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Review

Why do we yawn?

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ABSTRACT

Yawning is a phylogenetically old behaviour that can be observed in most vertebrate species from foetal stages to old age. The origin and function of this conspicuous phenomenon have been subject to speculations for centuries. Here, we review the experimental evidence for each of these hypotheses. It is found that theories ascribing a physiological role to yawning (such as the respiratory, arousal, or thermoregulation hypotheses) lack evidence. Conversely, the notion that yawning has a communicative function involved in the transmission of drowsiness, boredom, or mild psychological stress receives increasing support from research in different fields. In humans and some other mammals, yawning is part of the action repertoire of advanced empathic and social skills.

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1. Introduction

Yawning can be observed in most vertebrate species from foetal stages to old age. In mammals, it consists of an involuntary sequence of mouth opening, deep inspiration, brief apnea, and slow expiration (Walusinski and Deputte, 2004). It can be accompanied by other facultative motor acts such as stretching (Provine et al., 1987a). In humans, yawns last on average about 6 s, and the individual yawn duration and frequency remains remarkably stable over weeks (Provine, 1986). In birds and fish species, a mouth gaping similar to yawning can be observed, and yawning as opposed to other forms of mouth openings has been defined as a slow opening of the mouth, maintenance of the open position for more than 3 s, followed by a more rapid closure of the mouth (Baenninger, 1987). The homology of yawning between different species is controversial, but at least similar movement sequences and similar conditions of occurrence can be observed (Baenninger, 1987; Deputte, 1994).

Since yawning seems to be a phylogenically old and frequent phenomenon, one would expect that it provides some evolutionary advantage, i.e., that is has a certain useful function. Indeed, numerous hypotheses on the function of yawing have been posited throughout the centuries. They were usually derived from behavioural observations of yawns.

In mammals, it has been observed that more than 90% of yawns occur at rest whereas the remaining yawns seem to be triggered by social or emotional stimuli. These contextual differences have motivated a classification of yawning into “physiological” and “social” yawns, although the phenomenology of yawns does not depend on the context (Deputte, 1994; Walusinski and Deputte, 2004). In accordance with the distinction of physiological and social yawn contexts, the hypotheses on the function of yawning have emphasised either a physiological or a social role of yawning.

In contrast to the abundance of theoretical considerations, experimental data is relatively scarce. Yet, in the last few decades, an increasing number of studies have shed some light on its conditions and effects. Although the available data is still far from providing a complete or generally accepted account of the mechanisms and consequences of yawning, it does allow confronting some of the theoretical models with empirical observations. In this review, we will try to classify existing hypotheses according to their current experimental evidence.

All hypotheses postulating a physiological role of yawning share the common assumption that yawning regulates a particular body function, e.g., the blood oxygen level or the brain arousal level. Thus, the mechanisms of yawning are characterised as a homeostatic system with negative feedback regulation. Accordingly, physiological models necessarily make at least two different predictions that can be empirically tested: (i) yawning is triggered by up- or downturns of a given body state and, (ii) yawning acts on the corresponding body function. We will therefore review the evidence of each physiological hypothesis based on its predictions with regards to triggers and effects of yawning. In the case of social models of yawning, the postulated regulating function of yawning would not concern body functions of individuals but rather the communication within social groups. The predictions of this model as well as the corresponding evidence will also be reviewed.

This article will focus on normal yawning; a recent review on pathological yawns can be found elsewhere (Walusinski, 2009).

2. Anatomy and pharmacology

Numerous neurotransmitters, neuropeptides, and hormones have been found to be implicated in the control of yawning. Neuroendocrine substances as diverse as, among others, dopamine, acetylcholine, glutamate, serotonin, nitric oxide, adrenocorticotropic hormone (ACTH) related peptides, oxytocin, and steroid hormones facilitate yawning whereas opioid peptides have an inhibitory effect. Some of these mediators (e.g., dopamine, glutamate, oxytocin) interact in the paraventricular nucleus of the hypothalamus (PVN) and induce yawning via oxytoninergic projections to the hippocampus, the pons, and the medulla oblongata. Other pathways seem to be effective for serotonin, acetylcholine, and ACTH related peptides (Argiolas et al., 1987; Argiolas and Melis, 1998; Sato-Suzuki et al., 1998).

It would be crucial in our search for a purpose of yawning to understand the interaction of these pharmacological pathways with vigilance and respiration centres or with the mechanisms of communication and empathy. However, studies using an interdisciplinary approach of this kind are currently lacking.

3. Physiological hypotheses

3.1. Respiratory and circulatory hypotheses

For several centuries, at least since Hippocrates in the 4th century BC, scholars have thought that yawning might remove “bad air” from the lungs and increase oxygen circulation in the brain (Trautmann, 1901; Schiller, 2002; Matikainen and Elo, 2008).

3.1.1. Oxygen need and hypercapnia do not induce yawning

This hypothesis predicts that yawning is triggered when blood or brain oxygenation is insufficient, i.e., when oxygen (O_2) levels drop and the CO_2 concentration rises.

