; chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*). In primates, common expressions occur during play (e.g., play face) and submission context (e.g., the bared-teeth display) and it has been hypothesized that they are homologous to laughter and smiling in humans (Preuschoft and van Hooff, 1995; de Waal, 2003; Waller and Dunbar, 2005).

The role of signals as intentional communication systems can be investigated through behaviours usually put to use during playful activity (Palagi, 2009; Palagi and Mancini, 2011). The experience of social play taxes an animal’s ability to regulate the emotional response, thus shaping the skill to perform appropriate actions in the appropriate context and so increases social competence (Pellis and Pellis, 2006).

In primates, the typical expression of social play is the relaxed, open-mouth display (or play face, PF), which can be performed in two different configurations (van Hooff and Preuschoft, 2003). In some species (such as in *Pan* spp., *Theropithecus gelada, Macaca tonkeana*), play face (PF) and full play face (FPF) represent two different degrees of the same playful expression. In the PF, the mouth is opened with only the lower teeth exposed, whereas in the FPF the mouth is opened in a relaxed mood with both upper and lower teeth exposed (Palagi, 2008; Palagi and Mancini, 2011).

Figure 1.2 – One juvenile shows a PF during a play session in *Macaca fuscata.*

It has been hypothesized that these playful expressions are ritualized versions of the biting movement that precedes the play bite, a very common behaviour frequently used during rough and tumble play (Palagi, 2006; van Hooff and Preuschoft, 2003). The PF is widespread in almost all primate species, for this reason it is considered to be the most ancestral configuration of the playful facial displays in this taxon. On the other hand, the presence of FPF seems to follow a patchy pattern with a distribution apparently random in respect to phylogeny (Preuschoft and van Hooff, 1997). Humans (*Homo sapiens*), bonobos (*Pan paniscus*) and gorillas (*Gorilla gorilla*) habitually use FPF, whereas chimpanzees (*Pan troglodytes*) use the classical PF (Chevalier-Skolnikoff, 1982; Palagi, 2006; Palagi et al., 2007).

In some cercopithecine species, the use and structure of particular facial expressions can converge as a function of their tolerance and affiliation baseline levels (Thierry et al., 1989; Petit et al., 2008). For example, in Sulawesi macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*), and geladas (*Theropithecus gelada*), all well-known as the most tolerant cercopithecine species, the FPF is not a more intense version of PF but derives from the convergence between PF and the silent-bared teeth display, a facial expression used for affinitive purposes in these species (van Hooff and Preuschoft, 2003; Bout and Thierry, 2005).

Whatever the origins and distribution of playful facial expressions are, they play a pivotal role in managing playful interactions. The use of playful facial expressions is important to avoid any misunderstanding, cope with a playful interaction successfully, promote social affiliation, and favour cooperation (Pellis and Pellis, 2009). Adult geladas make an intense use of FPF that, from a perceptive point of view, is a more effective and less ambiguous because it can be visually perceived at longer distances compared to PF (Palagi, 2008; Palagi and Mancini, 2011). FPF may also have an important role especially when play occurs in a social situation that is highly tense, such as that following intra-group aggression. Similarly, in humans an increase in distress may be prevented by laughing appropriately (as a corrective response), thus maintaining a cooperative mood during play (van Hooff, 1989). In this view, human laughter and FPF in geladas (and other primate species) may be used as a counter mechanism to offset the chance of aggression.

Understanding others’ emotional states by using the same facial expressions instantly allows an individual to foresee playmates’ intentions (Palagi, 2008) and fine-tune its own motor sequences accordingly (Provine, 1996; Palagi and Mancini, 2011). The importance of imitation processes has been well described by Meltzoff and Moore (1994, p.83): "*Imitation is to understanding people as physical manipulation is to understand things*”. By matching one’s own behaviour with that of others, individuals are able to develop their complete sphere of social competence. This gives an individual the possibility to synchronize its activity with those of group members, to copy their behaviour, and to place its behavioural activity in the appropriate context.

The context of play, due to its plasticity, safety, and emotional involvement, provides a good substrate to investigate these imitation processes. So we can hypothesize that the ability to promptly respond with an imitative action is an adaptive behaviour. Different forms of imitation can be distinguished. Some forms are under voluntary and cognitive control, while others are more strictly linked to the emotional sphere of the subject (Dimberg et al. 2002; Iacoboni 2009). For example, in humans there are two possible responses to positive facial expressions: automatic responses (within 1.0 s) and non-automatic responses (within 5.0 s). The automatic affective laughter has been matched with the spontaneous Duchenne smile (a facial expression involving the contraction of both the zygomatic major and the orbicularis oculi muscles) and non-automatic laughter reflects the later evolved non-Duchenne smile (involving only the contraction of the zygomatic major muscle, a smile purely controlled and detached from any emotion) (Dimberg et al., 2000; Wild et al., 2003). The involuntary, automatic, mirroring and rapid response (e.g. the Duchenne smile) given by the receiver is called Rapid Facial Mimicry (RFM) and is distinguished by other forms of imitation (Iacoboni, 2009) because of the rapidity of the matched reply. In humans, other apes, and monkeys, RFM plays an important role in emotional contagion, that is the process by which one party is affected by another’s emotional or arousal state (Davila Ross et al., 2008, de Waal, 2008). There is evidence that facial mimicry in playful contexts correlates with the success of each playful interaction. For example in chimpanzees, play bouts last more when the play face is bidirectionally performed by the two players (Waller and Dunbar, 2005). Moreover, social play sessions characterized by facial replication, last longer than those sessions punctuated only by spontaneous laughter (Davila Ross et al., 2011).

It seems, therefore, that the emotional synchronization through playful facial mimicry goes hand in hand with the cooperative side of social play. In humans, facial responsiveness requires a mechanism of "redirection of the sender’s neural processing and perception toward one interactant and away from others" (Schmidt and Cohn, 2001, p. 14). For both sender and receiver, maintaining a social interaction and exchanging facial expressions imply high-energy costs in terms of attentional investment. In this sense, the presence of high levels of RFM during a playful interaction is a clear statement of honesty by the two players that can be translated into fair play. Recent observations in geladas seem to support this hypothesis. In this species play duration length goes hand in hand with rapid facial mimicry but not with delayed facial mimicry. In this perspective, the rapid and automatic response being, more than the delayed response, the expression of an emotional involvement could be directly linked to the real motivation of the subject to play (Palagi et al., 2009).

Such evidences suggest that play behaviour contains many clues that can be used to better understand the empathic abilities of diverse species. This is true particularly for species like *Macaca fuscata* and *Macaca tonkeana* that show inter-individual relationships diametrically opposed.

1.4. Post-conflict triadic interactions

Living in a social group confers several advantages to an individual, if we think of cooperation in locating the best resources, protection against intra-specific aggression, and detection/protection from predators (van Schaik, 1983; Wrangham, 1979). However, group living is not always an advantage, it also has costs. Group living implies sharing limited resources (such as food, mates, and space) that can often lead to competition and conflicts of interest (van Schaik, 1989; Walters and Seyfarth, 1987). But if group living is an adaptive behaviour it necessitates that costs are not greater than benefits, or at least that to reach a stable balance some mechanisms to manage conflicts need to evolve (de Waal, 1986). These mechanisms have been studied by Frans de Waal on a group of chimpanzees (*Pan troglodytes*) at the Arnhem Zoo in The Netherlands: he identified first a whole of post-conflicts behaviours that include "reconciliation" and "consolation" (de Waal and van Roosmalen, 1979). Reconciliation has been defined as certain friendly interactions between former opponents that occur shortly after an aggressive conflict (de Waal and van Roosmalen, 1979). It has been demonstrated that reconciliation functions in repairing relationships (de Waal, 1989), reassuring former opponents of restored tolerance (Cords, 1992), reducing stress in the victim (Aureli et al., 1989; Aureli and van Schaik, 1991), decreasing the probability of a second attack by either the former opponent or other group members (Aureli and van Schaik, 1991), and providing a signal indicating the termination of conflict (Silk, 1996, 1997, 2002).

Although reconciliation may be the best option to restore a balanced situation among group members, it has been argued that other types of PC (post-conflict) behaviour involving a third-party ("triadic" PC interaction) have a similar function (Cords, 1997; Das, 2000; Watts et al., 2000). Post-conflict third-party interactions are the affinitive contacts exchanged among one of the opponents of a previous aggressive incident and an uninvolved bystander (de Waal and van Roosmalen 1979; de Waal, 2008). Contacts directed to the victim and initiated by a third-party are labelled as "unsolicited" (de Waal and van Roosmaleen 1979) whereas contacts directed to the bystander and initiated by the victim are labelled "solicited" (Watts et al., 2000). This distinction has been done to underline the spontaneity of the gesture, because providing comfort to an individual that is probably anxious requires even a minimum empathic ability, to identify oneself with the emotional state of the victim. This is the reason why only spontaneous affinitive contacts offered by the victim to the bystander have been identified "consolation" (de Waal and van Roosmaleen 1979). Consolation is considered as one of the best candidates for evaluating the empathic potential in humans, since it produces clear benefits to the receiver (e.g. anxiety reduction) and it is preferentially directed to kin and friends (Burleson, 1983; Eisenberg, 1992; Eisenberg, 2000; Frith, 1989; Fujisawa et al., 2006; Zahn-Waxler and Radke-Yarrow, 1990). Up to now in non-human primates unsolicited triadic contacts have been found in great apes: chimpanzees (*Pan troglodytes*) (Wittig and Boesch, 2003, 2010; Kutsukake and Castles, 2004; Palagi et al., 2006; Koski and Sterck, 2007; Fraser and Aureli, 2008; Fraser et al., 2008; Romero and de Waal, 2010), gorillas (*Gorilla gorilla*) (Cordoni et al., 2006; Mallavarapu et al., 2006), and bonobos (*Pan paniscus*) (Palagi et al., 2004b). For apes, the actual consolatory function of unsolicited contacts – resulting from a benefit obtained by the receiver – and its possible empathic origin are still under debate (e.g. de Waal and Suchak, 2010; de Waal and Aureli, 1996; Koski and Sterck, 2007; Fraser et al., 2008). For instance, in two studies on chimpanzees, Kosky and Sterk (2007) detected no anxiety decrease in the victim after being consoled, whereas Fraser and collaborators (2008) found that consolation reduced anxiety levels in the recipient of aggressions.

In monkeys, to demonstrate the occurrence of unsolicited post-conflict affiliation, de Waal and Aureli (1996) applied to macaques the same observation protocol used for apes (*Macaca fascicularis, M. fuscata, M. sylvanus, M. nemestrina*), but the researchers failed to find any evidence for this kind of post-conflict affiliation. Further investigations in other catarrhines also failed to reveal unsolicited bystander affiliation (*M. fascicularis, M. mulatta, M. arctoides, M. fuscata, M. sylvanus, Chlorocebus aethiops, Erythrocebus patas, Papio anubis, P. hamadryas*; Watts et al., 2000; Schino et al., 2004). Only in two monkey species, *Macaca arctoides* (Call et al., 2002) and *Mandrillus sphinx* (Schino and Marini, 2012), evidences of unsolicited triadic contacts have been noticed. Yet, despite their presence, the “consolatory” function of unsolicited triadic contacts to reduce victim’s distress has not still been demonstrated. This is the reason why non-human primate scholars prefer to use, for monkeys, a less value-laden term as “unsolicited bystander affiliation” when referring to this type of post-conflict affiliation (Call et al., 2002).

The function of consolation as victim’s anxiety reducer and the possible empathic foundation of consolation are intertwined. In fact, the possible empathic nature of consolation can be inferred from biases in the direction of the comforting behaviour because friends and kin are expected to react more empathetically to each others’ distress than non-friends (Aureli and Schaffner, 2002; Romero and de Waal, 2010). This aspect has been investigated in chimpanzees and bonobos where consolation was found to be higher between strongly bonded compared to weakly bonded individuals, and between kin compared to non-kin (Romero et al., 2010; Fraser et al., 2008; Palagi and Norscia, submitted to PlosONE). Therefore, consolation has been associated with sympathetic concern (Romero et al., 2010; Fraser et al., 2008). However, Kosky and Sterck (2007) found in a group of chimpanzees that consolation was not skewed toward kin, being directed to both unrelated and related individuals in a comparable way.

If consolation is an alternative behavioural mechanism in alleviating physiological distress and reducing the probability of further attacks (de Waal and Aureli, 1996; Aureli, 1997; Arnold and Barton, 2001; Call et al., 2002), its occurrence in the absence of reconciliation is expected at higher rates than in the presence of it. Wittig and Boesch (2003) found that Taï chimpanzees seem to select the best postconflict interaction (reconciliation, third party solicited contact, consolation, renewed aggression, or redirected aggression), carefully weighing advantages and disadvantages. In fact, consolation events followed longer conflicts more than reconciliation events did. Therefore, consolation was probably offered when reconciliation was either not beneficial or was too risky for conflict participants. In the chimpanzee group of the Parc de Beauval, Palagi and collaborators (2006) found that aggressive interactions were characterized by a high intensity level, and consolation was more frequent than reconciliation; thus, they supposed that unsolicited contacts with third parties could have been an "alternative choice" to reconciliation when further aggression was more likely to occur. When aggression is particularly severe, reconciliation cannot be immediate, and consequently social stress reaches high levels. This could mean that both victims and third parties likely gain potential advantages by triadic contacts.

One of the benefits of consolation can be also the reduction of renewed aggressions on the victim by other group individuals (Victim Protection Hypothesis). The possible effect of consolation in reducing renewed aggressions has been tested for all group members (overall conflict levels) to assess the Tension Reduction Hypothesis (in chimpanzees: Palagi et al., 2006), for the consoler to verify the Self-protection Hypothesis (chimpanzees: Wittig and Boesch, 2010; mandrills: Schino and Marini, 2012), but only in bonobos a role of consolation as part of a possible victim-protection function has been found (Palagi and Norscia, submitted to PlosONE). Hence, assessing whether consolation follows an empathic gradient (being biased by emotional closeness) and whether it has an actual benefit for the victim are obligatory steps to understand if consolation may be driven by a basic form of empathy (e.g. sympathetic concern; sensu de Waal, 2008).

Differently from Japanese macaques (Schino et al., 2004), conflict resolution mechanisms such as reconciliation, quadratic affiliation, and peaceful interventions are common occurrences in Tonkean macaques (Thierry, 1985a; Petit and Thierry, 1994; De Marco et al., 2010; Demaria and Thierry, 2001; Ciani et al., 2012). It is remarkable that compared to all the other macaque species in which third-party affiliation has been investigated, Tonkean macaque is the only species which belongs to the most egalitarian level (Grade 4) (Thierry, 2000; De Marco et al., 2010). Therefore, investigate unsolicited triadic contacts in monkey species that are so different about their inter-individual relationships style could open new scenarios on a so intriguing and discussed behaviour.

1.5. The genus *Macaca*

All the species belonging to the genus *Macaca* constitute a monophyletic group of the cercopithecine subfamily. The fossil record indicates that macaques colonized Eurasia 5 to 6 million years ago via the Near East and then, they branched into several phyletic lineages that have been identified from morphological and molecular evidence (Chakraborty *et al*., 2007, Delson, 1980, Fooden 1976, 1982, Hoelzer and Melnick 1996, Ziegler et al., 2007). Today we recognize 20 species: with the only exception of *M. sylvanus*, that is the unique species living in North Africa and Gibraltar, the macaques distribution range goes from central (Afghanistan, China and India) to south-oriental Asia (Malaysia, Indonesia, Philippines) reaching the north of Japan (Groves, 2001). We can distinguish three main lineages of extant macaques, corresponding to three dispersal waves in Asia. The *silenus* lineage has the most disjunct geographical distribution, indicating an early dispersal (Fooden,). Only the pigtailed macaque has a large distribution range. The liontailed macaque is found in the evergreen forests of southern India. The other species of the lineage inhabit the Sulawesi and Mentawai Islands. The *sinica* lineage has a moderately fragmented distribution in southern Asia and is thought to be the second lineage to have dispersed. Four of its species are found in tropical and subtropical continental areas, while the fifth species, the toque macaque, lives on Sri Lanka. The most broadly and continuously distributed lineage is *fascicularis*, which is likely to be the third lineage to have dispersed. The longtailed macaque is present in equatorial and tropical regions; the other three species are found in subtropical and temperate Asia. The taxonomic position of two further species remains debated. The Barbary macaque, which lives in the montane forests of North Africa, is the most ancient taxon of the genus. It is alternatively classified as either being the only member of its own species group or one belonging to the *silenus-sylvanus* lineage. The stumptailed macaque inhabits broadleaf evergreen forests of southern Asia. It is either ascribed to its own species group or included in the *sinica- arctoides* lineage.

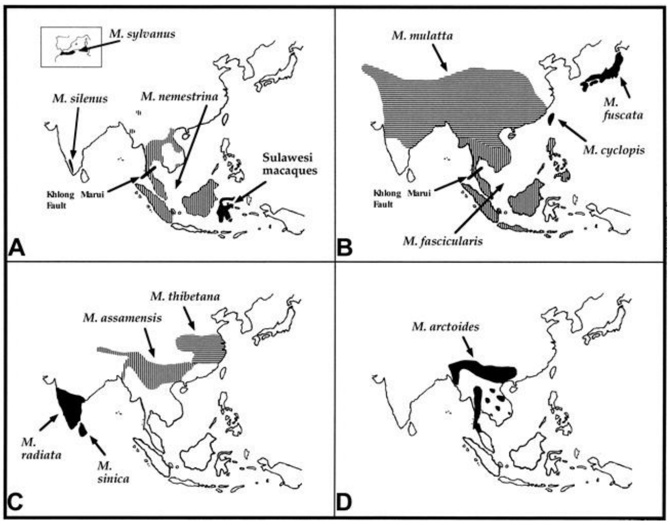

Figure 1.3 - Mappe di distribuzione dei gruppi di specie (*sensu* Fooden, 1980): (A) *silenus-sylvanus* group, (B) *fascicularis* group, (C) *sinica* group, (D) *arctoides* group (Tosi *et al*, 2003).

Macaques are semi-terrestrial primates that form *multi-male*, *multi-female* groups that permanently contain both adult males and females with offspring. The adult sex ratio is biased toward females. Neighboring groups have overlapping home ranges. Most males disperse and periodically transfer from one group to another. On the other hand, females stay in their natal group and maintain enduring relationships with their relatives, constituting matrilines that lead to the coexistence of several generations in the same group. Whereas the dominance status of males varies through their lifetimes, following shifts in their competitive abilities, the positions of females in hierarchies remain quite stable owing to kin-based alliances (Kummer, 1971, Thierry, 2004, Thierry, 2007).

Despite these common characteristics it has been proposed by Thierry (2000) to distribute all the macaques' species on a gradient ranging from more intolerant (despotic, Grade 1) to more tolerant (egalitarian, Grade 4) social systems (Matsumura, 1999) (see Table 1.1). This classification reflects different inter-individual relationships and a notable variability in temperament inside the genus *Macaca*. In fact the macaques species show a wide range of behaviours including aggression and affiliation patterns, dominance relationships and nepotism (Aureli *et al*, 1997; de Waal and Luttrell, 1989; Petit *et al*, 1997; Thierry, 1985; 1990). Despotic species like Japanese macaques (*Macaca fuscata*) have a strong, kin-centric power asymmetry between dominants and subordinates, marked submission behaviours, unidirectional conflicts, and low levels of social tolerance (Aureli *et al*, 1997; Kurland, 1977; Kutsukake and Castles, 2001). Whereas, egalitarian species such as Tonkean macaques

(*Macaca tonkeana*) have relationships which are minimally influenced by social rank and kinship ties. No formal indicators of subordination are present and the proportion of friendly interactions among non-kin is quite high (Butovskaja, 2004; Butovskaya and Kozintsev, 1996; Preuschoft and van Hooff, 1997).

Table 1.1 - Subdivision of macaques species based on the different social systems (Thierry, 2000; Flack and de Waal, 2004)

Social Organization	Species belonging to the class
Class 1 – Despotic High level of nepotism and strong asymmetries in aggressive behaviour with high intensity conflicts; very low post-conflict affiliation levels.	*M. mulatta, M. fuscata, M. ciclopi*
Class 2 Less rigid social system; strong asymmetries but medium-low intensity aggressions; higher levels of post-conflict affiliation.	*M. fascicularis, M. nemestrina*
Class 3 Social system intermediate between class 2 and class 4; restrained asymmetry with aggressive displays more than real conflicts.	*M. arctoides, M. assanamensis, M. radiata, M.silenus, M. sinica, M. sylvanus, M.thibetana*
Class 4 – Egalitarian High levels of tolerance and symmetry in aggressive interactions; frequent affiliation behaviours during post-conflict interactions	*M. maura, M. nigra, M. ochreata, M. tonkeana*

1.5.1. *Macaca fuscata*

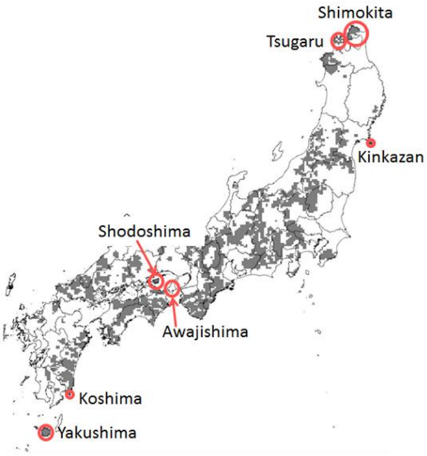

Figure 1.4 – A juvenile of *Macaca fuscata* from Olomouc Zoo (Czech Republic).
Figure 1.5 – Japanese macaques (*Macaca fuscata*) distribution in Japan (from Ministry of the Environment – Tokyo).

Macaca fuscata is an endemic Japanese species that represents the group of primates that inhabits the highest terrestrial latitudes (Fooden and Aimi, 2005). Groups can be composed of different matrilineal lines distributed in a stable and defined hierarchical scale, where females inherit automatically mothers' rank, often overtaking older sisters (Kawamura, 1958; Koyama, 1967). Adult males are rarely related with other group members (Sugiyama, 1976) and they get organized in hierarchical scales where the dominant tolerates other males but he is the only one that gets access to estrous females (Sprague *et al*., 1996). Moreover, males can use two means to go up the hierarchical scale: taking advantage of the dominant male death and maintaining good relationships with dominant females (Sprague *et al*., 1996).

Thierry (2000) classified *Macaca fuscata* as belonging to the first class that comprises the most despotic species. The social life of this species is governed by unbending rules, clear-cut dominance relationships and strong nepotism (Kawamura, 1958; Kurland, 1977). Inter-individual relationships are mainly asymmetric: subordinates tend to avoid dominants due to the high risk of injuries. This tendency can be observed during conflicts in which the direction is always from top-rank to low-rank individuals that never counterattack (Schino *et al.*, 2005; Majolo *et al*., 2005).

Clear submission signals have evolved to manage this asymmetric relationships, such as the typical facial expressions called *bared-teeth display*, *lipsmacking*, *teeth chatter*, *fear grimace* (Preuschoft, 2004).

