Interplay between Yawning and Vigilance: A Review of the Experimental Evidence

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Abstract

**Background:** Yawning is a phylogenetically old behavior of ubiquitous occurrence. The origin and function of this conspicuous phenomenon have been subject to speculation for centuries. A widely held hypothesis posits that yawning increases the arousal level during sleepiness; thus, providing a homeostatic regulation of vigilance. **Methods:** This chapter reviews experimental data on the relationship between yawning and vigilance that allow testing of the components and predictions of this hypothesis. **Results:** Behavioral studies and electroencephalographic (EEG) recordings of brain activity before and after yawning have provided consistent evidence that yawning occurs during states of low vigilance; thus, substantiating the notion that it is provoked by sleepiness. However, studies analyzing autonomic nervous activity and EEG-based indices of vigilance in yawning subjects did not find specific autonomic activations or increased arousal levels after yawning. **Conclusions:** The data therefore do not support an arousing effect of yawning or a role in regulation of vigilance or autonomic tone.

Yawning is a conspicuous behavior that can be observed in numerous animal species from fetal stages to old age. It is therefore not surprising that the question of what might be its cause and function has always aroused human curiosity.

For several centuries, at least since Hippocrates in the 4th century BC, scholars have attributed a respiratory function to yawning: it was thought that it increases oxygen levels in the brain \cite{1, 2}. 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 apnea \cite{3}. Indeed, experiments by Provine et al. \cite{4} have demonstrated that healthy subjects who are exposed to gas mixtures with high levels of CO\textsubscript{2} increase their breathing rate, but do not yawn more frequently.

Nevertheless, the idea that yawning might play an important role in regulating individual brain physiology has remained in the literature even after the rejection of
the respiratory hypotheses. A widely expressed proposition has speculated that yawning might be responsible for the homeostatic regulation of vigilance and brain arousal level [3, 5].

In this chapter, we review studies and experiments that have empirically assessed the functional relationship between yawning and vigilance. A mechanism that is capable of regulating brain activation would need at least 2 different components: an afferent loop that responds to states of low vigilance, and an efferent loop that acts on the brain arousal level. Accordingly, the vigilance hypothesis makes 2 different predictions that can be empirically tested: (1) yawning is triggered by drowsiness, and (2) yawning arouses the brain.

Before examining experimental data on these predictions, we will summarize different methods that allow the measurement of vigilance and arousal associated with yawning.

**Measuring Vigilance**

Arousal is a global activation of brain activity that progresses from brain stem structures to centers of the autonomic nervous system and to distributed cortical areas [6, 7]. The resulting autonomic and cortical activations can be assessed with non-invasive techniques.

The gold standard for non-invasive measurement of cortical activity is electroencephalography (EEG). Spontaneous brain activity produces electromagnetic oscillations in a variety of frequencies, which in turn correlate with specific aspects of human vigilance and arousal. Delta frequencies (<3 Hz) 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 [8]. In addition, low-frequency activity below ~6 Hz increases in anterior and central brain areas during the transition from wakefulness to sleep, and reaches a maximum over the fronto-central midline during drowsiness [9–11]. Alpha oscillations (approx. 8–12 Hz) have maximal amplitude when the recorded subject is awake, at rest, and has the eyes closed. Sleepiness is associated with a decrease and slowing of alpha activity, and with a topographical shift in an anterior direction along the midline of the scalp [9, 10, 12]. Increased arousal levels are also manifested by an attenuation of alpha oscillations in EEG, but, in contrast to sleepiness, they also induce an acceleration of alpha frequencies [13, 14].

Fluctuations in autonomous nervous activity produce, among other things, changes in heart rate [15] and sympathetic nerve activity [16], both of which were measured in studies of yawning.

Skin conductance was also shown to be a reliable indicator of the arousal level, reflecting both autonomic and cortical activities [13, 17].
Experimental Yawn Induction

Behavioral as well as electrophysiological analyses require a sufficient quantity of observable yawns. Several techniques have therefore been applied to induce yawning in test subjects.

In humans, yawning has a pronounced contagious effect which is frequently used for experimental purposes. Videos or photographs of yawning persons are shown to study participants who are recruited for analysis of yawning.

Yawning also occurs more frequently during boredom, and boring texts have been found to facilitate yawns [18].

Several studies interested in the relationship between yawning and vigilance have used sleepy subjects for their analyses [19–21], since the arousal hypothesis predicts that they yawn particularly often.

A vigilance test commonly used in clinical practice to evaluate the ability of patients to stay awake proved to be a useful tool for the investigation of yawning. The Maintenance of Wakefulness Test is a standardized test during which the subjects must try to stay awake while sitting alone in a quiet and darkened room [22, 23]. The test thus combines sleepiness with boredom and frequently induces yawning.

Yawning Occurs Preferentially during Drowsiness

Behavioral and neurophysiological studies provide converging evidence that yawning occurs preferentially during periods of drowsiness.

The frequency of yawning has a distinctive circadian distribution and occurs most frequently before and after sleep [24, 25], i.e. during periods of lower levels of vigilance and alertness. Furthermore, the yawning rate correlates with the individual's subjective feeling of drowsiness [28] and adjusts to individual circadian rhythms [26–28]. See also contribution by Giganti et al. (this volume, pp. 42–46) for further details on this aspect.

If yawning is triggered by drowsiness, we should be able to observe corresponding physiological signs of sleepiness before yawns. We used electroencephalography (EEG) to test this in human subjects. Indeed, delta power density over central midline brain areas (which is thought to represent sleep pressure and sleepiness) was found to be significantly greater before yawns than before control movements without yawning [19]. Thus, sleep pressure and drowsiness were significantly greater when subjects yawned than when they only moved. This finding provides further evidence for the notion that yawns are triggered by drowsiness.

