...seeing a dog and horse and man yawn, makes me feel how much all animals are built on one structure.

Charles Darwin, 1838 notebook.

Yawning: its cycles, its roles

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Charles Darwin is said to have qualified yawning as a piece of useless physiology. But, what about the continuity of this strongly stereotyped behaviour in poikilotherms and homeotherms inhabiting water, air and land, from reptiles with rudimentary, so-called archaic brains, to human primates? On the basis of knowledge flowing from phylogenesis and from sciences as diverse as ethology, embryology and neurophysiology, a coherent explanation can be developed. What a surprise, therefore, to find that yawning becomes a metaphor for Life and its three pillars: obtain energy, survive individually and as a group, reproduce. Indeed, we will show how yawning is linked to each of these behavioural pillars of vertebrate life.

Keywords : arousal, ethology, feeding behavior, physiology, sexual behavior, sleep, yawning

Yawning is a stereotyped behaviour akin to a reflex. Its function remains mysterious and physicians have tried ever since antiquity to assign it a physiological role. All theories about breathing and circulation proposed from the days of Hippocrates until the middle of the XXth century (Schiller 2002) have been debunked by contemporary physiological explorations. Neurophysiology is now starting to explain its cerebral mechanisms. Psychopharmacology has integrated it to preclinical tests on human and animals in order to better classify mechanisms of action in the various ancient and developing psychotropic families (Furukawa 1996, Smith 1999).

What is a yawn?

A yawn is a paroxystic respiratory cycle characterised by a standard cascade of movements over a 5-to-10 second period (Aubin & Garma 1988, Barbizet 1958) :

- an ample, slow and very deep inspiration, mouth wide open; in human, the expansion of the pharynx can quadruple its at-rest diameter, while the larynx opens up with maximal abduction of the vocal cords. Air inspiration is essentially through the mouth, and cannot happen through the nose or clenched teeth. Thus, the Equidae, who only breathe through the nose, must inspire through the mouth when yawning,
- a brief interruption of ventilation fluxes once the thorax is full, the acme state, often with accompanying limb stretching and eye occlusion,
- a passive, noisy and more or less gentle expiration, accompanied by the relaxation of all participating muscles. The mouth closes shut and the larynx returns to its normal position. Humans mention a unfolding feeling of well-being. The length of a yawn in a given individual seems fixed.

At the same time, there may be noises of varying intensity, with or without modulation. The movements of the thorax and the diaphragm do not differ from regular inspiration, but the importance of the pharyngolaryngeal opening associated with a visible lowering of the thyroid cartilage and hyoid bone is typical of yawning and absent in simulated yawning. Simultaneously, the eustachian tubes open up, which lowers hearing acuity briefly; the opening of the stomach cardia provokes an influx of intragastric air which is responsible for a sensation of abdominal fullness.

Therefore, yawning is not just a matter of opening one's mouth, but a generalised stretching of muscles, those of the respiratory tract (diaphragm, intercostal), the face and the neck. Curiously, it implies the simultaneous constriction of antagonist muscles, such as the mastication muscles (closing of the mouth) and the digastric muscles which play the greatest role and allow for a large opening of the mouth. All facial muscles come into play, leading to multiple comical expressions in no particular order; lacrimal secretions are briefly impeded by the compression of the lacrimal ducts, and a tear seeps through the eyelids. A drop of saliva escapes from the eversed lip when the mouth is wide open (Aloe 1994, Baenninger 1997).

Nevertheless, this association of complex and synergic movements is a very stereotyped behaviour that can be classified as a reflex due to its involuntary occurrence. Once on its way, the yawn can be willfully modulated, either by accentuating all its phases, or by minimising the opening of the mouth and the expiration, but it cannot be prevented.

It often comes in salvos of two or three cycles accompanied by stretching movements of the torso in hyperlordosis, with members hyperextended in the case of bipeds, essentially at wake-up time. Among quadrupeds, the back may take a very rounded position (carnivores). Non-human primates generally yawn is a seated position, sometimes lying down, exceptionnally while walking. At the acme of the yawning cycle, there can be either a raising of the shoulders (mangabeys) or a contraction of muscles in the nape of the neck in the shape of a "zebu hump" (macaques). The head is carried in cervical hyperextension during inspiration, followed by some flexion at expiration. It is associated with noisy utterances of varying modulations depending on the phase and the type of yawning. Yawning can be simultaneous with urination, defecation, an erection, even some vocalisation (Deputte 1998).

In human, lessened auditory acuity, closed eyelids, a sensation of physical fullness, cause a relative loss of contact with the environment. Yawning is often perceived as pleasurable, a moment of well-being, similar to the satisfactions of people who have a tics (Baenninger 1996).

Two respiratory and muscular characteristics are the starting point of studies on the cause of yawning among vertebrates, and set it apart from other types of mouth opening. Present among branchial-respiration fish and among birds, it is found from reptiles to mammals. Only the giraffe seems exempt, but it sleeps very little, in spurts of 1 to 30 minutes (Baenninger 1987, Luttenberger 1975, Rasa 1971).

Yawning circumstances

Among mammals, there are three types of morphologically identical yawns occurring in three distinct situations: situations relative to circadian rest-activity rhythms, situations relative to feeding, situations relative to sexuality or social interactions.

Situations relative to circadian rest-activity rhythms. In human, the most pronounced occurrences at at awakening in the morning, in association with the stretching of muscles (pandiculation), and as sleep is about to occur, without stretching, as well as in any condition of lessened vigilance (Baenninger 1996, Greco 1993). Repetitive and monotonous activities trigger repeated yawns as have shown studies of individuals at their work stations. Activities involving a weekly change of shift, called 3 times 8, help trigger episodes of somnolence preceded by salvos of yawning, lack of sleep and perturbations of circadian rhythms (Lal 2000). When driving a vehicle, particularly on long stretches of highways, repeated yawns are an alarm signal warning the driver about the risk of falling asleep (Cummings 2001, Kishida 1973, Koch 1987, Sakai 1975). R. Provine proposed to students that they watch both stimulating and monotonous videos (Provine 1986). Not surprisingly, he found a significant correlation between the frequency of yawns and the viewing of monotonous videos. Environmental conditions such as being confined to a small room or subjected to excessive heat proved to be factors that augment the frequency of yawns caused by boredom. M. Greco et R. Baenninger have established that the frequency of yawns is high under four daily life situations: reading, travelling in public transport, driving and waiting (Baenninger 1991, Greco 1993). In children, there is also a relationship between yawning and schooling rhythms and lifestyles. When children move from kindergarten, which is not really stressful, to the first year of grade school, where they learn to read and count, the proportion of yawners increases markedly (Carskadon 1992, Weinberg 1991).

G. Schino et F. Aureli have shown, through the study of subway users in Rome at rush hour, that there is no difference in the frequency of yawns between men and women (Schino 1989). Yawning evolves over the course of human ontogeny: from high frequency during the first year of life to a gradual reduction as age advances, in parallel with the decrease in the the total time spend asleep during the nycthemeron. Just as there are light and deep sleepers, there are light and deep yawners (Giganti 2002, Holditch-Davis 2003, Stoessl 1989).

