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**Visual Communication and Development of Social
Behaviour in gelada
(*Theropithecus gelada*)**

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- ABSTRACT -

Play is a fertile field to examine the role of facial expressions that we share with our common ancestors because the primate play face is homologous to human laughter. Here, we focus on the use of two playful expression variants, play face (PF) and full play face (FPF) in *Theropithecus gelada*. We recorded the behaviours of individual belonging to two colonies of geladas living at the NaturZoo (Rheine, Germany). Data were collected during a 6-month period in 2007 (June-November), a 4-month period in 2009 (June-September) and a 2-month period in 2010 (July-August).

Data showed that during ontogeny PF was replaced by FPF; in older subjects PF was virtually absent. The ontogenetic transition of facial expressions appears to reflect their different roles in communication.

In a second study we assessed the capacity to reproduce rapid imitative responses (RFM) and to evaluate the impact of these responses on affiliative behaviours. Here, we demonstrated that RFM is also present in a cercopithecoid species (*Theropithecus gelada*) and provided evidence of the link between behavioural matching and emotional connection. In fact, in the third study, we demonstrated that individuals with higher levels of matching also display prolonged sessions of play. We propose that RFM could be grounded in the automatic perception-action coupling of sensorimotor information occurring in the mirror neuron system. The capacity to match others' behaviour could have the advantage to synchronize the activity with those of the other group members and to learn the context in which an activity should be performed.

Finally, we investigated the ontogeny of RFM and found that it is also present in gelada newborns and is refined in the course of the first weeks of life. This naturalistic approach gave an important contribution to previous researches on imitative

behaviour suggesting that the infant's capacity to respond and solicit facial expressions is critically dependent on the type of social environmental feedback received by the mother and other individuals.

Our findings indicate that the building blocks of empathy linked to RFM in humans have homologous not only in apes, but also in cercopithecoids, suggesting a common evolutionary root in the basic elements of social communication.

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- CHAPTER 1 -

GENERAL INTRODUCTION

1.1 WHAT IS PLAY?

There are no doubts 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 behaviours with clear immediate significance, such as aggression, sex, feeding etc. (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 activities, which have no clear, immediate benefits and which involve an array of motor patterns, typical of serious functional contexts (e.g. agonistic, anti-predatory, 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 repetitive, 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 (Cordoni, 2009; Dolhinow, 1999; Pellegrini *et al.*, 2007). Clearly then, play joins and cuts across a variety of disciplines. It leads directly to inquiries connecting individual development with species adaptation. Thus, it is not surprising that comparative studies of play behaviour can make significant contributions to a wide variety of fields (Palagi, 2007).

1.2 PLAY AS A WINDOW INTO COMMUNICATION SYSTEMS AND SOCIAL COGNITION

One of the central issues in human evolution is the origin of human sociality. The power of the human brain can in part be explained by increasing social demands over the course of human evolution (Dunbar, 1998). Every adaptation, which allows successful interactions in social groups, modulated by a complex brain, contributes to social intelligence in human and nonhuman primates (Byrne, 1995). One of the most important factors for complex sociality is communication. Communication can be defined as a complex interplay between senders and receivers, each with their own targets (Bradbury & Vehrencamp, 1998). Communication is based on signals that can be considered as packets of energy. These packets are generated by a display/action of one organism (the signaler). They are selected to induce effects and therefore influencing the behaviour of another organism (the receiver) in a way that is adaptive either to one or both parties (Markl, 1983).

In primate evolution there was an increasing trend toward larger and more complex social groups. Moreover, individuals in primate societies rely less on olfactory than on visual cues to communicate (Fleagle, 1999). In humans and nonhuman primates, visual signals (e.g., body postures, movements, and

facial expressions) are crucial to transmit emotions and intentions between subjects (de Waal, 2003a). The ability to use the information present in visual signals and to respond to them discriminatively has been critical for the evolution of communication in social animals (Bradbury & Vehrencamp, 1998). In particular, facial expressions are involved in regulating many aspects of primate social life such as aggression, dominance-subordinate relationships, appeasement, and play (de Waal, 2003a).

Playful activity is characterized by a set of behaviours that could be of utmost interest for examining the role of signals as intentional communication systems (Palagi, 2009; Palagi & Mancini, 2011). Play behaviours could also be central in the development of the social competence of an organism and in regulating its physiology and emotional responses to social and environmental challenges. 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 provide accurate descriptions and detailed analyses of human facial expressions. Darwin

underlined the fact that human facial expressions have great similarities with the expressions of other animals. He interpreted this similarity as a sign of 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 behavioural patterns (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*). During play (e.g., play face) and submission contexts (e.g., the bared-teeth display) some similar expressions can occur. Specifically, play faces are homologous to laughter/smiling in humans (de Waal, 2003b; Preuschoft & van Hooff, 1995; Waller & Dunbar, 2005). 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 (*Pan troglodytes*, Waller & Dunbar, 2005), and bonobos (*Pan paniscus*, Palagi, 2009). 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 & Preuschoft, 2003). In

some species (such as in *Pan* spp. and *Theropithecus gelada*), play face (PF) and full play face (FPF) represent two different degrees of the same playful expression. In the PF (Figure 1.1a) the mouth is opened with only the lower teeth exposed, whereas in the FPF (Figure 1.1b) the mouth is opened in a relaxed mood with both upper and lower teeth exposed (Palagi, 2008; Palagi & Mancini, 2011).

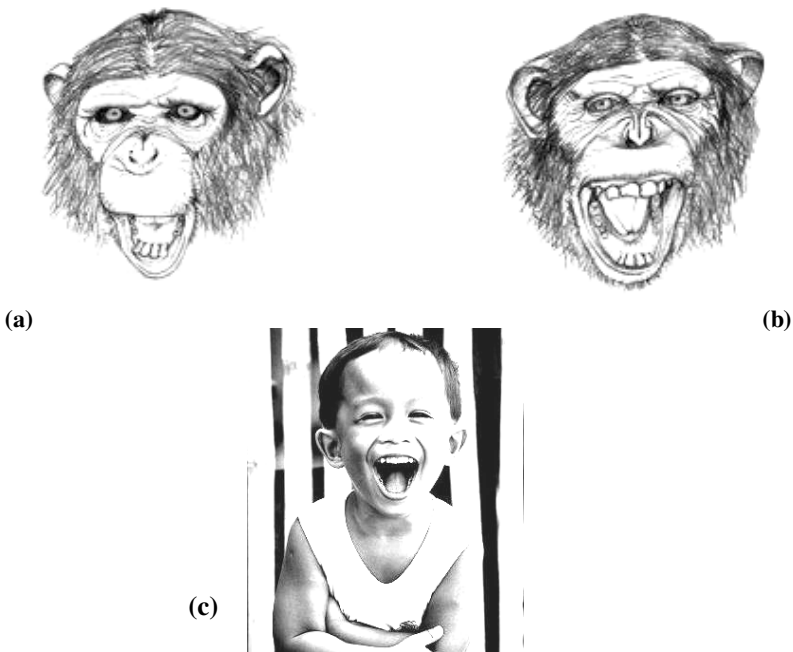


Figure 1.1 - Play face (a) and full play face (b) are two different degrees of the same playful expression. In the play face (a) the mouth is opened with only the lower teeth exposed, whereas in the full play face (b) the mouth is opened in a relaxed mood with both upper and lower teeth exposed. These facial expressions are homologous to human laughter (c). Drawing by Giorgia Tacconi

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 last assumption would be supported by the observation that bonobos (*Pan paniscus*) sometimes perform the play face (PF) 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-awareness, which are the precursors to more complex forms of cognition.

The capacity to express emotions is crucial also in primate communications to signal the internal states and to elicit in the receiver altruistic or empathic responses. The phenomenon of empathy is defined as the capacity to be affected by and share the emotional state of another, assess the reasons for the other’s state, and identify with the other, adopting his or her perspective (de Waal, 2008). The lowest common denominator of all empathic processes is that one party is affected by another’s emotional or arousal state (de Waal, 2008). More specifically, 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) or, more in general, to the capacity to reproduce in the observer a similar sensorimotor experience. In humans, facial imitation includes various expressions in adults (e.g. smiling/laughter, Lundqvist, 1995; yawning, Norscia & Palagi, 2011) and in infants (e.g. mouth opening, Meltzoff & Moore, 1977). In non-human primates, contagion has been found in monkey and ape yawning (Anderson *et al.*, 2004; Paukner & Anderson, 2006; Palagi *et al.*, 2009) and facial mimicry in neonatal oro-facial movements (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. In humans, RFM plays an important role in emotional contagion thus giving the responding subjects important advantages in cooperation and communication (Provine, 2005). The phenomenon of RFM has been recently found in the play activity of 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.

In conclusion, such evidences 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.

Despite the importance of the empathic mechanisms in the evolution of primate sociality, no study on RFM has been ever performed in monkeys. Moreover, most researches have described the distribution of playful facial displays without examining the way they are performed and their potential adaptive value and functions during the different phases of life. Based on these considerations, the main purpose of this work was to fill these gaps. In particular, we investigated in a monkey species, the gelada (*Theropithecus gelada*), the different communicative roles of playful facial expressions, the presence of RFM and its possible functions in regulating animal play activity. Moreover, we studied the affective mechanisms, such as neonatal matching behaviours, which play a crucial role in the development of infant's social behaviour and cognition.

- CHAPTER 2 -

THE GELADA (*Theropithecus gelada*)

2.1 GELADA AS MODEL SPECIES

The *Theropithecus gelada* is a cercopithecoïd species characteristic of the Ethiopian upland and, on the basis of facial features and geographic distribution, there are distinguished two subspecies: *T. g. gelada* e *T. g. obscurus* (Kingdon, 1997; Iwamoto, 1993).

Gelada social system is characterized by two main components: the individual reproductive units (one-male unit or OMU) and a cluster of units (band or herd) that share a common home-range. OMU consists of a single adult male, his reproductive females (ranging from 2 to 8) and their offspring (Dunbar & Dunbar, 1975). The social integrity of the unit is not maintained by the aggressive herding of males, as it occurs in hamadryas baboons (*Papio hamadryas*) (Kummer, 1968) which is a highly related species, but by the strength of the social affiliation among the unit members (Dunbar & Dunbar, 1975). The relationships within the unit involve the maintenance of power, most of which is hold by adult females (Dunbar, 1984). As it has been reported, in some cases, the strength of female positive bonds is sufficient to maintain the unit's integrity despite the absence of the alpha male (Dunbar & Dunbar, 1975).

Geladas (*Theropithecus gelada*) are an extremely playful species showing high levels of social play even as adults (Mancini & Palagi, 2009). They have a particularly rich repertoire of facial expressions (Dunbar & Dunbar, 1975) confirming that gelada sociality is mainly based on visual communication (for facial display's definitions, see Table 2.1). In particular, when performing full play face (FPF) geladas display the teeth and gums in a highly visible way, which makes the signal perceivable over long distances (van Hooff, 1972). Different from the relaxed FPF performed the great apes, the gelada FPF is characterized by the actively retraction of the upper lip, thus suggesting that bared-teeth display can be incorporated with the play face (PF) yielding a FPF (also named open-mouth bared-teeth display by Thierry *et al.*, 1989). Moreover, Palagi & Mancini (2011, see Chapter 3) observed that both during grooming sessions and playful events geladas frequently lip smacked (LS, lips are protruded and then smacked together repeatedly) toward conspecifics. This observation suggests that additional facial expressions can be recruited from other behavioural contexts and used for playful purposes. In addition to these important behavioural features, a recent finding of yawn contagion in geladas (Figure 2.1) suggests that these monkeys are sensitive to the emotional facial expressions of conspecifics especially

individuals with whom they are closely affiliated (Palagi *et al.*, 2009). Due to their social peculiarities, gelada are a good model species to verify differential functions on the use of specific (PF and FPF) and nonspecific (LS, used also in other social contexts) playful facial expressions and to investigate the communication rule that these expressions play during ontogenetic development.

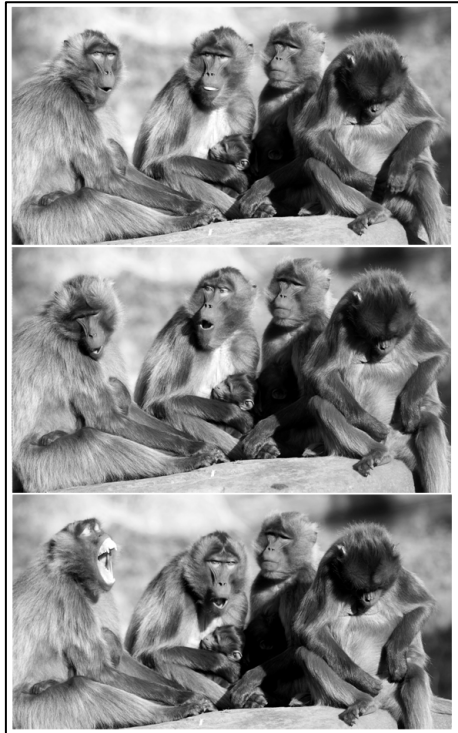


Figure 2.1 – Example of yawn contagion between gelada adult females. The sequence lasts less than 5 seconds.
(Photo by M. Pusceddu)

Table 2.1 - Gelada Facial Expressions (Dunbar, 1975)

CONTEXT	FACIAL EXPRESSIONS	DEFINITIONS
Affinitive, Greeting, and Sexual	GREETING FACE (GRE)	the mouth is closed with the teeth exposed via the active retraction of the mouth's angles.
	TEETH CHATTER (TCH)	facial display is often associated with LS
Maternal and Weaning	OPEN-MOUTH	the mouth is opened without the teeth and gums exposed. It is a typical neonatal facial display.
	TONGUE PROTUSION (TP)	facial display is often associated with LS
Play	FULL PLAY FACE (FPF)	the mouth is opened with the lower and upper teeth and gums are exposed via the active retraction of the lips relaxed, open-mouth expression with lower teeth exposed
	PLAY FACE (PF)	
Threat and Aggression	JAW FENCE (JF)	teeth and tongue are exposed with retraction of upper lip. Generally Rey (see below) is associated with this aggressive facial display
	RAISED EYEBROWS (REY)	revealing pale area above eyelids
	STARE WITH LOWERED HEAD (SLH)	threat display with fixed stare and lowered head
Submissive	BARED TEETH (BT)	frightened facial display: the mouth corners are withdrawn, the lips are retracted and the upper and lower teeth are exposed.
No context-specific*	LIPSMACK (LS)	lips are protruded and then smacked together repeatedly.
	YAWN (YW)	there are three different variants of yawning that are often associated with the vocalizations

* *Note: facial expressions present in different social context*

2.2 SUBJECTS AND HOUSING



Figure 2.2 – the gelada colony in outdoor facility of the *NaturZoo* (Rheine, Germany). (Photo by J. Achim, director of the *NaturZoo*)

We collected behavioural data during a 6-month period in 2007 (June-November), a 4-month period in 2009 (June-September) and a 2-month period in 2010 (July-August).

The colony of geladas (*T. gelada*) housed at the *NaturZoo* (Rheine, North Westfalia, Germany) was made up of two one-male units (OMUs) (for group's composition and age-class definition see Tables 2.2, 2.3 and 2.4). Individual identification was based on sex, age, and on distinctive external features (scars,

size, missing fur patches, fur colour, and facial traits). Kin relations between animals were known.

In 2007, the two OMUs were housed in the same enclosure and, in 2009-2010, they lived separately in two different enclosures. The animals' movements were due to management purposes. The two enclosures were composed by an indoor (rooms of about 36 m²) and outdoor facility (islands of 2,700 m² surrounded by a boundary ditch). The outside enclosures were located in an open, naturally hilly area equipped with trees, branches, ropes, and dens (Figure 2.2). The animals were fed with grass, vegetables, and pellets, which were scattered on the ground two times a day (9:30 a.m., 2:30 p.m.). Water was available *ad libitum*. No stereotypic or aberrant behaviours have been observed in this group. The research complied with current laws of Germany, Italy, and the European Community.

