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No evidence of contagious yawning in the red-footed tortoise *Geochelone carbonaria*

Anna WILKINSON[1, 2*], Natalie SEBANZ[3], Isabella MANDL[1], Ludwig HUBER[1]

[1] Department of Cognitive Biology, University of Vienna, Althanstrasse 14, Vienna, 1090, Austria

[2] Department of Biological Sciences, University of Lincoln, Lincoln, LN2 2LG, UK

[3] Donders Institute for Brain, Cognition and Behavior, Centre for Cognition, Radboud, University Nijmegen, P.O. Box 9104, 6500 HE Nijmegen, The Netherlands

Abstract Three hypotheses have attempted to explain the phenomenon of contagious yawning. It has been hypothesized that it is a fixed action pattern for which the releasing stimulus is the observation of another yawn, that it is the result of non-conscious mimicry emerging through close links between perception and action or that it is the result of empathy, involving the ability to engage in mental state attribution. This set of experiments sought to distinguish between these hypotheses by examining contagious yawning in a species that is unlikely to show nonconscious mimicry and empathy but does respond to social stimuli: the red-footed tortoise *Geochelone carbonaria*. A demonstrator tortoise was conditioned to yawn when presented with a red square-shaped stimulus. Observer tortoises were exposed to three conditions: observation of conditioned yawn, non demonstration control, and stimulus only control. We measured the number of yawns for each observer animal in each condition. There was no difference between conditions. Experiment 2 therefore increased the number of conditioned yawns presented. Again, there was no significant difference between conditions. It seemed plausible that the tortoises did not view the conditioned yawn as a real yawn and therefore a final experiment was run using video recorded stimuli. The observer tortoises were presented with three conditions: real yawn, conditioned yawns and empty background. Again there was no significant difference between conditions. We therefore conclude that the red-footed tortoise does not yawn in response to observing a conspecific yawn. This suggests that contagious yawning is not the result of a fixed action pattern but may involve more complex social processes [*Current Zoology* 57 (4): 477–484, 2011].

Keywords Reptile, Contagious yawn, Empathy, Nonconscious mimicry, Fixed action pattern

Contagious yawning is well documented in humans, however, little is known about its function and prevalence in the animal kingdom or the brain mechanisms underlying it. The function of yawning itself is also poorly understood. Yawning has been observed in a number of vertebrate taxa and, though it is likely that such a prominent and widespread behaviour serves a biological function, the nature of this function remains unclear (Guggisberg et al., 2007). It has been suggested that yawning may cause an increase in arousal which will reduce the probability of sleep. This is something which is likely to be important for vigilance in all animal species (Walusinski and Deputte, 2004, cited by Guggisberg et al., 2007). Another hypothesis suggests that yawning is a form of communication used to synchronize group behavior (Daquin et al., 2001) this could be for a variety of reasons, those postulated have included communicating drowsiness, social stress or even boredom (Guggisberg et al., 2007). This would potentially serve an important social function and it is possible that contagious yawning may have evolved as a result of this.

Experimental analysis of contagious yawning in humans has revealed that it occurs in 40%–60% of participants when they see (videos of) a yawning person (Platek et al., 2005). However, the mechanisms underlying contagious yawning remain poorly understood (Nahab et al., 2009). A number of hypotheses have been proposed to account for the occurrence of contagious yawning and current evidence to support or refute them is equivocal at best. It has been suggested that contagious yawning may simply be the result of a fixed action pattern for which the releaser stimulus is the observation of another yawn (Provine, 1986; Yoon and Tennie, 2010). Evidence to support this hypothesis comes from the fact that yawns follow a highly stereotyped

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∗ Corresponding author. E-mail: awilkinson@lincoln.ac.uk

pattern (Provine, 1986). Further, yawning in humans can be triggered by observing a yawn, hearing a yawn (Arnott et al., 2009) or even thinking about yawning (Provine, 1986). This hypothesis predicts that contagious yawning may be observed in all vertebrates that exhibit yawning behavior.

A second hypothesis suggests that nonconscious social mimicry, the tendency to adopt postures, gestures and mannerisms of an interaction partner (also known as the chameleon effect; Chartrand and Bargh, 1999) may control contagious yawning behavior (Yoon and Tennie, 2010). Non-conscious mimicry is assumed to reflect close links between perception and action. Many studies in macaque monkeys and humans have shown that when an individual observes another perform a particular action, corresponding action representations in the observer's action repertoire are activated (Rizzolatti and Sinigaglia, 2010). Nonconscious mimicry may occur when inhibitory processes that normally keep us from executing observed actions (Brass et al., 2005) are overridden. It has been shown to be modulated by specific social motivations e.g. the desire to affiliate with the social partner. This is well documented in humans and there is some evidence of this phenomenon in primates (Rizzolatti and Sinigaglia, 2010) but no research has directly examined this in terms of contagious yawning. This hypothesis would predict the presence of contagious yawning in species in which perception and action rely on common neural representations and social relations are of import.

