



Sharing the motivation to play: the use of signals in adult bonobos

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Gestures and facial displays are involved in regulating many aspects of mammal social life such as aggression, dominance–subordinate relationships, appeasement and play. Playful activity is an interesting behaviour for examining the role of signals as intentional communication systems. When animals play they perform patterns that are used in other serious contexts. To avoid miscommunication, many species have evolved signals to maintain a playful mood. Bonobos, *Pan paniscus*, with their flexible social relationships and playful propensity, may represent a good model species to test some hypotheses on adult play signalling. I analysed the potential roles of facial play expressions and solitary play in soliciting and regulating social play and found that adult bonobos used the play face (relaxed open-mouth display) in a selective manner. Play faces were more frequent during social than solitary play and, within social play, polyadic sessions (even though less frequent than dyadic sessions) were characterized by a higher frequency of signals. Following the rule of play intensity matching, play faces were more frequent when the two players matched in age and size (sessions among adults). Moreover, among dyads there was a positive correlation between the frequency of aggressive interactions performed and the frequency of play signals used, thus suggesting that signals are crucial in play negotiations among individuals showing high baseline levels of aggression. Finally, solitary play, especially when it involved pirouettes and somersaults, had an important role in triggering social play.

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Communication can be defined as a complex interplay between senders and receivers, each with their own targets (Bradbury & Vehrencamp 1998), and is based on signals that can be considered packets of energy generated by a display or action of one organism (the signaller) that is selected for its effects in influencing the probability pattern of behaviour of another organism (the receiver) in a way that is adaptive either to one or both parties (Markl 1983). Signals are based on different sensory modalities such as olfactory, acoustic or visual cues (see Hebets & Papaj 2005 for an extensive review).

The ability to use the information present in visual signals (e.g. body postures, movements and facial displays) and to respond to them discriminatively has been

critical for the evolution of communication in social animals (Andrew 1963; East et al. 1993; Bradbury & Vehrencamp 1998; Tomasello & Zuberbuhler 2002; Parr 2003a). In primate evolution, for example, there has been an increasing trend towards larger and more complex social groups in which individuals rely less on olfactory than visual cues, such as facial signals, for communication (Andrew 1963; Marler 1965).

Generally among mammals, facial displays are unambiguously social; a display may tell a receiver something about the motivational state of the sender, something about the immediate environment or both. In fact, such displays are performed with greater frequency in social situations and can be directly related to interactive consequences (Pellis & Pellis 1996; Schmidt & Cohn 2001; de Waal 2003). Therefore, facial displays can be considered cooperative systems, benefiting both signallers and receivers (Bradbury & Vehrencamp 1998; Van Hooff & Preuschoft 2003). For this reason, probably, gestures

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and facial displays are commonly involved in regulating many aspects of mammal social life such as aggression, dominance–subordinate relationships, appeasement, affiliation and play (Bekoff 1972; Kruuk 1972; Colmenares et al. 2000; Preuschoft & van Schaik 2000; Smuts 2002; de Waal 2003).

Playful activity is an interesting behaviour for examining the role of visual signals as communication systems. During a play session animals use patterns that are used mainly in other functional behaviours (i.e. predatory, antipredatory, mating) (Bekoff & Byers 1981; Fagen 1981, 1993). A major issue of theoretical importance, given this overlapping in behavioural patterns, has been how animals can discriminate between playful and non-playful intent (Pellis & Pellis 1996, 1997; Bekoff & Allen 1998). Visual signals are often associated with situations where the playful intentions of the performer may be ambiguous to the recipient. 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 (Loizos 1967; Fagen 1981; Drea et al. 1996; Bekoff 2001; Palagi 2006). During such situations signals appear to be crucial in avoiding escalation to real aggression and in prolonging the play session (Moynihan 1998; Burghardt 2005; Waller & Dunbar 2005). For example, Bekoff (1977, 1995) stressed the importance of play signals as ‘punctuation’ during interactions among group members in canids and showed that the bow (an individual crouches on its forelimbs, remains standing on its hindlegs and may wag the tail and bark) is used to initiate a play bout and is performed randomly during social play especially when the play includes elements of hostile origin.

Primates use a variety of facial displays that have been described in great detail (Darwin 1872; Chevalier-Skolnikoff 1973; Van Hooff 1973; Goodall 1986; Ladygina-Kohts 2002; de Waal 2003).

Tinbergen (1952) was first to define the process whereby expressive displays become ritualized and separated from their original function to serve a new function. Through this evolutionary transformation, displays become stereotypical and easy to recognize by receivers; consequently, the communicative message is maximized (see Bradbury & Vehrencamp 1998 for an extensive review).

Since facial displays are highly stereotypical and conservative in primates, researchers have identified specific facial expressions in related species, such as those used by macaques, *Macaca* spp., and chimpanzees, *Pan troglodytes*, particularly those occurring during play (e.g. the relaxed open-mouth face or play face (PF)) and submission (e.g. the bared-teeth display) that appear to be homologous with the expressions of laughter and smiling in humans (Van Hooff 1972, 1976; Preuschoft & Van Hooff 1995).

