Ethological Study of Yawning in Primates. 1. Quantitative Analysis and Study of Causation in Two Species of Old World Monkeys (Cercocebus albigena and Macaca fascicularis)

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Yawning is a common, species-typical behaviour in many vertebrate species that as attracted substantial popular, but relatively little scientific, attention (BARBIZET 1958; PROVINE 1986; PROVINE et al. 1987a). Yawning is commonly described in terms of its two principal components: a respiratory and a mouth-gape component. The act is also generally associated with other movements of head and body. Yawning bas mainly attracted physiologists who have focused more on the respiratory component (HEUSNER 1946). The conspicuousness of a yawn arises from the large opening of the mouth. If this mere stretching of the mandibles is considered to be yawning, yawning can also be said to exist in invertebrates (TACHET pers. comm.). If, however, both respiratory and gaping components are used to define a yawn, the gaping observed in fishes, reptiles, amphiblans could be considered only as analogous to yawning in mammals (PEIPER 1932; SAUER & SAUER 1967). The homology between human yawning and yawning in birds and even in herbivores is controversial (HEUSNER 1946), but remains unquestioned in rodents, carnivores and non-human primates. Yawning bas often been mentioned in the ethograms of many carnivores and rodent species in the 'Comfort movements, section (WILLIAMS & SCOTT 1954; LINDEMANN 1955; KOENIG, 1960; KUNKEL & KUNKEL 1964; GUNDLACH 1968), often in association with stretching ('Râkelsyndrom', TEMBROCK 1962). However this association could be considered to be facultative (HEUSNER 1946) and, during evolution, yawning could have become a separate action from stretching (PROVINE et al. 1987b). Yawning can be observed during the first h after birth in a variety of mammals, including humans (HFUSNER 1946; WILLIAMS & SCOTT 1954; REDICAN 1975; DE VRIES et al. 1982; DEPUTTE unpubl. data) suggesting control by lower levels in the brain stem (URBA-HOLMGREN et al. 1977). Primate yawning behaviour is especially interesting as it also occurs in a variety of social contexts, thus being more than a 'comfort movement' (TRoisi et al. 1990) and yawns occurring outside the transition between sleep and waking phases may have a communicative function (REDICAN 1975). In humans, the puzzling question about yawning is its social 'infectiousness', a well known but rarely studied process (PROVINE 1986; PROVINE 1989 a, b). This contagious effect is absent in non-human primates (DEPUTTE 1978).

Previous studies on primate yawning emphasize either its physiological basis or social contexts. In the latter case, studies have focused on individual differences in males or differences in frequency between age and sex classes (HADIDIAN 1980; TROISI et al. 1990). The goal of this ethological study on non-human primates is to analyse the causation and function of yawning quantitatively and to answer several questions: do yawns have one cause or several possible causes depending on the context? Does the morphology of a yawn change according to the context? Do yawns have a single function or several functions according to the context? Is yawning a physiological response, a social signal, or both? Do contexts within which yawns occur differ according to age and sex? If so, sex hormones could be responsible to the modulation of yawning frequency.

Although this study was conducted on mangabeys and macaques, two species of Old World monkeys, the emphasis is on the generality of causation and function across species rather

than on species-specific aspects of yawning. [...]

