

Contagious yawning in domestic dog puppies (*Canis lupus familiaris*): The effect of ontogeny and emotional closeness on low-level imitation in dogs

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Abstract

Contagious yawning is a well-documented phenomenon in humans and has recently attracted much attention from developmental and comparative sciences. The function, development and underlying mechanisms of the phenomenon, however, remain largely unclear. Contagious yawning has been demonstrated in dogs and several non-human primate species, and theoretically and empirically associated with empathy in humans and non-human primates. Evidence of emotional closeness modulating contagious yawning in dogs has, nonetheless, been contradictory. Humans show a developmental increase in susceptibility to yawn contagion, with typically developing children displaying a substantial increase at the age of four, when a number of cognitive abilities (e.g. accurate identification of others' emotions) begin to clearly manifest. Explicit tests of yawn contagion in non-human animals have, however, thus far only involved adult individuals. Here, we report a study of the ontogeny of domestic dogs' (*Canis lupus familiaris*) susceptibility to yawn contagion, and whether emotional closeness to the yawning model affects this. Thirty-five dogs, aged 4–14 months, observed a familiar and unfamiliar human repeatedly yawn or gape. The dogs yawned contagiously, but emotional closeness with the model did not affect the strength of contagion, raising questions as to recent evidence of emotionally modulated auditory contagious yawning in dogs. The dogs showed a developmental effect, with only dogs above 7 months evidencing contagion. The results support the notion of a developmental increase in dogs' attention to others and identification of others' emotional states and suggest that yawn contagion is underpinned by developmental processes shared by humans and other animals.

Keywords: *Canis lupus familiaris*, Yawning, Imitation, Contagion, Empathy, Development

Introduction

Contagious yawning (yawning in response to perceiving others' yawn, henceforth CY) is a well-documented phenomenon in humans (Provine 1986; Anderson and Meno 2003; Norscia and Palagi 2011). Viewing others yawn elicits yawning in 45–55 % of adults (under experimental conditions: Provine 1986; Platek et al. 2003), and the mere thought (Provine 1986), and sound (Arnott et al. 2009) of yawning is sufficient to evoke contagion. While the phenomenon has recently attracted much attention from developmental and comparative sciences (see Walusinski 2010), the function, development and underlying mechanisms remain largely unclear.

Recent research has emphasised that CY may be linked to and modulated by empathy (Platek et al. 2003; Anderson and Matsuzawa 2006; Palagi et al. 2009; Campbell and de Waal 2011; Norscia and Palagi 2011). The term empathy encompasses a spectrum of resonant emotional responses, ranging from basic 'affective empathy' to 'cognitive empathy'. 'Affective empathy' represents vicarious, visceral emotional responses to others' experiences. It has been argued that this affective element results from an automatic motor mimicry response to others' emotional expressions and is mediated by emotional closeness (Lipps 1903; Preston and de Waal 2002; Baron-Cohen and Wheelwright 2004). Affective empathy is therefore, effectively, a case of emotional contagion, which relies on two inter-linked processes: non-conscious mimicry and afferent feedback. Non-conscious mimicry (the so-called 'chameleon effect': Chartrand and Bargh 1999) is the tendency to mirror the behaviours of social partners, without awareness or intent. Since facial expressions tend to influence emotional experiences (e.g. smiling provides an afferent feedback: Niedenthal et al. 2005), the 'chameleon effect' can give rise to emotional contagion, whereby the mimicking and synchronisation of others' movements and facial expressions lead individuals to converge emotionally (Hatfield et al. 2009). While no empirical research has yet demonstrated that CY provides afferent feedback (increases sleepiness in the subject), CY may be considered an emotional contagion, arising non-conscious mimicry (Yoon and Tennie 2010). In contrast to 'affective empathy', 'cognitive empathy' is considered to emerge phylogenetically and ontogenetically with other 'indicators of mind' and requires a capacity for self-other differentiation and perspective-taking and that the subject represents the state of another's feelings (in terms of theory-of-mind), without this necessarily involving emotional matching (Preston and de Waal 2002).

