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SLEEP BREATHING PHYSIOLOGY AND DISORDERS • LETTER TO THE EDITORS

The evidence does not support long-term oxygenation as a functional explanation for the evolution of yawning

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Dear Editor,

In a recent paper in *Sleep and Breathing* entitled "Yawning and airway physiology: a scoping review and novel hypothesis", Doelman and Rijken [1] propose a novel hypothesis for the main function of yawning based on the physics involved in this stereotypical behaviour. In particular, they suggest that, by repositioning the muscles around the airway, yawning evolved to secure long-term oxygenation. Given the growing appreciation for the evolutionary significance of yawning [2], research uncovering new potential function(s) of this motor action pattern is of clear importance. Doelman and Rijken indeed provide a nice overview, including very detailed and useful visualizations, of the physics of a yawn, and as such their paper could function as a reference work. However, the exclusion criteria used for their scoping review are concerning, and the studies presented as evidence for their hypothesis either have important confounding variables, can be explained by other factors, or fail to even measure yawning. In addition, their paper neglects several phenomena related to yawning that their hypothesis cannot explain, as well as a myriad of studies that do account for these phenomena, yet that support an alternative hypothesis.

Doelman and Rijken attempt to dismiss or downplay existing functional hypotheses for yawning, some of which have strong empirical support, by stating that there are at least four popular hypotheses and thus a lack of consensus among the scientific community. This perspective is based on a common misconception with regard to the analyses of behaviour, i.e. considering these functional hypotheses as mutually exclusive. Yet, as these hypotheses concern different levels of analyses, both proximate as ultimate [3], they could work in parallel. For example, the brain cooling effect of yawning could induce brain arousal and/or vigilance [4], and the communicative function of yawning in yawn contagion should be considered a derived function, as yawning is not contagious for all species, whereas all vertebrates seem to show spontaneous yawning (e.g. [5]).

To our surprise, Doelman and Rijken mention that yawning has rarely been studied. Yet a quick PubMed search reveals 1326 studies on yawning (dating back to 1946; Fig. 1), with 424 in the last decade (2012–2021; mean $42.4 \pm$ SEM 2.45 publications/year). However, the authors refer to only 8 papers of the last decade in their paper, none of which investigates the evolutionary significance of yawning. As a consequence, Doelman and Rijken have overlooked a myriad of recent empirical studies that have investigated the function of yawning in great detail, the repercussions of which we will discuss below.

To investigate their newly proposed airway hypothesis, i.e. that yawning evolved to secure long-term oxygenation, Doelman and Rijken conducted a literature search relating the frequency of yawning with obstructive airway conditions. In doing so, they find a total of 13 studies that align with predictions of their hypothesis. We, however, have serious concerns with regard to the methods Doelman and Rijken use in their analyses of the literature, specifically with regard to their exclusion criteria. In the methods section, Doelman and Rijken refer to two exclusion criteria based on "Determinant and Outcome 2". They state that any paper that did not find a change in yawning frequency, yet was related to obstructive airway conditions, was excluded. They also state that any paper that suggested confounding factors, which could be an alternative reason for an increase in yawn frequency, was also excluded. In doing

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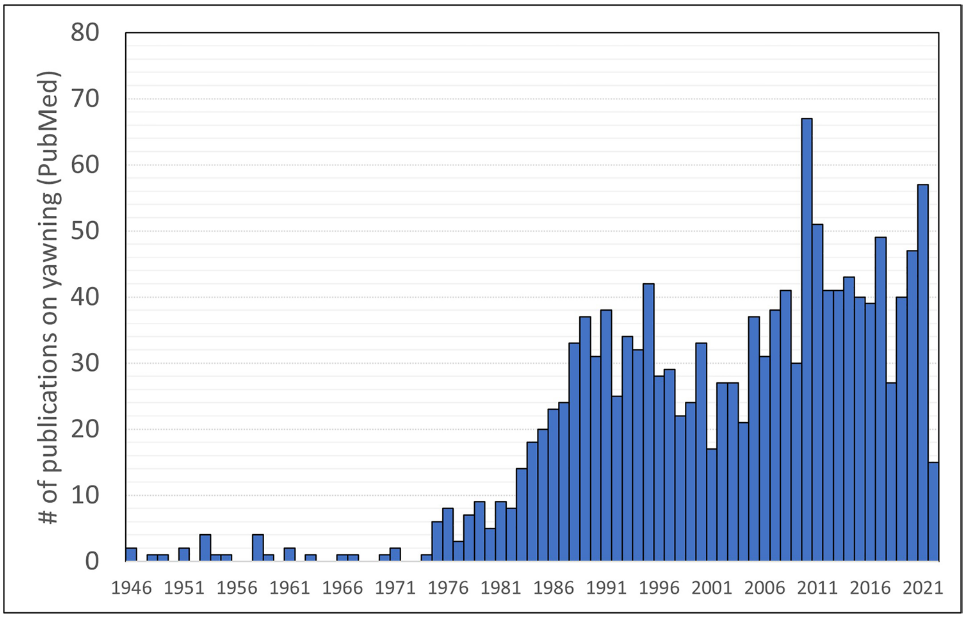

