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Animal behaviour

Yawn duration predicts brain weight and cortical neuron number in mammals

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Research indicates that the motor action pattern of yawning functions to promote cortical arousal and state change through enhanced intracranial circulation and brain cooling. Because the magnitude of this response likely corresponds to the degree of neurophysiological change, we hypothesized that interspecies variation in yawn duration would correlate with underlying neurological differences. Using openly accessible data, we show that both the mean and variance in yawn duration are robust predictors of mammalian brain weight and cortical neuron number (ρ-values > 0.9). Consistent with these effects, primates tend to have longer and more variable yawn durations compared with other mammals. Although yawning has long been considered a stereotyped action pattern, these findings reveal substantial variation in this response and highlight the importance of measuring yawn duration in future research.

1. Background

Yawning is characterized by a powerful gaping of the jaw with inspiration, a brief period of peak muscle contraction and a passive closure of the jaw with shorter expiration [1]. Yawn-like mandibular gaping patterns have been identified across vertebrate classes [2], though it remains unknown whether the jaw stretching observed in fish, amphibians and reptiles functions in the same way as yawns in birds and mammals [3]. Nonetheless, the relative ubiquity of this response in vertebrates suggests it is an evolutionarily conserved behaviour that holds basic and important adaptive value. Although the function to yawning remains debated [3–6], previous research supports a role in promoting cortical arousal and state change [7–11] through enhanced intracranial circulation and brain cooling [12–13].

Yawning is controlled by several neurotransmitters and neuropeptides [14] and has been linked with numerous neurological diseases and clinical conditions [15–16]. Despite the potential applications of studying differences in yawning as a marker of neural processing, variation in this response has yet to be fully explored. Naturalistic reports on the frequency of yawning across taxa are quite limited [17,18], and yawns have long been considered a stereotyped action pattern with limited variation in expression within or between species [8]. However, recent studies on non-human primates have identified previously overlooked variation in the mouth aperture associated with yawning, and it has been shown that different forms of yawning tend to correspond to distinct contexts and situations [18,19].

Another measure of variability that could be easily catalogued across species is the duration of yawning. Although early research examined average yawn duration in humans (approx. 6 s) [8], this variable has not been used in studies of non-human animals. Given that the primary circulatory effects associated with yawning are localized within the skull, differences in the duration or magnitude of this response likely correspond to the degree of neurophysiological change. Therefore, we hypothesize that differences in yawn duration will correlate with neurological variation between species.

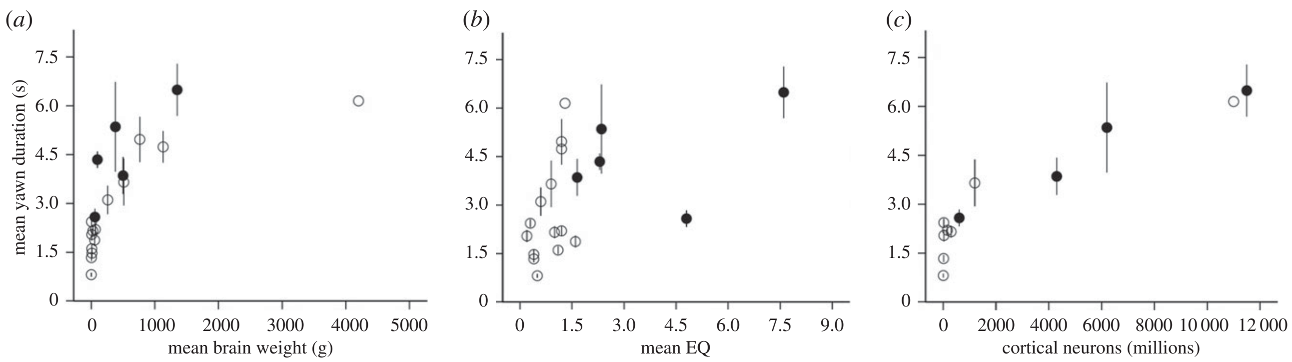

Figure 1. Average yawn duration (mean ± s.e.m.) in mammals is highly correlated with (*a*) brain weight, (*b*) EQ and (*c*) cortical neuron number. Filled circles represent primate taxa. (*a*,*b*) Taxa in order of average yawn duration: mouse; rat; rabbit; squirrel; fox; possum; cat; dog; hedgehog; white-fronted capuchin; lion; horse; gorilla; gibbon; walrus; camel; chimpanzee; African elephant; human. (*c*) Taxa in order of average yawn duration: mouse; rat; possum; cat; dog; hedgehog; white-faced capuchin; horse; gorilla; chimpanzee; African elephant; human. Note: variance is not available for African elephants.

Here, we examine this possibility by linking openly accessible videos of yawning from the Internet (primarily from www.youtube.com) to previously published brain parameters in a representative sample of mammalian taxa [20]. Based on previous research supporting a neurophysiological function to yawning, we hypothesized that mammals with larger brains would yawn longer, even when controlling for body size, and that yawn duration would correlate with number of cortical neurons.

