Investigating contagious behaviors in *Canis familiaris*

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Abstract

Contagious behaviors, and in particular contagious yawning, have been widely studied because of their unique features among social behaviors and because of their supposed link to empathy. Although many researchers have worked in this area, there is still a great deal unknown about the mechanisms of contagious behavior and in what species it occurs. The literature on contagious yawning in dogs is particularly conflicted, with mixed results in the literature and varied experimental methods. This paper includes two studies aimed at elucidating the literature. First, an experiment investigated differences in the modalities of contagion, comparing contagious yawning with contagious itching in *Canis familiaris*, the domestic dog. Neither contagion was significantly present in the experiment. Second, a meta-analysis of the canine contagious yawning literature found a significant effect of contagion, suggesting that contagious yawning does exist in canines. These results are discussed in the context of the literature, suggesting specific avenues for further clarifying research, and cautioning careful acceptance of contagious yawning in dogs, with a modest view in its relation to empathy.

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1. Introduction

One of the great paradoxes of science is the complexity of simplicity. Sometimes the most mundane and apparently simple phenomena can, in fact, be extraordinarily complex or difficult to understand rigorously. This is especially true in the domain of cognitive science; for all that we have learned, in many ways we are still woefully unaware of the mechanisms by which our own minds operate. This is made especially obvious when considering some of our most basic, seemingly uncomplicated behaviors. Take, for example, the yawn.

1.1 Yawning

Yawning is a behavior that all humans are familiar with, and is instantly recognizable with its characteristic mouth-gape. Yawning involves the inhalation of breath and the stretching of the eardrums, though it is frequently combined with closed eyes and the more obvious stretching of other body parts (Provine, 2005). Yawning is common to every human being, even before birth (Provine, 2005), and is something we have all experienced but tend to think about very little. Typically, we associate it with sleepiness, boredom, or fatigue, but for a behavior that we have all experienced and which comes naturally, there is still a surprising amount we do not yet know about yawning.

While many theories have been put forward, there is not yet a scientific consensus on why, exactly, we yawn in the first place. One theory that has received some favor is that yawning functions as a mechanism for rapidly exchanging oxygen and carbon dioxide in the lungs, bloodstream, and brain. This explanation is somewhat common publicly, and has long been the thesis taught in most medical schools (Provine, 2005). Yet, contradictory evidence casts doubt on this theory. Provine, Tate, and Geldmacher (1987) experimentally manipulated the oxygen and carbon dioxide conditions in the environment to examine whether rates of yawning would be influenced. However, they found that yawning incidence was not impacted by environment, with subjects breathing normal air (CO_2 concentration approximately 0.03%), compressed air (at normal CO_2 concentration, 0.03%), 3% CO_2, 5% CO_2, or 100% Oxygen. Furthermore, they found that exercise, a naturalistic setting in which the body would require a greater exchange of carbon dioxide for oxygen, had no impact on yawning incidence (Provine et al., 1987).

An alternative hypothesis for the origin of yawns is that yawning functions to decrease the temperature of the brain. This thermoregulatory hypothesis was first proposed by Gallup and Gallup Jr (2008), suggesting that yawning could be a compensatory cooling mechanism. This hypothesis has received a fair amount of support, with studies suggesting that brain temperature rises preceding a yawn, and decreasing immediately after the yawn in mammals (Shoup-Knox, Gallup, Gallup, & McNay, 2010). Similarly, a large body of evidence in support of the thermoregulatory hypothesis (Gallup & Eldakar, 2011, 2013; Gallup & Gallup Jr, 2007) comes from experiments that exploit one of yawning's most interesting features—its contagion.

1.2 Contagious yawning

It is commonly known that yawning is contagious. That is, when someone around you yawns, or even as you read about or think about yawning, you are more likely to yawn yourself. This effect has been shown robustly in scientific studies. Starting with some of the early work of Provine (1989), the stimulus of a yawning human being, either in video or image form, has been shown to produce yawning in subjects at a significantly higher rate than viewing video or images of smiles. Provine argues that this is evidence that contagious yawning is a released fixed-action pattern in humans; the releaser of a yawning face causes an unconscious, uncontrollable reaction in the observer where they yawn contagiously. Further research by Provine discovered that the relevant stimuli to this contagious yawn was the yawning face. Systematically controlling for what regions of the yawn stimulus were visible to the subjects showed that while a yawning mouth alone was not sufficient to create contagion, a yawning face, even with the mouth occluded, could create the contagion. But while the more gestalt stimulus of the yawning face was proven to generate contagion beyond just the yawning mouth, the yawning face is not the only stimulus capable of generating contagion yawning responses. A variety of studies have demonstrated that the auditory component of a yawn can generate contagion as well (Arnott, Singhal, & Goodale, 2009; Moore, 1942). Furthermore, both thinking about yawning and reading about yawning have been demonstrated to produce contagion as well (Provine, 2005).

More recent work has investigated the neurological underpinnings of yawning and its contagion, with some mixed results. A large body of research has focused on the role of mirror-neurons in yawn contagion, in particular, since mirror neurons characteristically fire when simulating the action of another actor (Cooper et al., 2012; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Haker, Kawohl, Herwig, & Rössler, 2013; Iacoboni, 2009). Arnott et al. (2009) found that in their study of contagious yawning following auditory stimuli, activity increased in the posterior inferior frontal gyrus, a characteristic part of the MNS. Similarly, Haker et al. (2013) saw activation of Broca's region in the right inferior frontal gyrus while subjects viewed yawning videos. Still, several studies have found no evidence of neural activity in regions associated with the mirror neuron system during contagious yawning (Nahab, Hattori, Saad, & Hallett, 2009; Platek, Mohamed, & Gallup Jr, 2005; Schürmann et al., 2005). While the body of neuroscience research on contagious yawning does not clearly show whether the MNS has an important role in contagious yawning, much of the neuroscientific evidence suggests that contagious yawning is closely related to our capacity to track the actions of others or our own selves (Platek et al., 2005). This puts the neuroscientific evidence in line with a leading hypothesis for why contagious yawning occurs; the capacity to yawn contagiously is probably linked to a capacity for empathy.

1.3 Contagious yawning and empathy

While there is a great deal to be said about the possible relationship between contagious behavior and empathy, it is first important to establish exactly what is meant by empathy in this context, as it has a variety of definitions in cognitive science. Most of the literature draws a distinction between two types of empathy, cognitive empathy and affective empathy (although even these terms are not used as a perfect standard across the field). Cognitive empathy refers to the capacity to understand another person's perspective and experience, while affective empathy refers to the capacity to share the emotional state of another individual (Davis, 1983). It is worth noting that the notion of cognitive empathy is closely related to the concept of theory of mind (ToM), which is generally described as an ability to infer the intentions and feelings of another individual. Shamay-Tsoory and Aharon-Peretz (2007) draw the further distinction between cognitive and affective ToM, where cognitive ToM refers to an ability to make inferences based on another's beliefs and affective ToM refers to an ability to make inferences based on another's emotions.

So in what forms, if at all, are empathy and theory of mind related to a capacity for contagious yawning? Lehmann (1979) argued that yawning's close link to boredom (an emotion) in humans meant that contagious yawning represented a form of emotional contagion. On this view, contagious yawning could be a form of affective empathy. However, as Massen and Gallup (2017) point out, it is a far cry to imagine that each time we catch a yawn from another individual, we are becoming instantaneously bored in the way an emotional contagion account would predict. It is far more likely that contagious yawning, if linked to empathy, would represent an early precursor or correlate to the more sophisticated forms of cognitive or affective empathy. Preston and de Waal (2002) include contagious yawning as an example of their Perception-Action-Model (PAM). This model aims to explain empathy, in all of its forms, within a framework of evolutionary psychology that accords better with the comparative, developmental, and environmental literatures. De Waal and Preston later describe contagious yawning as a clear example of motor mimicry (2017) fitting in their PAM, where motor mimicry is one of the evolutionarily ancient features of the capacity for empathy. In the "Russian Doll" model of empathy (de Waal, 2007), where more sophisticated forms of empathy have emerged over the course of evolution, motor mimicry is considered part of the innermost doll, one of empathy's earliest emerging dimensions. Yoon and Tennie (2010) largely agree with this placement of contagious yawning in the hierarchy of the PAM, arguing that contagious yawning may not truly represent any sort of sophisticated theory of mind, and indeed might not even be a truly contagious behavior, but might rather be a form of nonconscious mimicry.

Taking into account the theoretical underpinnings of the link between contagious yawning and the capacity for empathy, it seems that while contagious yawning should not necessarily provide evidence for a strong form of either cognitive or affective empathy, the presence or absence of contagious yawning may yet provide important insight into where and when the system that underlies richer forms of empathy (as in the perception-action-model) exists. In other words, where contagious yawning exists, rich forms of empathy have the possibility to exist, but only if evolutionary pressures have driven the further development of additional layers in the PAM. Where contagious yawning does not exist, especially if lacking other basic elements of the PAM, it is probable that rich forms of cognitive and affective empathy might also be absent.

This theoretical understanding of contagious yawning and its link to empathy is grounded in a wide array of empirical studies suggesting that these two concepts are linked. Several studies have suggested that individual trait differences in empathy predict increased susceptibility to contagious yawning (Arnott et al., 2009; Platek, Critton, Myers, & Gallup Jr, 2003). However, it is worth noting that quite a few other studies (Bartholomew & Cirulli, 2014; Gottfried, Lacinová, & Širůček, 2015) have used different scales meant to measure trait empathy, and have found no relationship to yawn contagion susceptibility (Massen & Gallup, 2017).

Another interesting approach to investigating the link between empathy and contagious yawning comes from experiments investigating non-neurotypical populations that are marked by a reduced capacity for empathy. Individuals with Asperger syndrome or high functioning autism have demonstrated lower empathy scores than age-matched controls (Baron-Cohen & Wheelwright, 2004). Further work in this area has highlighted that individuals with autism spectrum disorder (ASD) have no deficit in affective empathy, but only in cognitive empathy (Dziobek et al., 2008; Jones, Happé, Gilbert, Burnett, & Viding, 2010). Borderline personality disorder (BPD) has been characterized by a double dissociation in empathy from typical controls, where individuals with BPD show lower than average cognitive empathy, but greater than average affective empathy (Harari, Shamay-Tsoory, Ravid, & Levkovitz, 2010). Individuals with schizophrenia have been shown to have a global empathy deficit, showing reduced levels of both cognitive and affective empathy (Derntl et al., 2009). Individuals with psychopathy have a deficit in affective empathy, but show no deficit in cognitive empathy (Jones et al., 2010).

