Variation and Context of Yawns in Captive Chimpanzees (*Pan troglodytes*)

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Abstract

Primate yawns are usually categorised according to context (e.g. as a threat, anxious or rest yawn) but there has been little consideration of whether these yawns are best regarded as a unitary behaviour that only differs with respect to the context in which it is observed. This study examined the context and precise morphology of yawns in a group of 11 captive chimpanzees. Focal video sampling was used to describe the morphology and intensity of 124 yawns using ChimpFACS, a system for coding facial movements. Two distinct forms of yawn were identified, a full yawn and a yawn which is modified by additional actions which reduce the mouth aperture. These modified yawns may indicate some degree of voluntary control over facial movement in chimpanzees and consequently multiple functions of yawning according to context. To assess context effects, mean activity levels (resting, locomotion and grooming) and scratching rates were compared one minute before and after each yawn. Locomotion was significantly increased following both types of yawn, while scratching rates significantly increased following modified yawns but decreased following full yawns. In terms of individual differences, males did not yawn more than females although male yawns were of higher intensity, both in the degree of mouth opening and in the amount of associated head movement. These data indicate that yawning is associated with a change in activity levels in chimpanzees but only modified yawns may be related to increased arousal. Different types of yawn can therefore be differentiated at the morphological level as well as context level.

Keywords

INTRODUCTION

Yawning is a remarkable behaviour in terms of how readily it is recognized across all classes of vertebrates [e.g. Baenniger 1987; Gallup et al. 2009]. Yawning is generally considered to be an involuntary response dependent on certain eliciting factors, yet it seems to lack consistent functional context across species [e.g. Smith, 1999]. It has long been noted within the behavioral repertoire of primates [Darwin, 1867/2006; Redican, 1975], and is sometimes considered a physiological response [indicating rest or arousal, dependent on context] and sometimes interpreted as a communicative act. For example in relation to physiological states, Provine [1986] reported that in humans, yawns are most frequent in the hour immediately prior to and following sleep, suggesting a relationship to drowsiness. A study with individuals

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complaining of sleepiness showed that yawning correlates positively with drowsiness in this population, but measurements of cortical activity (EEG) and autonomic responses (heart rate) revealed that yawning did not function to increase arousal levels of the brain as has previously been suggested [Guggisberg et al., 2007]. Thus while yawns may be caused by sleepiness, their functional significance in this context remains unclear.

In nonhuman primates, two different types of yawn are generally distinguished according to context, both related to physiological states. First, as mentioned above for human yawns, true or rest yawns appear to correlate with states of drowsiness and relaxation. On the other hand, tension or aggressive yawns occur in conflict situations and may indicate high arousal [Deputte, 1994; Bertrand, 1969; Hadidian, 1980; Maestripieri et al. 1992; Schaller, 1963]. Wild chimpanzees, for example, are reported to yawn more in response to human proximity [Goodall, 1968; Nishida, 1970], while increased yawning was found in response to social tension in captive chimpanzees [Baker & Aureli, 1997]. Yawning is therefore often considered as a displacement behaviour [Mastriepieri et al. 1992] and used as a good indicator of stress in observational studies, although it is often grouped with other 'abnormal' or self-directed behaviors and not always analyzed independently [e.g. Pomerantz & Terkel, 2009]. As self-scratching is a reliable indicator of arousal in primates, increases in yawning seen in combination with higher rates of scratching are taken to indicate that these yawns are related to physiological arousal [Baker & Aureli, 1997; Kutsukake, 2003]. Altmann [1967] suggested that both true and tension yawns indicate levels of physiological arousal; true yawns being contingent upon drowsiness or fatigue, while tension yawns indicate elevated stress levels. More recently, yawning has also been implicated in thermoregulation in budgerigars [*Melopsittacus undulates*; Gallup etal., 2009], and field observations report increased yawning at higher temperatures in white-faced capuchins (*Cebus capucinus*, although the authors attribute this effect to increased time spent resting rather than thermoregulation [Campos & Fedigan, 2009]; see also [Gallup & Gallup, 2007], for a discussion of yawning as a brain cooling mechanism in humans).