Discussion : The description of yawns in grey-cheeked mangabeys and long-tailed macaques presented here complements those of a wide range of mammal species and especially other primates, including humans (MAYER 1921; BARBIZET 1958; DEPurrE 1974; HADIDIAN 1980; PROVINE 1986). A yawn is characterized by a maximal gaping of the mouth associated with a deep inhalation. Defining a yawn with these two components, maximum gaping and respiratory movements, suggests that a mammallan yawn is not homologous to gaping or so-called 'yawning' in other vertebrates such as birds, fishes, amphiblans and reptiles (DEPUTTE 1974), although comprehensive studies show a great similarity in the contexts of occurrence (fish: RASA 1971; birds: SAUER & SAUER 1967). The three phases of a yawn described in this study correspond to those described as 'Invariant' by MAYER (1921) and BARBIZET (1958) for human yawns: an 'active- inspiratory' phase, an 'acme' phase, and a 'passive expiratory' phase (actually MAYER distingulshed only 2 phases: inspiratory and expiratory, while dividing the first phase into 2 sub-phases, initial and acme). MAYER (1921) and BARBIZET (1958) also described, during the acme phase of the yawn, the partial or total closing of the eyes and, in the last phase, the noisy exhalation. Yawning in mangabeys and longtailed macaques is similar to yawning in humans, in Macaca nigra (HADIDIAN 1980), and many other primate species (DEPUTTE unpubl. data). The Type 1 yawn in grey-cheeked mangabeys during which the teeth are not exposed, has been observed in the black ape, but HADIDIAN (1980) considered it to be an 'Incomplete yawn'. In grey-cheeked mangabeys, the Type 1 yawn could not be considered to be an incomplete yawn because its duration is identical to that of the three-phase Type 2 yawn. This suggests that, despite the difference in the gaping components between the two types of yawn, the respiratory components are similar. The'zebu bump', observed at the end of the second phase of yawn, on the neck of seated long-tailed macaques, has also been noticed in several primate species (bonnet macaques, KAUFMAN & ROSENBLUM 1966; black ape, HADIDIAN 1980; pig-tailed and rhesus macaques, de Brazza's monkey, DEPUTTE unpubl. data). But it is absent in mangabeys that are yawning while seated. However, the 'zebu bump' is observed in any monkey yawning while assuming a quadrupedal stance. This suggests that the 'zebu bump' and shoulder shrug are analogous components associated with inflation of the chest; the 'zebu bump' occurs when the yawner maintains a fixed shoulder girdle. Head-raising while dropping the lower jaw allows a complete opening of the mouth and, consequently, maximum stretching of the masseters. All the movements occurring during a yawn suggest a dynamic stretching of facial muscles and the upper parts of the body, including the respiratory muscles.

The results of this study provide strong evidence for a primary physiological causation of yawning, suggested by the influence of the level of activity, of sex hormones, and of the emotion induced by social interactions.

Yawning and Level of Activity : Between 90 and 98 % of yawns are performed by quiet individuals while seated or lying. Thus, yawning is associated with a moderate to low level of muscular tonus. The daily distribution of yawns found in monkeys suggests that yawning mainly occurs during the waking phases, either after night sleep or day rest. In humans, yawning has also been demonstrated to be more frequent after waking than before sleeping (PROVINE et al. 1987a). In both species studied, the pre- and post-sleep peaks suggest that yawning is related to state changes. Outside pre- and post-waking periods, yawning occurs during transitions between locomotor activity and rest, and the greater the postural instability, the higher the probability of yawning (DEPUTTE 1978; DEPUTrE et al. 1994). The fact that yawning is primarily defined as a breathing movement (HEUSNER 1946; BARBIZET 1958; COMROE 1967) is well supported by the influence of locomotor activity on yawn duration: the more intense the locomotor activity, the

faster the breathing and the shorter the yawn. However, in humans, PROVINE et al. (1987b) showed that breathing rate and yawning rate are not related, suggesting that yawning is not primarily a respiratory act (cf. PROVINE 1986).