However, from self-observation most people will confirm that they do not yawn more frequently when they do exercise and need more oxygen than when they are at rest (Provine et al., 1987b). In accordance with this notion, experiments by Provine et al. (1987b) demonstrated that healthy subjects who are exposed to gas mixtures with high levels of CO_2 or physical exercise, do not yawn more frequently. Similarly, high levels of O_2 had no influence on the yawning rate. The study has some limitations, since the subjects had to use hand-held masks prone to leakage and had to count their yawns themselves by pressing a button to activate an event recorder. A potential effect of blood gas concentration might therefore have been hidden by confounding effects. Moreover, the effect of breathing low oxygen concentrations on the yawning rate has not been evaluated due to safety concerns. Nevertheless, the study clearly found significant effects of blood gases and exercise on breathing rates, which demonstrates that breathing and not yawning is the primary – if not only – physiological mechanism used for regulation of blood oxygenation. The breathing rate and yawning rate were found to vary independently, indicating that different central mechanisms are effective.

If yawning were critical for brain oxygenation, one would expect that infrequent yawners have to perform longer yawns to ensure similar oxygenation. However, no relationship between yawn frequency and duration has been observed in humans (Provine, 1986).

Although hypoxia is frequent in patients with heart or lung disease, no increased yawning is usually observed in these patients. Conversely, prolonged psychogenic hyperventilation with consecutive hypocapnia has been reported to be associated with automatic movements including yawns in some patients (Walusinski, 2009).

In anesthetised rats, local hypoxia in the paraventricular nucleus of the hypothalamus (PVN) – induced by injection of a chemical agent – did indeed produce a yawning response, which was interpreted as evidence for the respiratory hypothesis (Kita et al., 2000). However, the PVN does not respond to local hypoxia only but induces the same stereotyped yawning response also after stimulation with several other chemical agents and even after electrical stimulation (Sato-Suzuki et al., 1998; Seki et al., 2002). Thus, the observed yawns during local PVN hypoxia cannot be interpreted as specific hypoxia sensitivity of PVN neurons. Rather, they seem to result from an unspecific irritation of these cells. The study does therefore not provide convincing evidence for a causal link between hypoxia and yawning.

Fish species exposed to low water oxygen concentrations were found to respond with opening of the gill operculum (Hasler et al., 2009). Although this gill flaring response was named yawning in this study, it is not homologous to human yawning but rather seems to be a respiratory act.

Taken together, the occurrence of yawning during periods with too much blood oxygenation but not during periods with oxygen need is exactly the opposite of what would have been predicted by the respiration hypothesis and thus casts severe doubts on its correctness.

3.1.2. *Yawning does probably not increase brain oxygenation*

There are, to our knowledge, no studies that measured the change in blood oxygenation induced by yawning. However, yawning would be a much less effective way of increasing oxygen intake than rapid breathing, especially since the deep inspiration during yawning is followed by a period of relative apnoea (Baenninger, 1997). Indeed, the subjects in the study of Provine et al. (1987b) used increased breathing rates rather than increased yawning rates to compensate for high CO_2 concentrations and exercise.

Another mechanism by which yawning could theoretically increase tissue oxygenation is by increasing blood circulation. Indeed, yawning has been found to be associated with an activation of the autonomic nervous system (Greco and Baenninger, 1991; Askenasy and Askenasy, 1996; Guggisberg et al., 2007) which, by means of an increased heart rate and vasodilatation, might result in increased oxygen circulation. However, autonomic changes following yawning occur to the same amount also after simple body movements or after deep breaths (Greco and Baenninger, 1991; Guggisberg et al., 2007). They are thus unspecific and obviously due to the jaw movement and respiration rather than the yawning as such. In other words, the act of yawn does not induce more autonomic changes than the ones that already occur hundreds of times throughout the day due to simple breathing or moving. Hence, from an evolutionary perspective, yawning does not provide an advantage with regards to autonomic activity, and it therefore does not make sense to attribute a circulatory function to yawning.

Provine advanced a further argument against the respiratory hypothesis based on his analysis of the routes of inhalation and exhalation during yawning (Provine, 1986; Provine et al., 1987a,b). Unlike normal breathing, yawns cannot be performed through the nose if subjects have their mouth taped shut, which indicates that yawning does not have the degree of behavioural freedom of normal breathing. Furthermore, oral inhalation by itself was insufficient for a satisfactory yawn. The subjects in Provine's study reported a feeling of satisfaction only if they were allowed to open their jaw during yawns. A pleasant yawn depended therefore on the mouth gaping component but not on the respiratory component of yawning, which was interpreted as indirect evidence against a respiratory function of yawning.

3.1.3. *Conclusions*

The predictions of the respiratory hypothesis are not supported by current experimental data. Additional research is needed to test the effects of hypoxia on the yawning rate under more controlled conditions. Studies investigating the effects of yawning on blood and brain oxygenation are also missing. Given current evidence, it seems unlikely that yawning has respiratory or circulatory functions.

3.2. *The arousal hypothesis*

The idea that yawning might play an important role in regulating physiological brain processes has remained in the literature also after the appearance of evidence against the respiratory hypotheses. A widely expressed proposition now speculated that yawning might be responsible for the homeostatic regulation of vigilance and brain arousal level (Baenninger, 1997; Giganti et al., 2002; Walusinski and Deputte, 2004; Matikainen and Elo, 2008; Vick and Paukner, 2010).