On the other hand, the gaping mouth and teeth seen during yawning are a salient visual display. For example when viewing conspecifics, rhesus monkeys generally display a strong bias for viewing the eye region but when viewing conspecifics yawn, they focus equally on both eye and mouth region [e.g. Gothard et al., 2004]. It is thought that yawning displays the canine teeth, thereby acting as a threat signal [e.g. Darwin, 1867/2006; Redican, 1982] and triggering a 'canine contest' between males [Hall & DeVore, 1965]. In support of a display function, yawns are commonly reported as more frequent in males than in females for a variety of primate species, e.g., *Cercocebus albigena* and *Macaca fascicularis* [Deputte, 1994]; *Macaca nigra* [Hadidian 1980]; *Macaca fuscata* [Troisi et al. 1990]; *Gorilla gorilla*; [Parnell, 2002]. This sex difference in yawn production is less likely in species which do not have pronounced dimorphism in canine size, such as humans [Schino & Aureli, 1989]. Moreover, in male-male encounters, the dominant individual produces more yawns that the subordinate e.g. *Macaca arctoides* [Adams & Schoel, 1982] although presumably the subordinate is likely to be more anxious during these encounters. Thus, some yawns may be displays used to induce emotions in others, rather than serving to release tension in the individual. These lines of evidence strongly suggest that yawns are not necessarily related to arousal alone, but may also serve a communicative function.

It is unclear whether display and arousal yawns are a unitary phenomenon as both tension and communicative threat yawns may be seen in the context of conflict. As a result, a distinction is often made between directed and non-directed yawns; yawns directed at a recipient are considered displays while non-directed yawns are seen as an indicator of stress [Hall &Devore, 1965]. In another study of male mandrill (*Mandrillus sphinx*) behaviour, all individuals were reported to yawn but these were not considered to be a communicative threat yawns as the

majority (91%) was not directed at another animal, or they occurred when the animal was alone. Even during tense stand-offs between males, yawns were not directed at opponents, suggesting these were occurring as part of a stress response rather than as communicatory signal [Setchell & Wickings, 2005]. However, given that yawns are very salient visual signals [perceptible from most perspectives due to gaping mouth and/or pattern of accompanying head movement], it is difficult to determine the directedness of the display and to interpret whether the yawn is an act of intentional communication. Interestingly, Altmann [1967] suggests that adolescent baboons must learn to direct yawn displays at individuals appropriately, so that threat yawns may be a learned use of teeth baring when yawning due to conflict arousal. Anderson and Wunderlich [1988] reported that nonhuman primates may indeed have voluntary control over yawning production as well as direction; tonkean macaques (*Macaca tonkeana)* could learn to yawn when they received food rewards for doing so.

Recent years have also seen a growing interest in the phenomenon of contagious yawning; seeing another individual yawn can trigger yawning it the viewer, a robust finding in humans [Provine 1986, 1997; Platek et al. 2003] but recently also reported in chimpanzees [Anderson et al., 2001; Campbell et al, 2009], dogs [C*anis familiaris*; Joly-Mascheroni et al., 2009; but see also Harr et al., 2009], stumptail macaques [*Macaca arctoides*, Paukner & Anderson, 2006] and gelada baboons [*Theropithecus gelada*; Palagi et al., in press]. Since yawns frequently occur in the morning shortly after waking and in the evening when settling down for the night in nonhuman primates, they appear to occur in relation to changes in activity states, which has led to the suggestion that yawning in general and contagious yawning in particular serves as a communicative social cue to synchronize group activity [Deputte, 1994]. That is, an individual who is about to change its activity state may yawn as an indicator of this change, which may induce yawning and a similar activity change in others. Observational studies with humans suggest that yawning precedes increases in activity level even outside waking and sleeping times [Baenninger et al., 1996]. However, most studies (with the exception Palagi et al., in press), have relied on repeated video stimuli to induce yawning; it is unclear how prevalent spontaneous yawn contagion among nonhuman primates.