In primates, social play is often accompanied by a typical expression, the relaxed open-mouth display (PF/full play face (FPF) hereafter), which can be performed in two different configurations. In the FPF the mouth is opened in a relaxed mood with both the upper and the lower teeth exposed and in the PF the mouth is opened with only the lower teeth exposed (Loizos 1967; Van Hooff &

Preuschoft 2003; Waller & Dunbar 2005; Palagi 2006; Palagi et al. 2007).

These playful expressions have been interpreted as ritualized versions of the biting intention movement which precedes the play bite that is so common during rough and tumble play (Pellis & Pellis 1996, 1997; Van Hooff & Preuschoft 2003).

Since play occurs mostly in the juvenile phase, efforts to study and explain play signals have been focused primarily on immature subjects (Pellis & Iwaniuk 2000; Power 2000; Flack et al. 2004; Burghardt 2005). However, play can continue into adulthood also (Fagen 1981), but adult play signalling negotiations have been often neglected in this field of research (Pellis & Iwaniuk 1999; Palagi 2006).

Among the apes, bonobos are the most playful species and show high levels of both solitary and social play during adulthood (de Waal 1988, 1989; Enomoto 1990; Palagi 2006; Palagi & Paoli 2007). Bonobo society is characterized by a rich set of social dynamics in which adults negotiate and maintain their relationships through coalitions, tolerance, reconciliation and even conflict mediation (Furuichi 1989, 1997; de Waal 1989; Hohmann & Fruth 2000, 2002; Palagi et al. 2004, 2006).

Palagi (2006) suggested that play may become most important when relationships among individuals are less codified and structured according to rank rules. If adult–adult play has a fundamental role in the social assessment, then such play is expected to be retained within tolerant species rather than within despotic species. For this reason, bonobos with their flexible interindividual relationships and playful propensity may represent a good model species to test empirically some hypotheses on adult play signalling, whose mechanisms remain incompletely elucidated. In particular, I focused my analysis on play facial expressions and solitary play.

Prediction 1

During social play interactions, chimpanzees generally perform the PF, whereas bonobos tend to perform the FPF (de Waal 1988). By comparing the play behaviour in these two species, Palagi (2006) showed that bonobos displayed significantly higher levels of FPF than chimpanzees. Following this evidence, if the FPF typifies play signalling in bonobos, I expect significantly higher levels of this facial configuration than the PF (prediction 1a). Moreover, due to the negotiating and de-escalating function of play signalling (de Waal 2003; Waller & Dunbar 2005) I also expect higher levels of playful facial displays during social play than during solitary play (prediction 1b).

Prediction 2

Social play may comprise both dyadic and polyadic sessions. Polyadic play in chimpanzees is more unstable than dyadic play (Hayaki 1985). Since unexpected situations frequently occur during a play bout (Spinka et al. 2001; Van Hooff & Preuschoft 2003), I expect that, due to the difficulty for individuals to monitor all the partners

involved, polyadic play sessions have higher rates of play signals than dyadic play sessions.

Prediction 3

Research on who play fights with whom has shown that, when a choice is available, animals play with partners similar to themselves in age and size. To cope with a well-matched (and, therefore, risky) play session, however, several play signals may be useful to declare playful intentions (Mendoza-Granados & Sommer 1995; Power 2000; Burghardt 2005; Palagi et al. 2007). Accordingly, I expect that adult bonobos perform play facial displays to a higher extent during adult–adult than during adult–immature play sessions (prediction 3a).

Previous findings on play signalling in mammals suggested that signals may function for both soliciting and maintaining social play (Power 2000; Burghardt 2005). Thus, I expect a comparable frequency of playful facial displays both at the beginning and during the play session (prediction 3b).

Increasing evidence shows that species with higher degrees of aggressiveness have evolved more diverse play signals, which are used in redundant ways (Bekoff 1974; Henry & Herrero 1974; Drea et al. 1996). If play signals have important roles in play negotiation among individuals showing high levels of aggression, then among dyads I expect a positive correlation between the frequency of aggressive interactions performed and the frequency of play signals used (prediction 3c).

Prediction 4

Many researchers assert that imitation can play an important role in the social transmission of communicative signals and that imitation can be part of playing (see Miklósi 1999 for an extensive review). Thus, I hypothesize that observation of a group member playing may increase the behavioural propensity and motivation to play in the receiver. If solitary play has important roles in soliciting and triggering a social play session (in a sort of ‘play for the play itself’), I expect that the frequency of social play after a solitary play session is higher than the frequency of social play after other self-directed behaviours (prediction 4a).

It is often assumed that the performance of self-handicapping movements during play is a valuable play signal for the receiver (Loizos 1967; Pereira & Preisser 1998; Power 2000; Burghardt 2005). If prediction 4a is confirmed, I also expect that among adult bonobos some self-handicapping patterns performed during solitary play may be involved in soliciting play sessions (prediction 4b).