Examining the record of studies on contagious yawning that have been performed in these clinical populations, there seems to be evidence supporting the claim that reduced capacity for empathy is linked with lower rates of yawn contagion. Several studies have shown that individuals with ASD show a significantly impaired capacity to yawn contagiously (Giganti & Esposito Ziello, 2009; Helt, Eigsti, Snyder, & Fein, 2010; Senju et al., 2007), suggesting that the capacity for cognitive empathy might be closely associated with the capacity for contagious yawning. However, two more recent studies showed that children with ASD could show normal levels of contagious yawning when their atypical ability to attend to faces and social stimuli in general were accounted for. Specifically, Senju et al. (2009) found that children with ASD showed normal rates of contagious yawning when instructed to attend to the eyes of the yawn demonstrator, and Usui et al. (2013) found that using an eye-tracker to control the onset of the yawning stimulus similarly allowed children with ASD to yawn contagiously at normal levels. As Massen and Gallup (2017) argue, these more recent experiments might cast some serious doubt on the supposed link between impaired cognitive empathy and impaired contagious yawning, and could instead merely show that any deficits in contagious yawning in individuals with ASD are a result of attentional problems, not empathy deficits.

Beyond ASD, there is some other work investigating the possible link between empathy deficits in clinical populations and low levels of contagious yawning. Platek et al. (2003) found that contagious yawning was negatively influenced by schizotypal traits, and in a clinical population, Haker and Rössler (2009) found that individuals with schizophrenia showed below average contagious yawning, and Rundle, Vaughn, and Stanford (2015) found that higher trait psychopathy, and in particular more psychopathic scores on the affective component of the Psychopathic Personality Inventory-Revised, predicted lower levels of contagious yawning. While attention to the social element of the yawning stimulus was not precisely controlled in these studies, allowing the result to be explained by attentional effects, there is less reasons to believe that individuals with schizophrenia or subclinical psychopathy would fail to attend to social stimuli in the same way as children with ASD. Although there could be other explanations for the findings, there is some preliminary evidence that individuals with disorders characterized by empathy deficits also show some deficits in the capacity to yawn contagiously.

Researchers have also examined the relationship between empathy and contagious yawning by investigating the link between yawning contagion and gender. Christov-Moore et al. (2014) use a wide array of evidence to suggest that women have a significantly better capacity for affective empathy as compared to their male counterparts, although neural and behavioral evidence suggests that while there are certainly some sex differences in cognitive empathy, women and men exhibit similar levels of it. Two studies have found a sex difference in the incidence of contagious yawning, with women yawning contagiously more frequently than men (Chan & Tseng, 2017; Norscia, Demuru, & Palagi, 2016), although a good number of other studies have tracked sex differences in their analysis and found no effect (Massen & Gallup, 2017). In spite of mixed evidence, there is support for the linkage between empathy and contagious yawning from gender differences in the effect.

Additional evidence for contagious yawning being tethered to a capacity for empathy comes from the developmental trajectory of contagious yawning. Anderson and Meno (2003) found that children do not begin to show yawn contagion under about 5 years of age, while Millen and Anderson (2011) confirmed that infants and toddlers do not show contagious yawning, and Helt et al. (2010) also found a developmental effect in contagious yawning. It is worth noting that one study seems to suggest that this failure to elicit contagious yawning in children below four years might be a result of attentional problems, as Hoogenhout, van der Straaten, Pileggi, and Malcolm-Smith (2013) were able to find evidence of contagious yawning in three year olds when they were instructed to look at the demonstrator’s eyes. Nevertheless, the overall developmental trend comes in concert with a large body of work cataloguing when children tend to develop their ability to empathize. In particular, the apparent age at which children develop contagious yawning comes after their capacity for motor mimicry and emotional contagion, but rather seems to loosely coincide with the development of theory of mind (Wellman, Cross, & Watson, 2001), although some studies have suggested that ToM also appears much earlier in development (Onishi & Baillargeon, 2005). Taken altogether, the evidence for the relationship between empathy and contagious yawning from developmental studies is a bit muddled, but could suggest further evidence for the link between the two.

Finally, many studies have investigated the link between empathy and contagious yawning by examining how contagion is modulated by social closeness. Under the assumption that empathy increases with social closeness, which is widely held in the field (Preston & de Waal, 2002), several studies have examined whether individuals are more likely to catch yawns from individuals they are more socially close to. Norscia and Palagi (2011), Norscia et al. (2016), and Palagi, Norscia, and Demuru (2014) have all found evidence to support this effect in humans, with yawning contagion being higher between kin, then friends, then acquaintances, and finally strangers. Furthermore, this method of measuring yawn contagion as it pertains to a capacity for empathy has been used even beyond human samples. In fact, one of the greatest areas of interest in the contagious yawning literature, and the major focus of this paper, is the evidence for contagious behaviors and empathy in the comparative literature.

1.4 Contagious yawning in other non-human species

One of the most remarkable features of yawning is its ubiquity across the animal kingdom. In fact, most vertebrate animals yawn, including virtually all mammals, birds, reptiles, and fish (Provine, 2005). The widespread nature of yawning suggests that it is an evolutionarily ancient phenomenon. In comparative psychology, where an understanding of what mental capacities exist in other species affords us a better understanding of how our own minds function, this makes studies of yawning its contagion an excellent resource for understanding our own capacity to yawn and the roots of our contagious yawning response. However, while yawning seems to be present in most vertebrate animals, the evidence for contagious yawning across the animal kingdom is less robust (Massen & Gallup, 2017). This may point to contagious yawning having a more evolutionarily recent origin, or reflect contagious yawning's relationship to some other evolutionarily recent feature of certain species, perhaps even empathy.

Contagious yawning in non-human populations was first observed in non-human primates. In particular, experimental evidence suggests that contagious yawning exists in *Pan troglodytes* (Amici, Aureli, & Call, 2014; Anderson, Myowa–Yamakoshi, & Matsuzawa, 2004; Campbell, Carter, Proctor, Eisenberg, & de Waal, 2009; Campbell & De Waal, 2011, 2014; Madsen, Persson, Sayehli, Lenninger, & Sonesson, 2013; Massen, Vermunt, & Sterck, 2012). As one of our closest evolutionary relatives, chimpanzees represent a close analogue to humanity to investigate which functions of our psychology are evolutionarily set, and which are a result of human social factors. In fact, several of these studies attested further support to the link between contagious behavior and empathy by showing that contagion was stronger among socially closer individuals (Campbell & De Waal, 2011, 2014). The presence of contagious yawning in chimpanzees therefore supported the evolutionary root of the behavior, and opened the field to determine where in the phylogenetic tree contagious yawning could be found. The bonobo (*Pan paniscus*), our other closest evolutionary relative, has also been shown to exhibit contagious yawning, and the modulation of contagion by social closeness (Demuru & Palagi, 2012; Palagi et al., 2014), although other studies failed to find evidence for yawn contagion in bonobos (Amici et al., 2014; Stevens, Daem, & Verspeek, 2017). It is interesting that bonobos have shown contagious yawning less reliably than chimpanzees, as both species are equally related to humans, having diverged from a common ancestor between 4.5 and 6 million years ago (Locke et al., 2011), and bonobos are usually thought to be less aggressive, more tolerant, and possibly more empathetic (de Waal & Lanting, 1997; Hare, Melis, Woods, Hastings, & Wrangham, 2007; Rilling et al., 2012). Nevertheless, one study showed evidence for contagious yawning in chimpanzees, but failed to show yawning contagion in bonobos and also failed to show yawning contagion in two other species of great ape (Amici et al., 2014): gorillas (*Gorilla gorilla*, diverged 6-8 m.y.a., Locke et al., 2011) and in orangutans (*Pongo abelii*, diverged 12-16 m.y.a., Locke et al., 2011). Unfortunately, fewer studies have examined contagious yawning in great apes outside of chimpanzees, but nevertheless, it does seem that contagious yawning has evolved as least as early as our common ancestor with the *Pan* genus.

Contagious yawning has also been observed in a several species of Old World monkeys, including stumptail macaques, *Macaca arctoides*, (Paukner & Anderson, 2006) and gelada baboons (*Theropitichus gelada*), where once again yawning contagion was modulated by social closeness (Palagi, Leone, Mancini, & Ferrari, 2009). To date, no other primate species, including any New World monkeys, have demonstrated contagious yawning, although many remain untested. Locke et al. (2011) estimate that we diverged from Old World monkeys between 25 and 33 million years ago, although given the negative results that have been observed in other primate species, it is unclear whether contagious yawning is evolutionarily common to our primate ancestor, or has convergently evolved alongside other cognitive traits. However, this picture becomes even more complicated when considering that contagious yawning has also been documented outside of the primate order in phylogeny.

Contagious yawning has been demonstrated in rats (*Rattus norvegicus*), although in this experiment the researchers conclude that a link between contagious yawning and empathy is unlikely, since yawning was modulated by scent cues, but was inversely correlated with social closeness (Moyaho, Rivas-Zamudio, Ugarte, Eguibar, & Valencia, 2015). Evidence for contagious yawning also exists in domestic sheep (*Ovis aries*) (Yonezawa, Sato, Uchida, Matsuki, & Yamazaki, 2017), and there is some anecdotal evidence for contagious yawning in elephants (*Loxodonta africana*) (Rossman et al., 2017). Even outside of the mammalian class, contagious yawning has been shown in a species of social parrot, the budgerigar (*Melopsittacus undulates*) (Gallup, Swartwood, Militello, & Sackett, 2015). Especially in the case of the budgerigar, contagious yawning seems to be spread more widely throughout the phylogenetic tree than what might be suspected given the negative results among some species of great ape.

Together, these results seem to suggest that contagious yawning, if evolutionarily ancient, has been lost in many species descended from that common ancestor. In fact, it seems perhaps more likely that contagious yawning has evolved several times in evolution (though to definitively support this claim is beyond the scope of this paper), and may perhaps be tied to the evolution of other cognitive processes. In particular, given the hypothesized link between contagious yawning and empathy in humans, these two processes may be under one set of evolutionary pressures, likely one that drives development of higher processes in the perception-action-model (de Waal & Preston, 2017; Preston & de Waal, 2002).