In short, evidence appears to support both physiological and communicative explanations for yawning and as a result, there remains a lack of consensus as to what function or functions yawning might serve. As yawning is considered to be a stereotypical, fixed action pattern [Alcock, 1993; Smith, 1999], there has been very little attention paid to the specific morphology of yawns, for example, in relation to intensity and the muscle movements underlying the action. In a recent study with humans, the authors noted that individual phenomenology of yawns was not of interest [Guggisberg et al., 2007], which indicates that there may be variation in yawning which is systematically ignored because yawns are considered to be stereotypical, a self-reinforcing interpretation. Possible variation in precise yawn morphology becomes interesting when the different interpretations of yawning are considered. In humans, for example, there are slight differences between spontaneous and voluntary facial movements [see Ekman & Rosenberg, 2005] and yawn variation could indicate volition over facial movements. Although Redican [1975, 147] suggested that 'both human and perhaps nonhuman observers are faced with a difficult task in distinguishing the different forms of yawning in all but extraordinary circumstances,' there are some reports indicating differentiation between yawns in nonhuman primates. Macdonald [1965, cited in Redican, 1975] discerned at least two different types of yawn in a home reared hamadryas baboon (*Papio hamadryas*) and Palagi et al. [in press] describe three different types of yawns (teeth covered, teeth uncovered and gums revealed) in gelada baboons. In addition, in mandrill males some variation in yawns is suggested by the fact that most yawns reveal the canines but in adolescent males, the canines are covered by the lips during yawning, resulting in 'half yawns' [Setchell & Wickings, 2005]. Palagi et al [in press] report that induced yawns matched the triggering yawn type but only in female and not male geladas. However, as the precise facial actions which differ between yawns have not been

considered, the categorization of yawns primarily on the visibility of teeth and gums could reflect intensity only; none of the studies identifying yawn variations report whether different yawns are seen across different contexts.

Could an analysis of facial muscle actions seen during yawning reveal differences in facial movements according to different environmental contexts? The present study reports the results of an observational study of yawning in chimpanzees with the aim of detailing the form and potential functional significance of yawning in this species. Yawning in chimpanzees is primarily considered a displacement behaviour in both wild and captive chimpanzees [Baker & Aureli 1997; Goodall, 1968] and although contagious yawning was first reported in this species of nonhuman primates [Anderson et al., 2001] yawns are often omitted from ethograms of facial behaviour [e.g. Parr et al., 2005; van Hooff, 1967] and previous studies have not described variation in yawn morphology. Here we aim to provide a full morphological description of the chimpanzee yawn and to examine the effects of sex, and associated activity states on yawn morphology. By systematically analyzing both the context in which yawns occur and the precise morphology of yawns, in terms of component facial actions, using a modified version of FACS, or Facial Action Coding System [Ekman et al., 2002; ChimpFACS; Vick et al., 2007] and yawn intensities, we can assess whether there is perceptible functional variation in chimpanzee yawns.

METHODS

Subjects and Housing

Subjects were a captive group of 11 chimpanzees housed at Edinburgh Zoo, UK. The group comprised 7 adults (3 males, 4 females), 2 sub-adults (1 male, 1 female) and 2 juveniles (both males). They were housed in an indoor-outdoor enclosure connected via a tunnel system and enriched with climbing frames, ropes and nets. Subjects were restricted to their outdoor enclosure until 9.30am for cleaning and maintenance purposes, but otherwise had constant access to both areas throughout the day. Subjects were fed a diet of fruit and vegetables several times a day with the main feed occurring at 3.30pm; water was available ad libitum.

This research complies with the animal care regulations of the Royal Zoological Society of Scotland (RZSS, Edinburgh Zoo), the American Society of Primatology's Principles for the Ethical Treatment of Non Human Primates and all applicable UK legislation on conducting research with primates.

Sampling procedure

Focal observations were carried out during October and November 2005. Each chimpanzee was filmed for 20 minutes once a day using digital camcorders, 5 days a week. However, due to poor visibility for some areas of their enclosures not all chimpanzees could be filmed on all days. The resulting data are based on a total of 42 h observation. Focal samples were conducted between 9.30am and 3.00 pm, thus not including the main waking and resting periods in the early morning and late in the afternoon. Using focal sampling methods and video, we were able to systematically examine the general behavioral context proceeding, during and following each yawn.