METHODS

Study Group and Data Collection

Behavioural data were collected on a group of bonobos housed in the Apenheul Primate Park (Apeldoorn, The

Netherlands), first established in 1998. The composition of the group during the observation period (July–October 2000) included 11 individuals (see Table 1 for details). The wild-caught animals were collected from different sites on different occasions. Bonobos were housed in an enclosure with both an indoor and an outdoor facility (about 230 and 5000 m², respectively). The animals were able to move freely from the indoor to the outdoor enclosure after the first feeding session (at 0845 hours) and received food (milk enriched by vitamins and proteins, monkey chow, vegetables and fruit) four times a day at about 0845, 1230, 1430 and 1630 hours. Most of the food items were scattered on the floor. Water was available ad libitum and environmental enrichment in the forms of fresh branches, rice and nuts broadcasted in the grass to encourage foraging activity and renewal of the equipment in the indoor facility was provided. Sometimes a wooden block with holes filled with honey or yoghurt was provided. No stereotypic or aberrant behaviour characterized the study group.

The observations, carried out by me and an assistant (T. Paoli), were made over a 6-h period each day, encompassing both the morning and the afternoon. Data were collected using a tape recorder, and these records were later transcribed onto a computer. Before commencing systematic data collection, I and T.P. underwent a training period. We followed the same focal animals simultaneously and then compared and discussed data. The training (80 h) ended when the observations matched in 95% of cases (Martin & Bateson 1986).

Play session data were collected by focal animal sampling (about 41 h of observation per individual) (Altmann 1974) and included the following patterns: play bite, pirouette, acrobatic play, play retrieve, play run, play slap, rough and tumble play tickle, play push, play brusque rush, play recover a thing and play stamp (see Table 2 for the item definitions). A play session began when one

Table 1. Bonobos at the Apenheul Primate Park (Apeldoorn, The Netherlands)

Subject	Sex	Age	Date of birth	Origin, Arrival date
Hani (H)	M	Adult	1989, wild	Zaire, 1998
Mobikisi (MB)	M	Adult	1981, wild	Antwerpen, 1996
Mwindu (MW)	M	Adult	1985, wild	Zaire, 1998
Jill (J)	F	Adult	1985, captivity	San Diego, 1997
Rosie (R)	F	Adult	1989, wild	Zaire, 1998
Molaso (M)	F	Adult	1985, wild	Zaire, 1998
Zuani (Z)	F	Adult	1990, wild	Zaire, 1998
Lomela (LO)	F	Adult	1992, captivity	Frankfurt, 1998
Liboso (LI)	F	Juvenile	1997, captivity, Zuani's daughter	Zaire, 1998
Tarishi (T)	M	Infant	1998, captivity, Jill's son	Apenheul
Kumbuka (K)	F	Infant	1999, captivity, Molaso's daughter	Apenheul

M: male; F: female.

Table 2. Play behavioural patterns recorded during the observation sessions

Play patterns	Definition
Airplane	An adult lies on its back and raises an infant up with its hands and feet
Grab gentle	An animal gently massages another
Play push	An animal pushes a playmate with its hands or feet
Play bite	An animal gently bites a playmate
Play recover a thing	An animal chases a playmate and attempts to grab an object carried by it
Play slap	An animal slaps any part of a playmate's body
Tickle	An animal contacts the partner's body with its mouth or hands
Pirouette	One or more animals together turn, somersault or roll over on the ground or on vertical supports
Acrobatic play	One (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (e.g. branches)
Play run	An animal runs alone (solitary play) or chases a play partner (social play)
Play stamp	An animal jumps on a play partner with its feet
Rough and tumble play	Two or more animals grasp, slap and bite each other (typical of immature individuals)
Play brusque rush	An animal jumps with its four limbs onto a playmate
Play retrieve	An animal holds a playmate to avoid interruption of the session
Play invite	An animal approaches a possible play partner, pats it and then goes away (used to start a play session)

partner directed any playful behaviour to its playmate and ended when the participants ceased their activities or one moved away.

Both social and solitary play sessions were recorded; for social play we also recorded the names of the actors and receivers in the play session. For each play session, the number and the identity of the playmates in the session were also recorded, thus permitting distinction between dyadic (two players involved) and polyadic (more than two players involved) play sessions (Hayaki 1985).

Grooming and agonistic interactions were also recorded by focal animal sampling. Agonistic events comprised bite, hit, slap, chase, threaten and pull (see Kano 1980, 1996 for a description). For both grooming and agonistic contacts both the names of the individuals involved and the directionality of the action were registered.

Data Analysis and Statistics

To assess whether solitary play may have a triggering function for social play, I focused on the temporal associations between solitary and social play sessions. In the sequential analysis, I counted how many times an individual initiated a social play session with the performer of the solitary play immediately after his/her solitary performance. I excluded all sessions initiated by

the performer of the solitary play. The frequency of social play observed after a solitary play session was then compared with the frequency of social play observed after one of the following self-directed behaviours: feeding, walking or autogrooming. Then, I compared the play patterns involved in the solitary sessions that directly preceded social sessions with the play patterns used during the solitary sessions that were not directly followed by social sessions.

I used mainly nonparametric statistics (Siegel & Castellan 1988; Lehner 1996; Zar 1999). Particularly, the Wilcoxon signed-ranks test (corrected for ties) was used to assess the differences between the frequencies of play signals performed during the diverse playful contexts and to compare the frequencies of social play bouts occurring directly after a solitary play session and after a self-directed behaviour.