It stands to reason, therefore, that one of the species that has been most thoroughly studied in its capacity to yawn contagiously is *Canis (lupus) familiaris*, the domestic dog. Dogs have shown a remarkable attention to human social cues, above and beyond the abilities of both wolves (*Canis lupus*, dogs' closest genetic relative) and chimpanzees (one of our closest genetic relatives) (Hare, Brown, Williamson, & Tomasello, 2002). Although the theory is not without controversy (Udell, Dorey, & Wynne, 2008, 2010; Wynne, Udell, & Lord, 2008), one proposed explanation for this ability to understand human cues is that domestication has made dogs especially attuned to human social signals (Hare et al., 2010). But whether or not the process of domestication is responsible for the unique abilities dogs show in following human social cues, there is no denying that domesticated dogs have an important place in comparative psychology. Dogs are more distant from humans than our primate cousins in evolutionary terms, but dogs are raised in human environments, and the social interactions between dogs and humans are rich and complex. Furthermore, some experimental work in canines has suggested that dogs could possess a capacity for recognizing and responding to human emotions, approaching humans in distress with "comforting" behavior (Custance & Mayer, 2012) that resembles a human capacity to empathize. Dogs are poised, therefore, as an excellent species upon which to test the spectrum of the interaction between of our genetics and our social environment contagious yawning lies. And so it comes as no surprise that in investigating contagious yawning and its possible link to empathy, domesticated dogs have been one of the most studied species.

1.5 Contagious yawning in dogs

The first study to investigate contagious yawning in dogs was performed by Joly-Mascheroni, Senju, and Shepherd (2008). Departing from comparative studies on contagious yawning up to this point, the experimenters did not use a conspecific stimulus. Rather, a human experimenter demonstrated a fake yawn behavior, or a visual gaping-mouth control, to the dog. The experimenter would call the dog's name, and upon making eye contact, demonstrate the yawn or control behavior. This sequence was repeated for a duration of five minutes, and the yawning of the dog in response was recorded. Joly-Mascheroni et al. (2008) found evidence for contagious yawning, and a remarkably strong effect, with no dogs yawning in the control trials, but yawning appearing in 72% of the tested dogs in experimental trials. So it appeared that contagious yawning was not only present in dogs, but furthermore that dogs were able to catch yawns from humans. However, as additional researchers set out to replicate and extend the findings of this initial study, the picture of contagious yawning in dogs became increasingly muddled.

Harr, Gilbert, and Phillips (2009) used a slightly different method to examine whether yawn contagion existed in dogs, and found very different results. Attempting to test whether dogs would yawn contagiously in response to the yawns of conspecifics, Harr et al. used a method more similar to those employed with chimpanzees and other apes earlier, playing video recordings of dogs and humans yawning as the stimuli to induce contagion. Each participant dog was shown one minute clips of humans and dogs yawning, as well as open mouth controls for both conspecific and human model, followed by three minute observation periods. Ultimately, the result of this experiment did not provide evidence for contagious yawning at the population level, in response to dog or human yawns (Harr et al., 2009).

The next study to examine contagious yawning in dogs investigated whether social closeness might modulate the result. O’Hara and Reeve (2011) used several stimuli, in an attempt to replicate and extend both prior studies. They tested over two weeks, with both weeks involving a live yawn demonstration, a video recording of a conspecific yawn, an open-mouth control live demonstration, and an audio recording of a yawn. Each demonstration period lasted three minutes, and was separated by two minute observation periods. In the first week of testing, the yawn and control live demonstrations were performed by the dog’s guardian (i.e. owner), a socially close individual. In the second week, these demonstrations were instead performed by the experimenter, an unfamiliar, more socially distant individual. These researchers also set out to investigate an alternative explanation for yawning in dogs: stress. Dogs are known to exhibit yawning in times of stress and tension as a diffusionary behavior (Beerda, Schilder, van Hooff, de Vries, & Mol, 1998). Consequently, O'Hara and Reeve recorded heart rate, as a way to test if the dogs were yawning as a result of increased stress or general arousal. In their analyses, O'Hara and Reeve ultimately found no support for yawning contagion, comparing the incidence of yawning in conspecific and heterospecific yawning trials to the audio and visual controls. Furthermore, they found no significant differences between familiar and unfamiliar demonstrations, suggesting no modulation of contagion by social closeness (2011). Finally, they found no significant differences in heart rate. The researchers took their results as a suggestion that contagious yawning, if present in domesticated dogs, is not linked to a capacity for empathy, but is more likely a form of nonconscious mimicry as per Yoon and Tennie (2010).

Silva, Bessa, and de Sousa (2012), however, reignited the case for the empathy-contagious yawning hypothesis when their study found support for contagious yawning in dogs and, further, modulation of the effect by social closeness. In particular, these researchers tested if contagion could occur divorced from the social elements of a live demonstrator, and measured contagion after exposure to audio stimuli of yawns from the dog's guardian, the experimenter, and associated controls (yawn audio digitally reversed). Their results provided support for contagious yawning in dogs, with both familiar and unfamiliar yawns eliciting greater contagion than controls. Furthermore, their results also provide evidence for social closeness modulation, with familiar yawns creating a significantly higher number of contagious yawns than unfamiliar yawns, but no difference between familiar and unfamiliar control sounds (Silva et al., 2012). Departing sharply from the earlier study by O'Hara and Reeve, these data seemed to suggest a link between empathy (or at least social closeness) and contagious yawning in dogs, even with nothing more than auditory stimuli. Furthermore, Silva et al. (2012) found no significant differences in attention to the various stimuli, suggesting that the effect could not be accounted for by greater attention to the familiar stimulus, but rather seemed to reflect genuine modulation of contagion by social closeness.

And yet, the picture grows ever more complicated with the inclusion of data from Madsen and Persson (2013). These researchers once again reverted to a method relying on live demonstrations by familiar and unfamiliar humans, this time further investigating whether there existed a developmental effect for contagion in dogs by examining differences between dogs at different ages before fourteen months. This experiment's method departed a bit from the other studies utilizing live demonstrations of yawn and gape behavior, in that the experimenters interacted with the dogs throughout the experimental duration (cuddling, grooming, playing), and interspersed the experimental behaviors throughout. Testing durations were five minutes, with five minute observation periods between trials. These researchers found evidence for contagious yawning as compared to a control, but only in dogs older than seven months (Madsen & Persson, 2013). This fits with the findings in humans suggesting that contagious yawning has a developmental effect, as documented in studies with human children (Anderson & Meno, 2003; Helt et al., 2010; Millen & Anderson, 2011). However, Madsen and Persson (2013) did not find any evidence for the modulation of contagious yawning according to social closeness, adding some doubt to the proposed link with empathy.

Nevertheless, Romero, Konno, and Hasegawa (2013) conducted another study attempting to document the possible link between contagious yawning and social closeness in dogs. These researchers also employed the live demonstration method, with five minute demonstrations of yawning and gaping performed by experimenters and guardians. These researchers also used a heart rate monitor to collect the dogs' heart rates so as to address the possibility of tension yawns. Their data ultimately supported the presence of contagious yawning in dogs, and further supported the modulation of yawning contagion by social closeness. Furthermore, they recorded no significant differences in heart rate during the experiment, ruling out the possibility of increased yawning due to stress or arousal (Romero et al., 2013). These same researchers provided additional evidence for the link between contagious yawning and social closeness by providing observational evidence for contagious yawning and its social modulation in wolves (*Canis lupus*) (Romero, Ito, Saito, & Hasegawa, 2014). Wolves are able to interbreed with domesticated dogs, and are essentially the same species without the influence of domestication by humans.

Another recent study of contagious yawning in domestic dogs was performed by Buttner and Strasser (2014). These researchers used live demonstrations of yawns and mouth gapes performed by an unfamiliar experimenter, using a population of shelter dogs. The researchers also recorded salivary cortisol measurements from the dogs tested, as a way to see if yawns could be attributed to arousal or stress. Finally, the experimenter also performed a social object choice task, to see if dogs that exhibited yawn contagion were more attentive to human cues in this object choice context. Buttner and Strasser (2014) did not find evidence for contagion at the population level, and they also found no correlation between yawning contagion and performance on the object choice task. Finally, they found that among dogs that showed contagious yawning, cortisol levels remained constant during the duration of the experiment, whereas cortisol levels decreased over time for dogs that did not show contagious yawning. The researchers took this as data suggesting that contagious yawning in dogs is likely not linked to a capacity for empathy, but more likely occurs as a communicative function relating to increased arousal (Buttner & Strasser, 2014).

Most recently, an investigation of contagious yawning in dogs was carried out in Stewart et al. (2015). This paper, which examined the potential of citizen science platforms for investigating canine cognition, included in its battery of tasks a test of yawning contagion. Therefore, in methodology, this paper departs rather starkly from the rest of the literature, relying on guardians as experimenters. In the test condition, guardians were instructed to yawn at their dog every five seconds for thirty seconds, and live recorded any yawning behaviors in their dogs. As a control, the guardians said the word "yellow" every five seconds for thirty seconds. In experimenter, the dramatically shorter observation period of the study, and in its control behavior, this experiment departed from the literature. However, like the literature, this investigation yielded mixed results. Their analyses are split into two testing sessions, a beta version of the citizen science web platform (*N*=245), and the official live release version (*N*=277). In the beta dataset, Stewart et al. (2015) found a small, significant effect of contagious yawning, with 66 dogs yawning in the experimental condition and only 44 yawning in the control condition. In the live dataset, no difference was recorded, with 65 dogs yawning in the control condition, and 64 dogs yawning in the experimental condition. As a combined dataset, no significant effect was found.

Taken altogether, the literature concerning contagious yawning in *Canis (lupus) familiaris* is quite conflicted, with several studies suggesting that contagious yawning exists and several suggesting it does not. Furthermore, even among those researchers who believe contagious yawning does exist in domestic dogs, there is still considerable debate as to whether that contagion is related to a capacity for empathy or more likely related to some lower level form of arousal or mimicry. And so it is to these questions that the present paper documents two attempts to contribute to and clarify this literature. First, an extension and replication of the experiments performed heretofore, introducing a new modality of contagion (itch) in an effort to clarify under what domains, if any, contagion is linked to a capacity for empathy in canines. Second, a meta-analysis of the literature including this most recent extension, in an effort to summarize and clarify whether dogs do, in fact, exhibit contagious yawning.