For the descriptions of yawn morphology all yawns recorded were included (a total of 124, please see Table 1 for individual yawn frequencies). Yawns sometimes occurred in bouts and we only considered a yawn to be an independent event if it was separated by at least 1 minute from previous yawns. Using this definition, we recorded: 11 bouts of 2 yawns, 3 bouts of 4 yawns and one bout of 6 yawns (from 4 females and 3 males). For context analyses, only the first yawn observed in a bout was included in the data set (25 yawns were excluded from

analyses of context on this basis). Yawns were also excluded if the focal indiviudal could not be clearly observed for the full one minute interval pre and post yawning. Together, these exclusion criteria resulted in 73 yawns being included in the context analyses.

Coding procedure

Video microanalysis was used to describe facial movements, with individual data pooled so that each yawn was considered as a unit of analysis to allow variation to be more fully examined. In terms of variation in yawn morphology, all Action Units (AUs) were considered during coding (an AU is an independent unit of facial movement. For more information on ChimpFACS please see: http://www.chimpfacs.com/). Overall intensity of each yawn was coded using two measures. Yawns were coded in terms of the overall amount of head movement using an intensity scale of 1–5, with 1 being slight or no perceptible change in head position and 5 being large movements of the head in any direction during the yawn (a FACS intensity scale of A-E was not used as these describe only specific direction of head movement e.g. up, down etc rather than an overall measure of head movement). Yawn intensity was also measured using the degree of mouth opening seen (AU27 Jaw Stretcher using a standard FACS intensity scale of A-E, with A being subtle and E being highest intensity). Particular attention was also given to actions which serve to reduce the mouth aperture (AU8 Lips towards each other and AU22 Lip funneler) and these were recorded using one-zero sampling, that is, whether or not the action had occurred during the duration of the yawn [Martin & Bateson, 2007].

Inter rater reliability on yawn coding

For all yawns, the degree of head movement and mouth opening were coded by a second observer. Pearson correlations showed that both head movement (R = 0.37, P<0.001, N = 124) and for mouth opening intensity (R = 0.55, P<0.001, N = 124). For the coding of FACS action units, a second ChimpFACS coder reviewed a sample of yawns for AU8 and AU22 only (12% of all yawns); both coders showed consistency in determining whether an action to reduce the mouth opening had occurred; Cohen's kappa = 0.7 [Bakeman & Gottman, 1997].

RESULTS

The 124 yawns recorded occurred between 9.35am and 2.45pm, with two peak times: 10.00am–11.20am (40% of yawns were performed during this period), and 12.20pm–1.10pm (24% of yawns were performed during this period). Chimpanzees usually received some food items around 12 noon, which might explain the lack of yawns around this time (yawns were never observed when feeding) and perhaps also the peak in yawning shortly before feeding time.

1. Yawn morphology

Micro-analysis of yawns revealed that while all yawns can be identified by a mouth stretching action (AU 27 Jaw stretcher), they can vary in intensity and accompanying actions. Yawns usually occur with head movements and the amount of movement correlates positively with yawn intensity (degree of AU27; Spearman's Rho, R = 0.445, P <0.001, N = 124). There are two movements which significantly alter the form of the yawn, seen in ca. half the observed yawns (61/124 = 49.2%). These movements were an action which funnels the lips outwards (AU 22, Lip funneler, N= 20 = 16.1%) or the movement of the lips towards each other to reduce the mouth aperture (AU 8, Lips towards each other, N = 47, 37.9%). These actions reduce the visual salience of the gaping mouth and sometimes resulted in distinctly multi-peaked yawns (see Figure 1). Yawns were also occasionally accompanied by independent movements of brow raising (AU1+2, N = 4) cheek raising (AU6, N = 7) or nose wrinkling (AU 9, N = 4). When head movement was compared across full and modified yawns, there was more movement observed for modified than full yawns (mean full yawn = 2.95, modified = 3.17; T = 1.08,df = 122, P = 0.012). All individuals were seen to produce both full and modified yawns. There

was no consistent pattern of eye closure in relation to yawns. The eyes were closed at the apex of the yawn in 21 (45.7%) of the full yawns and in 19 (42.2%) of the modified yawns (these percentages exlcude 17 and 16 cases, respectively, where eye closure was not clearly visible at the apex of the yawn).

