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Why contagious yawning does not (yet) equate to empathy

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Highlights:

1 Contagious yawning has been linked with empathy

2 Evidence supporting this connection is inconsistent and inconclusive

3 More controlled studies are needed to explicitly test this association

Abstract:

Various studies and researchers have proposed a link between contagious yawning and empathy, yet the conceptual basis for the proposed connection is not clear and deserves critical evaluation. Therefore, we systematically examined the available empirical evidence addressing this association; i.e., a critical review of studies on inter-individual differences in contagion and self-reported values of empathy, differences in contagion based on familiarity or sex, and differences in contagion among individuals with psychological disorders, as well as developmental research, and brain imaging and neurophysiological studies. In doing so, we reveal a pattern of inconsistent and inconclusive evidence regarding the connection between contagious yawning and empathy. Furthermore, we identify study limitations and confounding variables, such visual attention and social inhibition. Future research examining links between contagious yawning and empathy requires more rigorous investigation involving objective measurements to explicitly test for this connection.

Keywords:

Yawning; contagious yawning; empathy; emotional contagion; attentional biases; neuroimaging

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1. INTRODUCTION

1.1. Yawning

Yawning is characterized by a powerful gaping of the jaw with deep inspiration, followed by a temporary period of peak muscle contraction with a passive closure of the jaw during expiration (Barbizet, 1958). Yawns are not under conscious control and, once initiated, go to completion with minimal influence of sensory feedback (Provine, 1986). Yawns have a more complex spatio-temporal organization than simple reflexes, and activate disparate physiological systems. In humans, yawns produce extended stretching of the orofacial musculoskeleton; are accompanied by head tilting, eye closure, tearing, salivating, and opening of the Eustachian tubes in the middle ear; and generate significant cardiovascular changes (Provine, 2012).

Yawning appears to be a universal human act that occurs throughout the lifespan, with an average duration of between four and seven seconds per yawn (Askenasy, 1989; Baenninger and Greco, 1991; Barbizet, 1958; Gallup et al., 2016; Provine, 1986). Self-report studies indicate that people yawn between six and 23 times per day, which depends upon an individual's circadian rhythm or chronotype (Baenninger et al., 1996; Provine et al., 1987a; Zilli et al., 2007). Evolutionarily conserved, yawning or a similar form of mandibular gaping behavior has been observed in all classes of vertebrates (Baenninger, 1987; Craemer, 1924; Gallup et al., 2009; Luttenberger, 1975). As further evidence that yawns are most probably phylogenetically old, ontogenetically this response occurs as early as 11 weeks gestation in humans (de Vries et al., 1982).

While the neural structures necessary for yawning appear to be located within the brainstem (Heusner, 1946), a recent case study demonstrated that electrical stimulation of the putamen, which has extensive connectivity between the brain stem and cortical regions, induces yawning in humans (Joshi et al., 2017). Pharmacological research on non-human animals indicates yawning is under the control of several neurotransmitters and neuropeptides in the paraventricular nucleus (PVN) of the hypothalamus; yawning is induced by dopamine, nitric oxide, excitatory amino acids, acetylcholine, serotonin, adrenocorticotropic hormone-related peptides, and oxytocin, and is inhibited by opioid peptides (Argiolas and Melis, 1998; Daquin et al., 2001). A more recent review has identified at least three distinct neural pathways involved in the induction of yawning, all of which converge on the cholinergic neurons within the hippocampus (Collins and Eguibar, 2010). Abnormal or frequent yawning is also symptomatic of numerous pathologies, including migraine headaches, stress and anxiety, head trauma and stroke, basal ganglia disorders, focal brain lesions, epilepsy, multiple sclerosis, schizophrenia, sopite syndrome, and even gastro-intestinal and some infectious diseases (reviewed by Daquin et al., 2001; Gallup and Gallup, 2008; Walusinski, 2010). The multifaceted motor expression and activation of yawning suggests it has a fundamental neurophysiological significance. Consistent with this view, recent comparative research demonstrates that yawn duration is robustly correlated with average brain weight and cortical neuron number across mammals (Gallup et al., 2016).

Attempts to identify the physiological function of yawning provides little consensus. Yawning has been hard to characterize functionally, primarily because there are numerous eliciting stimuli. Smith (1999) outlined over 20 functional hypotheses for why we yawn; however, few have received empirical support. Hypotheses range from increasing alertness (Baenninger and Greco, 1991; Baenninger et al., 1996), to inducing relaxation of social tension in groups (Sauer and Sauer, 1967), and to aiding in the removal of potentially infectious substances from the tonsils (McKenzie, 1994). Yawning has also been thought to be an indicator of hemorrhage (Nash, 1942), motion sickness (Graybiel and Knepton, 1976), encephalitis (Wilson, 1940), and rises in cortisol (Thompson, 2011).

One of the most well documented features of yawning relates to its circadian variation. In humans, yawning occurs with greatest frequency within the hours just after waking and right before sleeping (Baenninger et al., 1996; Giganti and Zilli, 2011; Provine et al., 1987a; Zilli et al., 2007), and this response follows a circadian pattern in other animals as well (Anias et al., 1984; Miller et al., 2012a; Zannella et al., 2015). Consistent with this evidence, it has long been suggested that yawns are representative of boredom, drowsiness, and fatigue (Barbizet, 1958; Bell, 1980; Suganami, 1977); yet, it is hard to reconcile these views with observations of Olympians yawning immediately prior to competition, musicians yawning while waiting to perform, and paratroopers yawning excessively leading up to their first free-fall (Provine, 2005). Despite the temporal association with sleep, and the fact that yawning frequency is positively correlated with subjective ratings of sleepiness throughout the day (Giganti and Zilli, 2011), the frequency of yawning is not significantly correlated to wakeup time, sleep time, or sleep duration (Baenninger et al., 1996; Zilli et al., 2007). In fact, subjective ratings of sleepiness account for less than 30 percent of the variance in spontaneous yawning frequency (Giganti and Zilli, 2011). Therefore, while the yawn/sleep relationship is significant, yawns are not simply signals of sleepiness or fatigue.

Due to the overt respiratory component of yawning, one commonly held belief is that yawns function to equilibrate oxygen levels in the blood (e.g., Askenasy, 1989). Despite the widespread acceptance of this hypothesis among both the layperson and medical physicians (Provine, 2005), it was tested and subsequently falsified 30 years ago. Provine et al. (1987b) demonstrated that neither breathing pure oxygen nor heightened levels of carbon dioxide increased yawning frequency in human participants, though each significantly increased breathing rates. It was also demonstrated in this report that physical exercise sufficient to double breathing rates had no effect on yawning. Therefore, contrary to popular belief, yawning and breathing are controlled by separate mechanisms (Provine et al., 1987b).