2. Study 1: An investigation of contagious yawning and contagious itch in canines

While it is among the most widely known and widely studied of its kind, yawning is by no means the only documented example of a contagious behavior. Laughter is another contagious behavior in humans (Provine, 1992), as is the sensation of itch (Schut, Grossman, Gieler, Kupfer, & Yosipovitch, 2015).

2.1 Contagious itch

Contagious itch was first demonstrated by Niemeier and Gieler (2000), where viewers of a presentation about itch—featuring images of insects, scratch marks, and allergic reactions—scratched themselves significantly more than viewers of a similar visual presentation on relaxing. It has since been replicated in experimental studies on humans many times. Images and videos of scratching, as well as images of irritants on skin, have been reliably shown to increase self-reported feelings of itchiness, as well as increased scratching (for review, see Schut et al., 2015). However, the precise mechanisms underlying contagious itch are not precisely known. Some researchers have suggested that contagious itch is related to the capacity for empathy, especially because participants in experiments often closely match in their assessments of their own itchiness and how itchy they believe the individual in stimuli images to be (Lloyd, Hall, Hall, & McGlone, 2013).

Notably, contagious itch has also been demonstrated in non-humans. Feneran et al. (2013) demonstrated contagious itch in rhesus macaques (*Macaca mulatta*), with observational evidence of macaques scratching themselves more often within 60 seconds of a cage-mate scratching an itch and with experimental evidence demonstrating macaques showed greater scratching behavior when watching a video of a conspecific scratching as opposed to control videos. Furthermore, Yu, Barry, Hao, Liu, and Chen (2017) found evidence for contagious itch in mice (presumably *Mus musculus*), with mice showing a greater incidence of scratching an itch after watching a mouse scratch an itch in an adjacent container, as well as a greater incidence of scratching after watching videos of a conspecific scratching as opposed to control videos. Yu et al. (2017) conclude that their experiment suggests that contagious itch is perhaps divorced from a capacity for empathy, both on account of the fact that the transmission of itch for mice occurs regardless of familiarity, whereas empathy in mice has been previously postulated only to exist among familiars (Langford et al., 2006), and on account of the fact that their neural data suggests artificial stimulation of gastrin-releasing peptide receptor cells in the superchiasmatic nucleus could effectively mimic contagious scratching behavior. In other words, contagious itch appeared to occur as a result of a low level, automatic activation of a cascade of neural networks, rather than as part of a higher cognitive/affective capacity for empathy (Yu et al., 2017).

Contagious itch therefore appears a useful behavior to use for comparison with contagious yawning. Both involve an automatic, unconscious response to a physically stereotyped action, both are present in humans and at least some non-human species, and while contagious yawning has a proposed link to empathy, contagious itch is perhaps motivationally distinct, and more essentially involves lower level activation. In this first experiment, it was investigated whether dogs (*Canis familiaris*) would show contagious yawning and contagious itch under similar circumstances, if at all. This experiment would also represent the first attempt to document contagious itch in canines, as well as the first test of heterospecific contagious itch in a non-human species.

2.2 Methods

In general, the method of this experiment followed the conventions established by Joly-Mascheroni et al. (2008) and followed widely in the literature; live demonstrations of yawns and control behaviors were performed in front of the dogs by the experimenter. However, this experiment differed in several domains from previous research, notably in the inclusion of two new behaviors, an itch and associated control behavior.

2.2.1 Subjects

Forty-five domestic dogs, of various breeds and ages were recruited to participate in this study. All participating dogs were pets, recruited from the subject pool for the Canine Cognition Center at Yale University. No dogs had participated in any earlier pilot studies on related questions. All participant dogs were current on standard immunizations, and informed consent was received from the guardians of each dog. Five dogs were excluded from data analysis on account of error in the experimental procedure (N=1), or because the experimenter deemed the dog to be uncomfortable or stressed (N=4), so a total of forty dogs were included in the full procedure and subsequent data analysis.

2.2.2 Stimuli

Both the yawning and yawn control stimuli were modeled closely on the stimuli from the literature. The yawn behavior lasted about six seconds, and involved the experimenter closing his eyes, leaning his head back, and performing a fake yawn in visual and auditory modalities. The yawn control behavior was a mouth-gape behavior, as in the literature. The experimenter stretched his mouth open noiselessly, leaving eyes open, for a total duration of about six seconds. While in a normal ecological setting, yawning is often accompanied by stretching of the limbs or other body parts, referred to as pendiculation, this experiment followed the standard of the literature by only exhibiting movement of the head and neck in the yawn and control behaviors. While this might reduce the ecological salience of the demonstration slightly (although work by Provine (2005) suggests that parsimonious yawning stimuli are still able to elicit contagion) the more constrained demonstration better controls against variance in demonstrations between subjects.

Both the scratching and control behaviors were original to this experiment. The scratching behavior was intended to strike a middle ground between a naturalistic human scratching behavior and the scratching behavior of dogs; it involved the experimenter reaching across his body with his right hand to scratch the area of his left collarbone with all four fingers. The fingers and hand of the experimenter moved in a scratching motion, at a rate of about 150 scratches / minute, for a duration of six seconds. This rate was found by the experimental team to satisfyingly mimic the sound and impression of a dog scratching itself, while remaining authentic to natural human scratching behavior. The itch control behavior was designed, like the yawn control, to match the experimental behavior in duration and motor activation silently. The experimenter bent his right elbow to hold his hand up straight in front of his right shoulder, with the wrist bent so that the forearm was almost perpendicular to the ground, while the palm of the hand lay parallel to the ground. The experimenter would rotate his forearm and wrist so that his hand, while remaining parallel to the ground, rotated leftward towards his chest, and then returned to its starting position. This rotation would occur at the same rate as the scratching behavior, approximately 2.5 Hz, for a duration of about six seconds.

There is some concern that the itching behaviors are not ecologically salient to dogs, especially because scratching behaviors by dogs are commonly performed with a hind leg, without crossing the body axis. However, the stimuli that was eventually performed was considered a good compromise between an ecologically valid human scratching behavior and a behavior that would be salient to dogs. Furthermore, evidence from the human contagious itch literature suggests that the localization of contagious itch is not tied to the location of a demonstration itch (Ward, Burckhardt, & Holle, 2013).

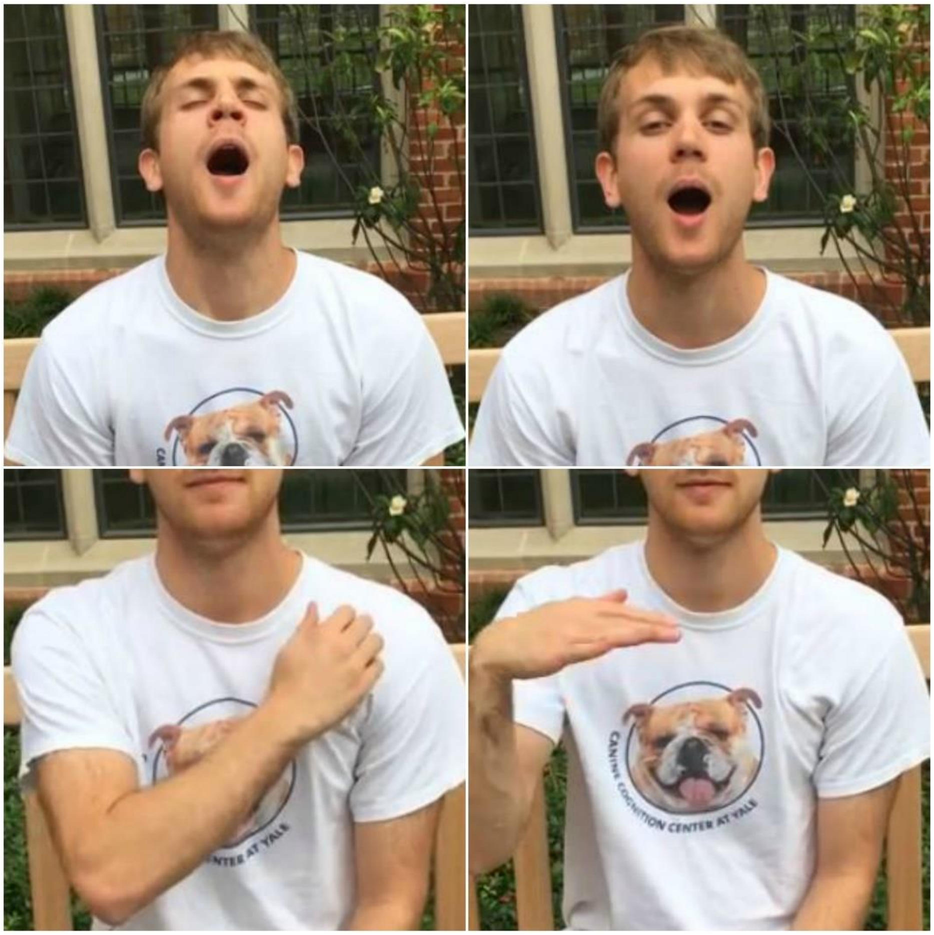

Figure 1- *The four stimuli used: yawning (top-left), the yawn control, open mouth-gape (top-right), the itch (bottom-left), and the itch control, arm rotation (bottom-right). All stimuli lasted six seconds; both the itch and itch control involved hand movement at 2.5Hz, with the hand either translating in a scratching motion, or rotating within the plane perpendicular to the ground.*

2.2.3 Procedure

All participants were tested in the same geographical location, in a closed room at the Canine Cognition Center in New Haven, CT. Guardians were seated in one corner of the room, with the subjects seated directly in front of them, facing the center of the room, and the experimenter. The experimenter was seated on a stool approximately 1 meter in front of the subject and facing the subject.

At the start of testing, the guardians were instructed to sit with their eyes closed, so as to avoid any possible social referencing effects or priming by the guardian (Pfungst, 1911). They held the subjects in place by a leash throughout the experiment.

The experiment was divided into four trials, the yawn, the yawn control, the itch, and the itch control (see Fig 2 below). Each section consisted of one minute in which the experimenter demonstrated the behavior, and one minute where the experimenter sat at rest with head down, as an observation period. The guardians were allowed to open their eyes during the observation periods of each section, but were instructed to sit quietly and let their dog rest. At the end of the first section, the experimenter would inform the guardian that the second would begin. After the second section, the experiment would pause, the guardian and dog would leave the room, and complete an unrelated experiment. Later in the session visit, sections three and four of the experiment would proceed exactly as described for parts one and two. The order for whether yawning or itching was tested first was counterbalanced, as was the order of whether the experimental behavior (yawn/itch) or the associated control was shown first. Each experimental behavior was completed immediately before or after its control.

