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PLAY AND PRIMATES: SOCIAL, COMMUNICATIVE, AND COGNITIVE ASPECTS OF ONE OF THE MOST PUZZLING BEHAVIOUR

Abstract - Play is extremely difficult to define and its benefits are not easily detectable. Due to its multifunctional nature, play represents a good opportunity to test some hypotheses on social, communicative, and cognitive aspects of animal and human behaviour. For this reason, comparative studies of social play can make contributions to a wide variety of fields (evolutionary biology, ethology, anthropology, psychology, and neuroscience). Here, we present data published in the last ten years by the primatologists of the Natural History Museum (University of Pisa) on a number of primate species in order to elucidate the importance of studying play behaviour in a comparative perspective. Firstly, we explore the immediate functions of adult social play especially in managing tension situations both within and between group members. Then, we discuss data on the importance of playful signals as tools in limiting competition and increasing cooperation that characterized each social play session. Finally, we provide new data on the presence of facial mimicry during play in a cercopithecoid species, a phenomenon homologous to human laughter contagion. The facial mimicry, up to now demonstrated only in apes and humans, is the expression of emotional contagion, a fundamental building block of empathy. In conclusion, such findings suggest that play behaviour also provides a good opportunity to investigate the affecting mechanisms at the basis of animal social cognition.

Key words - Social play, playful facial expressions, social bonding, communication, facial mimicry, social cognition.

Riassunto - *Gioco da primati: aspetti comunicativi, sociali e cognitivi di uno dei comportamenti più enigmatici.* Il gioco è, dal punto di vista etologico, un comportamento di difficile definizione, i cui benefici non sono facilmente identificabili. Tale difficoltà si può intuire dal fatto che questo comportamento non si identifica con una caratteristica in positivo, ma lo si descrive come qualcosa che non ha le peculiarità proprie dei comportamenti cosiddetti «seri» (agonistico, sessuale, anti-predatorio, ecc.). Tuttavia, grazie alla sua natura multifunzionale (definizione sulla quale, stavolta, l'intera comunità scientifica concorda), il comportamento ludico rappresenta un terreno fertile per saggiare alcune ipotesi sugli aspetti sociali, comunicativi e cognitivi del comportamento animale, uomo incluso. In quest'ottica, gli studi comparativi sul gioco sociale possono offrire un grosso contributo a numerose discipline scientifiche tra cui la biologia evolutiva, l'etologia, l'antropologia, la psicologia e le neuroscienze. Il presente lavoro si propone di discutere alcuni risultati ottenuti nel corso degli ultimi dieci anni dai primatologi del Centro Interdipartimentale Museo di Storia Naturale e del Territorio (Università di Pisa). I risultati, riguardanti numerose specie di primati, evidenzia-

no l'importanza dello studio del comportamento di gioco in una prospettiva comparata. Per prima cosa, vengono esplorate le funzioni immediate del gioco sociale negli adulti. Il gioco, sia in alcune specie di lemuri (proscimmie del Madagascar) sia nelle antropomorfe del genere *Pan*, viene utilizzato per gestire situazioni di particolare tensione sociale tra membri dello stesso gruppo come tra individui estranei. Viene poi discussa l'importanza delle espressioni facciali necessarie per limitare la competizione e favorire la cooperazione, caratteristiche queste peculiari per il mantenimento e l'efficacia di una sessione ludica. Infine, presentiamo dati che dimostrano la presenza in un cercopitecoide (gelada, *Theropithecus gelada*) del fenomeno di imitazione facciale delle espressioni di gioco (sorriso), fenomeno omologo al contagio della risata nell'uomo. L'imitazione facciale, finora dimostrata solo negli Hominoidea, è manifestazione esteriore del contagio emotivo: tassello fondamentale alla base delle più complesse capacità empatiche umane. In conclusione, tutti i risultati presentati indicano il gioco come un ottimo mezzo per esplorare i meccanismi affettivi alla base delle capacità cognitive che caratterizzano gli animali sociali.

