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FAIR PLAY AND HONEST SIGNALS IN IMMATURE CHIMPANZEES

Abstract - In primates, specific facial displays (PF, play face; FPF, full play face) often accompany play bouts and are considered an integral part of play development. In humans, laughter, a universal expression of joy, seems to derive from non-human primate play faces and pant-like vocalizations. Playful facial displays may represent honest signals that express the non-agonistic intent of players in order to maintain the session at a later time. Here, we examine the possible roles of facial displays during play sessions of immature chimpanzees (*Pan troglodytes*). Infants and juveniles performed PF and FPF with comparable frequency to maintain the playful mood. However, the use of playful expressions was fine-tuned in relation to the asymmetry of the session and of the receiver's identity. In infants, whose play sessions were the most unbalanced, we found a positive correlation between the play face frequency and the asymmetry degree that characterizes each single session. On the other hand, in juveniles, we found that the most of the facial signals was directed towards peers. This result is not surprising also considering the high complexity and competition levels characterizing juvenile play in chimpanzees. Probably, when play becomes more competitive, as it occurs in juvenile chimpanzees and adolescent humans, clear and fair signals are essential to maintain the session and to avoid it turning into aggression. Therefore, like human laughter, playful expressions do not give simple information, but positively influence the receiver's reaction. Independently of the playmate age, in chimpanzees, play facial signals, may have a role in advertising cooperative dispositions and intentions thus increasing the likelihood of engaging in honest social relationships. In social play, there are codes of conduct that regulate what is permissible and what is not. The existence of shared codes in immature individuals might contribute in developing some traits of social morality in adults.

Key words - Play face, Full play face, Social competence, Fair play, Codes of social morality.

Riassunto - *Giocare onestamente: l'uso dei segnali di gioco negli immaturi di scimpanzé* - Nei primati umani e non-umani, il comportamento di gioco è presente ad alti livelli principalmente nella fase immatura. Durante le sessioni ludiche, solitarie e sociali, i primati mostrano spesso specifiche espressioni facciali. Tali espressioni possono manifestarsi in due varianti: la faccia da gioco, bocca aperta e arcata dentaria inferiore scoperta e la piena faccia da gioco, bocca aperta ed entrambe le arcate dentarie scoperte. Nell'uomo, il sorriso sembra derivare dalla faccia da gioco dei primati non-umani e dalle vocalizzazioni a essa associate. La faccia da gioco rappresenta un segnale onesto, che esprime gli intenti non aggressivi degli individui coinvolti e permette di mantenere la sessione ludica più a lungo nel tempo. In questa ricerca sono stati analizzati l'uso e il ruolo delle espressioni di gioco negli individui immaturi di scimpanzé (*Pan troglodytes*). I piccoli e i giovani di scimpanzé, pur mostrando frequenze paragonabili di facce da gioco, sembrano modulare differenzialmente l'uso delle espressioni in relazione all'identità del ricevente e all'asimmetria della sessione. Nei piccoli, le cui sessioni ludiche sono particolarmente sbilanciate e asimmetriche, è stata riscontrata una

correlazione positiva tra frequenza di facce da gioco e grado di asimmetria della sessione, mentre, nei giovani, i segnali facciali sono diretti maggiormente ai coetanei. Quest'ultimo risultato non è sorprendente, considerando i livelli di complessità e di competizione che caratterizzano il gioco giovanile; nel momento in cui l'attività ludica diviene più competitiva, come accade anche negli adolescenti umani, segnali chiari e onesti sono essenziali per mantenere la sessione ed evitare che essa degeneri in un vero e proprio conflitto. Come nel caso del sorriso umano, anche le facce da gioco dei primati non-umani esercitano un'influenza positiva sul comportamento del ricevente. Negli scimpanzé, i segnali di gioco, indipendentemente dall'età dei giocatori, sembrano svolgere un ruolo fondamentale nell'indicare una disposizione a cooperare e a instaurare relazioni sociali oneste. Nel gioco, esistono codici di condotta che determinano ciò che è permesso e ciò che non lo è; negli immaturi di scimpanzé, la condivisione di tali codici può contribuire allo sviluppo di alcuni tratti della «moralità» riconducibili alla fase adulta.

