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Contagious Yawning

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Synonyms

Chasm; Gap

Definition

The yawn is a stereotyped and often repetitive motor act characterized by gaping of the mouth accompanied by a long inspiration of breath, a brief acme, and then a short passive expiration of breath.

> . . .seeing a dog and horse and man yawn, makes me feel how much all animals are built on one structure.
> Charles Darwin, 1838 notebook.

Introduction

Yawning is a universal everyday behavior shared by all vertebrate species. It is a stereotyped and often repetitive involuntary motor act characterized by gaping of the mouth and accompanied by a long inspiration of breath, a brief acme, and then a short expiration of breath. Yawning is not merely a simple opening of the mouth but a complex, coordinated movement involving a flexion followed by an extension of the neck and a wide dilatation of the pharyngo-larynx with strong stretching of the diaphragm and antigravity muscles (Provine 1986). Contagious yawning is the urge to yawn when thinking about, listening to, reading about, hearing, or viewing yawning. Ethologists use a better word, i.e., replication, or behavioral mimicry, whereas neurologists refer to echokinesis, a term coined by Jean-Martin Charcot (1825–1893). The widespread familiarity of contagious yawning is due in part to the fact that almost everyone has experienced the phenomenon and it occurs seemingly without volition. This behavior is well documented in humans; however, its function and prevalence in the animal kingdom and the brain mechanisms underlying it are only beginning to be understood.

Behavioral Framework

Yawning is morphologically similar in reptiles, birds, mammals, and fish, and no environmental input changes the sequence of movements (Walusinski and Deputte 2004). This behavior may be an ancestral vestige maintained throughout evolution with little variation, bearing witness to the early phylogenetic origins of yawning. Like any phylogenetically old behavior, yawning can be observed early in ontogeny, that is, at 12 weeks of fetal life in humans (Walusinski 2012). Behavioral and neurophysiological studies

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provide converging evidence that yawning occurs preferentially during rest, periods of drowsiness, and awakening. Hunger and satiety also trigger yawning. The frequency of yawning has a distinctive circadian distribution and occurs most frequently before and after sleep, that is, during periods of lower levels of vigilance and alertness (Fica and Salzarulo 2002; Walusinski and Deputte 2004).

When animals transition between behaviors, they are not merely responding in a passive way to the conditions of the environment, such as day-night succession. Rather, they are following internally generated signals produced by homeostatic processes originating in the hypothalamus (suprachiasmatic nucleus and paraventricular nucleus of the hypothalamus, where yawning is triggered). The resultant internal rhythm allows for the anticipation of transitions and triggers behavioral and physiological changes in accordance with those transitions. This results in two advantages: predictability and the possibility to detect the unexpected. Similar to sleep and hunger, yawning functions in this way and appears to be associated with transitions between periods of high and low activity or arousal. This universal form of yawning is internally elicited (Gupta and Mittal 2013; Krestel et al. 2018).

But other, externally elicited forms of yawning exist. Among mammals, morphologically identical yawns occur in situations relative to stress, social interactions, and sexuality (Kubota et al. 2014). Contagious yawning is a form of social interaction without language, triggered involuntarily. Nonconscious mimicry ("chameleon effect") refers to an individual's tendency to imitate a social partner's behaviors without either party's awareness or intent.

Yawning in the Animal Kingdom

Yawning conveys information to other conspecifics about dominance, state of arousal or tiredness, anxiety, or fear. The combinations of different types of signals (visual, acoustic, and olfactory) establish the interaction in either conspecifics or human counterparts. Indeed, a cross-species chameleon effect or contagiousness has now been documented for yawning between dogs and humans (Buttner and Strasser 2014; Harr et al. 2009). In nonhuman primates, teeth-bearing during yawning has led to the suggestion that this behavior reinforces dominant identity rather than signaling a threat (Deputte 1994). Accordingly, yawning has been compared with intimidating displays that dominant males usually show to subordinate males to display their dominant status. Chimpanzees, like humans, differ from Old World monkeys in that yawning by adult males is not a form of ritualized display expressed in situations of male-male confrontation.

Other ethological studies propose that yawning might induce relaxation of social tension and thus be a displacement activity, considered to indicate changes in behavioral state for the yawner and simultaneously to operate as a physiological capacity signal. In Sprague-Dawley rats, yawning associated with penile erections suggests that yawning behavior arises from the ritualization of pre-existing cues involved in perception of stimulating chemo-signals in a mating context (Moyaho et al. 2015).

Contagious Yawning

Contagious yawning has been observed in nonhuman primates (chimpanzees, bonobos, stump-tailed macaques, gelada baboons, and common marmosets) (Demuru and Palagi 2012; Palagi et al. 2009), in dogs (Harr et al. 2009), in wolves (Romero et al. 2014), in sheep (Yonezawa et al. 2017), in budgerigars, the only non-mammalian specie (Gallup et al. 2015), in rats (Moyaho et al. 2015), and in elephants (Rossman et al. 2017), but not in lemurs (Reddy et al. 2016) and tortoises (Huber and Wilkinson 2011). No data are available for other species. Animal studies have reported low levels of contagious yawning in dogs, significantly lower than 33%, the rate observed in chimpanzees (Harr et al. 2009). Contagious yawning seems to be more easily triggered when models are conspecifics or have a strong social bond with the observer. The

individuals that are more "reactive" when watching yawning of conspecifics are not more reactive when exposed to other behaviors (Anderson and Matsuzawa 2006).