Instead, the powerful gaping of the jaw appears to be the most important feature of this motor action pattern. Patients who cannot voluntarily open their mouth due to tetraplegia, for example, have been reported to extensively gape their jaws during yawning (Bauer et al., 1980; Geschwend, 1977), suggesting that the mandibular muscular contractions are essential for the proper function of this response. The importance of jaw stretching is also evidenced by the fact that people asked to clench their teeth while yawning report feeling left in mid-yawn, or being unable to experience the relief of completing a yawn (Provine, 1986). Similarly, clenched teeth yawns are perceived as unpleasant compared to positive hedonistic effects attributable to normal, uninhibited yawns.

To date, the comparative research supports a role of yawning in promoting state change (e.g., but not limited to, sleep/wake state changes) and cortical arousal. Provine (1986) first proposed the state change hypothesis based on observations that yawning was associated with numerous behavioral transitions. The general hypothesis was then extended to suggest that yawning facilitates a number of behavioral shifts such as from boredom to alertness, changes from one activity to another, and, importantly, between sleeping and waking (Provine, 1996, 2005). Consistent with this hypothesis, a large body of comparative research aligns with the view that yawning functions to stimulate or facilitate arousal during environmental transitions (reviewed by Baenninger, 1997). In support of this, yawning occurs in anticipation of important events and during behavioral transitions across vertebrate taxa. Baenninger (1997) also summarizes evidence from endocrine, neurotransmitter, and pharmacological studies that supports the view that yawning is an important mediator of arousal levels. Accordingly, it has been proposed that the adaptive function of yawning is to modify levels of cortical arousal. A recent reformulation of this idea proposes that yawns activate the attentional network of the brain (Walusinski, 2014). This notion is supported by research on humans, chimpanzees, and laboratory rats, showing that yawns reliably precede increases in activity (Anias et al., 1984; Baenninger et al., 1996; Giganti et al., 2002; Vick and Paukner, 2010). Individual variation in total yawn frequency per day among humans has also been linked to activity levels (Baenninger et al., 1996). People who are active, for example, tend to yawn less frequently than those who are less active. Also consistent with the view that yawning produces an arousing effect, yawns are common following stressful events, threats, and increases in anxiety (e.g., Eldakar et al., 2017; Liang et al., 2015; Miller et al., 2010; Miller et al., 2012b). In addition, numerous studies have revealed that yawning is associated with hormonally-induced penile erection (reviewed by Baenninger, 1997), a well-defined indicator of sexual arousal.

Further evidence for an arousing effect of yawning comes from various neurophysiological studies. For example, yawning in humans has been shown to produce significant changes in heart rate and skin conductance (Greco and Baenninger, 1991; Guggisberg et al., 2007), as well as sympathetic nerve activity (Askenasy and Askenasy, 1996). Research has shown that arousal responses in laboratory rats, as measured by electrocorticogram, are accompanied by yawning behavior following electrical, chemical, and light stimulation of the PVN of the hypothalamus (Kita et al., 2008; Sato-Suzuki et al., 1998, 2002; Seki et al., 2003). Furthermore, yawning is a common response among patients undergoing anesthesia (Kim et al., 2002), and actually produces a transient arousal shift as measured by electroencephalographic (EEG) bispectral index (Kasuya et al., 2005). This result has been interpreted as yawning representing a mechanism to enhance arousal during the progressive loss of consciousness caused by induction of anesthesia. It should be noted, however, that other studies have failed to show yawn-associated increases in cortical arousal as measured by EEG (see Guggisberg et al., 2010).

One mechanism by which yawns facilitate state change and arousal appears to be through enhanced intracranial circulation. Generally, yawning produces global increases in heart rate (Corey et al., 2011; Heusner, 1946) and blood pressure (Askenasy and Askenasy, 1996), and the jaw stretching and deep inhalation accompanying yawning produces profound intracranial circulatory alterations (Provine, 2012; Walusinski, 2014). The constriction and relaxation of facial muscles during a yawn increase facial blood flow, which, in turn, increases cerebral blood flow (Zajonc, 1985). The deep inspiration during yawning also produces significant downward flow in cerebrospinal fluid and an increase in blood flow in the internal jugular vein (Schroth and Klose, 1992). The pterygoid plexus, a network of small veins within the lateral pterygoid muscle activated by yawning, operates as a "peripheral pump" that aids venous return by the pumping action of the pterygoid muscle during yawning (Sinnatamby, 2006). Furthermore, cadaveric dissections suggest that the posterior wall of the maxillary sinus flexes during yawning, which could serve to ventilate the sinus system (Gallup and Hack, 2011).

In an attempt to unite the existing research linking yawning to state change, arousal, and enhanced circulation to the skull, it has recently been proposed that yawns may function to cool the brain by altering the rate and temperature of the arterial blood supply (Gallup and Gallup, 2007). While some researchers do not accept this as a viable explanation of yawning (Elo, 2010, 2011; Guggisberg et al., 2010, 2011; Walusinski, 2013), the basic predictions of the brain cooling hypothesis have been rigorously tested, supported and replicated. For example, evidence from both rats and humans shows that yawns are triggered by rises in brain temperature and produce a cooling effect to the brain and/or skull thereafter (Eguibar et al., 2017; Gallup and Gallup, 2010; Shoup-Knox et al., 2010; Shoup-Knox, 2011). Experimental research also shows that yawn frequency can be effectively reduced through behavioral brain cooling methods (Gallup and Gallup, 2007). The brain cooling hypothesis is also supported by varying lines of pharmacological and clinical evidence, as many medical conditions and pharmaceutical drugs alter brain/body temperature and yawn frequency in predicted ways (reviewed by Gallup and Eldakar, 2013; Gallup and Gallup, 2008). Furthermore, a growing number of studies have documented predicted changes in yawn frequency as a function of ambient temperature manipulation/variation, including data from laboratory experiments and naturalistic observations (Eldakar et al., 2015; Gallup et al., 2009, 2010, 2011; Gallup & Eldakar, 2011; Massen et al., 2014; Gallup, 2016).

1.2. Contagious yawning

While spontaneous yawns are triggered physiologically and are ubiquitous comparatively, other forms of yawning are driven by social stimuli. Research on some non-human primates, for example, has shown that some yawn-like displays, known as social tension or aggressive yawns, appear to hold a communicative function and are used as a threat display of the canine teeth (e.g., Deputte, 1994; Troisi et al., 1990; Redican, 1982). However, these "yawns" take on a different morphology and expression compared with typical spontaneous yawns. In some species, the signaler, rather than closing its eyes at the peak of the "yawn", fixes its attention on the target during the yawning display to monitor the effect of the yawn on the individual. These social displays are typically documented among non-human primate species with sexual dimorphism in body size, canine size, and aggressive competition (Darwin, 1872), and, in fact, sex differences in yawn frequency among primates are lost within species with limited sexual dimorphism in canine size (humans, Schino and Aureli, 1989; chimpanzees, Vick and Paukner, 2010). Therefore, researchers have questioned whether these displays can be classified as true yawns (Gallup, 2011).