The Friedman two-way analysis of variance was used to determine whether three or more samples (with blocked measurements or repeated measures) on the same individuals were significantly different. The Friedman two-way analysis of variance was also applied to assess differences in the distribution of the play patterns used after a playful facial display during social play and to investigate whether during solitary play some patterns are preferentially used. When the obtained value of the Friedman test was significant, to determine which pairs of samples differed significantly I used the Dunnnett multiple comparison test as suggested by Lehner (1996) and Zar (1999).

When applying nonparametric statistics, I made use of exact tests according to the threshold values as suggested by Mundry & Fisher (1998). Statistical analyses were performed by using Microsoft Excel, SPSS 12.0 (SPSS Inc., Chicago, IL, U.S.A.).

To correlate the play face distribution with the grooming and agonistic contacts (matrix-based data) I made use of a matrix permutation analysis. This method of analysis accounts for interdependency of the data within matrices that generally prevents evaluation of the probability of a correlation against a normal distribution. The matrices were permuted 10 000 times. Each analysis was carried out using the MatMan 1.0 Software by Noldus developed by de Vries et al. (1993).

All analyses were two tailed, and the level of significance was set at 5%.

RESULTS

Prediction 1

The analysis of the frequencies of play face (mean \pm SE frequency 0.008 ± 0.003) and full play face (mean \pm SE frequency 0.1975 ± 0.059) in adults revealed a significant difference with the former less frequent than the latter (Wilcoxon signed-ranks test: $T = 0$, $N = 8$, ties = 2, $P < 0.05$). The play face was present with extremely low frequency in only two subjects.

I found a significantly higher frequency of play signals during social play (mean \pm SE frequency 0.28 ± 0.018) than during solitary play (mean \pm SE frequency

0.07 ± 0.02) sessions (Wilcoxon signed-ranks test: $T = 0$, $N = 8$, ties = 2, $P < 0.05$).

Prediction 2

The analysis of the frequency of dyadic (mean \pm SE frequency 0.45 ± 0.094) and polyadic (mean \pm SE frequency 0.11 ± 0.034) sessions revealed that the former were significantly higher than the latter, with two subjects of the group never involved in polyadic play sessions (Wilcoxon signed-ranks test: $T = 0$, $N = 8$, ties = 2, $P < 0.01$; Fig. 1a). The polyadic play sessions comprised about 24% of the social play sessions performed. Among the polyadic sessions I recorded all but one as triadic sessions. When I tested for the distribution of playful facial displays according to the number of playmates involved in the session, I found that the animals performed play signals at higher rates during the polyadic sessions than during the dyadic sessions (Wilcoxon signed-ranks test: $T = 0$, $N = 6$, ties = 0, $P < 0.05$; mean \pm SE frequency of play signals during dyadic sessions 1.79 ± 0.439 ; mean \pm SE frequency of play signals during polyadic sessions 0.375 ± 0.106 ; Fig. 1b).

Prediction 3

With regard to the use of play facial displays by adults according to the age of the playmate, adults performed play signals with a higher frequency when playing with other adults (mean \pm SE frequency 0.330 ± 0.089) than during play sessions with immatures (mean \pm SE frequency 0.046 ± 0.015) (Wilcoxon signed-ranks test: $T = 0$, ties = 1, $N = 8$, $P < 0.05$; Fig. 2).

I also analysed the frequency of play sessions that became particularly violent (involving screaming and bared teeth in at least one of the playmates). Adult–adult play behaviour never escalated towards actual conflict. Escalation to violent play occurred only when at least one of the playmates was an immature. The mean \pm SE frequency of violent play/play session was 0.002 ± 0.00042 . I never observed the occurrence of play signals during play bouts that escalated into real conflicts.

Adult bonobos displayed play signals significantly more often to maintain (mean \pm SE frequency 0.221 ± 0.052) than to initiate (mean \pm SE frequency 0.033 ± 0.086) a social play session (Wilcoxon signed-ranks test: $T = 0$, $N = 8$, ties = 2, $P < 0.05$; Fig. 3a). The analysis of the patterns following playful facial displays (PRUN: play run; PS: pirouette/somersault; PBIT: play bite; PRE: play retrieve; see Table 2) revealed a high significant difference (Friedman test: $\chi^2_3 = 12.74$, $N = 8$, $P < 0.001$). For determining what pairs of play patterns differed significantly, I applied the Dunnett post hoc test and obtained the following results (PRUN versus PS: $q = 0.53$, $N = 8$, NS; PRUN versus PRE: $q = 2.65$, $N = 8$, $P < 0.01$; PRUN versus PBIT: $q = 0.74$, $N = 8$, NS; PS versus PBIT: $q = 0.51$, $N = 8$, NS; PS versus PRE: $q = 3.00$, $N = 8$, $P < 0.01$; PBIT versus PRE: $q = 3.73$, $N = 8$, $P < 0.01$; Fig. 3b).