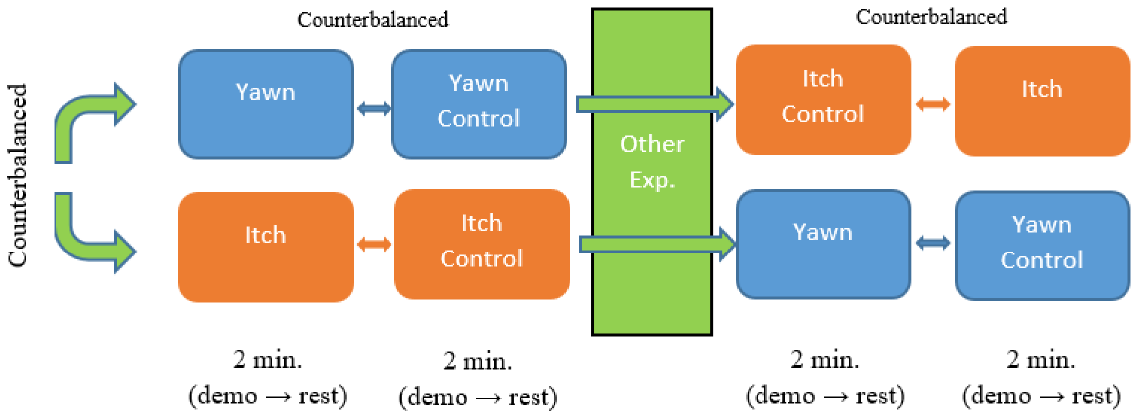

Figure 2- *The order of the experiment. Order of the presentation of modality (yawn or itch) is counterbalanced, as is the order of presentation of the controls and experimental blocks. Each block last two minutes, with one minute of demonstration, and one minute of observation.*

Within each trial, the first minute of demonstration followed the convention of the literature, and involved continuous demonstration for the full minute period. The experimenter would call the dog's name, make eye contact, and perform the behavior. As soon as the behavior was completed, the experimenter would repeat these steps, performing the sequence as many times as possible for one minute. At the end of one minute, the experimenter would tell the guardian they could open their eyes, and would sit quietly for one minute.

2.2.4 Data collection

During testing, the experimenter would keep track of yawns and scratching behaviors performed by the subject, but this live coding was only secondary. Throughout the experiment, a GoPro camera recorded the view of the subject from a position under the experimenter's seat, looking directly at the subject. The recordings from each session were blind coded later by the primary experimenter and an unfamiliar other, for yawns or scratching behaviors observed (scratching behaviors within scratching and control trials, yawning behaviors within yawn and control trials). A 100% reliability was found between coders with respect to yawns recorded, while a 96% reliability was found between coders with respect to scratching behaviors recorded.

2.2.5 Data processing

While data had intitially been tabulated separately for the period of time (1 min.) when a demonstration was being performed and the period of time (1 min.) meant for observation immediately following, the number of yawns or scratching behaviors within these two period were summed.

2.3 Results

Of the forty dogs included in analyses, seven dogs yawned in the experimental condition, and three dogs yawned in the control condition. Four dogs scratched themselves in the experimental condition, and two dogs scratched themselves in the control condition. No dogs yawned or scratched themselves more than once, and no dogs yawned in both control and experimental conditions nor scratched in both control and experimental conditions. This means that the number of behaviors exhibited and the number of dogs exhibiting those behaviors are the same.

A chi-square test of independence was performed to examine the relation between yawning stimulus and yawning response. The relation between these variables was not significant, ($\chi^2(2,40)=1.83$, $p=0.176$). A second chi-square test of independence was performed to examine the relation between itching stimulus and itching response. The relation between these variables was not significant, ($\chi^2(2,40)=0.72$, $p=0.396$).

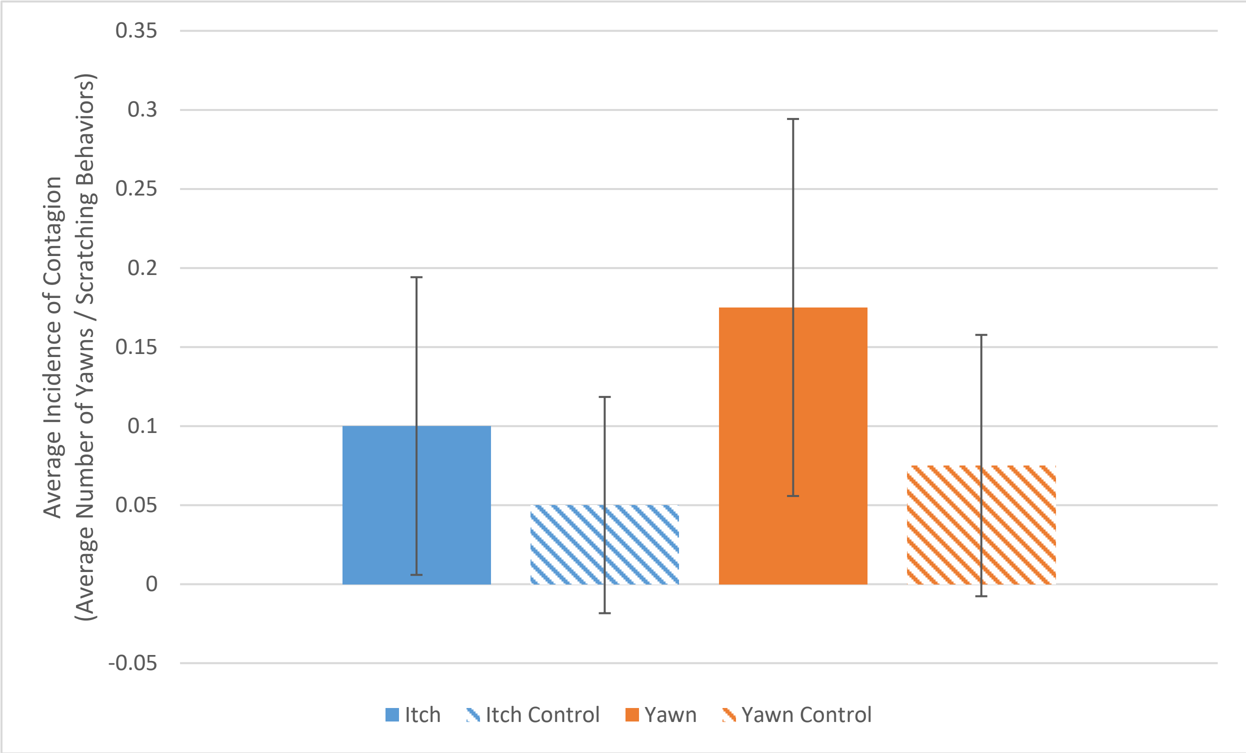

Figure 3- *The average number of yawns and scratching behaviors performed in each condition. Error bars represent 95% confidence intervals. There are no significant effects.*

2.4 Discussion

Overall, in this experiment, the incidence of yawning is much lower than reported in any previous study examining contagious yawning in dogs. While there is an effect, wherein more dogs did show yawning contagion in the experimental periods as compared to control periods, this effect is relatively small overall, and not significant. To this end, the present data corroborate the results from Harr et al. (2009), O'Hara and Reeve (2011), and Buttner and Strasser (2014), failing to show contagion. At the same time, they come in conflict with the results of Joly-Mascheroni et al. (2008), Silva et al. (2012), Madsen and Persson (2013), and Romero et al. (2013).

Furthermore, in the first investigation of contagious itch in canines, and the first study of itch contagion across species, the null hypothesis was again supported; dogs do not appear to demonstrate contagious itch, or at least not the contagious scratching of itch across species. The overall incidence of contagious scratching was even lower than contagious yawning, and while greater contagion was found in the experimental condition in comparison to the control, this effect is far from significant.

Nevertheless, it is perhaps incorrect to take these findings as definitive evidence for the absence of contagious yawning and itch in canines. This study differed from the literature on contagious yawning in some important ways, notably in having a much shorter observation window than in most of the experiments performed heretofore (2 minutes in each condition vs. 5 minutes in each condition previously). Only one other study investigating contagious yawning in dogs has used similarly short testing periods (Stewart et al., 2015), and this study also found low overall incidence of contagious yawning. The shorter testing period in this experiment was implemented for three reasons: in order to better fit with the testing conventions at the place of research, in order to avoid stress for the subjects and preserve their interest, and for theoretical reasons. While many studies investigating contagious yawning have implemented five minute-long periods of demonstration and observation, rarely would we consider a yawn we perform 250 seconds after our friend yawns an example of us catching that yawn from them. Certainly, five minute observation periods are standard in the literature, and this experiment's methodological departure could perhaps explain the extremely low incidence of yawning recorded. But recently, contagious yawning effects in general have come under scrutiny, with Kapitány and Nielsen (2017) arguing that several factors in the literature, long testing periods included, could be finding contagious yawning effects as Type I errors. The evidence of this paper is certainly insufficient to definitively suggest contagious yawning does not exist in canines. However, it does raise the need for further investigation into the latency of yawns in contagious yawning experiments.

Meanwhile, while this experiment does provide data suggesting that dogs do not scratch itches contagiously from a human demonstrator, there are many factors that deserve further exploration and explanation in this field. Perhaps chiefmost, this experiment utilized two novel stratching demonstrations, which were perhaps inadequate as modelled stimuli for canines. Humans and canines often scratch itches in methodologically distinct ways, on account of differences in anatomy and dexterity. It is definitely possible that the itch demonstration in this experiment was inadequate in producing contagion because it did not convey any meaningful information to the subjects. Further investigation of contagious itch in canines, especially using a conspecific demonstrator, might provide a clearer answer to the question.

Finally, the chief aim of this experiment's design was to investigate if there would be a difference between contagious yawning and contagious itch behaviors in canines that could possibly help elucidate the mechanism of contagious behaviors in dogs and their possible link to a capacity for empathy. While there was a slightly greater incidence of yawning behavior as compared to scratching behavior in the respective experimental conditions, there was no significant difference between these two behaviors. This could mean that contagious yawn and contagious itch, if present at all in canines, operate by a similar mechanism. Or this experimental design lacks sufficient power to demonstrate a difference between these two mechanisms. Either way, especially with so many unanswered questions about the presence of contagious behavior in dogs and its possible mechanisms, the present results do not do much to make the results of the field clearer. Therefore, a second study performed a meta-analysis of the contagious yawning literature in canines to elucidate any underlying trends in the data.