Multiple lines of psychological, clinical, developmental and neuroscientific evidence suggest that empathy, linked with social bonding, influences yawn contagion. For example, in human

adults, CY is positively correlated with visual self-recognition and performance on theory-of-mind tasks (Platek et al. 2003), two abilities that contribute to ‘cognitive empathy’. Moreover, CY is diminished in individuals with empathy-related disorders (schizotypy: Platek et al. 2003; autism: Senju et al. 2007, 2009; Giganti and Ziello 2009; Helt et al. 2010).

Typically, developing children begin to yawn contagiously at 4–5 years. (Anderson and Meno 2003; Helt et al. 2010; Millen and Anderson 2011), an age, at which a host of cognitive abilities (such as false-belief theory-of-mind understanding) begin to clearly manifest, and children begin to correctly identify the emotions of others (Wiggers and van Lieshout 1985; Wellman et al. 2001; Saxe et al. 2004; Singer 2006). While this is consistent with the suggestion that CY shares a developmental basis with ‘cognitive empathy’ and theory-of-mind capacities, CY has been recorded in a number of non-human species, of which none have passed the paradigmatic false-belief test of theory-of-mind understanding, suggesting that the phenomenon relies on processes other than those involved in ‘cognitive empathy’.

Aside from humans, CY has been recorded in chimpanzees (Anderson et al. 2004; Campbell et al. 2009; Campbell and de Waal 2011), gelada baboons, *Theropithecus gelada* (Palagi et al. 2009) and domestic dogs, *Canis lupus familiaris* (Joly-Mascheroni et al. 2008), with some suggestion of CY in stump-tailed macaques, *Macaca arctoides* (Paukner and Anderson 2006) and budgerigars, *Melopsittacus undulatus* (Miller et al. 2011). In contrast, no CY has been demonstrated in tortoises, *Geochelone carbonaria* (Wilkinson et al. 2011), a solitary species, lending some empirical support to the notion that CY serves to coordinate and synchronise group behaviour (e.g. Deputte 1994; Palagi et al. 2009).

For humans, the strength of the contagion is proportional to degree of familiarity (i.e. it is greatest in response to kin, then friends, then acquaintances and lastly strangers: Norscia and Palagi 2011). Moreover, adult chimpanzees are more likely to yawn contagiously in response to watching videos of familiar than unfamiliar conspecifics (Campbell and de Waal 2011), and among gelada baboons, social bonding predicts CY (Palagi et al. 2009). Overall, these findings are consistent with the notion that familiarity and emotional closeness increase empathy (Preston and de Waal 2002; de Waal 2008; Langford et al. 2006) and, consequently, CY.

Dogs are an interesting species for addressing questions regarding social cognition and the domestication thereof. By virtue of social domestication over the past 15,000 years (Miklósi 2008), dogs have been selectively bred for their function in human society (Cooper et al. 2003)

and attachment to humans (as if they were conspecifics: Topál et al. 2005). Dogs, for example, are sensitive to human emotions and respond to their owners' distress with enhanced negative emotional arousal (Jones and Josephs 2006) and behave seemingly to comfort owners as well as strangers, who pretend to be distressed (Custance and Mayer 2012).

Joly-Mascheroni and colleagues showed that 72 % of dogs tested yawned in response to viewing an unfamiliar human yawn (Joly-Mascheroni et al. 2008). Subsequent studies have, however, failed to replicate this result and found little evidence for hetero-specific as well as con-specific CY in dogs, and none suggests that dogs respond differently when viewing familiar and unfamiliar humans yawn (Harr et al. 2009; O'Hara and Reeve 2010). Consequently, doubts have been raised regarding the cross-species CY reported by Joly-Mascheroni and colleagues and have led to the suggestion that the results were explained by a high degree of 'tension yawns' (O'Hara and Reeve 2010), which may be evoked in situations of uncertainty (as yawning indexes social stress in dogs: Beerda et al. 1998).