A row-wise matrix permutation procedure revealed a positive correlation between the use of play signals

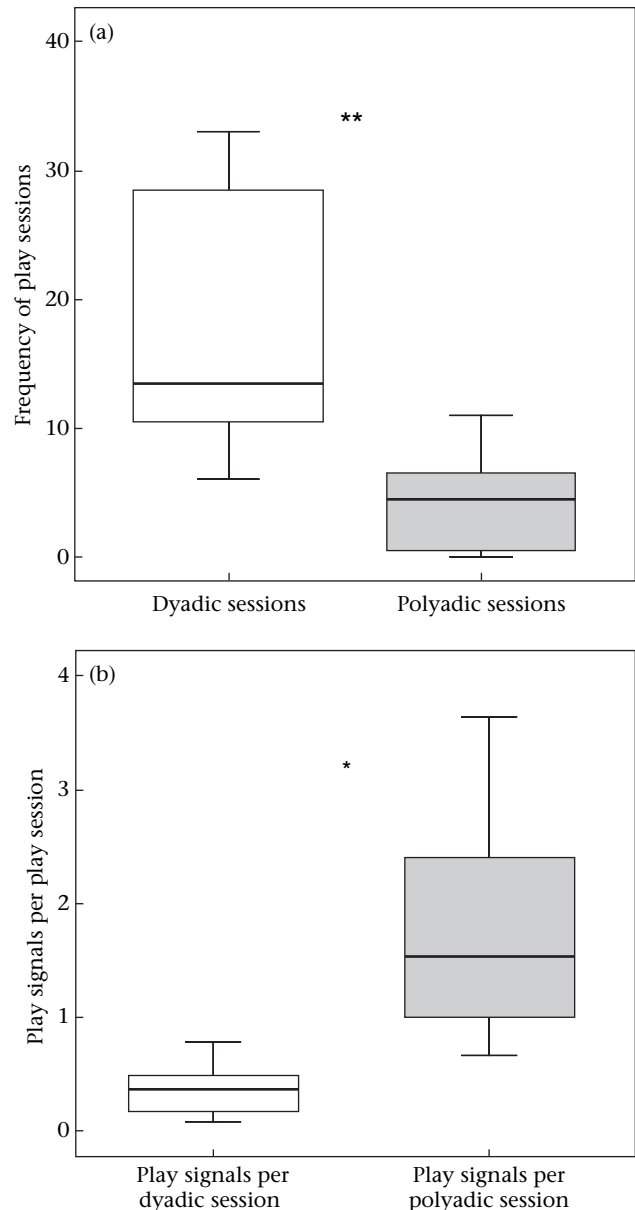


Figure 1. (a) Frequency of dyadic and polyadic play sessions between adult bonobos; $**P < 0.01$. (b) Frequency of play signals per dyadic and per polyadic play sessions performed by adult bonobos; $*P < 0.05$. Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

and the number of agonistic encounters between the playmates (play signals–agonistic encounters: $k_r = 17$, $\tau_{rw} = 0.27$, $N = 8$, $P < 0.05$). On the other hand, no correlation between the distribution of play signals and the grooming sessions was found (play signals–grooming: $k_r = 5$, $\tau_{rw} = 0.07$, $N = 8$, $P = 0.355$).

Prediction 4

The mean \pm SE percentage of solitary play sessions directly followed by social play was $47.7 \pm 4.0\%$. The

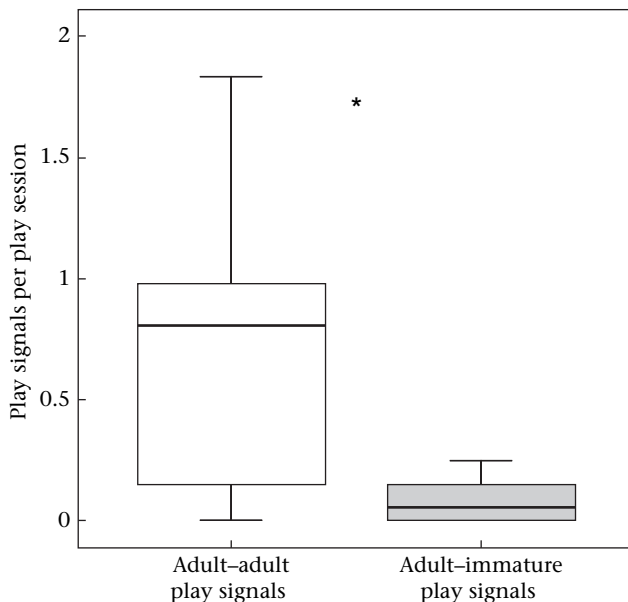


Figure 2. Frequency of play signals per play session performed by adult bonobos according to the age class of the playmates (other adults or immatures); * $P < 0.05$. Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

sequential analysis revealed that solitary play sessions increased the likelihood of social play compared to other self-directed behaviours (Wilcoxon signed-ranks test: $T = 0$, ties = 0, $N = 8$, $P < 0.01$; Fig. 4).