Among non-human primates, unspecific yawning is common to all species regardless of age and sex, and constant as to its parameters in a given male before canines push out and after they have reached full size (Deputte 1994,). Yawning happens before sleep but mainly after sleep (or various phases of daytime rest). This type of yawning which occurs during changes of life rhythms and activities is common throughout the animal kingdom (Anias 1984, Seki 2003). For instance, the ostrich yawns and stretches as soon as it has hatched, as well as throughout its life following a prolonged period of immobility, when it wakes up, etc. (Sauer 1967).

Situations relative to feeding. While observing lions at the Philadelphia zoo, R. Baenninger noted an increased frequency of yawning before feeding times, as well as in function of the outside temperature (maximum of 20 to 24°C) (Baenninger 1987). In the wild, carnivores yawn when they wake up and before they go hunting. Carrion-eating animals, such as hyenas, yawn repeatedly while circling a dead animal before tearing it to pieces. Similar observations of anticipatory yawning at meal time have been noted among mandrill monkeys in captivity (Anderson 1988).

Among birds, yawning immediately after eclosion can be interpreted as a feed-me signal addressed to the parents. The approach of any other member of the species elicits a fear recoil, which shows that the yawn is specifically related to the food-providing adults (Sauer 1967).

B. Holmgren has experimented on the effect the feeding rhythm of Sprague-Dawley rats has on the schedule of yawns, but under constant lighting conditions to eliminate the light-darkness rhythm. After three weeks of getting them used to one meal a day always at the same time, he found increases in the number of yawns in the hour preceding feeding time, as well as in the moving-about activity (Holmgren 1991). After three days of food deprivation, this behaviour faded away, as well as all spontaneous yawns or those pharmacologically induced with apomorphine. It would appear that, beyond a day-night rhythm, there is a rhythm associated with ingestion which is expressed by an increase in the frequency of anticipatory yawns (Naselo 1995). This condition is in correlation with a rise in the concentration of circulating corticosteroids.

Of note is the fact that hypocretine or orexine is a neuromediator involved in the stimulation of vigilance and appetite. It so happens that the injection of hypocretine in the paraventricular nucleus of the hypothalamus also triggers yawns (Sato-Suzuki 2002).

Though long claimed non-existent, yawning is also found in herbivores, but with a reduced frequency. The energy contribution of grasses is low, as opposed to that of meat. Herbivores spend a great amount of time feeding, do not sleep as much as carnivores and yawn infrequently. There is a correlation between the number of yawns, the duration of sleep, particularly of paradoxical sleep, and the calorific value of food intake. It seems logical to propose the following: the more an animal is under pressure from predators, the case of herbivores for instance, the less it sleeps and the less it yawns. The more it ingests a high amount of calories in a short span of time, the case of predators for instance, the more it can afford to sleep for long stretches and the more it yawns. The exception to this rule is found in non-human primates, the frugivorous, whose paradoxical sleep and number of yawns is comparable to that of carnivores (Baenninger 1987, Kaplan 1998).

In human, fasting is also a trigger of yawns (hypoglycemia). Culinary excesses with overeating and alcohol consumption quickly lead to somnolence accompanied by yawns (Cronin 1988).

Situations relative to sexuality or social interactions. Yawning also occurs outside the periods of sleep or rest, after various social interactions linked notably to sexuality or conflicts. Data is not available for all animal species (Askenazy 1989, Neunmann 1990). Examples used here refer to a fish and to macaque monkeys.

Microspathodon chrysurus, a fish of the Pomacentridae family, exhibits natural aggressivity (Rasa 1971). Yawning in fish, as observed in aquariums, is associated with an interruption of swimming motions, the stiffening of the body as a whole and of the fins, along with a wide opening of the mouth. This interruption of swimming motions translates into a tendency to sink vertically. In examining the behaviour of this fish, it is possible to identify yawns related to internal stimuli. As mentioned earlier, yawns develop before feeding time and during reduced motor activity; turbulent water forces regular swimming motion, which inhibits yawning. However, Microspathodon chrysurus also yawns in response to external stimuli. Two types of experiments involving calm waters have been conducted. Dangling a lure mimicking a conspecific or dangling a grey moving ball triggers an increase in the degree of excitation. Chronologically, there are 2 to 4 yawns in the 30 seconds following the dangling, then the body takes on a dark-green hue, swimming picks up speed with frequent direction changes at 90°, signalling a state of excitation that will last about 10 minutes. An immobile ball does not trigger the same reaction as the image of a conspecific. This fish lure may be the target of agressive attacks and will sustain this state of excitation as long as it is dangled, whereas the grey ball in motion will gradually lose its triggering effect. These observations confirm that yawning is the first manifestation that the level of excitation in the fish has increased, either because the water is being agitated or because a conspecific has been seen. Adding a surrenal- stimulating hormone (ACTH) to the aquarium water, which triggers the release of the stress hormone cortisol, starts the same chronology of events: yawning, darkening of the skin, agitated swimming (Myrberg 1972, Robins 1959) .

Males yawn more frequently than females, be it among rodents (rats, cobayes) or non-human primates. This behavioural characteristic is widely used in neurophysiological experiments (Berendsen 1986, Urba-Holmgren 1990, Moyaho 2002).

Among non-human primates, the frequency grows as secondary sexual traits develop (testicular drop, growth of canines), and reaches its maximum in adult males. Yawning is partially governed by androgens; the castration of adult macaques causes a marqued reduction of yawns, while injections of exogenous dihydrotestosterone re-establishes their frequency. The injection of a non-steroid anti-androgen (hydroxyflutamide) blocks the effects of testosterone injections, thus reproducing the effects of castration (Deputte 1994, Rodriguez-Sierra 1981, Troisi 1990).

Such yawns, which are basically restricted to adult males and dominant males in the group can be qualified as “emotivity yawns” (Deputte 1994), which indicates that they are triggered by a “psychic tension”. What communication value can yawning have in a social group? In such a context, anything that can be witnessed by a partner can have meaning. Over the course of evolution, actual communication signals have arisen to act as codes shared by all members of a given species and have led to the modification of the fellow creature’s behaviour to whom the signal is adressed or who has noticed it. The yawn can be perceived by a fellow creature without being specifically adressed to same. Such signal always appears at the end of an interaction during which a more or less significant quantity of signals, stricto sensu, have been exchanged. It has not been possible to detect any modification of the fellow creature’s behaviour at the sight of a yawn. Therefore, it can only be seen as having a secondary communication value. Since the emotiviy yawn is associated with a given individual, it can serve as a reinforcement of the particular rank this individual has in the group. Such a function cannot be assigned to an unspecific yawn which, though morphologically identical, is not associated with any individual in particular (Holmgren 1980, Redican 1975).