Parole chiave - Faccia da gioco, Piena faccia da gioco, Competenza sociale, Gioco onesto, Codici sociali di moralità.

INTRODUCTION

Play, defined as all activity that appears to an observer to have no obvious immediate benefits for the performer, involves motor patterns typical of other serious functional contexts, such as agonistic, anti-predatory, and mating behaviours (Bekoff, 2001; Burghardt, 2005; Martin & Caro, 1985; Pellis & Pellis, 1996). The difference between playful and serious contexts is not in the actual behavioural patterns performed, but in the way they are performed (Bekoff & Allen, 1998). Burghardt (2005) listed five criteria that behaviour must show to be considered play: a playful behaviour must be incompletely functional, rewarding/voluntary, structurally or temporally modified, performed in a repeated manner, and initiated in a relaxed context.

Specific actions, gestures, gaits and grimaces may be associated with a play session functioning as signals that communicate the playfulness of a potential dangerous act (Bekoff, 2001; Drea *et al.*, 1996; Fagen, 1981; Palagi, 2006). Human and non-human primates use specific facial displays that are considered as an integral part of play behaviour development (Cordoni & Palagi, 2011; Palagi, 2008; Palagi *et al.*, 2007; Pellis & Pellis, 1996; van Hooff & Preuschoft, 2003). In the

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great apes these facial expressions are performed in two different configurations: Play Face (PF), when the mouth is open with only the lower teeth exposed and Full Play Face (FPF), when the mouth is opened with upper and lower teeth exposed (Loizos, 1967). Some authors contend that PF and FPF are used differently in relation to the intensity of play (Palagi, 2008; Palagi *et al.*, 2007; Pellis & Pellis, 1996; Waller & Dunbar, 2005). In humans, laughter derives from non-human primate play faces and pant-like vocalization (van Hooff & Preuschoft, 2003). Play faces signal non-agonistic intents and induce a positive influence on the receiver's behaviour. Human and non-human apes smile spontaneously during pleasurable experiences. Smiles and play faces, being the expression of positive emotional states, reinforce the behaviours that elicited them in the first place (Davila-Ross *et al.*, 2011; Mehu *et al.*, 2007; Owren & Bachorowski, 2003). A deep investigation on the use and function of playful facial displays in non-human primates helps to shed light on the biological roots of smiling in humans.

During play fighting, animals use patterns of agonistic functional contexts that are not intrinsically different from their «serious» counterparts, thus, it may be hard to distinguish them. Animals seem to be able to use play signals appropriately when a clear statement of purpose is necessary (i.e., during competitive play or high complex play interactions) (Cordonì & Palagi, 2011; Pellis & Pellis, 1996). The ability to interpret such features of social signalling may represent a central issue in the evolution of behavioural flexibility and intelligence in primates.

In this study, we investigated if immature chimpanzees (*Pan troglodytes*) may use play faces in a strategic way in order to signal their benign intents. We predicted that chimpanzees may vary their playful expressions in frequency, timing, and type (PF & FPF) according to the age of playmates.

METHODS

From 2001 and 2004, we observed two chimpanzee colonies hosted at the ZooParc de Beauval, (France) and the Dierenpark Amersfoort (the Netherlands) (see Table 1). Both colonies lived in an enclosure composed by indoor and outdoor facilities equipped with trunks, lianas, ropes, rocks, and platforms. We focused our analysis on 15 immature individuals: 8 infants (0-3 yrs.) and 7 juveniles (4-7 yrs.). All individuals were observed for the same amount of time *via* focal animal sampling (Altmann, 1974): 31 hrs. of observation for the Beauval colony and 35 hrs. of observation for the Amersfoort colony.

For each play sessions we recorded: i) playmate identity, ii) play patterns and their chronological sequence

Tab. 1 - The chimpanzee colonies hosted at the ZooParc de Beauval and Dierenpark Amersfoort.