3.2.1. *Drowsiness induces yawning*

Yawning occurs preferentially during periods of drowsiness, as it is predicted by the arousal hypothesis. Behavioural studies consistently reported that yawns occur most frequently before and after sleep, i.e., during periods with lower levels of alertness (Greco et al., 1993; Provine et al., 1987a). The circadian distribution of yawns precisely reflects the individual sleep-wake rhythm (Giganti et al., 2007; Zilli et al., 2007, 2008). Furthermore, the individual subjective feeling of drowsiness correlates with increased yawning rates (Zilli et al., 2008).

We used electroencephalography (EEG) to objectively assess the vigilance of human subjects before and after yawns (Guggisberg et al., 2007). Spontaneous brain activity produces electromagnetic oscillations in a variety of frequencies which can be recorded by EEG and which in turn correlate with specific aspects of human vigilance and arousal. EEG recordings were obtained during Maintenance of Wakefulness Tests (MWT). The MWT is a standardized diagnostic tool that is widely used to assess the ability to stay awake in patients with excessive daytime sleepiness (Doghramji et al., 1997; Littner et al., 2005). During this test, the subjects must try to stay awake while sitting alone in a quiet and darkened room, a situation which frequently leads to spontaneous yawning. EEG segments of 16 subjects who had yawned at least 4 times during the test were analyzed. Fig. 1 (left panel) shows that delta (<3 Hz) power density over central midline brain areas was significantly greater before yawns than before control movements produced by the same subjects during the same test ($t(15) = 3.1$, $p = 0.008$) (Guggisberg et al., 2007). These control movements consisted in postural adjustments without yawning. What does this mean? Delta frequencies are known to increase with the duration of wakefulness and to decrease during sleep, and are therefore interpreted as an indicator of an individual's sleep pressure (Borbely et al., 1981). Thus, sleep pressure and drowsiness proved significantly greater when subjects yawned than when they moved only.

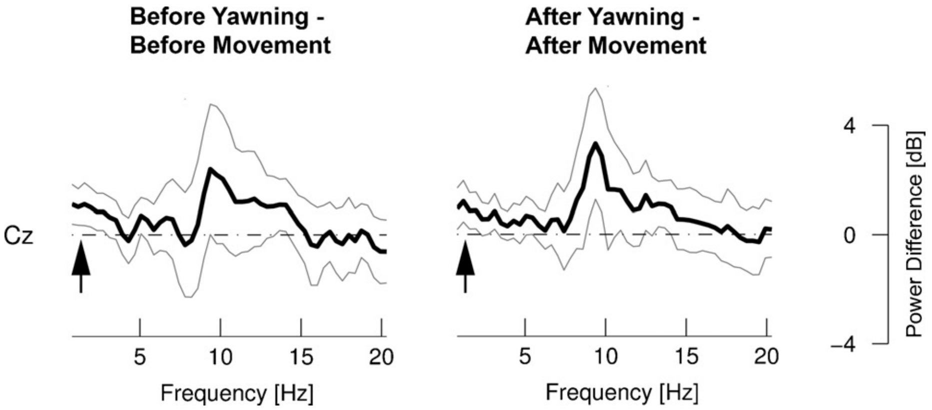

Fig. 1. Yawning is associated with EEG signs of sleepiness. The difference in power spectrum between yawning and postural adjustments without yawning was assessed. The figure shows the mean power difference ± 95% confidence interval across all 16 subjects studied in Guggisberg et al. (2007) for the vertex electrode (Cz) and for data segments before as well as after yawning/movements. Delta power was greater before and after yawning than before and after control movements of the same subjects (filled arrows), indicating that yawning is preceded and followed by greater sleep pressure and somnolence. Modified after Guggisberg et al. (2007), with permission.

3.2.2. Yawning does not produce an arousal

Arousals are defined as a global activation of brain activity that progresses from brain stem structures to centres of the autonomic nervous system and to distributed cortical areas (Moruzzi and Magoun, 1949; Sforza et al., 2000). They are accompanied by a typical acceleration of EEG activity. Several studies have therefore analyzed spectral EEG changes after yawns in humans to test the hypothesis that yawning has an arousing effect. However, the results were negative.

Two studies looking at 30 s samples of EEG before and after yawns were unable to find significant and lasting changes in EEG activity related to yawns (Laing and Ogilvie, 1988; Regehr et al., 1992). One of these studies reported transient increases in theta, spindle, and beta activity, but they only reached significance when the analysis was a priori limited to data segments between 10 and 20 s before and after yawning (Regehr et al., 1992). Furthermore, EEG power after yawning was not significantly different from EEG power after postural adjustments without yawning (Laing and Ogilvie, 1988).

In our analyses of EEG power spectra from patients undergoing MWTs, we observed that the increase in delta power over the vertex that was found before yawning (as compared to delta activity before postural adjustments without yawning, see Section 3.2.1) persisted to the same amount also after yawning (Fig. 1, right panel). Thus, yawning did not reverse the increased sleep pressure and drowsiness that seemed to have triggered it.