The testosterone-dependent yawn uncovers and exposes the male’s long canines. Non-human primates being essentially vegetarians, a utilitarian perspective would explain this behaviour as a ritualised exhibition of "weapons of dissuasion". But, this hypothesis is not supported by observation, certainly not among the white-cheeked mangabeys and the long-tailed macaques. In the case of the emotivity yawn, more particular to males therefore more susceptible to expose powerful canines, it occurs at the end of interactions involving exchanges of numerous communicative signals allowing for the specific pattern of this interaction. To the contrary of other signals, the yawn, and of course the canines, have very little chance of being noticed. An electromyographic analysis has shown that during the yawn the exposure of the canines is purely passive and dependent on the maximal opening of the mouth (Deputte 1980). This study has underlined an essential difference between a threat, a specific signal to stay away, and a yawn. Three characteristics support this difference:

a- Whereas the duration of a threat and its intensity are totally dependent of the partner's behaviour, the sequence of events during a yawn is unchanging and entirely independent of any behavioural trait of the partner.

b- Among all primates, a threat comprises at least an intense visual fixation aimed by the emitting party at the threatened one. While this visual fixation is accompanied solely by a retractation of the scalp among white-cheeked mangabeys, it involves the opening of the mouth among long-tailed macaques. This visual fixation is held as long as the partner has not backed off or ended the interaction. Yawning does not necessarily imply, at its inception, that the yawner is looking at a fellow being; once triggered, it involves the lifting of the head, usually accompanied by the closing of the eyes.

c- Finally, when a threat is a specific signal devoid of ambiguity, the canines remain hidden, whereas they are largely exposed during a yawn that is not in any way directed at a given partner. Under no circumstances can yawning be seen as a type of threat (Hadidian 1980, Hall 1962, Louboungou 1987, Napier 1985).

U. Halder and R. Schenkel (1972) have described the repeated yawns of bovids which, after having calved, lick the amniotic liquid and the embryonic sac. Is this an olfactive component of yawning resting of the mother's specific recognition of her calf later? (or a yet to be investigated ocytocine effect ? Melis 1994, 1997).

Cerebral structures controlling yawning among vertebrates

The facial bone structure and the brain become distinct starting from a common embryonic structure, the ectoblast (Fortin & Abadie 2000). The cephalic pole comprises an original embryological encephalo-facial and encephalo-cervical segmentation with a strict topographical correspondence: the naso-frontal and premaxillary structures are joined to the anterior brain; the maxillo-mandibular and anterior cervical structures are joined to the brain stem and its nerves. At the beginning of the third month, the embryo becomes a fetus with the occurrence of the first oral and pharyngal motor sequences under the control of the neurological development of the brain stem: development of the suction-deglution and yawning activity. Therefore, suction and yawning have the same embryological origin, which shows the importance of the brain stem in the neurophysiological development of the oropharyngeal activity co-ordinated with the respiratory, cardiac and digestive regulations which have the same neuroanatomical localisation (de Vries 1982). Starting at the 12th week of pregnancy, echography reveals yawning and suction activities, at a developmental stage when the brain stem is already individualised and the pituitary gland has become functional, whereas the extension of the temporal and frontal neocortex takes up to 22-24 weeks to reach completion (Masuzaki 1996, Petrikovsky 1999, Sherer 1991, Van Woerden 1988).

Until now, no specific cerebral structure has been identified as a yawning centre. A good number of clinical and pharmacological arguments indicate that yawning involves the hypothalamus (particularly the paraventricular nucleus), the bulbus and pontic regions, with frontal region connections in primates and to the cervical medulla (Daquin 2001, Gilbert 1988). Muscles which contract during a yawn are controlled by cranial nerves 5,7,9,10,11,12, cervical nerves C1-C4 (phrenic nerve) and dorsal nerves innervating the intercostals, or accessory breathing muscles. During the few hours of life of anencephalous babies, it has been noted that they yawn and stretch, a sign of the mammalian syndrome of awakening activity or " Rekel Syndrom " (Selbach 1953). Patients afflicted with the locked-in syndrome, still yawn, despite being paralysed (Blin 1994, Heusner 1946, Kranianski 2003, Topper 2003). This shows that yawning originates in the brain's archaic structures common to all vertebrates .

The central nervous system is based on a common overall organisational plan and reveals, from the most ancient to the most recent vertebrates, a gradual increase in complexity corresponding to life levels that are increasingly independent and functionally developed. Yawning helps understand the phylogenesis of the encephalon by inferring a functional organisational pattern of the nervous system similar to that advanced by Paul MacLean (1985) with the superposition of :

- an ancestral "reptilian" brain (brain stem and central gray nuclei), where yawning originates,
- a "paleomammalian" brain (limbic system) common to all mammifers, functioning as a synaptic and humoral interface, in fact the seat of the monkeys' emotivity yawn,
- a "neomammalian" brain characterised by human's cortical development, particularly the frontal lobes, seat of the "contagious" yawn.

Vigilance and yawning

Let's forget about the old theories disproved by contemporary explorations. Yawning does not oxygenate the brain (a marathoner would have to yawn at each stride!), does not alter the thyroid's activity (Provine 1987, Kita 2000). Ample inspiration hinders the venous return to the heart, thus increasing the peripheral venous pressure; this contributes indirectly to the flow of cephalo-rachidian fluid, but without any identifiable consequence (Oreskovic 2002, Schroth 1992).

Sleep and awakening regulation is controlled by some 15 different and redundant circuits, mainly located in the pons (adrenergic), the peduncle (dopaminergic), the hypothalamus (histaminergic), the Meynert basifrontal region (cholinergic). There are two permissive networks controlling awakening that must be inhibited for sleep to occur. Experiences realised on rodents and non-human primates confirm the role of each of these neurotransmitters in triggering yawning (Argiolas 1987, 1998, Cooper 1990, Daquin 2001) .

How is a yawn triggered?

At the moment there is no definite and irrefutable data on this. Here are some of the proposed mecanisms.

Vegetative data: the controls exercised by the autonomous nervous system (or vegetative) on the major vital functions are modulated by states of vigilance. The balance between sympathetic and parasympathetic activity is modified depending on the state of vigilance at play. There is a tendency to a progressive increase in vagal (parasympathetic) activity from waking to slow sleep with a peak during tonic paradoxical sleep, while sympathetic activity decreases almost proportionally. During sleep, this leads to a clear reduction of muscle activity in the upper respiratory airways. It reaches its maximum during paradoxical sleep, which is of longer duration at the end of the night, and combines overall peripheral muscular hypotonia with a tendency to collapsus of the upper respiratory airways (Ayappa 2003). At awakening, the yawning and stretching open the pharyngo-larynx to its maximum and activate the return of muscle tone, which increases cardiac frequency, blood pressure, muscle metabolism, all associated with a loosening up of articulations. Repeated stress experiments trigger the suppression of paradoxical sleep in association with the disappearance of yawning. This seems to confirm the close link between paradoxical sleep and yawning, which does not mean that the effect of stress does not count (Aubin 1988, Tufik 1995).

Reflex data: fatigue, boredom, lack of sleep, etc, have an impact on muscle tone, which is perceived by the nervous system (deep sensibility). The control of muscle tone in the nape of neck (trapezius) and of the masseters is one of the elements contributing to the triggering of our awakening. The modification of this tone would be the triggering event of the yawning reflex. During the powerful contraction caused by yawning, the spindles of the masticatory muscles (masseters, temporal, inner and outer pterygoid), which have receptors that respond to stretching, send influxes via afferent fibres of the Ia category, which are located in the mesencephalic root of the trifacial nerve. With the motoneurons of the same muscles these fibres form a monosynaptic link. This is the basis of the masseteric reflex. These fibres have projections on the reticular formation and the locus cœruleus (two structures involved in the awakening mechanisms) which are anatomically close to the nucleus of the trifacial nerve (motor nucleus of the mastication muscles). Through the massive contraction of the masseteric muscles, yawning stimulates those structures responsible for cortical activation. The fact that the amplitude of the masseteric reflex varies in parallel with the level of vigilance constitutes another argument (Aubin 1988, Lobo 1990).

