RESEARCH PAPERS

Differential Behavioural Effects of Silent Bared Teeth Display and Relaxed Open Mouth Display in Chimpanzees (*Pan troglodytes*)

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Abstract

This study examines the behavioural consequences of the silent bared teeth display (SBT) and the relaxed open mouth display (ROM) in the chimpanzee, and discusses functional similarities with smiling and laughing (respectively) in humans. Rates of affinitive behaviour increase (in relation to baseline levels) following SBT, suggesting that SBT is a signal of affinity. ROM is observed primarily during play, and dyadic play bouts are significantly longer when ROM is bidirectional, indicating that it may be a signal of play. Rates of affinitive behaviour also increased after ROM, suggesting that both displays may have a similar ultimate (evolutionary) function – social bonding; this could explain convergence of the two displays in humans.

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Introduction

The specific function of facial displays in primates is poorly understood, despite widespread acknowledgment of the likely importance of facial communication. Facial display repertoires have been described in great detail (Andrew 1963; Chevalier-Skolnikoff 1973; van Hooff 1973; Goodall 1986; Ladygina-Kohts 2002) and Parr et al. (1998) showed that chimpanzees (*Pan troglodytes*) can discriminate between the facial displays of conspecifics in matching tasks. Yet with the notable exception of work by van Hooff (1972, 1973) and Preuschoft (1992, 1995), empirical analysis of the behavioural context and function of displays in primates has been neglected.

van Hooff (1972) proposed that the silent bared teeth display (SBT) and the relaxed open mouth display (ROM) are possible primate homologues of smiling and laughing, respectively, in humans. van Hooff suggested that the two displays

have become emancipated from their original function in the ancestral primate (sensu Tinbergen 1952) and converged functionally in humans, (termed the Emancipation Hypothesis). However, smiling and laughter are used in similar contexts in human behaviour, which makes the suggestion that they have different phylogenetic origins seem puzzling. Others have therefore suggested that smiling and laughter are on a continuum of graded intensities (Andrew 1963), with smiling as a diminutive of laughing. Indeed, Redican (1982) even questioned the homology of the musculature involved, suggesting the risorius is used in the SBT (making it more similar to a human fear expression) whereas the zygomatic major is involved in the human smile. In the primate literature, SBT is often labelled 'fear grin', and has commonly been interpreted as expressing negative valence. It seems imperative, however, to determine function before ascribing emotional terms.

van Hooff (1972) used cluster analysis to define the social contexts in which SBT and ROM occur in chimpanzees (*P. troglodytes*), compared this to the equivalent social contexts in humans, and on the basis of this evidence hypothesized about the function of these two behaviour patterns in the two species. Preuschoft (1992, 1995) built on this work with detailed sequential analyses documenting the behavioural consequences of these displays in different macaque species (*Macaca* spp.). This latter approach documents not only the immediate context (similar to van Hooff 1972), but also examines how these displays function in social interaction sequences. Thus, although social context of SBT and ROM has been demonstrated in chimpanzees, their behavioural consequences in interaction sequences (and, hence, their function) has not. Additionally, the reasons for convergence in the two displays, leading to similarity between humans smiling and laughing, have yet to be explored.

van Hooff (1973) found that SBT and ROM occur in different behavioural contexts in chimpanzees: cluster analysis indicated that ROM is highly correlated with play elements and SBT is correlated with affinitive elements (despite the term 'fear grin'). In addition, Preuschoft (1992, 1995) conducted a comprehensive analysis of the behavioural consequences of SBT and ROM (in four species of macaque). By analysing the behaviour of dyads before and after the display from focal animal protocols, Preuschoft (1992) found SBT to be associated with submissive behaviours in barbary macaques (*Macaca sylvanus*) and followed by an increase in affinitive behaviour directed from the receiver of the display to the sender. SBT appeared to be used differently between the various species of macaque studied, possibly reflecting species differences between dominance style and submissive/affinitive signals (see Preuschoft 1995, for a full discussion of the Power Asymmetry Hypothesis of Motivational Emancipation). For example, in species like rhesus macaques (*Macaca mulatta*), the SBT is a signal of submission and directed only from subordinates to dominant individuals (de Waal & Luttrell 1985), whereas in more egalitarian species such as tonkean macaques (*Macaca tonkeana*; Preuschoft 1995), it is used in a variety of social affinitive contexts. The function of SBT has, therefore, previously been examined in two ways: in terms of immediate context and associated behaviour (chimpanzees: van Hooff 1973), and in terms of post-display contacts between sender and receiver (macaques:

Preuschoft 1992, 1995). Here, we aim to combine these two approaches in order to assess the function of SBT and ROM in chimpanzees.

