Yawning: An Evolutionary Perspective

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Introduction

Evolutionary analyses of human behavior have illuminated a number of fundamental questions (i.e., foraging, mating systems, communication, etc.), and a wide array of behaviors have been targeted for investigation (infanticide, polygyny, child abuse, homicide, etc.). In general, investigation has centered on complex behaviors organized into broader functional units based on their context, or in some cases, their outcome. Little attention has been given te, more basic behavioral units (Scott, 1950) (e.g., ingestive, eliminative) that serve as the foundation for all more complicated patterns. The ubiquity of these basic patterns across animal species may have contributed to their perceived lack of importance in understanding higher order and more complex behavior patterns. On the other hand, the systematic analysis of basic motor/behavior patterns [e.g., fixed action pattern (Lorenz, 1954; Lorenz & Tinbergen, 1938) or modal action pattern (Barlow, 1968)], characterized by: (1) being species typical (within classes of animals the behavior is typically found in all individuals); (2) consisting of movements that occur simultaneously or sequentially with a high degree of predictability; and (3) being repeatedly recognizable (Slater, 1978, p. 14) may be quite productive.

Evolutionary theory has rendered some aspects of human behavior, that were previously thought to be solely influenced and directed by cultural specific patterns of behavior, to be influenced by a long evolutionary history. It is true, however, that there are still a number of human behaviors that remain puzzling in spite of the analytical power of Darwinian evolutionary theory. Relatively little attention has been paid to the study of fixed or modal action patterns in humans, with one notable exception. One of the frequently overlooked behaviors in the study of human behavior, yawning is a virtually ubiquitous behavior among all vertebrate species (Heusner, 1946). Alcock (1993, p. 26) noted that a human yawn is one of the best examples of a fixed or modal action pattern in our species. The study of yawning, particularly in humans, is important because (1) it is a behavior pattern that we share with all vertebrates, (2) it occurs in several different contexts in essentially the same form, and (3) it is contagious (Moore, 1942; Provine, 1996), unlike sneezing, coughing or crying.

Previous studies of yawning in humans have centered on yawning and activity levels of individuals (Baenninger, Binkley & Baenninger, 1996; Provine, Hamernik & Curchack, 1987). In general, little attention has been paid to the evolution of yawning and in particular the identification of its ultimate function, although quite a bit of work has focused on its proximate or more immediate causation (Alcock & Sherman, 1994). Moreover, the ontogeny of yawning has been little studied, even though it has been reported to regularly occur in utero by the 15th week of pregnancy in humans (de Vries, Visser, & Prechtl, 1982; Egerman & Emerson, 1996; Sepulveda & Mangiamarchi, 1995; Sherer, Smith & Abrainowicz, 1991). Taken together these observations suggest that the evolution of yawning is a potentially important and largely overlooked behavior.

Description and Classification

A yawn is a very deep inspiration, taken with jaws wide open which ventilates all alveoli (not the case with normal quiet breathing) (Marieb, 1995). Yawning is characterized by a long inspiration followed by shorter expiration of air. Yawns are a strong prolonged reflex (311 seconds) which invoives a strong and coordinated contraction of a complex array of pharyngeal and associated muscles (Barbizet, 1958; Provine, Hamernik & Curchack, 1987). Yawning is closely related to the gape, but differs in a number of crucial components. The principle difference is the combination of two components: a respiratory and a mouth-gape component. Gaping simply involves a large opening of the mouth and stretching of the muscles of the mandible and maxilla, and thus is differentiated from yawning behavior seen in rodents, carnivores, primates and possibly birds and herbivores (Heusner, 1946). Gaping has been reported in a wide variety of vertebrate species [fish (Baenninger, 1987; Baerends & Baerends-van Roon, 1950; Morris, 1954; Peiper, 1932; Rasa, 1971), reptiles and amphibians (Cramer, 1924; McCutcheon, 1970)] but may only be analogous to yawning and not a true homologue. According to Heusner (1946), it is unclear whether birds (Delius, 1967; Sauer & Sauer, 1967) as well as herbivores (Barbizet, 1958; Cramer, 1924) actually yawn. Nevertheless, yawning has been described in carnivores (Bekoff, 1974; Leyhausen, 1979) and in a variety of primate species (Anderson & Wunderlich, 1988; Deputte, 1994; Hadidian, 1980; Hinde & Rowell, 1962; Scucchi, Maestripieri & Schino, 1991; van Lawick-Goodall, 1968; Wolfheim & Rowell, 1972).