Under this perspective, yawning is triggered by the stimulation of reticular activity and of the locus cœruleus, thus acting as a vigilance reflex, as confirmed by the nature of neurotransmitting secretions (Argiolas 1998).

Neurophysiology of yawning

The involvement of the dopaminergic system can be evidenced through the administration of small doses of apomorphine, a mixted agonist of the D1-D2 receptors of dopaminergic synapses which induces yawning (Eguibar 2003, Protais 1983). Strong doses make them disappear and cause motor stereotypies in animals or dyskenesias of the face in human. Such yawns induced by apomorphine are antagonised by typical and atypical neuroleptics, but not by domperidone, a blocking agent of peripheral dopaminergic receptors because it cannot cross the blood-brain barrier (Melis 1987). The disappearance of yawning in extrapyramical syndromes confirms the importance of the dopaminergic pathway. The correlate is that giving an injection of apomorphine to a parkinsonian triggers, during the next ten minutes, a yawn a minute, with a repeat cycle at the end of the test one hour later. Similarly, a parkinsonian who loosens up under the effet of L-DOPA yawns when this occurs (Blin 1988, Cooper 1990, Dubuc 1982, Evidente 1999, Goren 1998, Mogilnicka 1977, O'Sullivan 1999) .

Endogenous peptide system : Hypophysectomy prevents yawning from happening (Serra 1987). ACTH, MSH (melanocyte-stimulating hormone), LH-RH, all hypophysial peptides administered to rats by intrathecal injection, induce yawns and an erection (Gessa 1966, 1967). Ocytocine injected in the paraventricular nucleus of the hypothalamus (its destruction prevents any yawning) triggers yawns, while an ocytocine inhibitor prevents them (Argiolas 1987, de Wied 1999). The role of the paraventricular nucleus of the hypothalamus and of the pituitary gland is controlled by an ocytocinergic network which receives dopaminergic activating influences and opioid inhibiting influences (Sato-Suzuki 1998, 2002). This network reaches the hippocampus, on one hand, and the bulbopontine region (the one that probably commands yawning), on the other hand. At the level of the hypothalamic nucleus one finds a parallel between the activation or not of yawning and the presence or not of nitric oxide synthetase (NO) (Melis 1989, 1997, Ushijima 1988, Zarrindast 1999).

The serotoninergic influence has been demonstrated by various pharmacological experiments. For instance, mCPP (1-3-chlorophenyl-piperazine) which is selective for 5-HT2c receptors is a powerful inducer of yawns in human as well as animals. This probably explains the iatrogenic effect of yawn salvos in patients receiving serotoninergic antagonists such as antidepressants (serotonine reuptake inhibiting action). On the other hand, the stimulation of 5-HT1a and 5-HT2 receptors prevents the development of yawns induced by apomorphine, as well as by mCPP or nitric-acid inhibitors. The paraventricular nucleus of the hypothalamus, which receives major serotoninergic projections originating in the nucleus of the dorsal raphe, would be the seat of a modulation of dopaminergic and ocytocinergic neurons by the serotocinergic receptors of these neurons (Holmgren 1979, Matsumato 1989, Urba-Holmgren 1979).

There is probably a final cholinergic pathway because pilocarpine and physostigmine, muscarinic agonists (acethylcholinesterase inhibiting) are powerful yawn triggers that are inhibited by atropine or scopolamine, acting as antagonists. These experiments show that the cholinergic pathways are the terminal, or executive, link common to all mechanisms triggering pharmacologically induced yawns (Gower 1987, Hipolide 1999, Holmgren 1980, Skorzewska 1993, Urba-Holmgren 1977).

Role of sexual hormones : in castrated rats, the response to apomorphine or ocytocine disappears. An injection of testosterone restores erection, but it must be accompanied by injections of estradiol for the yawn-erection diptych to occur. Tamoxifen, an anti-estrogen, prevents the reoccurrence of yawns induced by apomorphine after a testosterone-estradiol treatment. In non-castrated rats, progesterone increases and estradiol inhibits yawns triggered by apomorphine, without impact on erection. However, tamoxifen prevents inhibition of this type of yawn by estradiol. Because of their structure, steroids offer an activation mechanism that differs from that of the other major hormones. Some hormones, such as ocytocine, are proteins that act on membrane receptors located outside the cell and cannot penetrate the double lipid layer of which cell membranes are made. But, steroidian hormones, given their lipid nature, cross the cell wall and act on the intracytoplasmic receptors, which gives them direct access to the nucleus and the regulation of genic expression. Differences in the concentration of these receptors in various cerebral regions are responsible for the differential action of these hormones. It also appears that these hormones act by modifying the microsomial metabolism of neurotransmitters. The facilitating effect of dihydro-testosterone on yawning would intervene at the cholinergic and serotoninergic level. There is as yet no proposed explanation regarding the reason for the disappearance of this phenomenon in human primates (Deputte 1994, Holmgren 1980, Melis 1994).

The curious phenomenon of contagious yawning

A famous saw states that a good yawner will induce yawning in seven people. Contagiousness is often mentioned. This term, though, is designed for infectious diseases when, through direct or indirect contact, a healthy individual becomes sick through the transmission of a virus or microbe. The replication of behaviour does not suppose the presence of a transmission agent. It would appear more appropriate, therefore, to refer to mimetism, a term proposed by W Baldwin in 1894, or to synchronous actions, rather than imitation which could involve a voluntary participation, which is not the case here.

Ethological studies of non-human primates show that at certain times an entire group goes about yawning, without the possibility for one member to be aware of another yawner, either by sight, hearing or smell. One could not consider this type of behaviour as comparable to replication among humans, but could link it, for instance, with a synchronous trigger of activities related to circadian rest-activity rhythms. Obviously, in the case of human, these two variants can be seen sometimes as one and the same. Given the above and other ethological observations, one can find that yawning replication is found only in human (Deputte 1994, Provine 1989).

This replication is triggered involuntarily. Neither does the yawner want to make others yawn, neither is the spectator-receiver of the replication aware of a need to yawn. The latter's yawn is also triggered involuntarily, but only and only if the level of vigilance allows for it. Indeed, the involvement in a sustained intellectual task (that is with high concentration or with an optimum level of vigilance) will not allow the triggering of a yawn. This point is fundamental to the human ethological explanation of the role of synchronisation of vigilance states between two individuals subjected to the transmission of yawning (Moore 1942, Baenninger 1987).

How is this replication triggered ? Sight is a powerful stimulant. R. Provine shows that 55% of spectators viewing a video showing 30 successive yawns will yawn within five minutes. The latency period varies from a few seconds to five minutes. The latency period and the duration of the viewing have not allowed for the precise identification of a rule, a type of specific synchronisation . R. Provine has also verified that there is no need whatsoever for the face of the yawner to be in a precise visual plane relative to the subject of the contagion. Face to face, at 90°, 180°, 270° relative to one another, contagion there is. The existence of a susceptibility to contagion among blind subjects confirms that sight is not the only trigger. Viewing part of the face only, such as a wide open mouth, does not trigger replication. Therefore a multimodal perception of the whole facial configuration and of audible respiratory moments is needed, along with co-ordinated dynamics for replication to happen (Provine 1986, 1989).

