NOT *JUST FOR FUN*! SOCIAL PLAY AS A SPRINGBOARD FOR ADULT SOCIAL COMPETENCE IN HUMAN AND NON-HUMAN PRIMATES

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ABSTRACT

Play is one of the most difficult behaviours to quantify and for this reason its study has had a very rocky history. Social play is ephemeral, difficult to distinguish from the other so called "serious" behaviours, not so frequent (especially in sexually mature subjects), fast and complex to describe. Due to its multifaceted nature, it has often been considered as a wastebasket category that has included all kinds of the behaviours not showing any immediate, obvious goal. Yet, play is widespread across the whole primate order and can have a strong impact on the development of cognitive, psychological and social skills of many species, including humans. Unlike functional behaviours that are specifically and economically performed to reduce uncertainty and to increase the opportunity to gain resources, play seems to introduce and increase uncertainty, creating new challenges for the animals. For this reason, social play has been hypothesized to be the engine of behavioural innovation in ontogeny. From the first mild and gentle interactions with the mother to the most sophisticated play fighting sessions and acrobatic action sequences with peers, play represents for juveniles (and not only for them!) a window onto the social and physical environment. In this review, I focus on social play and its relation to adult social competence. By playing, juveniles acquire competence to manage interactions with conspecifics, enlarge their social networks, and test their physical power and motor skills (i.e., long-term benefits). At the same time, I propose the view that play - due to its plastic and versatile nature - can be used in an opportunistic way, as a *joker* behaviour, throughout life to strategically obtain short-term or immediate benefits. I put forward the hypothesis that, during ontogeny, the *joker* function of play can be modulated according to the differing inter-individual relationships present in the diverse societies characterizing the primate order.

Key words: Play fighting; Ontogenetic and evolutionary pathways; Facial mimicry; Emotional sharing; Tolerant species;

αἰὼν παῖς ἐστι παίζων πεσσεύων • παιδὸς ἡ βασιληίη

Time is a child playing by moving the pawns: this is the realm of a child

Heraclitus (fragment 52)

Introduction

In 2005, Gordon Burghardt defined play by listing five different criteria that a behaviour has to accomplish to be included in the category of "play". Despite the precision and validity of Burghardt's definition, many authors are still defining play via *litotes* (from the Greek word λιτότής — a figure of speech which uses a negation with a term in place of using an antonym of that term). This is because it is easier to define play as what play 'is not' rather than what actually 'it is'. Since play occupies a diverse sphere than the so-called "serious" or maintenance behaviours (e.g., predatory, reproductive, defensive), in the past several authors have underlined (Bekoff and Allen 1998; Martin and Caro 1985) that play is a behaviour not producing obvious immediate and clear benefits (to the observer!). Actually, compared to "serious" behaviours, whose functions can be immediately detected and measured by the observer, understanding the real benefits of play remains an intriguing challenge. Play is assumed to be a time- and energy-consuming risky activity for subjects (Fagen 1993; Monteiro de Almeida Rocha et al. 2014; Palagi 2007), even though the real costs are largely unknown (Graham and Burghardt 2010). Therefore, at a first glance, play should have been counter-selected throughout the evolutionary process; however, there are data underlining the importance of play as a form of investment to acquire higher levels of competence. In Assamese macaques (*Macaca assamensis*), juvenile locomotor play implies considerable costs in term of reduced growth but it is highly advantageous in speeding up the acquisition of motor skills. Hence, play seems to have ontogenetic priority over the physical growth rates thus suggesting that it is a key factor in the ontogenetic process (Berghänel et al. 2015). This is an important piece of information that may explain why play is well represented in the animal kingdom (Burghardt 2005).

Play adaptive functions and, consequently, its significance in natural life history are difficult to identify for several reasons. First, when a behaviour is multifunctional (thanks to its plasticity and versatility) it may provide different advantages according to the context in which it occurs (Palagi et al. 2016a). The benefits of play can vary as a function of the species, the sex and age of the players, and their physiological and emotional state. This multi-functionality makes it hard to categorize all the single adaptive functions because they can overlap. Moreover, the benefits deriving from play can be immediate (Palagi et al. 2004; 2006) or delayed in time (Blumstein et al. 2013; Nunn 2014). This is troublesome for researchers who must often disentangle many different interacting factors in order to provide a reliable measure of the benefits produced by play. Hence, a strict separation between the potential immediate and delayed benefits may not make much sense, as immediate can often translate into delayed benefits. Obviously, trying to operationally separate the different benefits of play (immediate *vs* delayed) increases the possibility to quantify them but, at the same time, obfuscates the holistic perspective of the phenomenon whose multifuctionality is likely at the basis of its evolution.

In this review, I will discuss the possibility of the interception between the potential benefits of play with its communicative potential by spotlighting two main interacting factors that influence its distribution in the life history: ontogeny (from the infant to the adult stage) and sociality (from the most tolerant to the most despotic societies). I will also show how these two factors can affect each other thus delineating peculiar evolutionary pathways of play. Finally, I will introduce the importance of facial expressions and their mimicry in fine-tuning the playful sessions by taking into account the different degrees of social tolerance of the species.