Table 2.2 - *The Group of Gelada Baboons (Theropithecus gelada) Housed in the NaturZoo (Rheine, German), data collection in 2007.*

Subjects 2007	Year of birth	Mother	Sex class	Age class
Gerda (GD)	1978	Unknown	F	
Gertje (GJ)	1987	Gerda	F	
Gitta (GT)	1992	Gertje	F	
Albert (AL)	1993	Agathe	M	
Amadeus (AM)	1994	Afra	M	
Gloria (GL)	1994	Gertje	F	Adult: > 6 years
Gevia (GV)	1996	Gitta	F	
Gwladys (GW)	1997	Gesa	F	
Günni (GU)	1997	Gertje	F	
Hilfia (HI)	2001	Gevia	F	
Hector (HE)	2002	Gitta	M	
Hobbit (HO)	2002	Gloria	M	Sub-adult: 4.5–6 years
Jacques (JA)	2003	Gwladys	M	
Grigia	2003	Gloria	F	
Ti (T)	2003	Grace	F	
Herkules (HK)	2003	Gevia	M	Juvenile: 2.5-4.5 years
Bionda	2004	Gitta	F	
Hagos (HG)	2005	Gloria	M	
Hermine (ER)	2005	Gitta	F	Infant: 6 months–2.5 years
Jasper (JS)	2005	Gwladys	M	
Julie (JU)	2007	Günni	F	Black-Infant: 1-6 months
Hichele (HC)*	2007	Gevia	M	Early Bck-Infant: < 1 months

* *Note: black infants that were video-recorded since the birth.*

Table 2.3 – *The Group of Gelada Baboons (Theropithecus gelada) Housed in the NaturZoo (Rheine, German), data collection in 2009.*

Subjects 2009	Year of birth	Mother	Sex class	Age class
Gertje (GJ)	1987	Gerda	F	
Gitta (GT)	1992	Gertje	F	
Gloria (GL)	1994	Gertje	F	
Gevia (GV)	1996	Gitta	F	
Angel (AN)	1996	Agathe	F	
Alegria (AL)	1998	Aurora	F	
Adina (AD)	1998	Agathe	F	
Dominick (DO)	2001	Buffy	M	Adult: > 6 years
Hilfia (HI)	2001	Gevia	F	
Bangle (BA)	2002	Angel	F	
Bako (BK)	2003	Sereba	M	
Babs (BB)	2003	Alegria	F	
Grigia	2003	Gloria	F	
Ti (T)	2003	Grace	F	
Bionda	2004	Gitta	F	
Hagos (HG)	2005	Gloria	M	
Bern (BR)	2005	Adina	M	
Hermine (ER)	2005	Gitta	F	Sub-adult: 4.5–6 years
Bounty (BO)	2005	Alegria	F	
Belinda (BE)	2005	Angel	F	
Hichele (HC)	2007	Gevia	M	Juvenile: 2.5–4.5 years
Tommaso	2009	Adina	M	
Giada	2009	Alegria	F	Infant: 6 months–2.5 years
Alessia	2009	Babs	F	
Betta (Betta)	2009	Gitta	F	Black-Infant: 1-6 months
Luca (LU)	2009	Hilfia	M	
Davide *	2009	Angel	M	
Dusella (DU) *	2009	Bionda	F	Early Black-Infant: < 1 month
Dalia (DA) *	2009	Gloria	F	

* *Note:* black infants that were video-reordered since the birth.

Table 2.4 – *The Group of Gelada Baboons (Theropithecus gelada) Housed in the NaturZoo (Rheine, German), data collection in 2010.*

Subjects 2010	Year of birth	Mother	Sex class	Age class
Gertje (GJ)	1987	Gerda	F	
Gitta (GT)	1992	Gertje	F	
Gloria (GL)	1994	Gertje	F	
Gevia (GV)	1996	Gitta	F	
Angel (AN)	1996	Agathe	F	
Alegria (AL)	1998	Aurora	F	
Adina (AD)	1998	Agathe	F	
Dominick (DO)	2001	Buffy	M	Adult: > 6 years
Hilfia (HI)	2001	Gevia	F	
Bangle (BA)	2002	Angel	F	
Bako (BK)	2003	Sereba	M	
Babs (BB)	2003	Alegria	F	
Grigia	2003	Gloria	F	
Ti (T)	2003	Grace	F	
Bionda	2004	Gitta	F	
Hagos (HG)	2005	Gloria	M	
Bern (BR)	2005	Adina	M	
Hermine (ER)	2005	Gitta	F	Sub-adult: 4.5–6 years
Bounty (BO)	2005	Alegria	F	
Belinda (BE)	2005	Angel	F	
Hichele (HC)	2007	Gevia	M	Juvenile: 2.5-4.5 years
Tommaso	2009	Adina	M	
Giada	2009	Alegria	F	
Alessia	2009	Babs	F	
Betta (Betta)	2009	Gitta	F	
Davide	2009	Angel	M	
Dusella (DU)	2009	Bionda	F	Infant: 6 months–2.5 years
Dalia (DA)	2009	Gloria	F	
Dita (DI)	2009	Ti	F	
Debi (DE)	2009	Grigia	F	
Diana (DN)	2010	Hilfia	F	
Che (CH)	2010	Gevia	M	Black-Infant: 1-6 months
Giulia (GI) *	2010	Adina	F	
Filippa (FI) *	2010	Alegria	F	Early Black-Infant: < 1 month
Gaga (GA) *	2010	Hermine	F	
Alexandra *	2010	Belinda	F	

* *Note: black infants that were video-reordered since the birth.*

- CHAPTER 3 -

**“PLAYING WITH THE FACE: PLAYFUL FACIAL
‘CHATTERING’ AND SIGNAL MODULATION IN A
MONKEY SPECIES (*Theropithecus gelada*)”**



Photo by M. Pusceddu

ABSTRACT

Darwin (1872), in *The Expression of Emotions in Man and Animals*, underlined that human facial expressions represent a shared heritage of our species with nonhuman primates. Play is a fertile field to examine the role of facial expressions that we share with our common ancestors because the primate play face is homologous to human laughter. Here, we focus on the use of two playful expression variants (PF: play face, mouth opened with only the lower teeth exposed; FPF: full play face, lower/upper teeth and gums exposed via the active retraction of the upper lip) in *Theropithecus gelada*. During ontogeny PF was replaced by FPF; in older subjects PF was virtually absent. The ontogenetic transition appears to reflect the phylogenetic sequence of the two playful displays with FPF considered a derived form of PF. This age-trend bias of facial displays is probably due to their different roles in communication. The correspondence between facial signals emitted and elicited is a valuable criterion to evaluate playmates' attentional state. Adults were more sensitive than immatures in responding to the play faces of others. Probably, previous playful experience, social competence, and neural circuit maturation are at the basis of adult sensitiveness. Similar to humans, where unconscious laughing is deserved for close friends and/or relatives, FPF was extremely frequent during gelada mother-offspring play. Probably, under some intimate circumstances, facial displays should be primarily linked to the spontaneous expression of emotional states of the sender more than to the strategic transfer of actual information to the receiver.

Keywords: human laughter homology, ontogenetic transition, strategic signals

3.1 INTRODUCTION

In primates, the typical expression of social play is the relaxed, open-mouth display which can be performed in two different configurations (play face, PF; full play face , FPF) (van Hooff & Preuschoft, 2003). These playful expressions have been interpreted as ritualized versions of the biting intention movement which precedes the play bite so common during rough and tumble play (Palagi, 2006; van Hooff & Preuschoft, 2003). The process whereby expressive displays become ritualized and separated from their original function to serve a new function is called ontogenetic ritualization (Tinbergen, 1952).

Since the PF is widespread in almost all primate species, 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 & van Hooff, 1997). Humans (*Homo sapiens*), bonobos (*Pan paniscus*), and gorillas (*Gorilla gorilla*) habitually use FPF, whereas chimpanzees (*Pan troglodytes*) and siamangs (*Symphalangus syndactylus*) mainly use the classical PF (Chevalier-Skolnikoff, 1982; Palagi, 2006, 2008; Palagi, Antonacci, & Cordini, 2007).

In some cercopithecine species, the use and structure of particular facial expressions can converge as a function of their

different tolerance and affiliation baseline levels (Thierry *et al.*, 1989; Petit *et al.*, 2008). For example, in the tolerant species such as sulawesi macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*), and geladas (*Theropithecus gelada*), the FPF is not a more intense version of PF, but it derives from a convergence between silent-bared teeth (a facial display used more for affiliative purposes than submissive ones, for display definition see Table 2.1) and PF (van Hooff & Preuschoft, 2003; Bout & Thierry, 2005).

Due to social peculiarities, described in Chapter 2.1, gelada (*Theropithecus gelada*) are a good model species to verify differential functions on the use of specific (PF and FPF) and nonspecific (LS, used also in other social contexts) playful facial expressions.

In some macaque species (e.g., *Macaca tonkeana*, *Macaca silenus*) and in bonobos (*Pan paniscus*) PF is typically performed by infants. In these species during ontogeny PF is replaced by FPF so that in older individuals PF is virtually absent (Palagi, 2006, 2008; van Hooff, 1972). Due to their playfulness (Mancini & Palagi, 2009) and flexibility in the use of facial expressions (Dunbar & Dunbar, 1975), we aimed to investigate whether a similar ontogenetic transition between the two playful facial configurations was also present in geladas (*Theropithecus gelada*). We hypothesized that if variants of the same signal during

different phases of life had different communicative roles then there should be an age-trend bias in PF and FPF. A second hypothesis is that during playful sessions with a higher risk of escalation (e.g., rough sessions, age-mismatched sessions, post-conflict sessions) the FPF, used in a strategic way, is more effective than PF.

A facial display tells a receiver something about the motivational state of the sender. Due to its interactive nature, a facial expression is only considered efficient when the receiver responds appropriately. For example, in humans the probability that an infant will smile at his or her mother increases when the mother is most attentive and also smiling (Jones *et al.*, 1991). Therefore, the correspondence between facial signals emitted and elicited could be a valuable criterion to evaluate the attentional state of playmates (Schmidt & Cohn, 2001). We aimed to verifying whether in geladas such correspondence is present and whether the responsiveness to the stimuli is affected by the age of playmates.

LS is a facial expression present since the first week of life (Ferrari *et al.*, 2009a). It does not seem to show any qualitative variations, either during different phases of life, or in different behavioural contexts (Maestriperieri, 1997). LS may derive, *via* ontogenetic ritualization, from the consumption of particles

picked up during grooming sessions (van Hooff, 1967). This possibility suggests the positive nature of the display, which in many primate species, transmits a message of benign intent. For this reason, we also hypothesize that LS plays a complementary role in fine-tuning play sessions which are not punctuated by a sufficient number of playful facial displays.

Finally, since the level of negotiation in play can vary as a function of the diverse relationship quality of the two players, we further hypothesize that kinship can affect the distribution of playful facial displays, both in terms of frequency and in quality of the patterns performed (PF, FPF, and LS).

3.2 METHODS

3.2.1 Data Collection Procedure

We collected behavioural data during 6 months of observation (June-November 2007) on all subjects of the colony: 2 adult males, 8 adult females, 11 immature subjects (sub-adults, juveniles, infants and black infants; see Table 2.2 for group's composition and age-class definition). Data were collected vocally through a voice recorder, and the records were later computer-transcribed. For the data collection a rigorous and repeatable observation protocol was developed by E.P. Before starting systematic data collection, the three observers (one of them was G.M) underwent a training period (90 h). During the training phase (the trainer was E.P.), 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 & Bateson, 1986) and when the Cohen's kappa was higher than 0.70 (Kaufman & Rosenthal, 2009). Kappa coefficients were computed to assess the agreement for Play face (PF), Full Play Face (FPF) and Lip Smacking (LS). For each behavioural category we report the minimum value of kappa obtained by the three dyads of observers: $k_{PF} = 0.76$; $k_{FPF} = 0.83$; $k_{LS} = 0.72$. At weekly intervals, such procedure was replicated in order to control for the inter-observer reliability.

The observations took place daily over 6-hr periods that spanned morning (from 6:00 a.m.) and evening (until 10:00 p.m.). The animals of the two OMUs could interact and play freely with one another. The size of the island allowed the scattering of geladas and, consequently, the formation of small groups of animals that frequently changed. This situation, together with the good observational conditions, allowed us to easily collect data on play behaviour by all-occurrences sampling (Altmann, 1974).

We focussed on two playful expression variants (PF: play face; FPF: full play face; for definitions see Table 2.1) in *Theropithecus gelada* (Palagi & Mancini, 2011). Since, during playful events, immature and adult geladas frequently lip smacked (LS, for definition see Table 2.1) toward conspecifics. Like PF and FPF, LS involves motor muscles of the oro-facial area and it is a facial display used to signal benign intentions. Different from PF and FPF, LS is not a context-specific signal (i.e., it occurs in a variety of contexts) and it develops through an ontogenetic ritualization process of ingestive actions (van Hooff, 1967).

We recorded a total of 513 hr of observation on all the specific (PF and FPF) and nonspecific (LS) playful facial expressions.

A play session began when one partner invited another individual to play, or directed any playful behaviour toward a

group member. A play session ended when playmates ceased their activities, one of them moved away, or when a third individual interfered, thus interrupting the previous interaction. If another play session began after a delay ≥ 10 s, that session was counted as new.

To record Rough play and Gentle play we followed the description given by Pellis (1993) and Pellegrini (1995). Rough play, also called Rough and Tumble or Play Fighting, has been defined as a physically vigorous set of behaviours such as chasing and vigorous wrestling. Gentle play was characterized by the total absence of any kind of fighting element. See Table 3.1 for the definitions of the play patterns included in the two different behavioural play categories.

We evaluated at individual level the percentage of times in which a playful facial signal was followed by a bite as follows: we verified the presence of a play bite within the three patterns immediately occurring after a playful facial display and then we divided such amount per the total facial displays performed by each animal.

In order to verify whether social tension affects the use of playful facial displays, we applied the PC-MC method (de Waal & Yoshihara, 1983). We compared the facial displays occurring during Post-Conflict play sessions (within a 10-min time window

after an aggressive event) with those occurring during Matched-Control sessions (those playful encounters not preceded by any agonistic event or occurring outside the 10-min time window) (see Leone & Palagi, 2010 for the definition of post-conflict time-window).

To evaluate the probability of signal responsiveness we verify whether the receiver emitted a playful signal within a 3-s time window after a previous stimulus (PF or FPF) emitted by the sender. We used a 3-s criterion in order to be reasonably sure that the second facial expression was actually elicited by the previous one.

3.2.2 Statistical Analysis

When the analyses were carried out at the individual level, we employed nonparametric statistics (Siegel & Castellan, 1988). Mann-Whitney *U* test was applied to compare the overall frequency of PF, FPF, and LS between adult and immature subjects and the difference in the response to the facial stimulus. The Wilcoxon's matched pairs sign rank test was applied to compare the frequency of the three facial expressions according to age and kinship of the playmates. As kin we considered only mother-offspring dyads (parental coefficient 0.5) because within gelada society they show stable social bonds. The Wilcoxon's test

was also applied to compare the frequency of facial expressions performed i) during Post-conflict sessions versus Control sessions, ii) during Rough play versus Gentle play session, and iii) to initiate or maintain the play session. Moreover, the Wilcoxon's test was also applied to compare the responsiveness to the two different facial configurations.

To control for the possible correlations between the frequencies of the different facial displays (PF + FPF and LS) we employed the Spearman test. Non parametric statistical analyses were performed by using SPSS 12.0 and we used exact tests according to the threshold values as suggested by Mundry & Fisher (1998).

When the analysis was carried out at dyadic level we used randomization procedures to avoid pseudo-replication due to non-independence of data (the same individual is included in more than one dyad, therefore dyads are not independent data points). To compare the rates of facial expressions performed and received by immature subjects during adult-immature play, we applied the two paired sample randomization test. All the randomization tests were employed with a number of 10,000 permutations using the software Resampling Procedures 1.3 by David C. Howell, freeware.

Table 3.1 - Gentle and Rough Play Patterns Recorded During the Study.