The majority of recent research has attempted to explain the phenomenon of contagious yawning in terms of mental state attribution and, in particular, empathy (e.g. Platek et al., 2005). There are many different definitions of empathy (Vignemont and Singer, 2006), but in this context empathy is considered to be the understanding of another's feelings based on the capacity to infer others' mental states (Baron-Cohen et al., 2005). According to this view contagious yawning should only be observed in those species that possess mental state attribution, and thus we would expect to see little evidence of contagious yawning outside the higher primates.

Contagious yawning has been observed in non-human primates (chimpanzees *Pan troglodytes*, Anderson et al., 2004; stump-tailed macaques *Macaca arctoides*, Paukner and Anderson, 2006; gelada baboons *Theropithecus gelada*, Palagi et al., 2009) and dogs (*Canis familiaris*, Joly-Mascheroni et al., 2008, but see Harr et al., 2009). These studies interpret their data in terms of empathy. However the data presented in these papers do not allow the other hypotheses to be dismissed (see Yoon and Tennie, 2010 for further details) as the studies have focused on those species that may possess the ability to engage in some aspects of mental state attribution or fit the criteria for nononscious mimicry.

This study aimed to discriminate between the possible mechanisms controlling contagious yawning by asking whether contagious yawning is present in a species that is unlikely to show empathy or nonconscious mimicry: the red-footed tortoise *Geochelone carbonaria*. To our knowledge there is no evidence of social mimicry, mental state attribution or empathy in this species. There is evidence that this species possesses a sensitivity to visual social cues (Auffenberg, 1965), that it can follow the gaze direction of a conspecific (Wilkinson et al., 2010a) and can learn to access an otherwise inaccessible goal by observing the behavior of a conspecific (Wilkinson et al., 2010b). Further, research suggests that this species is highly visual and when available will use visual cues over both olfactory cues (Wilkinson et al., 2007) and over a highly successful response based behavior (Wilkinson et al., 2009). Taken together this makes them ideal subjects for examining this question. If contagious yawning is simply the result of a fixed action pattern for which the releaser stimulus is the observation of another yawn, then we would expect to observe it in this species; however, if it is controlled through social processes such as nonconscious mimicry or empathy then we would expect it to be absent.

1 Materials and Methods

1.1 Experiment 1

1.1.1 Subjects Seven captive-bred, red-footed tortoises *Geochelone carbonaria* participated in this study. The tortoises were housed in two groups in a heated (29 ± 4 ℃) and humidified room. They were group housed for at least 6 months prior to the onset of the experiment. The exact age of the tortoises was unknown; however all were juvenile or subadult with plastron (the lower part of the shell) lengths measuring 10.5 cm –17 cm at the start of the experiment (see Table 1 for individual sizes). The sex of some of our subjects was unknown as this species does not develop unambiguous sexually dimorphic traits until around the age of 5. However, Alexandra, the demonstrator, was female; two of the observers (Wilhelmina and Moses) were also female and another observer, Aldous, was male (see Table 1 for further details). None of the tortoises were experimentally naïve (e.g. Wilkinson et al., 2007; Wilkinson et al., 2009; Wilkinson et al., 2010a; Wilkinson et al., 2010b), but they had never previously been involved in a contagious yawning task or any similar experiment. Two of the tortoises (Wilhelmina and Aldous) lived in a group with the demonstrator.

1.1.2 Apparatus The study was run in a tank measuring 80 cm × 40 cm × 40 cm in a heated room, maintained at approximately 29^{o}C. The testing tank was separated by a screen; the lower part was made of metal fencing (40 cm × 17.5 cm) that the tortoises could see through. The upper part consisted of an opaque screen (40 cm × 22.5 cm; see Fig. 1).

1.1.3 Pretraining Prior to the onset of the study the demonstrator was trained to yawn when presented with a 2 cm × 2 cm red square shaped stimulus. The technique used for training was that of successive approximation. Initially whenever the demonstrator opened her mouth slightly in the presence of the red stimulus she was rewarded with a favored food. Once she started to readily open her mouth when presented with the stimulus she was then only rewarded when she opened it wide. Once she readily performed the gape like response she was rewarded for tilting her head back whilst her mouth was open. The resulting behavior appeared highly similar to a naturally occurring tortoise yawn. This training took 6 months.