The replication of yawning seems to originate at a basic level because it is independent of knowing the triggerer beforehand, independent of racial, education or socio-cultural characteristics, which indicates an absence of mnestic intervention. There is no need of explicit characterisation for the other party to be subjected to replication. There is need for a vigilance level situated between somnolence and sustained concentration and for the unconscious perception of the other party, while in a position to notice the rigorous chronology of the unfolding yawn via its visual and/or audio components of mouth opening, specific modifications of other facial traits, ventilation activity and sounds reflecting deep and prolonged inspiration (the acme), and expiration, but to a lesser degree (Platek 2003).

Following such perception, the motor trigger of the yawning reflex is also involuntary and stems from the setting into action of sub-cortical motor loops (gray nucleus – brain stem). In parallel, there is a conscious perception of the development of this phenomenon, of its stimulus and of its contextual valence through the interoception pathways, which lead to a conscious hedonist perception (Tong 2003).

Ethology allows for the distinction between two types of reactions regarding an external stimulus:
1°) reactions qualifiable as common programmes for the animal kingdom as a whole, notably all mammals. These reactions seem necessary for individual or group survival. They are contagious through non-verbal communication. This is a cognitive process of direct, immediate and non-conscious communication triggering innate or acquired motor patterns such as escape or avoidance. The replicated yawning in human can only be partly related to this archaic behavioural level. Its automatism is close to the latter. But its random component and its possible latency are quite different.
2°) reactions with cognitive participation of an emotional nature. An emotion expressed by a fellow being calls for decoding through an analytical treatment of the information. As a basis of social cognition, facial expressions reflecting emotions underly complex and flexible cognitive processes. Only human primates demonstrate the capacity to perceive others as agents endowed with intention, along with the ability to identify. This capacity to think about others and their desires is probably at the root of the complexity and sophistication of Homo sapiens' social bevaviour. (Theory of the mind). This is the basis of conscious empathy: to understand the feeling of the other, to feel personally what the other feels. The replication of yawning is akin to decoding an emotion, the other's state of vigilance, but at an unconscious, automatic level allowing for the synchronisation of the state of vigilance between individuals, which one could qualify as an instinctive, involuntary empathy. This capacity to in tune with unconscious affects rests on implicit communications, developed over the course of evolution, but whose neurobiological mechanisms are just starting to be understood (Adolphs 1996, 2001, Meltzoff 2002).

Research by J. Decety (2002) has helped identify participating cortical structures when a subject imitates the actions performed by an experimenter or when the subject's actions are imitated by an experimenter, in comparison to a situation where actions are produced without imitation: "As expected, over and above the regions involved in motor control, a network of activation common to the parietal cortex and the frontal lobe (dorso-median prefrontal regions) was detected between these two imitation situations. This network of shared activations is consistent with the hypothesis of a common coding between the actions of one's self and those of another individual. When taken together, the neurophysiological data pertaining to the neuronal implementation of the three types of activity (preparation, simulation and observation in view of imitating) involving motor representations show that there is a close functional equivalence between them".

The activation of the inferior frontal gyrus in the left hemisphere (which would correspond to the F5 region in the monkey) during the observation of actions can be explained by a silent verbalisation among the subjects. Indeed, this area belongs to Broca's region, the lesion of which provokes an aphasia. G.Rizzolati (1999) discovered in the macaque's ventral premotor cortex, in areas F4 and F5, groups of neurons called mirror neurons whose activity is correlated with the observation of another individual's action in function of its purpose, which shows the actions as being volitional. These neurons seem to exist in human. The bold speculation that supposes their involvement in this in-tune, mimetic yawning behaviour, is supported by the first functional imagery study, done by R. Hari (yet to be published), showing the activation of the sulcus temporalis superior (STS) at the sight of a yawner. In opposition to other banal facial movements, the STS is specifically stimulated by the viewing of a yawn. The STS was identified long ago as the structure involved in the perception of movement involving facial characteristics and the expression of the mouth. The activation difference between non-specific facial movements and a yawn points to the specific activation of the STS during a yawn. It so happens that the STS is an essential component of the mirror-neuron system identified by V. Gallese et G. Rizzolatti, that is the neurophysiological foundation of the ability to imitate. Another interpretation is that the STS is part of the analysis system of visual behavioural information and, in the typical case of yawning, recognises the kinesodic pattern of this behaviour and its contextual valence, enriched by the previous emotional knowledge (Platek 2003).

The perception of actions by another party would involve a simulation process that would lead to an understanding of intentions. This tuning-in on the part of the observer does not necessarily produce a movement or action. An inhibiting mechanism, activated in parallel and that can be located in the frontal area, would block the triggering of motor mimetic actions. Indeed, the study of human neurological pathology of frontal dysfunctions finds two circumstances where uninhibited imitation disturbs behaviours :
1°) The Gilles de la Tourette disease, affecting the prefrontal cortex, the basal limph nodes and the limbic system, combines four major elements: tics, the rare coprolalia behaviour, and the echolalia/echopraxia, echokinesis (Stern 2000).
2°) The prefrontal or premotor syndrome is associated with a kinetic aphasia (lesions to the left hemisphere) and selectivity troubles of motor patterns, leaving intact the superior functions: de-automation of activities accompanied by perseverance and rudimentary and erroneous imitation, echokenesis and cetopraxia.

Could the replication of yawning be an uninhibited behaviour, physiologically speaking, that through its mechanisms would be somewhat akin to these pathologies?

In human, at what age does the replication of yawning start? As early as 1952, Piaget had shown that the sensitivity to the replication of yawning in babies only appeared during its second year, whereas newborns yawn frequently, maintaining a precocious behaviour developed during fetal life. A. Meltzoff (1983, 2002) proposes an ontogenic interpretation of this discord. During its first six months of life, the baby is able to imitate hand movements because it perceives surrounding hands as its own. However, it does not have a conscious notion of itself as an individual nor any perception of its own facial movements. Once the mirror test shows that the baby has self-perception as an autonomous individual and has acquired the capacity for self recognition in a mirror, the mental development of imitation is rounded out by the capacity to copy mimics, which explains why it is only in the second that the baby becomes sensitive to yawning contagion.

To sum up, on the assumption that the development of the frontal (motor) and prefrontal (premotor) cortex is specific to bipeds, it can proposed that yawning replication is a real example of echokinesis, a word coined by JM Charcot (1890), which is characterised by three criteria:

- replication would be specifically human, to be interpreted as a behavioural mimetism,
- whereas upon observation of someone's motor behaviour what was seen is mimed through the motor areas of the observer and, more often than not, is not followed by motor actions consequent to frontal inhibition, yawning for its part is the result of uninhibited bevaviour, under certain conditions pertaining to vigilance,
- replication would have provided a selective advantage by allowing for an efficient synchronisation of vigilance levels between members of a group. It would be instrumental in a type of involuntary instinctive empathy, that would probably have appeared late in the evolution of hominids.

Some thoughts on human pathology

On Tuesday, Oct.23, 1888, Jean-Martin Charcot (1890) presented, during one of his celebrated Tuesday gatherings at La Salpêtrière, the observation of a young woman inconvenienced by 8 yawns a minute, that is 480 per hour! He qualified this as a form of hysteria, despite his examination revealing binasal hemianopsia, right-side cheirobrachial skin insensitivity to all stimuli, loss of smell. Given our contemporary knowledge, this points to a probable tumor in the sella turcica (Trautmann 1902).