Silk's (1996, 2002) Benign Intent Model of reconciliation behaviour argues that many of the behaviours used in post-conflict situations (such as lipsmacks and contact calls) simply signal that the individual concerned no longer has aggressive intentions. Silk's hypothesis contrasts with the original explanations for post-conflict interaction that focussed on relationship repair and long-term resolution (e.g. de Waal & van Roosmalen 1979). We suggest that SBT (in particular) serves to signal that the intentions of the sender are currently benign, non-aggressive and affinitive.

Despite the correlation with play behaviour in many primates, the signal value of ROM is poorly understood; indeed, few studies have demonstrated the functionality of play signals (see Bekoff & Byers 1981 for a review). Play fighting in many mammals involves the non-serious use of behaviour patterns derived from serious fighting (Pellis & Pellis 1997), which poses the interesting question of how animals distinguish between playful and non-playful intent (Pellis & Pellis 1996). ROM appears to be an exaggerated form of normal combat open mouth displays (Andrew 1963), and, at least in chimpanzees, it is accompanied by slow and rather conspicuous body movements. The behaviour is easily identified by human observers (and presumably also by conspecifics), but empirical evaluation of the occurrence of ROM, and its consequent effect on the behaviour of the interactants, is the only way to draw reliable conclusions about social function. The term used to describe ROM in chimpanzees is 'playface', and the cluster analysis of van Hooff (1973) found that ROM is strongly associated with play behaviour. If characteristics of play can be predicted by use of ROM, it will provide compelling evidence that ROM is indeed a signal of 'play'.

Here, we explore the behavioural consequences of both SBT and ROM in chimpanzees, in particular focusing on post-display aggressive, affinitive and play behaviours. We aim to (1) evaluate the effectiveness of SBT as a signal of benign intent (sensu Silk) and the effectiveness of ROM as a signal of play, and (2) investigate possible reasons for convergence of smiling and laughing in humans.

Methods

Study Group

Observations were conducted on the captive chimpanzee colony of Chester Zoological Gardens, Chester, England. At the time of study, the group consisted of five adult males, 14 adult females, one subadult male and nine subadult females, totalling 29 individuals. Individuals were split into two age categories based on Goodall (1986), but taking into account earlier reproductive maturity in captive animals: adults (> 11 yr) and subadults ($\leq$11 yr). The zoo maintains a non-invasive policy with respect to the chimpanzees, and currently the animals have no direct physical contact with humans (other than for essential veterinary intervention).

Two individuals (one adult male, one adult female) were wild-caught pre-1971, nine have had some human rearing intervention pre-1983 (three adult males, six adult females), and all other individuals have been colony-reared by their mothers.

Sampling Procedure

Focal observations were carried out on 26 individuals; the two youngest infants (one male and one female) and a juvenile with abnormal development (female) were excluded from focal observations because of lack of independence from the mother. They did, however, often feature as interactants. Focal samples (of 1 h duration) were conducted at 10.00, 11.00, 13.00 and 15.00 hours, Monday to Thursday during the period May to Jul. 2001 (inclusive of 1 mo to identify the group and streamline coding). The focal times avoided the regular feed at 14.30 hours, and ensured that all animals were present (animals were allowed access to the out of view area between approximately 16.00 and 09.00 hours each day). Focals were pseudo-randomly scheduled so that each individual was sampled in each time slot. Overall, 4×1 h focals were recorded per individual, totalling 104 h of observational data.

Coding Procedure

All the social behaviours described in the structural analysis of van Hooff (1973) (e.g. gnaw-wrestle, hit, hold out hand) including all SBT and ROM (defined in Table 1) that were displayed by or directed to the focal individual were recorded as and when they occurred (continuous focal sampling; Altmann 1974)

Table 1: Descriptions of SBT and ROM as used in methods

Facial display	Physical description (van Hooff 1973)
Silent bared teeth display (SBT; fear grin, fear grimace, silent grin)	The mouth corners are withdrawn and the lips retracted from teeth and gums. The mouth is kept practically closed (or) the mouth is widely open[a]
Relaxed open mouth display (ROM; playface)	The mouth is kept in a moderate-to-wide open position. The mouth-corners may be slightly withdrawn, but the lips retain their normal relaxed position, so that the upper teeth remain wholly or partly covered by the upper lip; the lower teeth are slightly bared. On some occasions the lips may slide further back, but the gums are hardly ever visible[b]

[a]Horizontal, open-mouth and vertical variants of SBT are distinguished (see van Hooff 1973). The vertical type was not seen in this study, and as the observed SBTs exhibited a range of mouth opening, both horizontal and open-mouth types were recorded and classed as SBT.