Grooming, play, agonistic support and mother-infant protectiveness are strongly related to the kinship: females prefer individuals of the same matriline and rank (Kawamura, 1958; Schino *et al*., 2003). Usually *M. fuscata* females do not permit interactions among subordinate young individuals and their infants (Maestripieri, 2004) and tend to restrict their chances to interact with other group members (Nakamichi and Shizawa, 2003).

1.5.2. *Macaca tonkeana*

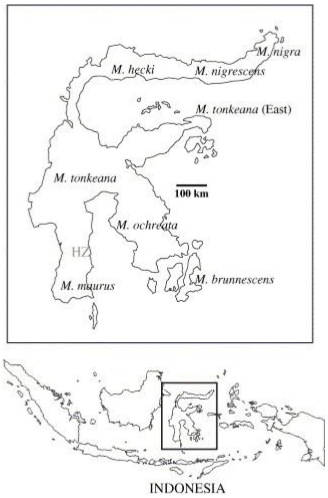

Figure 1.6 – An adult male of *Macaca tonkeana* from Parc de Thoiry (France) (photo by Julie Platel)

Figure 1.7 – Tonkean macaques (*Macaca tonkeana*) distribution on the island of Sulawesi (Indonesia) (from Schillaci et al., 2005)

Tonkean macaques are large black macaques found in the central region of the island of Sulawesi, Indonesia. This island has a peculiar biogeographic situation with highly endemic flora and fauna, probably due to relatively long period of isolation during geological time (Groves, 1976, 1980). On the island we can find seven allopatric taxa of macaques that derive from a single ancestral population: there are some evidences of gene flow between them, probably occurring in border areas between neighbouring groups (Groves, 1980; Camperio Ciani *et al*., 1989; Watanabe *et al*., 1991). They share many morphological, physiological, behavioural and molecular similarities (Fooden, 1969; Melnick and Kidd, 1985; Takenaka, 1985; Fooden and Lanyon, 1989).

Macaca tonkeana is one of the best known and studied Sulawesi macaque species (Thierry, 1984; Masataka and Thierry, 1993; Thierry *et al*., 2000b). It occupies a large part of tropical forests in the island central region (Thierry *et al*., 1994). Together with all other Sulawesi macaques, Tonkeans are classified as highly tolerant and egalitarian species and they are placed at the last class of the tolerance gradient proposed by Thierry (2000). A striking feature of Tonkean social relations is the symmetry observed during conflicts where both the competitors (the attacker and the threatened) react each other. In this way often the aggressive interaction becomes bidirectional. This does not depend on the kinship and it is regardless of age-and-sex class (Thierry, 1985). To understand dominance relationships in primates we usually observe the outcomes of agonistic interactions, where loser and winner are distinguished by which individual flees or submits. Such a criterion cannot be used in Tonkean macaques, where spontaneous displacements and supplantations are quite rare and ritualized submission signals are generally absent (Thierry, 1985, Thierry *et al*., 1994, Petit *et al*., 1997, Preuschoft, 2004). In Tonkean macaques also the *silent bared-teeth display*, that represents the typical macaques submission signal, acquire a different meaning. The jaw may be closed or open; in the last case it becomes impossible to distinguish this display from the relaxed open-mouth face usually seen in the context of play in monkeys. This facial expression signals peaceful intentions on the part of the emitter, and serves to initiate affinitive interactions (Thierry *et al*., 1989; van Hooff and Preuschoft, 2003). Another affinitive signal exhibited by *M. tonkeana* is *lipsmacking* that is the main facial expression displayed towards a higher-ranking individual in a non-aggressive context but may also be addressed to subordinates. Affinitive displays such as lipsmacks, grunts, and clasps of various forms usually occur at a high frequency (Thierry, 1984, 1985a and b; Demaria and Thierry, 1992). Tonkean individuals often switch from agonism to affiliation and, on rare occasions, mild punishment may even merge with genuine reconciliation.

Tonkean macaques social relations are characterized by the lack of formality that can be perceived during inter-individual contacts. In these situations they do not pay attention to the risks of approaching one another, even when the highest-ranking individuals are involved. For example, juveniles do not avoid adult males when passing by, they may contact them with impunity, and the latter tolerate their interference in matings (Thierry, 1986). Even if we can identify different matrilineal lines in the group, the social network of an individual is wide and not constrained by kinship, rank or age, even in the grooming or play mate choice (Butovskaya, 1993; Butovskaya and Kozintsev, 1996; Thierry *et al*., 1994). Mothers are quite permissive with their infants, who may interact with any other group members from an early age and this allows other females, kin or non-kin, to perform high levels of alloparental care (Thierry, 1985a; Thierry and Herrenschmidt, 1985, Maestripieri, 2004). Post-conflict conciliatory tendencies are not significantly greater among maternal kin than non-kin (Demaria and Thierry, 1992; Veenema *et al*., 1994). This does not mean that nepotism has no role in the social organization of Tonkean macaques: in coalitions for instance, help is mostly given to related partners, which results in dominance relations between matrilines. What is evident in this species is that kin-preferential behaviour is much less marked than in others, such as rhesus or Japanese macaques, and neither dominance asymmetries nor strong nepotism prevent individuals from interacting freely with all other individuals (Thierry, 1990).

Figure 1.8 – two juveniles Tonkean macaques (Photo by C. Scopa)

1.5.3 Subjects and Housing

Figure 1.9 and 1.10 – Macaques outdoor facilities respectively at the Olomouc Zoo (on the left) and at the Parc de Thoiry (on the right).

Behavioural data were collected on two groups of *Macaca fuscata* and one group of *Macaca tonkeana*. Individual identification was based on sex and other distinctive external features like scars, size, missing fur patches, fur colour and facial traits. Prepubertal individuals (infants and juveniles) were labelled as *immatures*, while fertile and sexually active subjects were labelled as *adults*. The study was conducted with no manipulation of animals. We adhered to ASAB guidelines for use of animals in research.

The first group of *Macaca fuscata* was housed in Parco Naturale di Cavriglia (Arezzo, Italy). During data collection (one month, April 2010) the colony was composed of three adult males, five adult females and seven immature subjects (ranging from one to four years of age) (for group's composition and age-class definition see Table 1.2). The animal enclosure was situated on a natural hill slope of about 500m^2 equipped with rocks, logs and a little pool. Food was distributed once a day (at about 9:00 AM) and water was available *ad libitum*.

The second group of *Macaca fuscata* was housed in the Olomouc Zoo (Olomouc, Czech Republic). During data collection (two months, June-July 2010) the colony was composed of five adult males, eight adult females, and 12 immature subjects (ranging from one to four years of age) (for group's composition and age-class definition see Table 1.2). Animals were housed in a large enclosure, about one hectare of pine trees forest enriched with ropes, wooden structures, shelters, and a natural stream. Food was distributed twice a day at 8.30 AM and 2:30 PM and water was available *ad libitum*.

The group of *Macaca tonkeana* was housed in the Parc Zoologique de Thoiry (Thoiry, France). During data collection (about three months, August-October 2010) the colony was composed of 30 adult males, 31 adult females, and six immature subjects (ranging from one to four years of age) (for group's composition and age-class definition see Table 1.3). The animals were housed in an enclosure with both indoor and outdoor facilities (182m^2 and 3 900m^2 respectively). The large outdoor grass area was equipped with pools, rope structures, trees and bushes. Food was distributed twice a day at 11:45 AM and 6.00 PM. Water was available *ad libitum*.

Tables 1.2 e 1.3 - Lists of animals belonging to the study groups.

Macaca fuscata CAVRIGLIA			*Macaca fuscata* OLOMOUC		
SUBJECT	**AGE CLASS**	**SEX**	**SUBJECT**	**AGE CLASS**	**SEX**
PR	Adult	♂	JK	Adult	♂
MB	Adult	♂	GS	Adult	♂
MC	Adult	♂	CS	Adult	♂
MR	Adult	♂	IN	Adult	♂
TT	Adult	♀	KR	Subadult	♂
PK	Adult	♀	AR	Adult	♀
GR	Adult	♀	RS	Adult	♀
MS	Subadult	♀	BU	Adult	♀
FA	Immature	♂	CT	Adult	♀
CA	Immature	♀	CH	Adult	♀
OP	Immature	♂	BEA	Adult	♀
TR	Immature	♀	VO	Adult	♀
MI	Immature	?	HE	Subadult	♀
RO	Immature	?	GA	Immature	♂
CI	Immature	?	BA	Immature	♂
			CL	Immature	♀
			RB	Immature	♂
			FI	Immature	♂
			GU	Immature	♂
			PI	Immature	♂
			AB	Immature	♂
			DR	Immature	♂
			AD	Immature	?
			GD	Immature	?
			JIRI	Immature	?

Macaca tonkeana **THOIRY**								
SUBJ.	**AGE CLASS**	**SEX**	**SUBJ.**	**AGE CLASS**	**SEX**	**SUBJ.**	**AGE CLASS**	**SEX**
AC	Ad.	♂	AM	Ad.	♀	CY	Imm.	♂
BE	Ad.	♂	AN	Ad.	♀	IN	Imm.	♀
CN	Ad.	♂	BT	Ad.	♀	LB	Imm.	♀
DA	Ad.	♂	CND	Subad.	♀	MC	Imm.	♂
EL	Ad.	♂	CD	Ad.	♀	PAN	Imm.	♀
EMA	Ad.	♂	CE	Ad.	♀	PR	Imm.	♀
ER	Ad.	♂	CL	Ad.	♀			
FX	Ad.	♂	EVA	Ad.	♀			
GE	Ad.	♂	FN	Subad.	♀			
GH	Ad.	♂	GL	Ad.	♀			
HS	Subad.	♂	GI	Ad.	♀			
JG	Ad.	♂	GV	Ad.	♀			
KU	Ad.	♂	LD	Ad.	♀			
LK	Ad.	♂	LE	Ad.	♀			
MI	Ad.	♂	MA	Ad.	♀			
MB	Ad.	♂	MV	Ad.	♀			
NEO	Ad.	♂	MT	Ad.	♀			
NQ	Ad.	♂	MG	Ad.	♀			
OT	Ad.	♂	MR	Ad.	♀			
PA	Ad.	♂	MO	Ad.	♀			
PE	Ad.	♂	PY	Ad.	♀			
PCH	Ad.	♂	PN	Ad.	♀			
PF	Ad.	♂	PIP	Ad.	♀			
RI	Ad.	♂	RZ	Ad.	♀			
RSC	Ad.	♂	SC	Ad.	♀			
SE	Ad.	♂	SP	Ad.	♀			
SK	Ad.	♂	TRT	Ad.	♀			
VA	Ad.	♂	VL	Ad.	♀			
ZZ	Ad.	♂	VE	Ad.	♀			
ZIG	Ad.	♂	VI	Ad.	♀			
			XE	Ad.	♀			

1.6. The arise of Primatology and its role in Anthropology

> [Paraphrasing some Roman or other we anthropologists say: "*Primatus sum, nihil primatum mihi alienum puto*", which, being translated, is "I am a primate; nothing about primates is outside of my bailiwick"]
>
> Earnest Hooton (1955)

Primatology is a relatively young discipline that began with the aim to elucidate the origins of human nature using morphological and behavioural comparisons among living nonhuman primates, fossil primates, and humans (Rodman, 1999). The study of primate behaviour and ecology is highly relevant to anthropology for two main reasons. First, the order Primates constitutes the appropriate context for comparisons with humans in all regards (Lévi-Strauss, 1968). Second, detailed understanding of the relationships between ecology and behaviour of living primates allows refined reconstructions of the origins of human behaviour (Rodman, 1999).

Modern primatological studies started with Ernest Hooton (1942, 1955) who in teaching human evolution underlined the importance of a comparative approach (including comparisons with primates behaviour). Then Clarence Ray Carpenter was one of the first scientists to conduct a primatological field study: he observed and documented the daily life of unhabituated gibbons during the Asiatic Primate Expedition (A.P.E.). The A.P.E. was sponsored by several universities of the United States, and was at that point the largest expedition purposely sent out to collect primates for scientific research and documentation. Carpenter (1940) described diet, individual behaviour, the monogamous social structure and territorial behaviour of gibbons. Another important figure for the rise of primatology was the Swiss anthropologist Adolph H. Schultz. At the Zurich institute of Anthropology he shifted the focus of his interests from physical anthropology to primatological studies (Stewart, 1983). His central aim was to understand the anatomical variability of many different species of primates in order to drawing appropriate broad evolutionary generalizations and sound taxonomic conclusions (Stewart, 1983). Sherwood Washburn (student of Hooton at Harvard) joined Schultz and Carpenter on the Asiatic Primate Expedition to Southeast Asia in 1937. His interdisciplinary approach, together with Kinji Imanishi studies of Japanese macaques, left a deep and important mark on primatology. They both addressed the importance of studying natural behaviour of nonhuman primates to reassemble the puzzle of human evolution (Rodman, 1999). Kinji Imanishi can be considered the "father" of Japanese primatology, due to his long-term study on a troop of *Macaca fuscata* at Koshima Island (Imanishi, 1960; Matsuzawa and McGrew 2008). He described some of the variations observed in the behaviour patterns of different social groups, such as the innovation, social transmission and modification of washing sweet potatoes in a freshwater stream and in seawater. These observations are considered one of the first documented examples of “cultural phenomena” in nonhuman primates (Matsuzawa and McGrew 2008).

The emergence of modern evolutionary biology, behavioural ecology and socio-biology (Wilson, 1975) also influenced primatological researchers. At that time anthropology lacked a firm tradition of observational study of naturalistic behaviour and primate studies began in a quasi-ethnographic mode, more descriptive than quantitative. With the passage of time, primate behaviourists borrowed the field techniques and theoretical orientations being developed by the recently emerged science of ethology. In fact, primatological observations changed dramatically to produce a flow of numerical data on time budgets, diets and so on (Clutton-Brock, 1977). The goal of these researches acquired a biological connotation, such as focusing on individuals and not only on group-phenomena or analysing social behaviour as a consequence of natural selection (operating on individual survival and reproductive success). Primatology’s development as a science also required the adoption of standardized methods of behavioural sampling. Altmann (1974) identified what is now considered the best observational techniques for the study of animal behaviour and her paper became the “How-To” manual for generations of primatologists. The aim has been, and still is, to employ the most appropriate sampling method for answering to research questions. This method should lead to the acquisition of unbiased behavioural data for objective comparisons with other animals, primates and humans (Strier, 2011). Further, behavioural samplings standardization helped the collection of quantitative data that could be more easily statistically compared.

Another important contribution to primatology came from Wilson (1975). He conveyed to a wide audience the message that natural selection, acting on the inclusive fitness of individuals, must be the primary process that generates social relations and social organizations. Even for nonhuman primates, variation in the social behaviour of individuals has fitness consequences that are acted on by natural selection, kin selection, and sexual selection. The current state of a social system is the result of a history of such selection on individuals (Rodman, 1999). Nonhuman primate behaviour, from that moment on, was interpreted in the light of new developments in evolutionary theory.

Cercopithecids, or Old World monkeys, share a large number of behavioural and ecological features with hominins. For example, they are extremely successful in terms of biomass and geographic coverage, they respond quickly to habitat change and often co-exist with humans. They also show opportunistic and eclectic feeding, such as omnivory, that contributes to this flexibility. Many cercopithecids are primarily adapted to relatively open habitats, such as grassland and woodland, but are also observed using more closed habitats (Rowell, 1966). It is increasingly apparent that Plio-Pleistocene hominins may also have occupied a variety of open and closed habitats (Reed, 1997; WoldeGabriel et al., 2001). So cercopithecids might be more ecologically similar to hominins than are apes. Comparisons between cercopithecid and hominins became prominent in the 1960s even if in the late 1970s and 1980s, they tended to be replaced by ape models. Obviously apes have a closer evolutionary relationship with humans than cercopithecid (Tanner, 1981). Traditionally, cercopithecid models have focused on the larger-bodied, terrestrial baboons (*Papio* spp.) and the gelada (*Theropithecus*). The relatively small macaques and the forest-living drills, mandrills, and mangabeys only rarely feature in comparisons, although the utility of macaques as referents has been later recognized (Schillaci and Froehlich, 2001). This represents a significant widening of the hominin-cercopithecid comparison and shows that comparative *taxa* should be selected on the basis of the hypotheses to be tested. The earliest well-cited baboon model was created by Washburn and DeVore (1961). They used field data to contextualize and reconstruct the possible social behaviour of early humans. Crook and Aldrich-Blake (1968) suggested that the interactions of Old World monkeys species might resemble those seen in early hominins under conditions of climatic and environmental change. Moreover, Rose (1976) examined the circumstances under which the olive baboon used bipedalism and argued that this behaviour could be used as a model for the development of bipedalism in pre-hominins. Also *Theropithecus* social behaviour has been used in at least one evolutionary scenario, with the relatively complex vocalizations used by geladas to convey information and emotion suggested as a model for the early stages of hominin language (Aiello and Dunbar, 1993). Although great apes are the obvious direct referents in studies of hominin cognition and cultural behaviour, the small number of extant apes makes detection of broad trends in brain evolution difficult. In a number of studies (Aiello and Dunbar, 1993) predictions for hominin behaviour and cognitive ability have thus been based on a catharrine (cercopithecid and hominoid) sample (Elton, 2006). By exploring the principles that underlie certain types of behaviours in modern primates, inferences about what was possible in hominins (under specific conditions) can be made (Strum and Mitchell, 1987). So, in some cases, the study of apes will provide the most appropriate baseline, but in others certain cercopithecid species will be more informative (Elton, 2006).

Today, the challenge for primatology is to elucidate the origins of human nature using morphological and behavioural comparisons among living nonhuman primates, fossil primates, and humans. For this reason two major components of anthropological primatology have evolved: paleoprimatology, which aims to uncover and interpret the fossil record of primate evolution, and the study of behaviour and ecology of living primates. The new paradigm of behavioural ecology and socio-biology proposed by Wilson (1975) was adopted by primatologists for the analysis and interpretation of variation in primate behaviour and ecology. Wilson argued that natural selection acted not at group level but at the individual level and after the spread of this paradigm, the focus of primatological studies turned from group-level phenomena and social relations to the study of individuals and social behaviour as a consequence of natural selection operating on individual survival and reproductive success.

Studies of behaviour and ecology of the living apes are particularly relevant for the reconstruction of the evolution of human behaviour (Foley, 1995).Variation in social behaviour of individuals has fitness consequences that are acted on by natural selection, kin selection, and sexual selection, and the current state of a social system is the result of a history of such selection on individuals. Grouping and group sizes of primates have been explained with reference to effects of predation, defence of resources, and female defence against male infanticide. Sexual dimorphism, dominance hierarchies, intra-sexual competition have been best interpreted through the action of sexual selection.

Comparative studies of primates indicate that the large brains of the genus *Homo* (enlarged cerebral cortex) evolved after bipedalism and human dental characters and probably depended on high-quality diets. Broad comparative studies have supported the hypothesis that large brains may have evolved in response to complex social environments. Aiello and Dunbar (1993) have applied comparative data on size of the neocortex, total cranial capacity, and group size of primates to understanding the timing and function of the origins of human language. The analysis indicates that neocortex size (relative to body weight) increases reliably with group size in primates and that time spent by group-living primates in social grooming also increases reliably with group size (Aiello, 1996; Dunbar 1991, 1995, 1998).

Another study that can be considered a milestone in the field of Primatology is that of Cheney and Seyfarth (1996) that performed a series of observational and experimental studies on vocal behaviour of cercopithecine monkeys. The results of this work lead to several important conclusions and inferences about nonhuman vocal communication: the calls of vervet monkeys have external referents and are functionally semantic (Seyfarth et al, 1980). Some vervet calls have acoustically differentiated meanings, and listeners respond to abstract meaning in some calls (Cheney and Seyfarth, 1990).However, although listeners may infer intentions from calls, intentionality is an inference of the listener rather than a true intention of the caller, calling monkeys apparently not intending to convey information to modify the current mental state of the listener (Cheney et al, 1996). This last result reveals that vocalizations of the vervets and baboons observed do not share the critical characteristic of human language, which is that the speaker intends to modify the behaviour of the listener.

These are just a few examples of the work that primatologists are doing to highlight similarities and differences among human and non-human primates. The field of Primatology is now looking ahead towards the primate social intelligence, and Frans de Waal has been one of the first scientists to start speaking of morality and empathy in non-human primates. He started his work paying a particular attention to deception, conflict resolution, and social strategies that are even now main areas of research for behavioural primatologists. Moreover, principal topics of his studies are cooperation, altruism and primate cognitive abilities (de Waal, 2008, 2011; Plotnik et al., 2006). In 2011, de Waal and his co-workers were the first to report that chimpanzees given a free choice between helping only themselves or helping themselves plus a partner, prefer the latter (Horner et al., 2011). In fact, de Waal does not believe these tendencies to be restricted only to humans and apes, but views empathy and sympathy as universal mammalian characteristics.

Therefore, the study of non human primates through morphological, genetic and behavioural studies could help anthropologists to fill the gap about the origin of man and its "human nature". As Washburn wrote: "...We are primates, products of the evolutionary process, and the promise of primatology is a better understanding of the peculiar creature we call man". It is my hope that this thesis research provides a further step in this process of understanding ourselves.

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2.

“SOCIAL TOLERANCE AND ADULT PLAY IN MACAQUE SOCIETIES: A COMPARISON WITH DIFFERENT HUMAN CULTURES”

(Francesca Ciani, Stefania Dall’Olio, Roscoe Stanyon, Elisabetta Palagi)

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ABSTRACT

Differences in play behaviour often illuminate complex ecological parameters and social differences. In primate societies, including humans, individuals acquire information through play. It is adults in every community that are most committed to managing social practices. In tolerant species, adults often participate in play to reinforce social networks and cooperation. The 20 macaque species are all organized in multi-male, multi-female groups but vary along a continuum from despotic/intolerant to egalitarian/tolerant social systems. These different social styles influence a wide range of behaviours including aggression and affiliation patterns, dominance relationships, and nepotism. Here, we test some covariation hypotheses by comparing play patterns in two macaque societies at opposite ends of the continuum: despotic Japanese macaques and tolerant Tonkean macaques. Our results show that these two species have striking differences in the distribution of social play according to the age and sex of the players. Our findings strongly indicate that play, one of the most plastic and versatile behaviours is sensitive to the quality of inter-individual relationships of a species, thus reflecting the nature of its social network. The different patterns of macaque play shows striking parallelisms with those coming from comparisons of different human cultures including: the distribution of social play according to the age and gender, player age-selection, partner preferences, and permissiveness of mothers. The adult play propensity of Tonkean compared to Japanese macaques indicates that adult-adult play is a good predictor for the polarity of changes in aggressiveness between different groups separated either genetically (taxa) or culturally (ethnies).

Key-words: adult social play; *Macaca fuscata*; *Macaca tonkeana*; playmate choice; mother protectiveness; despotism; tolerance; *Homo sapiens* societies.