2. Sex differences in chimpanzee yawns

There were 71 male yawns (57%), 53 female yawns (43%). Since there was a slight observation bias towards males (with 5 females and 6 males in the group), the expected yawning frequency of males and females did not differ from the observed yawning frequency (Chi-Square (1) = 0.181, P > 0.05). However, there was a tendency for males to yawn for longer than females: male mean yawn length = 4.65 sec, female yawn length = 4.01 sec, Mann-Whitney: Z = −1.846, P = 0.06, N = 11. In addition, males had higher intensity yawns in terms of both degree of jaw stretching (AU27; average males = 3.85, average females = 3.24, Z = 2.753, P < 0.01, N = 11) and the amount of head movement (average males = 3.25, average females = 2.76, Z = 2.67, P = 0.01, N = 11). Overall, male yawns tended to be longer, the mouth was more widely stretched, and there was more accompanying head movement than in female yawns.

3. Activity states pre-and post-yawn

The majority of yawns were observed while the chimpanzees were sitting (56.5%), although a large proportion of yawns were also observed when the chimpanzees were lying down (42.7%). Only one yawn was observed in a standing position (0.8%). Generally, there was no clearly discernible social context apparent; the chimpanzees appeared relaxed when yawning. When considering the 3 minute interval pre- and post-yawn, there were 7 instances where the yawn was displayed in close proximity to play bouts; 3 yawns that were displayed in close proximity to feeding; 2 yawns that were displayed before and after sexual contexts (both displayed by females); and 12 yawns that were either preceded or followed by extended grooming bouts. Only 3 yawns were connected to sleeping: two yawns were observed before the subject fell asleep, and one yawn was observed after a subject awoke and became alert. No other behavioral contexts were apparent.

Yawns for which the full 1 minute pre- and post interval was observed were categorized as full (N = 32) or modified (AU8 or AU22 present, N = 41) with no significant difference in the frequency of full and modified yawns. (Binomial test P = 0.35, N = 73), or the likelihood of yawn suppression between sexes (females 58% and males 54% of yawns; Binomial test, P = 0.714, N = 73).

Individual means for general activity levels (time spent walking, sitting, lying down and grooming] and rate of scratching were calculated for each chimpanzee for 1 minute pre and post each yawn type (see Table 2 for all group means and SDs). For time spent lying down, a repeated measures Anova (2 levels: before or after yawns, full or modified yawn) showed no main effects or interaction (timing: F = 1.78, df = −1,8 P = 0.22, yawn type: F = 0.71, df = 1,8, P = 0.42, interaction: F = 0.43, df = 1,8, P = 0.53). Analysis of amounts of time spent sitting, there was no main effect of timing (F = 2.30 df = 1,8,P = 0.17) or yawn type (F = 0.71 df = 1,8, P = 0.42) or an interaction between these (F = 0.12, df = 1,8,P = 0.92). Similarly, there were no main effects and no interactions for amount of time spent grooming (timing F = 3.87, df = 1,8, P = 0.09, yawn type: F = 0.49 df = 1,8, P = 0.50, or interaction: F = 0.87 df = 1,8, P = 0.38). For locomotion, there was a main effect of timing on the amount of locomotion, with locomotion increasing after a yawn (F = 5.59, df = 1,8, P = 0.05], but no main effect for yawn type (F = 0.01,df= 1,8, P = 0.98] and no interaction between these factors (F = 0.76, df= 1,8, P = 0.41]. In addition, there was no main effect of timing on rates of scratching (F = 0.20, df = 1,8, P = 0.67) or of yawn type (F = 0.01,df = 1,8, P = 0.94). However, there was a significant

interaction with less scratching following a full yawn and more scratching following a modified yawn (F = 6.85, df= 1,8,P < 0.01).