Investigators have attempted to identify and classify yawns, but have been largely unsuccessful in categorizing yawning behavior into clearly defined types based on fundamental motoric differences in yawning patterns. Attempts at classification have largely relied on functional differentiation of context to define the different types of yawns (Hadidian, 1980). Deputte (1994) recognized two contexts for yawns, the 'rest yawn' observed in transitions from rest to waking states and is synonymous with 'true yawns' (Altmann, 1967; Angst, 1975), and the 'emotion yawn' or the 'tension yawn' (Bertrand, 1969; Hinde & Rowell, 1962; Redican, 1975). Deputte (1994) notes that the 'emotion yawn' could also be called the social yawn since it is elicited by a number of social signals. Charles Darwin recognized that yawning occurred in several different contexts. He noted that, "... baboons often show their passion and threaten their enemies in a very odd manner, namely, by opening their mouths widely as in the act of yawning ... Some species of Macacus and Cercopithecus behave in the same manner" (Darwin, 1872, p. 136-7).

A cross-specific analysis of yawning suggests two broad functional explanations. One centers on the immediate physiological circumstances that are implicated in yawning; and the other, a possibly secondarily derived social communicatory function. Investigators do not agree on the functions of yawning, nor on its importance in the behavioral repertoire of any particular species. van Hooff (1967), in an important early review of facial displays in Old World monkeys and apes, does not include yawning as a social communicatory behavior. While Redican (1975), in a exhaustive review of facial expressions in nonhuman primates, devotes an entire section (pps.147-53) to the discussion of yawning,

Based solely on observational data, these two types of yawns (rest yawn and truc yawn) are motorically identical. In macaques, yawns are described as having three basic components: oral, postural and respiratory. These components are distinguished on behavioral bases since there is no temporal disruption in a yawn. In general, prior to the yawn the head is lifted backward and rotated sideways, the mouth is slightly open, but the teeth are not exposed. The second phase of the yawn is characterized by continued upward motion of the head, the mouth is fully open, often exposing the teeth and gums. A deep inhalation is also part of this phase. In the final phase, the head is lowered, the mouth closed rapidly and the lips covered with the teeth (Deputte, 1994). In a discussion of baboon behavior, Altmann (1967) suggests that one can distinguish truc yawns from those with socially implied functions, but only by context. Truc yawns are presumably stimulated by a lowered oxygen tension in the blood, while social yawns express conflict, anxiety or threat. The external manifestations of these two types of yawns are quite similar. The entire set of teeth including the canines may bc exposed, and as the yawn reaches a climax the head may bc thrown back (Redican, 1975).

While yawning, the mouth opens widely and roundly, usually fairly slowly, typically closing more swiftly. A swelling of the throat is usually visible, accompanied by a deep breath and closing of the eyes and lowering of the brows (Brannigan & Humphries, 1972, p. 58). Yawns have an average duration of 6 seconds, are difficult to stop midperformance and are infectious, stimulating yawning in other humans that observe or even hear the yawner. One of the most interesting characteristics of human yawning behavior is its high degree of contagion. After observing, hearing, reading, or thinking about yawning evokes a yawn (Provine, 1986,1989a,b). Oddly, this contagious feature of yawning has not been observed in nonhuman primates (Deputte, 1978). In addition to its contagious nature, yawning has been shown to have a truc circadian cycle in both humans and laboratory animals (Anfas, et ai., 1984; Greco, et al., 1993; Provine, et al. 1987).

Suggested Functions

Although overlooked in the human evolutionary literature, yawning has been used as a behavioral indicator of various types of experimental neurochemical interventions in laboratory animals for quite a while. Since it is clear that yawning occurs in at least two vastly different contexts (truc vs. emotional yawns), any discussion of the functional or evolutionary responses must keep these behavioral variants clearly separated. Table 1 lists the suggested functions of yawning behavior and distinguishes between truc and emotional yawns. One of the interesting aspects of Table 1 is the conspicuous absence of empirical verification of any of the propositions about yawning [except for the work of Provine and his colleagues (1986, 1987)]. In spite of the lack of research into the evolutionary basis of yawning, many of the proximate mechanisms implicated in the behavior have been identified. A variety of studies have shown that cholinergic, dopaminergic as well as serotonergic systems are implicated in the induction of yawning in laboratory animals (Brown, et al., 1990, 1991; Mogilnicka & Klimek, 1977; Mogilnicka, Boissard & Delini-Stule, 1984; Urbà-Holmerren, Holmgren & Anias, 1982; Urbà-Holmgren, et al., 1979; Yamada & Furukawa, 1980; Zarrindast & Poursoltan, 1989; Zarrindast, Fatehi & Mohagheghi-Badi, 1995; Zarrindast, Toloui & Hashemi, 1995; Zarrindast, et al., 1995). While these studies have enhanced our knowledge of the brain mechanisms and neurochemical pathways implicated in yawning behavior, none have attempted to link these neural mechanisms to the behavior of free-ranging animals. We are therefore still left with no satisfactory enipirical answer to our earlier question of the evolution of yawning.