More widespread forms of social yawning occur as a result of sensing yawns in others. This is known as contagious yawning (CY). Seeing, hearing (e.g. Massen et al., 2015), or even thinking about yawning can trigger yawns in humans, and it is suggested that attempts to shield a yawn do not stop its contagion (Provine, 2005). As expected, based on this distinct mode activation, CY does not follow the same diurnal pattern described above for spontaneous yawns, being much less related to sleepiness (Giganti and Zilli, 2011). Although the motor action patterns appear indistinguishable from one another, CY has only been documented within a few social species (see Table 1).

Given the relatively limited comparative evidence for CY, it can be concluded that this response is not simply a product of being social or gregarious, but rather serves some new social role. From an evolutionary perspective, it has been argued that CY is a more recently evolved behavior derived from the primitive spontaneous form (Gallup, 2011). Further differentiation between these two yawn-types, which is consistent with the proposed evolutionary framework, can be seen in terms of the developmental trajectory of these responses. For example, while spontaneous yawning among humans begins early on in utero (de Vries et al., 1982) and is very frequent among infants (Giganti et al., 2007), CY does not emerge until early childhood (Anderson and Meno, 2003; Helt et al., 2010; Hoogenhout et al., 2013).

The first findings of CY in chimpanzees, but not in monkeys, suggested a divergence of this trait phylogenetically separating the apes from the monkeys. However, recent studies have provided evidence for CY in some monkey species, whereas the picture among the apes has become less clear (see Table 1). Whereas all studies on chimpanzees indeed do report CY, results on bonobos are inconsistent, and the only study on gorillas and orangutans to date found no evidence for CY in these species. Consequently, the picture in the primate lineage is far from homogenous and the evolution of CY does not seem to be homologous. Instead, the evidence of CY in some, but not all, more distantly related mammal species, as well as in a bird species (see Table 1) suggests that this trait has evolved independently within several lineages. Nevertheless, the lack of consistent data on CY in multiple species within particular lineages (e.g. only a single bird species so far) makes any phylogenetically controlled analysis impossible, and consequently any conclusion about its phylogenetic history is premature. Moreover, the field most probably suffers from a publication bias in which null results (i.e. absence of evidence for CY in a given species) are less likely to be published. Therefore, a more systematic study of CY is needed across species of different orders or even classes. Specifically, more studies on reptiles and amphibians are needed.

Although CY is first and foremost a social trait, comparisons between closely related social- and non-social species would be particularly informative as to study both mechanistic as well as functional hypotheses. For example, other socially contagious behaviors (e.g., gaze-following) have been documented in non-social vertebrates (e.g. red-footed tortoise: Wilkinson et al., 2010) that do not show CY (Wilkinson et al., 2011).

Empirical investigations into the potential function(s) of CY are nearly absent from the literature, but there are currently two lines of thought. The first proposes a primarily communicative/signaling function to this behavior, whereby yawns serve to signal internal states to others within the group (Guggisberg et al., 2010; Liang et al., 2015). Given the characteristic social nature of this response, it perhaps makes intuitive sense to propose such a communicative function. However, there is no empirical support for this perspective. There is currently no evidence that yawning, outside of the aforementioned threat displays in non-human primates, provides a meaningful signal to receivers, and it is not clear what communicative benefits there would be to yawning (see Gallup and Clark, 2015). Yawns are limited in their role as social signals because they are under minimal voluntary control (Provine, 2012). Furthermore, any potential signal from yawning remains nonspecific since yawns occur under a variety of contexts (i.e., during changes in arousal, before and after sleep, during boredom, transitions in activity patterns, following stress) and are often misinterpreted in human social settings (see Gallup, 2011). Therefore, although CY is inherently social, experimental research is still needed to test the predictions of communication hypotheses.

An alternative approach to thinking about the potential function(s) of CY is to consider how the neurophysiological consequences of yawning within the individual (i.e., intracranial circulation, cortical arousal, brain cooling) would impact the collective, if passed along to members of the group. That is, instead of viewing these two yawn-types as independent actions, it may be useful to consider them as the same behavior produced by different triggers. Evolution fosters adaptations that accumulate upon existing architecture and, thus, both behaviors should share fundamental mechanistic pathways and may even possess similar functional outcomes. Consistent with this view, growing research shows that physiological variables that directly alter spontaneous yawn frequency (i.e., those that influence brain and body temperature) have the same effects on the spread of yawn contagion (Eldakar et al., 2017; Gallup, 2016; Gallup and Gallup, 2007, 2010). Therefore, when considering the neurophysiological changes surrounding spontaneous yawning, and the existence of CY in some gregarious species, the spreading of this behavior across the group could serve to heighten collective vigilance and facilitate an adaptive response to external stimuli under natural conditions (Gallup and Gallup, 2007). Although this hypothesis has not been directly tested, Miller et al. (2012b) provide some evidence in support of this view by demonstrating that within small groups of budgerigars yawning becomes more contagious following startling auditory disturbances. Further research is certainly needed to test these and other functional hypotheses for yawn contagion.

Table 1

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2. CONTAGIOUS YAWNING AND EMPATHY

2.1. Conceptual problems

Despite having a relatively poor understanding for why CY has evolved, the fact that CY is comparatively limited and shows a delayed developmental pattern indicates that it may reflect some higher-level social-cognitive capacity. Consistent with this perspective, over the last decade and a half, a large and growing body of research has focused on the potential connection between yawning and empathy (e.g., Platek et al., 2003; Platek et al., 2005; Palagi et al., 2009; Campbell and de Waal, 2010, 2014; Norscia et al., 2016). Empathy is a complex construct, representing the ability to understand, share and be affected by the state and/or feelings of others (Singer et al., 2004). Thus, if sensing yawns in others can reflexively trigger the same response, it seems that the action CY could be placed within a category of empathy. The proposed link between CY and empathy stems from a monograph on yawning that was published nearly 40 years ago (Lehmann, 1979), and more recently by its inclusion in the Perception-Action-Model (PAM) proposed by Preston and de Waal (2002). Lehmann (1979) notes that yawning is a sign of boredom (cf. Provine and Hamernik, 1986), and considers the latter an emotion. Subsequently, he concludes that CY thus constitutes emotional contagion (Lehmann, 1979). Emotional contagion in the basic sense represents a primitive form of empathic processing known as state matching (Preston and de Waal, 2002), whereby the observation of an emotional state in another elicits the same emotion in the observer. The contagion of an outward sign that correlates with an emotion, however, does not per association also indicate that the emotion is transmitted. In fact, it seems rather unlikely that people suddenly become bored when they see someone yawn as a result of uninteresting stimuli or stressed when sensing yawns elicited by anxiety-provoking situations. And if so, this still needs to be empirically verified and to date no data support such an effect. Instead, yawns that are initiated contagiously could be due to nonconscious mimicry or, mechanistic at an even lower-level, result from 'simple' behavioral contagion (Thorpe, 1963; Yoon and Tennie, 2010; Zentall, 2001).