2.1. INTRODUCTION

Defining play is a difficult matter. Compared to the so-called "serious" behaviours, whose modalities and functions are easier to be detected, play remains an intriguing challenge for researchers interested in the study of this ephemeral and controversial phenomenon. Burghardt (2005) listed five criteria to define play. Play is a behaviour which is not completely functional in the form or context in which it is performed because it does not seem to contribute to current survival (first criterion). Play is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic ("done for its own sake") (second criterion). Compared to other ethotypic behaviours, play is incomplete, exaggerated, awkward, or precocious and it generally involves patterns modified in their form, sequencing, or targeting (third criterion). During a play session, the behavioural pattern performance is repeated in a not rigidly stereotyped way (fourth criterion). Play generally occurs when animals are free from environmental and social stressors (fifth criterion). In complex mammalian societies, including human societies, play is one of the main means for individuals to acquire information about themselves and others (Paquette 1994; Pellis and Pellis 2006; Pellegrini et al. 2007; Pellis et al. 2010).

Play, in those species characterized by prolonged immaturity and extended parental care, (Fagen 1993), starts in infancy, peaks in juvenility, and decreases at puberty (rodents: Pellis and Pellis 2009; lemurs: Palagi et al. 2002; chimpanzees/humans: Cordoni and Palagi 2011; humans: Pellegrini 2009). However, in many species social play continues into adulthood (ungulates: Aldis 1975; rodents: Pellis 2002; canids: Bauer and Smuts 2007; non-human primates: Pellis and Iwaniuk 2000; humans: Power 2000), thus suggesting that this behaviour can provide benefits throughout life (Palagi et al. 2006; Antonacci et al. 2010). Play between adult and unrelated immature subjects could represent a sort of "social bridge" mechanism, which favours adult social networks (Palagi 2011). In fact, play serves to test the strength of inter-individual social bonds and cooperation (geladas: Mancini and Palagi 2009; chimpanzees: Palagi et al. 2004).

Adult-adult play in primates has been observed both in sexual and non-sexual contexts (Pellis and Iwaniuk 1999). Sexual play is useful for courtship mainly in solitary species (e.g. *Mirza*, *Daubentonia*, *Perodicticus* and *Pongo*), where males and females are unfamiliar with one another (Pellis and Iwaniuk 2000). Non-sexual adult play, occurs in those species characterized by higher levels of social aggregation and a more fluid, loose composition (e.g *Ateles*, *Cacajao*, *Pan*: Pellis and Iwaniuk 2000). More relaxed social organizations and less fixed dominance relationships help to maintain high levels of play between adults. For example, despite their phylogenetic closeness and similar social structure (*fission-fusion* society), bonobos and chimpanzees have striking differences. Bonobos have more egalitarian and tolerant social relationships (Hare et al. 2012), and are much more playful than chimpanzees (Palagi 2006).

Play at all ages can be viewed as a socially and culturally moulded behaviour. Therefore, variability in play often reflects important social system parameters in both animal and human societies such as cooperation, parental behaviour, tolerance and affiliation (Norbeck 1974; Thierry et al. 2000; Gosso et al. 2005; Palagi 2011).

Males and females show differences in locomotor play (mainly Rough-and-Tumble) (Pellegrini 2009), and juvenile males are generally more playful than females in catarrhine monkeys and apes (Owens 1975; Pereira 1984; Mendoza-Granados and Sommer 1995; Maestripieri and Ross 2004). However, no sex differences are found in tamarins and ring-tailed lemurs (Cleveland and Snowdon 1984; Gould 1990; Palagi 2009). In children from industrial as well as many preindustrial societies, gender differences in playful physical assaults and other forms of rough-and-tumble play, begin to emerge at about three years of age although the magnitude of sex difference in this form of play can vary across cultures (Whiting and Edwards 1973; 1988; Eibl-Eibesfeldt 1989). It has been suggested that sex differences in animal play are expected whenever males and females differ in their physical, behavioural and social features (Fagen 1981; Byers and Walker 1995; Špinka et al. 2001) because play can be used differently by adult males and females according to their role within the society (Palagi 2006).

Although the 20 species of the genus *Macaca* are organized in *multi-male*, *multi-female* social groups and have similar morphological features, they vary on a gradient ranging from more intolerant (despotic, Grade 1) to more tolerant (egalitarian, Grade 4) social systems (Matsumura 1999; Thierry 2000). These differences in social styles reflect species variability in temperament, thus influencing a wide range of behaviours including aggression and affiliation patterns, dominance relationships, and nepotism (Thierry 1985; 1990; de Waal and Luttrell 1989; Aureli et al. 1997; Petit et al. 1997). Despotic species like Japanese macaques (*Macaca fuscata*) have a strong, kin-centric power asymmetry between dominants and subordinates, marked submission behaviours, unidirectional conflicts, and low levels of social tolerance (Aureli et al 1997; Kurland 1997; Kutsukake and Castles 2001). Whereas, egalitarian species such as Tonkean macaques (*Macaca tonkeana*) have relationships which are minimally influenced by social rank and kinship ties. No formal indicators of subordination are present and the proportion of friendly interactions among non-kin is quite high (Butovskaya and Kozintsev 1996; Preuschoft and van Hooff 1997; Butovskaya 2004).

Many traits of social organization seem to be epigenetically correlated to the nature of inter-individual relationships and social play is considered to be one of them (Thierry et al. 2000; Hare et al. 2012). Hence, play should be a good indicator of the quality of social bonds both in despotic and egalitarian species. Recently, a correlation between styles of immature play fighting and the degree of cooperation was demonstrated in despotic and egalitarian macaque species (Petit et al. 2008; Reinhart et al. 2010). Nevertheless, it is adult individuals in every community that are most committed to managing social practices. Further, the assessment of tolerance level of a given species is generally based on adult relationships (Thierry et al. 1990; Schino et al. 2005). However, there are no quantitative and standardized data on adult macaque play in the literature. It was not known whether adult play in these species could be a good candidate to test some hypotheses. To fill this gap, we compared adult play distribution in two different species *M. fuscata* and *M.tonkeana* characterized by contrasting social styles.

Hypothesis 1

Adult and immature play frequency and distribution fluctuate according the degree of tolerance in a given species.

The degree of mother intolerance covaries across the diverse macaque species as a function of the difference in the quality of female relationships (Maestripieri 2004). Females of the most despotic and nepotistic species are often described as highly protective with their offspring, thus inhibiting contacts between their own infants and other group members (Maestripieri 1994; Thierry 2004). Therefore, we expect that immature social play is less frequent in *M. fuscata* than in *M. tonkeana* (Prediction 1a).

Due to the more fluid and flexible relationships typical of the egalitarian societies compared to the despotic societies (Pellis and Iwaniuk 2000; Thierry et al. 2000; Butovskaya 2004), we expect that adult-adult play levels differ between the two macaque species and, more specifically, we expect that adult play is more frequent in *M. tonkeana* compared to *M. fuscata* (Prediction 1b).

Hypothesis 2

Play may have different roles as a function of the sex of the players (Fagen 1981; Burghardt 2005; Pellis and Pellis 2009).

At sexual maturity males of both species (*M. tonkeana* and *M. fuscata*) leave their natal groups to join other groups (Gachot-Neveu and Ménard 2004). If play has competitive purposes (e.g. by testing others' fighting abilities: Pellis and Iwaniuk 2000; Maestripieri and Ross 2004; Palagi et al. 2007) and a role in improving the individuals' performance (Byers and Walker 1995; Byers 1998), we expect that in both species adult males show the highest play frequency (Prediction 2a).

In the most tolerant primate species, adult-adult play also functions to strengthen inter-individual relationships (*Propithecus verreauxi*: Antonacci et al. 2010; *Pan paniscus*: Palagi 2006; Palagi and Paoli 2007; *Theropithecus gelada*: Mancini and Palagi 2009; *Homo sapiens*: Peterson and Flanders 2005; Gray 2009). Therefore, we expect that Tonkean macaque females should show stronger, more relaxed, and less hierarchical social relationships compared to Japanese macaque females (Thierry 2004) and, consequently, also a higher adult-adult play frequency. Moreover, we do not necessarily expect that males of the two species show a difference in adult-adult play frequency (Prediction 2b).

2.2. METHODS

2.2.1.Data Collection Procedure

Observers collected data by using a tape recorder and a video camera. All occurrences sampling, focal-animal sampling (Altmann 1974) and Post-Conflict/Match-Control observations (de Waal and Yoshihara 1983; Kappeler and van Schaik 1992) were concurrently used. Observations were conducted only during working days to avoid the maximum concentration of visitors. Two observers collected data on *Macaca fuscata* groups and three observers followed the colony of *Macaca tonkeana.* Each observation day lasted eight hours, encompassing both morning and afternoon. Before starting systematic data collection, the observers underwent a training period (90 h). During the training phase (the trainer was S.D.), the same focal animal was followed by the observers simultaneously, and the data were then compared. Training was over when the observations matched in 95% of cases (Martin and Bateson 1986) and when the Cohen's kappa was higher than 0.70 (Kaufman and Rosenthal 2009).

We collected 166 hours of focal data for *Macaca fuscata* and 242 hours for *Macaca tonkeana*. Each member of each group was followed as focal animal every day and at different times of the day in order to obtain data covering entire the day in a balanced proportion. Via focal sampling we recorded all affinitive (grooming, proximity, contact sitting, play, touching, food sharing, co-feeding), self-directed (self-grooming, scratching, yawning), and neutral behavioural patterns (sitting alone, walking alone, feeding, foraging, resting) performed by animals.

Using all occurrences sampling we recorded play sessions and all aggressive encounters along with their i) relative intensity (high intensity conflicts included physical contact between opponents, slapping, biting, pulling, pushing; low intensity conflicts did not include any physical contact between opponents, threatening, chasing, fleeing), ii) outcome (decided conflicts were characterized by the absence of any sort of retaliation or counter-attack by the victim; undecided conflicts were characterized by victim counter-attack) and iii) presence/absence of agonistic supports by a third party. By all occurrences sample technique we collected 992 hours for *Macaca fuscata* and 1,176 hours for *Macaca tonkeana*.

After the last aggressive act of any given agonistic event, we followed the victim as the focal individual for a 5-min post-conflict period (PC). Control observations (MCs) took place on the next possible day at the same time as the original PC, on the same focal animal, in the absence of agonistic interactions during the 5 min before the beginning of MC and when the opponents had the opportunity to interact (de Waal and Yoshihara 1983). Both for PCs and MCs we recorded: starting time (min) and type of the first affinitive contact, initiator of the first affinitive behaviour (grooming, contact sitting, touching, sharing food and playing), and partner identity.

2.2.2. Data Analysis

To test whether the different captive conditions affected the behaviour of the animals and whether the colonies of the two species fell into the categories previously defined as despotic or egalitarian, we selected and compared five social parameters: incidence of decided aggressions, intensity of aggressions, presence of reconciliation, agonistic support rates, and levels of exchanged grooming. Since the assessment of the tolerance level of a given species is normally based on adult relationships, for preliminary analyses we considered only data from adult individuals.

One of the most effective mechanisms of conflict resolution is reconciliation, defined as a form of affinitive interaction between former opponents, which engage in friendly contacts (grooming, contact sitting, touching, sharing food and playing) shortly after a previous fight (de Waal and van Roosmalen 1979; Palagi et al. 2008;). Reconciliation functions in restoring the relationship between the opponents after a conflict, in resuming the benefits associated with valuable relationships, in reducing the probability of further conflicts and limit stress in the victim (Aureli et al. 2002).

Reconciliation analysis was carried out at the individual level. For each animal we determined the number of attracted, dispersed and neutral pairs over all PC-MC pairs. In attracted pairs, affinitive contacts occurred earlier in the PC than in the MC (or they did not occur at all in the MC), whereas in dispersed pairs the affinitive contacts occurred earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occurred during the same minute in the PC and the MC, or no contact occurred in either the PC or the MC. To avoid coding the same incident twice, for each individual we used only PC-MC pairs in which that individual was the focal animal, and entered them under its name. When dealing with reconciliation, we selected only victims for which we recorded at least 3 *PC-MC* pairs and calculated the *Corrected Conciliatory Tendency* (*CCT*) as described by Veenema et al. (1994). CCT was defined as ‘attracted minus dispersed pairs divided by the total number of PC-MC pairs’. Individual CCTs were used to determine the group mean CCT.

A play session began when one partner invited to play or directed any playful behaviour (for a complete description of play patterns see Table 2.1) towards a group member and ended when the playmates ceased their activities or separated. Two play bouts were considered as separated when a time frame of at least 10 seconds passed between the end of the first and the start of the new one. For both species, individual play frequencies were obtained dividing the number of play sessions with adult and with immature partners for individual observation time and dividing again respectively for the number of adult and immature subjects of the group. Due to the differences in the size of the troops and to be conservative as much as possible, we normalized the adult play sessions for the number of adult subjects that actually had the opportunity to interact (within a range of 15 meters from the play partners). The immature play sessions were always divided for the total number of immature subjects of the group (infants and juveniles together roamed the entire enclosure faster and more often than adults).

Table 2.1. Social play patterns recorded during the study.

Social Play Items	**Definitions**
Acrobatic play (acp)	Animals climb, jump and dangle from supports of the environment (i.e. branches)
Climb and stand on another (pcst)	An immature climbs/jumps and stands on an adult shoulders or back
Flip (pflip)	An animal jumps over the head or back of another ("leapfrog")
Gentle wrestling (gw)	Limbs entwined while sitting or laying: animals roll/twist together placing open mouths on each other
Play bite (pbit)	An animal gently bites a playmate
Play grab (pgra)	An animal gently grabs a playmate
Play kick (pk)	An animal gently kicks a playmate
Play pull (ppl)	An animal gently grabs and pulls a playmate
Play push (pps)	An animal gently pushes a playmate
Play retrieve (pre)	An animal holds a playmate to avoid its flight
Play recovering a thing (pre)	An animal chases a playmate and attempts to steal an object carried by it
Play run (prun)	An animal rapidly follows and chases a playmate
Play slap (psl)	An animal gently slap a playmate
Rough and tumble (rt)	Bipedal wrestling. Typically consists of: chasing, lunging, tackling, falling on the other, vigorous wrestling and mock biting

In case of deviation from normality (Kolmogorov-Smirnov $P < 0.05$) we applied non-parametric statistic. For intra-specific and dependent comparisons we employed the Wilcoxon matched pairs sign-rank test. The Mann-Whitney *U* and the Independent Sample t were applied to test for inter-specific and gender differences in the behavioural distribution. The level of significance was set at 5% for all the analyses. Statistical analyses were performed using Microsoft Excel and SPSS 12.00.

Preliminary Results

All the results performed to test whether the colonies of the two study species fell into the categories previously defined as despotic or egalitarian are reported in Table 2.2. Four out of five social parameters were found consistent with data from literature; on the other hand, the outcome of the analysis on aggression intensity shows contrasting results. Even though previous literature did not provide quantitative data on this issue, our finding does not appear out of tune. As it occurs in human societies, in which a rigid hierarchy is formally accepted to rule social relationships, in non-human species characterized by a crystallized ranking order, there is no need of high intense conflicts to maintain social stability. Indeed, sociobiologists consider dominance ranking one of the most powerful tools for reducing aggression propensity in a species (Preuschoft and van Schaik 2000).

Table 2.2 - Categories used to define a macaque society as despotic (Grade 1 – *Macaca fuscata*) or egalitarian (Grade 4 – *Macaca tonkeana*). Data from previous literature and statistical results from the present study are reported and compared. See the Method section for the definitions of the different parameters.

PARAMETERS	**DATA FROM LITERATURE**		**PRESENT STUDY**	
	M. fuscata **(Grade 1)**	***M. tonkeana*** **(Grade 4)**	***M. fuscata*** **(Grade 1)**	***M. tonkeana*** **(Grade 4)**
Incidence of undecided aggressions	**LOW** Demaria and Thierry, 2001; de Waal and Luttrell, 1989; Kutsukake and Castles, 2001; Petit et al., 1997; Thierry, 1985, 2000; Thierry et al., 2004.	**HIGH**	**LOW** Mann-Whitney U = 468; $N_{tonkeana} = 59$; $N_{fuscata} = 24$; P = 0.015	**HIGH**
Aggression intensity	**HIGH** Demaria and Thierry, 2001; de Waal and Luttrell, 1989; Kutsukake and Castles, 2001; Petit et al., 1997; Thierry, 1985, 2000; Thierry et al., 2004.	**LOW**	**LOW** Wilcoxon T=0; ties=0; N=14; P=0.0001	**HIGH** Wilcoxon T=164.5; ties=9; N=50; P=0.0001
Agonistic support	**LOW** Butovskaya, 1993; 2004; Flack and de Waal, 2004.	**HIGH**	**LOW** Mann-Whitney U = 291; $N_{tonkeana} = 59$; $N_{fuscata} = 18$; P = 0.003	**HIGH**
Reconciliation levels	**RARE** Demaria and Thierry, 2001; de Waal and Luttrell, 1989; Kutsukake and Castles, 2001; Petit et al., 1997; Thierry, 1985,2000; Thierry et al., 2004	**FREQUENT**	**RARE** mean CCT=4.13 ±4.13 SE Mann-Whitney U = 66; $N_{tonkeana} = 42$; $N_{fuscata} = 8$; P = 0.004	**FREQUENT** mean CCT=29.21 ±4.45 SE
Grooming	**LESS FREQUENT** Butovskaya, 1993; Mehelman and Chapais, 1988; Nakamichi and Shizawa, 2003; Singh et al., 1992; Thierry et al., 1990.	**MORE FREQUENT**	**LESS FREQUENT** Independent sample *t* test: t=6.34; N=21; df=80; P=0.0001	**MORE FREQUENT**

2.3. RESULTS

Hypothesis 1

Adult and immature play frequency and distribution fluctuate according to the tolerance degree of a given species.

Play sessions between immatures were significantly more frequent in *M. tonkeana* than in M. fuscata (Mann-Whitney U test = 3.00; $N_{immT} = 6$; $N_{immF} = 16$; $P = 0.0001$) (Figure 2.1). Japanese macaque infants still depending on mothers' support were eliminated from the analysis (Prediction 1a supported). Play sessions between adults were significantly more frequent in *M. tonkeana* than in *M. fuscata* ($U = 133.00$; $N_{adT} = 28$; $N_{adF} = 21$; $P = 0.0001$) (Figure 2.2) (Prediction 1b supported).

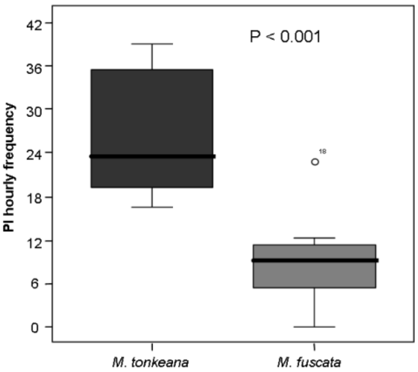

Figure 2.1 – Hourly play frequency between immature subjects (IMM-IMM) in *Macaca tonkeana* and *Macaca fuscata.* Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate the range of observed values. The boxplot shows both "mild" outliers and "extreme" outliers. Mild outliers are any score more than 1.5*IQR from the rest of the scores, and are indicated by open dots. IQR stands for "interquartile range", and is the middle 50% of the scores. Extreme outliers are any score more than 3*IQR from the rest of the scores, and are indicated by stars.

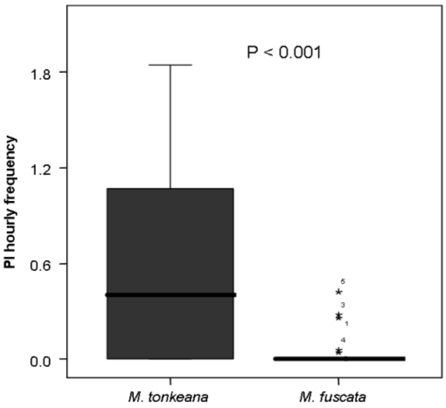

Figure 2.2 - Hourly play frequency between adult subjects (AD-AD) in *Macaca tonkeana* and *Macaca fuscata.*

Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate the range of observed values. The boxplot shows both "mild" outliers and "extreme" outliers. Mild outliers are any score more than 1.5*IQR from the rest of the scores, and are indicated by open dots. IQR stands for "interquartile range", and is the middle 50% of the scores. Extreme outliers are any score more than 3*IQR from the rest of the scores, and are indicated by stars.

When analyzing with whom adults play the most as a function of age, we found Japanese macaque adults playing significantly more with immatures (Wilcoxon signed-rank test: T = 54; N = 10; P = 0.007; mean SE per minute AD-AD: 0.0017 ± 0.0008; AD-IMM: 0.0066 ± 0.0017; Figure 2.3a), while no difference was found in play frequency between Tonkean macaques adult-adult and adult-immature sessions (Wilcoxon signed-rank test: T = 443; N = 58; P = 0.717; mean SE per minute AD-AD: 0.0480 ± 0.00950; AD-IMM: 0.0257 ± 0.0051; Figure 2.3b).

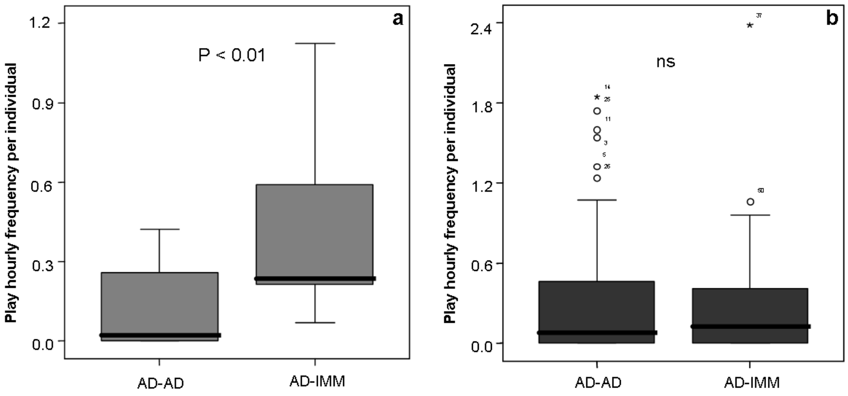

Figure 2.3 - Hourly play frequency performed by adults according to the age class of the playmates (AD-AD and AD-IMM) in *Macaca fuscata* (a) and *Macaca tonkeana* (b). The scale of the two graphs is appropriate to the observed distributions.

Hypothesis 2

Play may have different roles as a function of the sex of the players (Fagen 1981; Burghardt 2005; Pellis and Pellis 2009).