Besides delta power, alpha oscillations (~7.5–12.5 Hz) also reflect the individual vigilance level. They become faster and smaller in amplitude when the arousal level increases. Fig. 2A gives an example of the EEG power spectrum 30 min after oral ingestion of 250 mg caffeine (Barry et al., 2005). In contrast, drowsiness is associated with a slowing of alpha oscillations, and with a shift of alpha oscillations from mainly occipital towards central brain regions (Tanaka et al., 1997; De Gennaro et al., 2001a,b). Fig. 2B shows that alpha power after yawning showed a pattern that is typical for sleepiness: alpha rhythms decelerated, and shifted towards central brain regions after yawning, as compared to the data segments before yawning. Conversely, we did observe EEG markers of increased arousal levels after simple postural adjustments, as shown in Fig. 2C: alpha rhythms became faster and smaller after body movements. Hence, if yawning had an arousing effect – even if it were as small as the effect of simple postural adjustments – we would have detected it with our EEG analyses. Instead, we observed signs of progressive drowsiness after yawning.

Arousals are also accompanied by activations of the autonomic system. As already discussed in Section 3.1.2, yawning is indeed followed by activations of the autonomic system, which might indicate some elementary form of arousal. However, this automatic activation is entirely unspecific and related to the associated movement and respiration rather than yawning as such (Greco and Baenninger, 1991; Guggisberg et al., 2007).

Other studies have assessed the arousal level after yawning by measuring the skin conductance, which was shown to reflect both autonomic and cortical activities (Barry et al., 2005; Lawrence et al., 2005). Again, no specific increase in skin conductance could be observed after yawning (Greco and Baenninger, 1991). One study

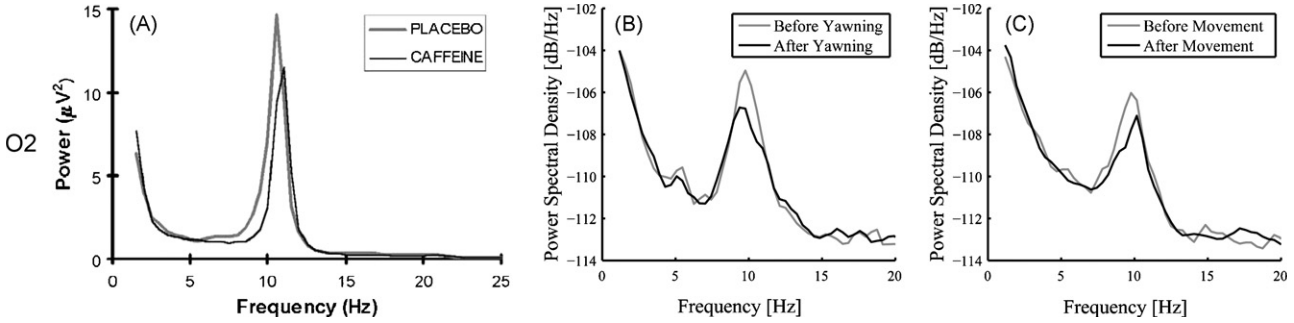

Fig. 2. Yawning does not increase the arousal level. (A) EEG power spectrum at a right occipital electrode (O_2) after ingestion of 250 mg of caffeine as compared to ingestion of Placebo (Barry et al., 2005). The increase in arousal level induced by caffeine is associated with an acceleration and amplitude decrease of alpha rhythms. (B) EEG power spectrum at electrode O_2 after yawning as compared to before yawning. No signs of an arousing effect can be observed. On the contrary, the slowing of alpha power observed after yawning indicates increased sleepiness. (C) EEG power spectrum after movements as compared to before movements. In contrast to yawning, simple postural adjustments did have an arousing effect qualitatively similar to caffeine. Modified after Barry et al. (2005) and Guggisberg et al. (2007), with permission.

even observed a yawning induced decrease in skin conductance, which would suggest a yawn-related decrease in arousal level (Baenninger and Greco, 1991).

One of the main arguments for an arousing effect of yawning has been derived from the observation that yawns are followed by a significant increase in motor activity (Baenninger, 1997; Giganti et al., 2002; Vick and Paukner, 2010). However, motor activity depends on numerous factors and more motor activity does not necessary point to an increased cerebral arousal level. Sleepy individuals trying to stay awake (e.g., during a boring meeting or during vigilance tests) typically present a motor restlessness with frequent changes of the body position (Guggisberg et al., 2007). Fig. 2C shows that these movements indeed do have an arousing effect measurable by EEG. Hence, the increased motor activity observed after yawns is probably not an indicator of an arousing effect of yawning, but an effective countermeasure against the underlying drowsiness.

An association of yawns and arousals is regularly observed in animal models of yawning. In anesthetized rats, electrical stimulation of the PVN or the application certain drugs leads to a stereotyped sequence of arousal reaction followed by yawning (Sato-Suzuki et al., 1998; Kita et al., 2000; Seki et al., 2002). However, since this arousal occurs before, not after, the actual yawning, it cannot be interpreted as a consequence of yawning, but rather corresponds to a requirement for yawning to occur during anaesthesia. Indeed, yawning almost never spontaneously occurs during sleep (Provine et al., 1987a; Greco et al., 1993; Giganti et al., 2007).

Yawning during induction of anesthesia has also been observed in humans, and recordings of the bispectral index have also suggested an accompanying arousal reaction (Kasuya et al., 2005). However, the bispectral index is sensitive to artifacts from cranial muscle activity which is abundant during yawning. Even if the observations of the study did not result from muscle artifacts, the same interpretation holds as for the data obtained in rats.