Yawning and Sex Hormones : Yawning is much more frequent in males than in females, and in adult than younger males. This observation is supported by other studies on non-human primates (Goy & RESKO 1972; WOLFHEIM & ROWELL 1972; TROisi et al. 1990). The adult male:female ratios of yawning frequency in this study approximate those given by TROISI et al. (1990) in their study of yawning in social groups of long-tailed and japanese macaques. Unlike in monkeys, no sex difference in yawning frequency has been detected in humans (PROVINE & HAMERNIK 1986; SCHINO & AURFLI 1989). The clear sex difference in yawning frequency in monkeys suggests a close relationship between yawning and androgens, especially testosterone. This relationship has been demonstrated in several studies: 1. Castration induces a significant decrease in yawning frequency, which is restored by injections of testosterone proprionate (GOY & RESKO 1972; PHOENIX et al. 1973; BIELERT 1976); 2. Injections of androgens into ovariectomized females or, during pregnancy, into mothers of female fetuses, increase yawning frequency in androgen-treated or pseudohermaphroditic fernales to a level comparable to those of normal same-age males (GOY & RESKO 1972; PHOENIX et al. 1973; POMERANTZ et al. 1986); and 3. Injections of a non-steroid anti-androgen, OH Flutamide, along with injections of testosterone proprionate, into castrated males inhibit the positive effect of exogenous testosterone on yawning frequency. Yawning frequency subsequently increases when anti-androgen injections are stopped and testosterone injections continued (DEPUTTE et al. 1994). However, the relationship between the blood level of testosterone and yawning frequency is nelther linear nor simple (ROBINSON et al. 1975; DEPUTTE et al, 1994).

Yawning and Social Interactions: Is Yawning a Communicative Signal? : Social contexts. The social contexts of yawning are diverse, especially in adult males. Most of the social situations associated with high yawning rates are related to conflict and interactions common in the male repertoire (e.g. initiation of play, mounts, etc.; Fig. 13). After an adult male grey-cheeked mangabey retrieves an infant and /or carries it, lie often yawns. In macaques, play between an adult male and an infant sometimes induces a yawn in the adult. Yawning is much more frequent after coercive gestures (threats, pushing away) than after open aggression, such as aggressive chase without actual contact. In macaques, adult male/female interactions, whether involving sexual components or just sitting in contact, represented more than 52 % of the social interactions inducing a yawn in males. Adult male/male mounts, or play interactions and rare affiliative interactions, sometimes lead to yawning. Mangabeys may yawn for less than 10 s after uttering an alarm call, suggesting a common cause in both events. Most of the social contexts inducing a yawn can be characterized as leading to psychological tension, an increase in arousal or a conflict of drives. All the social contexts of yawns described here are similar to those described by HADIDIAN (1980) in black apes, and confirin the widespread opinion that yawns are induced by psychological tension or mild stress (REDICAN 1975).

Yawning as a threat. A yawn is sometimes considered to be a mild threat gesture when the yawner faces his partner (HALL & DE VORE 1965; ALTMANN 1967; CHALMERS 1968). CHALMERS (1968) showed that, in black mangabeys, yawning while facing away froin a partner is associated with a tendency to flee. In addition, CHALMERS (1968) showed that the recipient of a yawn was as likely to flee as to stay, This does not suggest that yawning is a less severe threat than a stare. In aggressive encounterS, monkeys keep track of and constantly adjust their behaviour to that of their antagonist. By contrast, when yawning, an individual stops his ongoing activity and, by raising his head and/or closing his eyes, loses track of a partner's behaviour. HADIDIAN (1980) noted that yawns falled to elicit direct responses from partriers, and, thus, were not threats.

Moreover, duration and completion of 'true' communicative facial expressions depend on the partner's response: DEPUTTE & FONTENELLE (1980) demonstrated that, unlike primary communicative signals such as the open-mouth threat and lip-smacking, the duration and degree of completion of a yawn are independent of external events; a yawn is 'unfolded' continuously, whereas, in the open-mouth threat, there is a plateau in the opening of the mouth, and its duration and intensity depend on the opponent's response. A yawner bas little control over the completion of his yawn (PELLATT et al 1981; PROVINE 1986); even humans have difficulty in stifling a yawn, once initiated (PROVINE 1986).

Yawning as a 'canine display'. Another widespread and often cited opinion on yawning is that it is a 'canine display' (NAPIER & NAPIER 1967; VINE 1970). fhis hypothesis is consistent with the high frequency of yawning in adult males, but is not supported by empirical studies. Except for the influence of high-level activity, yawns associated with wake-up phases, and yawns elicited in social interactions are morphologically similar (REDICAN 1975). Yawns have the same form whatever the size of the canines (Fig. 4). Yawns do not change in form after the growth of the canines, and the change in yawning frequency during puberty occurs during the growth of canines, not after. Yawning displays in males are more likely associated with social status than canine size (DEPUTTE 1978). Females, possessing only short canines, yawn in the saine social contexts as males, although less often (HADIDIAN 1980).