[b]ROM can be accompanied by staccato rhythmic breathing, but this was not recorded because of variable distances between the focal animal and the observer (and therefore difficulty in hearing the vocalization).

using check sheets. Each social behaviour was then re-coded as an event using the behavioural categories of van Hooff (1973), which groups behaviours into distinct (exhaustive) social contexts (affinitive, aggressive, excitement, play and submissive). SBT and ROM were not re-coded as social events, and instead we used additional analyses (see below) to confirm the social context of these displays. For present purposes, the submissive and excitement categories were excluded as the research questions focused on affinitive, play and aggressive behaviour. A 15 min bout of grooming would be treated in the same way as a near-instantaneous crouch-present. This method was deemed most accurate given the speed of many behaviours (touching, hitting etc.), and difficulty in maintaining consistent time keeping in a real-time setting. However, the duration of play behaviours was recorded (to the nearest minute) as much variation in bout length was observed during pilot studies with the coding system. An interaction or behaviour was recorded as a new event if a different recordable behaviour occurred. For example, a grooming bout would be split into two events if one individual changed grooming partners.

To determine the social context of each display, other behaviours (whether produced by sender or receiver) that occurred while the animal produced the display were recorded and categorized using van Hooff's (1973) schema. For example, if ROM was accompanied by play behaviours (e.g. sender: mock biting, gnaw wrestling), the context was recorded as play, while if SBT was accompanied by affinitive behaviours (e.g. sender: hold out hand) or aggressive behaviours (receiver: hit) the context was recorded accordingly. If sender and receiver displayed different behaviours, preference was given to the sender's behaviour. If more than one behaviour accompanied the display the observer used the first behaviour, and if the display was instantaneous, the observer judged which behaviour was the closest temporally.

Analysis

All analyses were based on the focal periods and carried out on an individual subject basis. The frequency of displays performed was calculated for each individual, along with the proportion of displays sent within the same age cohort (age categories defined above) and frequency of displays associated with other behaviours. In addition, baseline rates of behaviour, calculated as the number of behavioural occurrences per minute (categorized as aggressive, affinitive and play), were determined for each individual by averaging across focal samples. As behaviours were counted only if the focal individual was the actor, a high baseline rate of affinitive activity means that the individual has exhibited a high rate of affinitive behaviour. Post-display rates of behaviour between sender and receiver were calculated for 10 min following the display (within the focal period), irrespective of who actually gave the display. If the focal sampling period finished prior to 10 min post-display, that particular display was discarded from the post-display analyses. Given that baseline rates included post-display behaviour, any significant differences between baseline and post-display are conservative.

Parametric analyses were used where the data were normally distributed and kurtosis or skewness $< \pm 2$; equivalent nonparametric analyses were used where the data did not meet these assumptions. All significance values are two-tailed.

Results

Display Frequency

A total of 87 SBT and 98 ROM (68 bidirectional, 30 unidirectional) were recorded. Subadults displayed more SBT than adults (subadults = 5.71 per 4 h focal period, adults = 2.44 per 4 h focal period; independent samples t-test; t = −3.07, df = 23, p < 0.005). Subadults also displayed more ROM than adults (subadults = 9.14 per 4 h focal, adults = 1.83 per 4 h focal; independent samples t-test; t = − 6.274, df = 23, p = <0.005). To examine the age composition of the display dyads, a repeated measures mixed ANOVA was conducted on the proportion of displays directed within the same age cohort (for SBT and ROM), with age (adult and subadult) as the between subjects measure. There was a significant effect of display ($F_{1,12} = 7.450$, p < 0.05), and a significant interaction between age and display ($F_{1,12} = 7.450$, p < 0.05). Pairwise comparisons showed there was a higher proportion of SBT displayed within same age dyads than was the case for ROM (paired t-test; t = 2.231, df = 13, p < 0.05), and a higher proportion of SBT dyads than ROM dyads were 'same age' for adults (paired t-test; t = 3.824, df = 6, p < 0.05) while no difference was found in the age composition of ROM and SBT dyads for subadults (paired t-test; t = 0.00, p = 1.00). Fig. 1 illustrates these differences between the two displays.