PLAY MODALITIES	SOCIAL PLAY ITEMS	DEFINITIONS
Gentle Patterns	ACROBATIC PLAY	one (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (i.e. branches)
	JUMPING	an animal jumps on equipment present in its environment
	PIROUETTING	an animal turns, somersaults or rolls over either on the ground or on vertical supports
	PLAY RUNNING	an animal rapidly following another, both with relaxed running gaits
	ROLLING	turning the body from side to side while supine; can be complete or incomplete rotation
	SOMERSAULT	turning the body one full rotation head over heels
	DANGLING	an animal holds an infant by its hands and allow it to dangle in the air
	AIRPLANE	an adult lies on its back and rises an infant up with its hands and feet
	OPEN-MOUTH-WRESTLING (gentle wrestling)	limbs entwined while sitting or laying; gorillas roll/twist together placing open mouths on each other
PLAY RECOVERING A THING	an animal chases a playmate and attempts to grab an object carried by it	
Rough Patterns	CLIMBING OR STANDING ON ANOTHER	an animal climbs or stands on the body of a conspecific
	PLAY BITE	an animal bites gently bites a playmate
	PLAY KICK	The partner's body is contacted either with the mouth or with the hands
	PLAY PULL	an animal grasps another playmate
	PLAY PUSH	an animal pushes another playmate with its hands
	PLAY RETRIEVE	an animal holds a playmate to avoid its flight
	PLAY SLAP	an animal slaps any part of the fellow's body
	ROUGH AND TUMBLE (rough wrestling)	vigorous bipedal wrestling. Typically consisted of chasing, lunging, tackling, vigorous wrestling, falling on the other, and vigorous mock biting

3.3 RESULTS

3.3.1 Strategic Use of Playful Signals as a Function of the Age of Playmates

All play signals (Full Play Face, FPF + Play Face, PF) occurred with the following frequencies: mean adult play signals per session: 2.075 ± 0.98 CI; mean immature play signals per session: 1.195 ± 0.22 CI. The comparison between the frequency of signals (FPF + PF per social session) performed by adult and immature individuals did not reveal any significant difference (see Table 3.2). The mean frequency of FPF and PF performed by adults were 1.770 ± 0.98 CI and 0.304 ± 0.17 CI, respectively. In immature individuals the mean frequency of the two different configurations were 0.460 ± 0.28 CI for FPF and 0.735 ± 0.15 CI for FP. The percentage of times in which a playful facial signal was followed by a bite (calculation made considering the three patterns immediately occurring after a playful facial display) were: adult PF, mean $0\% \pm 0.0$ CI; adult FPF, mean $3.0\% \pm 0.2$ CI; immature PF, mean $6.3\% \pm 1.6$ CI; immature FPF, $2.6\% \pm 1.8$ CI.

We carried out a comparison of the use of FPF according to the age of playmates. In order to evaluate such a difference, we compared the following ratio ($FPF_{ad}/(FPF_{ad} + PF_{ad})$) versus ($FPF_{imm}/(FPF_{imm} + PF_{imm})$). We found that adults used higher levels of FPF than immatures (Exact U Mann-Whitney = 12.50, $n_{ad} = 9$, $n_{imm} = 11$, $p = 0.003$; see Figure 3.1).

During adult-immature play, immatures received more FPF than they directed to adults (see Table 3.2); on the other hand, immatures performed more PF than they received by adults (see Table 3.2). However, as a whole the playful facial signals were mainly directed by adults to immatures (Two paired sample randomization test, $n = 47$ dyads, $t = 3.640$, $p = 0.0001$; see Figure 3.2).

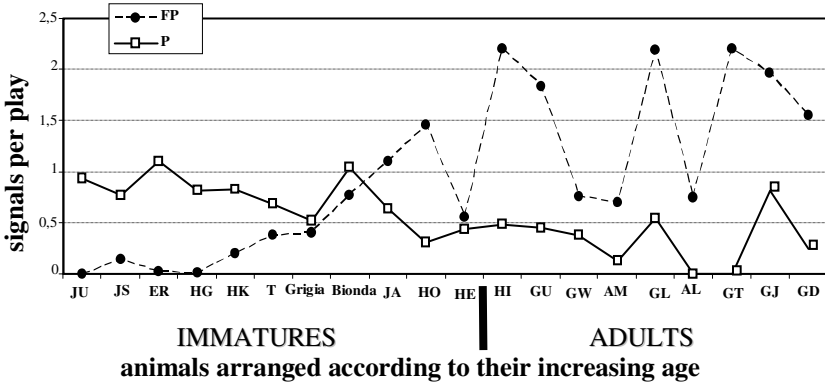


Figure 3.1 - Play face (PF) and full play face (FPF) per play session arranged by the increasing age of the subjects under study. For animal initials see Table 2.2.

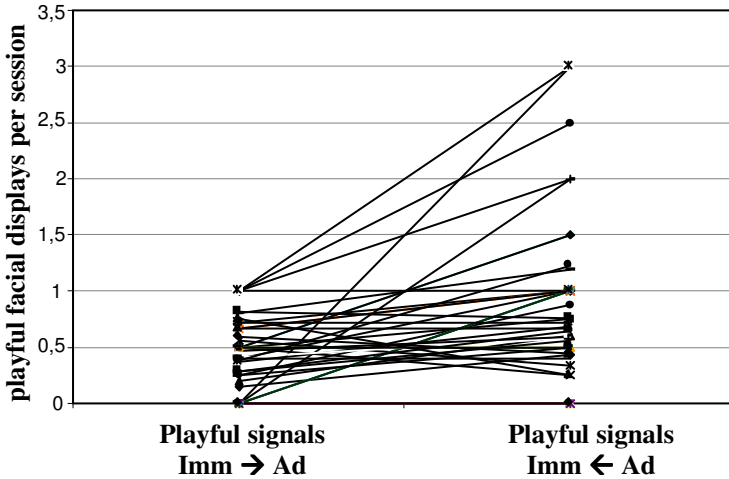


Figure 3.2 - Frequency of play signals per session performed by immatures toward adults (Imm → Ad) and performed by adults toward immatures (Imm ← Ad).

Then we compared the FPFs performed by adults both during adult-immature and adult-adult sessions ($FPF_{ad-ad}/FPF_{ad-ad} + PF_{ad-ad}$) versus ($FPF_{ad-imm}/FPF_{ad-imm} + PF_{ad-imm}$). Three adults were eliminated from the analysis because they did not engage in any adult-adult play session. Adults did not show any difference in the use of FPF according to the age of playmates (see Table 3.2). Similarly, we compared the FPFs performed by immatures during both immature-adult and immature-immature sessions ($FPF_{imm-ad}/FPF_{imm-ad} + PF_{imm-ad}$) versus ($FPF_{imm-imm}/FPF_{imm-imm} + PF_{imm-imm}$). Immature individuals used preferentially FPF during their sessions with adults than with other immatures (see Table 3.2).

We carried out a similar analysis on the use of Lip Smacking (LS) in the playful context. Adults showed higher frequency of LS (LS per play session) than immature individuals (see Table 3.2). Adults also used LS at comparable levels when playing with immatures and other adults (see Table 3.2). A similar result was also found for immature subjects. They did not show any difference in the use of LS according to the age of play partners (see Table 3.2).

Playful facial displays were performed both by adults and immatures to maintain more than to initiate a play session. In contrast to play signals, LS was performed at similar levels by adults and immatures both to maintain and to initiate a play session (see Table 3.2).

Post-Conflict play sessions were characterized by a higher number of playful facial displays (PF + FPF) compared to Control play sessions (see Table 3.2).

This difference was mainly due to the FPFs that occurred more frequently during Post-Conflict than Control play sessions (Exact Wilcoxon's $T = 14.00$, $n = 13$, ties = 0, $p = 0.027$; Figure 3.3a). The use of PF did not show any variation between the two contexts considered (Exact Wilcoxon's $T = 42.00$, $n = 13$, ties = 0, $p = 0.839$; Figure 3.3b). No difference was also found for LS (see Table 3.2). We included in this analysis only those animals (adults

and immatures) that played in both conditions (Post-Conflict/Control). It was not possible to carry out the same analysis on immature-immature play sessions due to their extremely low frequency in the Post-Conflict context.

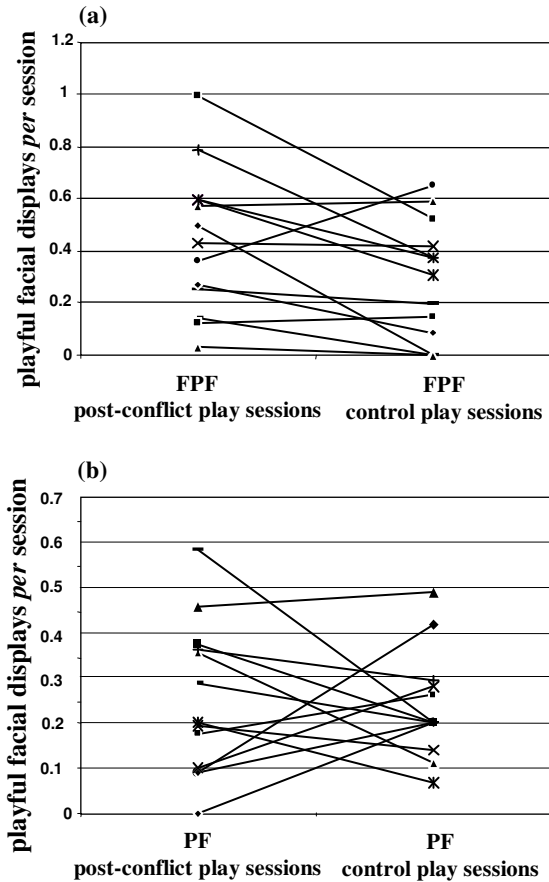


Figure 3.3 - Frequency of FPF (a) and PF (b) per play session occurred in Post-Conflict (play sessions occurring within a 10-min time-window after an aggressive event) and Control conditions (playful encounters not preceded by any agonistic event or occurring outside the 10 min time-window)

Considering only adult immature play, there was no difference in the overall levels of playful facial displays during Rough and Gentle play. Yet, FPF was more common during Rough than Gentle play sessions; on the other hand, PF did not show any difference between the two play modalities (see Table 3.2). This analysis was possible only on those animals (seven adults and seven immature subjects) which engaged in both Rough and Gentle play sessions.

Considering immature-immature play sessions, we found a significant difference in the use of playful facial displays according to the roughness of the play session ($R > G$). The difference in the overall play faces was mainly due to the use of PF which was particularly frequent during Rough sessions ($R > G$); on the other hand, no difference was found for FPF (see Table 3.2). This analysis was possible only on those animals (10 immature subjects) which engaged in both Rough and Gentle play sessions.

A similar analysis carried out on LS gave the following results. As for adult-immature play, there was no significant difference in the use of LS between Rough and Gentle sessions. Similarly, for immature-immature play no difference was found in the use of LS between the two play modalities (see Table 3.2).

3.3.2 Signal Responsiveness: The Age-Effect

The mean immature responsiveness to adult playful facial displays was $45.11\% \pm 17.4$ CI. The adults responded with a playful signal to an immature facial expression in $62.92\% \pm 16.2$ CI of cases. The level of adult responsiveness tended to be higher than that shown by immature subjects (see Table 3.2).

Adults elicited higher levels of immature response (PF + FPF) by performing PF more than FPF. Three adults were discarded from the analysis because they did not show both configurations when playing with immature subjects. On the other hand, immature PF and FPF elicited a comparable response by adult receivers (see Table 3.2). Four juveniles were eliminated from the analysis because they did not use both PF and FPF during their play sessions with adults.

3.3.3 The Complementary Use of Different Facial Displays

There was a significant negative correlation between playful signals (PF + FPF) and LS during overall play sessions (Spearman, $r_s = 0.48$, $n = 17$, $p = 0.045$; see Figure 3.4). In this analysis we included only those sessions where at least one pattern of both facial expressions was present (PF + FPF and LS). For this reason three subjects were excluded from the analysis. Taking into account kin relationships we did not find any significance difference in the use of play signals (PF + FPF) by adult females

toward their offspring (parental coefficient = 0.5) and other immature subjects (parental coefficient < 0.5; see Table 3.2). When we performed the same analysis for PF and FPF separately, we found an interesting result. PF frequency did not differ between the two conditions (kin vs. non-kin; see Table 3.2); on the contrary, adult females performed more FPF when they played with their offspring (see Table 3.2). The analysis of LS showed an opposite trend; in fact, adult females performed LS more frequently toward nonkin than toward kin (see Table 3.2).

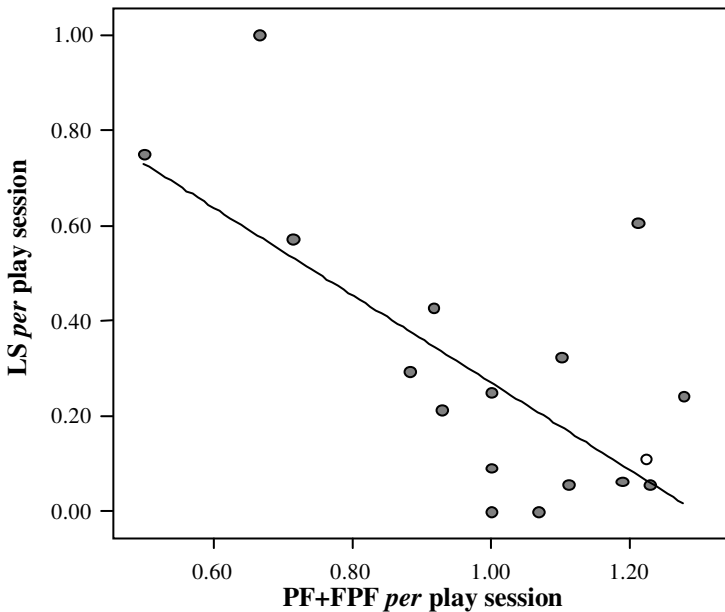


Figure 3.4 - Scatterplot showing the negative correlation between the frequency of play signals (FPF + PF) and LS per play session.

Table 3.2 - Summary of the Results Discussed in Chapter 3

Strategic use of playful signals as a function of the age of playmates	Statistic values	Sample size	<i>p</i>
Adult vs. immature play signals (PF+FPF)	Mann-Whitney's U=52.00	Nad=9 Nim=11	0.848
FPF performed vs. FPF received by immatures during Ad-Im sessions	Paired sample randomization test t=3.846	Ndyads=47	0.0001
PF performed vs. PF received by immatures during Ad-Im sessions	Paired sample randomization test t=2.314	Ndyads=47	0.0016
FPF performed by adults during Ad-Im vs Ad-Ad play sessions	Wilcoxon's T=4.50	Nad=7	0.250
FPF performed by immatures during Ad-Im vs. Im-Im sessions	Wilcoxon's T=3.00	Nim=11	0.010
Adult LS vs. immature LS	Mann-Whitney's U=8.00	Nad=9 Nim=11	0.029
LS performed by adults during Ad-Imm vs. Ad-Ad sessions	Wilcoxon's T=1.00	Nad=7	0.688
LS performed by immatures during Ad-Imm vs. Im-Im sessions	Wilcoxon's T=13.00	Nim=11	0.160
Adult play signals (PF+FPF) to initiate vs. maintain a session	Wilcoxon's T=0.00	Nad=9	0.004
Immature play signals (PF+FPF) to initiate vs. maintain a session (Im-Ad)	Wilcoxon's T=0.00	Nim=10	0.002
Immature play signals (PF+FPF) to initiate vs. maintain a session (Im-Im)	Wilcoxon's T=0.00	Nim=10	0.002
Adult LS used to initiate vs. maintain a session	Wilcoxon's T=13.00	Nad = 9	0.938
Immature LS to initiate vs. maintain a session (Im-Ad)	Wilcoxon's T=7.00	Nim=10	0.531
Immature LS to initiate vs. maintain a session (Im-Im)	Wilcoxon's T=12.00	Nim=10	0.461
Play signals (PF+FPF) in Post-Conflict vs. Control sessions	Wilcoxon's T=15.00	Nim+ad=13	0.032

LS in Post-Conflict vs. Control sessions	Wilcoxon's T=24.50	Nim+ad=13	0.274
Play signals (PF+FPF) in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=26.00	Nim+ad=14	0.104
FPF in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=22.00	Nim+ad=14	0.050
PF in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=40.00	Nim+ad=14	0.735
Play signals (PF+FPF) in Rough vs. Gentle sessions (Im-Im)	Wilcoxon's T=1.00	Nim=10	0.004
FPF in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=25.00	Nim=10	0.846
PF in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=1.00	Nim=10	0.0002
LS in Rough vs. Gentle sessions (Im-Ad)	Wilcoxon's T=27.00	Nim+ad=14	0.119
LS in Rough vs. Gentle sessions (Im-Im)	Wilcoxon's T=16.00	Nim=10	0.496
Signal responsiveness: the age-effect Adult vs. immature responsiveness	Mann-Whitney's U=25.00	Nad=9 Nim=11	0.055
Immature responsiveness to adult PF vs. adult FPF	Wilcoxon's T=1.00	Nad=6	0.060
Adult responsiveness to immature PF vs. immature FPF	Wilcoxon's T=9.00	Nim=7	0.844
Female play signals (PF+FPF) during play sessions with kin and non-kin	Wilcoxon's T=4.00	NAd-fem=8	0.219
Female PF during play sessions with kin and non-kin	Wilcoxon's T=6.00	NAd-fem=8	0.219
Female FPF during play sessions with kin and non-kin	Wilcoxon's T=2.00	NAd-fem=8	0.047
Female LS during play sessions with kin and non-kin	Wilcoxon's T=0.00	NAd-fem=8	0.016

Note: PF = play face; FPF = full play face; LS = Lip-smacking; Im= immatures; Ad = Adults; Ad-fem = Adult females

3.4 DISCUSSION

3.4.1 Strategic Use of Playful Signals as a Function of the Age of Playmates

In geladas, the two playful facial configurations (play face, PF, and full play face, FPF) followed an ontogenetic transition, with immatures using preferentially the PF (see Figure 3.5) and adults performing mainly the FPF (Figure 3.1 and 3.6). Adults showed comparable levels of FPF both during adult-immature and adult-adult play; on the other hand, the rates of immature FPF were higher when juveniles played with



Figure 3.5 - Play session between a black infant (right) and an infant (left). The black infant is performing a play face (PF). (Photo by P.F Ferrari)

adults than with peers. Yet, during age-mismatched sessions playful facial signals were generally directed from adults toward immatures thus showing a strong unidirectionality.