3.2.3. *Conclusions*

The experimental data suggests that yawning indeed occurs during progressive drowsiness, which is compatible with the notion that it is triggered by states of low vigilance. However, no specific arousing effect of yawning on the brain or the autonomic nervous system could be observed. Experimental evidence therefore suggests a rejection of the arousal hypothesis. The absence of an arousing effect of yawning does obviously not exclude that it might have some other form of activating function on brain metabolism or neuropharmacology, but these effects should not be named arousal.

3.3. *The sleepiness hypothesis*

Rather than attributing an arousing effect to yawning, some authors have suggested that it might lower the arousal level (Deputte, 1994). Studies assessing the arousal level after yawing have indeed found signs of decreasing wakefulness (see Section 3.2.2), which would be compatible with this notion. However, the observations could simply represent the drowsiness underlying yawning that continues to progress also after yawning. Thus, there is no established causal link between yawning and subsequent drowsiness. Moreover, if yawning had a soporific effect apart from being induced by drowsiness, it would be a self-reinforcing mechanism and would need to be controlled by other processes in order to ensure stability of the sleep-wake balance.

3.4. *The thermoregulation hypothesis*

Recently, another physiological function of yawning has been proposed: the regulation of brain temperature. It is postulated that yawning might cool down the brain when its temperature increases. The advocates of this model give a detailed description of their arguments in (Gallup and Gallup, 2008). Here, we provide a brief critique of the corresponding experimental evidence.

3.4.1. *Does brain hyperthermia trigger yawning?*

Yawning has a well-known contagious effect. In a recent experiment, the frequency of these contagious yawns (which were induced by having the subjects watch videos of yawning people) could be manipulated when the subjects held temperature packs on their forehead or when they breathed rapidly (Gallup and Gallup, 2007). For example, a cold pack on the forehead was associated with decreased contagious yawning whereas a warm pack increased the occurrence of contagious yawns. This was interpreted as evidence for a role of brain temperature in the generation of yawning. However, the experiment did not control for potential confounding factors. For instance, having an ice pack on one's forehead likely has a profound arousing effect whereas a nice and warm pack will promote sleepiness. It is therefore impossible to differentiate between effects of temperature and sleepiness in this experiment. The authors of the study acknowledge a correlation between the circadian rhythms of temperature and vigilance, but maintain that temperature is the decisive parameter in yawning generation. However, there is no evidence for the latter claim. On the contrary, there is evidence from behavioural and EEG studies that vigilance is one of the primary yawn triggering factors.

The same concern also applies to a second study of the same group performed in birds which were exposed to different ambient temperature conditions. A rapidly increasing room temperature was associated with more frequent yawns than relatively stable cold or warm temperatures (Gallup et al., 2009), which may again be due to uncontrolled factors such as differences in drowsiness or related to rapidly changing vs. stable temperatures.

The proponents of the thermoregulation hypothesis also advance anecdotal data of yawning frequency in patients with different brain diseases, but in the absence of direct comparisons and controls, the evidence remains inconclusive.

3.4.2. *Yawning does probably not cool down the brain*

The greatest challenge for the proponents of the thermoregulation hypothesis lies in demonstrating how yawning would be able to cool down the brain. It is suggested that the inflow of cool air during yawning ventilates heat off the brain. However, the proposition faces similar problems as the respiratory hypotheses discussed above. Yawning actually interrupts normal nasal breathing which seems to be a more efficient way of ventilation.

3.4.3. *Conclusions*

There is currently insufficient evidence for a thermoregulatory effect of yawning. The thermoregulation hypothesis seems to be counterintuitive and has important explanatory gaps which seem to be difficult to close.

3.5. *The ear pressure hypothesis*

Yawning has the much appreciated capacity to equalize air pressure in the middle ear with outside air pressure. It can thus relieve discomfort in the ear and hearing problems due to rapid altitude changes in air planes or elevators. This is achieved through contraction and relaxation of tensor tympani and stapedius muscles during yawning, which results in an opening of the Eustachian tubes and the aeration of the tympanal cavities (Laskiewicz, 1953; Winther et al., 2005). This observation has led to the postulation that yawning might be a “defence reflex” of the ear, which is triggered by rapid altitude changes or other conditions leading to air trapping in the middle ear (Laskiewicz, 1953).