A recent study, however, suggested that dogs are subject to auditory contagious yawning (i.e. as in humans, the mere sound of yawning is sufficient to evoke contagion) and that this is modulated by familiarity with the model yawner (Silva et al. 2012). To examine whether CY in dogs is modulated by familiarity (indexing empathy), dogs were played recordings of, respectively, yawns produced by their owner or an unfamiliar experimenter, and two control sounds consisting of a computer-reversed yawn from either the owner or experimenter. While the study showed that the sound of familiar yawns elicited more CY than unfamiliar yawns, the dogs' increased yawning to familiar yawns may have been induced by mildly heightened tension. Dogs recognise their owner's voice (Adachi et al. 2007) and have acute sound localisation. The dogs in Silva et al.'s study were tested in their homes, positioned facing two speakers, but without visual contact to the owner, from whom the recorded familiar yawns derived. The sound of their owner's yawns, emitted from two speakers immediately in front of the dogs, was from a direction where the owner was not (the owner was outside the testing room). Dogs sensing this discrepancy would likely experience uncertainty and consequently mild stress. The higher proportion of yawns to familiar stimuli may therefore have represented an increase in mild stress. Conversely, no such stress effect should be evident in response to the scrambled (reversed) familiar yawns, since identification of the owner's voice was likely impossible. By comparison, auditory CY in humans is evoked by the sound of unfamiliar yawns (Arnott et al. 2009), and CY in responses to viewing unfamiliar yawns has been demonstrated in a number of other studies (children: e.g. Senju et al. 2007; chimpanzees: Madsen et al. *in prep*;

dogs: Joly-Mascheroni et al. 2008), making the finding of an auditory CY effect in dogs, elicited only in response to familiar stimuli, puzzling. The methodological issues, detailed above, are sufficient to raise questions about the interpretation of the results, particularly given lack of evidence of empathy-based, familiarity biased CY in dogs exposed to familiar and unfamiliar human yawns presented by a live model (O'Hara and Reeve 2010). As all empirical results, evidence of a potential familiarity effect on CY must be evaluated in the light of the overall pattern of results.

One intriguing, yet unstudied aspect of CY in non-human animals is its developmental trajectory. While humans show a developmental increase in susceptibility to yawn contagion, explicit tests of the contagion in non-human animals have thus far only involved adults. One study of chimpanzees, however, indicated a potential age effect in susceptibility to contagion, as videoed stimuli of conspecific yawns failed to elicit yawning in any of three infants accompanying their mothers to the test (Anderson et al. 2004). There is, however, some evidence that the medium may obscure the message for younger and non-human subjects. For example, while neither videoed stimuli nor stories, in which a central character repeatedly yawned, have evoked CY in children below 5 years (Anderson and Meno 2003; Millen and Anderson 2011), live models have evoked CY in younger children (35 % of 4-year-olds tested: Helt et al. 2010; for observation of CY in a 12-month-old, see Piaget 1951, p. 40). There is some suggestion that dogs are sensitive to the medium, as only live (Joly-Mascheroni et al. 2008) and not videoed (conspecific and human) models (Harr et al. 2009) have elicited CY in this species.

In this study, we explored the ontogeny of dogs' susceptibility to yawn contagion and whether emotional closeness to the yawning model affects this. We wished to increase ecological validity and the probability of evoking CY in younger subjects by using live rather than videoed models. We used the same basic design as the first study of CY in dogs (Joly-Mascheroni et al. 2008), but strove to minimise the possibility of evoking 'tension yawns' by engaging the dogs in a bout of play and cuddling, without requiring eye contact with the experimenter prior to each yawn, thereby explicitly making the dogs attend to the yawning (as done by Joly-Mascheroni and colleagues). Calling the dogs' name and attention to the experimenter immediately prior to yawning may have endowed the behaviour with a puzzling and seemingly communicative function, and avoiding this addresses the critique by O'Hara and Reeve (2010) that 'tension yawns' might underlie the high frequency of CY found by Joly-Mascheroni and colleagues. Moreover, we included a 5-min baseline phase and a familiar experimenter.

We hypothesised that if CY is related to the development of empathy and emotional understanding in humans, a similar developmental effect might be found in dogs. We thus predicted that (1) older dogs show stronger evidence of CY than younger dogs. Since empathy and model identity may play a significant role in facilitating social behaviours, such as imitation (Meltzoff and Moore 1994; see de Waal 2001, for the ‘Bonding- and Identification- based Observational Learning’ model), we presented young dogs with a familiar yawning model, with whom they had a strong and positive emotional relationship (their owner), and an unfamiliar model. We predicted that (2) the dogs would be more likely to yawn contagiously to the familiar model and that this model would elicit more CY from the younger participants. We further predicted (3) yawning frequency to increase in response to viewing a human model performing repeated yawns, but not gaping (mouth opening and closing), or indeed when the experimenter performed none of the behaviours (baseline phase). While previous studies have used a variety of control behaviours (smiles, coughs, laughs and gapes, see Campbell and de Waal 2010), gaping has the advantage of mimicking much of the motor pattern of a yawn, while being a meaningless expression. If CY is an emotional contagion (Hatfield et al. 2009) and reflects perception and internalisation of the emotion and/or physical state that another’s yawning reflects, only yawn stimuli should evoke yawning. A comparison of the rate of yawning in response to yawning and gaping stimuli thus excludes a more motoric stimulus–response interpretation of CY.