Throughout this discussion we have assumed an evolutionary basis for such a widespread behavior like yawning. It is possible that yawning bas no immediate adaptive value, and is merely a byproduct of selection for other types of behavior. This possibility seems unlikely, however, given its highly contagious nature. It is reasonable to expect that a behavior that elicits a similar behavior in conspecifics so frequently and with no intention by the yawner has been the object of strong selective pressure. One of the reasons why yawning may have been overlooked and investigated only on a limited basis is the perception that the costs and benefits of yawning are relatively trivial. This may not be the case, at least in some situations. Tesfaye and Lal (1990), Tesfaye, Skorzewska & Lal (1990), Warner & Warner (1990), and Lurie (1990) all note that the costs of yawning can be quite high and can result in subluxation of the lower jaw. Subluxation of the temporomandibular joint results in the jaw being locked open, deviated either left or right, often leaving the affected individual unable to speak. Certainly, in a minority of cases, yawning may be very costly.

The interesting question still remains, i.e. the ultimate causation of yawning. As previously noted, in nonhuman species, yawning seems to serve two distinctly different ends. While there are marked similarities between the yawns of humans and nonhuman primates, the functional differentiation of human yawns is not so clear. Did yawning originate as a direct response to some physiological process and then subsequently co-opted as signal of underlying emotional state? Did yawning arise as a communicatory act and subsequently associate with an entirely different underlying physiological process? It is unlikely that we will ever know the answer to these questions with any degree of certainty for either humans or nonhumans. What we are left with are a set of best guesses based on an examination of the behavior as it manifests itself in modern humans, coupled with comparative observations of other vertebrate species.

The most compelling characteristic of human yawning that calls for an evolutionary explanation is its contagious nature coupled with the absence of this contagion in other yawning species. These observations suggest that yawning in humans has evolved as a fitness enhancing behavior pattern. Identification of a precise function for yawning is difficult, but perhaps the coordination of activity, whether it is preparing for sleep, increasing alertness (Askenasy, 1989), warding off respiratory infection (McKenzie, 1994) or preventing alveoli collapse (Forrester, 1988) are among its most important and enduring features. Clearly, our understanding of yawning as a coordinated human behavior would benefit from additional research and this research would likely yield a clearer picture of its adaptive nature.

Table 1: Summary of suggested functions of Yawning

Function	Evidence	Reference
1 Increase alertness		Baenninger & Greco (1991); Baenninger, et al. (1996)
2.Decrease alertness		Lehmann (1979)
3.Signals change in behavioral state		Greco, Baenninger. & Govern (1993)
4.Ensures proper articulation of temperomandibular joint	Yawning observed in fetus in 1 trimester	de Vries, et al. (1982)
5.Opens eustachian tubes		Laskiewiez (1953)
6.Component of primal stretch	Yawning and stretching seein to co-occur least at some times	Provine, et al. (1987)
7.Indicator of hemorrhage		Nash (1942)
8.Indicator of motion sickness		Graybiel & Knepton (1976)
9.Indicator of encephalitis		Wilson (1940)
10. Marker of increased choliner-gic and peptidergic activity		Dourish & Cooper (1990); Mogilfficka, et al. (1984)
1l. Marker of decreased dopami-ne activity		Dourish & Cooper (1990); Gilbert (1988)
12. Behavioral assay of neuro-chemical activity	ACTH, apomorphine, catechol-amine, estrogen, MSH, oxytocin, piribedil, physostigmine, pilocar-pine, serotonin, & testosterone,	Anias et al (1984); Cowan (1978); Phoenix & Chambers (1982); Urba-Holmgren et al. (1979)
13. Prevents atelectasis		Cahill (1978)
14. Induces relaxation of social tension in groups		Sauter & Sauer (1967)
15, Equilibrate C02 and/or 02 le-vels in the blood		Sauer & Sauer (1967)
16. Early manifestation of vaso-vagal reflex		Cronin (1988)
17. Correct imbalance in cere-bral oxidative metabolism		Lehmann (1979)
18. Renews surfactant film in lungs		Forrester (1988)
19. Expression of boredom, un-concern, or indifference		Barbizet (1958); Baenninger & Greco (1991)
20. Evacuation of potentially in-fectious substances from ton-sils		McKenzie (1994)

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