Fig. 1 Number of publications on yawning since 1946, based on PubMed search (24 Feb. 2022)

so, the authors admit that the research that either falsified their hypothesis or might have found proof for an alternative hypothesis was excluded.

Rightly so, the authors admit that their methods lack critical appraisal, and in the Discussion, they acknowledge the subjective nature of their exclusion criteria and the low level of evidence. However, this remains problematic. The scholarly literature on yawning is riddled with baseless hypotheses and unscientific proposals which only exacerbate the perceived lack of consensus in the field. As a result of these subjective exclusion criteria, the conclusions the authors draw from their results can be regarded biased and lacking rigor. A quick PubMed search on "obstructive airway conditions" alone results in 29,050 papers, suggesting that 29,038 papers do not report on such a temporal relationship, or given the exclusion criteria of Doelman and Rijken, report on opposing results. Consequently, the general results of the scoping review presented by Doelman and Rijken should be considered insignificant.

Doelman and Rijken acknowledge themselves how the temporal relations between yawning and obstructive airway should not be viewed as causal, and that the specific findings of the few studies that do align with their predictions are confounded by several factors. In particular, 11 out of the 13 total studies list sleepiness as a confounding variable. Perhaps the most well-documented feature of yawning is that it modulated by sleep/wake transitions and decrements in arousal/vigilance. As it specifically relates to the latter, Doelman and Rijken point out that seven of the articles that passed their exclusion criteria show an increase in yawn frequency during the induction of anaesthesia. Doelman and Rijken view anaesthesia solely as producing a collapse in the upper airway, and thus interpret these results as support for their hypothesis. However, anaesthesia induces other significant physiological changes that can also explain a rise in yawn frequency. Notably, anaesthesia triggers a progressive reduction in brain vigilance, which is a known trigger for yawning [6]. In fact, there is evidence that yawning during the induction of anaesthesia actually functions to counteract decrements in vigilance [7], which supports the arousal hypothesis.

Other features of the reviewed studies are problematic as well. For example, one study [8] reports on two cases of infants choking on food, and how this triggered repetitive yawning and other behaviors until all or part of the food was regurgitated. This, while a very interesting and thought-provoking set of cases, does not support a function in long-term oxygenation. If anything, it represents a short-term, acute, effect of airway physiology. Upon close inspection, another study fails to even measure yawning [9]. In addition, a case report of two women suffering from excessive bouts of yawning is included because one of them was diagnosed with sleep apnoea [10]. Doelman and Rijken take this as evidence for the positive association between obstructive airway and yawn frequency, but fail to acknowledge how the excessive yawning could not have been caused by sleep apnea since the other woman showed the same exact symptoms in the absence of this condition. Moreover, this case report provides a wealth of information demonstrating that both women suffered from thermoregulatory dysfunction and that their yawning frequency was effectively modified by methods of cooling/warming and conditions that modified brain and/or body temperature.

When researchers attempt to refute or discredit existing research while simultaneously presenting new functional accounts for a given phenomenon, as Doelman and Rijken

Table 1 Other documented effects that cannot be explained by the airway hypothesis

(1) The influence of nasal vs. oral breathing and carotid artery and forehead temperature on yawn frequency [23, 24]
(2) The link between yawn duration and brain size after accounting for body size [5]
(3) How chewing on gum decreases, rather than increases, yawning [25, 26]
(4) The connection between abnormal yawning and thermoregulatory dysfunction in the absence of breathing problem [27]
(5) Why there is a reduction in yawning frequency with senescence [28], as airway mechanics and lung function decline with age [29]
(6) The fact that fish, which have a completely different oxygenation system, also yawn [30]

do in their paper, a useful exercise is to examine how this new hypothesis can explain existing findings within the literature. For example, let us examine the relationship between yawning and ambient temperature. According to the brain cooling hypothesis, which remains the most empirically supported account of yawning (reviewed by [11], with responses to various critiques), the cooling function of yawning results in part from counter current heat exchange with the ambient air. Accordingly, yawn frequency is expected to be modulated by ambient temperature. As ambient temperatures rise above a thermal neutral zone, this should trigger compensatory cooling mechanisms, and yawning should therefore increase in frequency. However, as ambient temperatures continue to rise and begin to approach or exceed body temperature, yawning is expected to decrease as the deep inhalation of air at these temperatures would be counterproductive and fail to provide a cooling effect. Similarly, as ambient temperatures fall below a thermal neutral zone, cooling mechanisms would not be triggered, and thus, yawning should diminish. These ambient temperature predictions, collectively referred to as the thermal window model, are unique to the brain cooling hypothesis.