The ontogenetic transition from PF to FPF found in geladas seems to reflect the phylogenetic sequence of the two playful

facial configurations. FPF, which probably evolved independently several times in different lineages, is considered a derived form (apomorphism) of the most ancestral version (PF, plesiomorphism; Lockard *et al.*, 1977; van Hooff, 1972). 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 (*Macaca tonkeana*, *Macaca silenus*, *Pan paniscus* and *Theropithecus gelada*), features that promote the maintenance of a conspicuous play activity also during adulthood (Mancini & Palagi, 2009; Palagi, 2006). Differently from other “totipotent” signals, which can acquire different meanings as a function of the context and the species in which they occur (Bout & Thierry, 2005; De Marco & Visalberghi, 2007; Preuschoft & van Hooff, 1995; Thierry *et al.*, 1989), PF and FPF are context specific and, due to their nature, they are exclusively part of playful interactions. Therefore, the most conservative interpretation to explain the patchy phylogenetic pattern of FPF is that adults belonging to highly playful and tolerant species have the possibility to perform the display. Further support for such parsimonious interpretation comes from recent comparative studies on bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). In contrast to chimpanzees, bonobos live in an

egalitarian society characterized by high tolerance levels among companions.

Despite the phylogenetic closeness of the two species, Palagi (2006) found a striking difference in the adult playful attitude and in the use of playful facial signals. Adult bonobos are more playful than chimpanzees and perform higher levels of FPF. Moreover, FPF in bonobos shows the typical ontogenetic pattern apparently not present in chimpanzees.

3.4.2 What Can Be the Adaptive Explanation for the Ontogenetic Transition of Play Signals?

The function of playful facial displays can be twofold. They can play a role as communicatory displays and/or can be a prelude to lunging for a bite (Pellis & Pellis, 1997; Poole, 1978). Our data seem to support the first viewpoint; in fact, the percentages of play signals followed by a bite during social play were extremely low for both immature and adult subjects.

As already stated (see Introduction 3.1), in the notably tolerant cercopithecine species FPF can be viewed as a mixture of two different facial expressions - bared-teeth and play face - occurring during positive social interactions (e.g., affiliation, reconciliation, appeasement) and play, respectively (Thierry *et al.*, 1989). This is consistent with our finding showing the massive use of FPF by adult geladas. Moreover, from a perceptive point of

view, FPF is a more effective and less ambiguous facial display because it can be visually perceived at longer distances compared to PF (Palagi, 2008; Figure 3.5 and 3.6). In an elegant study, Flack, Jeannotte & de Waal (2004) demonstrated that adolescent chimpanzees increased their playful signals in presence of mothers of the younger playmates, especially when the roughness of play was high. Therefore, chimpanzees modulated play signals not only to manage the play session itself but also to manipulate the social context in which the session occurred. Under stressful situations, adult human beings use laughter instrumentally to maintain emotional and social homeostasis: emotionally “to laugh away one’s distress” or socially “to laugh to break the ice” (van Hooff, 1989, p. 128). Similarly, fine-tuning of the play session (Palagi *et al.*, 2007) and the “audience” effect (Russell & Fernandez-Dols, 1997) may have a role in the FPF selectivity by adult geladas. Intriguingly, even though the PF is the typical expression of gelada immature phase, infants and juveniles selectively used the FPF when playing with adults thus suggesting the value of such facial display during age-mismatched play sessions. Moreover, FPF has a strategic role during adult-immature sessions characterized by play fighting and those occurring after a serious aggressive event (Post-Conflict play). Probably, the bared-teeth component incorporated

within the gelada FPF can help to maintain a playful mood by adding an affiliative factor, especially useful during those interactions characterized by asymmetries in body size, age and status. When animals play fight they use patterns borrowed from other agonistic functional behaviours (Pellis & Pellis, 2009). Since these actions are not intrinsically different from their “serious” counterpart, it may be hard to distinguish them and, in these cases, more redundant and appeasement signals are required to avoid playful interactions escalating into real conflicts. FPF may also have an important role especially when play occurs in a highly social tension situation (after an intra-group aggression). In the parallel way, an increase of distress in humans may be prevented by laughing appropriately (as a corrective response) in a playful atmosphere thus maintaining a cooperative propensity and group integrity (van Hooff, 1989). In this view, laughter in humans and FPF in geladas (and other primate species) may be used as a counter mechanism to give real aggression no chance.



Figure 3.6 - Play session between an adult female and a juvenile male. Both animals show a FPF while having a face-to-face interaction. The face of the individuals performing FPF is not relaxed, but rather, the upper lip is actively retracted. A bystander (a juvenile male) is witnessing the session at close distance.
(Photo by M. Pusceddu)

3.4.3 Signal Responsiveness: The Age-Effect

The analysis on immediate signal responsiveness showed that adults were generally more sensitive than immature to playful facial expressions performed by playmates. This result could be linked to the immature selectivity in responding to adult PF more often than to adult FPF. In contrast, adults did not vary their own response as a function of immature signal modality. All these findings suggest that the “age-effect” has an impact on signal responsiveness as well.

Facial responsiveness (or contagion) 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, 2004). Maintaining a playful facial chattering implies high costs in terms of attentional investment. Schmidt & Cohn (2001, p. 14) suggested that, in humans, facial responsiveness requires attention and attention requires “the redirection of the sender’s neural processing and perception toward one interactant and away from others.” The suitability of the signal can be preserved only by paying attention to the receiver and to the progress of the social interaction. In this view, it seems that adult geladas are more inclined than immature subjects to undertake such attentional costs. Moreover, previous playful experience (Pellis & Pellis, 2006), social competence (Pellis & Pellis, 2009), and neural circuit maturation (Ferrari *et al.*, 2009b) may be at the basis of adult sensitiveness in responding to play faces of the other individual (see Figure 3.6). In this view, the selectivity shown by infants and juveniles to respond to PF more than to FPF could reflect the ontogenetic transition of the two facial displays. It would be interesting to investigate whether possible action-perception mechanisms (based on mirror neuron system, Ferrari *et al.*, 2009c) are at the basis of the playful facial responsiveness found in geladas. Particularly, if the phenomena

of rapid facial mimicry (Davila-Ross *et al.*, 2008) and matching response (Palagi *et al.*, 2009) are implied in the use of PF and FPF, separately.

3.4.4 The Complementary Use of Different Facial Displays

Lip smacking (LS) is present in many cercopithecine species and in a variety of social contexts. It may be used as a reassuring display after a conflict to communicate an intention to engage in affiliation (Leone & Palagi, 2010; Maestripieri & Wallen, 1997). Furthermore, LS is often associated with affiliative (e.g., grooming), sexual, and parental care behaviours (Andrew, 1963; Ferrari *et al.*, 2009a; van Hooff, 1967). In some macaque species, anecdotal reports suggest that LS occasionally is used to initiate playful activity (Preuschoft, 1992). In contrast to macaques, geladas punctuate their playful interactions with a certain amount of LS which is performed both to initiate and to maintain the session. Yet, LS does not seem to be used to manage vigorous and risky sessions, even though it is performed largely by adults during age-mismatched play interactions.

The negative correlation found between LS and playful displays suggests that nonspecific signals are recruited when the specific ones are not sufficient to negotiate the play session. This finding suggests that the meaning of the LS as an appeasement

signal is maintained during playful interactions. This interpretation is supported by the high levels of LS recruitment during those play sessions occurring between adult females and unrelated immature subjects: females frequently lip smacked to juveniles. An opposite kin-biased trend is shown by FPF, which appears to be more frequently used by mothers when playing with their own offspring.

The use of reassuring signals (LS in geladas, this work; conscious smiling in humans, DePaulo, 1992) between individuals sharing a low degree of familiarity could have the primary goal of self-presentation of the sender thus favouring the onset/maintenance of social cooperative interactions. On the other hand, different kinds of facial displays such as unconscious laughing in humans (Mehu & Dunbar, 2008; Schimdt & Cohn, 2001) and playful expressions in geladas could be reserved for close friends and/or relatives in leisure situations. Even though the emotional and adaptive interpretation of facial expressions cannot be completely disentangled, under some intimate circumstances (e.g., mother offspring play activity) facial displays could be primarily linked to the spontaneous expression of emotional states of the sender more than to the strategic transfer of actual information to the receiver.

- CHAPTER 4 -

**“RAPID FACIAL MIMICRY IN GELADAS: A
PLAYFUL FACIAL MATCHING TO BE EMOTIONALLY
CONNECTED WITH OTHERS”**



Photo by M. Pusceddu

ABSTRACT

Rapid facial mimicry (RFM) is an automatic response, in which individuals mimic others' expressions. RFM, only demonstrated in humans and apes, is grounded in the automatic perception-action coupling of sensorimotor information occurring in the mirror neuron system. In humans, RFM reflects the capacity of individuals to empathize with others. Here, we demonstrated that RFM is also present in a cercopithecoid species (*Theropithecus gelada*) and provided evidence of the link between behavioural matching and emotional connection. Mother-infant dyads showed not only higher levels of RFM compared to the unrelated dyads, but they also showed the fastest responses. Our findings indicate that the building blocks of empathy linked to RFM in humans have homologous not only in apes, but also in cercopithecoids. Moreover, data point to similarities in the modality in which mother-infant synchronous behaviours are expressed among primates, suggesting a common evolutionary root in the basic elements of mother-infant affective exchanges.

Keywords: Play face/Full play face; Response latency; Affective exchange; Emotional contagion; Mirror neuron system; *Theropithecus gelada*

4.1 INTRODUCTION

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. Numerous studies document that people mimic emotional facial expressions of others within 1,000 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 & Thunberg, 1998), whose congruent reactions are elicited more frequently and rapidly in response to a dynamic facial expression compared to a static one (Sato & Yoshikawa, 2007).

RFM has been proposed to be grounded in 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, they 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 & Palagi, 2011). Therefore, RFM could be advantageous to promote social connections and affiliative behaviours among individuals (de Waal & Ferrari, 2010; Paukner *et al.*, 2009). Despite the hypothetical link between the phenomenon of RFM and the inter-individual emotional connection, no study has ever empirically tested this hypothesis (emotional connection hypothesis, ECH). In line with this, RFM has never been investigated in mother-infant interactions, in which the emotional engagement is extremely high and thus, for

this reason, it could represent an optimal social model to verify this hypothesis.

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 with high levels of social tolerance (Davila-Ross *et al.*, 2008). In nonhuman primates RFM has been only investigated in the orang-utan, *Pongo pygmaeus*. In this study, orang-utans viewed a playful facial expression performed by a playmate and then produced a congruent expression within 1 sec. Such response appears to be homologous with RFM in hominoidea (Davila-Ross *et al.*, 2008).

Here we investigated the presence of RFM in a cercopithecoid species, the gelada (*Theropithecus gelada*). We focussed on geladas because they a) are extremely playful even as adults (Mancini & Palagi, 2009), b) show high levels of social tolerance (Leone & Palagi, 2010) and c) have a rich repertoire of facial expressions (Dunbar & Dunbar, 1975; Palagi & Mancini, 2011 or see Chapter 3; see Table 2.1 for facial displays definitions). In addition to these important behavioural features, a recent finding of yawn contagion in geladas suggests that they are sensitive to the facial expressions of conspecifics with whom they are closely affiliated (Palagi *et al.*, 2009).

Based on the ECH, we expect that RFM is present in all age classes of this monkey species (Prediction 1), and it is more frequent among closely related individuals, compared to unrelated ones (Prediction 2). Therefore, we predict that mother-infant dyads are characterized by more accurate and faster facial responses compared to unrelated dyads (Prediction 3).

4.2 METHODS

4.2.1 Data Collection Procedure

Dyadic play bouts (n=1121) of everyday social encounters of 18 adults (adults and sub-adults) and 16 immature subjects (juveniles, infants and black infants) were video-recorded during a 4-month period in 2009 (June-September) and a 2-month period in 2010 (July-August) (see Tables 2.3 and 2.4 for group's composition and age-class definition). Video-analysis was conducted using Kinovea v. 0.7.10 software.

We focussed our analysis on two playful expression variants in *Theropithecus gelada*: the play face (PF) and the full play face (FPF). Since, during playful events immature and adult geladas frequently lip smacked (LS) toward conspecifics, we measured LS as a control (for facial expressions definitions see Table 2.1).

Videometric analyses of facial displays were primarily conducted by G.M. Interobserver reliability was tested by G.M. and E.P. with one-frame accuracy (one frame/4msec). The mean

Cohen's kappa values obtained were: $k_{PF} = 0.78$; $k_{FPF} = 0.81$; $k_{LS} = 0.76$.

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 were the first playmates that emitted a facial stimulus (PF, FPF or LS). 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 a LS, 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 LS as the stimulus. Observers who never displayed PF, FPF, or LS in response to a previous stimulus were excluded from the analysis.

Furthermore, for PF and FPF, we distinguished the *matching-* from *non matching-response*. The *matching-response* occurred when the observer mirrored the same facial display of the trigger (stimulus PF/response PF; stimulus FPF/response FPF). In contrast, we defined a behaviour as a *non-matching-response* when the observer's reaction did not match the trigger's facial display (stimulus PF/response FPF; stimulus FPF/response PF).

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.

4.2.2 Statistical Analysis

Due to non-normal data distribution, we employed nonparametric statistics (Siegel & Castellan, 1988). To compare the frequency and the latency of the observer's response we applied the Friedman test when $k > 2$ and the Wilcoxon's matched pairs sign rank test when $k = 2$. The Mann-Whitney U-test was used to compare the frequency of responses for immature subjects and adults. Statistical analyses were performed using SPSS 17.0 software. Exact tests were used

according to the threshold values as suggested by Mundry & Fisher (1998).

4.3 RESULTS

4.3.1 Prediction 1

The frequency of the three types of response significantly differed (*congruent*, *incongruent*, and *no-response*) both in adult (Exact Friedman's $\chi^2 = 31.11$, $n = 18$, d.f. = 2, $p = 0.0001$) (Figure 4.1a) and in immature subjects (Exact Friedman's $\chi^2 = 28.50$, $n = 16$, d.f. = 2, $p = 0.0001$) (Figure 4.1b). The frequency of congruent responses was higher (*Median* = 0.99; *min value* = 0.67, *max value* = 1.00) than incongruent responses (*Median* = 0.01; *min value* = 0.00, *max value* = 0.34), but only when the trigger stimulus was a PF or a FPF (Exact Wilcoxon's $T = 0$, *ties* = 0, $n = 34$, $p = 0.0001$). When the trigger stimulus was a lip-smacking (LS) the congruent responses (*Median* = 0.00; *min value* = 0.00, *max value* = 1.00) did not significantly differ from the incongruent responses (*Median* = 1.00; *min value* = 0.00, *max value* = 1.00) (Exact Wilcoxon's $T = 80.50$, *ties* = 0, $n = 22$, $p = 0.134$). These results confirm the presence of RFM in geladas.