Methods

Participants

Participants were 35 domestic dogs, of various breeds, between 4 and 14 months of age (mean age = 7.23 mts., SD = 2.45, 22 males, 13 females, see supplementary materials, Table 1 for participant details). All dogs were healthy and experimentally naïve. The dogs were recruited through adverts and contacts with puppy schools in Denmark. Three dogs were excluded from analyses, due to, respectively, distractions, over-excitedness and poor owner yawning.

Design and procedure

The study used a repeated measures design, with two independent variables: experimenter familiarity (familiar and unfamiliar human model: the dog owner and a female researcher) and experimenter behaviour (yawning and gaping). Each participant received five 5-min phases presented in immediate succession, for a total duration of 25 min. A trial sequence consisted of a baseline phase followed by two phases, where the experimenter repeatedly either yawned or gaped. The yawning/gaping phases were each followed by a 5-min post-stimulus observation phase, during which interaction continued, but without the inclusion of the key behaviour (yawning or gaping). In all phases, the dog and experimenter engaged in calm interactions (cuddling, grooming, playing) while sitting/lying on the floor. During testing, the individual (owner/ researcher) not involved in the trial sat quietly behind the dog. If approached by the dog, the individual acknowledged (e.g. hugged) and encouraged the dog to re-engage with the experimenter. Pilots indicated that some dogs became nervous if trials were conducted in silence (an atypical context: prolonged engagement with a stranger, or the owner in a stranger's presence). The experimenter thus engaged in near-continuous talk to/with the dog and the individual not involved in the trial (thus implicitly drawing attention to yawning/gaping instances). The dogs were tested in their homes, between 9.00 and 20.00 h, and received two full trial sequences, one with the familiar and unfamiliar experimenter. Except for two dogs, all participants received a minimum 24-h interlude between trials with the familiar and unfamiliar experimenter (mean interlude = 3.51 ± 3.42 days, max = 14 days). The conditions (familiar/unfamiliar model, yawning/gaping) were counterbalanced across participants (see Suppl. Matr., Table 2).

Yawning phase

The experimenter repeatedly yawned while being within the participant's full or peripheral field of vision. Experimenters yawned as naturally as possible, with yawning defined as opening the mouth fully, drawing in air, tilting the head and body backwards, closing the eyes, and producing

a vocalisation during exhalation, for a total duration of 5–10 s.

Gaping phase

The experimenter performed repeated (non-yawning) mouth openings, that is, opening the mouth wide and closing it, without audible inhalation and exhalation of air (approx. 5 s duration), while within the participant's full field of vision.

Experimenters aimed to expose participants to 15 yawns and gapes, yet given the restive nature of the participants, yawns/gapes were often produced outside the participants' field of vision. The number of presented yawns and gapes therefore varied across subjects (mean \pm SD: yawning: 16.29 ± 2.02 , range = 12–25, gaping: 16.09 ± 2.10 , range = 13–25). Elicited yawns were recorded in real-time and verified by subsequent video-analysis (trials were recorded with two Panasonic camcorders, HDC-HS700S and HDC-SD700). We were careful not to include yawns seemingly reflecting tension¹; one dog displayed two 'tension yawns', which were excluded from the analyses. Trials from 10 % of a random selection of subjects were scored for inter-observer reliability (100 % agreement).