Playing for the future

Primates are extremely playful and spend a large amount of time engaging in any form of play (locomotor, object, and social), more than subjects belonging to any other taxa (Burghardt 2005). In this playful world, mother is the first playmate and the intimate dialogue between mother and offspring enhances cognitive skills in infants (Provine 1996, 1997). Tickling and laughing while engaging in a face-to-face contact are naturally observed in mother-infant interactions in many primate species and this practice has a fundamental role in infants' development (Dettmer et al. 2016). Its effectiveness relies on the multimodal nature of the behaviour which derives from the integration of different kinds of stimuli (auditory, tactile and visual). Provine (1996, 1997) stated that tickling does not involve a mere tactile reflex but it is a context-dependent social contact shared by the two interacting subjects, the tickler and the ticklee. Therefore, tickling play is a shared emotional experience and it is considered being at the basis of the development of mother-infant (or care-giver) inter-subjectivity (Ishijima and Negayama 2017). Hence, mother–infant sensory-motor play (e.g. tickling) cannot be simply interpreted as a physiological stimulation, but as a psychological investment on offspring. Touching is a cornerstone in infant-caregiver communication. In an elegant study on rhesus macaques (*Macaca mulatta*), Simpson and co-workers (2017) demonstrated that the neonates who received more tactile stimulation (e.g., tickling) were later less inhibited in their explorative behaviour and experienced less fear when approaching novel objects and new social partners. In short, social touching and stimulation in the neonatal phase translate into a proper behavioural development at both motor and emotional level.

Via interactive play with others, infants learn how to move and act upon their world (Bigelow et al. 2004; Rossmanith et al. 2014). The close linkage between play, interaction and learning finds support from studies carried out on preterm babies, who showed faster cognitive recovering when they were properly stimulated through sensory-motor play (Forcada-Guex et al. 2006; Håkstada et al. 2017; Treyvaud et al. 2009). In 1997, Feldman and Greenbaum demonstrated that the affect regulation and emotional synchrony characterising mother–baby play (facial expressions, manual actions, gazing, and 'motherese' vocalization) can be predictive of the development of symbolic competence in infants. In humans, mother–infant play is therefore one of the driving forces of infants' motor, social, cognitive and language development (Lifter et al. 2011).

In non-human primates, playful interactions between mothers and infants involve a multi-modal approach in which a true communicative exchange takes place especially during the first phases of life. In chimpanzees (*Pan troglodytes*), for example, infants are dependent upon their mothers for a prolonged period with weaning occurring between the ages of 3 and 5 years (Watts and Pusey 1993), with attenuation of infant energetic demand during the first 2 years and a marked decline in suckling frequency after the first 6 months (Thompson et al. 2012). Despite the energetic constraints due to lactation and carrying, during the first year of life chimpanzee mothers invest their energy and time in grooming and playing with their infants. Experiments of social isolation (Suomi 2005) and naturalistic observations in monkeys (Fairbanks 2000) have demonstrated that the first months of life represent a very sensitive period to acquire skills for proper socialization. This finding is also supported by a comparative analysis which demonstrates that the rates of social play are significantly associated with postnatal brain growth and longer period of lactation in primates, but not with longer juvenile periods (Montgomery 2014). Taken together, all these findings converge in indicating that the timing of play reflects changes in the timing of plasticity of neuronal and cognitive systems at a very early stage of life. In chimpanzees, the levels of investment in grooming and play differ between primiparous and multiparous mothers. Compared to multiparous females, primiparous females spend a larger amount of time in grooming and playing with their infants in the first year of life (Stanton et al. 2014); however, despite the difference in maternal investment, firstborns and laterborns are equally likely to survive. Although it remains to be determined whether primiparous females have the same social success of multiparous females (e.g., ability to engage in cooperation, to become dominant), it is possible that, by increasing their playing efforts, primiparous females compensate for their maternal inexperience and give their infants equal chance to survive.

Early mother-infant communication in chimpanzees often relies on tickling and gentle grabbing (Plooij 1979, 1984). These mother's gestures are also accompanied by facial expressions and vocalizations. If during such interactions the infant performs a relaxed open mouth (or play face), this is used by the mother to emphasize her tactile stimulation (e.g., Adamson and Bakeman 1984) in a sort of positive reinforcement. In macaques, mutual relaxed open mouth interactions are reported between mothers and infants (*Macaca mulatta*, Ferrari et al. 2009a). Such interactions often involve reciprocal replication, which translates into a mirroring effect between the two subjects. The proper stimulation through facial expressions by the mother and the appropriate mirror response by the infant increase the probability for the infant to develop a better social competence in the future. The neonates of rhesus macaques who were frequently stimulated by the mother and imitated her facial expressions spent more time in social play with peers one-year later (Kaburu et al. 2016).