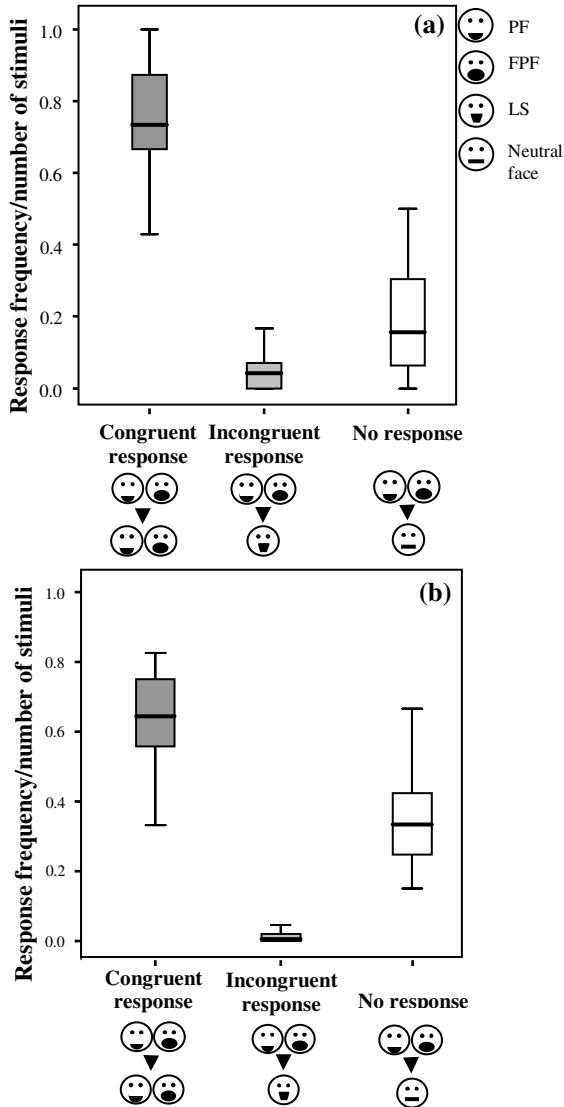


Figure 4.1 - Rapid facial mimicry in adult and immature individuals: RFM events per number of trigger stimuli, when the observer was an adult **(a)** and an immature individual **(b)**. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

Congruent responses were faster than incongruent responses (Exact Wilcoxon's $T = 46.00$, $ties = 1$, $n = 23$, $p = 0.014$) (Figure 4.2). Adult ($Median = 0.41$; $min\ value = 0.33$, $max\ value = 0.67$) and immature subjects ($Median = 0.37$; $min\ value = 0.31$, $max\ value = 0.45$) did not differ in the latency of their congruent responses (Exact Mann-Whitney $U = 52.50$, $n_{ad} = 11$, $n_{imm} = 12$, $p = 0.42$).

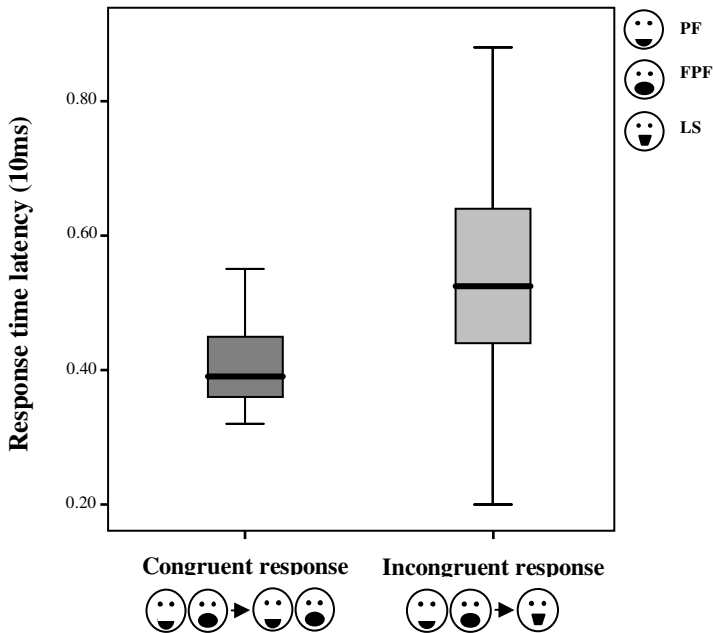


Figure 4.2 – Congruent vs incongruent response latency

Response time latency (10ms) recorded for congruent and incongruent responses. Data are referring to both adult and immature subjects. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

Since in elder subjects PF is virtually absent (during ontogeny PF is replaced by FPF, Palagi & Mancini, 2011), the matching analysis for PF was limited to immature subjects. When the stimulus was a PF or a FPF the observer reacted significantly more frequently with a matching (PF/PF or FPF/FPF; *Median* = 0.78; *min value* = 0.40, *max value* = 0.95) than a non-matching response (PF/FPF or FPF/PF; *Median* = 0.22; *min value* = 0.04, *max value* = 0.59) (Exact Wilcoxon's $T = 1.00$, *ties* = 0, $n = 16$, $p = 0.0001$). The matched responses were more rapid than the non-matching responses (Exact Wilcoxon's $T = 6.00$, *ties* = 1, $n = 16$, $p = 0.001$) (Figure 4.3).

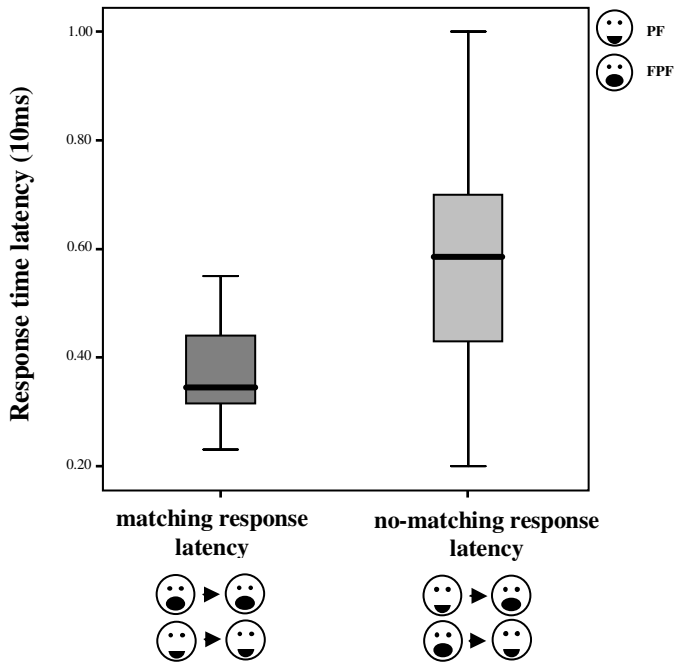


Figure 4.3 - Matching vs no-matching response latency

Response time latency (10ms) recorded for matching and non-matching responses. Data are referring to only immature subjects. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

4.3.2 Prediction 2

Though immature individuals were equally likely to play with their mothers and other unrelated adults (Exact Wilcoxon's $T = 52.00$, $ties = 0$, $n = 16$, $p = 0.433$), they showed higher levels of RFM with the former compared to the latter (Exact Wilcoxon's $T = 15.00$, $ties = 0$, $n = 13$, $p = 0.032$, Figure 4.4). Three immature subjects were excluded from the analysis because they have never played with other adults.

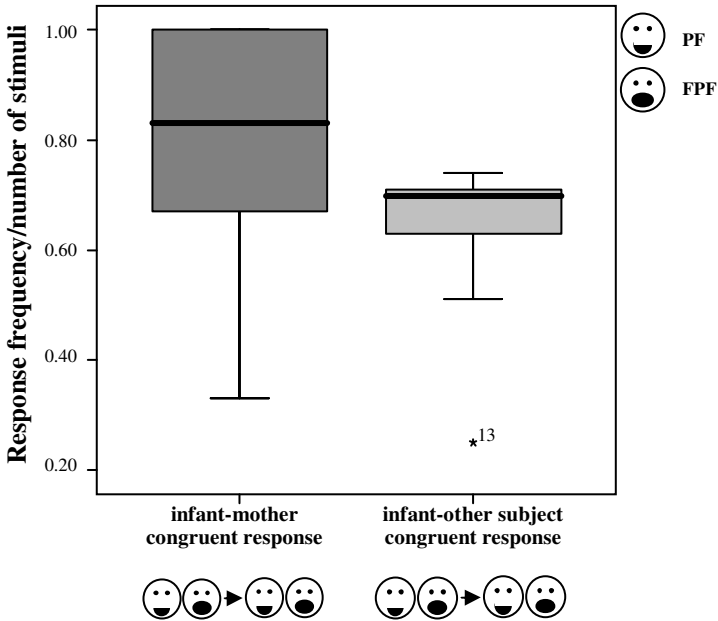


Figure 4.4 – Rapid facial mimicry: infant-mother dyads vs infant-other conspecific dyads: frequency of the congruent responses (RFM event per number of PF and FPF perceived) exchanged between infants and their mothers and between infants and other unrelated group-members. Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

4.3.3 Prediction 3

The reciprocal RFM was faster between mothers and offsprings than between unrelated adults and immature individuals (Exact Wilcoxon's $T = 5.00$, $ties = 1$, $n = 13$, $p = 0.006$, Figure 4.5).

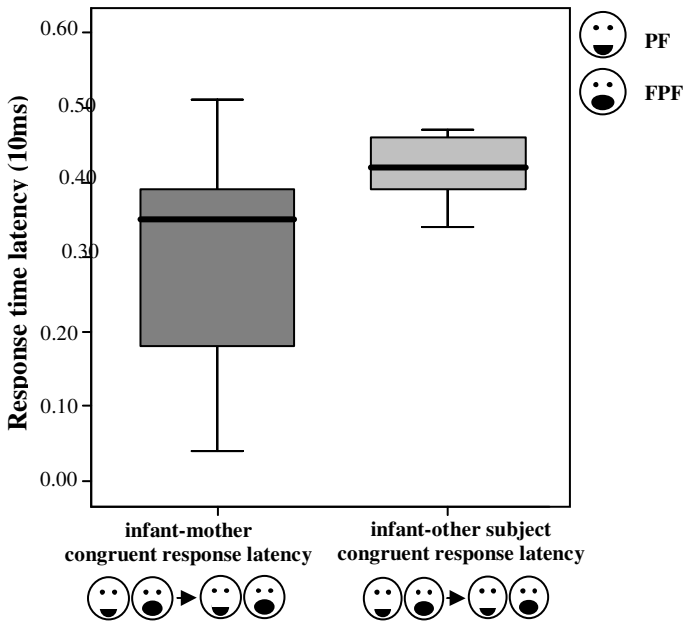


Figure 4.5 – Response latency: infant-mother dyads vs infant-other conspecific dyads

Response latencies for congruent responses exchanged between infants and their mothers, and congruent responses exchanged between infants and other unrelated group-member. Thick horizontal lines indicate medians; the height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

4.4 DISCUSSION

In the present study, we provide evidence that RFM occurs in a non-ape species, the gelada. Moreover, as expected, both immature and adult subjects mimicked play faces (PF/FPF) (Figure 4.6) but not lip-smacking (LS) (Prediction 1 supported). Since our analysis considered two different displays (PF and FPF), we additionally assessed the accuracy of geladas' RFM. The use of a third facial expression (LS) as a control gave further solidity to our findings. As we predicted, the RFM was not found



Figure 4.6 – An example of matching response in RFM

RFM during a play session between an adult (left) and an immature individual (right). The immature mimics the adult's full play face (FPF) (congruent and matching response). (Photo by P.F. Ferrari)

for LS, which is a signal that can elicit different behavioural responses depending on the target animal to which is directed and the context in which it is used (Maestriperi, 1997; see Chapter 3, Palagi & Mancini, 2011).

Why do play faces elicit mimicry? Different from LS, the primate play face (PF and FPF) is strongly linked to a positive emotional self-reward behaviour, that is play (van Hooff & Preuschoft,

2003), and it is considered homologous to human's laughter (for an extensive review see Niedenthal *et al.*, 2010). Human laughter is found across cultures and is the external manifestation of joy and happiness (Sauter *et al.*, 2010). The primate play face can, through RFM, evoke in the perceiver a similar positive emotional state (Decety & Meyer, 2008; Mehu *et al.*, 2007). Indeed, this ability to instantly understand the emotional states of others is adaptive, as it allows an individual to foresee the playmate's intentions (Palagi, 2008) and fine-tune its own motor sequences accordingly (see Chapter 3, Palagi & Mancini, 2011). Such ability is a prerequisite to avoid any misunderstanding, manage a playful interaction successfully, and promote social affiliation (Pellis & Pellis, 2009).

The presence of both PF and FPF in gelada immature subjects (see Chapter 3, Palagi & Mancini, 2011) allowed us to test the accuracy of RFM by examining the occurrence of facial matching (PF/PF; FPF/FPF). We found that animals exactly matched the facial expression perceived, a phenomenon already demonstrated for yawn contagion in the adult females of the same species (Palagi *et al.*, 2009). Moreover, compared to the non-matching response, the matching responses were characterized by shorter latencies. In humans (Niedenthal *et al.*, 2010; Norscia & Palagi, 2011), mimicking others' facial expressions facilitates the

recognition of the emotional state underlying such facial expressions. For example, Stel & van Knippenberg (Stel & Knippenberg, 2008) showed that blocking mimicry influenced humans' speed of facial expression recognition, but not the skill of categorizing facial expressions as positive (i.e. happiness, joy) or negative (i.e. sadness, anger). Moreover, humans scoring high levels of RFM tended to have also high levels of empathy (Stel & Knippenberg, 2008). Taken together, these findings strongly suggest that RFM is important in the recognition process when it requires fine distinctions of similar facial expressions conveying subtle differences in meaning (Palagi & Mancini, 2011), such as the processing of different smile types in humans (Niedenthal *et al.*, 2010).

In terms of proximate mechanisms responsible for RFM, it has been previously hypothesized that activating shared motor representation could explain it, at least in part. Individuals can understand the meaning of an action performed by another individual through a direct activation of a corresponding motor representation (Gallese *et al.*, 1996; Fogassi & Ferrari, 2010; Rizzolatti & Craighero, 2004). Normally, during action observation the motor output (i.e., the cortico-spinal tract, the muscles, etc.) is suppressed because some of the components of the motor network are not active. However, neural matching

mechanisms, in conjunction with other motor areas, can produce an overt activation of the observed behaviours (Ferrari *et al.*, 2009c; Kraskov *et al.*, 2009; Rizzolatti *et al.*, 2001). In humans, such mirroring activity may have implications for the capacity of individuals to empathize with others (Avenanti *et al.*, 2005; Norscia & Palagi, 2011; Pfeifer *et al.*, 2008; Zaki *et al.*, 2009). While the correlation between the activity of mirror system and empathy is supported by several fMRI (functional magnetic resonance imaging) investigations, more recently it has been also shown that behavioural synchrony and matching activate neural circuits involved in reward and positive affect. In fact, research using infrared spectroscopy demonstrated that in both mothers and infants there is an increase in activation of the orbitofrontal cortex in response to the smile of one's own infant or mother, respectively (Minagawa-Kawai *et al.*, 2009). Our findings provide further behavioural evidence of the link between behavioural matching and emotional connection; in fact, mother-infant dyads were characterized by higher levels of RFM compared to the unrelated dyads (Figure 4.7) (Prediction 2 supported) and by the lowest time delay in the response (Prediction 3 supported). The temporal coordination of face-to-face interaction that occurs between mothers and infants has been extensively documented in humans (Feldman, 2007). Such moments of affective matching are

important for the neuro-physiological maturation and for the functional attachment relationship of the infant with the caregiver (Feldman, 2010). RFM probably reflects one of the core elements of the mother-infant relationship and might represent an important indicator of the quality of such relationship.



Figure 4.7 - An example of incongruent response

Infant's incongruent response (right) to the facial expression of an unrelated female (left). Infant is performing a play face (PF) and adult female lip smacking (LS). (Photo by P.F. Ferrari)

In conclusion, our findings point to similarities across diverse primate taxa in the process in which synchronous behaviours are expressed. This suggests a common evolutionary root in the fundamental elements of affective exchanges which are at the basis of inter-individual emotional connection. In primates, including humans, the emotional connection, based on face-to-face interactions, is already evident in the mother-infant relationship and fundamental for sustaining and nurturing healthy attachment in the first phases of life (Ferrari *et al.*, 2009a). This affective

responsiveness is also central for the development of the infant's neuro-physiological system and behavioural competence, which are necessary to gain social advantages in the future.