1.1.4 Procedure The goal of this study was to test whether tortoises show contagious yawning. To do so, we used a demonstrator tortoise that was conditioned to yawn when presented with a red square-shaped stimulus. Observer tortoises were exposed to three conditions: A yawning condition in which they observed a single conditioned yawn; a control condition in which a conspecific was present but did not yawn; and a second control condition in which the red square-shaped stimulus was presented without the presence of the demonstrator. We measured the number of yawns for each observer animal in each condition.

The experiment was run between 19th August and 1st September 2009; trials took place in early afternoon. All tortoises were habituated to the apparatus before testing began. The observer tortoises received one trial a day and three trials for each condition. This resulted in each observer animal receiving nine trials. In general these studies present only one trial per condition, however, we wanted to examine behavior over time. Further, the number of trials was identical to that used in a recent (successful) study which investigated gaze following behavior in this species (Wilkinson et al., 2010a). The order of presentation was counterbalanced across subjects. At the onset of each trial the demonstrator was placed in the left hand side of the tank, after this one observer tortoise was placed in the right-hand side and allowed to observe the demonstrator. Each trial lasted 5 minutes and 30 seconds. After the trial was completed the tortoise was removed. Observer tortoises only received one trial per day to ensure that the demonstrator's conditioned yawn did not extinguish. Throughout the entire experiment an experimenter (IM) observed and documented the observer tortoises' behavior. Any yawn that occurred within the trial time was recorded.

Experimental condition: The conditioned stimulus was presented to the demonstrator tortoise. This resulted in the demonstrator performing a single conditioned yawn in each experimental trial. The tortoise yawn is characterized by the extension of the neck, the head being tilted back and the mouth opening in a large gape. The

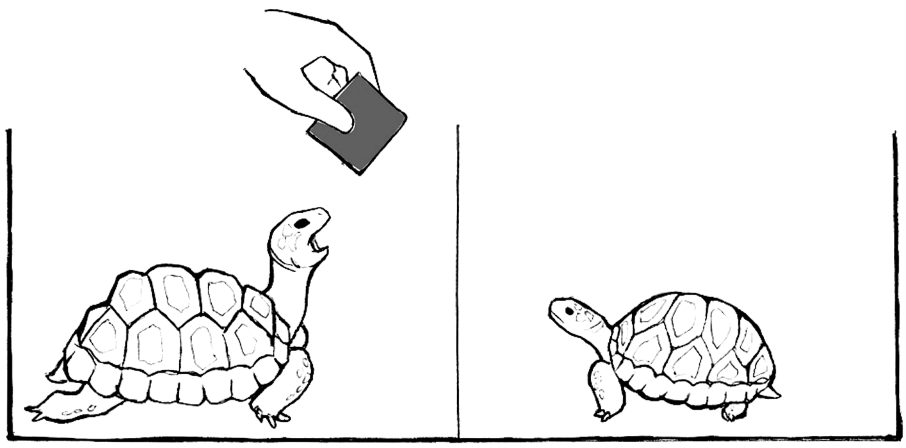

Fig. 1 A diagram of the experimental setup in Experiment 1 and 2

yawn is extremely clear and cannot be mistaken for another behavior. The tortoise does not open its mouth in this way in any other circumstance. When eating the mouth is less open and head position and body posture are quite different from that observed in a yawn. A trial only counted if the demonstrator performed the yawn whilst the observer was watching (judged as facing towards the demonstrator). If the observer was not watching then the trial was stopped, the observer removed and the trial re-run later. An observer yawn was counted if the observer tortoise yawned within 5 minutes and 30 seconds of observing the demonstrator yawn. This was based on the trial times used in previous contagious yawning experiments with animals.

No yawn control: To rule out the possibility that the presence of another animal caused the subject to yawn, we included a control condition in which the demonstrator was present, but the stimulus was not presented. This was identical to the experimental condition except that the stimulus was not presented and thus the demonstrator did not perform a conditioned yawn. On the rare occasion that the demonstrator happened to yawn, the trial was aborted and excluded from analysis. This only occurred once. The trial started after the observer tortoise was placed in the apparatus and had turned to face the demonstrator tortoise. Each trial lasted 5 minutes and 30 second and we recorded all yawns.