Nonetheless, the automatic and reflexive copying of behavior remains an interesting adaptive response in social animals. Although relatively understudied, so far researchers have identified contagion of several behaviors; e.g. contagious itch and associated scratching (humans: Holle et al., 2012; rhesus macaques: Feneran et al., 2013; Japanese macaques: Nakayama, 2004; mice; Yu et al., 2017), contagious stretching (budgerigars: Miller et al., 2012a; Gallup et al., 2017), contagious sniffing (humans: Arzi et al., 2014), contagious "jump-yip" displays (prairie dogs: Hare et al., 2014), contagious scent-marking (common marmosets: Massen et al., 2016), contagious laughter (humans: Provine, 2005) and contagious play (ravens: Osvath and Sima, 2014; keas: Schwing et al., 2017). Apart from the studies on play and laughter that clearly represent emotional contagion (Osvath and Sima, 2014; Provine, 2005; Schwing et al., 2017), the other studies acknowledge that emotional contagion transcends superficial motor mimicry (Hare et al., 2014), and either do not mention empathy at all, or only when referencing papers on contagious yawning (Arzi et al., 2014; Feneran et al., 2013; Gallup et al., 2017; Massen et al., 2016; Miller et al., 2012), or empirically dismiss a link between the contagion of the specific behavior and empathy (Holle et al., 2012; Yu et al., 2017).

Empathy is notoriously difficult to define, and among others (e.g. Davis, 1983; Singer, 2006), Preston and de Waal (2002) emphasize its multifaceted nature. In their seminal paper they specifically focus on the process and include empathy within the PAM; i.e. they superimpose empathy on the PAM and argue that empathy thus includes all phenomena that share the same mechanisms. Consequently, they continue, that this should also include facilitation behaviors like imitation or the yawn reflex. The hierarchical structure of their proposed model (see also the "Russian Doll Model" in de Waal, 2008) thus specifies CY as a prerequisite for empathy (Preston and de Waal, 2002), which has led multiple researchers to infer that there is a direct link between CY and empathic processing. But, one could argue that a brain is also a necessary prerequisite for empathy, and, as for CY, arguing that any animal with a basal ganglion of a particular size thus should be empathic is based on the fallacy of assuming that having a brain is sufficient for having empathy (i.e., the fallacy of the converse, or affirming the consequent). Instead, one should also consider that there might be more primitive systems in which CY is included, which do not posses empathy. CY may be a primitive root of what evolved into empathy, or may involve a separate trend as a social coupling mechanism. Consequently, conceptually there is no reason to assume that the presence or degree of CY is representative of empathic capacities.

2.2 A critical review of empirical evidence

Even when considering these conceptual shortcomings, discussion of the connection between CY and empathy is rather persistent within the literature, as by now many studies have produced data that *seem* consistent with several derived hypotheses that predict inter-individual differences, developmental trajectories and certain underlying neural as well as hormonal or neurotransmitter patterns. Here, we critically review these hypotheses, the data and their implications.

2.2.1. Inter-individual differences

2.2.1.1. Questionnaire- and cognitive measures of empathy.

Perhaps the most logical prediction derived from the proposed link between CY and empathy is that people who are more empathic should be more susceptible to CY. This prediction has now been tested in several studies using questionnaire and cognitive measures of empathy. One obvious limitation to these studies is that all the tests are purely correlational and thus do not allow for causal inference. Whereas several of such studies indeed did show a significant relationship between an individual's susceptibility to CY and several questionnaire- or cognitive measures of empathy in healthy human populations, others find no such connection (see Table 2). As with defining empathy, measuring it through questionnaires and cognitive tasks also takes a multifaceted approach. This approach is needed when dealing with such a complex phenomenon, but it does impair overall analyses and the reproducibility of results, and with regard to links to CY the picture becomes rather unclear. For example, CY is correlated with some scales and appears to be unrelated to others, and to date no two studies on CY have used the same measurements of empathy. Notably, of the 22 identified tests for this relationship, only six (27.3%) are significant in the predicted direction. The emerging literature on this topic is rather unbalanced, with the papers showing predicted results being most often cited when discussing this connection. This creates a problem for progress in the field, since one could just as well interpret the few positive results as false positives, or type I-errors.

Table 2

2.2.1.2. Links to psychological 'disorders'

There are many other approaches to examining the connection between CY and empathy. Rather than looking at empathic abilities on a continuous scale, several CY researchers have studied populations that are impaired with regard to their empathic abilities. To date, researchers have focused on individuals with schizophrenia and Autism Spectrum Disorder (ASD), as both conditions have been linked with reductions in empathy (e.g., Baron-Cohen and Wheelwright, 2004;

Derntl et al., 2009). Consistent with the proposed link between CY and empathy, the first studies of this nature reported a lack of CY or diminished susceptibility to CY in ASD patients (Giganti and Esposito Ziello, 2009; Helt et al., 2010; Senju et al., 2007) and in people with schizophrenia (Haker and Rössler, 2009). These findings were taken as strong support for utilizing CY as a behavioral measure of empathic processing, and drew a great deal of attention from researchers and the media. More recent follow-up studies have revealed that at least for ASD patients this effect is mainly due to an attention bias; i.e. individuals with ASD typically focus less on the facial expressions of others. In fact, when children with ASD were specifically instructed to fixate on the eyes of the stimuli they were just as likely to yawn in response to CY stimuli when compared to typically developing children (Senju et al., 2009). Similarly, in a study in which an eye-tracker controlled the onset of the yawn and control stimuli to ensure that the participants paid attention, CY was found at similar rates both in ASD and typically developing children (Usui et al., 2013). Therefore, while initially this line of research was quite promising and widely cited in support of the CY/empathy connection, further research in this area has cast doubt on this interpretation.

2.2.1.3. Sex differences

The potential for sex differences in CY has also recently been explored. Quite some research by now has revealed that there is a strong difference in empathic qualities between men and women (reviewed in Christov-Moore et al., 2014), and thus Norscia and colleagues (2016) predicted that the susceptibility of CY, as a proxy for empathy, should be lower among men in comparison to women. When these authors then indeed found a difference between men and women in CY using observational methods, they used this as evidence to back up the claim that CY is indeed a marker of empathic processing. Aside from representing circular reasoning, the authors did not find a difference in CY susceptibility between men and women. What they report is a difference in the frequency of yawns, following exposure to yawns from others, between men and women that were already shown to be susceptible, thereby greatly reducing their sample. This remains the only reported sex difference in CY among humans despite numerous psychological investigations of this behavior in men and women. In their review, Gallup and

Massen (2016) found no support for such a bias. Of the 17 other previously published studies that analyzed for sex differences, and the one since then (Eldakar et al., 2017), no such difference was found. The lack of a sex difference in CY appears to be a robust and highly reproducible effect. The sole sex difference presented by Norscia et al. (2016) seems a false positive. This effect has not been demonstrated in any other animal species (see Table 1), though it is unclear whether other non-human animals show sex differences in empathy.