These first playful interactions, relying on an exchange of tactile and visual stimuli with the mother, lay the foundation for more complex social playful interactions that infants will engage with their peers. There is a general consensus on the positive role of social play in fostering some motor and social skills not only in primates but also in other mammal species (Burghardt 2005; Norscia and Palagi 2016; Pellis and Pellis 2009).

Social play, and particularly play fighting between peers, seems to be fundamental for the development of infants at a later stage and represents a springboard to enter social world. In wild chimpanzees, Heintz and coworkers (2017) found that infants who frequently engaged in social play achieved motor (e.g., locomotor independence from the mother) and social skills (e.g., social grooming towards unrelated subjects) at an earlier age. In 1986, Goodall observed that when juvenile chimpanzees began to groom others they tended to engage in less social play sessions. The shifting between social play and grooming along with age supports the hypothesis that these behaviours share the role of favouring the formation and maintenance of social bonds. This hypothesis has been recently tested through a social network analysis on wild Japanese macaques (*Macaca fuscata*) (Shimada and Sueur 2017). Although the authors found that social play and grooming negatively correlated as a function of the age of the subjects, social play, rather than social grooming, reflected the association among juvenile macaques in their daily activities. Therefore, it seems that in *Macaca fuscata* social play is an important means for immature subjects to build those social relationships which will be fundamental for their social life.

What makes social play so important in leading immature subjects to become socially competent adults

Social, free play is a challenging behaviour which is constantly pervaded by elements of uncertainty (Burghardt 2017; Palagi et al. 2016a; Špinka et al. 2001). Play strikingly differs from ritualization. Ritualized behaviour relies on a temporal and hierarchical organization of fixed and repeatable sequences of motor patterns (Tinbergen 1952). The elaboration and incorporation of many behavioural patterns extracted from different functional systems into ritualization is well known in the contexts of feeding, courtship, agonism and parent–offspring interactions (Burghardt 1973). Also in play, many behavioural patterns are recruited from the 'serious' domains, but such patterns are arranged in an infinite variety of combinations. In some cases, new motor patterns (e.g., postures, gestures, facial expressions) are produced (or 'invented') to increase the level of unpredictability. An elucidating example is the *Blindman's bluff game* which is not rare both in human and non-human primates (Palagi et al. 2016a). By actively covering their own eyes via hands or objects (e.g., large leaves, cloths) bonobos (*Pan paniscus*), for example, walk on horizontal branches while trying to maintain equilibrium and avoid falling down. This kind of play can be performed during locomotor/solitary play, but it seems to be particularly highly rewarding during social play when animals try to catch playmates (Palagi 2012). It is therefore clear that the object used to cover the eyes is a means to create a novel, self-handicapping situation, with which the subject has to cope (Figure 1).

In a naturalistic study on preschool children, Cordoni and colleagues (2016) found that most of the aggressive interactions occurred during free play and involved 3-year old children. This result can be explained by the lower level of social competence of younger children (3 years) compared to the older ones (5 years). Aggressive conflicts in younger children are mainly due to their inability to limit their roughness during play fighting and to reach a friendly compromise over the possession of a toy which translates into coercive strategies of resource control. As children grow older, they develop more sophisticated tactics of interacting with peers (e.g., self-handicapping and self-restraint) that can be based on the development of empathic and cognitive abilities (intrinsic factors) and on their social previous experience (extrinsic factors).

Whatever the species considered, play fighting bears the risk of escalation into serious fighting. This is because the practice, despite its apparently free-flowing performance, involves a very high number of uncertain modules which increases the level of risk. The player immediately reacts after the actions produced by playmates apparently without any evaluation of the risk. During play fighting, it seems that rules are completely missing. However, rules are present and, in case they are not followed, the session can escalate into overt aggression (Cordoni et al. 2017; Pellis et al. 2010). This can occur, for example, when one playmate uses disproportionate force or fails to adhere to the rules of turn-taking, thus making the play session unbalanced (Palagi et al. 2016a; Pellegrini 2009; Pellis and Pellis, 1998, 2017; Pellis et al. 2010). A free play session involves rules that have to be created by the players *hic et nunc* (here and now) and that can flexibly vary along with sex, age, bonding of the players, but also with the roughness and type of the session itself. Therefore, each playful encounter is characterized by different rules that are incessantly changed. This agreement could not be reached without highly sophisticated and complex communication. For this reason, play fighting is considered by ethologists, sociobiologists and comparative psychologists a window into social cognition and communication (Palagi et al. 2016a) and a fertile field with which to explore the evolution of shared intentionality (Heesen et al. 2017).

Specific facial expressions, vocalizations, movements, gestures, and postures can be recruited during play fighting to signal the non-seriousness of the context, thus reducing the uncertainty and prolonging the session (Bekoff 1995; Cordoni and Palagi 2011, 2013; Mancini et al. 2013a; Palagi and Cordoni 2012; Palagi et al. 2016a; Waller and Dunbar 2005; Weigel and Berman 2017).

The play domain creates unique experiences and gives juvenile subjects the opportunity to become skilled not only in synchronizing their motor actions but also managing their emotions when they come across new and unpredictable situations that are difficult to manage.