Parole chiave - Gioco sociale, espressioni facciali ludiche, legami sociali, sistemi di comunicazione, imitazione facciale, cognizione sociale.

WHAT IS PLAY?

There are no doubt about what play is, and there are few uncertainties when it comes to understanding when animals and children play. The difficulty to find a clear definition derives from the fact that it is not possible to describe a distinctive characteristic of play; it is only possible to state that play lacks certain characteristics that are typical of serious behaviours (Fagen, 1981; Power, 2000).

Some authors attempted to define play as a functionless behaviour, but the notion that mammalian play has no obvious benefit involves a subjective interpretation on the part of the observer (Martin & Caro, 1985). Play has probably many benefits but they are not easily detectable. Recently, researchers of different disciplines gave a more comprehensive definition of play behaviour in mammals. Ethologists, sociobiologists, and anthropologists defined play as all activity, which has no clear, immediate benefits and which involves an array of motor patterns, typical of serious functional contexts

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(e.g. agonistic, antipredatory, and mating behaviour). However, the main difference between playful and serious contexts is not in the actual behavioural patterns, but how they are performed (Martin & Caro, 1985; Pellis & Pellis, 1996). Burghardt (2005) listed five criteria that a behaviour must follow to be considered play. A playful behaviour must be incompletely functional, voluntary and autotelic, structurally or temporally modified repetitious, and initiated in a relaxed context. Such definition is applied to the diverse play types such as solitary acrobatic play (locomotor-rotational), object play, and social play (Power, 2000).

Social play is widespread in mammals, including humans. It 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 (Dolhinow, 1999; Pellegrini *et al.*, 2007; Cordoni, 2009). Clearly then, play joins and cuts across a variety of disciplines. It leads directly to inquiries connecting individual development with species adaptation. It is not surprising that comparative studies of play behaviour can make contributions to a wide variety of fields (Palagi, 2007).

SOCIAL PLAY IN MANAGING TENSION SITUATIONS BETWEEN AND WITHIN SOCIAL GROUPS

Some authors (Fagen, 1993; Bekoff, 1995) suggest that if two or more individuals play for long periods, *cooperation* has to occur much more frequently than conflict of interest, especially when playmates are unfamiliar. Failure to negotiate and cooperate prevents animals from playing together and can lead to a decline of play frequencies. In this view, social play can be viewed as a balance between *cooperation* and *competition*. Therefore, the ability to maintain a playful session is a good index of the willingness to invest in a social relationship and it is not surprising that play is used to manage tension situation within and between primate social groups, including humans.

Xenophobia (from Greek: *xénos*, foreign and *phobos*, fear) indicates aversion to strangers which is expressed, in its extreme form, through a violent reaction of the residents. This phenomenon, addressed as «xenophobia principle» by socio-biologists, is widespread in animals (Wilson, 2002, p. 286). In primates, xenophobic reactions include target aggressions (ringtailed lemurs, *Lemur catta*, Jolly, 1966), agonistic chasing (sifaka, *Propithecus verreauxi*, Benadi *et al.*, 2008), cooperative attacks (rhesus macaques, *Macaca mulatta*, Wade, 1974), coalitionary killing (chimpanzees, *Pan troglodytes*, Wrangham, 1999), and warfare (humans, *Homo sapiens*, Cashdan, 2001). The power of play in limiting xenophobia is a well-known phenomenon in humans (Peterson & Flanders, 2005; Gray, 2009). Antonacci *et al.* (2010) demonstrated that also in one of the most basal group of primates (the lemurs) play works in regulating xenophobia. Sifaka (*Propithecus verreauxi*) live in cohesive multi-male/multi-female groups and show temporary variations in group composition, especially during the mating season (Norscia *et al.*, 2009), when