DISCUSSION

Microanalyses indicate that yawns can be differentiated in terms of intensity (amount of head movement, degree of mouth opening) and accompanying facial movements, i.e. chimpanzees may modify their yawns with the addition of facial movements which reduce the mouth aperture. Interestingly, these modified yawns were accompanied by more head movement than full yawns, perhaps indicating the yawns were being directed away from others, i.e. non directed yawns [Hall & Devore, 1969]. The presence of these additional movements could indicate that chimpanzees may have some voluntary control over facial actions and that these actions may be used to reduce the salience of the yawn by reducing the mouth aperture. Unfortunately, given the focal video sampling method (needed for microanalyses) and the enclosure layout, it was not possible to accurately record the presence and orientation of other group members; we cannot ascertain whether yawns were directed towards or away from conspecifics, whether yawning was more likely in the presence of dominant others, or whether the behaviour of non-focal individuals differed in response to the different types of yawns.

Factors such as social relationships and specific yawn types should be more fully examined using both experimental and observational methods if we are to better understand yawning in nonhuman primates. Another factor which may impact upon yawning rates may be the presence of human observers; we know that the presence and behaviour of visitors can impact upon zoo housed primates [e.g. Hosey, 2000], and higher visitor density or noise, or even the sustained proximity of the researchers (particularly in the inside areas where proximity was higher), may have elevated stress and increased the yawning rates observed [Baker & Aureli, 1997]. On the other hand, these primates were well habituated to visitors and the study was conducted in winter, that is, outside the peak season for visitor numbers so we would expect any visitor effects on behaviour to be less pronounced.

As in humans s [Provine & Hamernik 1986; Schino & Aureli 1989], we did not find any sex difference in yawn frequency, but male yawns were longer in duration and of higher intensity. There was no sex difference in the tendency to modify yawns with additional facial actions. In humans, women are reported to cover their yawns more than men [Schino & Aureli, 1989] but we cannot compare this finding with any yawn modification seen in primates without studying human yawn morphology in more detail. It would be interesting to look in more detail at yawning morphology in species which use yawns as part of a threatening display, in terms of both intensity [e.g. Setchell & Wickings, 2005; Palagi et al, in press] and also whether additional modifying actions can be identified.

The results also indicate that similar to humans [Baenninger et al., 1996], yawning in chimpanzees is related to a change in general activity levels with increased locomotion during the 1 minute interval following a yawn. This effect seems to be independent of yawn morphology and indicates that yawning may relate to synchronization of group activity and indicate changes in activity. Although chimpanzees yawns are not generally considered as a display [e.g. van Hooff, 1967], if yawns reliably indicate a change in activity state, they may be a source of information for other group members, and help with synchronizing group behaviors. Given that there were increased levels of self scratching following a modified yawn, while full yawns led to reduced self-scratching, the modified yawns seem to be associated with arousal [e.g. Baker & Aureli, 1997; Pomeratz & Terkel, 2009] while full yawns may be considered true or rest yawns. The overall pattern of results indicates that chimpanzee yawns are not used in display but rather reflect physiological factors. However, the phenomenon of yawn contagion in chimpanzees [Anderson et al. 2001; Campbell et al. 2009] indicates that

yawns may also be signals as they might impact upon receiver behaviour. It remains to be seen whether conspecifics perceive any difference in yawn types. In humans, attempts to suppress a yawn do not prevent it inducing yawns in human observers [Provine, 1997] but it would nonetheless be interesting to test these different yawn types within a contagious yawning paradigm similar to Anderson et al [2001]. It is apparent that a combination of experimental methods and detailed and systematic observations of spontaneous behaviour are both necessary to untangle the complexities of yawning in primates.