Self-handicapping is a widespread phenomenon occurring during play. Animals can put themselves into disadvantageous and vulnerable positions by reducing their strength and velocity whenever their playmates are mismatched in age or size (Bauer and Smuts 2007; Bekoff 2001; Lutz and Judge, 2017). Self-handicapping movements involving unnatural body/head positions in relation to gravity or strong limitation in sensory perception (as in the *Blindman's bluff game*) can be read by the playmates as honest signals of an individual's playful intention (Špinka et al. 2001). Bonobos, for example, use this communicatory tactic to elicit a playful response in the receiver. Palagi (2008) demonstrated that in this species play fighting was more frequent when preceded by acrobatic, self-handicapping solitary play than by any other self-directed behaviour. Solitary pirouettes, hanging upside down and somersaults performed by a subject seemed to trigger the response in the receiver that read the self-handicapping behaviour as an invitation to play (Figure 2).

In rats, Pellis and coworkers (2017) demonstrated that, for a juvenile, playing with peers is much more effective than playing with an adult subject because adults tend to limit and restrain their roughness thus giving to the immature subject high levels of advantage. Instead, juvenile-juvenile play requires high level of fine modulation and both subjects have to cooperate if they want to engage in a successful interaction. In this context, juveniles experience higher opportunities than adults to engage in self-handicapping behaviours so that the 'attacker' can become the 'defender' and *viceversa*. This de-escalating strategy has a strong impact on the success of social play, as it is predicted by the *Retroactive Function Hypothesis* of self-handicapping behaviour (Pellis and Pellis 1996), and is a very demanding and critical activity for the development of appropriate executive functions. The de-escalation strategy seems to be very fundamental in those animals which show high level of competition during play such as despotic species. Indeed, there is a large body of literature which underlines the importance of the tolerance experienced by a given species on the development of a huge variety of communicative components. In tolerant species, social interactions among individuals are highly variable, not structured or codified according to rank or kin rules (Flack and de Waal 2004). The different actions and their combinations are characterized by a high degree of freedom which translates into a high degree of unpredictability (Butovskaya 2004; Freeberg et al. 2012). The plasticity characterizing such social interactions requires a notable ability to properly communicate and negotiate each action. This holds true especially for the play domain: the free activity *par excellence*. In this view, the more the play is free from social constraints, the more it is effective in developing new communicative components: it is what occurs among juveniles and adults belonging to tolerant species (Ciani et al. 2012; Palagi 2008; Palagi et al. 2016b).

In despotic primate and non-primate species, juvenile individuals tend to refrain from playing with unmatched partners. For example, juveniles of rhesus macaques tend to avoid engaging in play with mismatched subjects (Kulik et al. 2015) and, when play occurs between males, it is generally characterized by short sessions (Yanagi and Berman, 2017). In South American sea lions (*Otaria flavescens*), a very competitive and highly dimorphic species, juveniles accurately select their playmates by limiting the number of players *per* session and by playing more with age- and size-matched peers. This hyper-selectivity is probably at the basis of the low level of escalation recorded during play in South American sea lions (Llamazares-Martín et al. 2017a).

In a very recent comparative study, Cordoni and colleagues (2018) demonstrated that lowland gorillas (*Gorilla gorilla gorilla*) tended to limit the number of play partners compared to chimpanzees, with the latter engaging in higher level of polyadic play. Even though gorillas tackled more balanced and less risky play sessions compared to chimpanzees, in the former play fighting escalated more frequently into serious aggression. In gorillas, play asymmetry increased along with the number of players thus explaining the strong limitation of polyadic play in this species. All these constraints put in action by immature gorillas translate into a virtual absence of playful interactions involving adults. All these findings led the authors to conclude that inter-individual bonding can account for the differences in play dynamics and distribution in the great apes. If, from one side, the strong preselection and constraints guarantee safer and less risky playful interactions; on the other side, it limits the possibility for juveniles to come across unpredictable situations and develop appropriate communicative strategies which will be useful in the future. Under these limitations, play is bridled and not completely functional because it is deprived of one of its most important features: the unpredictability. The '*a priori* selection' seems to be lacking in tolerant and more cooperative species (Palagi 2006).

The relaxed social relationships characterizing the tolerant and cooperative species make social play highly pervasive in its form and diffusion (Palagi et al. 2016b). Geladas (*Theropithecus gelada*), a tolerant species living in a multilevel society, engage in play in a highly promiscuous way, independently from their age, sex, size, kin, and rank (Mancini and Palagi 2009; Mancini et al. 2013a,b) (Figure 3). Macaques are organized along a continuum from intolerant (e.g., Japanese macaques, *Macaca fuscata*) to tolerant species (e.g., Tonkean and crested macaques, *Macaca tonkeana* and *Macaca nigra*) and, for this reason, they are good models to test some hypotheses about the possible linkage between playful communication and tolerance (Petit et al. 2008). Compared to Japanese macaques, Tonkean macaques show lower levels of selection about playmates. Immature subjects engage in social play with peers and also with other adults irrespective of their relatedness and gender (Ciani et al. 2012). Moreover, Tonkean macaques play more and for longer compared to Japanese macaques, suggesting a greater ability to manage the playful interactions (Scopa and Palagi, 2016). Play fighting in Japanese macaques is highly competitive with reduced physical contact (Reinhart et al. 2010); on the contrary, play fighting in Tonkean macaques is more cooperative and less defensive (Reinhart et al., 2010).