The behavioural patterns recorded during solitary play were acrobatic play (ACP 48.7%), pirouette/somersault (PS 30.6%), play run (PRUN 17.8%), object play manipulation (PMAN 1.6%) and play stamping (PSTA 1.3%) (see Table 2). Due to the low frequencies of PMAN and PSTA, I selected ACP, PS and PRUN to elucidate whether a particular play pattern was more frequently involved in the solitary play sessions directly followed by social sessions. The analysis of the frequency distributions of ACP, PS and PRUN performed during the solitary play not directly followed by social play revealed no statistical differences (Friedman test: $\chi^2_2 = 1.23$, $df = 2$, $N = 8$, $P = 0.585$). On the contrary, the Friedman test revealed a statistical difference in the distributions of ACP, PS and PRUN performed during the solitary play directly followed by social play ($\chi^2_2 = 12.07$, $df = 2$, $N = 8$, $P < 0.001$). For determining which pairs of play patterns differed significantly, I applied the Dunnett post hoc test and obtained the following results (ACP versus PS: $q = 3.53$, $N = 8$, $P < 0.01$; ACP versus PRUN: $q = 1.41$, $N = 8$, NS; PS versus PRUN: $q = 3.50$, $N = 8$, $P < 0.01$; Fig. 5).

DISCUSSION

Adult bonobos use preferentially the full play face compared to the play face and the frequency of play signals is significantly higher during social play than during solitary play, even though the play signals are displayed also in solitary play (prediction 1 confirmed). Moreover, polyadic

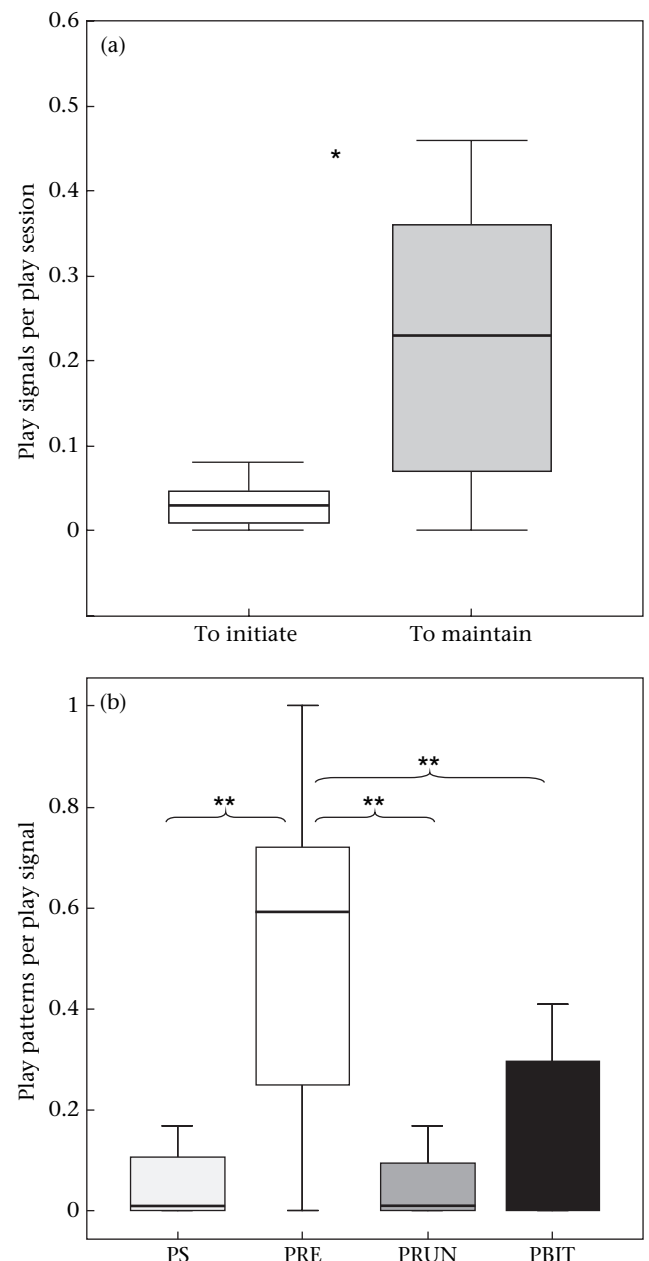


Figure 3. (a) Frequency of play signals per play session performed by adult bonobos at the beginning of (to initiate) and in the middle of (to maintain) a play session; * $P < 0.05$. (b) Frequency of play patterns between adult bonobos following a play signal during the social play sessions; ** $P < 0.01$. (PS: pirouette/somersault; PRE: play retrieve; PRUN: play run; PBIT: play bite). Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

play sessions, although rarer than dyadic sessions, had higher frequencies of playful facial displays (prediction 2 confirmed). In adult bonobos, the use of play expressions appears to be highly selective according to (1) the age class of playmates; (2) the timing of the performance during the play session (within the session more than at the beginning of it); and (3) the baseline frequency and direction of aggression between the playing dyads