SUBJECTS (INITIALS)	SEX CLASS	YEARS/AGE CLASS	SIBLINGS RELATIONSHIP	RESIDENCE
Christmas (CR)	Female	6.5/Juvenile	LE's sister	Beauval
Isabel (IS)	Female	5.5/Juvenile		Beauval
Melie (ME)	Female	3.5/Infant		Beauval
Rachel (RA)	Female	1.0/Infant		Beauval
Tsavo (TS)	Male	7.0/Juvenile	BZ's brother	Beauval
Benji (BE)	Male	6.0/Juvenile	MA's brother	Beauval
Leo (LE)	Male	4.0/Juvenile	CR's brother	Beauval
Makury (MA)	Male	2.5/Infant	BE's brother	Beauval
Bazou (BZ)	Male	2.0/Infant	TS's brother	Beauval
Bibi (BI)	Female	7.0/Juvenile	KR's sister	Amersfoort
Chura (CH)	Female	6.0/Juvenile		Amersfoort
Ghafula (GA)	Female	3.5/Infant	IT's sister	Amersfoort
Ituri (IT)	Female	0.5/Infant	GA's sister	Amersfoort
Karibuna (KR)	Male	2.5/Infant	BI's brother	Amersfoort
Kumi (KU)	Male	2.0/Infant		Amersfoort

(see Table 2) and iii) circumstance in which play took place (e.g. feeding). Moreover, during the performance of playful facial displays (PF and FPF) we registered the signaller's and the receiver's identity (directionality) and the exact chronological sequence of the visual signals.

Due to the non-normality of data and the small sample size (N=15), nonparametric statistical tests were ap-

Tab. 2 - Play behavioural patterns recorded during the observation sessions both at the Beauval and the Amersfoort colony.

PLAY PATTERN	INITIAL	DEFINITION
Acrobatic Play	ACP	An animal climbs, jumps, and dangles from supports in its environment (e.g., branches, ropes, etc.) in solitary or social way
Pirouetting	PIRO	An animal performs rolling over either on the ground or on vertical supports in solitary or social way
Play recovering a thing	PRCO	An animal chases a playmate and attempts to grab an object it is carrying
Play run	PRUN	An animal runs alone (solitary play) or chases a play partner
Somersault	SO	An animal flips over either on the ground or on vertical supports in solitary or social way
Play bite	PBIT	An animal gently bites a playmate
Play brusque rush	PBR	An animal jumps with its four limbs on a playmate
Play push	PPS	An animal pushes a playmate either with its hands or feet
Play retrieve	PRE	An animal holds a playmate to prevent its flight
Play slap	PSL	An animal slaps any part of a playmate's body
Play stamping	PST	An animal jumps on the ground (solitary) or on a playmate with its feet
Object play manipulation	OPM	An animal shakes, dangles, throws, an object of its environment in solitary or social way (when the action is directed to a playmate; the pattern does not imply any kind of contact between the two animals)
Tickle	TK	An animal contacts the partner's body with its mouth or hands

plied to the analyses performed at the individual level (Siegel & Castellan, 1988). When performing dyadic comparisons 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).

RESULTS

Play signal rates (PF *plus* FPF) do not correlate with the chimpanzees' ages (Spearman $r_s = -0.074$, $N = 15$, $p = 0.794$; Fig. 1). Nevertheless, the levels of play fa-

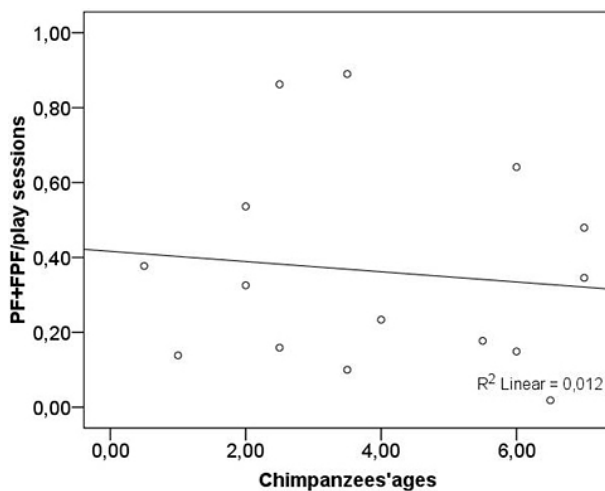


Fig. 1 - Correlation between the levels of play facial displays (PF *plus* FPF *per* play session) and chimpanzees' ages.

cial displays positively correlate with the complexity of play sessions (*Play Complexity Index* = number of types of play patterns forming a single session on the total number of patterns forming that session. Spearman $r_s = 0.811$, $N = 15$, $p = 0.00001$; Fig. 2).