Both individual phases and the subsequent 5-min post- observation phases were used as means of comparisons (i.e. the yawning and post-yawning, as well as gaping and post- gaping, phases were collapsed). We used independent t tests to assess differences in the number of yawns and gapes produced by experimenters and Spearman's correlations to test for a relationship between the numbers of presented and elicited yawns. Data were analysed at both group level (number of yawns across conditions) and individual level (number of individuals that yawned across conditions). Wilcoxon signed ranks matched pairs tests were used to compare within-participant differences in the rate of elicited yawns to yawn and gape stimuli, and familiar and unfamiliar stimuli, and Friedman's tests to compare the mean number of yawns per minute across the baseline, yawn and post-yawning, and gaping and post- gaping phases (mean number of yawns per minute was used, as the duration of the three conditions compared differed). Mann–Whitney tests were used to compare rate of contagious yawning by age. McNemar Chi-square tests were used to assess whether different numbers of dogs yawned across conditions, and a repeated measures binomial logistic regression (generalised linear mixed model, GLMM) was used to assess interactions between age, condition and familiarity. Data were analysed using SPSS Statistics 20 for Macintosh (SPSS, IBM Inc.). Values reported are mean \pm SEM, and all statistics were two- tailed.

¹ Tension yawns and 'sleepy' yawns are morphologically identical, only distinguished by the context and the co-occurrence of either, none or all of a number of associated behaviours, e.g. lip licking, scratching, body shaking ('shaking it off'), panting, whimpering or sneezing.

Results

Eighty-nine per cent (31 of 35) of dogs yawned during the experiment. Twelve per cent of yawns appeared in the baseline phase, 13 % in the gaping phase, 17 % in the post-gaping phase, 26 % in the yawning phase and 32 % in the post-yawning phase. The number of yawns ($t_{(68)} = 0.83$, $P = 0.41$) and gapes ($t_{(62)}^2 = 1.61$, $P = 0.11$) made by the two experimenters did not differ significantly, nor was there a relationship between the number of presented and elicited yawns ($r = 0.06$, $P = 0.62$, Spearman's test). Moreover, the frequency of yawning in the yawn condition was not influenced by the order of presentation (i.e. yawn or gape condition first: $U = 136.5$, $z = 0.27$, $P = 0.79$, Mann-Whitney test), nor the time of day of testing (9–12, 12–17, 17–20: familiar experimenter: $X^2_{(2)} = 0.63$, $P = 0.73$, Friedman test unfamiliar experimenter: $X^2_{(2)} = 0.81$, $P = 0.67$), nor did it differ significantly between the sexes ($U = 117.50$, $z = 0.89$, $P = 0.37$).

Yawn contagion

To assess the strength of yawn contagion, phases where the familiar and unfamiliar models yawned were collapsed to represent 'yawn stimuli', and familiar and unfamiliar gaping phases were considered 'gape stimuli'. On average, yawn stimuli elicited nearly twice as many yawns (mean = 2.7 ± 0.33 , range = 0–8) as gape stimuli (mean = 1.4 ± 0.25 , range = 0–6), a statistically significant difference² ($N = 35$, $z = 3.46$, $P = 0.001$, Wilcoxon test, Fig. 1). Moreover, there was a difference in the mean number of yawns per minute across the baseline (0.06), the collapsed gape/post-gape phase (0.07) and yawn/post-yawn phase (0.13, $X^2_{(2)} = 18.73$, $P = 0.000$, Friedman test), with significant differences being between the yawn/post-yawn phase and baseline ($N = 35$, $z = 3.36$, $P = 0.001$, Wilcoxon test), and yawn/post-yawn and gape/post-gape phase ($N = 35$, $z = 3.46$, $P = 0.001$), while not between baseline and gape/post-gape phase ($N = 35$, $z = 0.70$, $P = 0.49$). A similar pattern emerged when comparing the number of individuals that yawned more to the yawn than gape stimuli (62 %, 22 of 35 dogs) with those that yawned more to the gape than yawn stimuli (17.14 % 6 of 35, $P = 0.004$, McNemar test). The overall difference between the number of individuals that yawned in the yawn and gape conditions, however, only (yet closely) approached significance ($P = 0.05$). There was no statistically significant difference with respect the number of dogs that yawned uniquely to yawn ($n = 9$) and gape stimuli ($n = 3$, $P = 0.15$). The dogs showed a trend towards exhibiting more yawning in the post-yawn (55 %) than yawn phase (45 %), with 26 % of dogs yawning uniquely in the post-yawn phase and only 9 %

² Analysis was based on 64 (rather than 70) trials, as the number of gapes could not be reliably coded in six trials (as the experimenter at times faced away from the camcorders).

uniquely in the yawn phase, although this failed to reach significance ($N = 35$, $z = 0.78$, $P = 0.44$, Wilcoxon test; $P = 0.15$, McNemar test).