Behavioural Context

There was a highly significant difference in the frequency of ROM exhibited in the behavioural contexts of 'affinitive', 'aggressive', 'play' and 'other' behaviours (Fig. 2: Friedman one-way ANOVA; n = 26, df = 3, $\chi^2 = 33.83$, p < 0.005), mainly because of a high frequency of displays produced in 'play' contexts. There was also a significant difference in the frequency of SBT produced in different contexts (Fig. 2: Friedman one-way ANOVA; n = 26, df = 3, $\chi^2 = 11.47$, p < 0.05). The very low frequency of SBTs in 'play' contexts explains this result: when 'play' was removed from the analysis, no difference was found in the frequency of SBT within 'affinitive', 'aggressive' and 'other' contexts (Friedman one-way ANOVA; n = 26, df = 2, $\chi^2 = 1.909$, p = 0.39).

These analyses confirm that ROM occurs most frequently with 'play' behaviours, whereas SBT is significantly less frequent in 'play' contexts but does not differ between the other contexts. A highly significant difference was found between the frequency of SBT and ROM associated with a 'play' context (Wilcoxon signed ranks test; n = 26, Z = −3.52, p < 0.005).
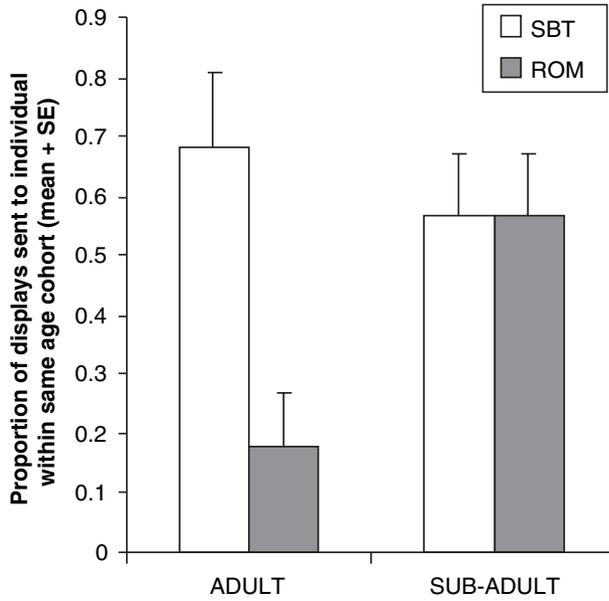
Fig. 1: Proportion of SBT (total 87) and ROM (total 98) directed at another individual within the same age cohort, showing differences between adults (> 11 yr) and subadult (≤11 yr)
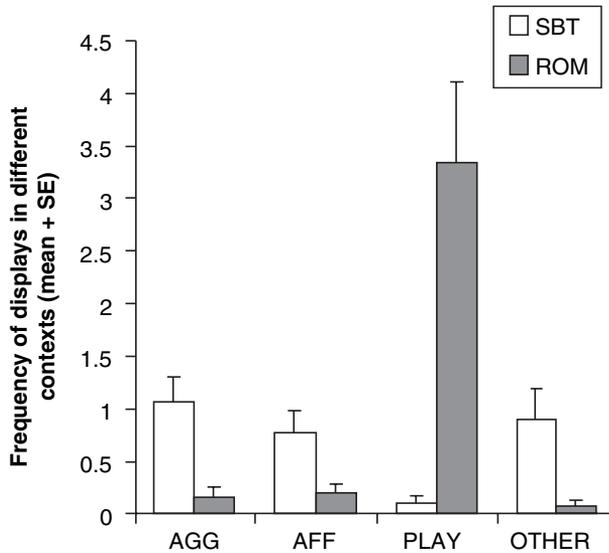

Fig. 2: Mean individual frequency of SBT and ROM (per 4 h focal time period) accompanied by other behaviours (categorized as aggressive, affinitive, play and other; van Hooff 1973)

Rates of Behaviour

Within-subjects analyses were conducted on baseline and post-display rates of behaviour to establish whether each display resulted in a change in behaviour of the sender. Degrees of freedom differ between analyses as not all individuals displayed SBT and ROM (18 displayed SBT, 17 displayed ROM and 13 displayed both) within the focal period, and so different sample sizes are used in each comparison.