3. Study 2: A meta-analysis of contagious yawning in canines

Studies of contagious yawning in dogs have led to mixed results, leaving the literature at large without a clear picture of whether or not contagious yawning exists in canines, and further leaving the potential mechanism of this contagion unknown. This meta-analyses aims to make clear the overall trend in the literature, using all published studies examining contagious yawning in canines thusfar and including the data from Study 1 of this paper.

3.1 Methods

Papers were gathered in response to the question "Do dogs show contagious yawning behavior?" Using the electronic database Google Scholar, the scientific literature was searched form the earliest entries to 22 February 2018 for peer-reviewed publications that focused on the investigation of contagious yawning in dogs. In conducting this search, the first 200 hits of each search were reviewed. Furthermore, the reference section of each relevant article was also reviewed for any additional articles that were considered appropriate. Searches were conducted using terms relevant to the subject and typical methods of studies investigating contagious yawning. These terms include *Canis* yawning, *Canis* contagious behavior, *Canis* contagion, *Canis* yawn gape, *Canis* yawning empathy, *Canis* yawning social, *Canis* social contagious behavior.

The criteria for selection included that papers be written in English. Furthermore, papers were only included in the analysis if they investigated contagious yawning in dogs; studies involving the study of spontaneous yawning in dogs were not included. Only studies that examined contagious yawning in domesticated dogs were included, excluding one study investigating contagious yawning in wolves. One peer-reviewed study was included in the analysis which did not appear given the criteria of the literature search that had been established at the outset. This paper, by Stewart et al. (2015) was considered relevant by the author, as it included in a battery of measures a test of yawning contagion as opposed to a live human control, and so was included even though it did not appear in the literature search as established beforehand. Finally, one non peer-reviewed study was included in the analysis, performed in Study 1 of this paper, referred to henceforth as Bowers et al.

Overall, nine studies were included in the meta-analysis, representing 722 dogs from five different countries. The studies included are summarized below in Table 1.

Author	**Year**	**Country**	**N**
Bowers et al.	NA	USA	40
Buttner & Strasser	2014	USA	58
Harr et al.	2009	UK	15
Joly-Mascheroni et al.	2008	UK	29
Madsen & Persson	2013	Finland	35
O'Hara & Reeve	2011	UK	19
Romero et al.	2013	Japan	25
Silva et al.	2012	Portugal	29
Stewart et al.	2015	USA	522

Table 1- *Characteristics of study included in meta analysis*

3.2 Results

A random effects model meta-analysis, using restricted maximum likelihood, of contagious yawning in canines yielded a weighted average Hedges' *g* significantly greater than zero (g=0.45, 95% CI [0.17,0.73] N= 9, z= 3.12, p=0.001). The total heterogeneity of the meta-analysis was 74.04%, with a Q value of 30.12, p=.0002.

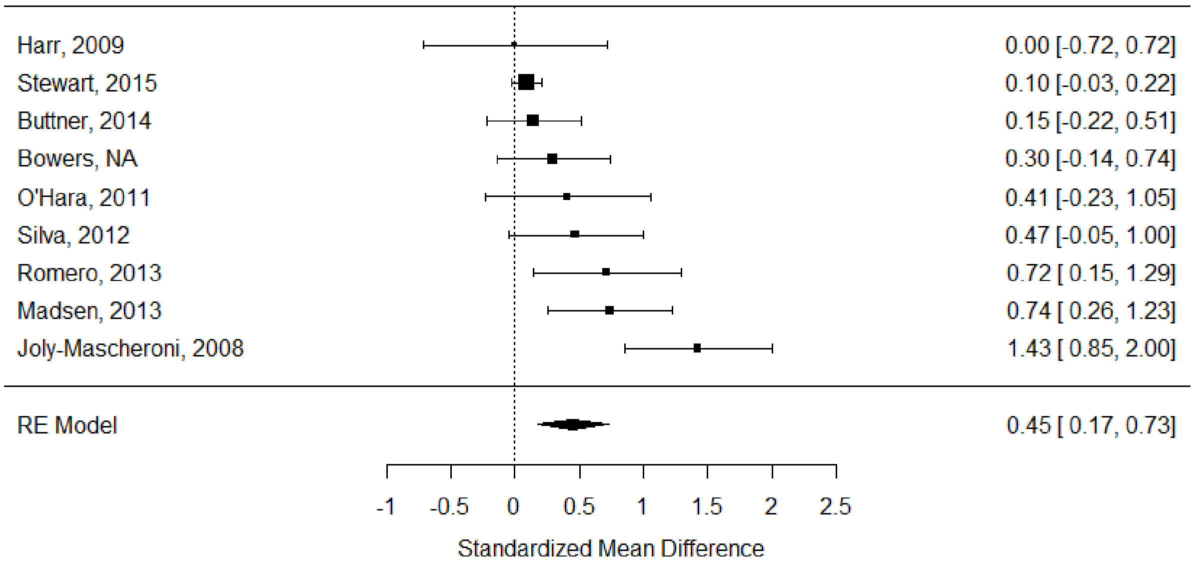

Figure 4- *Forest plot visualizing the meta-analysis of contagious yawning in canines. A significant effect of contagious yawning is found.*

An analysis was also run on only those studies that controlled for stress yawning in their analyses, whether by explicitly excluding stress yawns from their analysis (Harr et al., 2009), finding no significant differences between experimental and control conditions in physiological measures of stress (O'Hara & Reeve, 2011; Romero et al., 2013), or by taking steps in the experimental method to minimize stress (Madsen & Persson, 2013; Silva et al., 2012). The summary effect remained significant, and actually became more significant (r=0.53, 95% CI [0.27,0.78] N= 5, z= 4.04, p< 0.0001). Heterogeneity of this restricted model was also dramatically reduced, with 0.00% heterogeneity, Q=3.43, p=0.49.

Looking once more at the main model, including all studies, several tests were performed to examine whether there might be a file-drawer problem. Neither Egger's test (z= 1.38, p= 0.17) nor a rank correlation test (Kendall's tau= 0.28, p= 0.3585) were significant, suggesting that there is no significant publication bias in the literature.

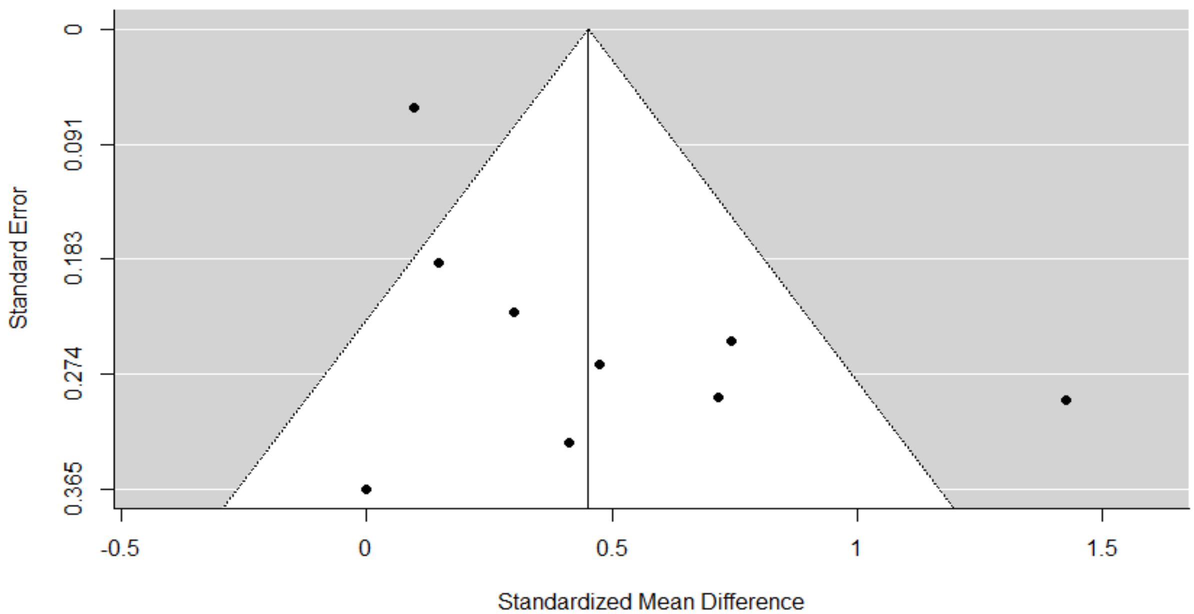

Figure 5- *Funnel plot for meta-analysis of contagious yawning in canines, no evidence for publication bias is found.*

3.3 Discussion

The meta-analysis, while modest in its summary effect, suggests that there is some evidence for contagious yawning in domesticated dogs, after all. Especially promising is the consistency of the effect when controlling for stress yawns in the sample, suggesting that the effect persists in spite of what has been considered a notable confound in the literature. In fact, the effect is stronger in those studies that controlled for stress yawns, and the heterogeneity of the model is dramatically lower, suggesting there is no additional factor that is explaining the variation between studies. However, with a literature as conflicted as this one, and with a modest effect overall, it is worth remarking upon the fact that contagious yawning in dogs does not seem to be as robust as it appears in humans.

Furthermore, while this meta-analysis does have the advantages of greater statistical power, it does not fully and definitively explain the results of the literature to this point. As lamented by Campbell and de Waal (2010), there is a large amount of methodological variation in the study of contagious yawning, and this makes generalizing between studies difficult. In the canine literature alone, tests for contagious yawning have used at least three different control behaviors, observation periods have varied, observation locations have varied, guidelines for interacting with the dogs during testing are not standardized, etc. Outside of the normal variation of statistical chance, perhaps the most explanatory variables are experimental duration and demonstration stimuli. Among the notable negative results in the literature, Bowers et al. and Stewart et al. (2015) used dramatically shorter testing durations, and Harr et al. (2009) and O'Hara and Reeve (2011) both included video demonstrations as part of their stimuli. These differences could explain some of the variation in the literature, but on the other hand, especially in a time when contagious yawning no longer seems a scientific surety (Kapitány & Nielsen, 2017), it is important to remain open to the possibility that contagious yawning may not exist in dogs.