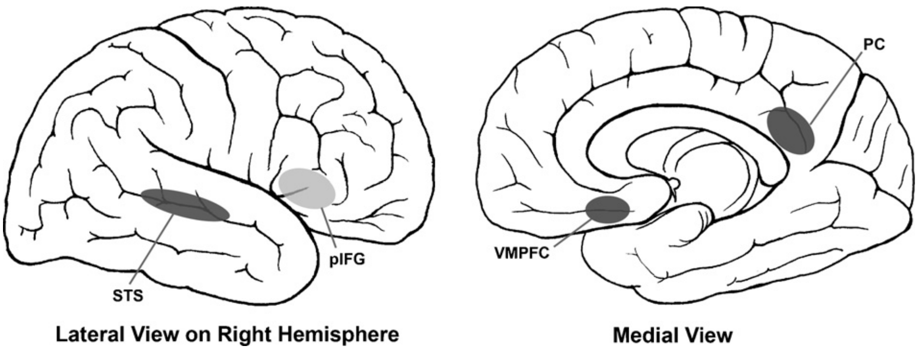

Fig. 3. Schematic illustration of brain regions found to be involved in human contagious yawning in different fMRI studies. Contagious yawning activates the right posterior inferior frontal gyrus (pIFG, light grey shading, Arnott et al., 2009) which is part of the mirror neuron system responsible for action observation and imitation (Rizzolatti and Craighero, 2004). Furthermore, human subjects watching other persons yawn specifically activate regions that are part of a network responsible for empathy and social behaviour (Saxe et al., 2004; Carrington and Bailey, 2009): the bilateral posterior cingulate (PC, Platek et al., 2005), the bilateral superior temporal sulcus (STS, Schurmann et al., 2005), or the bilateral ventromedial prefrontal cortex (VMPFC, Nahab et al., 2009), all in dark grey shading.

However, there is to our knowledge no systematic investigation that would confirm increased yawning rates under rapidly changing ear pressure conditions. Also, yawning is not the only mechanism to open the Eustachian tube; swallowing, chewing, and the Valsalva manoeuvre have the same effect (Laskiewicz, 1953; Winther et al., 2005). The middle ear pressure release of yawning does therefore not represent by itself an indispensable evolutionary advantage. Equalization of ear pressure seems to be a useful effect that yawns have in common with other contractions of oropharyngeal muscles rather than the primary purpose of yawning.

3.6. *The state change hypothesis*

Rather than suggesting a single physiological function of yawning, Provine attempted to combine the multiple behavioural state changes associated with yawning (wakefulness to sleep, sleep to wakefulness, alertness to boredom, etc.) within a single framework. He proposed that "yawning is a vigorous, widespread act that may stir up our physiology and facilitate these transitions" (Provine, 1986, 2005).

This approach has the advantage that it might integrate findings from different research fields. However, the proposition does not go beyond a mere description of the behavioural changes associated with yawning and does not give insights into how or why the proposed state changes might be achieved. Given the current scarcity of experimental evidence for any physiological function of yawning, the combination of several physiological states within a single concept also lacks empirical support.

3.7. *Other physiological hypotheses*

Several other variants of a regulatory function of yawning on body physiology have been proposed (Smith, 1999). To name only a few: yawning prevents lung atelectasis (Cahill, 1978); yawning renews surfactant films in lungs (Forrester, 1988); yawning ensures intermittent evacuation of the palatine tonsillar fossae (McKenzie, 1994). None of these propositions has been experimentally tested.

4. The social/communication hypothesis

In many cultures, yawning is interpreted as a sign of boredom and sleepiness and is therefore considered to be rude (Schiller, 2002). Thus, yawning seems to communicate a message that is almost universally understood. Moreover, yawning frequently occurs in social contexts. A communicative function of yawning has therefore long been suspected. The hypothesis states that yawning is a non-verbal form of communication that synchronizes the behaviour of a group (Barbizet, 1958; Provine, 1986; Weller, 1988; Deputte, 1994).

4.1. *Yawning has physiological and social triggers*

Yawning can be triggered by several different physiological body states as well as social contexts. Drowsiness (see above) and boredom (Provine and Hamernik, 1986) are well documented precursors of yawning. Observations in animals further suggest that yawns may be facilitated by hunger or mild psychological stress (Deputte, 1994). The communication hypothesis accounts for all these inductors by stating that they generate yawning to transmit the corresponding information to other members of a social group. The number of possible yawning triggers must of course not be unlimited; otherwise the transmitted message would be too ambiguous. Indeed, all triggers of yawning mentioned above have in common that they are mildly to moderately unpleasant while not presenting an immediate threat.

4.2. *Social effects of yawning*

The social hypothesis predicts that yawning has some impact on the behavioural organization of a social group. Communication should result in better synchronization of group behaviour. Such effects have indeed been observed in Ostriches (Sauer and Sauer, 1967), but studies that test the prediction in a controlled fashion are lacking.

4.3. *Contagious yawning*

Yawning has a well-known contagious effect in humans (Baenninger, 1987; Provine et al., 1987b; Provine, 1989a,b; Platek et al., 2003) and this effect is now frequently used to induce yawning for research purposes. Recent studies have accumulated evidence that this contagiousness depends on an intact social competence of the yawning individual. The susceptibility to contagious yawning correlates with empathic skills in healthy humans (Platek et al., 2003) and is reduced in patients with disorders affecting the ability of social interaction, such as autism (Senju et al., 2007) and schizophrenia (Lehmann, 1979; Haker and Rossler, 2009). In patients with schizophrenia, the occurrence of yawns has been interpreted as a positive sign indicating that the patient is in an accessible mood (Lehmann, 1979).

Watching or hearing other persons yawn activates a complex network of brain regions related to motor imitation, empathy, and social behaviour. Fig. 3 illustrates the brain regions that have been reported to activate in different functional magnetic resonance

Table 1
Summary of the predictions made by different hypotheses on the function of yawning and of their current experimental evidence.