Affinitive behaviour between sender and receiver in the 10 min following an SBT display was significantly higher than baseline rates for the sender (Fig. 3: paired sample t-test; $t = 3.17$, df $= 17$, $p < 0.05$). Affinitive behaviour 10 min post-ROM was significantly more frequent than baseline rates (Wilcoxon signed ranks test; $n = 17$, $Z = -2.68$, $p < 0.05$) but there was no significant difference between the rates of affinitive behaviour post-SBT and post-ROM (Wilcoxon signed ranks test; $n = 13$, $Z = -0.35$, $p = 0.724$).

Rates of aggressive behaviour did not differ significantly between post-SBT and baseline (Fig. 4: Wilcoxon signed ranks test; $n = 18$, $Z = -1.194$, $p = 0.232$), or between post-SBT and post-ROM (Wilcoxon signed ranks test; $n = 13$, $Z = -1.401$, $p = 0.144$). There was, however, a significant reduction in aggressive behaviour post-ROM compared with baseline levels (Wilcoxon signed ranks test; $n = 17$, $Z = -2.033$, $p < 0.05$).

Rates of play behaviour were significantly higher post-ROM compared with baseline levels (Fig. 5: Wilcoxon signed ranks test; $n = 17$, $Z = -2.38$, $p < 0.05$), and higher post-ROM than post-SBT (Wilcoxon signed ranks test; $n = 13$, $Z = -2.30$, $p < 0.05$). There was, however, no significant difference between post-SBT and baseline rates of play (Wilcoxon signed ranks test: $n = 18$, $Z = -1.29$, $p = 0.198$).

Play bouts during which both participants displayed ROM (bidirectional events) were significantly longer than bouts during which only one participant displayed ROM [mean bidirectional bout length, 2.35 ± 20 min ($\bar{x} \pm$ SE); mean
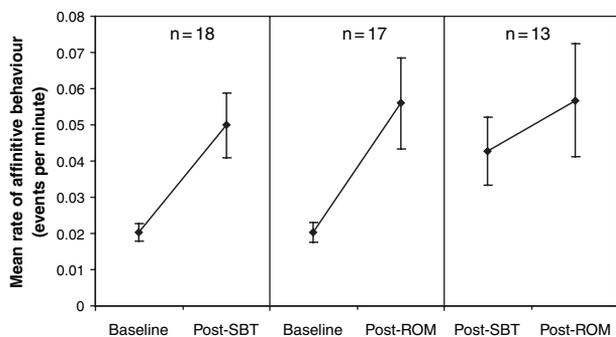

Fig. 3: Mean ($\pm$SE) individual rate of affinitive behaviour at baseline, and between sender and receiver following SBT and ROM (10 min post-display). Pairwise comparisons are shown (and not all individuals displayed both SBT and ROM)
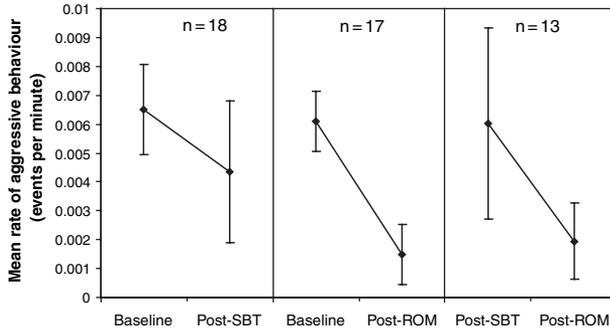
Fig. 4: Mean (±SE) individual rate of aggressive behaviour at baseline, and between sender and receiver following SBT and ROM (10 min post-display). Pairwise comparisons are shown (and not all individuals displayed both SBT and ROM)