Infant and juvenile chimpanzees do not show any difference in the use of the two variants of play face (PF and FPF) in order to maintain the playful session (*Play Signal Index* (PSI) = $[(PF-FPF)/(PF+FPF)]$; Exact Mann Whitney $U = 23$, $N_{\text{Infants}} = 8$, $N_{\text{Juvéniles}} = 7$, $p = 0.588$; mean infant PSI = $0.32 \pm 0.11SE$, mean juvenile PSI = $0.33 \pm 0.12SE$).

We defined an *Asymmetry Index* (AI) as the number of unidirectional patterns performed by individual A *minus* the number of unidirectional patterns performed by individual B on the total number of patterns (unidirectional *plus* bidirectional) forming the session. Considering infants, our findings show a positive correlation between the play face frequency and the AI that characterizes their play (Correlation via randomization $r = 0.735$; $N = 10$, $p = 0.042$). Further-

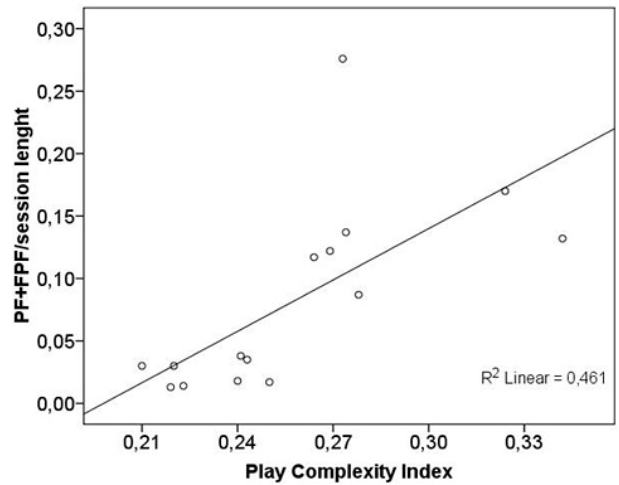


Fig. 2 - Correlation between the rates of play facial displays (PF *plus* FPF *per* play session) and the complexity level of play sessions (*Play Complexity Index*).

more, infants directed play signals towards peers and juveniles with comparable levels (Exact Wilcoxon's $T = 14$, ties = 0, $N = 8$, $p = 0.641$; Fig. 3a), whereas, juveniles tended to direct most of their play signals towards other juveniles rather than towards infants (Exact Wilcoxon's $T = 2$, ties = 0, $N = 7$, $p = 0.058$; Fig. 3b).

DISCUSSION

During immaturity, chimpanzees do not show any quantitative difference in the use of play facial displays in relation to the age-class (infants and juveniles). Moreover, playful expressions, independently of the two variants (PF and FPF), are mainly performed to maintain play session at a later time. Nevertheless, infant and juvenile chimpanzees fine tune their play signals according to the complexity level and asymmetry degree of the session and to the receiver's identity.