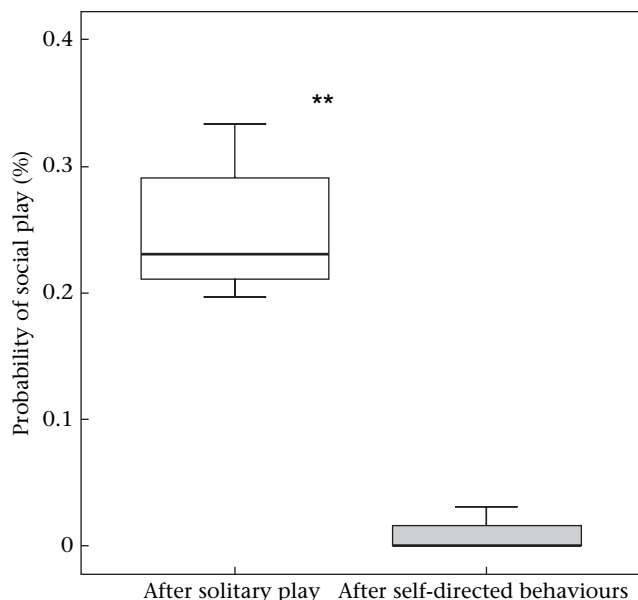


Figure 4. Probability (%) of social play after solitary play behaviours and after self-directed behaviours (feeding, walking, autogrooming); $**P < 0.01$. Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

(prediction 3 only partially confirmed). Finally, solitary play sessions, particularly when characterized by pirouettes and somersaults, appear to have an important role in soliciting social play (prediction 4 confirmed).

Previous studies (de Waal 1988, 2003; Palagi 2006) elucidated the differences in the use of the two grades of the

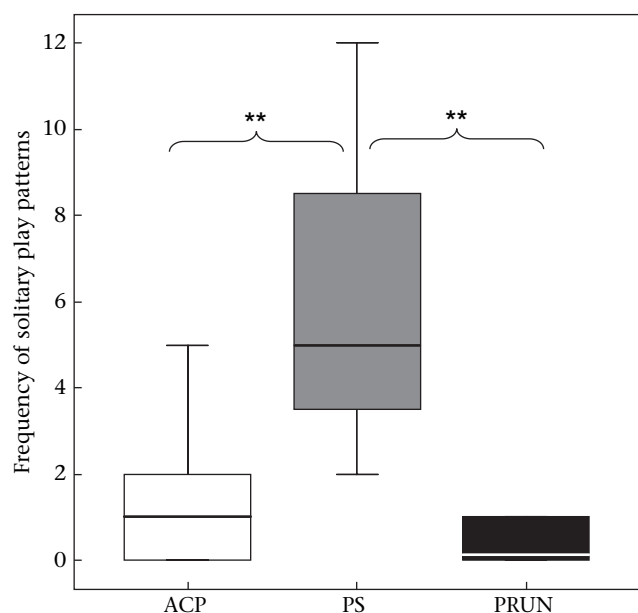


Figure 5. Frequency of patterns used during those solitary play sessions that were directly followed by social play sessions; $**P < 0.01$. (ACP: acrobatic play; PS: pirouette/somersault; PRUN: play run). Thick horizontal lines indicate medians; height of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

playful facial displays (PF and FPF) in the *Pan* genus, with bonobos using the FPF more frequently than chimpanzees. In particular, I interpreted this greater tooth exposure as signifying a higher intensity of play, which I found in bonobos (Palagi 2006). This flexibility in the performance of play signals both within and between the two species may derive from the gradedness of signals, which is striking in the facial expressions of the great apes (de Waal 2003). In monkeys, the facial expressions are generally fixed, whereas in hominoids they may show a gradient of intensity, which appears to be associated strictly with the emotions experienced by the animals (Parr 2003b). This theory is supported by the observation that bonobos (like chimpanzees) sometimes perform the play face also while engaged in solitary play conversely to macaques, capuchins, and marmosets (Van Hooff & Preuschoft 2003; De Marco & Visalberghi 2007; unpublished data). Van Hooff & Preuschoft (2003, page 257) affirmed that this 'private emotional expression' may suggest not only a playful intent directed to a potential partner but also a capacity for self-reflection or self-awareness, which are the precursors to more complex forms of cognition in social communication. However, the peak frequency of play faces occurred during the social sessions, thus emphasizing the important function of such signals in play communication (Waller & Dunbar 2005; Palagi et al. 2007). This evidence is supported by previous findings. Palagi & Paoli (2007) showed that play sessions involving contact between the participants had higher frequencies of play faces than play sessions characterized exclusively by the presence of locomotor patterns. Contact play involving cooperation and reciprocity is one of the most sophisticated and complex forms of social interaction, during which the playmates have to trust each other to maintain the rules of the game (Bekoff 2001; Dugatkin & Bekoff 2003). This appears to be crucial when the play session involves animals with similar age and size; this could be the reason that, among adult bonobos, play faces are particularly frequent. Some studies (Pellis et al. 1993; Pellis & Iwaniuk 2000; Palagi 2006) emphasized that contact play (in its more intense variants, e.g. play fighting) may be used to maintain social bonds, test for weakness of play partners and, therefore, gain social advantage especially when relationships among adults are not codified and structured according to rank rules. Among adult bonobos, play fighting might be a form of competitive interaction that functions to test a partner's willingness to invest in a relationship and simultaneously to show willingness to accept vulnerability (Palagi 2006). Since this form of complex social interaction is risky and an escalation of roughness among adults may be particularly dangerous, a clear declaration of intent is needed. This hypothesis is also supported by an interesting finding reported for spider monkeys, *Ateles geoffroyi*. In this species, the characteristic head shake (regarded an affiliative signal; Eisenberg 1976) was found to be more frequent during play fighting among adult dyads than during play fights involving immatures. Moreover, this pattern was used in 74% of cases immediately before a bite or bite attempt (Pellis & Pellis 1997).