While Doelman and Rijken do not address the literature on yawning and ambient temperature and how it relates to their own hypothesis, the existing literature on the relationship between ambient temperature and airway obstruction allows us to derive some basic predictions. In general, decreases in temperature are associated with diminished lung function [12]. Studies show that cold temperatures increase airway obstruction and acute exacerbation, and lead to an overall decline in lung function among individuals with chronic obstructive pulmonary disease [13, 14]. Similarly, studies show that obstructive sleep apnoea is more severe at colder room temperatures [15], and scores on the apnea–hypopnea index are inversely correlated with ambient temperature [16]. Other studies have found decrements in pulmonary functioning at both high and low temperatures [17]. Thus, for warm temperatures, the predictions of the airway hypothesis might vary based on the condition and characteristics of the sample (e.g. old vs. young) and the range of temperature being assessed; in some cases, a decrease in yawn frequency might expected by the airway hypothesis, while in other cases an increase in yawn frequency might be expected. For colder temperatures, however, the prediction is clear: yawning should increase given the decline in lung function.

So how do these alternative hypotheses explain the findings pertaining to yawning and ambient temperature? In support of the brain cooling hypothesis, and contrary to what would be expected if yawning functioned to promote long-term oxygenation, the frequency of yawning shows an inverted U-shape with ambient temperature [18]. Yawning increases in frequency with initial rises in temperature outside a thermal neutral zone, but then begins to diminish in frequency as temperatures approach or exceed body temperature[19–22]. Moreover, at low temperatures, yawning decreases in frequency [18], despite decrements in airway obstruction at low temperatures. Collectively, these findings provide compelling support for the brain cooling hypothesis and are in contrast to what would be expected based on the airway hypothesis. Given the importance of ambient temperature on lung function [12], we can conclude that long-term oxygenation is not a main function of yawning.

Doelman and Rijken's hypothesis also fails to account for a number of other phenomena related to yawning. For brevity, we present these in Table 1.

Whereas we do not refute the predicted physical consequences of yawning and how associated muscle repositioning could widen the airway lumen, and we applaud Doelman and Rijken for providing such a nice overview of the physics involved in this process, any new hypothesis for why we yawn should be both supported by convincing evidence and account for existing phenomenon, at least as well as competing hypotheses. Based on the scoping review performed by Doelman and Rijken, we are skeptical of any proposed support for any long-term oxygenation effect, and as acknowledged by these authors, a function in short-term oxygenation has already been falsified [31]. Moreover, predictions derived from the airway hypothesis are not supported by the existing literature. In addition, this hypothesis fails to account for a number of documented effects on yawning. In sum, Doelman and Rijken provide speculations to account for some of the intraspecific variation observed regarding yawning frequencies of a few selected studies, which, to this point, do not improve our understanding of yawning nor of its evolutionary function.