In addition to the meta-analysis reported in this paper, there is some strong potential in this analytical approach for further elucidating the literature on this subject. In particular, while Egger's test and a rank correlation test did not find any significant evidence for a publication bias, the random effects model could be improved with the addition of any potential unpublished data on contagious yawning in dogs. Furthemore, although the data was not publicly available to perform such an analysis, a meta-analysis could also be performed on those studies that investigate an effect of social modulation on contagion, to discern whether contagious yawning in dogs has any relationship to social closeness and, by extension, a capacity for empathy.

As it stands, there is perhaps some additional evidence to suggest that contagious yawning remains an intriguing piece of evidence for investigating a capacity for empathy in our domestic canines. Given the evidence from neural data, studies of clinical populations, and developmental and comparative studies, there does seem to be evidence that contagious yawning is linked to a capacity for empathy in *some* way. However, to suggest that contagious yawning coincides with a rich capacity for cognitive or affective empathy as seen in humans is perhaps overly bold. Nevertheless, likely in its functioning as part of the perception-action-model, contagious yawning may still be a useful way of investigating the underlying processes of empathy and other social behaviors in canines, in other species, and in ourselves.

4. General discussion

This paper makes two contributions to the investigation of canine cognition and the study of contagious behaviors more generally. First, a replication and extension finds limited evidence for contagious yawning in dogs, and further provides the first piece of evidence suggesting a lack of contagious itch behavior in dogs. In particular, this first result suggesting a lack of contagious itch in canines merits further investigation. If the contagious yawning literature is any indication, there remains a strong possibliity that contagious itch does exist in dogs, and either random variation or some methodological shortcoming of this experiment have obfuscated a real effect.

Second, a meta-analysis performed in this paper of the canine literature provides modest support for contagious yawning. The present meta-analysis can help researchers to have greater faith in studies demonstrating contagious yawning in canines, and allow for the exploration of additional factors that explain the specific conditions that increase or affect contagion. For instance, a systematic analysis of the latency of yawning contagion in canines (and generally among other species) could greatly improve our understanding of what truly counts as yawning contagion, and what is more likely a result of environmental circumstances (like stress) or an instance of spontaneous yawning. Another promising avenue for research is the comparison of different modalities of behavior contagion. Although Study 1 in this paper provided no evidence for contagious itch in canines, exploration of this and other possible contagions (contagious sniffing, perhaps) might provide insight into what sorts of behaviors take on the unique connection to sociality as to become contagious.

Lastly, it is the hope of the author that this paper also serves as an introduction to the richness of the contagious behavior literature, and of cognitive science more generally. As evidenced by this paper, the phenomenon of contagious yawning, and behavioral contagion generally, is quite complex and deeply interesting. The aim of cognitive science is to understand the mind, and in this pursuit it is easy to marvel at our more complex mental abilities. But even the most basic, mundane behaviors can in fact be signposts to sophisticated cognitive abilities, and great depths of complexity and intricacy.

Author Contributions

The literature review and research performed to write the introduction of this paper was performed by Bowers. The methods of the experiment in study 1 of this paper were designed by Bowers, Professor Santos, and the lab manager, Mikey Bogese. These methods were based on an earlier pilot study designed by Santos and Bogese and performed by Bogese, which examined only contagious itching. The experiment in Study 1 was performed by Bowers, with Bogese present for consultation, and Santos advising. An initial analysis of the data was performed by Santos and Bowers, although all figures in this paper were produced by Bowers. The meta-analysis constituting Study 2 was performed by Bowers, in consultation with graduate students Angie Johnston—who helped Bowers to establish a criteria for the literature search component of the meta-analysis—and Gordon Kraft-Todd, who advised Bowers on the statistical approach of the meta-analysis. After the literature search was conducted by Bowers, Kraft-Todd performed an analysis of the data which informed the writing of a draft of this thesis. Bowers then performed the meta-analysis himself, under advisement by Kraft-Todd to ensure accuracy, and produced all analyses found in this final draft. Santos provided advisement and revision on the updated draft of the paper.

References

Amici, F., Aureli, F., & Call, J. (2014). Response facilitation in the four great apes: is there a role for empathy? *Primates*, *55*(1), 113-118.

Anderson, J. R., & Meno, P. (2003). Psychological influences on yawning in children. *Current psychology letters. Behaviour, brain & cognition*(11, Vol. 2, 2003).

Anderson, J. R., Myowa–Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences, 271*(Suppl 6), S468-S470.

Arnott, S. R., Singhal, A., & Goodale, M. A. (2009). An investigation of auditory contagious yawning. *Cognitive, Affective, & Behavioral Neuroscience, 9*(3), 335-342.

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of autism and developmental disorders, 34*(2), 163-175.

Bartholomew, A. J., & Cirulli, E. T. (2014). Individual variation in contagious yawning susceptibility is highly stable and largely unexplained by empathy or other known factors. *PloS one*, *9*(3), e91773.

Beerda, B., Schilder, M. B., van Hooff, J. A., de Vries, H. W., & Mol, J. A. (1998). Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Applied Animal Behaviour Science, 58*(3), 365-381.

Buttner, A. P., & Strasser, R. (2014). Contagious yawning, social cognition, and arousal: an investigation of the processes underlying shelter dogs' responses to human yawns. *Animal cognition, 17*(1), 95-104.

Campbell, M. W., Carter, J. D., Proctor, D., Eisenberg, M. L., & de Waal, F. B. (2009). Computer animations stimulate contagious yawning in chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20091087.

Campbell, M. W., & de Waal, F. B. (2010). Methodological problems in the study of contagious yawning *The mystery of yawning in physiology and disease* (Vol. 28, pp. 120-127): Karger Publishers.

Campbell, M. W., & De Waal, F. B. (2011). Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PloS one, 6*(4), e18283.

Campbell, M. W., & de Waal, F. B. (2014). Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. *Proc. R. Soc. B, 281*(1782), 20140013.

Chan, M. H., & Tseng, C.-H. (2017). Yawning Detection Sensitivity and Yawning Contagion. *i-Perception, 8*(4), 2041669517726797.

Christov-Moore, L., Simpson, E. A., Coudé, G., Grigaityte, K., Iacoboni, M., & Ferrari, P. F. (2014). Empathy: Gender effects in brain and behavior. *Neuroscience & Biobehavioral Reviews, 46*, 604-627.

Cooper, N. R., Puzzo, I., Pawley, A. D., Bowes-Mulligan, R. A., Kirkpatrick, E. V., Antoniou, P. A., & Kennett, S. (2012). Bridging a yawning chasm: EEG investigations into the debate concerning the role of the human mirror neuron system in contagious yawning. *Cognitive, Affective, & Behavioral Neuroscience, 12*(2), 393-405.

Custance, D., & Mayer, J. (2012). Empathic-like responding by domestic dogs (Canis familiaris) to distress in humans: an exploratory study. *Animal cognition, 15*(5), 851-859.

Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of personality and social psychology*, *44*(1), 113.

de Waal, F. B. (2007). The 'Russian doll'model of empathy and imitation. *On being moved: From mirror neurons to empathy,* 35-48.

de Waal, F. B., & Lanting, F. (1997). *Bonobo: The forgotten ape*: Univ of California Press.

de Waal, F. B., & Preston, S. D. (2017). Mammalian empathy: behavioural manifestations and neural basis. *Nature Reviews Neuroscience, 18*(8), 498.

Demuru, E., & Palagi, E. (2012). In bonobos yawn contagion is higher among kin and friends. *PloS one, 7*(11), e49613.

Derntl, B., Finkelmeyer, A., Toygar, T. K., Hülsmann, A., Schneider, F., Falkenberg, D. I., & Habel, U. (2009). Generalized deficit in all core components of empathy in schizophrenia. *Schizophrenia research, 108*(1), 197-206.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research, 91*(1), 176-180.

Dziobek, I., Rogers, K., Fleck, S., Bahnemann, M., Heekeren, H. R., Wolf, O. T., & Convit, A. (2008). Dissociation of cognitive and emotional empathy in adults with Asperger syndrome using the Multifaceted Empathy Test (MET). *Journal of autism and developmental disorders, 38*(3), 464-473.

Feneran, A. N., O'donnell, R., Press, A., Yosipovitch, G., Cline, M., Dugan, G., . . . Shively, C. A. (2013). Monkey see, monkey do: contagious itch in nonhuman primates. *Acta dermato-venereologica, 93*(1), 27-29.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*(2), 593-609.

Gallup, A. C., & Eldakar, O. T. (2011). Contagious yawning and seasonal climate variation. *Frontiers in evolutionary neuroscience, 3*, 3.

Gallup, A. C., & Eldakar, O. T. (2013). The thermoregulatory theory of yawning: what we know from over 5 years of research. *Frontiers in neuroscience, 6*, 188.

Gallup, A. C., & Gallup Jr, G. G. (2007). Yawning as a brain cooling mechanism: nasal breathing and forehead cooling diminish the incidence of contagious yawning. *Evolutionary Psychology, 5*(1), 147470490700500109.

Gallup, A. C., & Gallup Jr, G. G. (2008). Yawning and thermoregulation. *Physiology & behavior, 95*(1-2), 10-16.

Gallup, A. C., Swartwood, L., Militello, J., & Sackett, S. (2015). Experimental evidence of contagious yawning in budgerigars (Melopsittacus undulatus). *Animal cognition, 18*(5), 1051-1058.

Giganti, F., & Esposito Ziello, M. (2009). Contagious and spontaneous yawning in autistic and typically developing children. *Current psychology letters. Behaviour, brain & cognition, 25*(1, 2009).

Gottfried, J., Lacinová, L., & Širůček, J. (2015). Contagious yawning and empathy. *E-Psychology, 9*(4).

Haker, H., Kawohl, W., Herwig, U., & Rössler, W. (2013). Mirror neuron activity during contagious yawning—an fMRI study. *Brain imaging and behavior, 7*(1), 28-34.

Haker, H., & Rössler, W. (2009). Empathy in schizophrenia: impaired resonance. *European archives of psychiatry and clinical neuroscience, 259*(6), 352-361.

Harari, H., Shamay-Tsoory, S. G., Ravid, M., & Levkovitz, Y. (2010). Double dissociation between cognitive and affective empathy in borderline personality disorder. *Psychiatry research, 175*(3), 277-279.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*(5598), 1634-1636.

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619-623.

Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: a response to Udell et al.(2008) and Wynne et al.(2008). *Animal Behaviour*.

Harr, A. L., Gilbert, V. R., & Phillips, K. A. (2009). Do dogs (Canis familiaris) show contagious yawning? *Animal cognition, 12*(6), 833-837.