Fig. 5: Mean (±SE) individual rate of play behaviour at baseline, and between sender and receiver following SBT and ROM (10 min post-display). Pairwise comparisons are shown (not all individuals displayed both SBT and ROM)
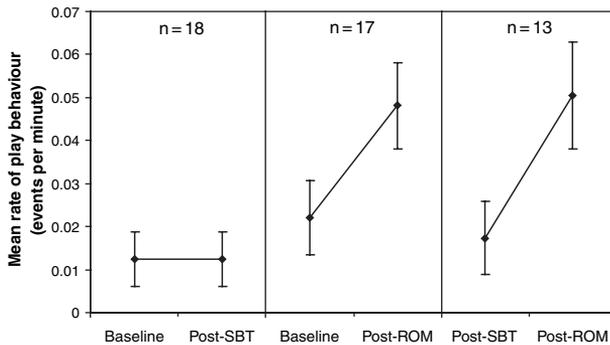
unidirectional bout length, 0.85 ± 0.13 min; Wilcoxon signed ranks test; n = 18, $Z = -3.55$, p < 0.005]. [For the purposes of this analysis, all play bout lengths were recorded to the nearest minute, with all instantaneous playing contacts estimated as lasting a nominal 0.10 min (6 s), and the mean taken for each individual.] Note that ROM was considered bidirectional only if both individuals exhibited ROM at the start of the play bout.

Discussion

The SBT was observed in a range of social situations, and accompanied by varying behaviours in the sender and receiver of the display. Therefore, SBT was not strictly a response to aggression, and signal meaning may depend on varying social contexts, or function may be applicable to different contexts. In contrast,

the vast majority of ROMs were observed during play situations, illustrating that ROM has a strong relationship with play behaviour, and signal meaning may explicitly reflect play situations. It seems that SBT and ROM occur in dissimilar behavioural contexts, implying that if SBT and ROM share phylogenetic origins with human smiling and laughing (respectively), these displays are rooted in different motivational complexes, thus confirming van Hooff's (1972) and Preuschoft's (1992, 1995) hypothesis.

In addition, clear differences in age composition of dyads were found between the two displays. Interactants in SBT dyads were mainly in the same age cohort (adult + adult, or subadult + subadult), whereas interactants in ROM dyads usually involved a subadult (adult + subadult, or subadult + subadult). In species where SBT is primarily a response to aggression (submissive signal), SBT is displayed strictly up the dominance hierarchy (e.g. rhesus macaques, de Waal & Luttrell 1985). Absolute dominance rank was not determined during this study (and, indeed, has been very difficult to define for the Chester Zoo chimpanzees: see also Bellingham 2002), but as juveniles and adolescents are usually subordinate to adults (see Goodall 1965) age can be taken as a broad estimate of dominance. This shortcoming notwithstanding, the data presented here support the suggestion that SBT is not primarily a signal of submission directed from youngers to elders (and perhaps from subordinates to dominants), but is used flexibly in this species.

There is a clear increase in affinitive behaviour between sender and receiver post-SBT compared to baseline levels in the sender. This could be explained in one of two ways:

1. The SBT is an honest signal of benign intent (sensu Silk) and the interactants are consequently motivated to act affinitively because of reduced uncertainty regarding the others' intent. Therefore, the sender has declared status (which is benign and non-aggressive) and so both interactants may now act affinitively, or because the affinitive interaction has a benefit in itself (which was the motivation for signalling benign intent).

2. SBT is most commonly used as a response to aggression as a signal of fear and/or submission, and is correlated with an increase in affinitive peaceful post-conflict behaviour, but is not causal.

No difference was found in the frequency of SBT in aggressive, affinitive and other behavioural contexts, which suggests that, at least in this study, SBT is not especially associated with aggressive behaviour of the receiver. Therefore, of the two explanations offered, the former seems the most appropriate. The increase in affinitive behaviour may serve to facilitate social cohesion in a similar manner to human smiling by facilitating appeasement and reinforcing friendliness.

Play bouts between two participants are significantly longer when both individuals exhibit ROM; this can be explained if ROM is an honest reflection of the sender's motivation to play and therefore a signal of play. Alternatively, it may be the case that ROM is not a signal of play, but rather a play behaviour in itself (similar to mock biting/gnawing) that is associated with motivation to play, and therefore longer play bouts. Although motivation to play is possibly a

necessary proximate explanation for ROM production, we do not feel this is a sufficient ultimate explanation for three reasons. Firstly, despite the fact that all recorded play bouts included play behaviours by both parties, and both individuals thus presumably had some motivation to play, ROM was not always exhibited. Secondly, if ROM is not a signal of play then its presence should be no more associated with longer play bouts than other play behaviours. We have shown here that play bouts in the absence of bidirectional ROM are shorter, illustrating that this is not simply an effect of play inducing more play. Thirdly, ROM is distinguishable from other play behaviours (e.g. mock biting) by its stereotyped nature (see Table 1) and can be classified apart from other facial displays by conspecifics (Parr et al. 1998). Given the clear relationship with play behaviours (and possibly with play motivation), it seems unlikely that this information has not been used by conspecifics (through the course of evolution) as a signal of motivation and intention to play. If, as we suggest, the participants are signalling their intention and motivation to play using ROM, play bouts will be longer when both individuals use them for the following reasons:

1. Both individuals are motivated to play.

2. Both individuals have increased certainty from the ROMs that the play behaviours are non-aggressive.

It is well known that other behaviours (such as staccato rhythmic vocalizations) accompany ROM, which can be heard by the receiver when the face is not visible. These may further serve to reduce ambiguity, and indeed may be more salient to conspecifics than the visual characteristics of ROM (Parr 2004). Comparisons have been made between this vocalization and the vocalized element of human laughter (van Hooff 1972; Provine 2000). Laughter (and perhaps ROM) may induce the production of endorphins in the brain (Panksepp & Burgdorf 2003), which in itself might increase motivation to continue the play bout, and as such act as a proximate mechanism for continued play.

In addition, rates of affinitive behaviour increase in relation to baseline levels following ROM. This suggests that ROM strengthens affiliative bonds between individuals and therefore aids social cohesion in a similar manner to SBT. This raises interesting questions concerning the evolution of laughing in humans. If ROM and human laughing share a common phylogenetic origin, the bonding effect seen in humans (and seen here in chimpanzees) can be explained as follows. Nonhuman primates 'play' using exaggerated mock-aggressive movements, and these movements are confirmed as non-aggressive by 'play' signals such as ROM. Combining aggressive movements with honest signals of 'playful' intent is perhaps an effective method of building trust and gaining certainty over future interactions. Demonstrating the ability to be aggressive while causing no harm is an obvious way of displaying non-aggressive intent, yet this explanation contrasts with that of Pellis & Pellis (1997) who argue that play signals need to be unambiguous and unrelated to aggressive movement (as in the case of the head shake in the spider monkey). ROM and human laughter can thus be considered meta-signals declaring 'I have no intention to be aggressive and I can demonstrate this by showing aggressive potential but

causing no harm'. It would be interesting to explore the relationship between human laughter and potential aggression (play fighting, teasing etc.) to test this suggestion.

Research in this area focuses on the function, meaning and signal value of facial displays, with the aim of discovering how these behaviours are interpreted by others, yet the research literature is itself inconsistent in its identification of each display (see Goodall 1965, 1986; Chevalier-Skolnikoff 1973; van Hooff 1973; Ladygina-Kohts 2002). This study used the comprehensive descriptions of van Hooff (1973) throughout, but Ekman (1982) noted that before development of the Facial Action Coding System (Ekman & Friesen 1978) descriptions of human facial behaviour were difficult to match between studies. A similar common language for nonhuman primate facial movement would undoubtedly benefit this area of research.

Given that:

1. there is morphological similarity between human smiling and SBT, and human laughing and ROM;

2. SBT is used (in the chimpanzee) in social situations as an affinitive signal, as is the human smile (Lockard et al. 1977);

3. SBT is used (in primates) flexibly depending on dominance style (Preuschoft 1995);

4. ROM is used (in the chimpanzee) in play situations as a signal of play, and human laughing is primarily associated with recreation as well as playful situations in both children and adults (Lockard et al. 1977);

5. both ROM and SBT are associated with increased affinitive behaviour, suggesting that both may have a role in social cohesion.

These findings would seem to support van Hooff's (1972) emancipation hypothesis at the expense of the alternative hypothesis that human smiling is a diminutive of laughing (Redican 1982). In particular, our finding that ROM and SBT are used in quite different contexts contradicts an essential assumption of the latter hypothesis, namely that both displays have the same motivation.

During the course of human evolution, smiling seems to have become more and more flexible as an affinitive signal, indicating benign intentions and facilitating peaceful interactions, whereas laughing, however, remained primarily recreational. Increased vocal ability was recruited with ROM, which allowed more efficient transmission and may have been selected for because it facilitated social bonding (Dunbar 1996, 2004). The superficial similarities between the two displays may have arisen and led to structural convergence [as seen in tonkean macaques (*M. tonkeana*); Thierry et al. 1989], because both became increasingly related to social cohesion and therefore have similar ultimate (evolutionary) function.

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