Acknowledgments

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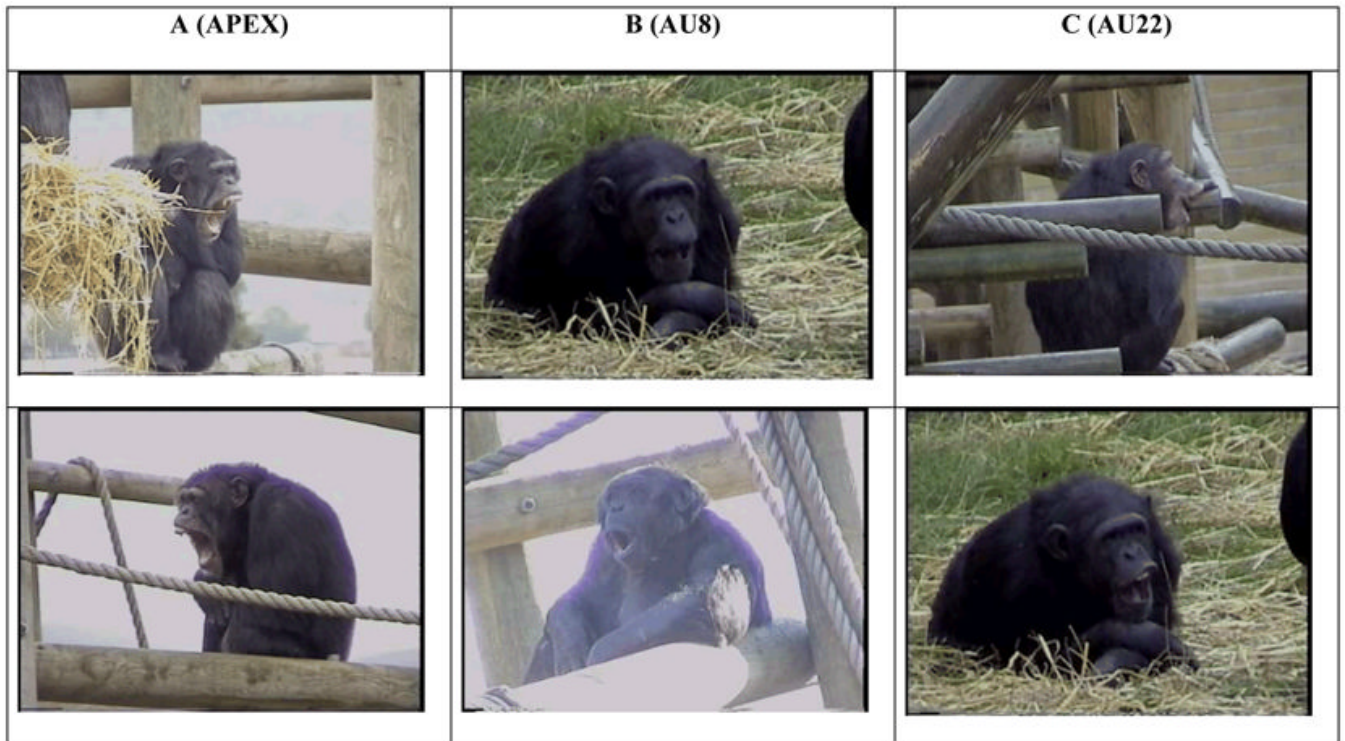
FIGURE 1.
All stills were extracted from an unambiguous yawn video sequence: A) Full yawns at apex
B) Yawns modified with AU8 Lips toward one another C) Yawns modified by AU22 Lip
funneler.

Table 1

Individual yawn frequencies.

	Name (age)	Frequency
Males	Ricky (44)	5
	Louis (29)	10
	David (30)	20
	Qafzeh (13)	3
	Kindia (8)	24
	Liberius (6)	9
Females	Cindy (41)	11
	Emma (24)	11
	Lucy (29)	13
	Lindsey (21)	12
	Kilimi (12)	6

Table 2

Mean (and standard deviations) amount of time (in seconds) spent in each behaviour in the minute before and after yawns. Individual means were used to calculate these group means.

	All yawns		Full yawn		Modified yawn	
	Before	After	Before	After	Before	After
Lie	22.03 [7.36]	21.29 [7.27]	25.67 [25.97]	24.40 [25.68]	18.39 [24.89]	18.17 [23.57]
Sit	37.64 [7.46]	37.01 [7.72]	34.33 [25.97]	33.65 [26.83]	40.95 [24.92]	40.38 [25.05]
Locomote	0.37* [0.32]	1.85* [0.71]	0	2.18 [3.15]	0.74 [1.81]	1.51 [2.86]
Groom	12.10 [2.46]	8.97 [3.04]	12.43 [1.45]	11.68 [15.18]	11.76 [9.92]	6.26 [6.36]
Scratch [Rate per minute]	1.32 [0.34]	1.19 [0.22]	1.66* [1.41]	0.88* [0.84]	0.99* [0.79]	1.51* [1.18]

*
= significantly different at P< 0.05 level.