- CHAPTER 5 -

**“FAST IS BETTER. RAPID FACIAL REPLICATION
PROLONGS GELADA PLAYFUL CONTACTS”**



Photo by M. Pusceddu

ABSTRACT

The primate play face is homologous with human laughter which, across cultures, is the external manifestation of joy and happiness. Through facial mimicry, the play face evokes in the perceiver a similar positive emotional state. This emotional resonance is adaptive, as it allows an individual to foresee playmates' intentions and fine-tune its own motor sequences accordingly. Facial replication can be fast (automatic response within 1.0 s) and delayed (non-automatic responses within 5.0 s). Different from the former, the latter is probably less spontaneous and genuine, not completely linked to the subject's emotional state. Here, we demonstrated that in geladas, although both rapid and delayed replication increased the duration of playful contacts, the former was more effective than the latter in prolonging them. Rapid facial replication, or mimicry, can lead to a greater synchronization and intent matching between the two players thus increasing their trust and cooperation levels. In an evolutionary perspective, our findings suggest that rapid facial mimicry not only was already present in the common ancestor of cercopithecoids and hominoids, but that it has probably played a role also in favouring cooperation and trust, which in humans reach their maximum expression.

Keywords: play face, rapid facial replication, delayed facial replication, play duration length, *Theropithecus gelada*

5.1 INTRODUCTION

Facial displays regulate many aspects of social life such as aggression, dominance-subordinate relationships, appeasement, and play (de Waal, 2003a). Play is an interesting behaviour for examining the role of signals in intentional communication systems (Palagi, 2008). Recently, Pellis & Pellis (2009) suggested that the social play experience affects animal's ability to regulate its emotional response, and this, in turn, affects its ability to perform actions and facial expressions in the appropriate context, thus increasing social competence.

The non-human primate play face is homologous with human laughter (Preuschoft & van Hooff, 1995) which, across the diverse cultures, is the external manifestation of joy and happiness (Sauter *et al.*, 2010). Through facial mimicry, the play face evokes in the perceiver a similar positive emotional state (Decety & Meyer, 2008; Mehu *et al.*, 2007). Understanding instantly others' emotional states is adaptive, as it allows an individual to foresee playmates' intentions (Palagi, 2008) and fine-tune its own motor sequences accordingly (see Chapter 3, Palagi & Mancini, 2011). This ability is a prerequisite to avoid any misunderstanding, manage a playful interaction successfully, promote social affiliation, and favour cooperation (Pellis & Pellis, 2009).

Primate play bouts last more when the play face is bidirectional (Waller & Dunbar, 2005). In chimpanzees, play sessions are sensitive not only to the presence of spontaneous laughter by the two players but also to its replication, or mimicry, in the perceiver. Social play sessions characterized by facial replication lasted more than those sessions punctuated only by spontaneous laughter (Davila Ross *et al.*, 2011).

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).

Chimpanzees not only produce affective laughter (rapid replication) but also laughter that represents a blend of both affective and non-automatic traits (delayed replication). Both of facial replications were equally effective in prolonging the duration of the chimpanzee play sessions (Davila Ross *et al.*, 2011).

Mancini *et al.* (submitted, see Chapter 4) provided evidence that rapid facial mimicry (RFM, congruent facial reactions to the

emotional facial displays of others) occurs in a non-ape species, the gelada (*Theropithecus gelada*), and that both immature and adult subjects mimicked within 1 sec the play faces of others. This finding suggests that an emotional connection through facial communication is also present in cercopithecoids.

Here, we demonstrate that in geladas, although both rapid and delayed facial mimicry increased the duration of playful contacts, the former was much more effective than the latter in prolonging them.

5.2 METHODS

5.2.1 Data Collection Procedures

Dyadic play bouts (n=1121) of everyday social encounters of 18 adults (adults and sub-adults) and 16 immature subjects (juveniles, infants and black infants) were video-recorded during a 4-month period in 2009 (June-September) and a 2-month period in 2010 (July-August) (see Tables 2.2 and 2.3 for group's composition and age-class definition). Video-analysis was conducted using Kinovea v. 0.7.10 software.

We focussed our analysis on two playful expression variants in *Theropithecus gelada*: the play face (PF) and the full play face (FPF). Since, during playful events immature and adult geladas frequently lip smacked (LS) toward conspecifics, we measured LS as a control (for facial expressions definitions see Table 2.1).

Videometric analyses of facial displays were primarily conducted by G.M. Interobserver reliability was tested by G.M. and E.P. with one-frame accuracy (one frame/4msec). The mean Cohen's kappa values obtained were: $k_{PF} = 0.78$; $k_{FPF} = 0.81$; $k_{LS} = 0.76$.

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 triggers were the first playmates that emitted a facial stimulus (PF, FPF or LS). 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.

We distinguished four play bout conditions: i) *no facial expressions* (absence of PF/FPF), ii) *facial expressions without response* (PF/FPF perceived without replication), iii) *incongruent facial response* (PF/FPF stimulus and LS response), and iv) *congruent facial response* (PF/FPF stimulus and PF/FPF response).

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 4 seconds (delayed replication). Considering the two time domains and the congruence of response, we distinguished four play bout conditions: i) *incongruent delayed facial response* (1-5 s), ii) *incongruent rapid facial response* (<1 s), iii) *congruent delayed facial replication* (1-5 s), and iv) *congruent rapid facial replication* (<1 s).

5.2.2 Statistical Analysis

Due to non-normal data distribution, we employed nonparametric statistics. To compare the individual mean length of the sessions we applied the Friedman test. In case of significant difference among the play session conditions, we employed the Dunnett's multiple comparison test to determine what pairs of conditions significantly differed. Exact tests were used according to the threshold values as suggested by Mundry & Fisher (1998).

5.3 RESULTS

The play duration length significantly differed across the four conditions (no facial expressions, facial expressions without response, incongruent facial response and congruent facial response) (Exact Friedman's $\chi^2 = 19.800$, $n = 20$, $df = 3$, $p = 0.000$). The Dunnett's post-hoc test revealed that sessions characterized by congruent facial response were longer than those with no facial expressions ($q = 4.41$; $p < 0.01$), facial expressions without response ($q = 2.84$; $p < 0.01$) and incongruent response ($q = 3.13$; $p < 0.01$). Moreover, those sessions characterized by the presence PF/FPF but without any facial response were longer than those sessions characterized by the absence of any facial expression ($q = 4.02$; $p < 0.01$), but did not significantly differ from incongruent facial response sessions ($q = 0.89$; $p > 0.05$) (Figure 5.1).

The duration lengths of play interactions characterized by incongruent DF response, incongruent RF response, congruent DF replication, and congruent RF replication significantly differed as well (Exact Friedman's $\chi^2 = 10.079$, $n = 14$, $df = 3$, $p = 0.015$). The Dunnett's post-hoc test revealed that sessions characterized by the presence of congruent RF replication were longer than those with congruent DF replication ($q = 4.27$; $p < 0.01$), those characterized by the presence of incongruent DF response ($q = 2.01$; $p < 0.05$) and incongruent RF response ($q =$

3.86; $p < 0.01$). Finally, no difference in play duration length was found between the other session's conditions: incongruent DF response vs incongruent RF response ($q = 1.86$; $p > 0.05$); incongruent RF response vs congruent DF replication ($q = 1.20$; $p > 0.05$) and incongruent DF response vs congruent DF replication ($q = 0.03$; $p > 0.05$) (Figure 5.2).

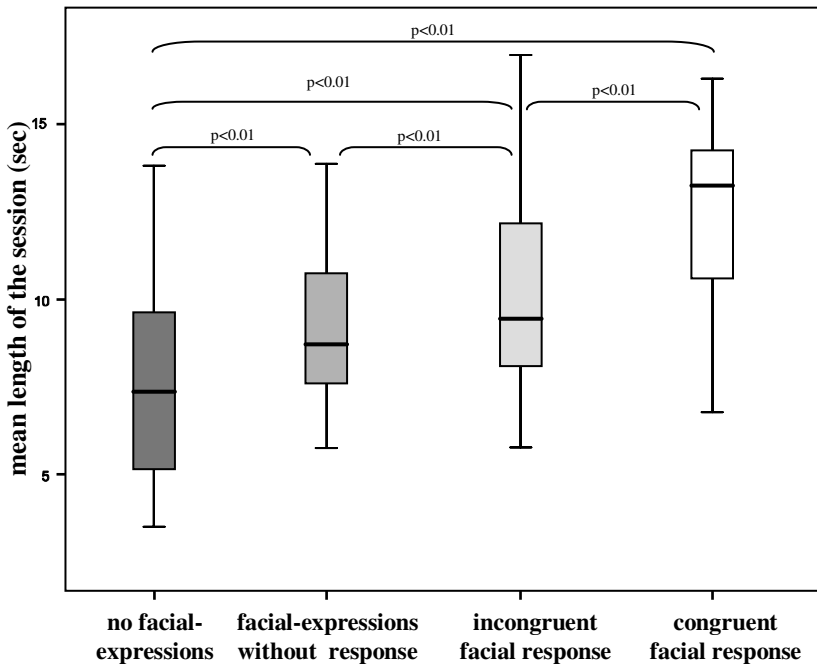


Figure 5.1 - Duration lengths of play sessions characterized by no facial expressions, facial expressions without response, incongruent facial response, and congruent facial replication.

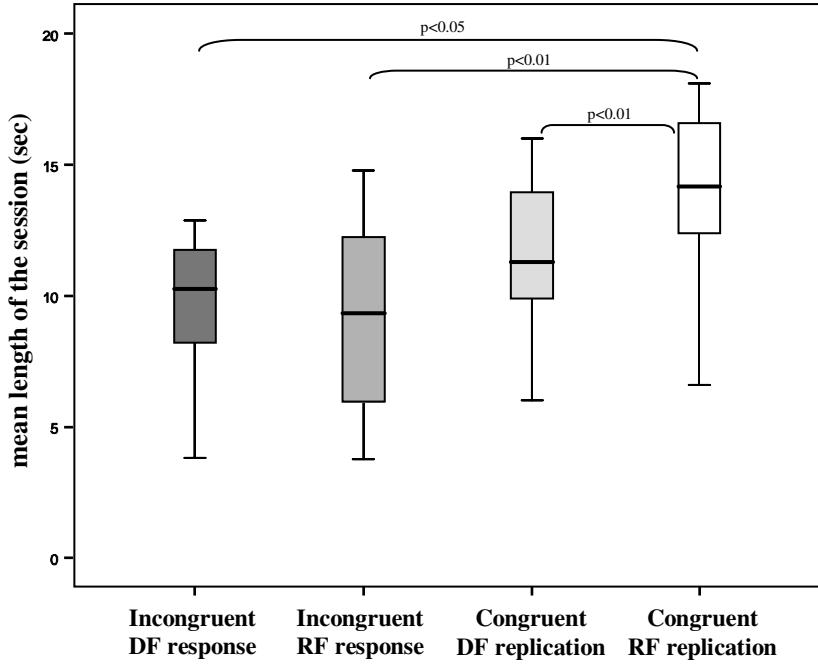


Figure 5.2 - Duration lengths of play sessions characterized by incongruent delayed facial (DF) response, incongruent rapid facial (RF) response, congruent delayed facial (DF) replication, and congruent rapid facial (RF) replication. Only significant results are reported.

5.4 DISCUSSION

In many social interactions uncertainty typically exists about the extent of cooperation to be expected from the interaction. Since trust and cooperation are widely observed in humans and other animals, we have to ask which signals might be used to identify trustworthy partners. One of the proposed functions of human smiling is to advertise cooperative intentions and thereby increase the likelihood that a social partner would invest resources in a relationship. In humans, true smile and laughter, involving strong emotional component, would be honest signals of altruistic propensity because they are not easy to produce voluntarily (Mehu *et al.*, 2007). In animals, facial responsiveness to partners' signals allows individuals to detect contingencies in their social world (see Chapter 3, Palagi & Mancini, 2011), to synchronize their activity (Palagi *et al.* 2009), and to learn the appropriate context in which an action can be performed (Pellis & Pellis, 2009).

In geladas, the longest playful interactions were those characterized by facial congruent replication, this suggests that the effectiveness of the trigger's playful facial expression is amplified when it is replicated by the observer (Figure 5.1). The facial replication, compared to the mere perception of the stimulus (presence of facial expression and incongruent

response), provides an additional representation of the same stimulus, which allows playmates who mimic to receive more input about laughter than playmates who do not mimic (Maringer *et al.*, 2011). Being able to prolong the playful interactions is advantageous for the playmates. Indeed, play is one of the best social tools which lead the individuals to increase their social competence (Pellis & Pellis, 2009), to reinforce social bonds (Mancini & Palagi, 2009), and to manage tension situations (Norscia & Palagi, 2011).

In geladas, the latency of response played a role in the duration of the play session as well. The climax in the play duration length was reached when the facial replication was rapid (within 1 s), thus suggesting that the automatic response is more efficient than the delayed one (Figure 5.2). Although internal and external factors can delay the affective replication, one of the proximate causes could be the suppressing action of the mirror neuron system (Kraskov *et al.*, 2009). Different from the rapid response, the delayed replication is probably less spontaneous and genuine. The rapid facial replication, due to its automatic and spontaneous nature, evokes in the subject the corresponding emotional state underlying the facial expression perceived (facial feedback theory, Niedenthal *et al.*, 2010). This facial and emotional response can lead to a greater social

synchronization and intent matching between the two players thus increasing their trust and cooperation levels, essential features to manage a playful interaction.

In an evolutionary perspective, our finding on geladas means that playful facial replication not only was already present in the common ancestor of cercopithecoids and hominoids, but that it already played a fundamental role in favouring cooperation and trust, which in humans reach their maximum expression.

- CHAPTER 6 -

**“A NATURALISTIC APPROACH TO STUDY NEONTAL
IMITATION IN GELADAS (*Theropithecus gelada*)”**



Photo by M. Pusceddu

ABSTRACT

This work assessed under semi-natural conditions the presence of rapid neonatal imitative responses (Rapid Facial Mimicry, RFM) in a monkey species, the gelada (*Theropithecus gelada*). In particular, our data demonstrated, for the first time in a non-ape species, that newborns are able to respond promptly (within 1 sec) and specifically to facial stimuli received by their mothers or by any other group members. Some authors have suggested that the RFM mechanism can be grounded in the perception-action coupling of automatic sensorimotor information that occurs in the motor brain areas. In this perspective, our results seem to indirectly support the hypothesis of the involvement of a mirroring mechanism in RFM. The study was conducted on 8 geladas infants that, at birth, remained with their mothers in a stable and well bonded social group, in which they had the opportunity to interact freely with other group members. This naturalistic approach gave an important contribution to previous researches on imitative behaviour suggesting that the infant's capacity to respond and solicit facial expressions is critically dependent on the type of social environmental feedback received.

Keywords: neonatal imitation, Rapid Facial Mimicry, mirror neuron system, *Theropithecus gelada*

6.1 INTRODUCTION

Matching one's own behaviour with that of others allows individuals not only to detect contingencies in the social world but also to recognize behaviours by mapping the sensory information related to others on the own motor knowledge. This process could allow an individual to synchronize its activity with those of its group members and to learn the context in which an activity should be performed (Suboski, 1990; Rizzolatti *et al.*, 2001). In humans, imitation is a form of behavioural matching that plays a key role in supporting cultural traditions by facilitating the transmission of knowledge and skills from one generation to another (Tomasello *et al.*, 1993; Matsuzawa *et al.*, 2001). Tracking signs of imitative mechanism early in life is important to understand its development and the biological features eliciting it (Ferrari *et al.*, 2006).