males start roaming and visiting other groups in search of receptive females. Subjects of both sexes can mate with multiple partners in their own and neighbouring groups. Even though mate choice is a prerogative of females, a strong intra-sexual competition is present between males. The plasticity characterizing sifaka groups provided a rare opportunity to determine if adult play facilitates the integration of unfamiliar individuals. Antonacci *et al.* (2010) found that aggression rates between resident and outgroup males were significantly higher than those between residents. However, aggressions between resident and outgroup males significantly decreased after the first play session and became comparable with resident-resident aggression levels. The presence of strangers in a well-established group implies the onset of novel social circumstances, which sifaka males cope with by two different tactics: grooming with ingroup males and playing with outgroup ones. The grooming peak, concurrently with the visit of outgroups, probably represented a social shield adopted by resident males to make their pre-existing affiliation more evident to the stranger «audience». Being mostly restricted to unfamiliar males (Fig. 1), adult play in sifaka appears to have a role in managing new social situations more than in maintaining old relationships. In particular, Antonacci *et al.*'s (2010) findings indicate not only that play is the interface between strangers but also that it has a specific function in reducing xenophobia. In conclusion, in sifaka play appears to be an ice-breaker mechanism in the critical process that «upgrades» an individual from stranger to familiar.

Primate play, as other social behaviours, has a role in mitigating tension and preventing conflict escalation between group-members (chimpanzees, *Pan troglodytes*; Palagi *et al.*, 2004; bonobos, *Pan paniscus*; Palagi *et al.*, 2006; Tacconi & Palagi, 2009; uistiti, *Calithrix jacchus*; Norscia & Palagi, 2011).

In the two *Pan* species, researchers have widely documented anticipation of competition at feeding time. Chimpanzees limit aggression over food by grooming (Fig. 2) and play (celebration) (Koyama & Dunbar, 1996; Palagi *et al.*, 2004), whereas bonobos use sociosexuality as a reassurance mechanism when food is present (Fig. 3). Palagi *et al.* (2006) examined the function of play in the context of conflict prevention in a bonobo colony. The distribution of social play, grooming, and sexual contacts in periods around feeding and in a control condition were examined. Play frequencies were significantly higher during prefeeding than in any other condition (Fig. 4a), thus not supporting the commonly held view that social stress suppresses play. Further, there was a significant positive correlation between adult-adult play and rates of cofeeding (two or more animals feed in physical contact while sharing their food). During feeding, adults engaged in their highest levels of sociosexual behaviours (Fig. 4b). In conclusion, bonobos apparently cope with competition and social tension via two different mechanisms of conflict management: play to prevent tension, e.g., prefeeding, and sociosexual behaviours as reassurance mechanism once the tense situation has emerged.