References

1. Doelman CJ, Rijken JA (2022) Yawning and airway physiology: a scoping review and novel hypothesis. Sleep Breath *in press*.
2. Gallup AC (2022) The causes and consequences of yawning in animal groups. Anim Behav 187:209–219
3. Tinbergen N (1963) On aims and methods of ethology. Z Tierpsychol 20(4):410–433
4. Gallup AC, Meyers K (2021) Seeing others yawn selectively enhances vigilance: an eye-tracking study of snake detection. Anim Cogn 24(3):583–592
5. Massen JJM, Hartlieb M, Martin JS, Leitgeb EB, Hockl J, Kocourek M, Olkowicz S, Osadnik C, Verkleij JW, Zhang Y, Němec P, Gallup AC (2021) Brain size and neuron numbers drive differences in yawn duration across mammals and birds. Commun Biol 4(1):1–10
6. Guggisberg AG, Mathis J, Herrmann US, Hess CW (2007) The functional relationship between yawning and vigilance. Behav Brain Res 179(1):159–166
7. Kasuya Y, Murakami T, Oshima T, Dohi S (2005) Does yawning represent a transient arousal-shift during intravenous induction of general anesthesia? Anesth Analg 101(2):382–384
8. Evans EB (1978) Yawning in pharyngeal obstruction. BMJ 1(6110):443–444
9. Zaharna M, Rama A, Chan R, Kushida C (2013) A case of positional central sleep apnea. J Clin Sleep Med 9(3):265–268
10. Gallup GG, Gallup AC (2010) Excessive yawning and thermoregulation: two case histories of chronic, debilitating bouts of yawning. Sleep Breath 14(2):157–159
11. Gallup AC, Eldakar OT (2013) The thermoregulatory theory of yawning: what we know from over 5 years of research. Front Neurosci 6:188
12. Kang G, Zhang H (2019) The effects of temperature on lung function. Respir Care 64(11):1454–1454
13. Donaldson GC, Seemungal T, Jeffries DJ, Wedzicha JA (1999) Effect of temperature on lung function and symptoms in chronic obstructive pulmonary disease. Eur Respir J 13(4):844–849
14. Zhang Y, Liu X, Kong D, Fu J, Liu Y, Zhao Y, Yang J, Fan Z (2020) Effects of ambient temperature on acute exacerbations of chronic obstructive pulmonary disease: results from a time-series analysis of 143318 hospitalizations. Int J Chron Obstruct Pulmon Dis 15:213
15. Valham F, Sahlin C, Stenlund H, Franklin KA (2012) Ambient temperature and obstructive sleep apnea: effects on sleep, sleep apnea, and morning alertness. Sleep 35(4):513–517
16. Cassol CM, Martinez D, da Silva FABS, Fischer MK, Lenz MDCS, Bós ÂJG (2012) Is sleep apnea a winter disease? Meteorologic and sleep laboratory evidence collected over 1 decade. Chest 142(6):1499–1507
17. Lin Z, Gu Y, Liu C, Song Y, Bai C, Chen R, Chen S, Kan H (2018) Effects of ambient temperature on lung function in patients with chronic obstructive pulmonary disease: a time-series panel study. Sci Total Environ 619:360–365
18. Massen JJM, Dusch K, Eldakar OT, Gallup AC (2014) A thermal window for yawning in humans: yawning as a brain cooling mechanism. Physiol Behav 130:145–148
19. Gallup AC, Miller ML, Clark AB (2009) Yawning and thermoregulation in budgerigars. Melopsittacus undulatus Anim Behav 77(1):109–113
20. Gallup AC, Miller ML, Clark AB (2010) The direction and range of ambient temperature change influences yawning in budgerigars (Melopsittacus undulatus). J Comp Psychol 124(2):133
21. Gallup AC, Miller RR, Clark AB (2011) Changes in ambient temperature trigger yawning but not stretching in rats. Ethology 117(2):145–153
22. Eldakar OT, Dauzonne M, Prilutzkaya Y, Garcia D, Thadal C, Gallup AC (2015) Temperature-dependent variation in self-reported contagious yawning. Adapt Hum Behav Physiol 1(4):460–466
23. Gallup AC, Gallup GG Jr (2007) Yawning as a brain cooling mechanism: nasal breathing and forehead cooling diminish the incidence of contagious yawning. Evol Psychol 5(1):92–101
24. Ramirez V, Ryan CP, Eldakar OT, Gallup AC (2019) Manipulating neck temperature alters contagious yawning in humans. Physiol Behav 207:86–89
25. Gallup AC (2020) Chewing on gum alleviates chronic bouts of excessive yawning. Hum Ethol 35:67–74
26. Gallup AC, Engert K (2019) Chewing on gum alters the expression of contagious yawning. Hum Ethol 34:93–103
27. Gallup AC, Gallup GG Jr (2008) Yawning and thermoregulation. Physiol Behav 95(1–2):10–16
28. Zilli I, Giganti F, Uga V (2008) Yawning and subjective sleepiness in the elderly. J Sleep Res 17(3):303–308
29. Kim J, Heise RL, Reynolds AM, Pidaparti RM (2017) Aging effects on airflow dynamics and lung function in human bronchioles. PLoS ONE 12(8):e0183654
30. Baenninger R (1987) Some comparative aspects of yawning in Betta splendens, Homo sapiens, Panthera leo, and Papio sphinx. J Comp Psychol 101(4):349
31. Provine RR, Tate BC, Geldmacher LL (1987) Yawning: no effect of 3–5% CO2, 100% O2, and exercise. Behav Neural Biol 48(3):382–393