The developmentally earliest form of imitation occurs in newborn's face-to-face interactions with social partners. Since birth, infants can accurately match conspecific's facial expressions (tongue protrusion, open mouth and lip protrusion). This phenomenon was reported in human newborns over 30 years ago (Meltzoff & Moore, 1977), and remains a thriving research topic within social sciences. Part of the persistent interest in neonatal matching mechanism lies on the fact that, from the publication of

the first report, it was clouded in controversy. Several hypotheses have been put forward to identify which mechanisms might underlie neonatal imitation (Meltzoff & Decety, 2003; Jones, 2009; Ferrari *et al.* 2006). One of them claims that, in humans, neonatal imitation is probably accomplished through active inter-modal matching (AIM), mediated by innate representational systems (Meltzoff & Moore, 1977; 1983; 1989). The AIM hypothesis is supported by the evidence that neonatal matching behaviour is present at birth in human and non-human primate infants (chimpanzees, Myowa-Yamakoshi *et al.*, 2004; rhesus macaques, Ferrari *et al.*, 2006). The presence of this phenomenon in other primate species points to similarities in the process in which matching behaviour is expressed, suggesting a common evolutionary root in the basic elements of neonatal imitation in this taxon (Myowa-Yamakoshi *et al.* 2004; Ferrari *et al.* 2006).

A neurophysiological support for the AIM hypothesis proposes that the phenomenon of neonatal facial imitation can rely on a rudimentary mirror mechanism already present at birth that allows the newborn to match the facial features via an internal motor representation (Ferrari *et al.*, 2006; Casile *et al.*, 2011). The idea of a mirror system specialized for imitation was suggested by the discovery of 'mirror' neurons in the macaque premotor and parietal cortex (Gallese *et al.* 1996; Ferrari *et al.*,

2003; Fogassi *et al.*, 2005). Single-cell recordings demonstrated that each neuron responded whenever a particular action was either observed or performed by the monkey (Gallese *et al.* 1996; Rizzolatti *et al.* 1996). In addition, recently a class of mirror neurons responding to facial expressions such as lip smacking and tongue protrusion has been found (Ferrari *et al.*, 2003). The mirror neurons hypothesis is also supported by a recent electroencephalogram study in newborn rhesus macaques showing the activation of sensorimotor cortex during observation and imitation of facial expressions (Ferrari *et al.* in press). Infants clearly demonstrate an innate ability to process facial information also when reared in absence of facial stimuli until the second year of life. Despite the deprivation period, macaque infants preserve the capability to recognize and discriminate facial stimuli (Sugita, 2008). These results suggest that the basic mechanisms for perceiving simple facial displays (lip smacking and tongue protrusion), and the ability to map them on the observer's motor repertoire could be pre-wired thus suggesting the innate nature of the phenomenon (Casile *et al.*, 2011; Ferrari *et al.* in press).

Another explanation of the imitation's origins holds that neonatal capacity of mimic is mediated by an "innate releasing mechanism" based on simple reflexes such as the Moro reflex (Thelen & Smith, 1994; Gottlieb, 2007). Indeed, data obtained

under laboratory conditions indicate that the ability to match the behaviours of others, although present at birth (Anisfeld *et al.*, 2001), disappears at a later stage, at approximately 2-3 months of age in humans and chimpanzees (Jacobson, 1979; Abravenal & Sigafos, 1984; Myowa-Yamakoshi *et al.*, 2004) and in the second week of life in rhesus macaques (Ferrari *et al.*, 2006), to recur later in the course of infant's development. According to Jones (2009) these findings suggest that there is no heritable, modular, specialized mechanism for imitation but, instead, imitative behaviour seems to emerge out at the moment of the infant's acquisition of different kinds of knowledge and motor, cognitive and social skills.

The lack of neonatal imitation at a later stage could be due to the setting under which the experimental trials were conducted. In fact, rearing conditions and the unnatural source of stimuli might account for the limited number of expressions matched and the short time course in which neonatal imitation was observed. It is also possible that infants that are separated from the mother at birth lack the rich social input required to adequately respond to expressions and to maintain such responsiveness over time (Ferrari *et al.* 2006). Moreover, the facial stimuli provided by the experimenter were most likely less salient for monkeys than those routinely provided by conspecifics

(i.e., the mother or group members). These factors could have reduced the effectiveness of the stimulus and, consequently, the amplitude and time course of the imitative response. In addition, because the infant was not emotionally attached to the experimenter, the possible functional meaning of neonatal imitation might have been masked or could not emerge in its complexity (Ferrari *et al.*, 2006).

Based on these considerations, our main purpose is to investigate if in geladas (*Theropithecus gelada*), living under natural conditions, the phenomenon of facial imitation and its possible developmental trajectory is present during the first weeks of life. At birth, gelada newborns remained with their mothers in a stable and well bonded social group, in which they had the opportunity to interact freely with other group members (Figure 6.1). Under such conditions, the newborn received a large amount of different stimuli from its social environment. In order to ascertain that the infant response was actually elicited by the facial expression perceived, we focused our analysis to the responses which were very rapid and occurred within 1 sec from the stimulus perceived. This form of imitation, known as Rapid Facial Mimicry (RFM), has been previously described in anthropoids such as humans, *Homo sapiens* (Beall *et al.*, 2008; Dimberg & Thunberg, 1998) and in orang-utans, *Pongo pygmaeus*

(Davila-Ross *et al.*, 2008). We recently described RFM also in the gelada (Mancini *et al.* submitted, see Chapter 4). The restriction of our analysis to responses that were rapid could possibly have excluded other imitative responses that occurred after a delay as in other works (Ferrari *et al.*, 2006; Paukner *et al.*, 2011; Myowa-Yamakoshi, 2005). However, as also described by others (Ferrari *et al.*, 2009) this methodology has the advantage to restrict the type of responses that from a neurological point of view could be attributed to a direct activation of the descending pathways likely originating in mirror and motor areas. Thus, the hypothesis of a mirror mechanism involvement could be directly tested by using this behavioural analysis.



Figure 6.1 – Example of gelada newborn (called Gaga) that freely interacts with their mother (called Hermine) and other adults female. The early black infant is performing an open mouth display (OM). (Photo by P.F. Ferrari)

6.2 METHODS

6.2.1 Data Collection Procedures

We collected behavioural data during a 6-month period in 2007 (June-November), a 4-month period in 2009 (June-September) and a 2-month period in 2010 (July-August).

For test the presence of RFM in the early stage of life, we video-reordered 8 early black infants (for age-class definitions see Table 2.2, 2.3, 2.4) for the first 15 days of life. We have collected 1904,49 minutes of video recordings.

We focussed our analysis on three infant's facial expression: open mouth (OM, facial display limited at the first stage of infant's life), lip-smacking (LS) and play face (PF) (for facial expressions definitions see Table 2.1). Video analysis was conducted on each infant using Kinovea v. 0.7.10 software. Videometric analyses of facial displays were primarily conducted by G.M. Interobserver reliability was tested by G.M. and E.P. with one-frame accuracy (one frame/4msec). The mean Cohen's kappa values obtained were: $k_{PF} = 0.78$; $k_{OM} = 0.83$; $k_{LS} = 0.76$.

To be reasonably reliable in asserting that the facial expression performed by the infant was actually elicited by the facial expression (LS or PF) performed by mother or other conspecifics (trigger), criteria were that the infant looked at the face of the trigger and did not show any facial expression 1sec

prior to the trigger's stimulus. Chewing behaviours and biting transitional faces were excluded from the analysis to reduce uncertainties.

After the trigger's stimulus (LS or PF), we categorized the infant's behaviour into three possible responses: *congruent*, *incongruent*, and *no-response*. When the infant mimicked the trigger facial expression (PF-response/PF-stimulus; LS-response/LS-stimulus), the response was labelled as *congruent*. When the observer responded with another facial expressions (PF-response/LS-stimulus; LS-response/PF-stimulus; OM-response/LS-stimulus; OM-response/PF-stimulus), the response was labelled as *incongruent*. When the infant did not show any facial reaction (neutral face) we categorized the absence of response as *no-response*.

6.2.2 Statistical Analysis

Due to non-normal data distribution, we employed nonparametric statistics (Siegel & Castellan, 1988). To compare the frequency infant's response we applied the Friedman test when $k > 2$ and the Wilcoxon's matched pairs sign rank test when $k = 2$. Statistical analyses were performed using SPSS 17.0 software. Exact tests were used according to the threshold values as suggested by Mundry & Fisher (1998).

6.3 RESULTS

The infant's responsiveness index (frequency of response/frequency of non-response) was significantly higher in the second week than in the first week of life (Exact Wilcoxon's $T = 0.00$, $ties = 0$, $n = 8$, $p = 0.008$) (Figure 6.2). Similarly, the congruence index (congruent responses/incongruent responses) was significantly higher in the second week than in the first week of life (Exact Wilcoxon's $T = 0.00$, $ties = 0$, $n = 6$, $p = 0.031$) (Figure 6.3).

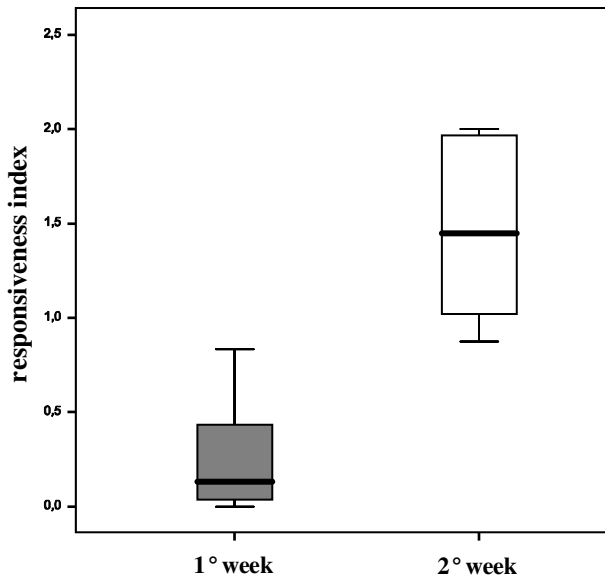


Figure 6.2 – Infant's responsiveness index (frequency of response/frequency of no-response) in the first and second week of life. Thick horizontal lines indicate medians; the height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

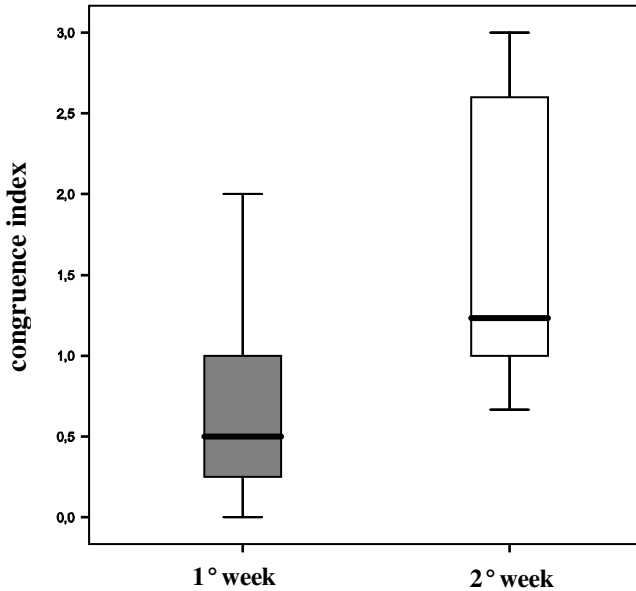


Figure 6.3 – Infant’s congruence index (congruent responses/incongruent responses) in the first and second week of life. Thick horizontal lines indicate medians; the height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

In the second week, the infant’s responsiveness index was significantly higher in response of other conspecifics stimuli than of mother stimuli (Exact Wilcoxon’s $T = 0.00$, $ties = 0$, $n = 6$, $p = 0.031$). Instead, the infant’s congruence index did not show any difference between mother and other conspecifics stimuli (Exact Wilcoxon’s $T = 1.00$, $ties = 1$, $n = 6$, $p = 0.125$). Two infants were excluded from the analysis because they did not show any

frequency of non-response or incongruent response. It was not possible to carry out the same analysis on the data of the first week due to the small size of the sample.

In the first week, when LS was the stimulus, the three types of infant's response (OM, LS, PF) significantly differed (Exact Friedman's $\chi^2 = 8.667$, $n = 8$, $df = 2$, $p = 0.011$). The Dunnett's post-hoc test revealed that OM- and LS-response significantly differ from PF-response (OM>PF: $q = 2.36$, $p < 0.05$; LS>PF: $q = 1.92$; $p < 0.05$). OM-response did not significantly differ from LS-response ($q = 1.41$, $p > 0.05$)

In the second week, when LS was the stimulus, the three types of infant's response (OM, LS, PF) significantly differed (Exact Friedman's $\chi^2 = 12.800$, $n = 8$, $df = 2$, $p = 0.001$). The Dunnett's post-hoc test revealed that LS- and PF-response were significantly higher than OM-response (LS>OM: $q = 4.24$, $p < 0.01$; PF>OM: $q = 4.24$; $p < 0.01$). Moreover, LS-response did not significantly differ from PF-response (LS=PF: $q = 0.00$, $p > 0.05$) (Figure 6.4). When we considered PF as the triggering stimulus, the three types of infant's response (OM, LS, PF) significantly differed (Exact Friedman's $\chi^2 = 11.273$, $n = 8$, $df = 2$, $p = 0.001$). The Dunnett's post-hoc test revealed that PF-response was higher than both OM- and LS-response (PF>OM: $q = 2.74$, $p < 0.01$; PF>LS: $q = 2.46$; $p < 0.01$). Moreover, LS-response did not

significantly differ from OM-response (LS=OM: $q = 1.41, p > 0.05$) (Figure 6.5).

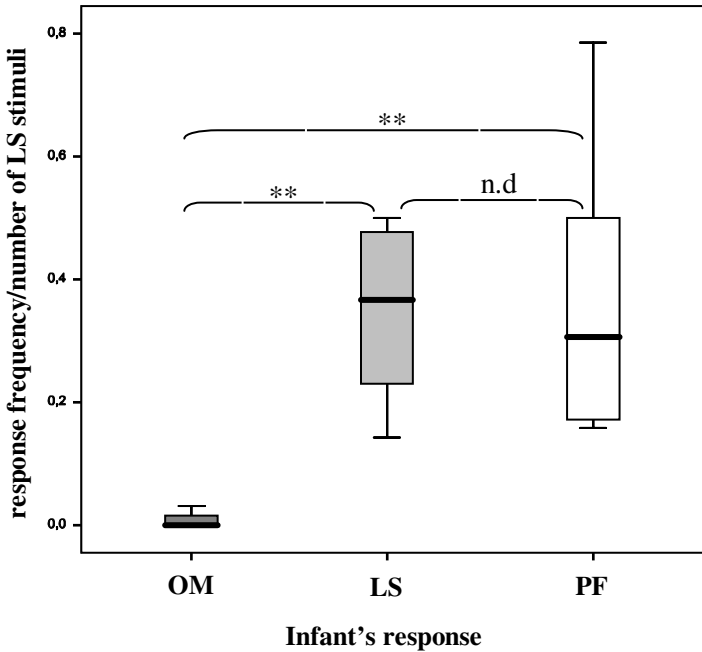


Figure 6.4 – Infant's response per number of Lip Smacking (LS) stimuli during the second week of life. Infant's response with three possible kind of facial expressions: open mouth (OM), lip smacking (LS) and play face (PF). Thick horizontal lines indicate medians; the height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

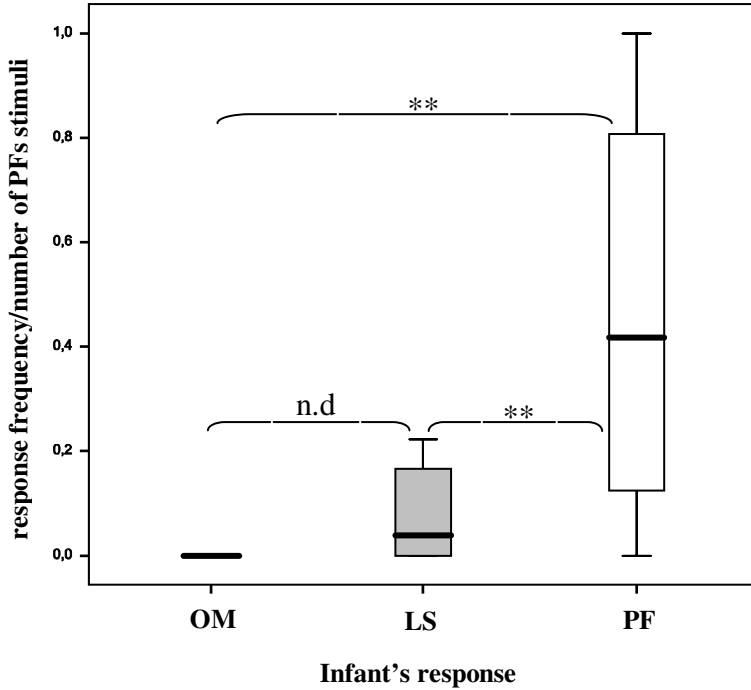


Figure 6.5 – Infant’s response per number of Play Faces (play face, PF or full play face, FPF) stimuli during the second week of life. Infant’s response with three possible kind of facial expressions: open mouth (OM), lip smacking (LS) and play face (PF). Thick horizontal lines indicate medians; the height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.