The intra-species comparison indicates that, in Japanese macaques, there is a significant gender difference in the frequency of the overall adult play levels (including both adults and immatures) with males involved in almost all sessions (Mann-Whitney U test=14; N_f = 13; N_m = 8; P = 0.002; Figure 2.4a) (Prediction 2a supported for *M. fuscata*). In Tonkean macaques, no difference was found in the frequency of play by adult males and females (U = 424.5; N_f = 31; N_m = 30; P = 0.50; Figure 2.4b) (Prediction 2a not supported for *M. tonkeana*). Additionally, the inter-species comparison indicates that adult males of *M. fuscata* played significantly more with immatures than adult males of *M. tonkeana* (U = 45; $N_{tonkeana}$ = 29; $N_{fuscata}$ = 8; P = 0.005; Figure 2.5a). On the contrary, the rates of adult–immature play of *M. fuscata* females were significantly lower than those of *M. tonkeana* adult females (U = 86; $N_{tonkeana}$ = 31; $N_{fuscata}$ = 13; P = 0.002; Figure 2.5b). Finally, adult males of both species played with other adults at similar rates (U = 74.5; $N_{tonkeana}$ = 28; $N_{fuscata}$ = 8; P = 0.151), while females showed a dramatic difference (U = 26; $N_{tonkeana}$ = 30; $N_{fuscata}$ = 13; P = 0.0001). We never observed adult females of *M. fuscata* engaging in play sessions with other adults (Prediction 2b supported).

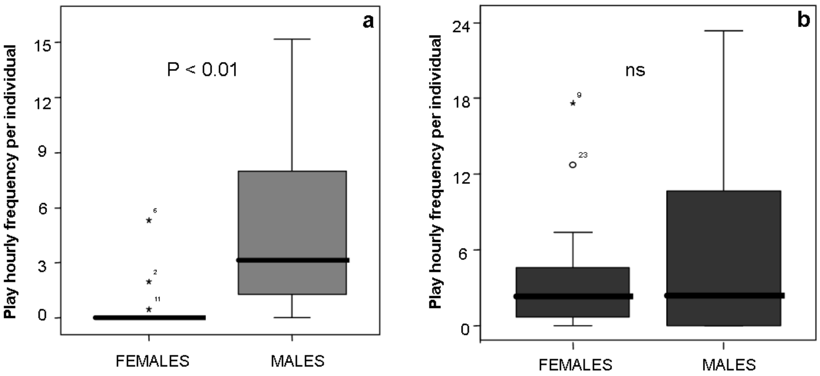

Figure 2.4 - Hourly play frequency performed by adults (AD-AD + AD-IMM) according to sex class in *Macaca fuscata* (a) and *M. tonkeana* (b). The scale of the two graphs is appropriate to the observed distributions.

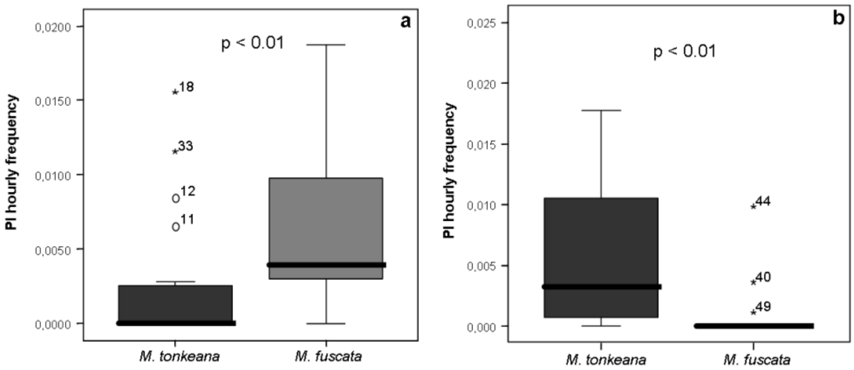

Figure 2.5 - Hourly play frequency performed by adult males with immature partners in *Macaca tonkeana* and *M. fuscata* (a) and performed by adult females with immature partners in *M. tonkeana* and *M. fuscata* (b). The scale of the two graphs is appropriate to the observed distributions.

2.4. DISCUSSION

Macaca tonkeana and *Macaca fuscata*, two species occupying the opposite extremes in the social tolerance gradient of the genus (Thierry 2000), showed striking differences in the distribution of social play according to the age and sex of the players. Immature Tonkean macaques had higher social play levels than immature Japanese macaques (*Hypothesis 1*, Prediction 1a supported). The adults of *M. fuscata* preferred to play with immature subjects than with other adults. In *M. tonkeana*, adults did not show any preference for play partners according to their age; in fact, adult-adult and adult-immature play levels did not differ (*Hypothesis 1*, Prediction 1b supported). We found a difference in social play distribution between adult males and females in *M. fuscata*, where the former played more than the latter (*Hypothesis 2*, Prediction 2a supported for Japanese macaques). In contrast, no gender difference in play propensity was found for *M. tonkeana* (*Hypothesis 2*, Prediction 2a not supported for Tonkean macaques). The difference in the adult play between the two species has to be ascribed to the diverse play levels characterizing the adult females. In fact, Tonkean macaque females played significantly more than Japanese macaque females, whereas no difference was found between males of the two species (*Hypothesis 2*, Prediction 2b supported). When we focused on adult-adult play, no playful session was recorded for Japanese macaque females throughout the entire period of observation.

These findings taken together strongly indicate that play, a highly plastic and versatile behaviour (Pellis and Pellis 2009), is sensitive to the quality of inter-individual relationships of a species, thus reflecting the nature of its social network. Infant social play is affected by the degree of mothers' permissiveness which, in turn, is strictly linked to the adult tolerance levels (Maestripieri 2004). The social inhibition, characterizing the despotic species, can increase the protectiveness level of Japanese macaque mothers, who should limit their infants' social contacts with other group members. The mothers of other macaque despotic species, like rhesus macaques, generally protect their infants from the attention of other adult females; in fact, in absence of group members, infants spent more time far from their mothers (Hinde and Spencer-Booth 1967). This inhibitory control provokes a limitation of the relational sphere of the infant, thus creating the conditions for an increased social canalization (Berman 1982). The narrow social canalization provoked by mother inhibitory control on infants can result in a more limited propensity to play also later in life, e.g. during juvenility. The restrictive experiences in early infancy can mould a more restrictive personality that rejects play with strangers, especially with adults. This is particularly true for despotic species in which play is enriched by more competitive elements compared to play performed by egalitarian species (Reinhart et al. 2010).

Data on macaques show striking parallelisms with those coming from different human cultures (Eisenberg 1990; Hewlett and Boyette, 2012). The personality traits of hunter-gatherer and farmer people strongly differ. Success in farming depends on adhering to consolidated and true methods. Creativity is risky, because if a crop is lost a whole year's food supply is lost too. These societies are generally hierarchically structured, so obedience towards high-ranking individuals is often essential to social and economic success. On the other hand, for hunter-gatherer people success requires continuous, creative, intelligent adaptation to the ever-changing environmental conditions (Barry et al. 1959, DeVore et al. 1968, Gould 1969). In farming societies, where various forms of hierarchy such as gender or age inequality exist, there is a strong control on infants and play behaviour is heavily discouraged. On the contrary, in hunter-gatherer societies characterized by mobility, small population size, minimal gender and age hierarchy, parents leave their infants free to play and to interact with other group members independently from kinship and age (Gray 2009; Hewlett et al. 2011). In these societies, child care and education are structured to maximize children's opportunities for play and to minimize any sense of being dominated by adults (Hewlett et al. 2011). By increasing child play opportunities, hunter-gatherers allowed their children to develop fully the characteristics of personal autonomy that are essential to hunter-gatherer success, especially cooperation and sharing with others. For example, in !Kung people, the mother-child relationship is set in a dense social community of people sharing frequent, reciprocal, and high quality bonds (Konner 1977). Alloparental care is well-represented and other adults and children are more likely than mothers or fathers to engage infants in any type of play (Hewlett 1991). Hunter-gatherer children are much more likely to be closer to adult-child mixed groups (both kin and nonkin) than are farmers (Konner 2005). Specifically, Ngandu and Bofi farmer children (Central Africa Republic) usually spend 59% of their day in groups composed by children only, whereas Aka and Bofi hunter-gatherer children (Central Africa Republic) spend only 18% of their day in proximity of child only groups (Hewlett et al. 2011). Also in those animal societies characterized by egalitarian relationships, there is a less selection in choosing a play partner as a function of its age (Palagi and Paoli 2007). Our findings on the player age-selection in the two macaque species fit with this statement. Adult Tonkean macaques did not show any preference between adult and immature playmates; whereas, adult Japanese macaques rarely played together and selectively chose immature subjects as play partners. The same findings have been obtained for the two *Pan* species, bonobos and chimpanzees. In the more egalitarian species, the bonobo, adults play with other adults as much as with infants and juveniles of the group; on the other hand, play in adult chimpanzees is strongly canalized in favour of immature subjects (Palagi and Paoli 2008). The absence of players' age-related selection has also been demonstrated in geladas (*Theropithecus gelada*), another egalitarian cercopithecine species (Dunbar and Dunbar 1975). Specifically, adult gelada females played with other group members independently of their age (Mancini and Palagi 2009). In hamadryads (*Papio hamadryas*), a strong despotic baboon species (Leone et al. 2010), adult play is essentially oriented towards immature subjects (Palagi, unpublished data). As a whole, these findings on non-human primates strongly suggest a covariation between adult-adult play propensity and the degree of tolerance characterizing a given society and human primates are not an exception. This play peculiarity is also evident in *Homo sapiens*. For example, hunter-gatherer societies show a fluid structure, consensual decision making, and rules for sharing that resemble those of their cooperative social play (Gray 2009; Sutton-Smith and Roberts 1970), which is typically informal and non-competitive (Marshall 1976). In these populations, the fluidity of social relationships is correlated with different cultural and ecological conditions and can promote the persistence of a playful attitude, in a number of adult social practices such as hunting and gathering activities, religious beliefs and practices, sharing meat and good acts, and even their most common methods of punishing offenders within their group (Norbeck 1974; Gray 2009). All activities which are performed through "humor and ridicule" of others (Gray, 2012). Indeed, in humans, smiling (in its more emotionally-linked version, e.g. Duchenne smile) is used to advertise cooperative propensity and thereby increase the likelihood that a social partner would invest resources in a relationship (Mehu et al., 2007). Specifically, Gray (2009, p. 490) reports that "[...]. Such humor, which is also common among people everywhere in social play, no doubts serves a bonding function. Laughing together helps create a feeling of closeness and shared identity. Good nature teasing is a way of acknowledging yet accepting one other's flaws."

Our findings on gender differences in adult social play practices support the covariation hypothesis for the genus *Macaca* (Thierry et al. 2000). Adult-adult play across species is mainly shaped by their similarity in the nature of inter-individual social relationships rather than by their phylogenetic closeness (Pellis and Iwaniuk 2000). In fact, play between adults has been reported only for those taxa which show i) fluid social organization (*Ateles* sp., *Cacajao* sp., *Pan paniscus*: Pellis and Iwaniuk 2000; *Crocuta crocuta*: Fagen 1981; *Tursiops truncatus*: Kuczaj et al. 2006; ii) high levels of tolerance with reduced hierarchical steepness (*Propithecus verreauxi*: Antonacci et al. 2010; *Pan paniscus*: Palagi 2006), and iii) alliances and cooperative behaviour (*Canis lupus*: Cordoni 2009; *Callithrix jacchus*: Norscia and Palagi 2011; *Theropithecus gelada*: Mancini and Palagi, 2009). It is worth noting that the role of females in these animal groups is central for social group cohesion (*Propithecus verreauxi*: Jolly 1966; *Theropithecus gelada*: Dunbar and Dunbar 1975; *Pan paniscus*: Kano 1982; Furuichi 2011; *Canis lupus*: ; Mech 1970; Cordoni and Palagi 2008; *Callithrix jacchus*: Snowdon and Cronin 2007; *Crocuta crocuta*: Drea and Frank 2003; *Tursiops truncatus*: Wells 2003; *Homo sapiens*: Hewlett et al. 2011). It seems, therefore, that the fluid social organization, the absence of strong sex-based hierarchical structure, and the presence of cooperative and tolerant interactions favour male and female role equality, which is evident in the sex distribution of adult play activity.

In conclusion, Tonkean compared to Japanese macaques maintain into adulthood some traits (e.g. play, tolerance) typical of the juvenile phase. Recently, it has been suggested that a self-domestication process, which is the natural selection for reduced aggressiveness within a species, could be at the basis of the retention of juvenilized traits into adulthood (Hare et al. 2012). The authors, who have coined the term “self-domestication syndrome” to account for the numerous differences between bonobos and chimpanzees, suggest applying the same theoretical explanation also to Tonkean macaques, which share with bonobos many behavioural characteristics such as social cohesiveness (De Marco et al. 2011; Thierry et al. 1994), low competitive relationships (Petit et al. 1992), a large use of positive facial expressions (Thierry et al. 1989), and a relaxed and playful mood of infant nurturing (Petit et al. 2008; Reinhart et al. 2010; this paper). Moreover, the present study demonstrating the adult play propensity of Tonkean compared to Japanese macaques indicates that adult-adult play is a good predictor for the polarity of changes in aggressiveness between different groups separated either genetically (taxa) or culturally (ethnies).

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3.

"UNDERSTANDING EACH OTHER. THE ROLE OF FACIAL EXPRESSIONS TO MANAGE DIFFERENT STYLES OF PLAY"

(Stefania Dall'Olio, Roscoe Stanyon, Elisabetta Palagi)

in preparation

ABSTRACT

Information exchanged during play sessions can be helpful to enhance social competence, promote the creation and development of social bonds, and increase tolerance levels that in turn affect conflict management. Rapid facial mimicry (RFM) is an involuntary, rapid, and automatic response, in which an individual mimics the facial expression of another individual. Two time domains are identified to describe replication of human positive expressions: automatic responses and non-automatic responses (within 5.0 s). Here, we investigated the presence of RFM in two macaque species located at the opposite sides of a classification based on social style: *Macaca fuscata* (despotic) and *Macaca tonkeana* (tolerant). RFM was present in both macaque species but only for specific playful facial expressions (play face, PF or full play face, FPF). Moreover, both species responded with the identical facial expression (mirroring responses) to the stimulus emitted by a playmate suggesting an elevated accuracy of RFM. The efficacy of the communication system during play seems to be a fundamental prerequisite to avoid any misunderstanding, manage a playful interaction successfully, and promote social affiliation in the social group. Finally, Japanese macaques used more rapid automatic responses (within 1.0 s) during social play than Tonkean macaques. This is probably due to the different styles of play performed by the two species: *Macaca fuscata* play is generally enriched of more competitive elements compared to *Macaca tonkeana* play. It is likely that *Macaca fuscata* needs a means to speed up the signal exchange, thus limiting the risk that the playful sessions could escalate into an overt aggression.

Key-words: Facial mimicry, Play face/Full play face, *Macaca fuscata*, *Macaca tonkeana*, Rapid Facial Mimicry, Competition/Cooperation

3.1. INTRODUCTION

Managing social relations among group members requires the use of an effective visual communication system (Palagi, 2008; Bradbury and Vehrencamp, 2011; Parr et al. 2005). Charles Darwin (1872) was the first to describe facial expressions and to underline their communicative connotation, with particular attention on the strong similarities between animals and human displays. Even though unconscious processes are probably at the basis of the phenomenon, the use of facial expressions for communication regulates many aspects of non-human primate social life such as aggression, dominance-subordinate relationships, appeasement, and play (de Waal, 2003). Information exchanged during play sessions can be helpful to enhance social competence (Byers and Walker, 1995; Brueggerman, 1978; Pellegrini et al., 2007), promote the creation and development of social bonds (Palagi et al., 2004, 2006, 2007), and increase tolerance levels that in turn affect conflict management (Aureli and de Waal, 2000). Moreover, for an individual living in a social group, it is fundamental to learn to behave and respond in the appropriate way to different situations and stimuli. Recently, Pellis and Pellis (2009) suggested that the social play experience affects animal's ability to regulate the emotional response, and this, in turn, affects the ability to perform actions and facial expressions in the appropriate context, thus increasing the capacity of living in a social group.

Facial mimicry is an involuntary, rapid, and automatic response, in which an individual mimics the facial expression of another individual. This phenomenon can be distinguished from other voluntarily and cognitive forms of imitation (Dimberg et al., 2002; Iacoboni, 2009) because of the rapidity of the response involving exclusively the face. Two time domains are identified to describe replication of human positive expressions: automatic responses (within 1.0 s) and non-automatic responses (within 5.0 s). The automatic affective laughter has been matched with the spontaneous Duchenne laughter and non-automatic laughter reflects the later evolving non-Duchenne laughter (purely controlled and detached from any emotion) (Dimberg et al., 2000; Wild et al., 2003). Numerous studies document that people mimic emotional facial expressions of others within 1000 ms (Dimberg et al., 2000). Rapid facial mimicry (RFM) has been widely described in children (Beall et al., 2008; Jones, 2009) and adult humans (Dimberg and Thunberg, 1998), whose congruent reactions are elicited more frequently and rapidly in response to a dynamic facial expression compared to a static one (Sato and Yoshikawa, 2007). RFM was considered as linked to the automatic perception-action coupling of sensorimotor information that occurs in motor brain areas (Ferrari et al., 2009a). Neurophysiological evidence of this coupling is derived from the discovery of mirror neurons in the premotor and parietal cortices of monkeys (Gallese et al., 1996; di Pellegrino et al., 1992; Ferrari et al., 2003). In fact, these neurons fire when a monkey performs an action and when it observes a similar action performed by another individual (Ferrari et al., 2003). Functional brain imaging studies in humans showed that the observation of facial emotions activates, similarly to monkeys, not only shared motor representations in premotor and parietal areas but also in insular and cingulate cortices, being these latter directly involved in processing visceromotor sensations. During the observation of a specific facial expression, the observer's covert motor activation results in the experience of a matching emotional state (Carr et al., 2003; Caruana et al., 2011; Pfeifer et al., 2008; Singer et al., 2004). In this perspective, human RFM has been theorized to be central in connecting the emotional experience of two individuals. This theoretical account is also supported by behavioural studies showing that the frequency of RFM is higher among friends and kin than among unfamiliar individuals (Feldman, 2007; McIntosh, 2006; Norscia and Palagi, 2011; Demuru and Palagi, 2012). Therefore, RFM could be advantageous to promote social connections and affinitive behaviours among individuals (emotional connection hypothesis, ECH) (de Waal and Ferrari, 2010; Paukner et al., 2009). Considering the importance that RFM might play in social interactions, it has been proposed that RFM may not be confined to humans, but may also be present in other nonhuman primates (Davila-Ross et al., 2008). RFM has been discovered in an ape species (*Pongo pygmaeus*) by Davila-Ross and collaborators (2008). Primates show two kinds of playful facial displays, the play face, where only the lower teeth are exposed, and the full play face where both upper and lower teeth are exposed (van Hooff and Preuschoft, 2003; Palagi, 2008). In orangutans it has been demonstrated that subjects responded, within 1 sec, with a play face to the same facial display performed by a playmate, thus suggesting that the positive emotional contagion and empathy, which in humans are linked to RFM, are homologous within the Hominoidea. Another ape species showed evidence of RFM: chimpanzees not only produce affective laughter (rapid replication) but also laughter that represents a combination of both affective and non-automatic traits (delayed replication), and both these facial replications were equally effective in prolonging the duration of the chimpanzee play sessions (Davila Ross et al., 2011).

Here, we investigated the presence of RFM in two macaque species: *Macaca fuscata* and *Macaca tonkeana*. Inside the genus *Macaca*, social style of the different species is viewed as a continuum from extremely despotic to extremely tolerant in which group members tend to show the opposite characteristics (Thierry, 2000). The despotic species show rigid, linear, steep hierarchies enforced with low levels of bidirectionality, counter-aggression, or reconciliation (Balasubramaniam et al. 2012a, 2012b; Thierry, 2000). On the contrary, the tolerant species show relaxed inter-individual relationships with frequent bidirectional conflicts, high levels of reconciliation and counter-aggression, and low levels of kin bias (e.g. Demaria and Thierry, 2001; Petit et al., 1997). Due to these striking differences we decided to compare species located at the opposite sides of the social style classification proposed by Thierry (2000): *Macaca fuscata* and *Macaca tonkeana*. Yet, whether social style affects the ability to respond in a congruent way to others' playful facial displays, thus permitting a better play fine-tuning, is still not known. To fill this gap we tested the following predictions.

If the ability to respond in an appropriate manner is adaptive, we expect to find the phenomenon both in *M. fuscata* and *M. tonkeana* due to their basic cognitive similarities (Call, 2004) (*Prediction 1*). Moreover, for an effective play communication, the facial replication should be accurate. In this view, we expect that the frequencies of mirroring responses (PF-PF, FPF-FPF) should be higher than non-mirroring response frequencies (PF-FPF, FPF-PF) for both species (*Prediction 2*). Finally, due to the more competitive connotation of social play in Japanese macaques compared to Tonkean macaques (Reinhardt et al., 2010; Ciani et al., 2012), we hypothesize that in *Macaca fuscata* rapid responses (within 1 sec) should overtake delayed responses (from 1 to 5 sec) (*Prediction 3*).

3.2. METHODS

3.2.1. Data Collection Procedure

We collected data on 19 subjects (9 adults, 10 immatures) of *Macaca fuscata* during June/July 2010 and on 46 subjects (40 adults, 6 immatures) of *Macaca tonkeana* from August to mid-October 2010. We selected for the analyses only those subjects for whom we recorded at least one playful session. We conducted a video-analysis on 68 (*M. fuscata,* individual mean: 3.57) and 235 (*M. tonkeana*, individual mean: 5.10) diadic play bouts using Kinovea v. 0.7.10 software.

According to the literature dedicated to the topic, we focused our analysis on two playful expression variants in *Macaca fuscata* and *Macaca tonkeana*: the play face (PF) and the full play face (FPF). Since, during playful events other playful expressions were observed (in *Macaca fuscata*: bared-teeth, BT; scalp-retraction, SR; in *Macaca tonkeana*: bared-teeth, BT; scalp-retraction, SR; lip-smacking, LS; tongue-protrusion, TP), we used these expressions as a control (for facial expressions definitions see Table 2.1).

Videometric analyses of facial displays were primarily conducted by S.D. Inter-observer reliability was tested by S.D. and E.P. with one-frame accuracy (one frame/4msec). The mean Cohen's kappa values obtained were *k*PF = 0.75; *k*FPF = 0.86; *k*LS =0.67. To test for the presence of RFM, we measured the facial displays of one individual (the observer, hereafter) to see whether the observer's expressions varied as a function of the facial displays of the play partner (the trigger, hereafter) within a 1-s time window. The trigger was the first playmate that emitted a facial stimulus (PF/FPF or BT/SR/LS/TP). In order to be reasonably sure that the facial expression performed by the observer was actually elicited by the facial expression performed by the trigger, we considered only those interactions in which the observer looked at the face of the trigger and did not show any facial expression in the 1s prior to the trigger's stimulus. Chewing behaviours and biting transitional faces were excluded from the analysis to reduce uncertainties.