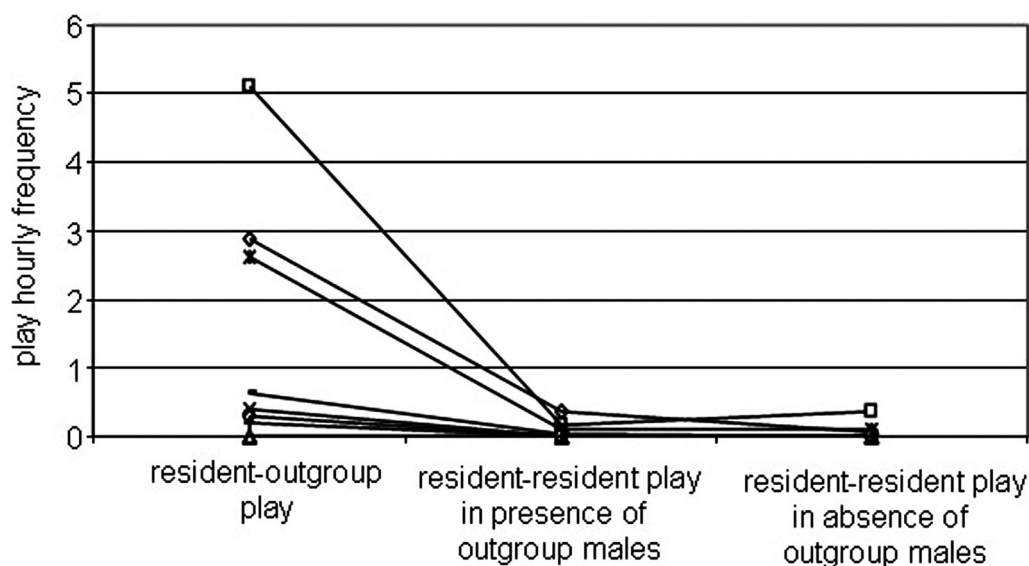


Fig. 1 - Play hourly frequency distribution recorded in sifaka groups at Berenty (Madagascar) as a function of males' group membership (Antonacci *et al.* 2010).

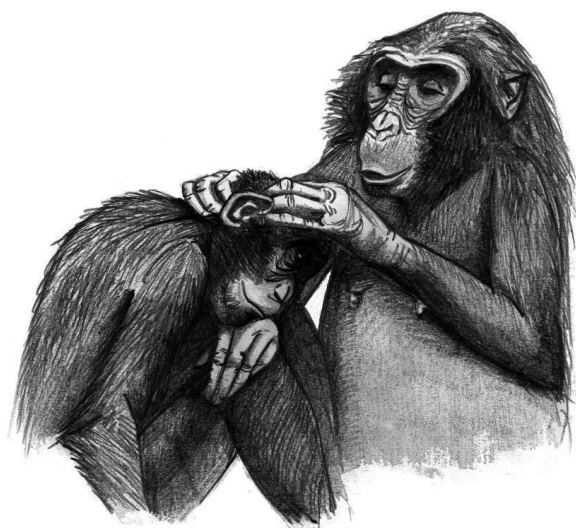


Fig. 2 - Drawing representing a grooming session between two bonobos. One animal cleans (i.e. removes ecto-parasites) the fur, extremity, or orifice of another by hand and/or mouth. In primates, grooming plays an important role in forming social bonds and affiliation between group-members. Drawing by Georgia Tacconi.



Fig. 3 - Drawing representing a ventro-ventral genito-genital rubbing between two females. One of the typical female homo-sexual contacts used by bonobos to reduce tension and increase their social affiliation. Two females rub their genital areas against one another. They can assume ventro-ventral, dorso-dorsal or ventro-dorsal positions. Drawing by Georgia Tacconi.

PLAY AS A WINDOW INTO COMMUNICATION SYSTEMS AND SOCIAL COGNITION

In humans and nonhuman primates, visual signals (e.g., body postures, movements, and facial displays) are crucial to transmit emotions and intentions between subjects (de Waal, 2003). The ability to use the informa-

tion present in visual signals and to respond to them discriminatively has been critical for the evolution of communication in social animals. In particular, facial displays are involved in regulating many aspects of primate social life such as aggression, dominance-subordinate relationships, appeasement, and play (de Waal, 2003). Playful activity is an interesting behaviour