Within the comparative literature, several studies show sex differences in CY, but these depend on the sex of the initial yawner rather than the observer (see Table 1). These patterns are opposite for the two pan species; i.e. among chimpanzees the yawns of males are more contagious (Massen et al., 2012), whereas among bonobos the yawns of females are more contagious (Demuru and Palagi, 2012). This pattern may reflect attention biases towards the more dominant group members (cf. Emory, 1976; Deaner et al., 2005) and a subsequent higher likelihood of CY, because in chimpanzee societies males are the dominant sex whereas among bonobos females are of higher rank. Two studies reported an interaction effect of the sex of the stimulus and of the responder. Massen and colleagues (2012) found that CY in chimpanzees was especially prevalent among male responders, while Palagi and colleagues (2009) found that CY in gelada baboons is much more common among females. Again, rather than supporting a connection with empathy, this differential response could be explained by attentional biases due to the dominance structure of chimpanzee societies and the matrilineal structure of gelada societies.

2.2.1.4. Familiarity

By far, the majority of studies examining the proposed link between empathy and CY have tested for familiarity/in-group biases in this response. The idea being that empathy increases with the degree of familiarity between individuals (reviewed in Preston & de Waal, 2002), and if CY is indeed a proxy for empathy, the probability of yawn contagion should also increase with familiarity of the stimulus (first spontaneous yawner) to the responder. Indeed, several studies in humans (Norscia and Palagi, 2011; Palagi et al., 2014; Norscia et al., 2016; but see Massen et al., 2015), and in other animals (see Table 1) show that CY susceptibility is higher when the stimulus is of the same group, a kin member, or a friend, and correlates positively with measures of relationship quality or social closeness. However, the evidence for a familiarity bias for CY is quite mixed comparatively, with several other studies failing to find such a relationship (see Table 1).

Although consistent with links to empathy, a higher incidence of CY between familiar individuals suffers from a large confound related to the issues already mentioned, namely that attention in general is biased by familiarity: humans (Méary et al., 2014) but also monkeys (Whitehouse et al., 2016) for example show an attention bias towards in-group members and away from unfamiliar conspecifics. In fact, in humans gaze avoidance is common among strangers in both natural and experimental contexts (Zuckerman, 1983; Laidlaw et al., 2011). Moreover, research shows that humans detect the faces of in-group members quicker (Jackson and Raymond, 2006), and facial identity and expression are perceived more integrally when the face is more familiar (Ganel and Goshen-Gottstein, 2004). Additionally, in-group faces are perceived more holistically than out-group faces (Michel et al., 2006), and familiarity increases the detection of visual change in faces (Buttle and Raymond, 2003), like for example when someone starts yawning. Non-human primates also pay more attention to kin than to nonkin (Schino and Sciarretta, 2016).

Importantly, several studies examining the relationship between CY and familiarity have not considered attention biases at all. Some researchers controlled for attention biases by excluding individuals from their analyses that did not pay attention (Palagi et al., 2009; Massen et al., 2012; Romero et al., 2014), by only showing stimuli when subjects were paying attention (Romero et al., 2013), or by repeating a stimulus when an individual was not paying attention (Madsen et al., 2012, 2013). Others measured the effect of attention and found either no difference in general attention between familiar or unfamiliar (Silva et al., 2012), in-group out-group (Gallup et al., 2015), and even differences in the direction opposite to the prediction (i.e. out-group > in-group: Campbell and de Waal 2011, 2014).

However, attention is difficult to define (when is someone paying attention?), and general attention may not be so informative giving the specific biases mentioned above. Two studies so far, have used an eyehole while experimentally showing chimpanzees yawn stimuli, which should guarantee attention, and still find an in-group bias (Campbell and de Waal, 2011), and a familiarity bias in inter-species contagion with regard to chimpanzees catching yawns from either familiar or unfamiliar humans (Campbell and de Waal, 2014). Whereas we applaud this method to account for biases in general attention, it remains unclear exactly what the chimpanzees in these experiments, or the animals/humans in any other study are paying attention to; e.g. the actual yawn of the individual in the stimulus, or more specific features, like in the example of out-group chimpanzees, the size of its canines (see above)?

In sum, a familiarity bias for CY is far from universal across species tested so far (Table 1), and unless researchers can rule out the confound of familiarity biases in general attention and implement measures for monitoring what individuals are paying attention to in CY studies, any documented familiarity bias in CY remains inconclusive with regard to the proposed link between empathy and CY. Furthermore, an in-group or familiarity bias in behavioral contagion could be adaptive in a variety of ways (i.e., group coordination and vigilance, Miller et al., 2012b; Gallup et al., 2017), and can be explained without any connection to empathy. It is also possible that CY is a non-adaptive byproduct of social facilitation that evolved in the context of ecologically relevant group coordination.

2.2.2. Developmental

Whereas spontaneous yawning has been recorded in fetuses of 11 weeks and older (de Vries et al., 1982; Reissland et al., 2012), its contagious counterpart normally does not emerge before the age of 4-5 years (Anderson and Meno, 2003; Millen and Anderson, 2010; Helt et al., 2010). Similar ontogenetic patterns have been reported for chimpanzees, geladas and dogs, whereby CY among juveniles is lower when compared to adults (Madsen and Persson, 2012; Madsen et al., 2013; Palagi et al., 2009). Additionally, the contagiousness of yawning seems to wane in old age (Giganti et al., 2012; Massen et al., 2014; Bartholomew and Cirulli, 2014), though this result needs to be taken with caution as it may be due to a general decrease in yawn frequency among the elderly (Zilli et al., 2008) and/or visual and auditory sensory decline. The relatively late development and subsequent decrease in CY among elderly populations is consistent with the developmental stages of empathy, of which some also only develop relatively late (see below) and diminish at old age (Maylor et al., 2002). However, the fact that the developmental trajectories, or the first occurrence, of specific traits are in parallel does not mean they are directly linked, and could be due to a third unknown factor. Moreover, the age at which CY emerges in children occurs when cognitive facets of empathy are also developing rather than the more ‘simple’ responses like emotional contagion (newborns: Hoffman, 1982; Singer, 2006), or the development of self-awareness, as measured by the mirror-mark test (age 18-24 months; Amsterdam et al., 1972). In fact, the development of CY parallels that of first order mentalizing, or theory of mind, as attested by the Sally–Ann test (Baron-Cohen et al., 1985; Perner et al., 1987). Nevertheless, there have been no explicit connections between CY and theory-of-mind, probably since the latter has been notoriously difficult to evaluate in animals that nonetheless show CY, or for that manner in non-human animals in general (but see Krupenye et al., 2016).

Moreover, like the differences between ASD and typically developing individuals, some of the sex differences between animals, and possibly the familiarity effects, at least one study investigating CY in children indicates that the developmental effects are due to a lack of attention. When, for example, children at the age of 3 years where primed to make eye contact before witnessing a yawn, they also displayed CY (Hoogenhout et al., 2013). Similar developmental patterns regarding attention in non-human animals (e.g. chimpanzees: Bard and Leavens, 2014; dogs: Wallis et al., 2014) may, consequently, also account for the developmental patterns of CY in these species. And finally, the inverted U-shaped developmental trajectory of attention in humans (Craik and Bialystok, 2006), with a decrease with senescence (e.g. Quigley et al., 2010) may also explain the reduction of CY in the elderly. Future research is needed to examine this possibility.