If the disappearance of yawning, indicative of an extrapyramidal syndrome, or of hypopituiarism syndrome, is exceptionnally the cause of complaints, family-medicine practice shows that excessive yawning is a source of embarassment in social circles (Walusinski 2000). There are multiple causes to excessive yawning, that is salvos of 5 to 20 yawns a number of times a day. Of short duration, they are banal, from the point of view of the observer, at the onset of a vagal malaise, or in the case of neurovegetative disorders (dyspepsia, migraine-like syndromes). All insults to the brain stem, the thalamus and the hypothalamo-hypophyseal region can be involved: tumors with intracranial hypertension, infections, temporal epilepsy (Muchnik 2003)vascular accidents, degenerative diseases, etc. The development of psychotropic drugs has given rise to a rich iatrogenic pathology (Beale 2000, Cohen 1992, Modell 1989): anti-epileptics, antidepressants, apomorphine, anticholinesterases, sismotherapy, morphinic or methadone withdrawal are triggers of yawn salvos (Argiolas 1987, Blin 1991, Cerbo 1997, Fanciullacci 2000, Golberg 1983, Jacome 2001). Finally, after having eliminated the other organic causes, it seems possible to individualise a particular type of chronic motor tic disorder, typified by tics associated with yawn salvos relieved with haloperidol.

Conclusion

Found from reptiles with the most archaic brains to human primates, the persistance of yawning shows its importance throughout evolution which has conserved it as a stereotypic action in both its pattern and function for millions of years. Its ethology, particularly among non-human primates, shows its association with the three fundamental pillars of life: nourishment, individual and group survival, and reproduction. In human, it conserves a function comparable to that of animals: stimulation of vigilance, at awakening or when sleep is needed. A prefrontal activity, characteristic of human, seems to facilitate the transmission of yawning and would lead to group homeostasia (or empathy, but yet to be investigated; Carr 2003). Numerous cerebral diseases affecting the brain stem or the thalamo-hypophyseal region can trigger repeated yawn salvos.

Yawning is a very pertinent model allowing for the understanding of a principle of causality non only through ethological observations but also through neurological determinisms regarding neuroanatomy, on the one hand, and neurotransmitters and hormones, on the other.

References

(A complete review can be found at : http://www.yawning.info)

Adolphs R., Damasio H., et al. (1996) Cortical Systems for the Recognition of Emotion in Facial Expressions. The Journal of Neuroscience 16:7678-7687

Adolphs R. (2001)The neurobiology of social cognition. Current Opinionin Neurobiology 11:231-239

Aloe F. (1994) Yawning. Arq Neuropsiquiatr 52:27-36

Anias J., Homgren B., et al. (1984) Circadian variation of yawning behavior Acta Neurobiol Exp 44:179-186

Anderson J.R., Wunderlich D. (1988) Food-reinforced yawning in Macaca tonkeana American Journal of Primatology. 16:165-169

Argiolas A., Melis M.R., et al. (1987) Yawning: neurochemistry, physiology and pathology Cephalagia 7:131-137

Argiolas A., Gessa G.L. (1987) Paraventricular nucleus lesion prevents yawning and penile erection induced by apomorphine and oxytocin but not by ACTH in rats Brain Research 421:349-352

Argiolas A., Melis M.R. (1988) The neuropharmacology of yawning Eur Pharmacol. 343:1-16

Askenasy J.J. (1989) Is yawning an arousal defense reflex? J Psychol 123:609-621

Aubin H.J., Garma L. (1988) Le bâillement Psychiatrie "&" Psychobiologie 3:275-286

Ayappa I., Rapaport D. (2003) The upper airway in sleep: physiology of the pharynx Sleep Med Reviews 7: 9-33

Baldwin W. (1894) Imitation: a chapter in the natural history of consciousness Mind 3:26-55

Baenninger R. (1987) Some comparative aspects of yawning in Betta sleepnes, Homo Sapiens, Pantera leo and Papio sphinx J.Comp. Psycho 101:349-354

Baenninger R., Greco M. (1991) Some antecedents and consequences of yawning Psychological Record 41:453-460

Baenninger R., Binkley S., et al.. Field observations of yawning and activity in humans. Physiol Behav 59:421-425

Baenninger R. (1997) On yawning and its functions Psychonomic Bulletin & Review 4:198-207

Barbizet J. (1958) Yawning J Neurol Neurosurg Psychiat 21:203-209

Beale M.D., Murphree T.M. (2000) Excessive yawning and SSRI therapy. Int J Neuro-psychopharmacol 3:275-276

Berendsen H.G., Gower A.J. (1986) Opiate-androgen interactions in drug-induced yawning and penile erections in the rats Neuroendocrinology 42:185-190

Blau J.N. (1991) Migraine postdromes: symptoms after attacks Cephalagia 11:229-231

Blin O., et al. (1988) Induction of yawning by low doses of apomorphine Psychiatr et psychobiol 3:195-199

Blin O., Azulay J.P., et al. (1991) Apomorphine-induced yawning in migraine patients: enhanced responsiveness Clin Neuropharmacol 14:91-95

Blin O., Rascol O., et al. (1994) A single report of an hemiplegic arm stretching related to yawning: further investigation using apomorphine administration J Neurosci 126:225-227

Carr L., Iacoboni M. et al. (2003) Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas PNAS 100: 5497-5502

Carskadon M.M. (1991)Yawning elicited by reading : is an open mouth sufficient stimulus ? Sleep research 20:116

Carskadon M.M. (1992) Yawning elicited by reading: effects of sleepiness. Sleep research 21:101

Cerbo R., Barbanti P., et al. (1997) Dopamine hypersensitivity in migraine: role of the apomorphine test Clin Neuropharmacol 20::36-41

Charcot J.M. (1890) Leçons du mardi de la Salpétrière Lecrosnier et Babé ed Paris 2:1-11

Cohen A.J. (1992) Fluoxetine-induced yawning and anorgasmia reversed by cyproheptadine treatment. Clin Psychiatry 53:174

Cooper S.J., Dourish C.T. (1990) Neural basis of drug induced yawning In Neurobiology of stereotyped behaviour Oxford ed

Cronin T.G. (1988) Yawning : en early manifestation of vasovagal reflex AJR 150:209

Cummings P. et al. (2001) Drowsiness, counter-measures to drowsiness, and the risk of a motor vehicle crash Injury Prevention 7:194-199

Daquin G., Micallef J. et al. (2001) Yawning Sleep Medicine Reviews 5:299-312

Decety J., Chaminade T., et al. (2002) A PET exploration of neural mechanisms involved in reciproal imitation NeuroImage 15: 265-272

Deputte B.L., Fontenelle A. (1980) Menace et bâillement chez MacacFascicularis: intérêt de l'étude électromyographique comparée. Biology of Behaviour 5:47-54

Deputte B.L., Johnson J. et al. (1994) Behavioral effects of an antiandrogen in adult male rhesus Macaques Hormones and Behavior 28:155-164

Deputte B.L. (1994) Ethological study of yawning in primates Ethology 98:221-245

de Vries M.P., Visser G., et al. (1982) The emergence of fetal behaviour Early Human Developpement 7:301-322

de Wied D. (1999) Behavioral pharmacology of neuropeptides related to melanocortins and the neurohypophyseal hormones Eur J Pharmacol 30:1-11