In a previous study, Cordoni and Palagi (2011) showed that play between infant chimpanzees is characterized by a higher degree of asymmetry compared to juveniles; on the other hand, juvenile play sessions are characterized by higher complexity levels. In play, more the complexity, more the unpredictability. The training for the unexpected hypothesis (Špinka *et al.*, 2001) predicts that play is a means by which animals learn to manage fluctuating social conditions and unexpected challenges. A complex play interaction (e.g. play fighting), particularly if performing with peers, is more self-rewarding and, concurrently, more effective in testing own abilities and social relationships with group-members compared to less heterogeneous interaction. However, unpredictability may also represent a higher risk for the players to incur in misunderstanding and, con-

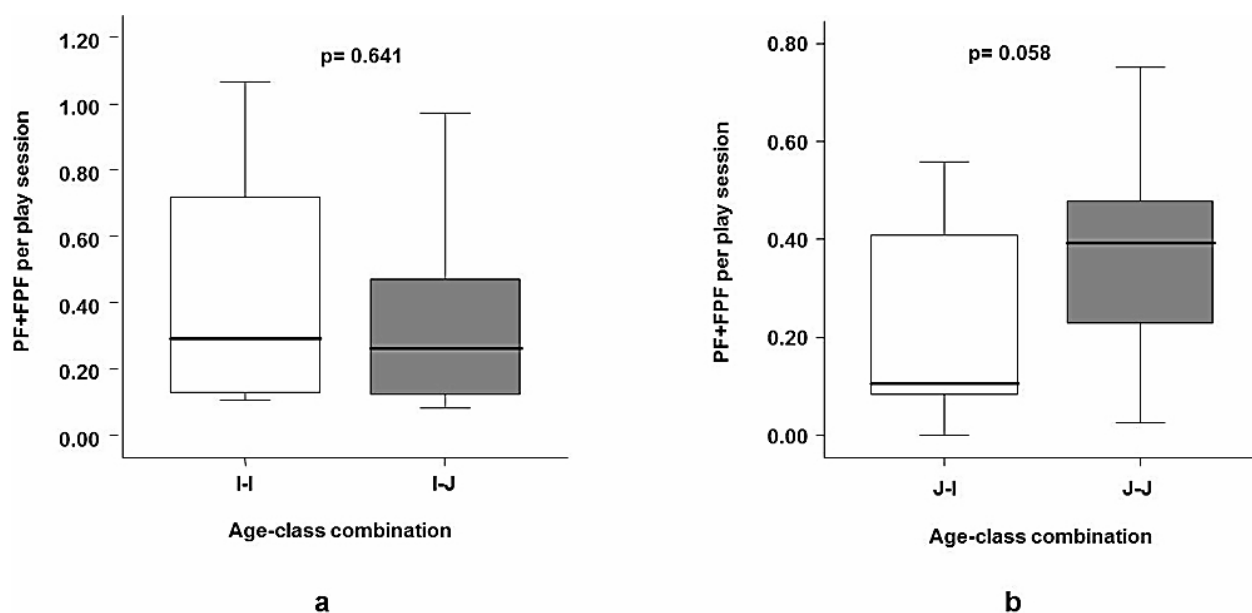


Fig. 3 - Play signal rates (PF plus FPF per play session) directed by infants towards peers and juveniles (a) and by juveniles towards infants and peers (b).

sequently, in overt aggressions. Flack and colleagues (2004) showed a significant increase in the frequency of play faces performed by an older chimpanzee playmate when the mother of the younger play partner was in close proximity. This finding suggests that older playmate may strategically use play faces as appeasing signals in order to avoid a misinterpretation and an aggressive intervention of younger playmate mother. Accordingly, the players for clarifying their own intentions have to make a redundant use of honest play signals (Bekoff, 2001; Palagi, 2008; Pellis & Pellis, 1996). When play becomes unbalanced, as it occurs in infant chimpanzees, or more competitive, as it occurs in juvenile chimpanzees and human adolescences (Pellegrini, 2009; Smith, 2010), the play faces, like laughter (Duchenne laughter; Gervais & Wilson, 2005), may have a role in advertising cooperative and fair dispositions thus increasing the likelihood of engaging in solid social relationships. Play signals can have a dual role by representing a shield for the performer and, concomitantly, a declaration of «good intents» for the receiver, thus maintaining the session as fairly as possible. In 2001, Bekoff (p. 82) stated that «*animals often have social expectations when they engage in various sorts of social encounters the violation of which constitutes being treated unfairly because of a lapse in social etiquette*». Playful facial displays, strictly linked to the emotions in apes, may be even effective to convey a truthful message thus representing a building block of the codes of morality in animals.

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