Communicative value of a yawn. Yawns following an interaction or a display have more chance of being percelved than any other yawns. The communicative behaviours exchanged during the interaction and/or display could have attracted the attention of elther one or a few partriers. The recipient (s) can then learn from yawns by integrating information available from the yawner's previous and subsequent demeanor. Therefore, any yawn preceded by a social interaction, and not only the 'averted tension yawn' as ALTMANN (1967) proposed, could be considered as being secondarily communicative (cf. BOLWIG 1959). A yawn could be viewed as an 'uneasiness' indicator similar to other physiological indicators such as scratching, pilo-erection, defecation, and micturition. This communicative value of the yawn is consistent with that proposed by several authors (CARPENTER 1940; BOLWIG 1959; HALL & DE VORE 1965; HALL 1968; POIRIER 1970; HADIDIAN 1980). Yawning could be classified as a 'displacement activity' (cf. DEPUTTE 1978; PROVINE 1986).

Speculations about the Function of Yawning : Yawns are primarily related to drowsiness, waking phases, or to social interactions or events. These primary contexts of yawning suggest discrimination between 'rest yawns' and 'emotion yawns'. The 'rest yawn', representing more than 90 % of all yawns, is synonymous with 'physiological' or 'true yawning' (ALTMANN 1967; ANGST 1974, 1975, pers. comm.). In primates, the 'emotion yawn', which accounts for 10 % of the total number of yawns, is synonymous with the 'tension yawn' (HINDE & RoWELL 1962; BERTRAND 1969; FEDICAN 1972; REDICAN 1975), with'transition yawning(ANGST 1974, 1975, pers. comm.), or with 'anxious' yawning (BOLWIG 1959; HALL 1968). The 'emotion yawn' could also be called a 'social yawn' as it is triggered by a variety of social stimuli.

Despite the fact that a yawn is characterized by conspicuous respiratory movements, simple respiratory functions have been refuted as being the cause of yawning (HEUSNER 1946; PELLATT et al. 1981; PROVINE 1986; PROVINE et al. 1987a; H. GAUTIER pers. comm.). The second conspicuous characteristic of a yawn is a vigorous stretching of the muscles of the upper body and face. HADIDIAN (1980) considers a yawn to be a 'facial stretch' and that this stretching is the main physiological function of the yawn (cf. LEWY 1921; PROVINE et al. 1987b). The furictions of a yawn could, therefore, be 'as diverse and plentiful as those of other types of stretches' (PROVINE et al. 1987b). Actually, this 'facial stretch' has a relaxing effect and is pleasurable to the yawner (PROVINE 1986; PROVINE et al. 1987a). The relaxing effect is

supported by the fact that monkeys yawn when groomed: BOCCIA et al. (1989) demonstrated the relaxing effect of grooming on the groomee.

Yawning is involved in behavioural state changes and, more generally, after increases of arousal level. Yawning may be associated with neural mechanisms lowering arousal level. Thus, it seems paradoxical that adult males yawn in bouts when they wake up. It could be suggested that the waking phase of adult males especially slow to wake (SCHALLFR 1963) is characterized by large oscillations of arousal before adjustment to the rest of the metabolism. Yawning might be one of the consequences of the activation of arousalregulating structures. It may help adjust the balance between general metabolism and arousal. Because of its high dependence on physiological processes, especially those related to arousal and sex hormones, yawning is an easy-to-observe and useful indicator of physiological correlates of behaviour. Thus, yawning should be included in both behavioural and 'physiological' ethograms (cf. CANDLAND 1974). Yawning can bc considered in an ethological paradigm because it can be elicited by internal metabolic events and by external social stimuli, both of which are modulated by the hormonal environment. Yawning is, therefore, a key topic for multidisciplinary research involving ethologists, psychologists, endocrinologists, neurologists and neurophysiologists.