2. Methods

The Roth & Dicke [20] paper on mammalian brain evolution and intelligence was used as a guide for identifying yawns across a representative sample of mammalian taxa [20]. This publication provides average brain weight, encephalization quotient (EQ) and cortical neuron number (where applicable) for 29 selected mammalian taxa (see [20] p. 251, table 1). Using this list, one researcher attempted to find up to a dozen individuals yawning from each mammalian taxa (though this number was only achieved for humans) by using openly accessible video clips from the Internet. This resulted in primarily accessing www.youtube.com, along with the video search tool on www.google.com. Once a video was identified, the researcher noted the time(s) at which the yawn(s) on the clip occurred and the duration of all yawning events using the operational definition provided by Barbizet [1] to the nearest 0.01 s using the stopwatch feature on an iPhone. When possible, the researcher also noted for each yawn whether the animal was an adult or subadult. In order to obtain inter-rater reliability on yawn duration, a second research assistant who was blind to the hypothesis was provided with the same list and set of instructions, but in this case was asked to identify only two to three yawns from each taxon. As expected, this additional search resulted in a significant overlap in the videos initially identified (37.7%). Both researchers also independently scored an additional set of seven videos, and the overall inter-rater reliability for yawn duration for video clips scored by both research assistants was very high ($r = 0.960$). A third researcher then confirmed all yawns from both searches.

The average yawn duration was calculated for each taxon by summing all the respective durations from that group and dividing by the number of yawners. In cases where the same individual displayed multiple yawns in a given video, the average duration for this animal was used as a single data point when generating the overall average for that taxon to avoid pseudo-replication. One video with multiple yawning clips from a litter of kittens was excluded owing to the inability to distinguish between individuals. There were also nine cases where the start or end of the yawn was not clear (e.g. video began when the animal was already yawning, the animal was looking away during the execution of the yawn or there was no clear endpoint to identify), and these were removed from the analysis. In addition, there were a total of five videos with URLs that were no longer available on www.youtube.com, and thus could not be confirmed and were removed. Lastly, two videos that were duplicates with different URLs (one rat, one chimpanzee) were also removed from the analysis. In total, 205 full yawns were confirmed from 177 individuals across the following 24 taxa (see supplementary material for URLs and full dataset): African elephant (1), camel (5), capuchin monkey (1), cat (9), chimpanzee (9), dog (12), fox (10), gibbon (6), gorilla (7), hedgehog (12), horse (7), human (27), lion (7), marmoset (3), mouse (6), opossum (9), rabbit (12), rat (13), rhesus monkey (2), sheep (3), squirrel (8), squirrel monkey (1), walrus (4) and white-fronted capuchin (3). In addition, the overall mean yawn duration from nine African elephants was provided from the lead investigator of an ongoing study (Ben Hart 2016, personal communication).

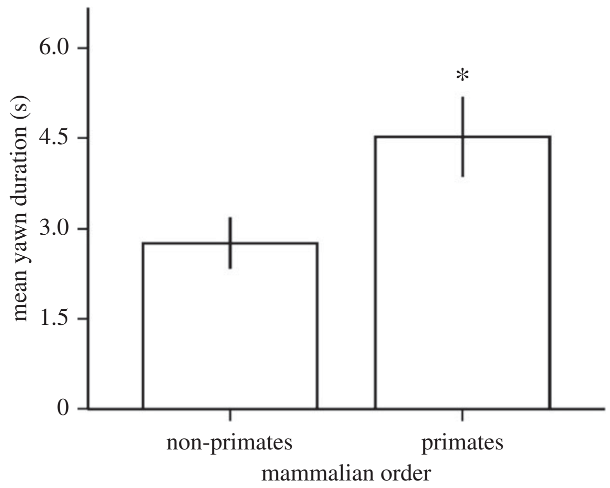

Figure 2. Bar graph compares the average yawn durations (mean ± s.e.m.) of primates and other mammals.

The taxon averages for yawn duration were then linked to the brain weight, EQ and cortical neuron data [20]. In cases where ranges were applied for brain weight and EQ, the average of the ranges was used. Standard error of mean (s.e.m.) duration

Table 1. Suggested research topics related to yawn duration, cognition and neural processing.

• Investigate whether yawn duration predicts similar neurological parameters in other vertebrates
• Examine how variation in more specific neuroanatomical structures predicts yawn duration across different species
• Explore whether differences in yawn duration predict variability in brain size and neuroanatomy within a species
• Investigate whether within-species variability in yawn duration correlates with measures of cognitive ability
• Determine whether within-subject yawn duration varies as a function of cognitive load or cortical arousal
• Explore whether within-subject variability in yawn duration follows a circadian pattern
• Examine whether variation in yawn duration correlates with changes in neural activity (EEG) in humans
• Explore whether yawn duration differs within human populations with reduced brain/cognitive functioning
• Determine whether spontaneous and contagious yawns vary in duration or magnitude
• Investigate how yawn duration varies across the lifespan*

*Note: Analyses in the electronic supplementary material begin to address this question.

was used as a measure of variance. Owing to the non-normal distribution of all variables of interest (as measured by skewness and kurtosis), a non-parametric Spearman's correlation was used to assess the linear relationships. Given notable differences in brain size and cortical neuron number among primates, a Mann–Whitney test was used to compare average yawn durations and s.e.m. of yawn duration between primates and other mammals. Because brain parameters were based on adult averages, analyses below were performed using only taxa with at least three representative adult yawns. This reduced the original sample from 24 to 19 taxa and from a combined 186 to 109 individual data points. Importantly, however, none of the following results change when including the remaining taxa with fewer than three adult yawns, combining all adult and subadult data or just using subadult data (see electronic supplementary material).