In adult bonobos the frequencies of play sessions and agonistic contacts were not significantly correlated (Palagi & Paoli 2007). However, in the present study there was

a positive correlation between the level of aggression and the frequency of play face performed by each adult dyad (a selective use of play signals). In a comparative study of play signals in three species of canids (domestic dogs, timber wolves, and coyotes), Bekoff (1974) showed that the most aggressive species, the coyote, was the most likely to precede the play session with play invitation signals and the most likely to use play signals during the session. All these results suggest that aggressiveness among the individuals may predict their reliance on play signals in facilitating social play. On the other hand, a previous study showed a positive correlation between grooming and play distribution in adult bonobos (Palagi & Paoli 2007). However, the absence of any correlation between grooming and play signal rates found in the present study suggests that among those players sharing good relationships the use of play signals is less selective.

Due to its contagious nature, social play often involves more than two animals (Hayaki 1985; Pedersen et al. 1990; Loranca et al. 1999; Miklósi 1999). For example, in domestic piglets about the 20% of all play interactions are triadic (Špinka et al. 2001); in chimpanzees about 12% (Hayaki 1985) and in *Lemur catta* about 15% (unpublished data) are triadic. When a third individual intervenes playfully in a dyadic bout the play session may shift into a polyadic bout. During polyadic sessions, the level of unpredictability and the number of opportunities to respond and cope with unexpected situations increase. Managing this kind of situation may be considered a social challenge in which the appropriate use of play signals may have a crucial role. My finding of the selective use of play signals during polyadic sessions appears to corroborate this hypothesis.

I also found that playful facial expressions are generally performed during the session and not at the beginning of it: therefore, the signals appear to be important in maintaining a playful mood and not in soliciting a session. The most frequent pattern recorded after a play face is the play retrieve (see Table 2). This pattern is generally used when an individual holds a playmate to prevent interruption of the session. After a play retrieving by one of the two partners, the play session usually continues (unpublished data). The strict temporal association between play signals and play retrieves may indicate the play promoting function of such signals once the play session has begun.

Other communication mechanisms are probably involved in the start of a play session. Špinka et al. (2001, page 146) argued that 'self-handicapping movements and positions used to practise for awkward situations were good precursors for signals of an individual's playful intention'. Bonobos appear to use this communicatory tactic to elicit a playful response in the receiver (play for the play itself). About 50% of the solitary play sessions were followed by social play. Moreover, social play was more frequent when preceded by solitary play than by other self-directed behaviours and, particularly, the solitary play sessions directly preceding the social sessions had high rates of pirouettes and somersaults. An animal, when pirouetting rapidly, cannot leap or run precisely due to the difficulty in evaluating distances and

directions. When a receiver detects a conspecific performing a self-handicapping movement, the nonharmful intentions of that animal are intrinsically available. Moreover, the playful mood of the 'sender' may increase the behavioural propensity to play in the receiver.

One of the major questions is what kind of process can be the basis of this common use of pirouettes and somersaults to elicit play in adults. It is often assumed that the performance of communication signals is little affected by learning (Tagliatalata et al. 2003). However, one important exception exists, the cultural transmission of communication displays in the great apes, which sometimes create or invent new communicative signals by modifying pre-existing behavioural patterns (ontogenetic ritualization as defined by Tomasello & Call 1997). Tomasello et al. (1989) observed that a juvenile chimpanzee may initiate a play bout by slapping the potential playmate. If the receiver realizes that such an interaction always begins with the initiator raising her/his arm in preparation for slapping, the receiver may anticipate by responding when only the first movement is given. The initiator may perceive the anticipation of the receiver, realize that the arm raising by itself is sufficient to elicit a play response and thus, at some future encounter, use the same pattern to invite play. It is possible that a similar mechanism may be the basis of the use of pirouettes/somersaults for inviting play in adult bonobos, although it has to be stressed that most evidence of ontogenetic ritualization is reported for immature subjects. However, since an action that motivates play does not need to be an intentional signal to attract a partner to play (play contagion is well known in many animals including rats), there can be alternative explanations and my data are insufficient to discriminate between them. Whatever the origin of the use of pirouettes as play signals, among the adult bonobos of the Apenheul colony this tactic seems to be effective to motivate a receiver to play. It could be interesting to investigate this issue in other bonobo groups to assess whether the mechanism play for play itself is present and what kind of pattern is involved mainly in this peculiar play invitation.

Clearly, additional investigation on play signalling is necessary. Because social play is such a widespread behaviour, research on how animals share the intention to play should explore a variety of possible signals across a wide range of taxa not only to document the presence or absence of specific play signals but also to identify the factors (e.g. social structure, interindividual relationships, intensity of play, partner preference) that may predict the frequency, nature, variety and use of play signals within a given species.

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