Age differences

Older (7–14 mts) but not younger dogs (4, 5 and 6 mts) yawned significantly more in the yawning than gaping condition (older: $n = 21$, $z = 3.20$, $P = 0.001$; younger: $n = 14$, $z = 1.41$, $P = 0.16$, Wilcoxon test, Fig. 1). A similar pattern emerged when considering the number of dogs, as dogs above 7 months were more likely to yawn in the yawn than gape condition, than dogs aged 4–6 months.

Social modulation

There was no significant difference in the number of elicited yawns to neither yawn ($N = 35$, $z = 0.19$, $P = 0.85$, Wilcoxon test) nor gape ($N = 35$, $z = 0.42$, $P = 0.67$) stimuli presented by the familiar or unfamiliar experimenters. Nor was there was a difference in the number of dogs yawning in the yawn and gape conditions with the familiar and unfamiliar experimenter ($F = 2.34$, $P = 0.13$, GLMM), nor an interaction effect between age group and experimenter familiarity ($F = 1.53$, $P = 0.22$). However, while older dogs (7–14 mts) yawned significantly more during the yawn than baseline phase, regardless of whether the experimenter was familiar ($N = 21$, $z = 2.89$, $P = 0.004$, Wilcoxon test) or unfamiliar ($N = 21$, $z = 2.55$, $P = 0.011$), the difference between the yawn and gape phases only reached significance in trials involving an unfamiliar experimenter ($N = 21$, $z = 3.08$, $P = 0.002$), while it only approached significance for the familiar experimenter ($N = 21$, $z = 1.77$, $P = 0.076$).