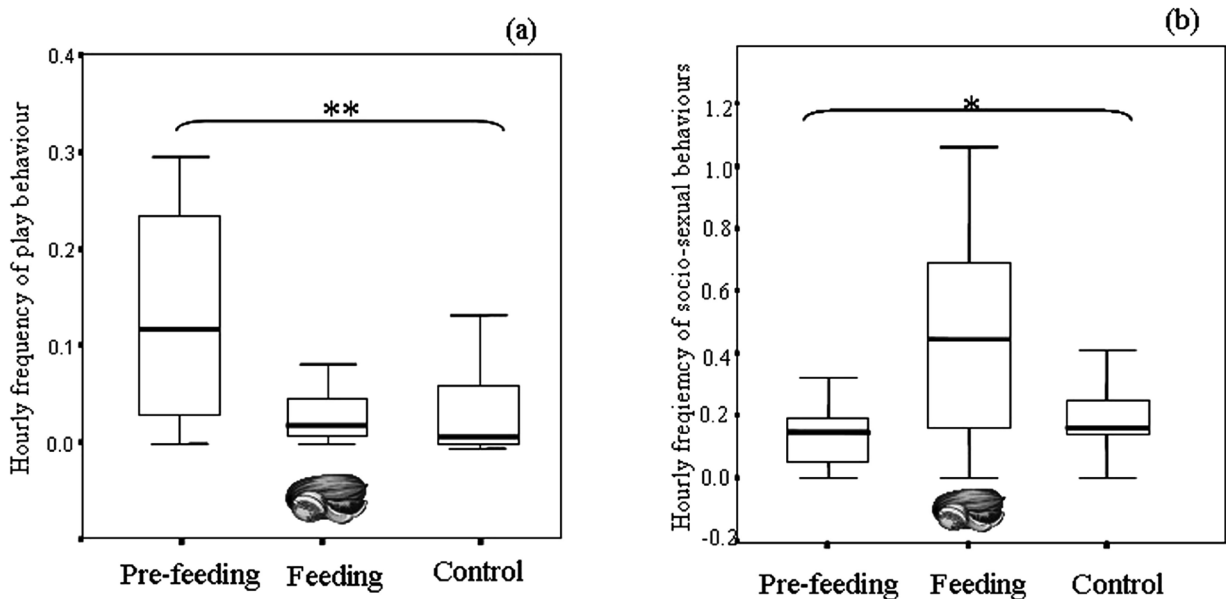


Fig. 4 - Hourly frequency distribution of play (a) and socio-sexual behaviours (b) in three different conditions: Pre-feeding (the last 25 min block before food provisioning), Feeding (the 25 min block starting from food provisioning), Control (the time block from 1000 h to 1200 h, the farthest from feeding times, when bonobos showed high activity levels, and a sufficiently long time span to represent a control condition). Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed value (Palagi *et al.*, 2006) (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

for examining the role of signals as intentional communication systems (Palagi, 2009; Palagi & Mancini, 2011). Recently, Pellis & Pellis (2006) suggested that the social play experience affects animal's ability to regulate its emotional response, and this, in turn, affects its ability to perform appropriate actions in the appropriate context, thus increasing social competence.

Charles Darwin, in *The expression of emotions in man and animals* (1872) was the first to underline that human facial expressions have great similarities with the expressions of other animals. He interpreted this to represent a shared heritage of our species which provided a behavioural argument for the evolutionary continuity between humans and other species. Apparently, human facial expressions, such as smiling, have their origin in ancestral nonhuman primates (van Hooff & 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.; chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*). In primates, the typical expression of social play is the open-mouth display (or play face, PF) which can be performed in two different configurations (van Hooff & Preuschoft, 2003). In some species (such as in *Pan* spp. and geladas, *Theropithecus gelada*), PF and full play face (FPF) represent two different degrees of the same playful expression. In the PF (Fig. 5a) the mouth is opened with only the lower teeth exposed, whereas in the FPF (Fig. 5b) the mouth is opened in a relaxed mood with both upper and lower teeth exposed (Palagi,