6.4 DISCUSSION

Our data confirm that gelada newborns are able to respond promptly (within 1 sec, RFM) to facial stimuli received by their mothers or by any other group members. Recently, Ferrari *et al.* (2009) have suggested that the RFM mechanism can be grounded in the perception-action coupling of automatic sensorimotor information that occurs in the motor brain areas. In this perspective, our results seem to support the hypothesis of the involvement of a mirror mechanism in rapid neonatal imitative responses. In fact, this hypothesis implies that, at birth, infants are pre-wired to recognize and imitate facial stimuli due to the presence of a rudimentary mirror neuron system (Ferrari *et al.*, 2006; Johnson, 2005; Lepage & Théoret, 2007; Park *et al.*, 2009; Pascalis & Kelly, 2009; Ferrari *et al.*, in press). In the course of the cognitive/motor ability maturation and the subsequent social experience, infant's neuronal system is refined and completed (Casile *et al.*, 2011). Therefore, it is not surprising that imitative abilities of gelada infants increase gradually in the second week of life and that, at this stage, they are able to selectively respond to the stimuli received by their own mothers and by other conspecifics. This imitative capacity seems to refine and to be better tuned in the course of ontogeny; in fact, older immature subjects (> 1 month) showed higher levels of RFM during playful

interactions with their mothers compared to those with unrelated subjects (see Chapter 4, Mancini *et al.* submitted).

From the first to the second week of life geladas increased their specificity in the facial response. While in the first week the infants did not seem to be able to mimic the facial stimuli perceived, in the second week they responded selectively, reacting in different manners to different kinds of facial stimuli. Actually, infants mimicked play faces (PF/FPF) but not lip-smacking (LS). This finding seems to be predictive of the responsiveness capability in the later stages of development and within specific social contexts (i.e. play); in fact, the same response trend was found during play activity for both immature (> 1 month) and adult subjects (see Chapter 4, Mancini *et al.* submitted). Probably, different response effects required different types of stimulation. Furthermore, it is also possible that the timing of imitative responses could differ according to the type of social interactions and facial display. In fact, in contrast to PF, a context-specific playful facial expression, the RFM was not found for LS, an unspecific signal that can elicit different behavioural responses depending on the target animal to which it is directed and the context in which it is used (Maestriperi, 1997; see Chapter 3, Palagi & Mancini, 2011). This result could explain why the neonatal imitation in infants tested in laboratory conditions,

disappears at 2-3 months of life in humans (Jacobson, 1979; Abravenal & Sigafos, 1984) and chimpanzees (Myowa-Yamakoshi *et al.*, 2004) and at 2 weeks of life in rhesus macaques (Ferrari *et al.*, 2006). In those studies, the facial stimuli (limited to LS, TP and OM) provided by the experimenter were probably less salient than those routinely provided by conspecifics (i.e., the mother or group members). Other methodological differences could also account for the differences obtained in this study compared to other accounts. In fact, we did not analyse in the current study possible imitative responses that were present after 1 second of delay. Moreover, Meltzoff and Moore (1992) proposed that the observed “disappearance” of imitative response may be because older infants react to conspecifics by engaging in social play interaction (e.g. smiling) more vigorously than neonates. This claim suggests that, once a certain degree of cognitive and motor development is reached, infants do not lose the imitative ability but, on the contrary, they acquire the competence to discriminate and select the stimulus received. Therefore, we suggest that the loss of imitation is mainly due to the loss of motivation to respond to unspecific stimuli (LS). Probably, the attention and reactivity of older infants are catalyzed and triggered by the specific facial expression (PF)

typical of playful activities, the infant's main behaviour used to socialize with others.

In conclusion, the naturalistic approach we adopted gave an important contribution to previous researches on imitative behaviour. Our data strongly suggest that the infant's innate capacity to respond and solicit facial expressions is critically dependent on the type of social environmental feedback received.

- CHAPTER 7 -

GENERAL DISCUSSION

Charles Darwin, in *The Expression of Emotions in Man and Animals* (1872), was the first to point similarities between human facial expressions and the expressions of other animals, underlining the presence of a shared heritage among the different primate species. In this evolutionary perspective, several studies on non-human primates have suggested that facial displays typical of play behaviour (play faces) are homologous to laughter/smiling in humans (de Waal, 2003b; Preuschoft & van Hooff, 1995; Waller & Dunbar, 2005). Therefore, playful activity is characterized by a set of behaviours that could be of utmost interest for examining the role of visual signals as intentional communication systems (Palagi, 2009).

Theropithecus gelada is a cercopithecoid species characterized by some peculiar features, such as high levels of social play even as adults (Mancini & Palagi, 2009), high levels of tolerance (Palagi & Leone, 2010) and a rich repertoire of facial expressions (Dunbar & Dunbar, 1975, Palagi & Mancini, 2011 or see Chapter 3; for facial display's definitions, see Table 2.1). In particular, we recognize two playful expression variants (Palagi & Mancini, 2009): play face (PF, mouth opened with only the lower teeth

exposed) and full-face play (FPF, lower/upper teeth and gums exposed via the actively retraction of the upper lip). In addition, Mancini & Palagi (2011, see Chapter 3) observed that during playful events geladas frequently lip smacked (LS, lips are protruded and then smacked together repeatedly) toward conspecifics. This observation suggests that additional facial expressions can be recruited from other behavioural contexts and used for playful purposes. Finally, the recent finding of yawn contagious suggests that this monkeys are sensitive to the emotional facial expressions of conspecifics, especially individuals with whom they are closely affiliated (Palagi *et al.*, 2009). For these reasons, gelada is a good model to verify differential functions on the use of specific (PF and FPF) and nonspecific (LS, used also in other social contexts) playful facial expressions and to investigate the communication role that these expressions play during ontogenetic development.

Here, we demonstrated that in geladas during ontogeny facial expressions related to play undergo developmental changes. The PF, typically performed by immatures, is replaced by FPF so that in older individuals PF is virtually absent (see Chapter 3, Palagi & Mancini, 2011). 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). This age-trend bias of facial displays is probably due to their different roles in communication. In fact, our data show that during playful sessions with a higher risk of escalation (e.g., rough sessions, age-mismatched sessions, post-conflict sessions) the FPF is more effective than PF (see Chapter 3, Mancini & Palagi, 2011). These results suggest that, in a highly social tension situation, FPF may be used in a strategic way as corrective response to maintain cooperation and social integrity and to avoid the possibility of a new aggression (van Hooff, 1989).

On the contrary, LS does not seem to be used to initiate or maintain play interactions and to manage vigorous and risky sessions, even though it is performed largely by adults during age-mismatched play interactions. The negative correlation found between LS and playful displays suggests that nonspecific signals are recruited when the specific ones are not sufficient to negotiate the play session (see Chapter 3, Mancini & Palagi, 2011). This finding suggests that the meaning of the LS as an appeasement signal is maintained during playful interactions. This interpretation is supported by the high levels of LS recruitment during those play sessions occurring between adult females and

unrelated immature subjects (see Chapter 3, Mancini & Palagi, 2011).

Further, the analysis on immediate signal responsiveness showed that adults were generally more sensitive than immatures to playful facial expressions performed by playmates (see Chapter 3, Mancini & Palagi, 2011). Previous playful experience (Pellis & Pellis, 2006), social competence (Pellis & Pellis, 2009), and neural circuit maturation (Ferrari *et al.*, 2009b) may be at the basis of adult sensitiveness in responding to social stimuli of the other social members. This result is also in line with a recent study demonstrating that gelada adults are more affected by facial expressions such as yawning compared to immatures (Palagi *et al.*, 2009).

Our data also provide new information on the capacity of monkeys and, more in general of nonhuman primates, to emotionally connect with other individuals. One of the phenomenon often considered and used as an index of affiliation and emotional proximity is emotional contagion. 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) or, more in general, to the capacity to reproduce in the observer a similar sensorimotor experience. In humans, rapid facial mimicry (RFM, involuntary, rapid and automatic response, in which an individual mimics the facial expression of another individual within 1 second) plays an important role in emotional contagion thus giving the responding subjects important advantages in cooperation and communication (Provine, 2005). In non-human primates, the phenomenon of RFM has been recently found in the play activity of an ape species (Davila-Ross *et al.*, 2008).

Despite the importance of such phenomenon in the evolution of primate sociality, no study on RFM has ever been performed in monkeys. In this context, the current work is the first to demonstrate the presence of RFM phenomenon in a cercopithecoid species. In particular, we found that during play activity both adult and immature geladas (> 1 month) rapidly mimic the specific playful facial expressions (PF and FPF) (see Chapter 4, Mancini *et al.* submitted). The use of a third facial expression (LS) as a control gave further strength to our findings. As we predicted, the RFM was not found for LS, which is a signal that can elicit different behavioural responses depending on the target animal to which is directed and the context in which it is used

(Maestripieri, 1997; see Chapter 3, Palagi & Mancini, 2011; see Chapter 4, Mancini *et al.* submitted). The presence of both PF and FPF in gelada immature subjects (see Chapter 3, Palagi & Mancini, 2011) allowed us to test the accuracy of RFM by examining the occurrence of facial matching. We found that immatures exactly matched the facial expression perceived (PF/PF; FPF/FPF) and that, compared to the non-matching response, the matching responses were characterized by shorter latencies (see Chapter 4, Mancini *et al.* submitted). These findings strongly suggest that RFM is important in the recognition process when it requires fine distinctions of similar facial expressions conveying subtle differences in meaning (see Chapter 3, Palagi & Mancini, 2011; see Chapter 4, Mancini *et al.* submitted), such as the processing of different smile types in humans (Niedenthal *et al.*, 2010).

Moreover, mother-infant dyads were characterized by higher levels of RFM compared to the unrelated dyads and by lower latencies to respond (see Chapter 4, Mancini *et al.* submitted). This result is also supported by behavioural studies showing that the frequency of RFM is higher among friends and kin than among unfamiliar individuals, suggesting that familiarity play a key role in the acquisition of social skills (Caruana *et al.*, 2011; Feldman, 2007; Norscia & Palagi, 2011). Therefore, similarly to

other imitative behavioural phenomena, RFM could be advantageous to promote social and emotional connections among individuals (de Waal & Ferrari, 2010; Paukner *et al.*, 2009) and appears to play an important role in the bond between individuals.

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; in chimpanzees, Waller & Dunbar, 2005; in bonobos, Palagi 2009). Recently, Davila Ross *et al.* (2011) discovered that, in chimpanzees, the play interaction is prolonged by the facial replication (or facial mimicry) in response to playful facial stimuli of the playmates. In this regard, the data on gelada add fundamental information to understand the communicative role of facial matching behaviours. In fact, play interactions characterized by RFM (rapid facial mimicry: facial response within 1 sec) are longer than those play characterized by DFM (delayed facial mimicry: facial response within 5 seconds, Wild *et al.*, 2003) (see Chapter 5). Different from the rapid response, the delayed responses of DFM might be due to increased emotional processing. Alternatively, although not necessarily in contrast with the previous hypothesis, we proposed that the modulation of this response is probably under the control of the same neural

processes involved in the rapid response but it seems that it is subjected to stronger to inhibitory influence. Consequently, the late response observed in DFM may be perceived by play partners as a signal linked to the expression of an internal emotional state communicating a low tendency to be involved in a play session and this would explain its lower effectiveness in prolonging play interaction (see Chapter 5).

In contrast, the rapid facial replication, due to its automatic and spontaneous nature, evokes in the subject a fast and corresponding emotional state underlying the facial expression perceived (facial feedback theory, Niedenthal *et al.* 2010). This facial and emotional response can lead to a greater social synchronization and intent matching between the two players thus increasing their trust and cooperation levels, essential features to manage a playful interaction (see Chapter 5).

Matching one's own behaviour with that of others allows individuals not only to detect contingencies in the social world but also to recognize behaviours by mapping the sensory information related to others on the own motor knowledge. This process could allow an individual to synchronize its activity with those of its group members and to learn the context in which an activity should be performed (Ferrari *et al.*, 2006; Paukner *et al.*, 2009; Rizzolatti *et al.*, 2001; Suboski, 1990). Some authors reported

the presence of imitative ability also in the early stage of life, underling the importance that this mechanism plays in the development of infant's social behaviour and cognition.

This work assessed for the first time, under semi-natural conditions, the presence of rapid neonatal imitative responses (Rapid Facial Mimicry, RFM) in a monkey species, the gelada (*Theropithecus gelada*). In particular, our data demonstrated that newborns are able to respond promptly (within 1 sec) and selectively to facial stimuli received by their mothers or by any other group members and that this imitative capacity seems to refine and to be better tuned in the course of ontogeny (see Chapter 6). The phenomenon of RFM can be grounded in the perception-action coupling of automatic sensorimotor information that occurs in the motor brain areas (Ferrari *et al.*, 2009c). In this perspective, our results seem to indirectly support the mirror neuron system hypothesis: infants are pre-wired to recognize and imitate facial stimuli due to the presence of a rudimentary mirror neuron system (Ferrari *et al.*, 2006; Ferrari *et al.*, in press; Johnson, 2005; Lepage & Théoret, 2007; Park *et al.*, 2009; Pascalis & Kelly, 2009), that very likely develops during the intrauterine period (Del Giudice *et al.*, 2009; Ferrari *et al.*, 2009c) when the fetus shows the first motor/intentional behaviours (Castiello *et al.* 2011; Myowa-Yamakoshi, 2004; Zoia, 2007) and

facial movements that can be used in the post-natal period (Hata *et al.* 2005).

Our study was conducted on 8 geladas black infants that, at birth, remained with their mothers in a stable and well bonded social group, in which they had the opportunity to interact freely with other group members. This naturalistic approach gave an important contribution to previous researches on imitative behaviour suggesting that the infant's capacity to respond and solicit facial expressions is critically dependent on the type of social environmental feedback received (see Chapter 6). The effects of these social interactions would be that of not only giving a meaning to infant's facial expressions but also to contextualize them within the appropriate social situations (Del Giudice *et al.*, 2009; Casile *et al.* 2011). Therefore, the mirror neurons system for facial expressions, might be shaped by the social environment based on the quality and frequency of the sensory feedback that infant received. These early interactions might have profound effects on the brain during development. For example, those circuits linking visual information concerning biological motion with those responsible of motor control could be reinforced through Hebbian learning (Casile *et al.*, 2011) strengthening those coupling visuomotor anatomical connections which have been described by neuroanatomical and

neurophysiological works in the adult monkeys and by neuro-imaging studies in humans.

In conclusion, our findings point to similarities across diverse primate taxa in the process in which facial matching behaviours are expressed. In a bottom-up perspective (de Waal & Ferrari, 2010), the imitative phenomena described in this thesis are part of a complex communication systems that could be considered as the building blocks of more complex behavioural pattern involved in social cognition, suggesting a common evolutionary root among primates in the fundamental elements of affective exchanges which are at the basis of inter-individual emotional connection. In primates, including humans, the emotional connection, based on face-to-face interactions, is already evident in the first phases of life (Ferrari *et al.*, 2009a). This affective responsiveness is probably central for the development of the infant's neuro-physiological system and behavioural competence, which are necessary to gain social advantages in the future. In fact, some studies demonstrated that, in absence of appropriate emotional responses by the mothers (e.g. depressed mothers), infant employ auto-regulative behavioural strategies that, under certain conditions, can have negative effects on its later ability to self-regulate emotions throughout social life (Feldman, 2007; Gianino & Tronick, 1988; Tronick, 1989). Therefore, behavioural

synchrony, such as facial matching behaviour, seem to have a fundamental role in affective coordination and could have an important impact in the development of social competences and empathy. In primate societies, this synchronous mechanisms seem to be evolutionarily ancestral and, then, may have played a key role in evolving altruistic behaviours and empathetic abilities (Casile *et al.*, 2011; Ferrari *et al.*, 2009a).

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