2.2.3. Brain studies

The proposed link between CY and empathy has also garnered a lot of interest within studies employing brain-imaging methods, whereby researchers can examine how humans exposed to yawn stimuli show increased activity in areas of the brain implicated in empathic processing, such as the mirror neuron system (e.g., Cooper et al., 2012; Haker et al., 2013). The argument here is that to empathize or sympathize with someone, we need to be able to project that individual's feelings or emotions onto our own mind first, before we can act appropriately (Leslie et al., 2004). Mirror-neurons that fire both when observing an action and when performing that action (di Pellegrino et al., 1992) seem to be able to fulfill that function. To date, the results with regard to the involvement of mirror neurons in CY are inconsistent, as a number of studies fail to show any increase in activity within these brain regions while observing yawning stimuli (Schürmann et al., 2004; Platek et al., 2005). These and other studies, however, show specific activation in a variety of other brain areas that have been linked to empathy-related capacities; i.e. the right posterior superior temporal sulcus and bilaterally in the anterior STS (Schürmann et al., 2004), the posterior cingulate and precuneus (Platek et al., 2005), the ventromedial prefrontal cortex (Nahab et al., 2009), and the right posterior inferior frontal gyrus (Arnott et al., 2009). In fact, the most consistent feature of imaging studies examining CY is their inconsistency. Whereas one could argue that the increased activity of multiple areas across these samples reflects the multi-faceted connection between CY and empathy, they are not activated in parallel across different studies, and the single neurological components linked with empathy may perform different functions when activated alone compared to when the system operates as a whole (Bechtel 2008). As a larger issue with functional imaging studies, the activation of one single brain area may result in multiple behavioral patterns (Krakauer et al., 2017), and consequently it is difficult to draw causal relationships. Therefore, behavioral studies are still needed (Krakauer et al., 2017), and behavior is exactly what is missing in these neuroimaging studies.

Specifically, while these studies claim that they show the involvement of particular brain regions involved in CY, what they actually show is how the brain reacts to sensing yawns in others, and the contagiousness of this yawn is either suppressed, as participants are not allowed to move in imaging studies, not reported in for example the one EEG study (Cooper et al., 2012), and possibly absent. In one study participants had to score whether they felt contagion or not (Haker et al., 2013), yet the analyses were not restricted to those contagiously rated stimuli. In another study the participants were asked to rate the contagiousness of auditory stimuli on a 4-point scale (Arnott et al., 2009), and here they indeed showed that activity of the right posterior inferior frontal gyrus was highest after listening to yawn stimuli that were highly rated for contagiousness. However, the stifling of CY responses either through collars or constraining cushions (Nahab et al., 2009; Schürmann et al., 2004), or because participants were told to lie still (Arnott et al., 2009; Haker et al., 2013), deserves careful consideration, since in and of itself this could involve heightened self-awareness (cf. Provine, 1986) and subsequent activation of empathy related brain areas specifically during exposure to yawn stimuli. Another important and related issue to consider is how the widespread social stigma surrounding yawns may impact these studies. Because yawning is often considered rude or disrespectful (Schiller, 2002), and CY appears to be actively inhibited by social presence in laboratory settings (Gallup et al., 2016), simply sensing yawns during an imaging experiment could activate areas more generally related to social cognition (Takahashi et al., 2004). Thus, neuroimaging studies reporting areas of brain activation in response to yawning stimuli should be interpreted with caution.

One study recently investigated whether the administration of intranasal oxytocin alters CY in a sample of male college students (Gallup and Church, 2015). Given that oxytocin has been implicated in various forms of empathic processing (Gonzalez-Liencres et al., 2013; De Dreu and Kret, 2015), and intranasal oxytocin increases emotional empathy in men (Hurlemann et al., 2010), one might expect that it should also increase the susceptibility of yawn contagion. However, while the results clearly demonstrated a change in behavior from that intranasal oxytocin, this manipulation did not increase CY susceptibility. In fact, oxytocin appeared to inhibit the expression of yawning, perhaps by enhancing social awareness of this response (see above). These findings and others highlight the complex social nature of CY in humans.

3. Future directions

Despite the rather inconsistent and indirect empirical evidence reviewed above, we are not advocating that researchers should discard the possibility of a direct connection between empathy and CY. Particularly, the ability to identify a behavioral marker of empathy, a phenomenon that has been notoriously difficulty to define (or measure for that matter), would be of tremendous impact to the behavioral sciences. Unfortunately, direct tests for a connection between CY and empathy are lacking. Therefore, we propose some methodological and conceptual advances that could be made to more explicitly test this connection. In addition, we briefly highlight some more general methodological issues within the study of CY.

We propose that future research examining the link between CY and empathy begin to focus on use of experimental methods, while including a more multifaceted approach to measuring empathy (e.g., cognitive vs. emotional, multiple subjective and objective measures). In particular, a fruitful yet previously overlooked approach to studying this connection would be to directly manipulate one variable to witness its effects on the other. If CY represents a primitive form of empathy, then manipulating empathy responses should alter the expression of CY. To date, only one study has attempted to employ such an approach through the peripheral administration of oxytocin in humans (Gallup and Church, 2015). Similarly, if CY activates neural pathways tied with empathic processing, studies could actively induce or inhibit CY to test how this alters empathy responses thereafter. This research approach could investigate how a combination of both subjective and objective (neurophysiological) measurements of varied forms of empathy (1) correlate with, (2) affect, and (3) are affected by CY. Future research in this area, both on humans and non-human animals, should help elucidate the proposed empathy/CY connection.

Moreover, we feel that future research should approach CY from the bottom up as a behavioral phenomenon first, and then investigate it with a holistic approach considering all 4 of Tinbergen's whys (Tinbergen, 1963). Consequently, researchers should not only consider developmental and/mechanistic questions about CY, but as mentioned before, also focus more on functional explanations of CY (e.g., group vigilance; Gallup and Gallup, 2007; Miller et al., 2012b) and more rigorously investigate its phylogeny to elucidate whether CY has emerged through convergent, parallel or homologous evolution.

3.1. Methodological problems & advances

In 2010, Campbell and de Waal wrote a very informative paper on the methodological problems in the study of CY (Campbell and de Waal, 2010). They argued, rightfully, that the field suffers from a strong variation in methods used to study CY, which makes comparisons between studies very difficult. Fortunately, some of their issues are partly resolved and by now, for example, most experimental studies do use a non-yawn stimulus as a control condition to compare yawning rates. Additionally, Campbell and de Waal (2010) noticed that there are large between-study differences in the number of yawns displayed to subjects and the duration of the yawns shown. Whereas recent studies show that the latter represents biologically relevant variation (Gallup et al., 2016), the former remains a problem when comparing results between studies. Though it should be noted that for proof of concept tests (CY in a species; yes or no?), when well controlled, this does not constitute a problem. Campbell and de Waal (2010), also noticed differences with regard to the analyses used within various studies; i.e. either population level comparisons of yawn frequencies in yawn and control conditions, or binomial analyses of whether an individual yawned or not in either condition. Studies using the latter method often report percentages of individuals that showed CY and Campbell and de Waal (2010) argued that these percentages are not informative given the wide range of stimuli used. However, the comparisons of yawn frequencies between test and control conditions can suffer from the self-contagious effect of yawning (i.e., one yawn often triggers several subsequent yawns in the same individual), so we advocate for the use of both analyses. Most importantly, however, we agree with Campbell and de Waal (2010) that authors must acknowledge the differences in methods used when making comparisons between existing studies.