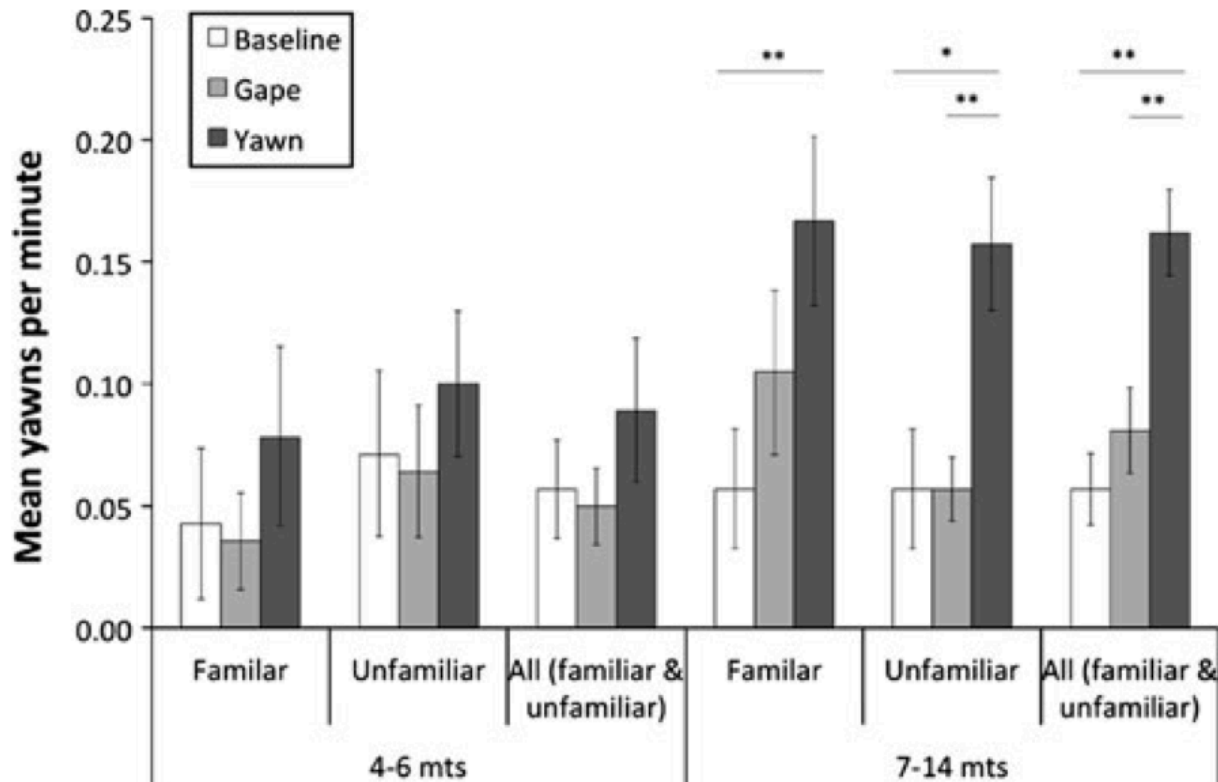


Fig.1 Mean rate of yawning per minute (\pm SEM) across the baseline, gape and yawn conditions with a familiar and unfamiliar model, as well as data from the familiar and unfamiliar conditions collapsed ($F = 3.70$, $P = 0.007$, GLMM). Moreover, age (months) correlated positively with the number of elicited yawns in the yawning condition ($r = 0.36$, $P = 0.03$, Spearman's test) and not in the gaping condition ($r = 0.18$, $P = 0.31$).

Discussion

The current study confirms previous results showing that dogs ‘catch’ human yawns. Viewing an unfamiliar human yawn elicited yawning in 69 % of 4–14 months old dogs, compared to 72 % of adult dogs, tested using the same basic paradigm (Joly-Mascheroni et al. 2008). While the failure to replicate the results of the original study (by Harr et al. 2009; O’Hara and Reeve 2010) has led to questions raised as to the veracity of the findings and the suggestion that the results stemmed from elicitation of ‘tension yawns’, the present study reduced potential stress in the dogs, yet confirmed the original findings.

The study demonstrates that, like humans (Senju 2010; Helt et al. 2010), dogs are subject to a developmental increase in susceptibility to yawn contagion, as dogs above the age of 7 months yawned contagiously, while dogs between 4 and 7 months showed little evidence of contagion. While studies of CY in dogs above the age of one have shown no age effect (Joly-Mascheroni et al. 2008; Harr et al. 2009; O’Hara and Reeve 2010), it is likely the developmental trend is more pronounced at younger ages. Indeed, while explicit tests of CY in other non-human species have thus far only involved adults, a potential age effect on the contagion has been suggested by the failure to elicit CY in three infant chimpanzees (Anderson et al. 2004). While an explicit test of a larger sample of chimpanzees is needed to confirm this suggestive trend, the pattern of results suggests that the ontogenetic emergence of CY reflects developmental processes shared by humans and other animals.

The CY response in younger dogs is delayed compared to that of adult dogs. In contrast to the study by Joly-Mascheroni et al. (2008), in which adult dogs yawned in only the 5-min yawn phase (in which they viewed a human yawn), more puppies yawned in the 5-min post-yawn phase (61 %) than the preceding yawn phase (39 %, when tested under comparable conditions, i.e., with an unfamiliar experimenter). While such a ‘spill-over effect’ may be accounted for by a self-reinforcing and accumulating effect of yawning, more than twice as many dogs yawned uniquely in the post-yawn phase (37 %) compared to the yawn phase (17 %) further supporting the notion of a delayed effect. In contrast to adult dogs, the puppies seemed to generalise the yawn response to the gaping stimuli. While adult dogs showed no yawning in response to the control (gape) condition (Joly-Mascheroni et al. 2008), 46 % of puppies yawned during the gaping/post- gaping condition (in trials with an unfamiliar experimenter—a pattern similar to that exhibited in trials with a familiar experimenter). Given the similarity of the studies, it seems plausible that, ontogenetically, dogs’ CY response is initially generalised and evokable by the

gaping stimulus which, while not reflecting the same physical/emotional state as a yawn (e.g. sleepiness), mimics much of the motor pattern. This suggests that the CY response becomes progressively more accurate with age, possibly reflecting increased awareness of changes in the environment, and an improvement in the identification of others' emotions, which in children co-emerges developmentally with susceptibility to yawn contagion (i.e. at 4–5 years of age: e.g. Singer 2006; Helt et al. 2010).