Social play is a phenomenon that appears very early in ontogeny, for this reason its diverse distribution, dynamics and effectiveness have to be searched in the first stage of life. If a society is relaxed and tolerant, mothers leave their infants free to interact not only with peers but also with other adults (Figure 4). This low level of social canalization expands the relational and emotional sphere of infants and increases the propensity to play also later in life. The enlarged experiences in early infancy can mould a more confident and sociable personality (Adams et al. 2015) that makes the individuals more prone to engage in social play with strangers, especially with adults (Ciani et al., 2012; Mancini and Palagi 2009; Palagi et al. 2016b; Petit et al. 2008; Reinhart et al. 2010; Scopa and Palagi, 2016). In this view, play seems to be the true engine that fosters and sustains the emotional and cognitive development of individuals especially if they live in a socially tolerant network.

Why it is so important to be playful adults

Once the adult phase has been reached, many experiences have been done, the cognitive capacities have been completely developed, both physical and social environment are familiar to the subject who is generally able to put in place the proper behaviour that each context requires. If the sole function of play were to provide training during immaturity to develop cognitive and physical abilities, then social play should be limited to the juvenile period. It is undeniably true that social play follows a bell-shape curve through ontogeny with a peak in the juvenile phase (Fagen 1993); however, many species of animals, and especially primates, continue to play as adults (Pellis and Pellis 2009; Norscia and Palagi 2011, 2016; Palagi 2007). Consequently, it is reasonable to argue that adult social play can serve immediate functions and that the behaviour is strategically used whenever it is needed (Palagi 2011). Adults can play when they need to solve or prevent disputes, to anticipate and buffer forthcoming periods of social tension or to keep the attention of a partner away from a resource. Play is used by adults to gain advantages at an immediate level and to establish good relationships at a short-term level. Therefore, the exploration of adult play is a window onto complex cognitive abilities enacted to manipulate social situations (Palagi et al. 2016).

Social play between adults seems to have an important role when individuals do not meet regularly either because they are mainly solitary or because they live in fluid societies (Pellis and Iwaniuk 1999, 2000). In solitary species (e.g. the genera *Mirza*, *Daubentonia*, *Galago*, *Perodicticus*, and *Pongo;* Norscia and Palagi 2016), adult social play seems to have a courtship function. In these species, play fighting is reported between males and females around the mating period with most of the scholars arguing that it can serve as an ice-breaker mechanism after long periods of separation.

As extensively discussed in the previous section of this review, the key social feature favouring social play is the propensity for tolerance (Ciani et al. 2012; Palagi 2006; Reinhart et al. 2010). This holds true not only for juvenile play but also for adult play. The social tolerance hypothesis finds support in the research on adult play in lemurs. Sifakas (*Propithecus verreauxi*) and ringtailed lemurs (*Lemur catta*) represent two good model species to test the influence of tolerance on adult social play in strepsirrhines. In *Lemur catta*, the most despotic lemur species (Norscia and Palagi 2016), play between adults is virtually absent and most of the sessions recorded in the wild involved at least one juvenile (Palagi et al. 2014). Under captive conditions, adult-adult play has been observed between males and females although strictly limited to the pre-reproductive period (Palagi 2009). In *Propithecus verreauxi*, a species showing more relaxed relationships and low propensity to aggression (Norscia and Palagi 2015; Norscia et al. 2009), adult-adult play is frequent. Via social play adult males have access to new groups via reducing their xenophobic propensity. One month before females enter the oestrus phase, which lasts no more than 72 h, adult males start roaming and visiting other groups. As almost all the other lemur species, females are the dominant and the choosing sex (Norscia and Palagi 2016). Immediately after the arrival of the out-group males and the very mild attempts to keep them away, the resident males begin to play with them at a very high frequency and stop their mild aggression thus indicating that play fighting was used in strategic way (Antonacci et al. 2010). Interestingly, resident males engage in play with the out-group males and concurrently direct more grooming to the other resident males. A clear-cut functional dichotomy between grooming and play is evident: grooming is used by resident males to maintain and reinforce their pre-established relationships and play fighting is used to establish new relationships. Play between unfamiliar males limits the escalation of overt aggression that is not beneficial to resident males because they can do very little against the mate choice operated by the females. Even though they won the disputes against the out-group males (with a high risk of injury and elevated energetic costs), they would not have any guarantee to gain female access. In this case, the social tolerance typical of *Propithecus verreauxi* makes play fighting extremely advantageous to solve sexual competition in a peaceful way.