Whereas we encourage the use of experimental tests of CY as it allows for an easier titration of different variables that may or may not influence this reponse, we acknowledge that observational studies of CY are paramount for our understanding of its ecological relevance (e.g. function). The problem with observational studies, however, is the difficulty in defining whether a yawn is spontaneous versus when it is caused by sensing another yawn. This difficulty becomes apparent in the literature particularly when comparing the timeframes within which a second yawn is considered dependent on / infected by the previous (see Kapitány and Nielsen, 2017): e.g. 20 sec. (Miller et al., 2012b) vs. 5 min. (Palagi et al., 2009). Whereas first of all it seems rather implausible that the contagious effect of a yawn can last 5 minutes, increasing these timeframes (in the absence of comparable control conditions) also significantly increases the possibility that some spontaneous yawns are considered contagious (Kapitány and Nielsen, 2017). Generally, studying CY observationally by defining a yawn to be caused by another yawn of a different individual within a certain time ignores the (random) distribution of spontaneous yawns and thus may contain false positives. Using very short timeframes this problem becomes less problematic, but the measurement of CY is nevertheless influenced by an individual's/species' frequency of spontaneous yawning, which in turn may be influenced by several factors (see introduction). Therefore, we advise testing whether the observed 'clumping' of yawns and the frequency of such 'clumps' differs from random behavior; i.e. random 'clumps' of spontaneous yawns (cf. Sokal and Rohlf, 1995), as has been done in some studies (Miller et al., 2012a; 2012b; Massen et al., 2016). A comparison of presumed CY with baseline rates of spontaneous yawns using survival analysis may also be a useful approach (Schino, Di Giuseppe and Visalberghi, 2009).

Finally, we highlight recent technological advances that could allow for better and more controlled studies of CY in relation to empathy. First, as attested by our review of the literature above, attention biases remain a large confound within this literature. Recent advances in eye-tracking have given us a very powerful tool to examine what people are paying attention to, and this method has now also been reliably used to study attention biases in non-human animals including apes (Krupenye et al., 2016) and dogs (Somppi et al., 2013). Therefore, when studying inter-individual differences in CY, the use of eye-tracking devices can help determine in more detail what humans and other animals are attending to within the stimulus presentation. Eye-tracking data could also be used for assuring equal exposure to test or control stimuli, familiar or unfamiliar stimuli, or of individuals from different populations (cf. Usui et al., 2013).

Second, with regard to brain imaging research we highlighted the problem that subjects within these studies are forced to inhibit their yawn responses, and that such inhibition in a laboratory setting may introduce a confound regarding neurological activity measured in the brain. Unfortunately, real-time fMRI remains very vulnerable to movement artifacts (Magland and Childress, 2014). Therefore, we welcome neuroimaging studies that do allow subjects to actually yawn when they feel the urge to do so, using methods that are robust to such movement. For example, recent advances in EEG hardware and analyses now allow this method to be used when subjects are in motion, opening novel research opportunities (Reis et al., 2014). Similarly, albeit with lower definition, near-infrared spectroscopy and topography (Jobsis, 1977) allows for movement, and has, for example, recently been suggested as a useful tool to characterize children with ASD (Li et al., 2016). Such technological advances, when applied appropriately to the study of CY, would greatly improve our neurobiological understanding of this phenomenon and could help elucidate possible links between CY and empathy.

4. Conclusion

In this review, we critically evaluated the research on the proposed link between CY and empathy. We first question the conceptual basis for this link, and second find that the current empirical evidence supporting this connection to be indirect, inconclusive and in some cases absent. The aforementioned review of the literature demonstrates results that are mixed and inconsistent with regard to this association. For nearly all areas examined, there exist studies reporting data both for and against the proposed association. Studies examining inter-individual differences related to empathy and CY provide evidence that is quite contradictory, and in fact, differences in empathy measures in humans prove to be a poor predictor of CY. Despite the fact that women have repeatedly been shown to score higher on empathy measures, only one study has discovered any difference in the measurement of CY between men and women, but that study did not report any difference in susceptibility to CY. Experiments examining CY within populations with well-defined deficits in empathy, such as ASD, provide mixed support for this connection depending upon whether participants are instructed to pay attention to the stimuli presented within the study. Furthermore, the large and growing body of studies investigating in-group/familiarity biases in CY provides no overall trend, particularly within the comparative literature. The majority of these studies also suffer from confounds related to biases in the degree and types of visual attention toward in-group versus out-group members, or related to levels of affiliation. The overlap in the developmental trajectory of CY and empathy is certainly consistent with a connection between the two, but this is simply correlational and further research is needed to more closely examine the development of empathic processing and the susceptibility to CY in tandem. Recent data also shows that developmental changes in CY may be more related to changes in visual processing. The various neuroimaging studies show no clearly convergent or consistent areas of activation within the brain following exposure to yawn stimuli, and fail to consider confounds related to the active inhibition of this response and social stigma of yawning when in the presence of others. When taken together, the proposed connection between CY and empathy should be viewed with caution. We propose the use of more rigorous and direct experimental manipulations to explicitly test this connection within future research.

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Table 1. Non-human species in which CY has been studied, whether the studies were experimental or observational, sample sizes, whether the species showed CY or not, whether there was a sex effect and which, and whether there was an effect of familiarity and which (In vs. out-group, Kin vs. non-kin, Familiar vs unfamiliar, or a continuous effect of relationship quality (RQ)).

Species	**Studies**	**Exp. / Obs.**	**n**	**CY: yes / no**	**Difference in suscepti-bility between ♂♂&♀♀**	**Difference in contagious-ness of yawns of ♂♂&♀♀**	**Interaction between sex of stimulus and receiver**	**Familiarity (In/Out group; Kin; Fam.vs. Unfam; RQ)**	**Comments**
MAMMALS									
<u>Primates:</u>									
Great Apes									
Pan troglodytes	Anderson et al., 2004	Exp.	6	Yes	-	-	-	-	
	Campbell et al., 2009	Exp.	24	Yes	No	-	-	-	Stimuli were computer animated chimpanzees
	Campbell and de Waal, 2011	Exp.	23	Yes	No	-	-	In>Out-group	
	Massen et al., 2012	Exp.	15	Yes	No	♂♂>♀♀	♂♂>♂♀ = ♀♂>♀♀	No	
	Madsen et al., 2013	Exp.	33	Yes	-	-	-	No	Stimuli were familiar or unfamiliar humans
	Amici et al., 2014	Exp.	14	Yes	-	-	-	-	Contagion only with conspecifics and not with humans.
	Campbell and de Waal, 2014	Exp.	19	Yes	-	-	-	Fam.>Unfam.	In addition to the 2011 study, here the stimuli were familiar and unfamiliar humans and baboons.
Pan paniscus	Demuru and Palagi, 2012	Obs.	12	Yes	No	♀♀>♂♂	-	Kin; RQ	
	Amici et al., 2014	Exp.	4	No	-	-	-	-	Stimuli were both live humans and videos of conspecifics
	Palagi et al., 2014	Obs.	(12) +4	Yes	No	No	-	RQ	Note that this study only contains limited additional data for bonobos with regard to the Demuru & Palagi 2012 study
	Stevens et al., 2017	Exp.	8	No	-	-	-	-	

