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Primate Play Laughing: a Comparison Between Immature Great Apes and Humans

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Introduction

In primates, playful interactions are often accompanied by specific facial expressions (van Hooff and Preuschoft, 2003). In the great apes, these expressions can be performed in two different ways: play face, where the mouth is opened with only the lower teeth exposed, and full play face, where the mouth is opened with upper and lower teeth exposed (Loizos, 1967). The use of the two expressions is plastic as a function of different factors such as play intensity (van Lawick-Goodall, 1968), playmate identity (Flack *et al.*, 2004), and context (Palagi and Mancini, 2011). Playful facial displays may have a role in signaling non-agonistic intent to a playmate and in expressing emotion both during social and solitary play sessions (Palagi, 2006; van Hooff and Preuschoft, 2003). The non-human primate play face is homologous with human laughter (van Hooff and Preuschoft, 2003) which, across the diverse cultures, is the external manifestation of joy and happiness (Sauter *et al.*, 2010). Primate laughter is considered a multifunctional behavior, because it reduces stress in subjects that face new situations, mitigates social ambivalence within a group, and triggers play interactions (see Gervais and Wilson, 2005 for an extensive review). If in the great apes, like it occurs in humans, playful facial expressions cover different roles and convey different information, we expect that they vary in frequency and form in relation to play intensity (Contact or Locomotor-Rotational play), playmate identity (sex of playmate), and number of players (dyadic or polyadic bouts). To test these hypotheses we collected data on two chimpanzee colonies (*Pan troglodytes*) and contrasted our findings with those coming from human literature on play facial communication.

Materials and Methods

The study was carried out on two groups of *Pan troglodytes* hosted at the ZooParc de Beauval (France) and the Dierenpark Amersfoort (The Netherlands). The Beauval colony was composed by 10 adults, 5 immature males, and 4 immature females. The Amersfoort colony was made up of 11 adults, 2 immature males, and 4 immature females. Both colonies lived in large enclosures of about 500 m^2. Observations took place over a 6-hour period, 6 days per week (Beauval: October 2001- February 2002; Amersfoort: May-October 2004). Data on play were collected by focal animal sampling method (Beauval: 31 hrs *per* individual; Amersfoort: 35 hrs *per* individual) (Altmann, 1974). A play session began when one partner directed any playful behavior towards a playmate and ended when the participants stopped their activities or one of them moved away (Palagi, 2008). If the bout started again after a delay of 10 s it was counted as a new play session. We recorded: i) playmates'identity, ii) playful patterns iii) circumstance in which play took place (e.g. feeding, sexual). Social play patterns included: object manipulation, bite, pirouetting/somersaults, acrobatic play, run, slap, tickle, push, and recovering a thing. We distinguished between locomotor-rotational (LR-play, absence of any pattern involving physical contact, Palagi and Paoli, 2007) and contact play (C-play). We also recorded the number of playmates and distinguished between dyadic (two players involved) and polyadic (more than two players involved) play. For Play Faces (PF) and Full Play Faces (FPF), we registered signaler and receiver identity (directionality).
To analyze the preferential use of PF or FPF respect to the total amount of playful signals performed, we used the following index [(FPF)/(PF+FPF)].
Data analysis focused on the 15 immature individuals. Due to the small sample size nonparametric statistical tests were applied. We made use of exact tests according to the threshold values suggested by Mundry and Fischer (1998). All the analyses were two-tailed and the level of significance was set at 5%.