Helt, M. S., Eigsti, I. M., Snyder, P. J., & Fein, D. A. (2010). Contagious yawning in autistic and typical development. *Child development, 81*(5), 1620-1631.

Hoogenhout, M., van der Straaten, K., Pileggi, L.-A., & Malcolm-Smith, S. (2013). Young children display contagious yawning when looking at the eyes. *J Child Adolesc Behav, 1*(101), 2.

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual review of psychology, 60*, 653-670.

Joly-Mascheroni, R. M., Senju, A., & Shepherd, A. J. (2008). Dogs catch human yawns. *Biology Letters, 4*(5), 446-448.

Jones, A. P., Happé, F. G., Gilbert, F., Burnett, S., & Viding, E. (2010). Feeling, caring, knowing: different types of empathy deficit in boys with psychopathic tendencies and autism spectrum disorder. *Journal of Child Psychology and Psychiatry, 51*(11), 1188-1197.

Kapitány, R., & Nielsen, M. (2017). Are yawns really contagious? A critique and quantification of yawn contagion. *Adaptive Human Behavior and Physiology, 3*(2), 134-155.

Langford, D. J., Crager, S. E., Shehzad, Z., Smith, S. B., Sotocinal, S. G., Levenstadt, J. S., . . . Mogil, J. S. (2006). Social modulation of pain as evidence for empathy in mice. *Science, 312*(5782), 1967-1970.

Lehmann, H. E. (1979). Yawning: a homeostatic reflex and its psychological significance. *Bulletin of the Menninger Clinic, 43*(2), 123.

Lloyd, D., Hall, E., Hall, S., & McGlone, F. (2013). Can itch-related visual stimuli alone provoke a scratch response in healthy individuals? *British journal of dermatology, 168*(1), 106-111.

Locke, D. P., Hillier, L. W., Warren, W. C., Worley, K. C., Nazareth, L. V., Muzny, D. M., . . . Minx, P. (2011). Comparative and demographic analysis of orang-utan genomes. *Nature, 469*(7331), 529.

Madsen, E. A., & Persson, T. (2013). Contagious yawning in domestic dog puppies (Canis lupus familiaris): the effect of ontogeny and emotional closeness on low-level imitation in dogs. *Animal cognition, 16*(2), 233-240.

Madsen, E. A., Persson, T., Sayehli, S., Lenninger, S., & Sonesson, G. (2013). Chimpanzees show a developmental increase in susceptibility to contagious yawning: a test of the effect of ontogeny and emotional closeness on yawn contagion. *PloS one, 8*(10), e76266.

Massen, J. J., & Gallup, A. C. (2017). Why contagious yawning does not (yet) equate to empathy. *Neuroscience & Biobehavioral Reviews, 80*, 573-585.

Massen, J. J., Vermunt, D. A., & Sterck, E. H. (2012). Male yawning is more contagious than female yawning among chimpanzees (Pan troglodytes). *PloS one*, *7*(7), e40697.

Millen, A., & Anderson, J. R. (2011). Neither infants nor toddlers catch yawns from their mothers. *Biology Letters, 7*(3), 440-442.

Moore, J. E. (1942). Some psychological aspects of yawning. *The Journal of General Psychology, 27*(2), 289-294.

Moyaho, A., Rivas-Zamudio, X., Ugarte, A., Eguibar, J. R., & Valencia, J. (2015). Smell facilitates auditory contagious yawning in stranger rats. *Animal cognition, 18*(1), 279-290.

Nahab, F. B., Hattori, N., Saad, Z. S., & Hallett, M. (2009). Contagious yawning and the frontal lobe: an fMRI study. *Human brain mapping, 30*(5), 1744-1751.

Niemeier, V., & Gieler, U. (2000). Observations during itch-inducing lecture. *Dermatology and Psychosomatics/Dermatologie und Psychosomatik, 1*(Suppl. 1), 15-18.

Norscia, I., Demuru, E., & Palagi, E. (2016). She more than he: gender bias supports the empathic nature of yawn contagion in Homo sapiens. *Royal Society open science, 3*(2), 150459.

Norscia, I., & Palagi, E. (2011). Yawn contagion and empathy in Homo sapiens. *PloS one, 6*(12), e28472.

O'Hara, S. J., & Reeve, A. V. (2011). A test of the yawning contagion and emotional connectedness hypothesis in dogs, Canis familiaris. *Animal Behaviour, 81*(1), 335-340.

Onishi, K. H., & Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs? *Science, 308*(5719), 255-258.

Palagi, E., Leone, A., Mancini, G., & Ferrari, P. F. (2009). Contagious yawning in gelada baboons as a possible expression of empathy. *Proceedings of the National Academy of Sciences, 106*(46), 19262-19267.

Palagi, E., Norscia, I., & Demuru, E. (2014). Yawn contagion in humans and bonobos: emotional affinity matters more than species. *PeerJ, 2*, e519.

Paukner, A., & Anderson, J. R. (2006). Video-induced yawning in stumptail macaques (Macaca arctoides). *Biology Letters, 2*(1), 36-38.

Pfungst, O. (1911). *Clever Hans:(the horse of Mr. Von Osten.) a contribution to experimental animal and human psychology*: Holt, Rinehart and Winston.

Platek, S. M., Critton, S. R., Myers, T. E., & Gallup Jr, G. G. (2003). Contagious yawning: the role of self-awareness and mental state attribution. *Cognitive brain research, 17*(2), 223-227.

Platek, S. M., Mohamed, F. B., & Gallup Jr, G. G. (2005). Contagious yawning and the brain. *Cognitive brain research, 23*(2-3), 448-452.

Preston, S. D., & de Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and brain sciences, 25*(1), 1-20.

Provine, R. R. (1989). Faces as releasers of contagious yawning: An approach to face detection using normal human subjects. *Bulletin of the Psychonomic Society, 27*(3), 211-214.

Provine, R. R. (1992). Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. *Bulletin of the Psychonomic Society, 30*(1), 1-4.

Provine, R. R. (2005). Yawning: the yawn is primal, unstoppable and contagious, revealing the evolutionary and neural basis of empathy and unconscious behavior. *American scientist, 93*(6), 532-539.

Provine, R. R., Tate, B. C., & Geldmacher, L. L. (1987). Yawning: no effect of 3–5% CO_2, 100% O_2, and exercise. *Behavioral and Neural Biology, 48*(3), 382-393.

Rilling, J. K., Scholz, J., Preuss, T. M., Glasser, M. F., Errangi, B. K., & Behrens, T. E. (2012). Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Social cognitive and affective neuroscience*, *7*(4), 369-379.

Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. *PloS one*, *9*(8), e105963.

Romero, T., Konno, A., & Hasegawa, T. (2013). Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. *PloS one, 8*(8), e71365.

Rossman, Z. T., Hart, B. L., Greco, B. J., Young, D., Padfield, C., Weidner, L., . . . Hart, L. A. (2017). When yawning occurs in elephants. *Frontiers in veterinary science, 4*, 22.

Rundle, B. K., Vaughn, V. R., & Stanford, M. S. (2015). Contagious yawning and psychopathy. *Personality and Individual Differences, 86*, 33-37.

Schürmann, M., Hesse, M. D., Stephan, K. E., Saarela, M., Zilles, K., Hari, R., & Fink, G. R. (2005). Yearning to yawn: the neural basis of contagious yawning. *Neuroimage, 24*(4), 1260-1264.

Schut, C., Grossman, S., Gieler, U., Kupfer, J., & Yosipovitch, G. (2015). Contagious itch: what we know and what we would like to know. *Frontiers in human neuroscience, 9*, 57.

Senju, A., Kikuchi, Y., Akechi, H., Hasegawa, T., Tojo, Y., & Osanai, H. (2009). Brief report: does eye contact induce contagious yawning in children with autism spectrum disorder? *Journal of autism and developmental disorders, 39*(11), 1598.

Senju, A., Maeda, M., Kikuchi, Y., Hasegawa, T., Tojo, Y., & Osanai, H. (2007). Absence of contagious yawning in children with autism spectrum disorder. *Biology Letters, 3*(6), 706-708.

Shamay-Tsoory, S. G., & Aharon-Peretz, J. (2007). Dissociable prefrontal networks for cognitive and affective theory of mind: a lesion study. *Neuropsychologia, 45*(13), 3054-3067.

Shoup-Knox, M. L., Gallup, A. C., Gallup, G., & McNay, E. C. (2010). Yawning and stretching predict brain temperature changes in rats: support for the thermoregulatory hypothesis. *Frontiers in evolutionary neuroscience, 2,* 108.

Silva, K., Bessa, J., & de Sousa, L. (2012). Auditory contagious yawning in domestic dogs (Canis familiaris): first evidence for social modulation. *Animal cognition, 15*(4), 721-724.

Stevens, J., Daem, H., & Verspeek, J. (2017). *Bonobos do not yawn along with video models of yawning conspecifics. Conference Paper.* Paper presented at the 15th Conference of the German Primate Society.

Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., . . . Kaminski, J. (2015). Citizen science as a new tool in dog cognition research. *PloS one, 10*(9), e0135176.

Udell, M. A., Dorey, N. R., & Wynne, C. D. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour, 76*(6), 1767-1773.

Udell, M. A., Dorey, N. R., & Wynne, C. D. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological reviews, 85*(2), 327-345.

Usui, S., Senju, A., Kikuchi, Y., Akechi, H., Tojo, Y., Osanai, H., & Hasegawa, T. (2013). Presence of contagious yawning in children with autism spectrum disorder. *Autism research and treatment, 2013*.

Ward, J., Burckhardt, V., & Holle, H. (2013). Contagious scratching: shared feelings but not shared body locations. *Frontiers in human neuroscience, 7*, 122.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child development, 72*(3), 655-684.

Wynne, C. D., Udell, M. A., & Lord, K. A. (2008). Ontogeny's impacts on human–dog communication. *Animal Behaviour, 76*(4), e1-e4.

Yonezawa, T., Sato, K., Uchida, M., Matsuki, N., & Yamazaki, A. (2017). Presence of contagious yawning in sheep. *Animal Science Journal*, *88*(1), 195-200.

Yoon, J. M., & Tennie, C. (2010). Contagious yawning: a reflection of empathy, mimicry, or contagion? *Animal Behaviour, 79*(5), e1-e3.

Yu, Y.-Q., Barry, D. M., Hao, Y., Liu, X.-T., & Chen, Z.-F. (2017). Molecular and neural basis of contagious itch behavior in mice. *Science, 355*(6329), 1072-1076.