Yawning Does Not Produce Arousal

The arousal hypothesis predicts that yawning reduces sleepiness or increases the arousal level. Several studies have tested this prediction by investigating spectral EEG
changes and markers of autonomic activity after yawns in humans. However, no corresponding evidence could be found.

Laing and Ogilvie [20] recorded the EEG of healthy human subjects who spontaneously yawned before going to sleep. Thirty-second samples of EEG before and after yawns from 4 participants were subjected to a spectral analysis. Spectral power in the theta, alpha, or spindle frequency bands did not significantly change after yawning. Furthermore, EEG power in these bands before and after yawning was not significantly different from EEG power before and after postural adjustments without yawning.

In a second study by this research group, analyses were extended to a larger population of 12 subjects and to more frequency bands. Again, no lasting changes in EEG activity attributable to yawning could be observed when pre- and post-yawn samples were compared. Transient decreases in delta activity as well as transient increases in theta, spindle, and beta activity were noted, but they only reached significance when the analysis was a priori limited to data segments between 10 and 20 s before and after yawning [21].

We analyzed EEG recordings of 16 patients who underwent Maintenance of Wakefulness Tests to elucidate the origin of excessive daytime sleepiness or non-restorative sleep and who had yawned at least 4 times during the test [19]. None of the included subjects had brain lesions, metabolic disorders or hormonal disorders that could have affected the physiological mechanisms underlying yawning. We observed that the increase in delta power over the vertex that was observed before yawning (as compared to delta activity before postural adjustments without yawning) persisted to the same amount after yawning. Thus, yawning did not reverse the increased sleep pressure and drowsiness that seemed to have triggered it. The EEG after yawning even showed a pattern that is typical of a decreased [9, 10, 12] rather an increased arousal level: alpha rhythms decreased, 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. Alpha rhythms became faster and smaller after body movements, a pattern that is qualitatively similar as – but quantitatively smaller than – the spectral changes that can be observed 30 min after oral ingestion of 250 mg caffeine [13]. Hence, if yawning had 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.

Several studies have observed that yawning is followed by increases in heart rate, i.e. by activation of the autonomic system. However, this activation occurs to the same amount after simple movements without yawning or during respiration. It is therefore entirely unspecific and related to the associated movement and respiration rather than yawning as such [15, 19]. In other words, the act of yawning 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 an autonomic function to yawning.

Other studies have assessed the arousal level after yawning by measuring the skin conductance [13, 17]. Again, no specific increase in skin conductance was found after yawning in one study [15], and another study even observed a yawning-induced decrease in skin conductance, i.e. a decrease in arousal level [29].

Arousal reactions associated with yawning have been observed in anesthetized rats [30–32], but this arousal started before, not after, the actual yawning. It can therefore not be interpreted as a consequence of yawning, but rather corresponds to a requirement for yawning to occur during anesthesia. Indeed, yawning almost never spontaneously occurs during sleep [24–26]. Another study has inferred yawning-related arousals from recordings of the bispectral index in humans during induction of anesthesia [33]. However, the bispectral index is sensitive to contaminations from cranial muscle activity which is abundant during yawning. Even if the observations of the study did not result from contaminations, the same interpretation holds as for the data obtained in rats.

One of the arguments for an arousing effect of yawning has been the observation that yawns are associated with a significant increase in motor activity [3, 34]. However, motor activity depends on numerous factors and does not necessarily correlate with the cerebral arousal level. Based on our observation of an arousing effect of body movements, we have suggested that the increased motor activity observed after yawning may not be an indicator of an arousing effect of yawning, but an effective countermeasure against the underlying drowsiness [19].

Discussion

The experimental data suggest that yawning indeed occurs during progressive drowsiness, which is compatible with the notion that it is triggered by states of low vigilance. However, numerous studies using various experimental techniques were unable to observe a specific arousing effect of yawning on the brain or the autonomic nervous system.

It might be argued that the arousing effect of yawning was not accessible to EEG recordings or measurements of autonomic activity. However, vigilance changes are typically manifested diffusely over the whole brain, and EEG is considered the gold standard to measure it. Moreover, even small arousing reactions, such as the ones induced by simple body movements, could be detected.

Another argument might postulate that the arousing effect of yawning occurred with a delay that was greater than the 10- to 30-second post-yawn period analyzed in the different studies. However, central regulation mechanisms typically respond
with a much shorter latency than 30 s, and it would be unclear why in the case of vigilance regulation it would ‘wait’ for such a long time. Furthermore, the non-significant changes of the EEG during the first seconds after yawning points to decreased rather than increased arousal levels.

In contrast to the lack of direct empirical evidence for an arousing effect of yawning, an increasing number of studies have accumulated evidence for an important social function, at least in humans. Yawning has a strong contagious effect in humans and primates. The susceptibility to contagious yawning correlates with social skills in healthy subjects [35] and is reduced in patients with disorders affecting the ability of social interaction, such as autism [36] and schizophrenia [37]. Furthermore, watching other persons yawn activates brain regions related to empathy and social behavior [38–41]. These findings suggest that the regulating function of yawning might not take place in individuals but rather be effective in social groups. Thus, yawning may be a non-verbal form of communication that helps synchronize the behavior within groups [42–45].

Despite some progress in yawning research in the last few years, yawning remains insufficiently understood to establish a generally accepted model of the origin and purpose of yawning. More data on the neural and pharmacological processes that precede, accompany and follow yawns are needed. Given the relatively solid evidence for social yawns, future research should also address the anatomical connections and functional interactions between social cortical networks and centers responsible for yawning control.

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References