Results

We found no evidence for directionality of signals (PF + FPF) as a function of sex (Mann-Whitney's U=28, N_{F-M}=8, N_{M-F}=7, p=1.0).
Play signals had comparable frequency in dyadic (D) and polyadic (P) play sessions (Wilcoxon's T=44, N=15, p=0.389). To evaluate the incidence of FPF in both D and P sessions we compared the following indices: (FPF_D/FPF_D+PF_D) *vs* (FPF_P/FPF_P+PF_P). We found no significant

difference between such indices (Wilcoxon's T=43, N=15, p=0.893).
Play signals were more frequent during C- than LR-play sessions (Wilcoxon's T=0, N=15, p=0.00001). Moreover, the incidence of FPF during C-play (FPF_C/FPF_C+PF_C) was higher compared to the incidence of FPF during LR-play ($FPF_{LR}/FPF_{LR}+ PF_{LR}$) (Wilcoxon's T=0, N=15, p=0.00001) (Fig. 1).

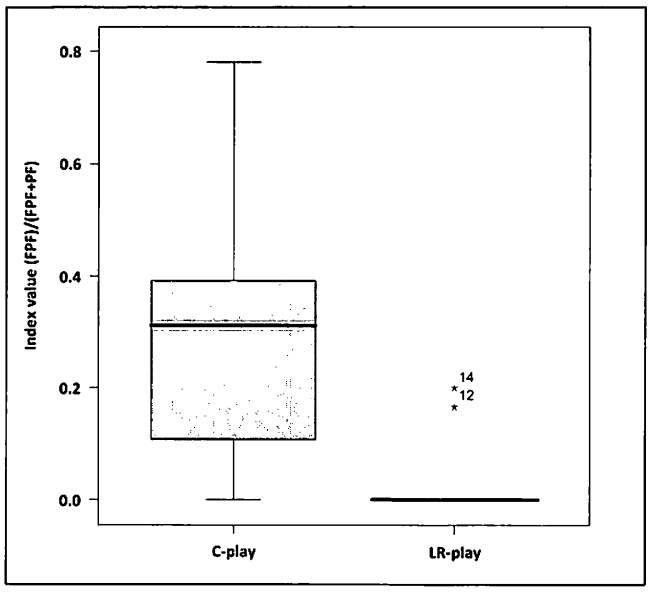

Fig. 1. *Index value distribution (FPF/FPF+PF) as a function of the two different types of playful interactions (LR-play and C-play). Thick horizontal lines indicate medians; height of the boxes corresponds to inter-quartile range; thin horizontal lines indicate range of observed values.*

Discussion

In immature chimpanzees, playful signal rates did not differ according to the sex and number of players involved in the session. The main factor affecting the play face distribution appears to be the intensity of play (C-play). Our data fit with findings coming from children literature; in fact, no difference was found in the laughing activity of boys and girls (preschoolers and toddlers) in different social contexts (Gervais and Wilson, 2005).
Even though there are no data on humans and other primates about the use of smiles according to the number of playmates, many efforts have been done in studying the role of such facial expression according to the roughness of play.
When play becomes more competitive, as it occurs in chimpanzees and humans, there needs to be clearer signaling (like full play faces) to maintain the session and to avoid it turning into overt aggression (Pellegrini, 2009). Also the other apes, like bonobos (*Pan paniscus*, Palagi 2008) and lowland gorillas (*Gorilla gorilla gorilla*, Palagi *et al.*, 2007), perform more full play faces during their riskiest playful contacts (e.g. during play fighting and when it occurs under reduced escape conditions), thus suggesting that animals are perfectly aware of the potential dangerous situations they are living. Therefore, like true human laughter, the playful expressions in apes seem to have a role in advertising cooperative intentions, thus increasing the likelihood of engaging in solid social relationships.
Is contact physical play just a "useless" activity, or is it really important in apes'and children's development? Primates (including humans) need to understand the meaning of play faces to enjoy such physical contact play. Pellegrini (2009) found that in children the frequency of peer contact play correlated to ability to understand play signals. Although it is difficult to prove a cause/effect relationship, it might be that children and apes with more difficulty in understanding others'emotional expressions engage in contact physical play less frequently and efficiently. This deficiency is not adaptive as, through contact play, immature animals can acquire the social competence that will be necessary to them later in life.

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