Eguibar J.R. et al. (2003) Behavioral differences between selectively bred rats: D1 versus D2 receptors in yawning and grooming Pharmacology, Biochemistry and Behavior 74: 827–832

Evidente V.G., Hardy K. (1999) Yawning in Parkinson's disease Neurology 15:428

Fanciullacci M., Alessandri M., et al. (2001) Dopamine involvement in the migraine attack. Funct Neurol 15:171-181

Fortin G., Abadie V., et al. (2000) Genetic and developmental models for the neural control of breathing in vertebrates Respir Physiol 122:247-257

Furukawa T. (1996) Yawning behavior for preclinical drug evaluation Meth Find Exp Clin Phamacol 18:141-155

Gessa G.L. (1966) Stretchings and yawnings induced by adrenocorticotrophic hormone Nature 5047:426-427

Gessa G.L. (1967) Stretching and yawning movements after intracerebral injection of ACTH Revue Canadienne Bioliologie 26:229-236

Giganti F., Hayes M.J., et al. (2002) Yawning and behavioral states in premature infants Developmental Psychobiology 41:289-96

Gilbert D. (1988) Is Yawning a brainstem phenomenon ? The Lancet 8580:596

Goldberg R.L. (1983) Sustained yawning as a side effect of imipramine Int J Psychiatry Med 13:277-280

Goren J.L. (1998) Yawning : an aura for an L Dopa induced "off" in Parkinson diesease Neurology 50: 823

Gower A.J. (1987) Effects of acetylcholine agonists and antagonists on yawning and analgesia in the rat Europ J Pharmacology 139:79-89

Greco M., Baenninger R., (1993) On the context of yawning: when, where, and why ? Psych. Rec. 43:175-183

Hadidian J. (1980) Yawning in old world monkey, Macaca nigra Behaviour 75:133-147

Hall K.L. (1962) Behaviour of monkeys towards mirror-images Nature 196:1258-1261

Halder U., Schenkel R. (1972) Das Riech-Gähnen bei Rindern (Bovinae) Z Säugertierkunde 137:232-245

Hari R. (2003) Abstract congress NeuroImage 2, Sup 1: S1-S101

Heusner A.P. (1946) Yawning and associated phenomena Physiological Review 25:156-168

Hipolide D.C., Lobo L.L., et al. (1999) Treatment with dexamethasone alters yawning behavior induced by cholinergic but not dopaminergic agonist Physiol Behav 65:829-832

Holditch-Davis D. (2003) Development of behaviors in preterm infants: relation to sleeping and waking Nurs Res 52:307-317

Holmgren B., Urba-Holmgren R. (1980) Interaction of cholinergic and dopaminergic inflences en Yawning Behavior Acta Neurobiol Exp 40:633-642

Holmgren R., Holmgren B., et al. (1979) Serotonergic modulation of yawning.Pharmacol Biochem Behav 11:371-372

Holmgren R., Holmgren B. (1980) Sex hormone influences on yawning behavior Acta Neurobiol Exp 40:515-519

Holmgren B., Budelli R. et al. (1991) Food Anticipatory Yawning Rhythm in the Rat Acta Neurobiol Exp 51:97-105

Jacome D. (2001) Primary yawning headache Cephalalgia 21:697-699

Kaplan, J.R. (1998) Frequencies and contexts of gape yawn displays of free-ranging patas monkeys (Erytrocybus patas.) American Journal of Primatology 45:215

Kishida K. (1973) Temporal change of subsidiary behavior in monotonous work Journal of Human Ergology 2:75-89

Kita I., Sato-Suzuki I., et al. (2000) Yawning responses induced by local hypoxia in the paraventricular nucleus of the rat Behavioural Brain Research 117:119-126

Koch P. (1987) Variation of behavioral and physiological variables in children attending kindergarten and primary school Chronobiol Int 4:525-535

Krasnianski M., et al (2003) Yawning despite trismus in a patient with locked-in syndrome caused by a thrombosed megadolichobasilar artery Clin Neurol Neurosurg 106: 44-46

Lal S., Tesfaye Y., et al. (2000) Effect of time-of-day on yawning response to apomorphine in normal subjects Neuropsychobiology 4:178-180

Lobo L.L., Neumann B.G., et al. (1990) Effects of REM sleep deprivation of ACTH-induced yawning Pharmacology 40:174-178

Louboungou M., Anderson J.R. (1987) Yawning, scratching, and protruded lips : differential conditionability of natural acts in Pigtail Monkeys Primates 23:367-375

Luttenberger F. (1975) The problem of yawning in reptiles Z Tierpsychol 37:113-37

Masuzaki H. (1996) Color Dopplerimaging of foetal yawning Ultrasound in obstetric & gynecolgy 8:355-356

Matsumoto S., Yamada K. et al., (1989) Potentiation by serotonergic inhibition of yawning induced by dopamine receptor agonists in rats Pharmacol Biochem Behav 32:815-818

MacLean P. (1985) Evolutionay psychiatry and the triune brain Psychological Medecine 15:219-221

Melis M.R., Argiolas A., et al (1987) Apomorphine-induced penile erection and Yawning : site of action in brain Brain Research 415:98-104

Melis M.R., Argiolas A., (1989) Evidence that apomorphine induces penile erection and yawning by releasing oxytocin in the central nervous system European Journal of Pharmacology 164:565-570

Melis M.R., Argiolas A. (1994) Apomorphine and Oxytocin induced penile erection and yawning in intact and castrated male rats : effect of sexual steroids Neuroendocrinology 59:349-354

Melis M.R., Argiolas A., (1997) Role of central nitric oxide in the control of penile erection and yawning Prog Neuropsychopharmacol Biol Psychiatry 21:899-922

Melis M.R. et al. (1997) Prevention by morphine of apomorphine- and oxytocin-induced penile erection and yawning: involvement of nitric oxide Naunyn-Schmiedeberg's arch Pharmacol 600;:355-395

Melis M.R. et al. (1997) Oxytocin increases nitric oxide production in the paraventricular nucleus of the hypothalamus of male rats: correlation with penile erection and yawning Regulatory Peptides 69: 105-111

Meltzoff A.N., Moore M.K. (1983) Newborn infants imitate adult facial gestures Child Dev 54:702-709
Meltzoff A., Prinz W. (2002) The Imitative Mind: Development; Evolution; and Brain Bases; Cambridge Ed

Modell J.G. (1989) Repeated observations of yawning, clitoral engorgement, and orgasm associated with fluoxetine administration J Clin Psychopharmacol 9: 63-65.