Observational surveys and experimental analysis of contagious yawning in humans has revealed occurrence in 65%–75% of the entire population. There is still no consensus as to whether women exhibit more contagious yawning than men (Gallup and Massen 2016). At any rate, individuals who conform spontaneously to normative social influence, and who are most receptive to advertising messages, also appear most susceptible to contagious yawning. People who scored higher on measures of empathy and mental state attribution skills were more likely to show contagious yawning (Palagi et al. 2014). These observational data, among others, are produced for linking contagious yawning and empathy.

How is contagious yawning triggered? Sight is a powerful stimulant. In spectators viewing a video showing 30 successive yawns, 55% will yawn within 5 min. The latency period varies from a few seconds to 5 min. There is no need for the face of the yawner to be in a precise visual plane relative to the subject receiving the contagion. Face to face, at 90°, 180°, and 270° relative to one another, replication occurs. The existence of a susceptibility to contagion among blind subjects confirms that sight is not the only trigger. Viewing only part of the face, such as a widely opened mouth, does not trigger replication. Therefore, a multimodal perception of the whole facial configuration and of audible respiratory moments is necessary for replication to happen, along with coordinated dynamics (Provine 1989). By animals as by humans, individual yawning in response to perceiving someone else yawn varies as a function of a host of variables that have yet to be clarified.

The Neural Basis for Contagious Yawning

Contagious yawning is a primitive expression of cognitive processes involved in self-awareness and theory-of-mind, that is, the capacity to build knowledge of mental states and to attribute them to others. In humans, contagious yawning first appears around 5 years of age, probably linked to the acquisition of a theory-of-mind. Humans who performed better at self-recognition and theory-of-mind exhibited more contagious yawning (Senju 2010). Yawning operates as a low-level form of nonconscious mimicry, which is necessary for involuntarily decoding the mental states of others, notably their emotions. The link between empathy and contagious yawning has empirical support but remains controversial (Massen and Gallup 2017). In line with this possible association, the empathic modeling hypothesis predicts that species that do not recognize themselves in mirrors and do not show evidence of mental state attribution ought to fail to show evidence of contagious yawning (de Waal and Preston 2017; Provine 2012).

Both developmental and neurophysiological research suggests that resonance between observed and executed actions is supported by the mirror neurons system (MNS). Brain areas that constitute the MNS, namely, the premotor area in the frontal lobe, the inferior parietal lobule, and the superior temporal sulcus, participate in the imitation of motor acts and expressions. These human mirror regions are homologous with area F5 of the ventral premotor cortex in macaques (Rizzolatti 2005). These regions are also interconnected with the insula and show activation in functional MRI studies of imitation, emotional states, and thus, empathy (Anderson and Matsuzawa 2006). The ventromedial prefrontal cortex also integrates affective signals to guide emotionally adapted behaviors. Thus, motor acts and affective states can transfer from a target to an observer in a bottom-up, goal-relevant manner through shared representations for perception and action. In this way, observing an affective posture or expression drives feed-back from peripheral motor representations to activate associated emotional states. Contagious yawning recruits brain areas that have been implicated in social cognition (empathy), self-processing, theory-of-mind, and emotional contagion mechanisms (motor mimicry-MNS). Contagious yawning is the most basic expression of motor mimicry and emotional

contagion, a rudimentary form of involuntary empathy (Brown et al. 2017; de Waal and Preston 2017). Whatever underlies contagious yawning, it does not appear to be based either on conscious imitation or higher-level, "conscious" empathy. Regardless, contagious yawning presents a powerful tool to explore the root of empathy in animal evolution (Provine 2014).

An Error to Avoid

Equating physiological and communicative functions of yawning with non-social and social contexts, respectively, is inaccurate as both forms may occur in a social context. Indeed, ethological studies of nonhuman primates or South-African ostriches, for example, show that, at certain points, an entire group yawns. In this case, there is no contagious yawning but a synchronous behavior related to circadian rest-activity rhythms.

Conclusion

Contagious yawning is an example where, through evolution, a behavior can be recycled for different purposes according to the increasing complexity of the central nervous system, correlated with the richness of social interactions. Yawning is managed by the phylogenetically oldest part of the brain, namely, the diencephalon and brainstem. Contagious yawning occurs by neocortex activation, which is necessary for the complex interactions of social life between individuals. It remains to be seen whether contagious yawning has any effect on the activity levels of other group members. Further research, especially in wild populations, should examine the regulating effect of yawning on synchronized group behavior in order to test its communicative function. Contagious yawning offers a neglected but fruitful avenue of investigation in the growing fields of developmental, affective, and social neuroscience.

Cross-References

- ▶ Contagion
- ▶ Emotional Contagion
- ▶ Empathy
- ▶ Grooming
- ▶ Imitation
- ▶ Sleep

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Further Reading

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