After the trigger emitted a specific play signal (stimulus: PF or FPF), we categorized the observer's behaviour into three possible responses: *congruent*, *incongruent,* and *no-response*. When the observer responded with a PF or a FPF, the response was labelled as *congruent*. When the observer responded with another expression (BT/SR/LS/TP), the response was labelled as *incongruent*. When the observer did not show any facial reaction (neutral face) we categorized the absence of response as *no-response*. As a control, the same analysis was conducted considering BT/SR/LS/TP as the stimulus. Observers who never displayed PF, FPF, or BT/SR/LS/TP in response to a previous stimulus and observers with less than 2 opportunities to see the trigger stimulus were excluded from the analysis.

Furthermore, to test the accuracy of the response, we distinguished the *mirroring* (stimulus PF/response PF; stimulus FPF/response FPF) from *non mirroring-response* (stimulus FPF/response PF; stimulus PF/response FPF).

Following the criteria used for human studies (Dimberg et al. 2000; Wild et al. 2003), the facial responses were measured for two time domains: within the first second after the onset of a facial display (PF/FPF or LS) emitted by a playmate (rapid replication) and within the next 5 seconds (delayed replication). Considering the two time domains and the congruence of response, we distinguished two facial expressions: i) congruent rapid facial replication (<1 s), ii) congruent delayed facial replication (1-5 s). The latencies were measured starting from the onset of the trigger stimulus and ending with the onset of the observer's facial response with 10-ms accuracy.

Table 2.1 – Description of facial expressions observed during play sessions in *Macaca fuscata* and *Macaca tonkeana*.

FACIAL EXPRESSION	DESCRIPTION
Play face (PF)	Relaxed, open-mouth expression with lower teeth exposed.
Full play face (FPF)	The mouth is opened with the lower and upper teeth exposed.
Scalp retraction (SR)	The scalp is retracted, ears may be flattened against the head while the individual looks at a partner. This may be associated with physical approach. This is an invitation to play or engage in an affinitive interactions.
Bared-teeth (BT)	The upper lip or both lips are vertically retracted, exposing the teeth and sometimes the gums. The corners of the mouth may be drawn back. The jaw may be either closed or opened to various degrees. The scalp is often raised and the ears flattened.
Lip-smacking (LS)	Lips are protruded and then smacked together repeatedly. The mouth may be slightly open with the tongue moving back and forth. The lips often produce an audible sound.
Tongue protrusion (TP)	The tongue is drawn out and inside the mouth repeatedly

3.2.2. Data Analysis

Nonparametric statistics were applied when the distribution of a given dataset deviated from normality (Kolmogorov-Smirnov $P < 0.05$). The level of significance was set at 5% for all the analyses. All the statistical tests were two tailed. Statistical analyses were performed using Microsoft Excel and SPSS 12.00 (SPSS Inc., Chicago, IL, U.S.A.). To evaluate the frequency of the observer's response we applied the Friedman test when $k > 2$. In case of significant difference of Friedman test, we employed the Dunnett's multiple comparison test to determine what conditions significantly differed. To measure the frequency of matching *vs* non-matching responses we used the Wilcoxon's matched pairs sign rank test. The same test was applied to compare congruent rapid and delayed responses. Exact tests were used according to the threshold values as suggested by Mundry and Fisher (1998).

3.3. RESULTS

3.3.1. *Prediction 1* - Presence of Rapid Facial Mimicry (RFM)

The frequency of the three types of response (*congruent*, *incongruent*, and *no-response*) significantly differed both in *Macaca fuscata* (Exact Friedman's $\chi 2$ = 25.000, n = 16, d.f. = 2, p = 0.0001) and in *Macaca tonkeana* (Exact Friedman's $\chi 2$ = 55.882, n = 32, d.f. = 2, p = 0.0001) but only when the trigger stimulus was a PF or a FPF (see Figure 3.1a and b; Figure 3.2a and b). When the trigger emitted a PF/FPF the frequency of *congruent* responses was higher than *incongruent* responses (*Macaca fuscata* - *congruent*: mean 0.63±0.06 SE – *incongruent*: mean 0.005±0.004 SE – *no responses*: mean 0.40±0.07 SE) (congruent-incongruent: Dunnett's test: q=0.697, df=2, N=19, p<0.01; congruent-no responses: Dunnett's test: q=1.634, df=2, N=19, p<0.01; incongruent-no responses: Dunnett's test: q=4.663, df=2, N=19, p=ns) (*Macaca tonkeana* - *congruent*: mean 0.53±0.44 SE – *incongruent*: mean 0.10±0.03 SE; – *no responses*: mean 0.40±0.04 SE) (congruent-incongruent: Dunnett's test: q=2.015, df=2, N=19, p<0.01; congruent-no responses: Dunnett's test: q=0.916, df=2, N=19, p<0.01; incongruent-no responses: Dunnett's test: q=6.309, df=2, N=19, p=ns).

In Japanese macaques when the stimulus emitted by the trigger was a BT or a SR the difference among *congruent*, *incongruent* and *no-responses* disappeared (Exact Friedman's $\chi 2$ = 4.526, n = 7, d.f. = 2, p = 0.115). Differently, in Tonkean macaques when the stimulus emitted by the trigger was a BT/SR/LS/TP there was still a difference among the three types of responses (Exact Friedman's $\chi 2$ =16.965, n = 28, d.f. = 2, p = 0.0001), but the frequency of congruent responses was lower than that of incongruent responses (*Macaca fuscata* - *congruent*: mean 0.05±0.05 SE – *incongruent*: mean 0.57±0.17 SE – no responses: mean 0.38 ±0.17 SE) (*Macaca tonkeana* - *congruent*: mean 0.07 ±0.04 SE – *incongruent*: mean 0.35±0.76 SE; – no responses: mean 0.58±0.08 SE) (congruent-incongruent: Dunnett's test: q=3.228, df=2, N=19, p=ns; congruent-no responses: Dunnett's test: q=3.556, df=2, N=19, p=ns; incongruent-no responses: Dunnett's test: q=1.799, df=2, N=19, p<0.01). These results confirm the presence of facial mimicry both in *Macaca fuscata* and *Macaca tonkeana*.

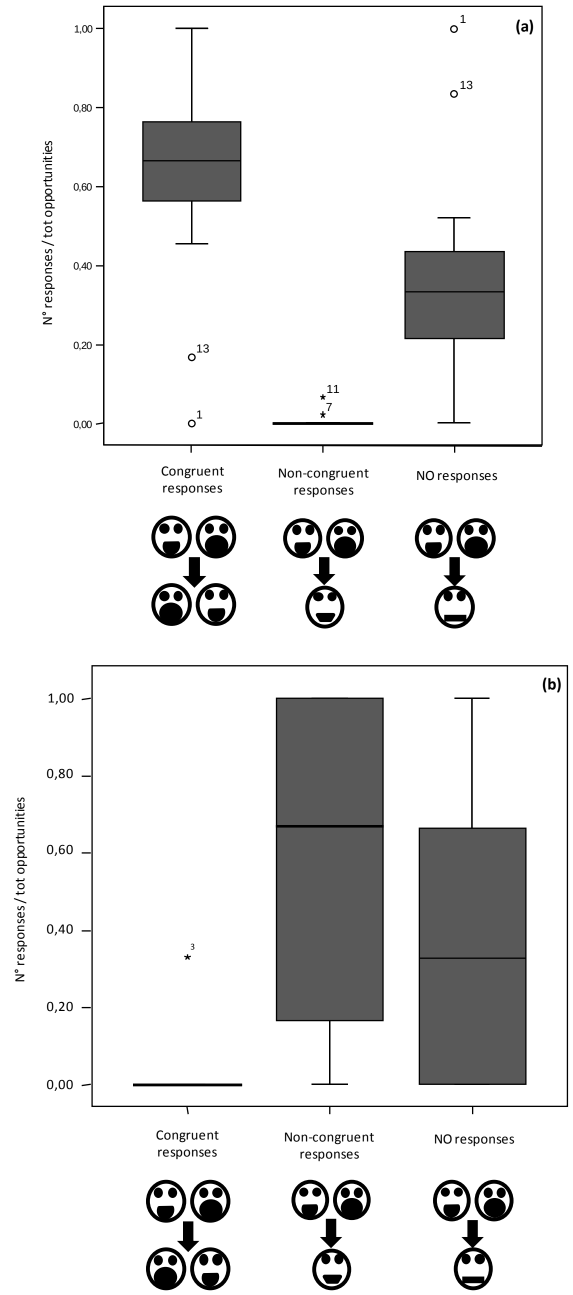

Figure 3.1a e 3.1b – Facial mimicry in *Macaca fuscata.* Facial Mimicry events per number of trigger stimuli (opportunities), when the trigger emitted a playful specific signal (PF/FPF) **(a)** and when the trigger emitted a playful aspecific signal (BT/SR) (control condition) **(b)**. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

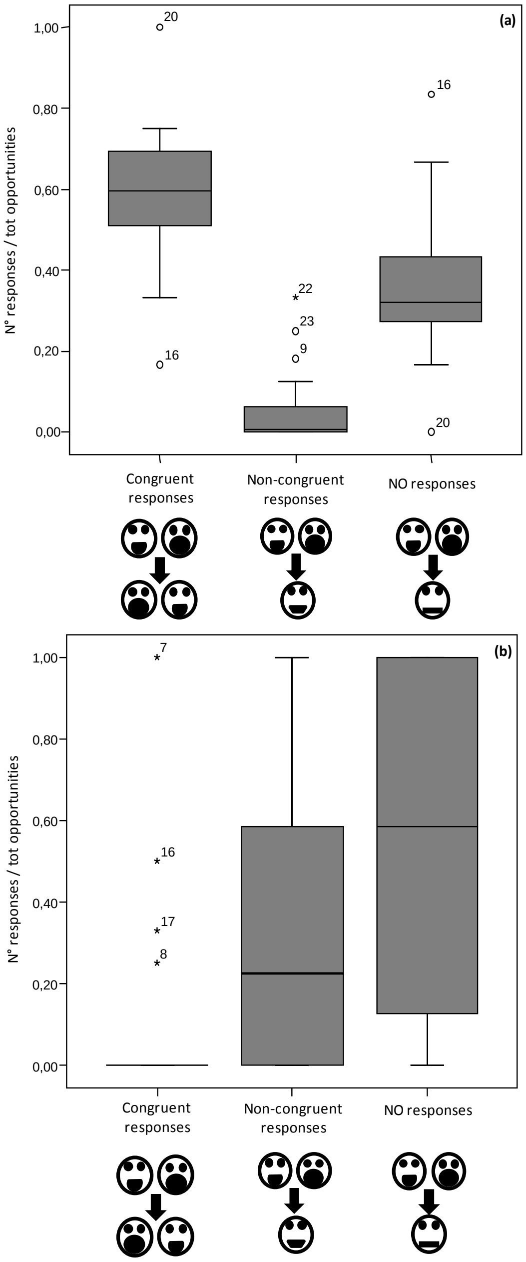

Figure 3.2a e 3.2b – Facial mimicry in *Macaca tonkeana.* Facial Mimicry events per number of trigger stimuli (opportunities), when the trigger emitted a playful specific signal (PF/FPF) **(a)** and when the trigger emitted a playful aspecific signal (BT/SR) (control condition) **(b)**. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

3.3.2. *Prediction 2* - Mirroring responses

In *M. fuscata* when the stimulus was a PF or a FPF the observer reacted significantly more frequently with a mirroring (PF/PF or FPF/FPF; *Median* = 1.00; *min value* = 0.67, *max value* = 1.00) than a non-mirroring response (PF/FPF or FPF/PF; *Median* = 0.00; *min value* = 0.00, *max value* = 0.33) (Exact Wilcoxon's $T = 0.00$, *ties* = 0, $n = 17$, $p = 0.0001$) (see Figure 3.3a). The same result was found for *M. tonkeana*: mirroring responses (PF/PF or FPF/FPF; *Median* = 0.95; *min value* = 0.00, *max value* = 1.00) were more frequent than non-mirroring response (PF/FPF or FPF/PF; *Median* = 0.05; *min value* = 0.00, *max value* = 1.00) (Exact Wilcoxon's $T = 102.00$, *ties* = 3, $n = 39$, $p = 0.0001$) (see Figure 3.3b).

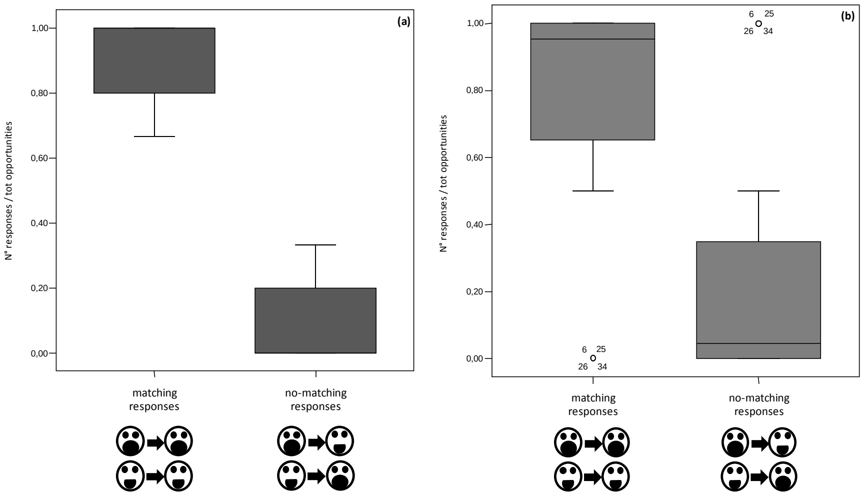

Figure 3.3a and 3.3b – Mirroring *vs* non-mirroring responses frequency in *Macaca fuscata* (a) and *Macaca tonkeana* (b). Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

3.3.3. *Prediction 3*: Rapid and Delayed Facial Replication

For both species we compared the frequency of congruent rapid facial replication (<1 s) and congruent delayed facial replication (1-5 s). In *Macaca fuscata* we found a significant difference, with congruent rapid response levels higher than congruent delayed response levels (Paired Samples T test: T=3.458, N=17, df=16, p=0.003) (see Figure 3.4a). On the contrary, *Macaca tonkeana* did not show any significant difference between rapid and delayed congruent responses (Paired Samples T test: T=0.644, N=39, df=38, p=0.524) (see Figure 3.4b).

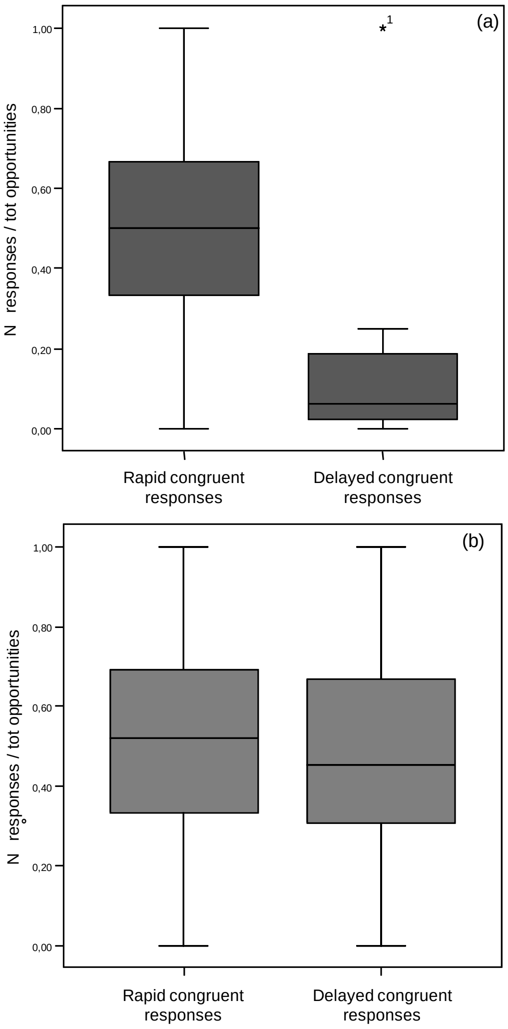

Figure 3.4a and 3.4b – Rapid congruent responses frequency *versus* Delayed congruent responses frequency in *Macaca fuscata* (a) and *Macaca tonkeana* (b). Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

3.4. DISCUSSION

In this study, we demonstrated that RFM is present in *Macaca fuscata* and *Macaca tonkeana* and that, for both species, facial replication functions only with specific playful facial expressions, such as PF or FPF (*Prediction 1* supported). The RFM mechanism failed to occur if the stimulus emitted by the trigger belonged to a category of unspecific playful signals, such as SR/BT (used in *Macaca fuscata* play) or LS/BT/TP/SR (used in *Macaca tonkeana* play). About the origin of PF and FPF, the main hypothesis is that they probably share a common origin with homologous facial expressions, such as human's smiles (Niedenthal et al., 2010). Human smile is the external manifestation of a positive emotional state and it is shared by many different human cultures (Sauter et al., 2010). The primate play face could, through RFM, evoke in the perceiver the same positive emotional state experienced by the trigger (Decety and Meyer, 2008; Mehu et al., 2007). During a playful session a positive feedback set up, determined by the mutual facial replication implemented by the players. Therefore, it is not surprising that these two playful signals are the only used for rapid facial imitation because they hold a positive emotional connotation that is probably perceived and self-evoked by both playmates (van Hooff and Preuschoft, 2003). As suggested by Pellis and Pellis (2009) the efficacy of the communication system during play is a fundamental prerequisite to avoid any misunderstanding, manage a playful interaction successfully, and promote social affiliation.

In support of this interpretation our data on the accuracy of RFM show that the frequencies of mirroring responses (PF-PF, FPF-FPF) are higher than frequencies of non-mirroring responses (PF-FPF, FPF-PF) for both species (*Prediction 2* supported). During play sessions, macaques not only replicated the display specific of the playful context, but they responded with the identical facial expression. This highly sophisticated kind of communication is common at the two species, mirroring the facial expression of others probably helps the players to synchronize their actions by anticipating the subsequent motor patterns. This process is easily understandable if we consider that the neural basis that macaques share includes mirror neurons system (Ferrari et al., 2006; Paukner et al., 2009; Rizzolatti et al., 2001). The mirroring capacity leads an animal to match also the same behaviour with that of others. This allows an individual to recognize behaviours by mapping the sensory information related to others on the own motor knowledge. The presence of imitation since the early days of life highlights the importance of the imitative phenomena in social and cognitive development (Ferrari et al., 2006). Such phenomena appear to be even more important later in life when an animal faces the need to identify the appropriate context in which an action should be performed. In humans, high levels of RFM are related to high levels of empathic behaviours showed by the subjects. There is experimental evidence that an impairment of mimic abilities provokes in the subject a reduced capacity of recognizing facial expressions and of experiencing the emotional state underpinning them (Stel and Knippenberg, 2008).

Finally, the main difference between the two macaque species resides in the levels of congruent rapid responses (within 1 sec) displayed in contrast with levels of congruent delayed responses (from 1 to 5 sec). The key to understand how the different social style influences the RFM mechanism seems to be related to the speed of the responses, with Tonkean macaques showing no difference between the two time domains, and Japanese macaques using more rapid responses during social play (*Prediction 3* supported). This difference can be ascribed to the different styles of social play the species adopt. In a comparative study involving the same species, Reinhart and collaborators (2010) found that Japanese macaque play is enriched of more competitive elements than that of Tonkean macaques. Moreover, in Japanese macaques adult social play is almost entirely performed by males (see Chapter 2) that are probably more interested than females in measuring others' and their own competitive abilities. When in play competition overcomes cooperation, the probability of misunderstanding would be higher. The high frequency of rapid mimicry in Japanese macaques seems to be a means to speed up the signal exchange, thus limiting the risk that the playful sessions could escalate into an overt aggression. The automatic response is characterized by a higher efficacy in communicating the intention of the player compared to the delayed response, probably due to the more spontaneous and immediate connotation of facial responses. On the other hand, when social play is more cooperative, as in Tonkean macaque play, a major use of congruent rapid responses does not seem essential. In this view, different social styles can affect not only play modality (competitive *vs* cooperative, symmetric *vs* asymmetric, rough *vs* gentle) but also the communication used to manage so different play moods. For this reason, studying communication in play can open a window on social cognition in animals.

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4.

“BEYOND HUMAN AND NON-HUMAN APES. TONKEAN MACAQUES CONSOLE THEIR FRIENDS”

(Elisabetta Palagi, Stefania Dall'Olio, Roscoe Stanyon)

submitted to PNAS

ABSTRACT

In many social species, conflicts have clear beginnings, but quite ambiguous endings. In some cases the victim can receive a friendly, spontaneous contact from a bystander not involved in the previous agonistic encounter. In the only two monkey species where it was found, unsolicited bystander affiliation appears to lack the consolatory function demonstrated for humans and great apes (in these species "consolation"). Here, we tested different hypotheses potentially predicting unsolicited bystander affiliation in macaques. We focused on two species placed at the opposite ends of a classification based on different social styles: *Macaca tonkeana* (tolerant) and *Macaca fuscata* (despotic). Due to this diversity, we expected to find the use of bystander affiliation as a post-conflict resolution mechanism in *Macaca tonkeana*, but not in *Macaca fuscata*. Our findings revealed striking differences in the use of bystander affiliation, with Japanese macaques never showing this post-conflict strategy. On the contrary, in Tonkean macaques bystander affiliation was frequent in absence of reconciliation, reduced victim's anxiety, and was mostly directed towards friends. Besides, it had a role in protecting the victims against renewed aggression. Thus, it seems that the Consolation Hypothesis, more than any other hypotheses formulated to explain the phenomenon, could explain the presence of this intriguing post-conflict mechanism in *Macaca tonkeana*.

Key-words: *Macaca fuscata*; *Macaca tonkeana*; third-party affiliation; consolation; victim protection; anxiety alleviation

4.1. INTRODUCTION

For social animals, including humans, aggression can have dramatic consequences not only for the two individuals involved but also for the whole group or community (Moynihan, 1998; Aureli and de Waal, 2000; Esteban et al. 2012; von Rohr et al. 2012). Conflict can generate further conflicts (Watts et al. 2000; Palagi and Cordoni, 2009; Barash and Lipton, 2011) and/or can affect the affinitive interactions among all group members (de Waal, 2000; De Marco et al. 2010; Ellemers 2012).

Since the pioneer work by de Waal and van Roosmalen (1979) much research was focused on conflict management in social animals. The most effective conflict resolution mechanism is reconciliation defined as affinitive interaction between former opponents in the first minutes after a fight (de Waal and van Roosmalen 1979; Palagi et al. 2008). Reconciliation reduces the probability of further attacks, limits anxiety in the victim, and act to restore the benefits associated with good relationships between the opponents (for a review see Aureli et al. 2002).