Another illuminating example of the importance of social tolerance in favouring the use of social play in a strategic way comes from the two *Pan* species. Chimpanzees and bonobos are two sister species sharing a long evolutionary history, and the same social structure, both living in a fission-fusion society (Palagi and Demuru 2017). Both species show male philopatry with between-group differentiation in male kinship being extremely similar (Ishizuka et al. 2018). Despite such strong similarities, bonobos and chimpanzees are characterized by strong differences in adult social play (Palagi 2006, 2007). Bonobos are much more playful than chimpanzees, with social play involving concurrently more than two players. According to the social bridge hypothesis (Palagi 2011), adult individuals that rarely play together in dyadic interactions may be involved in polyadic play thanks to additional playmates who are motivated to join the session. These 'third parties' would represent a sort of bridge between two socially unconnected individuals, thus enlarging their social network. In the long run this mechanism may favour the formation of large parties, a peculiarity of bonobo social organisation (Kano 1992). Bonobo society is characterized by a wide array of cooperative activities in which adult individuals continuously negotiate their relationships through alliances and affiliation (Clay and de Waal 2013; Furuichi 2011; Palagi 2006; Palagi and Demuru 2017; Palagi and Norscia 2013).

Contrary to chimpanzees which are highly xenophobic and aggressive towards the individuals of other communities (Goodall 1986; Wrangham 2018), bonobos of different communities frequently engage in affiliation and sexual contacts to buffer social tension thus reducing the risk of attacks (Furuichi 2011; Tan et al. 2017). During such encounters, subjects can also play together. In the Congo river basin, Behncke (2015) observed an alpha male of a community play with a young adult male belonging to another community. It has been recently demonstrated that in bonobos the average relatedness among males within communities was significantly higher than that among males between communities, therefore, differentiation in male kinship is similar in bonobos and chimpanzees. Hence, the differences in hostility towards males of different groups between bonobos and chimpanzees cannot be explained by kinship and the inter-community social/playful exchange recorded in bonobos is necessarily linked to other factors, maybe to their true social, tolerant nature. Data on play in adult bonobos (e.g., inter-community, polyadic), again, support the social tolerance hypothesis, which predicts that the more a society is tolerant, the more play is freely expressed.

In conclusion, when play is present in all its possible forms and at every age, the behaviour becomes a strategic tool to manipulate social situations and enlarge social networks, thus favouring social integration and, in turn, potentially increasing individual fitness.

Let me see your face and look at mine! Tolerance, facial expressions and mimicry

The degree of freedom characterizing playful social interactions in the most tolerant species seems to be also at the basis of the redundancy and complexity of signals that these species have evolved (van Hooff 1967; Micheletta et al. 2013; Palagi and Mancini, 2011). Larger facial display repertoires and playful cooperative tendency could be favoured by natural selection in tolerant species which need to continuously negotiate their ever changing relationships (Dobson 2012; Palagi and Scopa 2017).

Spontaneous facial expressions, as opposed to fake or manipulative expressions (Calvo et al. 2013), are considered as honest signals informing the observers about the internal emotional state of the performer (de Waal 2003; Gallese 2003; Gallese et al. 2004; de Waal and Preston 2017). During play, facial expressions communicate emotions and intentions (Demuru et al. 2015; de Waal 2003) and have an important role in managing the play session (de Waal 2003; Mancini et al. 2013a; Palagi 2008; Pellis and Pellis 2009). During play, a specific facial expression, the relaxed open-mouth display, has been observed in many primate (ring-tailed lemurs: Palagi et al. 2014; Norscia and Palagi 2016; macaques, Scopa and Palagi 2016; Preuschoft 1992; Preuschoft and van Hooff 1995,1997; geladas, Palagi and Mancini 2011; great apes, Cordoni and Palagi 2013; Palagi 2006, 2008; Palagi and Cordoni 2012; Palagi et al. 2007; Waller and Cherry 2012) and non-primate species (American black bear, Henry and Herrero 1974; domestic dogs, Palagi et al. 2015; South American sea lions, Llamazares-Martín et al. 2017b).

To communicate their playful mood, many primate species can show two different configurations of the relaxed open-mouth display: the play face, in which only the lower teeth are exposed, and full play face, in which both upper and lower teeth are exposed (Palagi 2008; van Hooff and Preuschoft, 2003). In some cases, such as in geladas, gorillas and Tonkean macaques, the full play face can derive from a convergence of the play face and the bared-teeth display (a signal of appeasement, submission and/or affiliation) as the full play face seems to contain some morphological modules of both expressions (Palagi and Mancini 2011; Waller and Cherry 2012). The play face, however, is not the unique facial expression punctuating social play; other facial displays can concur in modulating the sessions and operating as de-escalating elements. In geladas, for example lip-smacking, a facial expression signalling appeasement or affiliation, is often performed (Palagi and Mancini 2011). In Tonkean macaques, not only lip smacking but also the bared teeth display is frequent during play fighting (Scopa and Palagi 2016). There is a strong correlation between the variability of facial expressions performed in the play domain and the level of tolerance shown by a species (Freeberg et al. 2012). Such a high plasticity in facial displays should be useless if receivers were not be able to contextualize and codify each facial expression in a proper way. It has been recently demonstrated that black crested macaque (*Macaca nigra*) can use facial expressions of others as pointers to potential actions at least in some contexts (Waller et al. 2016). In this view, a facial expression can be considered as a reliable, honest signal that anticipates the actions of others, thus reducing uncertainty in the receiver. This is extremely adaptive especially in tolerant species when animals have to deal with unpredictable social playful interactions. But what informs playmates that their facial expressions have been correctly caught and detected?