Mogilnicka E., Klimek V. (1977) Drugs affecting dopamine neurons and yawning behavior. Pharmacol Biochem Behav 7:303-305

Moore J. (1942) Some psychological aspects of yawning The Journal of General Psychology 27: 289-294

Moyaho A., Valencia J. (2002) Grooming and yawning trace adjustment to unfamiliar environments in laboratory Sprague-Dawley rats J Comparative Psychology 116; 263-269

Muchnik S., Finkielman S., et al (2003) Yawning and temporal lobe epilepsy Medicina (B Aires) 63:137-139

Myrberg A. (1972) Ethology of the bicolor damselfish Eupomacentrus partitus Animal behaviour monographs 5:197-283

Napier J.R., Napier P.H. (1985) Yawning serves as a visual signal in primates. The Natural History of the Primates. British Museum, London

Naselo A., Tieppo C., et al. (1995) Apomorphine induced yawning in the rat : influence of fasting and time of day Physiology & Behavior 57:967-971

Neumann B.G., Troncone L.R., et al. (1990) Modifications on dopaminergic and cholinergic systems induced by the water tank technique: analysis through yawning behavior Arch Int Pharmacodyn Ther 308:32-38

Oreskovic D., Klarica M. et al. (2002) The formation and circulation of cerebrospinal fluid inside the cat brain ventricles : a fact or an illusion ? Neuroscience letters 327:103-106

O'Sullivan J.D., Lees A.J., et al. (1999) Yawning in Parkinson's diseas Neurology 52:428

Petrikovsky B., Kaplan G., (1999) Fetal yawning activity in normal and high-risk fetuses: a preliminary observation. Ultrasound Obstet Gynecol 13:127-130

Piaget J. (1952) Play, dreams, and imitation in childhood New York Norton Press

Platek S.M., Critton S.R., et al (2003) Contagious yawning: the role of self-awareness and mental state attribution Cogn Brain Res 17: 223-227

Protais P., Dubuc I., Constentin J. (1983) Pharmacological characteristics of dopamine agonists on yawning behavior in rats Eur J Pharmacological 94:271-280

Provine R.R., Hamernik H.B. (1986) Yawning: effect of stimulus interest Bulletin Psychonomic Soc 24:437-438

Provine R.R. (1986) Yawning as a stereotyped action pattern and reasing stimuls Ethology 72:109-122

Provine R.R., Tate B.C. (1987) Yawning: no effect of 3-5% CO2, 100% O2, and exercise Behav Neural Biol 48:382-393

Provine R.R., Hamernik H.B., (1987) Yawning : relation to sleeping and stretching in humans. Ethology 76:152-160

Provine R.R. (1989) Contagious Yawning and infant imitation Bulletin Psychonomic Soc 27:125-126

Provine R.R. (1989) Faces as releasers of contagious yawning: on approach to face detection using normal human subjects Bulletin Psychonomic Soc 27:211-214
Rasa O.A. (1971) The causal factors and function of yawning in microspathodon Chrysurus (Pices : Pomacentridae) Behaviour 39:39-57

Redican W.K. (1975) Facial expressions in nonhuman primates Primate Behavior: Developments in Field and Labaratory Research (Roseblum, L. A., Ed.) Academic Press, New York 4:103-194

Rizzolatti G., GalleseV. (1999) Resonance behaviors and mirror neurons Archives Italiennes de Biologie 137;:85-100

Robins C. et al. (1959) Some aspects of the behavior of the blennioid fish Chaenopsis ocellata Poey Proceedings of the zoogical society of London 44; 77-84

Rodriguez-Sierra J. (1981) Testosterone potentiation of the effectiveness of ACTH on the induction of the strech-yawning syndrome in male Guinea Pigs Hormones and Behavior 15:77-85

Sakai K., Takahashi Y. (1975) Driving and subsidiary behavior of taxi drivers working alternate-day shifts Hum Ergol (Tokyo) 4:115-127

Sato-Suzuki I., Kita I. et al. (1998) Stereotyped yawning responses induced by electrical and chemical stimulation of paraventricular nucleus of the rat Journal of Neurophysiology 80: 2765-2775

Sato-Suzuki I., Kita I., et al., (2002) Cortical arousal induced by microinjection of orexins into the paraventricular nucleus of the rat Behavioural Brain Research 128:169-177

Sauer F., Sauer E. (1987) Yawning and other maintenance activities in the South African Ostrich The Auk 84:571-587

Schiller F. (2002) Yawning ? Journal of the History of the Neurosciences 11:392-401

Schino G., Aureli F. (1989) Do men yawn more then women ? Ethol. sociobiol. 10:375-378

Schroth G., KloseU. (1992) Cerebrospinal fluid flow; Physiology of respiration-related pulsations. Neuroradiology 35:10-15

Seki Y, Nakatani Y., et al (2003) Light induces cortical activation and yawning in rat Behav Brain Res 140: 65-73

Selbach C., Selbach H. (1953) Das Rekel-Syndrom als Wirkungsfolge eines biologischen Regelsystems. Monatschr.f. Psychiat .u. Neurol 125:671-682

Serra G. et al (1987) Hypophysectomy prevents ACTH-induced yawning and penile erection in rats Pharmacology Biochem Beh 26:277-279

Sherer D.M., Smith S.A., (1991) Fetal yawning in utero at 20 weeks gestation. J Ultrasound Med 10:68

Skorzewska A., Tesfaye Y, et al. (1993) Effect of scopolamine on spontaneous yawning in men. Neuropsychobiology 27:17-20
Smith E.O. (1999) Yawning: An Evolutionary Perspective Human evolution 14:191-198

Stern E., Silbersweig D.A., et al A (2000) functional neuroanatomy of tics in Tourette syndrome. Arch Gen Psychiatry 57:741-8

Stoessl A.J. (1989) Effects of ageing on the behavioural responses to dopamine agonists: decreased yawning and locomotion, but increased stereotypy Brain Research 495:20-30

Tong F. (2003) Cognitive neuroscience: primary visual cortex and visualawareness Nature Reviews Neuroscience 4:219-229

Topper R. et al. (2003) Involuntary stretching during yawning in patients with pyramidal tract lesions: further evidence for the existence of an independent emotional motor system European J Neurology 10;495-499

Trautmann R.F. (1901) Le bâillement Thèse Bordeaux (France), 40:1-86

Troisi A., Aureli F.,et al. (1990) The influence of age, sex, rank on yawning behavior in two species of macaques (Mfascicularis, Mfuscata) Ethology 86:303-310

Tufik S. et al. (1995) Effects of stress on drug induced yawning Physiology & behavior 58:1881-1884

Urba-Holmgren R., et al. (1977) Is yawning a cholinergic response? Nature 267: 261-22

Urba-Holmgren R., Holmgren B., et al. (1979) Serotonergic modulation of yawning Pharmacol Biochem Behav 11:371-372

Urba-Holmgren R., Trucios N. et al.,(1990) Genotypic dependency of spontaneous yawning frequency in the rat Behav Brain Res 40:29-35

Ushijima I., Mizuki Y., (1988) Multifocal sites of action involved in dopaminergic-cholinergic neuronal interactions in yawning Psychopharmacology (Berl) 95:34-37

Van Sweden B., Vanderhoven L., (1994) Excessive yawning Acta Neurol Belg 94:150-151

Van Woerden E.E., Van Geijn H.P., et al. (1988) Fetal mouth movements during behavioral states 1F and 2F. Eur J Obstet Gynecol Reprod Biol 1988:97-105

Weinberg W.A., Brumback R.A. (1990) Primary disorder of vigilance: a novel explanation of inattentiveness, daydreaming, boredom, restlessness, and sleepiness. J Pediatr 116:720-5

Walusinski O. (2000) Pourquoi bâillons-nous ? La Revue du Praticien Médecine Générale (Paris) 14:259-263

Zarrindast M.R., Fazli-Tabai S.,et al. (1999) Influence of different adrenoceptor agonists and antagonists on physostigmine-induced yawning in rats. Pharmacol Biochem Behav 62:1-5

A complete review and the nature of the authors' work can be found at :
http://www.yawning.info