After a conflict the victim can also receive a friendly, spontaneous contact from a bystander not involved in the agonistic encounter (de Waal and van Roosmaleen, 1979; Palagi et al. 2008; Fraser et al. 2009; Romero et al. 2010). This first spontaneous post-conflict affinitive contact directed by a third party to the victim as documented for humans and great apes, was coined as consolation (chimpanzees, *Pan troglodytes*: Wittig and Boesch 2003, 2010; Kutsukake and Castles 2004; Palagi et al. 2006; Koski and Sterck 2007; Fraser and Aureli 2008; Fraser et al. 2008; Romero and de Waal, 2010; gorillas, *Gorilla gorilla*: Cordoni et al. 2006; Mallavarapu et al. 2006; bonobos, *Pan paniscus*: Palagi et al. 2004; humans, *Homo sapiens*: Fujisawa et al. 2006; Burleson 1983; Eisenberg 1992). The terms “consolation” or “comfort” include a hypothesis about the function of the post-conflict mechanism as distress alleviation. For this reason, non-human primate scholars prefer to use a less value-laden term as “unsolicited bystander affiliation” when referring to this type of post-conflict affiliation (Call et al. 2002).

To demonstrate the occurrence of unsolicited post-conflict affiliation in monkeys, de Waal and Aureli (1996) applied to macaques the same observation protocol used for apes (*Macaca fascicularis, M. fuscata, M. sylvanus, M. nemestrina*), but the researchers failed to find any evidence for this kind of post-conflict affiliation. Further investigations in other catarrhines also failed to reveal unsolicited bystander affiliation (*M. fascicularis, M. mulatta, M. arctoides, M. fuscata, M. sylvanus, Chlorocebus aethiops*, *Erythrocebus patas, Papio anubis, P. hamadryas* Watts et al. 2000; Schino et al. 2004). In the only two monkey species where it was found, bystander affiliation appears to lack consolatory function (*Macaca arctoides,* Call et al. 2002; *Mandrillus sphinx,* Schino and Marini 2012). Outside of primates, third-party affiliation towards victims was observed in rooks, *Corvus frugilegus* (Seed et al. 2007), ravens

(*Corvus corax*, Fraser and Bugnyar, 2010), dogs (*Canis familiaris*, Cools et al. 2008), and wolves (*Canis lupus*, Palagi and Cordoni, 2009). However, in all these cases there was no evidence of consolation. To date, only chimpanzees, bonobos, and humans appear to provide distress alleviation in conspecifics (consolation, Fraser et al. 2008; Palagi and Norscia, under review; comfort, Zahn-Waxler and Radke-Yarrow 1990).

Here, we focussed on unsolicited third-party affiliation towards victims (hereafter, third-party affiliation) in *Macaca tonkeana* and *Macaca fuscata*. The 20 species of the genus *Macaca* are phylogenetically closely related and all are organized in multi-male, multi-female social groups that vary on a gradient ranging from more intolerant (despotic, Grade 1) to more tolerant (egalitarian, Grade 4) social systems [Matsumura 1999; Thierry 2000]. These differences in social styles influence a wide range of behaviours including aggression and affinitive patterns, dominance relationships, and nepotism [Thierry 1985; 1990; de Waal and Luttrell 1989; Aureli et al. 1997; Petit et al. 1997]. Despotic species like Japanese macaques (*Macaca fuscata*) have a strong, kin-centric power asymmetry between dominants and subordinates, marked submission behaviours, unidirectional conflicts, and low levels of social tolerance [Aureli et al 1997; Kurland 1977; Kutsukake and Castles 2001]. Whereas egalitarian species, such as Tonkean macaques (*Macaca tonkeana*), have relationships which are minimally influenced by social rank and kinship. No formal indicators of subordination are present and the proportion of friendly interactions among non-kin is relatively high [Butovskaya and Kozintsev 1996; Preuschoft and van Hooff 1997; Butovskaya 2004]. Different from Japanese macaques [Schino et al. 2004], conflict resolution mechanisms such as reconciliation, quadratic affiliation, and peaceful interventions are common occurrences in Tonkean macaques [Thierry, 1985; Petit and Thierry, 1994; De Marco et al., 2010; Demaria and Thierry, 2001; Ciani et al. 2012]. For these reasons we might expect to find third-party affiliation in *Macaca tonkeana* and to confirm its absence in *Macaca fuscata* (Prediction 1). Moreover, we expect that in *Macaca tonkeana* third-party affiliation towards victims functions as a substitute of reconciliation when it fails to occur (Wittig and Boesch, 2010; Palagi et al. 2004; Palagi and Cordoni 2009; Romero et al. 2010; Fraser and Aureli, 2008; Fraser et al. 2008) (*Substitute of reconciliation hypothesis*; Prediction 2).

The *Self-Protection Hypothesis* (direct benefits for the bystander) predicts that third party affiliation protects the bystander from redirected aggression (chimpanzees: Wittig and Boesch, 2010; mandrills: Schino and Marini 2012). In order for this function to be in place, redirection should be common and affiliation should be received primarily from individuals that are frequently the target of redirection and from individuals ranking lower than the victim (presumably more at risk). If in Tonkean macaque third-party affiliation functions in protecting the bystander by redirection, we expect high levels of redirection in this species (Prediction 3). If Prediction 3 will be supported, we also expect that bystanders offering contact to the victims are those individuals ranking lower than the victim and/or those receiving the highest levels of redirection (Prediction 4).

One of the benefits of third-party affiliation can derive from a lowered probability for the victim to receive further aggressions by other group members (*Victim Protection Hypothesis*). However, the effect of third-party affiliation in reducing renewed aggressions has been tested for all group members (overall conflict levels) to assess the *Tension Reduction Hypothesis* (in chimpanzees: Palagi et al 2006), for the bystander to verify the *Self-Protection Hypothesis* (chimpanzees: Wittig and Boesch, 2010; mandrills: Schino and Marini 2012), but never for the victim as a part of a possible victim-protection function. Therefore, the next step of our research was to investigate if third-party affiliation protects the victim against further conflicts (*Victim Protection Hypothesis*) and/or if it has a role in reducing the spreading of aggression to the whole group (*Tension Reduction Hypothesis*). If third-party affiliation functions to protect the victim (*Victim Protection Hypothesis*), we expect it to significantly reduce the probability of renewed attacks on him/her (Prediction 5). If third-party affiliation reduces tension at group level (*Tension Reduction Hypothesis*) and limits the risk of bystanders to be involved in a subsequent conflict, we expect it to significantly reduce the probability of aggression among all group members (Prediction 6), with an indirect benefit for the bystander. We need to underline that the *Victim Protection* and *Tension Reduction Hypotheses* are not mutually exclusive.

The final step of this work was to test for the consolatory function of the third-party affiliation (*Consolation Hypothesis*). If the *Consolation hypothesis* explains the presence of third-party affiliation in Tonkean macaques, we expect third-party affiliation should console the victim by reducing him/her anxiety (measured by scratching levels) (Prediction 7) and it should be primarily received from friends (i.e. individuals frequently exchanging grooming) (Prediction 8).

4.2. METHODS

4.2.1. Subjects and Housing

Behavioural data were collected on a group of *Macaca tonkeana* (Parc Zoologique de Thoiry, France) and on a group of *Macaca fuscata* (Olomouc Zoo, Czech Republic).

The colony of Tonkean macaque was composed of 30 adult males, 31 adult females, and 9 immature subjects (1-4 years of age). The animals were housed in an enclosure with both indoor and outdoor facilities (182 m2 and 3900 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 AM and 6.00 PM and water was available *ad libitum*. Data were collected from August to October 2010 and from August to October 2011.

The colony of *Macaca fuscata* was composed of five adult males, eight adult females, and 12 immature subjects (ranging from one to four years of age). Animals were housed in a large enclosure, about one half a hectare of pine trees forest enriched with ropes, wooden structures, shelters, and a natural stream. Food was distributed twice a day at 8.30 AM and 2.30 PM and water was available *ad libitum*. Data were collected from June to July 2010.

4.2.2. Data Collection

Individual identification was based on sex and other distinctive external features such as scars, size, missing fur patches, fur colour and facial traits. Prepubertal individuals (infants and juveniles) were labelled as immatures, while fertile and sexually active subjects were labelled as adults. Three observers collected data by using a tape recorder and a video camera. All occurrences sampling, focal-animal sampling (Altmann 1974) and Post-Conflict/Match-Control observations (PC-MC, de Waal and Yoshihara 1983; Kappeler and van Schaik 1992) were used concurrently to collected data on adult subjects.

To limit the influence of visitors, the observations were conducted during working days avoiding holidays and weekends. Each observation day lasted 8 hs, encompassing both morning and afternoon. Before starting systematic data collection, the observers underwent a training period (90 hs). During the training phase (the trainer was S.D.), the same focal animal was followed by the observers simultaneously, and the data were then compared. Training was over when the observations produced a Cohen's kappa higher than 0.70 (Kaufman and Rosenthal 2009). We checked for observation reliability at the beginning of each month obtaining values never below 0.70.

We gathered data via focal animal sampling collecting about 547 hs (individual mean 8.96 ±1.41 SE) for *Macaca tonkeana* and about 96 hs (individual mean 7.30 ± 0.52SE) for *Macaca fuscata.*

Each individual was followed as the focal animal every day and at different times of the day in order to obtain data covering the entire day in a balanced proportion. Using focal sampling we recorded all affinitive (grooming, proximity, contact sitting, play, touching, food sharing, co-feeding), self-directed (selfgrooming, scratching, yawning) and neutral behavioural patterns (sitting alone, walking alone, feeding, foraging, resting) performed by animals.

Via all occurrences sampling (1,248 hs for *Macaca tonkeana* and 326 hs for *Macaca fuscata*) we recorded all aggressive encounters and specifically (1) victim's and aggressor's identity (2) intensity (high-intensity conflicts, which included physical contact between opponents - slapping, biting, pulling, pushing - and low-intensity conflicts, which did not include any physical contact between opponents - threatening, chasing, fleeing) and (2) outcome (decided conflicts were characterized by the absence of any sort of retaliation or counterattack by the victim; undecided conflicts were characterized by victim counterattack).

After the last aggressive act of any given agonistic event, we followed the victim as the focal individual for a 5 min post-conflict period (PC). Control observations (MCs) took place on the next possible day at the same time as the original PC, on the same focal animal, in the absence of agonistic interactions during the 5 min before the beginning of MC and when the opponents had the opportunity to interact (less than 15 m) (de Waal and Yoshihara 1983). For both PCs and MCs we recorded 1) starting time (minute), 2) type of the first affinitive contact, 3) initiator of the first affinitive behaviour (grooming, contact sitting, touching, sharing food and playing) and 4) partner identity. A third party was defined as any individual other than the victim and the aggressor. If the focal animal went out of sight during the PC or MC periods, those observations were discarded from the analysis.

4.2.3. Data Analysis

To verify the occurrence of post-conflict contacts initiated by bystanders, we used the method pioneered by de Waal and Yoshihara (1983). For each animal we determined the number of attracted, dispersed and neutral pairs over all PC-MC pairs. In attracted pairs, affinitive contacts occurred earlier in the PC than in the MC (or they did not occur at all in the MC), whereas in dispersed pairs the affinitive contacts occurred earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occurred during the same minute in the PC and the MC, or no contact occurred in either the PC or the MC. To avoid coding the same incident twice, for each individual we used only PC-MC pairs in which that individual was the focal animal. As a measure of third-party affiliation we used Third-party Contact Tendency (TCT), which is equal to the numbers of attracted pairs minus the numbers of dispersed pairs divided by the total number of pairs.

To evaluate which behaviour is preferentially used in third-party affiliation, via the same methodology we calculated TCTs for the three different clusters of post-conflict third-party affiliations (cluster 1 - grooming, contact sitting, touching and playful contacts; cluster 2 - sexual contacts; cluster 3 - kiss, mouthing, face sniffing, cheek-to-cheek, holding face). For each cluster we scored an attracted pair when any of the behaviours belonging to that cluster occurred earlier in the PC than in the MC period and, conversely, a dispersed pair when they occurred first in the MC period.

Scratching was recorded as a behavioural measure of anxiety experienced by the subject (Aureli and de Waal 1997, Baker and Aureli 1997, Maestripieri et al. 1992, Troisi 2002; Palagi and Norscia, 2011; Sclafani et al., 2012). We defined scratching as a repeated movement of the hand or foot during which the fingertips are drawn across the individual’s fur. A new scratching bout was assigned when the scratched body part changed, or when scratching was resumed after more than 5 s.

We used Friedman’s test to compare scratching rates during three conditions: PC-no contact (absence of third-party affiliation), PC-contact (presence of third-party affiliation) and MC (Matched Control). In case of significance across the three conditions, we ran the Dunnett's multiple comparison test (post-hoc test) to determine which pairs of conditions differed significantly (Siegel and Castellan, 1988). We excluded from the analysis those events of triadic unsolicited contacts, which were preceded by conciliatory (reconciliation) or triadic affiliation actively requested by the victim.

Via Linear Mixed Model (LMM) we evaluated which factors could explain the variation in the frequency of third-party contacts. The frequency of third-party affiliation was calculated as the number of contacts normalized on the number of opportunities. Opportunities equalled the number of PCs in which one individual was the victim, excluding those in which third-party was involved in the conflict as aggressor. Data entered into analysis were relative to the individual PC-MC observations. The third-party affiliation frequency was the dependent variable. Moreover, we considered the following factors: intrinsic features of dyad’s member (rank and sex) and relationship quality between dyad’s members: strong (friends), medium, and weak. Third-party's and victim's rank, their gender and relationship quality were entered as fixed variables (Table 1).

To determine the ranking position of each subject we calculated the frequency of aggressions in which that subject was the victim on the total number of aggressions in which that subject was involved. For this distribution, three rank levels were recognized: high (if an animal’s position fell into the upper quartile), medium (if an animal’s position fell into the inter-quartile) and low (if an animal’s position fell into the lower quartile).

Since for our sample kin relationships were unknown, we categorized the affiliation levels between dyads using grooming levels collected during focals (excluding PCs and MCs) and calculating the quartile points of dyadic scores for each focal individual. Dyads with scores falling into the upper quartile were considered as strongly bonded (friends) and those with scores falling in the inter-quartile were considered as medium bonded. All the other dyads were labelled as weakly bonded.

Third party and victim identities were entered as random factors (nominal variables). We tested models for each combination involving the variables of interest (see Table 4.1), spanning from a single-variable model to a model including all the fixed factors (full model). To select the best model, we used Akaike's Corrected Information Criterion (AICc), a measure for comparing mixed models based on the -2 (Restricted) log likelihood. The AICc corrects the Akaike's Information Criterion (AIC) for small sample sizes. As the sample size increases, the AICc converges to AIC. The model with a lower value of AIC was considered to be the best model.

Table 4.1 – Description of the variables used in LMM analysis

NAME	TYPE
DEPENDENT VARIABLE	
Frequency of triadic unsolicited affiliation	Scale (positive integer values)
FIXED EXPLANATORY VARIABLES	
Individual characteristics	
Victim's and Third Party's Rank	Ordinal (1=high; 2=medium; 3=low)
Victim's and Third Party's Gender	Ordinal, dichotomous (1=male; 0=female)
Relationship characteristics	
Relationship quality	Ordinal (1=weakly bonded individuals; 2= medium bonded individuals; 3= strongly bonded individuals - friends)
RANDOM VARIABLES	
Victim's and Third Party's Identity	Nominal

To assess if third-party post-conflict affiliation can be considered as a substitute of reconciliation, we divided the PCs according to the presence or absence of reconciliation and, subsequently, according to the presence or absence of third-party contacts. Then, we used Wilcoxon matched-pairs signed-ranks test to compare the frequency of triadic contacts in absence and presence of previous conciliatory contacts.

In order to test whether third-party affiliation protects victims against further attacks or has a role in limiting the spreading of aggression within the social group, we compared the frequency of further aggressions (attacks towards the victim or among group members after the previous fight) in presence or absence of triadic affiliation. Only the events not characterized by reconciliation were considered for this analysis.

Nonparametric statistics was applied when the distribution of a given dataset deviated from normality (Kolmogorov-Smirnov $P < 0.05$). The level of significance was set at 5% for all the analysis. All the statistical tests were two tailed. Statistical analyses were performed using Microsoft Excel and SPSS 12.00 (SPSS Inc., Chicago, IL, U.S.A.).

4.3. RESULTS

Prediction 1

We focused on adult subjects as victims collecting a total of 876 PC-MC for Tonkean macaques and 148 PC-MC for Japanese macaques. We analyzed every possible third-party contact between victims and third parties. We entered into the analysis only those subjects who had at least five PC-MC during which reconciliation did not take place (N=43 for Tonkean and N=10 for Japanese macaques). In *Macaca tonkeana*, attracted pairs were significantly more frequent than the dispersed pairs (Paired samples t-test: t=6.266, N=43, df=42, p=0.0001; mean TCT = 21.36 ±3.6 SE) (Figure 4.1b); whereas, no significant difference was found for *Macaca fuscata* (Wilcoxon signed-ranks test: T=2.50, N=13, ties=8, p=0.157; mean TCT = -0.1% ±4.4 SE) (Figure 4.1a) (Prediction 1 supported).

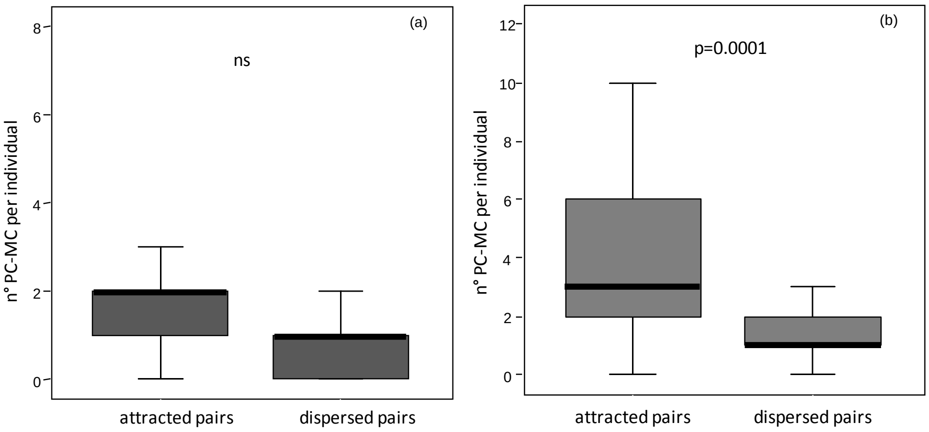


Figure 4.1a and 4.1b – Number of attracted versus dispersed pairs for *Macaca fuscata* (a) and *Macaca tonkeana* (b).

Substitute of reconciliation hypothesis

Prediction 2

To examine the time association between reconciliation and third-party affiliation, we counted how many triadic contacts occurred in absence/presence of reconciliation, normalizing data on the total PCs for each individual. The minimum PC number required for each animal to be included in the analysis was five. The test revealed that third-party affiliation was more likely in absence of reconciliation (mean 0.246 ±0.026 SE) than when it was present (mean 0.096 ±0.015 SE) (Wilcoxon signed-ranks test: T=136, N=52, ties=9, p=0.0001) (Prediction 2 supported).

Self-Protection Hypothesis

In the group of *Macaca tonkeana*, redirection was virtually absent with 52 on 61 victims never redirecting an attack against a bystander (individual mean 0.028 ±0.017 SE) (Prediction 3 and 4 not supported).

Victim Protection Hypothesis

To understand if third-party affiliation has a role in victim protection, we calculated the frequency of further aggression directed towards the victim (in absence of reconciliation) according to the presence/absence of third-party affiliation. We found that the presence of triadic contacts significantly reduced the probability of further attacks against the victim (Wilcoxon signed-ranks test: T=-3.934, N=43, ties=21, p=0.0001) (Figure 4.2a; Prediction 5 supported).

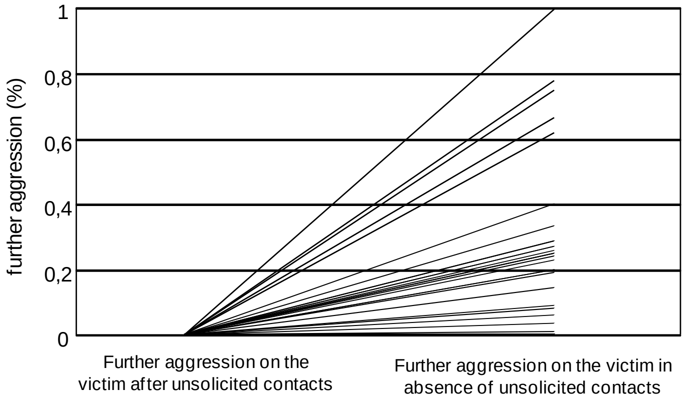


Figure 4.2a - Frequency of further aggression directed towards the victim after a conflict (in absence of reconciliation), according to the presence/absence of third-party affiliation.

Tension Reduction Hypothesis

We wanted to substantiate if third-party affiliation played a role in limiting the spreading of aggression and, therefore, limiting the risk of bystanders to be involved in a subsequent conflict. Consequently, we calculated the probability of further aggression among other group members (excluding the victim) according to the presence/absence of third-party affiliation. We did not find any significant difference between the rates of further aggression among other group members in the presence or in the absence of third-party affiliation (Wilcoxon signed-ranks test: T=-1.739, N=43, ties=11, p=0.12) (Figure 4.2b; Prediction 6 supported).

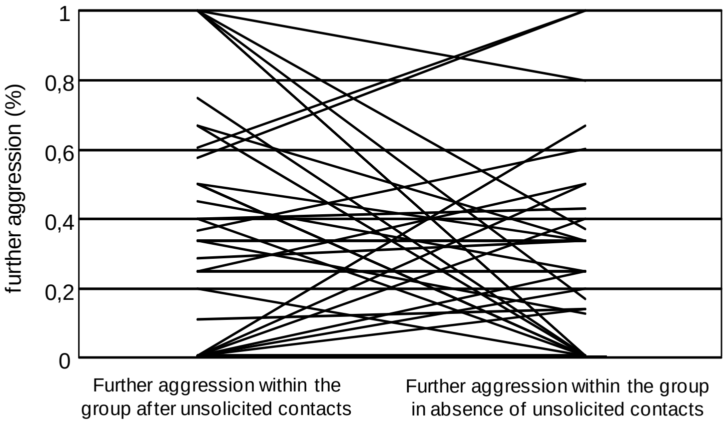


Figure 4.2b – Frequency of further aggression among group members (excluding the victim) after a conflict, according to the presence/absence of third-party affiliation.

Scratching rates were significantly different across the three conditions: without contacts (PC-no contact), following third-party contacts (PC-contact), and matched-control (MC) (Friedman: Chi-square=7.885, N=37, df=2, p=0.019). We found that scratching rates in PC-contact did not differ from those in MC (Dunnett's test: q=0.183, df=2, N=37, n.s.). Both scratching rates in PC-contact and in MC were significantly lower than those recorded in PC-no contact (PC-contact vs PC-no contact: Dunnett's test: q=4.379, df=2, N=37, p<0.001; MC vs PC-no contact: Dunnett's test: q=3.223, df=2, N=37, p<0.01) (Figure 4.3). This analysis was focused on those subjects, which we could observe in all the three conditions (N=37) (Prediction 7 supported).