The ability to correctly decode information conveyed by facial displays and to properly respond to them has been critical for the evolution of social communication in primates (Allen et al. 2014; de Waal 2003; Schmidt and Cohn 2001). Face-to-face interactions, due to their interactive nature, are only considered efficient when the receiver responds appropriately. In South American sea lions, for example, the duration of each play session was positively affected by the amount of reciprocity of relaxed open-mouth displays performed by the players. The reciprocation was particularly high during dyadic encounters, when the players had the highest probability to engage in face-to-face interactions (Llamazares-Martín et al. 2017b).

In humans, the probability that a newborn smiles at its mother increases when she is most attentive and also smiling. It has been recently demonstrated that the behavioural facial displays, such as mirroring a smile, that mothers used preferentially to respond to infant expressions, created a positive feedback on the occurrence of the same facial expressions by the infant (Murray et al. 2016). Therefore, the correspondence between facial signals emitted and elicited is a reliable measure to evaluate the attentional state of the interacting subjects (Schmidt and Cohn 2001). Maintaining a playful facial chattering implies a certain amount of cost in terms of attentional investment and the effectiveness of a signal can be optimized only by paying attention to the receiver and to the outcome following the social interaction (Palagi and Mancini 2011). In this view, facial responsiveness allows animals to detect contingencies in their social world, to synchronize their motor sequences, and to perform a proper action into the right context (Provine 1996; 2004).

The importance of facial mimicry in maintaining a playful mood is becoming more and more evident (Palagi and Scopa 2017). The term *rapid facial mimicry* implies the unconscious and unintentional activation of a congruent facial expression in response to the mere observation of the facial expression of others (Hess and Fischer 2013). Facial mimicry recorded during free play is an extremely rapid phenomenon which often occurs within the first 500 ms after the perception of the stimulus (Seibt et al. 2015). Rapid facial mimicry seems to be driven by the automatic perception-action coupling of sensorimotor information that occurs in the mirror neuron areas (Clay et al. 2018; Ferrari et al. 2009b). It means that during the observation of a specific facial expression, the observer’s motor activation results in experiencing a matching emotional state with the trigger, in a sort of *same face-same emotion* effect. This is why, in human and non-human animals, rapid facial mimicry is considered one important phenomenon to emotionally connect two individuals (Palagi and Scopa 2017; Palagi and Norscia 2018) (Figure 5 and 6).

Compared to reciprocation, rapid mimicry is more effective in prolonging the playful session. The short reaction time appears to convey more information to the playmate. The immediateness of the response means that not only the stimulus has been perceived but that it has been accurately decoded and interpreted. In this view, rapid mimicry facilitates communicative exchanges and behavioural synchronization in the sequence of players' actions. This hypothesis is strongly supported by the new findings putting in relation the presence of rapid mimicry during the play sessions and the duration of the session itself. In all the species in which rapid mimicry has been demonstrated, it has been found to be fundamental in prolonging the play sessions (dogs, Palagi et al. 2015; chimpanzees and gorillas, Palagi et al. in press; geladas, Mancini et al. 2013b; Tonkean macaques, Scopa and Palagi 2016).