Anecdotally, there was some suggestion that the dogs may have internalised the emotion that yawning reflects. Although difficult to measure consistently (in the absence of a physiological measure), a considerable number of the dogs (43 %) responded to the yawning condition with a clear reduction in arousal (to the extent that the experimenter needed to prevent [e.g. playfully shake] five dogs from falling asleep during the yawning/post-yawning phase). This effect was not observed in the gaping/post-gaping phase, providing some, albeit anecdotal, suggestion that yawn contagion provides an afferent feedback (Hatfield et al. 2009) and elicits a similar, synchronous state in the observer.

CY in young dogs may help adjudicate between cognitive (2) and affective (3) empathy as the key mechanism underlying cross-species CY. In contrast to affective empathy, cognitive empathy considered to involve theory-of-mind attribution and perspective-taking, of which there is no evidence for the former in dogs and the latter emerges developmentally late in children and chimpanzees (in chimpanzees not until around 4.5 year: Povinelli et al. 1994). CY in young dogs thus suggests that the phenomenon is underlain by processes less cognitively complex than cognitive empathy. There is ample evidence that the affective and cognitive components of empathy have different developmental trajectories in humans (see Decety 2010) and that affective empathy precedes cognitive empathy, ontogenetically and phylogenetically (Preston and de Waal 2002). Thus, it seems possible that non-conscious mimicry and the development of affective empathy (as well as an improvement in the identification of others' emotions) are sufficient to explain the distribution of yawn contagion, ontogenetically as well as phylogenetically.

Studies of CY in dogs have produced conflicting results, yet have deployed a variety of methodological designs, of which the effect on CY is largely unknown, thus complicating comparison of results across studies (Campbell and de Waal 2010). To date, in visual paradigms, only designs that have presented live human models (Joly-Mascheroni et al. 2008; present study), rather than videoed human (Harr et al. 2009) or conspecific (O'Hara and Reeve 2010)

models, have elicited CY in dogs. This difference may be accounted for by videoed stimuli having been displayed on laptops optimised for human viewing (in terms of flicker rates) and that many dogs attend little to 2D screens (pers. obs.). Interestingly, O'Hara and Reeve (2010) failed to show evidence of yawn contagion in dogs viewing a live human model yawn. While puzzling, it is possible that the shorter duration of stimulus presentation (3 min, with no post-yawn observation phase) and the smaller sample size (19 dogs), of which 37 % resided at a dog rescue centre, and thus possibly had disrupted attachment to humans, may account for these differences in results. Moreover, while the human models in O'Hara and Reeve's study yawned "from the neck up only" (p. 337), models in the present study were asked to yawn as naturally as possible, thus mostly also engaging the arms and upper body (e.g. raising the chest and shoulders during deep inhalation) and tilting the body axis backwards. Since dogs seem to pay much attention to body movements and posture, the absence of these cues may contribute to the failure to demonstrate CY in dogs by means of paradigms using only facial movements.

Model familiarity failed to predict yawning in both younger and older puppies. Contrary to prediction, a positive emotional bond with the model was thus insufficient to elicit CY in young dogs. While the strength of contagion was similar when older puppies viewed a familiar and unfamiliar model (i.e. they yawned with similar frequency to yawns presented by the two models types), familiar gapes elicited a higher (though statistically non-significant) number of yawns than unfamiliar gapes.

Consequently, the difference between yawns elicited by familiar gapes and yawns failed to reach significance. This slight increase in yawns in response to familiar gapes may be accounted for by elicitation of tension yawns, when subjects viewed their owner repeatedly gape—an unusual behaviour from a familiar individual.

While recent research has emphasised that CY may be linked to and modulated by empathy, a social modulation of the contagion has thus far only been demonstrated in adult individuals (humans: Norscia and Palagi 2011; chimpanzees: Campbell and de Waal 2011; gelada baboons: Palagi et al. 2009; for potentially controversial results with dogs, see Silva et al. 2012) and not very young individuals (humans: Millen and Anderson 2011; dogs: present study; chimpanzees: Madsen et al. in prep.). Jointly, this raises the possibility that in species that exhibit an empathy-based social modulatory effect on CY, the effect emerges only at later stages of development ('developmental hypothesis of empathy modulation of CY').

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