3. Results

Analyses revealed that average yawn duration is a robust predictor of brain size and cortical neuron number across mammals. In particular, average yawn duration was highly correlated with brain weight ($\rho_{19} = 0.911$, $p < 0.001$; figure 1*a*), and this relationship remained significant after taking into account relative brain size (EQ) ($\rho_{19} = 0.651$, $p < 0.005$; figure 1*b*). Yawn duration was also highly correlated with the number of cortical neurons between taxa ($\rho_{12} = 0.951$, $p < 0.001$; figure 1*c*). The steepest rises in yawn duration (approx. 0.8–2.6 s) occurred within a narrow range of brain weight and cortical neuron number (approx. 0.3–60 g; 4–600 million), with a comparatively smaller difference in duration observed for larger brain masses and cortical neurons (60–4200 g; 600–11 500 million). As expected from these overall relationships, yawns from primates were significantly longer than from other mammals ($Z = 2.129$, $p < 0.05$; figure 2).

Furthermore, within-taxon variance in yawn duration was highly correlated with mean duration ($\rho_{18} = 0.902$, $p < 0.001$) and all three neurological parameters (brain weight: $\rho_{18} = 0.921$, $p < 0.001$; EQ: $\rho_{18} = 0.632$, $p < 0.005$; cortical neurons: $\rho_{11} = 0.966$, $p < 0.001$). Similarly, variance in yawn duration was higher for primates compared with other mammals ($Z = 2.224$, $p < 0.05$). Importantly, within-taxon variance in yawn duration was not related to taxon sample size ($\rho_{18} = 0.057$, $p = 0.821$) and therefore does not reflect sampling error.

4. Discussion

Although yawning has been considered a stereotyped action pattern [8], we document substantial variation in the duration of this response in mammals. In particular, we found that both the mean and variance in yawn duration are robust predictors of brain weight and cortical neuron number (ρ-values > 0.9). Consistent with these results, we also found that primates tend to have longer and more variable yawn durations compared with other mammals. These results apply irrespective of variation in the mouth aperture of yawns in some non-human primates [18,19].

These combined effects represent a striking scaling relationship between brain and behaviour. Importantly, neither the size of the body nor the anatomical structures specific to yawning (cranium and mandible) are driving these effects, because gorillas, camels, horses, lions, walruses and African elephants all have shorter average yawns than humans. Furthermore, having a larger skull does not necessitate more variable motor pattern duration. Instead, differences in yawn duration appear to be specifically linked to interspecies variation in brain size and complexity, with cortical neuron number being the most significant factor. Future research should investigate whether mean and variation in yawn duration also predict similar brain parameters recently documented across avian taxa [21].

These findings are consistent with the view that yawning holds a basic neurophysiological function. In particular, previous research suggests that yawning is an adaptation to enhance intracranial circulation and brain cooling [11–13], which in turn could promote cortical arousal and state change [7–9]. While the neural structures necessary for yawning appear to be located within the brainstem [22], based on these results, we hypothesize that the neurophysiological consequences of yawning affect the brain more globally, whereby longer yawns may be necessary to more effectively modulate cortical arousal for animals with larger and more complex brains. Furthermore, we predict that the greater within-taxon variance in yawn duration observed for large-brained mammals may be related to increased cognitive capacities and more variable behavioural repertories. We note that while a primarily social/communication (i.e. signalling) function to yawning has been posited [4], it is unclear how such an explanation would account for the current effects.

Provine [8, p. 120] stated, 'yawning may have the dubious distinction of being the least understood, common, human behavior'. Unfortunately, 30 years later, we still know relatively little about the biological significance of this evolutionarily conserved response. The difficulty in uncovering the ultimate function(s) of yawning may, in part, be owing to the fact that it can be elicited by numerous stimuli and researchers have by and large overlooked subtle distinctions in the expression of this behaviour. Based on the current findings, we believe yawn duration deserves further attention. We close by offering suggestions for future research in this area (table 1).

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material.

Ethics. No ethics approval was required for this research.

Authors' contributions. A.C.G. conceived of the study, designed the study and performed the analysis. A.M.C. and A.J.P. performed the data collection. A.C.G., A.M.C. and A.J.P. contributed to the writing of this manuscript, approved the final version, and agreed to be accountable for all aspects of the work.

Competing interests. We have no competing interests.

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