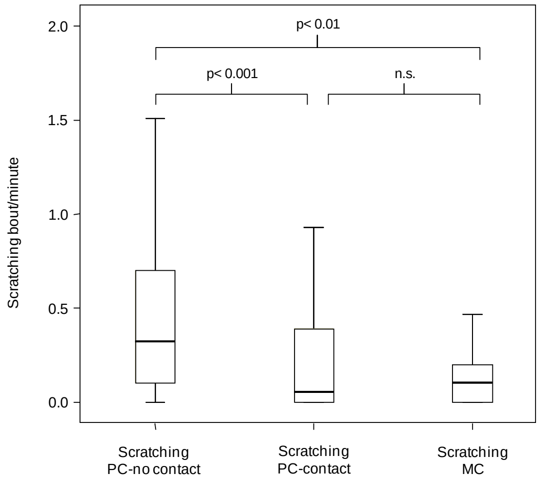


Figure 4.3 - Scratching rates in *Macaca tonkeana*: without contacts (PC-no contact), following third-party contacts (PC-contact), and matched-control (MC).

Prediction 8

We evaluated which variables could explain the distribution of third-party affiliation via Linear Mixed Model (LMM) (Table 1). Victim and third-party sex, rank, and relationship quality were entered as fixed factors. This analysis included subjects who had more than 3 opportunities for contact after the conflict. The best model (AICc=-497.333) included the relationship quality and the victim's rank (Table 4.2).

Table 4.2 – Best LMM explaining the occurrence of triadic unsolicited affiliation (AICc = -497.333)

	Numerator df	**Denominator df**	**F**	**Significance level**
Intercept	1	40.577	210.24	0.0001
FIXED FACTORS				
Relationship quality	2	113.834	8.461	0.0001
Victim’s rank	2	37.641	4.323	0.020
RANDOM FACTORS	**Variance**	**SE**		
Victim’s identity	0.002221	0.000605		
Responder’s identity	0.000000	0.000000		

df: degrees of freedom; SE: standard error

Relationship quality positively affected the frequency of third-party affiliation (number of triadic post-conflict contacts/number of opportunities), which increased alongside the tightness of the social bonding (Figure 4.4).

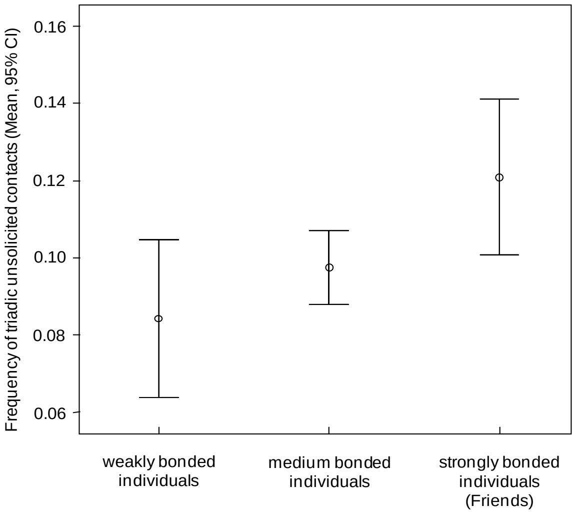


Figure 4.4 – Frequency of triadic affinitive contacts in respect of the relationship quality between victim and bystander (weakly, medium and strongly bonded individuals).

Moreover, third-party affiliation was higher when the victim occupied a high-ranking position (Figure 4.5).

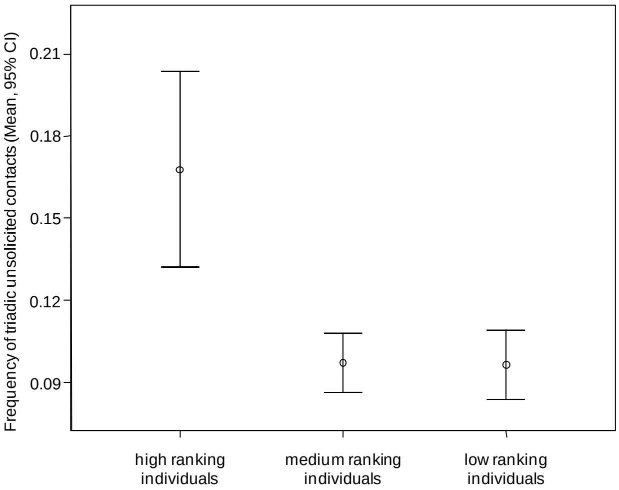
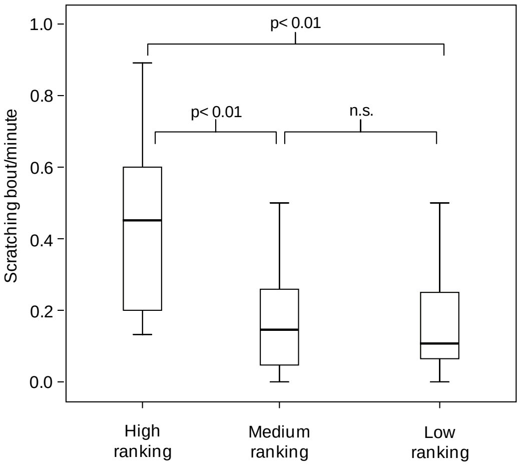
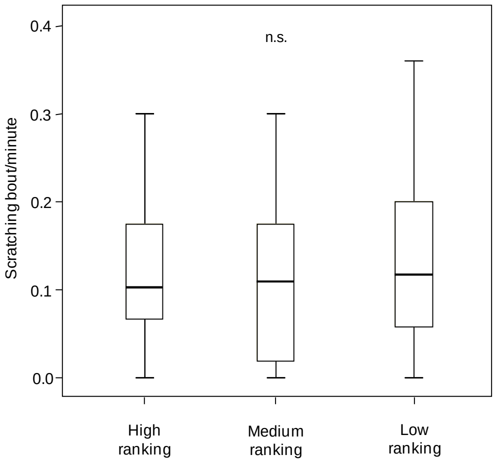


Figure 4.5 – Frequency of triadic affinitive contacts in relation to the victim's rank (high, medium and low ranking individuals).

During the period PC-no contact (absence of any kind of affinitive interactions after the aggression), high-ranking subjects showed higher scratching levels than medium and low-ranking conspecifics (Kruskal-Wallis Chi-square=12.662; N_{high}=13; N_{medium}=23; N_{low}=13; df=2; p=0.002; N_{high} vs N_{medium}, Dunn test Q=3.213, p<0.01; N_{high} vs N_{low}, Dunn test Q=3.023, p<0.01; N_{medium} vs N_{low}, Dunn test Q=0.289, n.s.) (Figure 4.6a). The difference in the scratching levels according to ranking position disappeared under the MC condition (Kruskal-Wallis Chi-square=0.471; N_{high}=13; N_{medium}=23; N_{low}=13; df=2; p=0.790) (Figure 4.6b).

Figure 4.6a and 4.6b – Scratching rates for high, medium and low ranking victims after a conflict without triadic contacts (a) and in presence of triadic contacts (b).





4.4. DISCUSSION

In this research we discovered for the first time in a catarrhine monkey species (*Macaca tonkeana*), that third-party affiliation can provide comfort to recipients of aggression. Our findings could allow us to use the term "consolation", instead of third-party affiliation, not just for human- and non-human apes, but also for a monkey species.

Macaca fuscata and *Macaca tonkeana* differ strikingly in the use of third-party affiliation, with Japanese macaques never showing this post-conflict strategy (Prediction 1 supported). In *M. tonkeana*, third-party affiliation reduces anxiety in the victims when reconciliation does not occur (Prediction 2 and 7 supported). Further third party-affiliation protects the victim against further conflicts (Prediction 5 supported), and is mostly directed towards friends (Prediction 8 supported). It does not seem that third-party affiliation has any effect in reducing the likelihood of further attacks among group members (Prediction 6 not supported) or it has any role in limiting redirection by the victim (Prediction 3 and 4 not supported). All these factors make it difficult to not acknowledge that third-party affiliation has a consolatory function in *M. tonkeana*.

In many social species, conflicts have clear beginnings, but quite ambiguous endings. Reconciliation is a means to end the conflict and restore the relationship between former opponents (Aureli et al. 2002). In Tonkean macaques, consolation occurred more frequently in absence of reconciliation, suggesting that the potential consolers are sensitive to the need of the victim to be contacted after an aggression, especially if the previous agonistic event is not formally resolved and the victim, a friend, is still suffering anxiety (Romero et al. 2010).

Since third-party affiliation does not reduce the probability of further aggression among other group members (including the "potential consoler"), the focus of the consolatory act does not seem to be the group, but the victim. Consolation reduces the probability of the victim to be attacked again and, therefore, could directly reduce the victim's anxiety. As required by the consolation hypothesis the action is predominately directed towards friends. Whether in *Macaca tonkeana* consolation produces any direct benefits for the consoler remains unclear, because we do not know if the actor is aware or can potentially learn about the long-term consequences of its action (de Waal and Suchak, 2010). However, even assuming that animals are capable of understanding long-term consequences, they have no way to know if the favour will be repaid in the future.

Our data on *Macaca tonkeana* also show that consolation is not only directed towards friends, but also towards high-ranking individuals. Romero et al. (2010) suggested that dominant chimpanzees may suffer higher levels of anxiety when losing to a subordinate. Indeed, our analysis revealed that high-ranking macaques suffer significantly more post-conflict anxiety than medium- and low-ranking individuals (Figure 4). Even though we cannot exclude that consolation can also provide benefits to the consoler, we can nevertheless hypothesize that the potential consolers are sensitive to the greater distress experienced by dominant subjects. The reduction of anxiety has been considered as one of the most informative parameters to interpret consolation as a possible expression of sympathetic concern in apes (Fraser et al., 2008; Romero et al. 2010). Some scholars ascribed the absence of consolation in monkeys to the different cognitive and empathic abilities characterizing them in respect to apes (de Waal and Aureli, 1996; Watts et al. 2000, Schino et al. 2004). In stump-tailed macaques, Call et al. (2002) documented the presence of third-party affiliation, which seems to have a purely appeasement function. Recently, a similar result has been found in *Mandrillus sphinx* (Schino and Marini, 2012) where third-party affiliation seems to protect bystanders from victims' redirections. One of the possible explanations of why consolation in *Macaca tonkeana* is beneficial to the victim can be attributed to the peculiar inter-individual relationships of this species (Matsumura 1999; Thierry 1985, 1990; de Waal and Luttrell 1989; Aureli et al. 1997; Petit et al. 1997). Compared to all the other macaque species in which third-party affiliation has been investigated, Tonkean macaque is the only species which belongs to the most egalitarian level (Grade 4) (Thierry 2000; De Marco et al. 2010).

In order for cognitive and empathic capacities of a species to emerge through the expression of a behavioural mechanism, specific social conditions might be needed to favour such a mechanism. For this reason, investigating behavioural patterns driven by certain, even basic forms of empathy (Preston and de Waal, 2002) requires the choice of an appropriate species. In conclusion, we suggest that M. tonkeana might be a good model to investigate the evolution of the empathic abilities in order to understand the full phylogenetic range of this intriguing phenomenon.

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5. CONCLUSIONS

Individuals influence each other through social interactions. Due to the presence of social constraints, the evolutionary processes can facilitate the origin of some behavioural patterns whereas others are not favoured (Thierry, 1997). The covariation hypothesis states that any significant variation in a single character induces a set of correlated changes in social organization (Petit et al., 2008; Thierry et al., 2000).

The twenty macaques species represent a monophyletic group (Delson, 1980; Morales and Melnick, 1998). The species of this genus were classified based on patterns of aggression, reconciliation, affinitive, dominance relationships, and nepotism along a 4-grade scale continuum (Thierry 1985, 1990, 2000; de Waal and Luttrell, 1989; Aureli et al., 1997; Petit et al., 1997). Grade 1 species such as rhesus and Japanese macaques are characterized by rigid, despotic social systems in which most conflict are unidirectional, high-intensity aggression is common, reconciliations are infrequent and nepotism is rampant (Thierry 1985a, 1990, 2000; de Waal and Luttrell, 1989; Aureli et al., 1993; Butovskaya, 1993; Chaffin et al., 1995; Petit et al., 1997; Schino et al., 1998; Kutsukake and Castles, 2001). On the other hand, the Sulawesi macaques such as Tonkean macaques are at the opposite end of the continuum, in grade 4. Here the majority of conflicts are bidirectional, with most aggressive acts inducing protests or counter-attacks. Species from grades 4 display high rates of specific affinitive contacts like clasps and embraces, and they are characterized by the development of special behaviours that reduce social tension and facilitate social contact (Thierry, 1984; de Waal, 1989; de Waal and Luttrellk, 1989; Matsumura, 1991; Abegg, 1998).

To understand how evolutionary processes shape the primate societies we need to trace the patterns of their social organization back to the behaviour of individuals. To help fill this gap the aim of this thesis was to analyze and compare social behaviours that can be influenced by social tolerance, using as models two species located at the opposite sides of the classification proposed by Thierry (2000): *Macaca fuscata* (grade 1) and *Macaca tonkeana* (grade 4). In fact, behaviours based on basic forms of empathic abilities (like consolation and facial imitation mechanism) and social activities like play can be modulated in different ways in relation to different social styles, but this topic has not been fully investigated before.

Play is a highly plastic and versatile behaviour (Pellis and Pellis 2009) that can be modulated by the nature of inter-individual relationships of a species. The data generated in this thesis support the hypothesis that the degree of tolerance of a species can influence adult and immature play frequency and distribution. Immature Tonkean macaques had higher social play levels than immature Japanese macaques (see Chapter 2, Ciani et al., 2012) showing that there is a clear ontogeny of play influenced by the social milieu. The more fluid and flexible relationships typical of the egalitarian societies compared to the despotic societies (Pellis and Iwaniuk 2000; Thierry et al. 2000; Butovskaya 2004) probably influence the degree of mothers' permissiveness. As proposed by Maestripieri (2004) the degree of mother intolerance covaries across the diverse macaque species as a function of the difference in the quality of female relationships. Females of the most despotic and nepotistic species are often described as highly protective with their offspring, thus inhibiting contacts between their own infants and other group members (Maestripieri 1994; Thierry 2004). This inhibitory control provokes a limitation of the relational sphere of the infant, thus creating the conditions for an increased social canalization (Berman 1982) that can result in a more limited propensity to play also later in life. Data on macaques can show striking parallelisms with those coming from different human cultures (Eisenberg 1990; Hewlett and Boyette, 2012). Similarly to the Tonkean macaques, social style in hunter-gatherer populations show high levels of mobility, small population size, minimal gender and age hierarchy. Parents leave their infants free to play and to interact with other group members independently from kinship and age (Gray 2009; Hewlett et al. 2011). In these societies, childcare and education are structured to maximize a child's opportunities for play and to minimize any sense of being dominated by adults (Hewlett et al. 2011). In contrast, a similarity between Japanese macaque society and farmers ethnies can be found in the existence of various forms of hierarchy such as gender or age inequality, a strong control over infants which are strongly discouraged from playing together. By increasing child play opportunities, hunter-gatherers allowed their children to develop fully the characteristics of personal autonomy that are essential to hunter-gatherer success, especially cooperation and sharing with others.

Moreover, in those animal societies characterized by egalitarian relationships, there is less selection in choosing a play partner as a function of age (Palagi and Paoli, 2007). Our findings on the player age-selection in the two macaque species supports this conclusion. Adult Tonkean macaques did not show any preference between adult and immature playmates; whereas, adult Japanese macaques rarely played together and selectively chose immature subjects as play partners (see Chapter 2, Ciani et al., 2012). The same findings were obtained for the two *Pan* species, bonobos and chimpanzees. In the more egalitarian species, the bonobo, adults play with other adults as much as with infants and juveniles of the group; on the other hand, play in adult chimpanzees is strongly canalized in favour of immature subjects (Palagi and Paoli, 2008). As a whole, these findings on non-human primates strongly suggest that a covariation between adult-adult play propensity and the degree of tolerance characterizing a given society and human primates are not exceptions.

Our findings on gender differences in adult social play practices support the covariation hypothesis for the genus *Macaca* (Thierry et al. 2000). We found a difference in social play distribution between adult males and females in *M. fuscata*, where the former played more than the latter. In contrast, no gender difference in play propensity was found for *M. tonkeana*. To explain this result we propose that Tonkean macaques have features in common with other species in which adults play: i) fluid social organization (*Ateles* sp., *Cacajao* sp., *Pan paniscus*, Pellis and Iwaniuk 2000; *Crocuta crocuta*: Fagen 1981; *Tursiops truncatus*: Kuczaj et al. 2006), ii) high levels of tolerance with reduced hierarchical steepness (*Propithecus verreauxi*: Antonacci et al. 2010; *Pan paniscus*: Palagi 2006), and iii) alliances and cooperative behaviour (*Canis lupus*: Cordoni 2009; *Callithrix jacchus*: Norscia and Palagi 2011; *Theropithecus gelada*: Mancini and Palagi, 2009). The difference in the adult play between the two species has to be ascribed to the diverse play levels characterizing the adult females. In fact, Tonkean macaque females played significantly more than Japanese macaque females, whereas no difference was found between males of the two species (see Chapter 2, Ciani et al., 2012). It is worth noting that the role of females in these animal groups is central for social group cohesion (*Propithecus verreauxi*: Jolly 1966; *Theropithecus gelada*: Dunbar and Dunbar 1975; *Pan paniscus*: Kano 1982; Furuichi 2011; *Canis lupus*: ; Mech 1970; Cordoni and Palagi 2008; *Callithrix jacchus*: Snowdon and Cronin 2007; *Crocuta crocuta*: Drea and Frank 2003; *Tursiops truncatus*: Wells 2003; *Homo sapiens*: Hewlett et al. 2011). It seems, therefore, that the fluid social organization, the absence of strong sex-based hierarchical structure, and the presence of cooperative and tolerant interactions favour male and female role equality, which is evident in the sex distribution of adult play activity. Therefore, we can conclude that adult-adult play across species is mainly shaped by the similarity in the nature of their inter-individual social relationships rather than by their phylogenetic closeness (Pellis and Iwaniuk 2000).

The role of signals as intentional communication systems can be investigated through behaviours usually put to use during playful activity (Palagi, 2009; Palagi and Mancini, 2011). Information exchanged during play sessions can be helpful in enhancing social competence, promote the creation and development of social bonds, and increase tolerance levels that in turn affect conflict management. Our data on the presence of Rapid Facial Mimicry (RFM) indicate that it is a mechanism used by both macaque species but only for specific playful facial expressions (play face, PF or full play face, FPF) (see Chapter 3). During a playful session a positive feedback set up, is determined by the mutual facial replication implemented by the players. Therefore, it is not surprising that these two playful signals are only used for rapid facial imitation because they hold a positive emotional connotation that is probably perceived and self-evoked by both playmates (van Hooff and Preuschoft, 2003). This process failed to occur if the stimulus emitted by the trigger was a signal used during playful sessions but not specific to this context. As suggested by Pellis and Pellis (2009) the efficacy of the communication system during play is a fundamental prerequisite to avoid any misunderstanding, manage a playful interaction successfully, and promote social affiliation.

Moreover, both species responded with the identical facial expression (*mirroring responses*) to the stimulus emitted by a playmate suggesting an elevated accuracy of RFM (see Chapter 3). Mirroring the facial expression of others probably helps the players to synchronize their actions by anticipating the subsequent motor patterns. This process is easily understandable if we consider that the neural basis. Macaques share the mirror neurons system (Ferrari et al., 2006; Paukner et al., 2009; Rizzolatti et al., 2001), which seems to be at the basis of the development of emphatic abilities. The mirroring capacity leads animals to match their behaviour with that of others. This allows individuals to recognize behaviours by mapping the sensory information on the own motor knowledge. The presence of imitation in macaques from the earliest days of life highlights the importance of the imitative phenomena in social and cognitive development (Ferrari et al., 2006) in these species. Such phenomena appear to be even more important later in life when an animal faces the need to identify the appropriate context in which an action should be performed.

Finally, Japanese macaques used more rapid automatic responses (within 1.0 s) during social play than Tonkean macaques (see Chapter 3). This is probably due to the different styles of play performed by the two species: *Macaca fuscata* play is generally enriched by more competitive elements compared to *Macaca tonkeana* play (Reinhart et al., 2010). In fact, in Japanese macaques adult social play is almost entirely performed by males (see Chapter 2) that are probably more interested than females in measuring others' and their own competitive abilities. When during play, competition overcomes cooperation, the probability of misunderstanding should be higher. The high frequency of rapid mimicry in Japanese macaques allows signal exchange to speed up, thus limiting the risk that the playful sessions might escalate into overt aggression. The automatic response is characterized by a higher efficacy in communicating intentions than the delayed response, probably due to the more spontaneous and immediate connotation of facial responses. On the other hand, when social play is more cooperative, as in Tonkean macaques, a major use of congruent rapid responses does not seem necessary. In this view, different social styles can influence not only play modality (competitive vs cooperative, symmetric vs asymmetric, rough vs gentle) but also the communication used to manage such different play moods. Clearly, studying play communication can open a window on social cognition in animals.

The last topic on which we directed our interest was post-conflict management, that is the use of different mechanisms to minimize disruptions caused by the arise of an aggressive event, in order to maintain group coherence and restore social relationships (de Waal, 1986). Escalation of conflicts can be prevented by various management strategies, such as signalling formal dominance, performing rituals, respecting possession and reconciliation (e.g., de Waal, 1992; Cords and Killen, 1998; Koyama, 2000; Preuschoft and van Schaik, 2000). In some cases the victim can receive a friendly, spontaneous contact from a bystander not involved in the agonistic encounter (de Waal and van Roosmaleen, 1979; Palagi et al. 2008; Fraser et al. 2009; Romero et al. 2010). This first spontaneous post-conflict affinitive contact directed by a third party to the victim as documented for humans and great apes, was coined as consolation, a term that includes a hypothesis about its function as distress alleviation (chimpanzees, *Pan troglodytes*: Wittig and Boesch 2003, 2010; Kutsukake and Castles 2004; Palagi et al. 2006; Koski and Sterck 2007; Fraser and Aureli 2008; Fraser et al. 2008; Romero and de Waal, 2010; gorillas, *Gorilla gorilla*: Cordoni et al. 2006; Mallavarapu et al. 2006; bonobos, *Pan paniscus*: Palagi et al. 2004; humans, *Homo sapiens*: Fujisawa et al. 2006; Burleson 1983; Eisenberg 1992). For this reason, non-human primate scholars prefer to use a less value-laden term as “unsolicited bystander affiliation” when referring to this type of post-conflict affiliation in monkeys (Call et al. 2002). In the only two monkey species where it was found, “unsolicited bystander affiliation” appears to lack the consolatory function demonstrated for humans and great apes (in these species: “consolation”).

Macaca fuscata and *Macaca tonkeana* differ strikingly in the use of third-party affiliation, as we have demonstrated in this work: Japanese macaques never showed this post-conflict strategy. In this research we discovered for the first time in a catarrhine monkey species (*Macaca tonkeana*), that third-party affiliation can provide comfort to recipients of aggression (see Chapter 4).