Hypothesis	Inductor of yawning		Consequence of yawning		Global evidence
	Predicted	Evidence	Predicted	Evidence	
Respiratory/circulatory	Hypoxia, hypercapnia	Negative	Increase of blood or brain oxygen	Missing	Negative
Arousal	Drowsiness	Good	Brain arousal	Negative	Negative
Sleepiness	Drowsiness	Good	Drowsiness	Inconclusive	Inconclusive
Thermoregulation	Brain hyperthermia	Inconclusive	Brain cooling	Missing	Inconclusive
Ear pressure	Rapid middle ear pressure change	Missing	Middle ear pressure release	Good	Inconclusive
State change	–		Facilitation of state transitions	Missing	Missing
Other physiological	Various	Missing	Various	Missing	Missing
Communication	Drowsiness, boredom, stress	Good	Contagiousness synchronization of group behaviour	Good inconclusive	Good

imaging (fMRI) studies when human subjects observe yawns of others. The so-called mirror neuron system is important for action understanding and imitation (Rizzolatti and Craighero, 2004) and mirror neurons in the right posterior inferior frontal gyrus also seem to be recruited for contagious yawning (Arnott et al., 2009). The mirror neuron activity is however not specific to yawning but occurs to the same amount also during observation of other movements (Nahab et al., 2009; Arnott et al., 2009). Activations that are more specific to contagious yawns have been observed in the posterior cingulate (Platek et al., 2005), the bilateral superior temporal sulcus (Schurmann et al., 2005), or the ventromedial prefrontal cortex (Nahab et al., 2009). The fMRI activations in these areas were significantly greater when the study subjects watched other persons yawn than when they watched control face movements of others. Although different studies have reported divergent areas to be implicated in contagious yawning, all of them seem to be part of a distributed neural network related to empathy and social behaviour (Saxe et al., 2004; Carrington and Bailey, 2009).

In children, no contagious yawning can be induced before the age of five (Anderson and Meno, 2003), suggesting that the contagiousness of yawning depends on mechanisms that have to develop during childhood in parallel with the empathic capacity to understand mental states of others (Saxe et al., 2004).

In animals, contagious yawning has been consistently observed in chimpanzees (Anderson et al., 2004; Campbell et al., 2009; Vick and Paukner, 2010), whereas it seems to be absent in lions (Baenninger, 1987). In old-world monkeys (Baenninger, 1987; Paukner and Anderson, 2006; Palagi et al., 2009) and dogs (Joly-Mascheroni et al., 2008; Harr et al., 2009), different studies showed divergent results, but contagious yawning occurs at least in some individuals. The findings from animal studies therefore also support the notion that contagious yawning mostly occurs in individuals and species with advanced empathic and social skills.

In monkeys, the contagiousness of yawning correlates with the level of grooming contact between individuals (Palagi et al., 2009), i.e., it is higher in animals that are socially and emotionally close to each other.

In summary, research on contagious yawning has revealed that yawns are part of the action repertoire of empathic and communicative processes in adult humans and some other mammals, which provides strong evidence for a social role of yawns in these species.

4.4. *Other social modulators of yawning*

Social contexts were found to have an important impact on the yawning rate. In animals, the hierarchical position within a social group influences the frequency of yawning: group leaders initiate more yawns than subordinates (Hadidian, 1980). This difference in the yawning rate may correspond to the greater importance of communications from leaders than from other individuals for the synchronized behaviour of the group (Sauer and Sauer, 1967), and may thus also be explained within the framework of the communication hypothesis.

There are however also yawns that are independent of social modulation. Yawning also occurs when individuals are alone and in non-social animals. This might be used as an argument against the communication hypothesis and for the need to postulate an additional physiological effect of yawning. However, the existence of yawns during aloneness does not contradict the communication hypothesis in general; it merely shows that the generators of yawning lack a negative feedback mechanism checking for the presence of other individuals. Hence, the message of yawning seems to be triggered by certain body states and “sent out”, no matter whether there are other individuals that might actually receive it.

In humans, the presence of other humans may even have a suppressive effect on the yawning rate. If human subjects feel socially observed, they completely stop yawning even if the usual conditions of yawning are met (Baenninger and Greco, 1991; Provine, 2005). This suppression may result from arousing effects inherent to social observation. Alternatively, the negative connotation of yawning in human society may push the individuals to hide or inhibit yawns when they are felt to be inappropriate.

4.5. *Conclusions*

The communication hypothesis has the best experimental evidence among all propositions on the function of yawning. It is the only model that can account for social effects of yawning such as contagiousness and for the different physiological states and social contexts that can trigger it.

Missing elements of this model include controlled studies observing a regulating effect of yawning on synchronized group behaviour and data on the neuropharmacological mechanisms underlying the social inductors and effects of yawning. It is also far from clear whether the findings of contagious yawns derived mostly from studies in humans and primates can be generalized to other forms of yawns and to yawns in other species. The social aspects of spontaneous (non-contagious) yawns, particularly in species and individuals who are not susceptible to contagious yawning, have received little research interest so far.

5. Discussion

In 1986, Robert R. Provine, the pioneer in yawning research, wrote that “yawning may have the dubious distinction of being

Table 2
Some open questions for future research.