Species	Studies	Exp. / Obs.	n	CY: yes / no	Difference in suscepti-bility between ♂♂&♀♀	Difference in contagious-ness of yawns of ♂♂&♀♀	Interaction between sex of stimulus and receiver	Familiarity (In/Out group; Kin; Fam.vs. Unfam; RQ)	Comments
Gorilla gorilla	Amici et al., 2014	Exp.	5	No	-	-	-	-	Stimuli were both live humans and videos of conspecifics
Pongo abelii	Amici et al., 2014	Exp.	4	No	-	-	-	-	Stimuli were both live humans and videos of conspecifics
Old world monkeys									
Lophocebus albigena	Deputte, 1978	Obs.	13	No	-	-	-	-	
Macaca fascicularis	Deputte, 1978	Obs.	13	No	-	-	-	-	
Mandrillus sphinx	Baenninger, 1987	Obs.	4	No	-	-	-	-	
Macaca arctoides	Paukner and Anderson, 2006	Exp.	22	Yes	-	-	-	-	Contagious yawns were accompanied by an increase in scratching suggesting mediation by stress.
Theropithecus gelada	Palagi et al., 2009	Obs.	21	Yes	-	-	♀♀>♂♂	RQ	
New world monkeys									
Callithrix jacchus	Massen et al., 2016	Obs.	14	No	-	-	-	-	Low yawn frequency and thus very little stimulus yawns
Strepsirrhini									
Lemur catta	Reddy et al., 2016	Exp.	17	No	-	-	-	-	
Varecia variegata	Reddy et al., 2016	Exp.	11	No	-	-	-	-	
<u>Rodents:</u>									
Rattus norvegicus	Moyaho et al., 2015	Exp.	158	Yes	-	-	-	Unfam.>Fam.	Using strains of high (HY) and low-yawning (LY) rats, only the former showed evidence of CY
<u>Ovis:</u>									
Ovies aries	Yonezawa et al., 2017	Exp.	12	Yes /No	-	-	-	-	The co-occurrence of yawning in natural context was 11%, while there was no evidence of CY in response to video stimuli

Species	Studies	Exp. / Obs.	n	CY: yes / no	Difference in suscepti-bility between ♂♂&♀♀	Difference in contagious-ness of yawns of ♂♂&♀♀	Interaction between sex of stimulus and receiver	Familiarity (In/Out group; Kin; Fam.vs. Unfam; RQ)	Comments
<u>Loxodonta</u>									
Loxodonta africana	Rossman et al., 2017	Obs	9	-	-	-	-	-	No direct tests, but six postulated instances
<u>Equus</u>									
Equus caballus	Malavasi, 2014	Obs.	8	No	-	-	-	RQ	Poster: Analyses rather unclear
<u>Canis</u>									
Canis familiaris	Joly-Mascheroni et al., 2008	Exp.	29	Yes	No	-	-	-	Inter-species test; i.e. the dogs caught humans yawn
	Harr et al., 2009	Exp.	15	No*	-	-	-	-	Both human and dog stimuli
	O'Hara and Reeve, 2011	Exp.	22	No	-	-	-	No	Human stimuli
	Silva et al., 2012	Exp.	29	Yes	-	-	-	Fam.>Unfam.	Auditori human stimuli
	Madsen and Persson, 2013	Exp.	35	Yes	-	-	-	No	Human stimuli
	Romero et al., 2013	Exp.	25	Yes	No	-	No	Fam.>Unfam.	Human stimuli
	Buttner and Strasser, 2014	Exp.	60	No	-	-	-	-	CY in 12 (out of 60) dogs seem to be stress induced as they showed elevated cortisol levels
Canis lupus	Romero et al., 2014	Obs.	12	Yes	No	No	-	RQ	
<u>Felis:</u>									
Pantera leo	Baenninger, 1987	Obs.	5	No	-	-	-	-	
BIRDS									
<u>Parrots:</u>									
Melopsittacus undulatus	Miller et al., 2012a	Obs	21	Yes	-	-	-	-	
	Gallup et al., 2015	Exp.	16	Yes	-	-	-	No	
REPTILES									
<u>Tortoise:</u>									
Geochelone carbonaria	Wilkinson et al., 2011	Exp.	7	No	-	-	-	-	
FISH									
<u>Osteichthyes:</u>									
Betta splendens	Baenninger, 1987	Obs.	19	No	-	-	-	-	

Table 2. Questionnaire- and cognitive measures of empathy, in different studies, with sample size n, and the relationship with contagious yawning (+ positive, - negative, or no relationship)

Measure of Empathy	Study	N	Relationship with CY
Raine's (1991) Schizotypical Personality Questionairre	Platek et al., 2003	65	-
Baron-Cohen's (1985) First Order false Believe Task	Platek et al., 2003	45	+
Keenan and colleagues' (1999) Left hand advantage self-face recognition task	Platek et al., 2003	21	+
Baron-Cohan and Wheelwright's (2004) empathy quotient	Arnott et al., 2009	10	+
Davis' (1980) Interpersonality Reactivity Index (IRI):			
IRI-fantasy scale	Haker and Rössler, 2009	45	+
	Bartholomew and Cirulli, 2014	328	no
	Gottfried et al., 2015	59	no
IRI-perspective taking scale	Haker and Rössler, 2009	45	no
	Bartholomew and Cirulli, 2014	328	no
	Gottfried et al., 2015	59	no
IRI-personal distress scale	Haker and Rössler, 2009	45	no
	Bartholomew and Cirulli, 2014	328	no
	Gottfried et al., 2015	59	no
IRI-empathic concern scale	Haker and Rössler, 2009	45	no
	Bartholomew and Cirulli, 2014	328	no
	Gottfried et al., 2015	59	no
Lilienfield and Widows' (2005) Psychopathic Personality Inventory-Revised (PPI-R): overall	Rundle et al., 2015	135	no
PPI-R fearless dominance subscale	Rundle et al., 2015	135	no
PPI-R Self-centered impulsivity subscale	Rundle et al., 2015	135	no
PPI-R Coldheartedness subscale	Rundle et al., 2015	135	-
Doherty's (1997) Emotional Contagion scale	Bartholomew and Cirulli, 2014	328	no
Baron-Cohan and colleagues' (2001) Reading the Mind in the Eye test	Gottfried et al., 2015	59	no