Interestingly, the level of tolerance of a species seems to be a good predictor not only for the amplitude of the facial repertoire used during play but also for the presence of the rapid facial mimicry phenomenon. The genus *Macaca* has once again provided a good model with which to test this hypothesis - Tonkean *versus* Japanese macaques. Despite the larger repertoire of facial expressions performed during play by Tonkean macaques (e.g., play faces, lip smacking, bared-teeth), the frequency of play faces used during play does not differ between the two species (Scopa and Palagi 2016; Pellis et al. 2011). Moreover, in both species the play faces were performed in all possible bodily orientations, including when the performer was out of the line of sight of the potential receiver. Nevertheless, when the researchers focussed on the presence of rapid facial mimicry, the difference emerged: the phenomenon was present in Tonkean macaques but not in Japanese macaques (Scopa and Palagi 2016). Psychologists, evolutionary biologists and neuroscientists have converged on the fundamental role of rapid, automatic mimicry in developing positive emotional contagion and empathy in humans (Prochazkova and Kret 2017). Hence, in our species, rapid mimicry is not simply a temporal linkage between perception and behaviour, but rather a behavioural phenomenon which is unconsciously activated and motivated by social affiliation and cooperation. While mimicry is an automatic and unconscious process, its presence correlates with the presence of an affiliative shared goal between the two interacting subjects. This means that i) *Homo sapiens* does not simply mimic motor facial actions, but the meaning underlying such actions, which convey emotional or social signals and ii) *Homo sapiens* mimics emotions when a sort of affiliation between the trigger and the mimicker is present. Therefore, rapid facial mimicry can be modulated by previous social experiences and by the immediate social context subjects are experiencing (Fischer and Hess 2017). If we apply the principle of parsimony (de Waal 2012), we should interpret the data on rapid facial mimicry in tolerant and despotic macaque species as an indicator of a different attitude of cooperation put in place while playing. The tolerant playful nature typical of Tonkean macaques (Ciani et al. 2012; Reinhart et al. 2010) can promote rapid mimicry which, in turn, fosters the emotional exchange between the players. This facial-emotional dialogue sustains the playful mood which, in turn, translates into longer sessions. Interestingly, the phenomenon was recorded not only in immature but also in adult subjects who, in this species, frequently engage in social play (Ciani et al. 2012; Reinhart et al., 2010; Scopa and Palagi 2016). Being skilled in maintaining prolonged playful interactions is beneficial for both immature and adult subjects living in tolerant societies because they increase the opportunity to promptly assess and renegotiate their relationships in groups whose social networks and bonding fluctuate independently from rank, nepotism or kinship. It is possible that the unpredictability of playful contacts typical of tolerant species could have positively selected those automatic and unconscious phenomena, such as rapid facial mimicry, which are at the basis of cooperation and coordination during play.

Conclusion

Play is a sort of *passepartout* which can open many doors. If we look at the multiple contexts in which social play can change its function we can easily understand the importance of this behaviour. Play is plastic in both its motor executions and roles. These two factors are strictly interconnected because the context in which a subject chooses to play can affect its modality. If I play with a peer to test his/her strengthen I will adapt my roughness accordingly. This continuous fine-tuning determined by the different roles that play can have in different contexts requires complex skills in the selection of playmates, self-control and ‘awareness’ that one can play that game without incurring in dangerous situations. This holds true independently from the age of the players. Both immature and adult subjects have to follow *hic et nunc* rules to make their playful sessions successful. We are naturally prone to think about immature and adult play as two disentangled phenomena, but this clear-cut division appears to be a pure operative necessity more than an actual difference. During the immature phase play can also have immediate or short-term functions as it occurs in adults. Flack and colleagues (2004) found that juvenile chimpanzees increased their play faces when their infant playmate’s mother was present, especially when they increased their roughness. This demonstrates that juvenile chimpanzees opportunistically use play signals not only to regulate the play session itself but also to manipulate the social context (in this case, the mother of the playmate) in which the session occurs. Therefore, it would be wrong to study immature play by starting from the preconception that play at that age produces exclusively long-term benefits. Immature play serves not only to develop capacities to efficiently deal with serious situations, but it also serves to learn to play, at least in some tolerant and cooperative species. Adults can opportunistically use play as a manipulative social tool because they have acquired the technique of playing during their immaturity. However, detecting long-term benefits is extremely complex. This is because both cognitive and physical development, especially in species with long periods of immaturity, depend on many epigenetic factors and play is only one of them. To solve the problem, at least in part, the comparative approach can be useful. It is now clear how play can be sensitive to some factors linked to the degree of social freedom of subjects within their groups. Studying the ontogenetic pathways while taking into account the social background in which the individual takes its first steps appears to be the best way to really understand the importance of play throughout development.

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Legends to figures

Figure 1 - Solitary *Blindman's bluff game* performed by an adult bonobo female. The full play face is visible under the white sheet. (Photo: Elisabetta Palagi)

Figure 2 - An infant male of bonobos hanging upside down in one of the most classical examples of self-handicapping. The subject is performing a full play face while a playmate is biting his feet (not visible in the image). (Photo: Elisabetta Palagi)

Figure 3 - Two sub-adult males of geladas engaging in a play fighting session. The phenomenon of rapid facial mimicry is evident with a perfect mirroring exchange of facial expressions (full play face). (Photo: Elisabetta Palagi)

Figure 4 - An adult bonobo female playing with an unrelated infant. The 'airplane' (an adult lies on its back and raises infant up with its hands and feet, Palagi 2006) is a very frequent playful pattern during adult-infant play. The infant is performing a full play face. (Photo: Elisabetta Palagi)

Figure 5 - In geladas black infants often play with other subjects of the group independently from their ages. (a) A black infant performs a full play face and a juvenile female responds with a bared-teeth display (incongruent response). On the right, the mother of the black infant is completely relaxed. (b) A black infant performs a full play face and the juvenile female responds in a congruent way with a full play face (rapid facial mimicry). The mother begins to tickle the throat of the black infant. There is a shifting from dyadic (a) to polyadic play (b). (Photo: Elisabetta Palagi)

Figure 6 - Rapid facial mimicry between an infant male and an infant female during a play fighting session in bonobos. (Photo: Elisabetta Palagi)

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5a & 5b

Figure 6