2008; Palagi & Mancini, 2011). The non-human primate play face appears to be homologous with laughter in humans (Preuschoft & van Hooff, 1995). Within social play, laughter seems to have a similar effect across the Hominidae, that is avoiding misinterpretation and prolonging play sessions in humans (Gervais & Wilson, 2005), chimpanzees (Waller & Dunbar, 2005), and bonobos (Palagi, 2009). In bonobos, Palagi & Paoli (2007) showed that play sessions involving contact between the participants had higher frequencies of play faces than play sessions characterized exclusively by the presence of locomotor patterns. Contact play, involving cooperation and reciprocity, is one of the most sophisticated and complex forms of interaction, during which the playmates have to trust each other to maintain the rules of the game (Dugatkin & Bekoff, 2003). This appears to be crucial when the play session involves animals with similar age and size; this could be the reason why, among bonobos, play faces are particularly frequent. Some studies (Pellis *et al.*, 1993; Pellis & Iwaniuk, 2000; Palagi, 2006) emphasized that contact play may be used to maintain social bonds, test for weakness of play partners and, therefore, gain social advantage especially when relationship among adults are not codified and structured according to rank rules. In a cercopithecoid species, *Theropithecus gelada*, PF and FPF followed an ontogenetic transition, with immature subjects using preferentially the PF and adults performing mainly the FPF (Palagi & Mancini, 2011). Such ontogenetic transition seems to reflect the phylogenetic sequence of the two playful facial configurations. FPF,

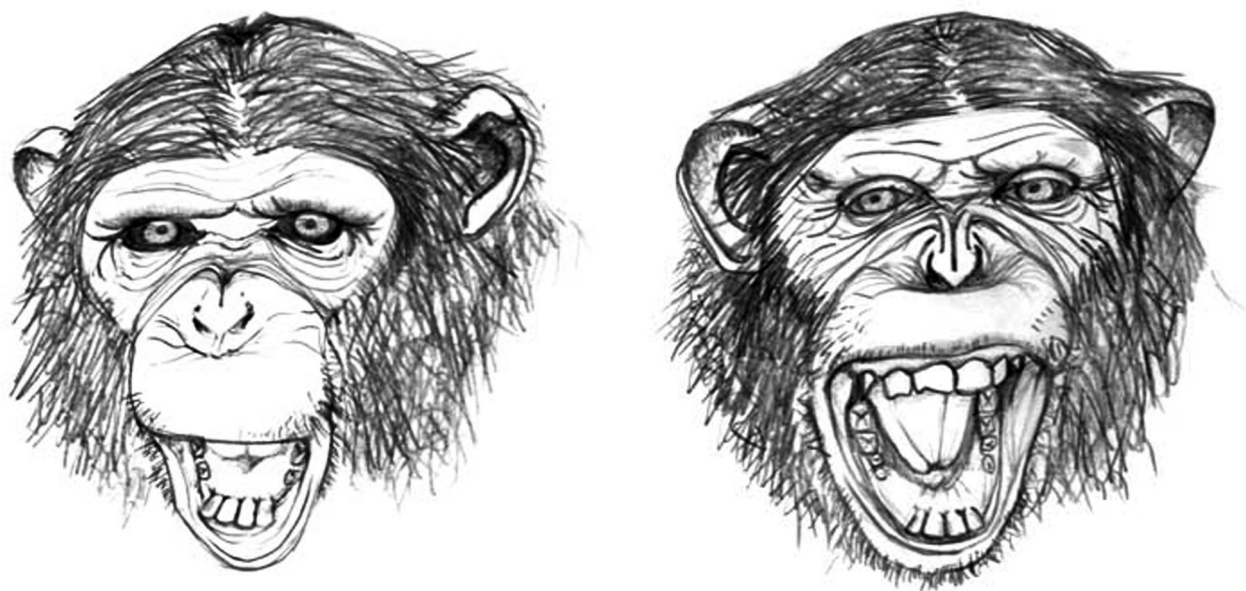


Fig. 5 - Play face (a) and full play face (b) are two different degrees of the same playful expression. In the play face (a) the mouth is opened with only the lower teeth exposed, whereas in the full play face (b) the mouth is opened in a relaxed mood with both upper and lower teeth exposed. These facial expressions appears are homologous of human smile and laughter. Drawing by Giorgia Tacconi.