Our findings allow us to use the term “consolation”, instead of third-party affiliation, not just for human- and non-human apes, but also for a monkey species. The reduction of anxiety has been considered as one of the most informative parameters to interpret consolation as a possible expression of sympathetic concern in apes (Fraser et al., 2008; Romero et al. 2010). Some scholars ascribed the absence of consolation in monkeys to the different cognitive and empathic abilities characterizing them in respect to apes (de Waal and Aureli, 1996; Watts et al. 2000, Schino et al. 2004). In stump-tailed macaques, Call et al. (2002) documented the presence of third-party affiliation, which seems to have a purely appeasement function. Recently, a similar result has been found in *Mandrillus sphinx* (Schino and Marini, 2012) where third-party affiliation seems to protect bystanders from victims’ redirections. One of the possible explanations of why consolation in *Macaca tonkeana* is beneficial to the victim can be attributed to the peculiar inter-individual relationships of this species (Matsumura 1999; Thierry 1985, 1990; de Waal and Luttrell 1989; Aureli et al. 1997; Petit et al. 1997). Compared to all the other macaque species in which third-party affiliation has been investigated, Tonkean macaque is the only species, which belongs to the most egalitarian level (Grade 4) (Thierry 2000; De Marco et al. 2010).

Moreover, in *M. tonkeana* third-party affiliation can be considered as a substitute of reconciliation (see Chapter 4), that is the main means to end the conflict and restore the relationship between former opponents (Aureli et al. 2002). In Tonkean macaques, consolation occurred more frequently in absence of reconciliation, suggesting that the potential consolers are sensitive to the need of the victim to be contacted after an aggression, especially if the previous agonistic event is not formally resolved and the victim, a friend, is still suffering anxiety (Romero et al. 2010).

Our data also provide evidence that third party-affiliation protects the victim against further conflicts, and is mostly directed towards friends. On the other hand, it does not seem that third-party affiliation has any effect in reducing the likelihood of further attacks among group members or it has any role in limiting redirection by the victim (see Chapter 4). All these factors make it difficult to not acknowledge that third-party affiliation has a consolatory function in *M. tonkeana.* Since third-party affiliation does not reduce the probability of further aggression among other group members (including the "potential consoler"), the focus of the consolatory act does not seem to be the group, but the victim. Consolation reduces the probability of the victim to be attacked again and, therefore, could directly reduce the victim's anxiety. As required by the consolation hypothesis the action is predominately directed towards friends. Whether in *Macaca tonkeana* consolation produces any direct benefits for the consoler remains unclear, because we do not know if the actor is aware or can potentially learn about the long-term consequences of its action (de Waal and Suchak, 2010). However, even assuming that animals are capable of understanding long-term consequences, they have no way to know if the favour will be repaid in the future.

Our data on *Macaca tonkeana* also show that consolation is not only directed towards friends, but also towards high-ranking individuals (see Chapter 4). Romero et al. (2010) suggested that dominant chimpanzees may suffer higher levels of anxiety when losing to a subordinate. Indeed, our analysis here revealed that high-ranking macaques suffer significantly more post-conflict anxiety than medium- and low-ranking individuals. Even though we cannot exclude that consolation can also provide benefits to the consoler, we can nevertheless hypothesize that the potential consolers are sensitive to the greater distress experienced by dominant subjects.

In conclusion, our study adds behavioural evidences that a species social style affects inter-individual interactions in different social contexts, such as during play activity and in tense situations. In a society characterized by high levels of tolerance and relaxed relationships, social behaviours that are absent in highly despotic societies can arise, for instance consolation. Moreover, play and communication during play can assume different connotations in relation to the social substrate in which they are expressed. Therefore, the different degree of social tolerance that macaques show is the key to understand how behavioural patterns can evolve and being shaped by social constraints.

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ANNEX 1

ETHOGRAM (*Macaca fuscata*, *Macaca tonkeana*)

(from Dunbar, 1975; Thierry et al., 2000)

GENERAL BEHAVIOURS (postures, locomotor and physiological behaviours, neutrals)

Approach (ap): an animal moves closer to another one. The approach has to be followed by an interaction (event or state).

Attempt Confiscated Food (acf): an animal tries to steal food to another one, but it can't.

Chewing (chw): the animal is chewing (food, bark, anything else..)

Climbing (climb): the animal is climbing.

Co-Feeding (cofeed): two animals eat together, sharing the same food (typically seen between mother and infant).

Confiscating food (cf): an animal steals food to another one.

Defecating (def): an animal is defecating.

Drinking (dr): the animal is drinking.

Feeding (f): the animal is eating.

Following (fol): an individual walks or runs after a moving partner.

Food Begging (food beg): the infant asks for food to its mother.

Foraging (for): looking actively for food.

Fore and Hind Limbs Suspension (fhsu): the animal hangs on a support using all limbs, or using one hand and one feet. This posture is also used during *acrobatic play*..

Forelimbs Suspension (fsu): the animal hangs on a support using only the forelimbs while the hind limbs are moved freely. This posture is also used during *acrobatic play*.

Geophagy (geo): the animal is eating soil (this behaviour has never been observed in *M. tonkeana*).

Hind Limbs Suspension (hsu): the animal hangs on a support using only the hind limbs while the forelimbs are moved freely. This posture is also used during *acrobatic play*..

Leaving (lea): an animal leaves another one with whom it has had an interaction (event or state).

Licking (lk): an individual is licking a substrate.

Lying Down (ld): the animal is lying.

Object Carrying (oc): an animal brings something (food, stones, objects..) using its forelimbs; this behaviour is generally associated with *walk and stand bipedally.*

Pushing Away (pa): an animal pushes another one away; sometimes a mother can moves away her infant using feet.

Resting (r): the animal stands still, it's inactive and alone.

Rubbing Chin (rch): an animal scrubs its chin on a support.

Rubbing Nose (rno): an animal scrubs its nose on a support.

Running (run): the animal is running.

Searching Food (src food): the animal is searching around for something to eat

Sit (sit): the animal is sitting alone.

Slide Down (sd): the animal descends a support.

Sniffing (sn): the animal is sniffing (food, genitals, ground..)

Urinating (uri): an animal is urinating.

Walk (wlk): any type of movement except *run;* this behaviour includes *standing*, that is standing still on all fours.
Walk and Stand Bipedally (wsb): the animal walks without using the upper limbs and usually it is associated with *object carrying*.

AFFILIATIVE BEHAVIOURS

Attempt of Grooming (aog): an animal tries to groom another one, but the first one prevents it pushing away its arm or avoiding it (sometimes infants do it with their mothers).
Grooming (gr): an individual cleans the skin or fur of a partner. The hair is brushed and parted using hands. Particles are picked using hand or the mouth, teeth or tongue. An individual grooms a passive partner.
Huddle (hu): an individual passes one or both hands, or one or both arms around the body of another in multiple combinations. This is an affinitive contact that may be accompanied by *lipsmacking*.
Mouthing (mou): an individual brings its mouth toward that of another, while looking or smelling. The mouth can be open or not, contacts may occur. This is an affinitive contact that may be directed toward an infant clinging to the mother, for instance. In rare instances, mouthing the penis of a male infant was observed .
Proximity (px): two or more animals are sitting together at a distance that does not exceed an arm or leg's length.
Reciprocal Grooming (rgr): two animals groom each others.
Request of Grooming (rog): an individual presents a body part (e.g., chest, head, side, back) to a partner at proximity, or lies against it. This frequently induces grooming by the partner.
Sitting in Contact (sitc): two (or more) animals are sitting together with a physical contact.
Touch (tou): an individual contacts another lightly with hands. This affinitive contact does not involve *push, grab* or *pull*.

SELF-DIRECTED BEHAVIOURS

Head Shaking (hs): the animal shrugs head and shoulders; this behaviour occurs in conditions of social tension and agonistic contexts. (This was observed especially in males).
Scratching (scr): a repeated movement of the hand or foot during which the fingertips are drawn across the individual’s fur. This is a self-directed behaviour that may occur before or between approaches and social interactions.
Self-grooming (sgr): an individual cleans the skin or fur of itself. The hair is brushed and parted using hands. Particles are picked using hand or the mouth. This solitary activity may occur at rest or in the context of social tension.
Self-injury (self inj): the animal bites itself strongly, especially the ends (hands and feet), sometimes even pulling at its fur.
Support Shake (shk): a violent shaking of an environmental object (e.g. branch, fence), producing an audible noise. The performer holds the object and repeatedly flexes and straightens the limbs. This behaviour may be followed by *yawning*. It occurs in conditions of social tension, agonistic contexts or play. It may serves to attract the attention on the performer.

Yawning (y): an involuntary intake of breath through a wide open mouth. During a yawning display, the mouth is partially opened, forming an oval shape. Then the head is tossed back and the mouth is opened to the fullest extent before to be rapidly closed with head returning to the normal position. Macaques perform two different yawning displays: the first type with covered teeth (1°grade) and the second type with uncovered teeth (2°grade). During agonistic contexts macaques perform the tension yawn, gaping is brief and there is no real preliminary stage. It can be followed by *support shake* or *stamping*.

AGGRESSIVE BEHAVIOURS (or threatening)

Aggressive Bite (abit): an individual bites another one.
Aggressive Crouching (acr): an individual presses the body against the ground with the four limbs flexed in response to an attack or a threat. This submissive act may be accompanied by screaming vocalizations.
Aggressive Grab (agra): an individual vigorously grabs or pulls another one. This is an aggressive act.
Aggressive Pull (apl): an animal vigorously pulls another one.
Aggressive Push (aps): an individual pushes away hard another one, using hand or body.
Aggressive Slap (asl): an individual hits another with the flat of its hand.
Aggressive Stamping (ast): a rhythmic trot or a jump followed by an abrupt landing with stiff limbs. It may be followed by *yawning*.
Avoid (av): an individual walks away when displaced, threatened or attacked.
Chase (ch): an individual runs after a fleeing individual. The pattern is associated with aggression.
Crash to the ground (ctg): the aggressor pushes roughly the victim to the ground and often the victim screams. This behaviour may be combined with *aggressive push*, *aggressive grab*, *aggressive slap* and it may occur in high intensity aggressions.
Dismiss (dism): an individual threats another one that walks away. This behaviour may be followed by *displacement*.
Displacement (disp): an individual takes the place of another individual, which simultaneously moves away.
Fight (fgh): struggle (term used when it is difficult recognize bites, slaps, pushes…)
Fleeing (fl): an individual runs away when threatened, attacked or chased.
Staring (st): an animal fixes its gaze on another individual. The scalp may be retracted or not. The head may be thrust forward. The performer is tense. This expression acts as a low-level threat aimed at warning or stopping the addressed individual.
Tail Lift (tli): an animal holds its tail in a vertical position. This signal can occur in aggressive contexts.
Threat (thr): an individual threats another one during aggressive contexts (e.g. simulated attack).

SEXUAL BEHAVIOURS

Anogenital Inspection (ing): an individual closely looks at or smells a partner's ano-genital region.
Attempt of Mount (atmo): an animal tries to mount another one.

Disoriented-mount (dismo): an individual climbs upon a partner in a position not suited for intromission: either frontally, from the side, against the back or a lying individual, or sitting on the back. This behaviour can be used during play.

Dorso-ventral Copulation (dvco): complete mating with mount, penetration and *thrusting* (pelvic pushes). The female is crouched and its receives the male from back. This behaviour ends with male's ouster.

Ejaculation (ej): an emission of semen, occurring during genital self-stimulation or *mounting*.

Genital-self Stimulation (gs): an individual manipulates its own genitals. This may lead to erection and ejaculation in males. This may also be performed by rubbing the genitals against a support.

Intromission (i): an insertion of the erect penis in the female genitals during *mounting*.

Looking Backward (lbw): a subject turns the head to look at another individual, usually during a mount/copulation. Looking backward can be performed during play sessions and may induce *play chasing*.

Mount (mo): an individual climbs ventro-dorsally upon a standing partner. The mounter may or may not grip the legs of the partner. The behaviour may represent a *copulation* or an affinitive interaction.

Parading (par): a female walks back and forth in front of a male. This may induce *mounting* by the male especially when performed by females exhibiting perineal swelling. This behaviour does not normally occur in Tonkean and moor macaques but some occurrences might have been observed.

Positioning (po): an individual pushes or grasps the pelvic region of a recipient to raise or orient it toward himself for *anogenital inspection* or *mounting.*

Post-Mount Flight (pm fl): after a mating, the female runs away some meters from the male.

Present Rear (pr): an animal directs its back to another animal. It can be accompanied by *looking back*. When this behaviour occurs during perineal swelling, the female crouches to the ground having up its rear. This may induce *anogenital inspection, mounting, grooming* or it may follows a *threat*.

Pushing Back (pubk): the male pushes the female on its rear (or somewhere else) in order to mount it.

Reaching back (rb): a mounted individual extends its arm backwards toward the mounter. It may grasp/pat the mounter's limb or penis. This may be accompanied by *looking backward*.

Thrust (th): a back and forth pelvic motion. A series of thrusts is generally performed by a mounting individual. It may also occur in individuals performing *disoriented mounts* or in females self-stimulating their genitals against a support.

MOTHER-INFANT BEHAVIOURS

Attracting (attr): an individual brings another toward itself with hand. This may be a mother attracting an infant on its belly. This may be also an individual pulling the partner's fur to initiate contact or an affinitive interaction, as in grooming or play.

Climbing (cl): an immature individual climbs over an older individual. This may be an infant crawling and exploring on any part of its body.

Dorsal Carrying (dc): an infant is transported on the back of a carrier. The infant holds on, grasping the fur of the carrier.

Examination (ex): an individual manipulates the body of another. This is often directed toward infants and may include pulling the limbs, handling the genitals and lifting or turning over.

Lift and Nuzzle Infant Rear (lni): an animal lifts up an infant's rear and sniffs it.

Nipple Holding (nip hold): an infant holds a nipple in its mouth. It may or may not suck.

Pick Up (pk up): an individual approaches and picks up an infant that is moving freely.

Restrain (re): an animal restrains or drags another animal, forbidding this one to leave. This behaviour often occurs in mothers that restrain infants.

Suckling (sk): an infant is suckling at its mother's nipple.

Suckling Rejection (skr): a mother forbids its infant to suckle, pushing away it from nipples.

Take Over (tko): an individual takes an object that another holds. This may involve taking of an infant carried on a partner's back. The partner may tolerate the action, move away or protest.

Ventral Carrying (vc): an individual transports an infant in a ventral position from one location to another. The infant may be clinging and/or the carrier may support it with one or both hands. Occasionally, the carrier supports the infant clinging to an odd part of the body (e.g. an arm).

Ventral Contact (veco): an infant maintains contact with the ventral surface of an older individual. The infant may face the ventral surface of its partner or sit sideways or outward.

VOCALIZATIONS

Alarm Call (alc): a loud emission with high intensity and tones; it may be repeated one or more times. (This is an alert vocalization).

associated with *staring, chase* and aggression.

Bark (ba): a loud and brief vocalization that may be repeated, the mouth forming a O shape. It is

Gecker (gk): a vocalization frequently reported as a distress cry emitted by an infant (*Temper tantrum*: when a mother rejects its infant).

Grunt (gru): a grunting sound, often emitted in series, and uttered in affinitive interactions and contacts.

Loud Call (loc): a high-pitched vocalization emitted by adult males either in non-specific situations or in the context of arousal and social tension (e.g., social conflict, separation of mates from the main group, presence of a stranger). It is composed of phrases consisting of frequency-modulated units.

“Mew” Call (mew): a continuous wail with variables pitches; it often occurs in juveniles and infants, with closed-mouth. (This is a medium-stressed vocalization).

Pre-Feeding Call (voc): this high-pitched vocalization is emitted in the lapse before feeding time.

Screaming (scrm): a long shrill vocalization accompanied by the *open mouth bared-teeth* display. It is typically emitted by an individual in conflict with a stronger individual and seeking refuge near a supporter, or may be uttered by an individual while avoiding another.

FACIAL EXPRESSIONS

Avoid Looking (alk): an individual turns the face and thus the gaze, resulting in avoidance of eye contact with another individual which is interacting or attempting to interact.

Bared-Teeth (bt): the upper lip or both lips are vertically retracted, exposing the teeth and sometimes the gums. The corners of the mouth may be drawn back. The jaw may be either closed or opened to various degrees. The scalp is often raised and the ears flattened. In *M. tonkeana* this is an affinitive display, commonly observed during affinitive interactions and social play. It may be used to initiate a positive interaction and is frequently associated to an approach. In *M. fuscata* the bared-teeth is used as a submission signal, in response to a threat. It could be without vocalization (**silent bared-teeth**).

Close Looking (cl): an individual physically brings face close to another one's face to establish visual contact. This behaviour is typically performed after an approach or toward an infant clinging to the mother.

Fear-Grimace (fgr): lower and upper lips are retracted, exposing the teeth.

Lipsmacking (ls): lips are protruded and then smacked together repeatedly. The mouth may be slightly open with the tongue moving back and forth. The lips often produce an audible sound. The display is used during affinitive interaction, as observed in *M. tonkeana*. It may also end a conflict, and acts as an appeasement or reassurance signal, as observed in *M. fuscata*.

Mutual Gaze (mg): the interaction that an animal starts to draw the attention of an infant. It may occur between mother and infant, or adult and infant (no kin). It may be associated with *lipsmacking*.

Open Mouth Threat (omt): this facial expression is accompanied by staring and it is associated with aggressions; the ears may be flattened against the head and the body is stiff. The mouth is open wide with corners retracted, partially exposing the teeth .

Scalp Retraction (sr): the scalp is retracted, ears may be flattened against the head while the individual looks at a partner. This may be associated with physical approach. This is an invitation to play or engage in an affinitive interactions. In *M. fuscata* this behaviour has been observed in aggression contexts like threat signal, but in *M. tonkeana* it could be used in play session to invite a partner.

Teeth Chatter (tch): an animal chatters its teeth together.

Tongue Protrusion (tp): the tongue is drawn out and inside the mouth repeatedly (it may occurs during a play session mixed together with others facial expressions). It may occur in *facial-mimcry* between mother and infant.

GESTURAL COMUNICATION

Beg with Hand (bwh): an animal touches another animal with one or two hands, round its chin or mouth; this behaviour may occur while the second animal is chewing.

Extended Arm (exta): an animal stretches out its arm toward another animal.

Finger/Hand in Mouth (fm/hm): an animal puts its fingers or the whole hand in another animal's mouth.

Foot/Leg Gesture (foot/leg): an animal stretches out its foot or leg toward another animal.

Gentle Touch (gtou): an animal touches another one with its finger or hand (back or palm) slightly.

Grab Face (gf): an animal grabs another one's face to get a visual contact with it.

Hand Lead (hl): an animal grabs another one's hand to be in contact with it; the grab is not so heavy to move the fellow.

Hunchover (hover): an animal scrolls down its arm on the fellow's back without establish a long contact (less than 2 sec).

Move (move): an animal shakes an object (branch, straw, ecc..) or an arm just in front of another animal.

Nose Wipe (nw): an animal touches his own nose, from up to bottom (it is common during stressful events).

Pat (pat): an animal touches quickly and repeatedly its fellow; palms are flattened.

Rub Eyes (rey): the animal rumples its eyes. This behaviour may be followed by *yawning*.

Slap Ground (slapg): the animal hits the ground or something fixed in the environment (an enclosure or a wall), palms are flattened.

ETHOGRAM ~PLAY~

Acrobatic Play (acp): one (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (branches).

Airplane (air): an adult lies on its back and rises an infant up with its hands and feet (in macaques usually the animal is sitting).

Bow (pbow): an individual crouches on its forelimbs, remains standing on its hind legs swinging its body.

Climb or Stand on Another (pcst): an animal climbs or stands on the body of a conspecific.

Drag (pdr): an animal trails the fellow by its arms or feet.

Eye Cover (eyecov): an animal covers up its fellow's eyes during a play session.

Full Play Face (fpf): the mouth is opened with the lower and upper teeth exposed, gums are visible via the active retraction of the lips.

Grab Genitals (grgen): an animal grabs another one's genital during a play session. This has been observed between males.

Head Right & Left (headrl): the animal shakes its head right and left, while it's biting something or someone (like a dog).

Jump (pjump): an animal jumps on equipment present in its environment.

Leapfrog (cav): an animal jumps beyond the fellow.

Moon Walk (mw): walking backwards.

Object Play (opc): holding an object in hands manipulating it (even with food that it will be not eaten)

Object Steal (objst): an animal appropriates of another one's object during a play session.

Own-Body-Part Play (obpp): an animal manipulates parts of its own body (solitary play).

Pirouetting (piro): an animal turns or rolls over on vertical supports.

Play Bite (pbit): an animal bites its playmate.

Play Brusque Rush (pbr): an animal jumps on another one; it has been observed in infants playing with adults.

Play Crouching (pcr): an individual presses the body against the ground with the four limbs flexed during a play session.

Play Face (pf): relaxed, open-mouth expression with only the lower teeth exposed.

Play grab (pgra): an animal vigorously grabs or pulls another during a play session.
Play Invitation (pinv): An individual approaches another to initiate play. This may employ a variety of patterns: *play face* or *full play face*, *play grab*, *play chase*, *play slap*, etc.
Play Kick (pk): an animal kicks another playmate.
Play Mount (pmo): An individual climbs ventro-dorsally upon a standing partner. The behaviour may represent an affinitive interaction during a play session.
Play Pull (ppl): an animal grabs another playmate.
Play Push (pps): an animal pushes another playmate with its hands.
Play Recovering a Thing (prco): an animal chases a playmate and attempts to grab an object carried by it.
Play Retrieve (pre): an animal holds a playmate to avoid its flight.
Play Roll (pro): turning the body from side to side while supine; can be complete or incomplete rotation.
Play Running (prun): an animal runs (seen during solitary play or social play).
Play Shaking Someone (pshk): an animal grabs the playmate to shake it.
Play Slap (psl): an animal slaps any part of the fellow’s body.
Play Turn Around (pta): to play ring-a-ring-a-roses (running around an object or an animal).
Rough and Tumble (rt): vigorous bipedal wrestling. Typically consisted of chasing, lunging, tackling, vigorous wrestling, falling on the other and vigorous mock biting (term used when it is not possible to distinguish clearly what the animals are doing).
Shake Rope (scuot): an animal shakes the rope where another animal is walking or stringing up.
Slide (sli): an animal drifts to the ground using legs and feet.
Slide Down (sd): an animal drifts down from a tree, or a rope or something else present in the environment.
Solitary Play (pso): a generic play involving one animal (excluded *object play*).
Somersault (pso): an acrobatic movement in which an animal turns head over heels on the ground and finishes on feet.
Swinging (psw): an animal oscillates hanging up on a support.
Tug of War (tirf): two animal compete for an object and they both pull it in their own direction.
Vertical (ver): an animal handstands during a play session.
Wriggle (wrg): an animal wriggles away from playmate’s grab.

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