- How is yawning to be defined in different species?
- Are there systematic differences between different yawn morphologies with regards to physiological and metabolic mechanisms?
- Are there systematic differences between animal species with regards to physiological and metabolic mechanisms?
- Are there functionally significant inter-individual differences in yawning?
- Is it possible to completely suppress yawns in animals? Which would be the behavioural, physiological or social consequences?
- Does yawning change brain oxygenation?
- Which are the effects of yawning on brain metabolism and on brain neuropharmacology?
- Do rapid changes in middle ear pressure induce an increase in yawning rate?
- Which are the structural and functional connections between social systems, the paraventricular nucleus of the hypothalamus (PVN), and motoneurons in the medulla responsible for yawning execution?
- Does yawning have a specific synchronizing effect on group behaviour?

the least understood, common human behaviour." (Provine, 1986). Today, more than two decades later, this may well still be the case. In particular, the centuries-old question of why we yawn still awaits a corroborated answer. None of the numerous propositions on the function of yawning has currently sufficient experimental support or links to neuropharmacological mechanisms.

Nevertheless, the preceding sections (which are summarized in Table 1) may have demonstrated that the emphasis of models on yawning has changed. Whereas traditional hypotheses were mostly characterized by the quest for a physiological function of yawning in individuals, these propositions now face severe explanatory problems or lack empirical evidence. In contrast, the idea that yawning might rather serve a social function in groups of individuals receives increasing support from studies in different fields. It emerges that yawning might communicate unpleasant but not immediately threatening states to other members of a group in order to enhance behavioural synchronization.

This social hypothesis of yawning is also the only model that can account by itself for all elements associated with yawns. For instance, contagious effects or social contexts of yawning cannot be explained when assuming a purely physiological function. Physiological hypotheses therefore have to postulate social effects in addition to a physiological effect of yawning, whereas the physiological triggers of yawning form an integral part of social models. Hence, the social hypothesis has not only the best experimental support but is also the most parsimonious model.

From an evolutionary perspective, the communicative value of yawning may yield sufficient advantage to explain its persistence and frequent usage in many vertebrate species. The capacity to exchange information about the physical and mental state of each individual seems indeed to be crucial for the survival of a group. There is therefore no need to postulate additional physiological functions of yawning to explain its selection during evolution.

One may argue that the difficulties with physiological models results from an oversimplification of a complex phenomenon.

There might be different types of yawning that assume different functions which are unrecognized if all yawns are inappropriately pooled. However, the data from observational studies does not support this notion. Although numerous yawn morphologies and contexts have been described (Provine, 1986; Deputte, 1994; Baenninger, 1987; Palagi et al., 2009; Vick and Paukner, 2010), the different studies did not converge on a consistent classification into well-delimited types. Furthermore, most studies found no functional or contextual differences among the different yawning morphologies (Provine, 1986; Deputte, 1994; Baenninger, 1987; Palagi et al., 2009). Vick and Paukner (2010) interpreted differences in the scratching rate after "full yawns" vs. "modified yawns" with additional voluntary face movements of chimpanzees as evidence for a selective arousal effect of modified yawns only, but we have seen above that indirect behavioural markers of arousals are problematic. The current limited data therefore seems to suggest that yawning is a single mechanism associated with a continuum of behavioural manifestations rather than a discrete set of functional entities.

On the species level, the generators and functions of yawning may have evolved differently in different species, and yawns may even be a residual of earlier life forms with no remaining function at all in some species.

However, in the absence of evidence for systematic differences in the mechanisms and functions of yawning between species or yawn morphologies, this call for more complexity does not withstand the simplicity and elegance of the social model of yawning.

In conclusion, current data suggests that we might have to get used to the idea that yawns have a primarily social rather than physiological function.

6. Future research directions

Several lessons can be learned from research of the last three decades. Experience with the respiratory and arousal hypotheses demonstrates that one must be careful when interpreting indirect or anecdotal evidence. Although both hypotheses had some arguments and indirect evidence on their side, direct measurements showed negative results. In order to differentiate between specific features of yawning and nonspecific coexisting elements, it is important to include control groups or conditions during experiments.

The lack of controlled experimental studies on yawning illustrates the need for research programs in all related fields. Some of the specific questions that could be addressed are listed in Table 2.

All current models on the function of yawning are derived from observations of the phenomenology and contexts of yawning, which may result in a negligence of aspects that are not behaviourally evident. An exploration of the neural and metabolic mechanisms may give new hints on the functions of yawning that were hitherto unsuspected or on the mechanisms of existing concepts. Future research should therefore systematically assess behavioural, physiological, and social features of yawning and combine observational with interventional techniques. This requires interdisciplinary strategies that would overcome limitations of traditional techniques. For example, a combination of interventional approaches [e.g., administration of yawn-inducing or -inhibiting drugs (Argiolas and Melis, 1998), experimental lesions of brain structures involved in yawn-generation such as the PVN (Argiolas et al., 1987), manipulation of environmental conditions] with systematic behavioural observations during wakefulness may increase the value of both animal models and observational approaches.

A multimodal approach of this kind also seems to be necessary to resolve long-standing controversies on whether different types of yawning exist and on whether yawns in different species are homologous. Future studies addressing these issues should systematically compare not only behavioural but also social, functional, and physiological parameters when trying to classify yawns within and across species.

Besides this explorative approach, there is also a need for hypothesis-driven research based on the current models of yawning. Numerous open questions related to the hypotheses discussed above remain unanswered; Table 2 lists only a few.

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