which probably evolved independently several times in different lineages, is considered a derived form (apomorphism) of PF (Lockard *et al.*, 1977). Yet, it is interesting to note that the species in which such ontogenetic transition was observed are generally characterized by egalitarian and tolerant social relationships (bonobos, *Pan paniscus* and geladas, *Theropithecus gelada*), features that promote the maintenance of a conspicuous play activity also during adulthood (Mancini & Palagi, 2009). Under tension situations, humans use laughter instrumentally to maintain emotional and social homeostasis (van Hooff, 1989). Palagi & Mancini (2011) found that, as humans do, adult geladas use the playful facial expression in a strategic way. When play sessions take place during a period of high social tension (after an aggression), geladas use selectively the FPF that, from a perceptive point of view, is a more effective and less ambiguous display because it can be visually perceived at longer distances compared to PF. This finding suggests that the «audience» effect has a role in the choice of particular facial expressions selected by geladas. In monkeys, the facial expressions are generally fixed, whereas in hominoids they may show a gradient of intensity, which appears to be strictly associated with the emotions experienced by the animals (Parr, 2003). This theory is supported by the observation that bonobos sometimes perform the play face also while engaged in solitary play. van Hooff & Preuschoft (2003) affirmed that this «private emotional expression» may suggest not only a playful intent directed to a potential partner but also the capacity for self-reflection or self-aware-

ness, which are the precursors to more complex forms of cognition. However, the peak frequency of play faces during social interactions underlines the interactive function of the visual signals (Waller & Dunbar, 2005; Palagi *et al.*, 2007).

Emotional contagion enables individuals to experience and understand the same emotions as their social partners and, consequently, allows animals to detect contingencies in their social world, to synchronize their activity, and to learn the context in which an action can be performed (Provine, 1996). This empathic phenomenon is closely linked to facial imitation (Decety & Jackson, 2006). In humans, facial imitation includes various expressions in adults, e.g. smiling/laughter (Lundqvist, 1995) and yawning (Platek *et al.*, 2003), and in infants, e.g. mouth opening (Meltzoff & Moore, 1977). In non-human primates, facial mimicry has been found in monkey and ape yawning (Anderson *et al.*, 2004; Paukner & Anderson, 2006; Palagi *et al.*, 2009) and neonatal imitation (e.g. Ferrari *et al.*, 2006).

Rapid Facial Mimicry (RFM) is an involuntary, rapid, and automatic response, in which an individual mimics the facial expression of another individual. This phenomenon has to be distinguished by other voluntarily and cognitive forms of imitation (Iacoboni, 2009) because of the rapidity of the matched response (face involvement). In humans, RFM (congruent facial reactions to the emotional facial displays of others) plays an important role in emotional contagion thus giving the responding subjects important advantages in cooperation and communication (Provine, 2005). The phe-

nomenon of RFM has been recently found in an ape species (Davila-Ross *et al.*, 2008). More specifically, it has been demonstrated that in the orang-utan, *Pongo pygmaeus*, 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. Despite the importance of such phenomenon in the evolution of primate sociality, no study on RFM has been ever performed in monkeys. Mancini *et al.* (unpublished data) found that geladas (*Theropithecus gelada*), a cercopithecoid species, rapidly mimic the specific playful facial expressions: PF and FPF. Additionally, the authors used lip-smacking as control. Lip-smacking (a facial signal where lips are protruded and then smacked together repeatedly) is a non specific-play visual expression for reassurance and appeasement functions. Mancini *et al.* (unpublished data) found evidence of RFM for both adult and immature geladas, whose response was highly congruent in presence of play faces (PF and/or FPF), but incongruent in presence of lip-smacking. The presence of RFM in this species indicates that this phenomenon, well-known in humans, has homologous not only in apes, but also in cercopithecoids. In conclusion, such findings suggest that play behaviour provides a good opportunity to investigate the fundamental building blocks of empathy, a neural affecting mechanism at the basis of animal social cognition.

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