No demonstrator control: We included a control condition in which this stimulus was presented, but the demonstrator was absent, to rule out the possibility that the subject responded to the red-square shaped stimulus. This was identical to the experimental condition except that the demonstrator compartment was empty. For this control we analyzed whether the subject yawned in the 5 minutes and 30 seconds following the presentation of the stimulus.

1.1.5 Data analysis The percentage of trials in which a tortoise yawned was calculated for each individual for each condition on the basis of the total number of yawns divided by the total of possible yawns multiplied by 100. The figures display an average of this across individuals. Given the small sample size non-parametric statistics were used for analysis. A Friedman's was used to analyze the number of yawns across conditions.

1.2 Experiment 2

Experiment 2 examined the hypothesis that contagious yawning would occur if the subject were presented with multiple yawns. Thus the tortoises were presented with yawns for the first minute of the trial (2–3 yawns) in the experimental condition. Further, observation of the tortoises' behavior in the different conditions of Experiment 1 revealed that they yawned slightly earlier in the experimental condition than in the control conditions. It is possible that, in the control condition, when no other tortoise was present the observer tortoises settled down to rest. Therefore the trial time was reduced to 3 minutes for Experiment 2.

1.2.1 Subjects, Apparatus, and Procedure The tortoises in Experiment 1 participated in Experiment 2. The Apparatus was the same as that used in Experiment 1. The experiment was run between 10th December 2009 and 18th December 2009; trials took place in the early afternoon. The procedure was identical to that used in Experiment 1 except that in the experimental condition the demonstrator tortoises performed conditioned yawns for the first minute of the trial. This resulted in 2–3 conditioned yawns per trial (resulting in 6–9 in total per animal). To reduce the possibility that the tortoises yawned as the result of resting in the tank the total trial time was reduced to 3 minutes (including the demonstration phase) for each condition.

1.3 Experiment 3

We examined the possibility that the lack of differential responding observed in the first two experiments was because the conditioned yawn did not appear as a yawn to the tortoises. It is possible that some element of a real yawn was not reflected in the conditioned behavior of the demonstrator. We therefore presented the observer tortoises with video stimuli which displayed a real yawn, a fake yawn or an empty background.

1.3.1 Subjects, Apparatus, and Procedure A Sony Vaio laptop (VGN-CR31S) was placed in the demonstrator side of the tank. The screen was 14.1-in and the resolution set at 1280 × 800 pixels. The video stimuli were presented silently via this laptop. Three clips of Alexandra performing real yawns and conditioned yawns were recorded. In addition three clips containing only empty background were also recorded. The clips were edited and sequenced to produce three different videos. Each video contained six 10 second clips (each clip was presented twice within a video) of real yawns, conditioned yawns or background. Each clip was preceded by a 5 second white screen and matched for total length. This resulted in a stimulus presentation time of 1 minute 30 seconds. A further 30 seconds of white screen was presented after the stimulus presentation had finished. This resulted in each video being 2 minutes in length. The video length made up the total trial time for each observer tortoise for each condition, the trial time was therefore 2 minutes for each condition.

The tortoises in Experiment 1 and 2 participated in Experiment 3. The testing tank was the same as that used in Experiment 1 and 2. Each animal received three trials per condition. The experiment was run between 15th February 2010 and 17th March 2010; trials took place in the early afternoon. The procedure was identical to that used in Experiment 2 except that the stimuli were presented via laptop. The laptop was placed on the left-hand side of the experimental tank (where the demonstrator had been in previous experiments). It was turned on and displayed a white screen before the start of each trial. The observer tortoise was then placed on the right-hand side of the experimental tank. When the tortoise was looking at the screen the experimenter started the video sequence. In all other respects the procedure was identical that used in Experiment 2.

2 Results

2.1 Experimental 1

Fig. 2 presents the percentage of yawns observed in each condition. A Friedman's test revealed that there was no difference in the tortoises behavior across conditions (χ^2 = 3.82, *df* = 2, *P* = 0.15). Table 1 shows the number of responses in each condition for each animal. Overall response rate was poor with three of the six tortoises not responding in any of the conditions. However, of the three that did respond two responded more in the conditioned yawn condition than in the control conditions.

2.2 Experiment 2

Fig. 3 presents the percentage of yawns observed in each condition. A Friedman's test revealed no difference in the tortoises behavior across condition (χ^2 = 3.00, *df* = 2, *P* = 0.22). Examination of the individual data revealed that only two tortoises (Wilhelmina and Aldous) yawned in this experiment. Wilhelmina yawned in all conditions (conditioned yawn = 2, no demonstration = 1, stimulus only = 2) whereas Aldous only yawned once (in the stimulus only condition).

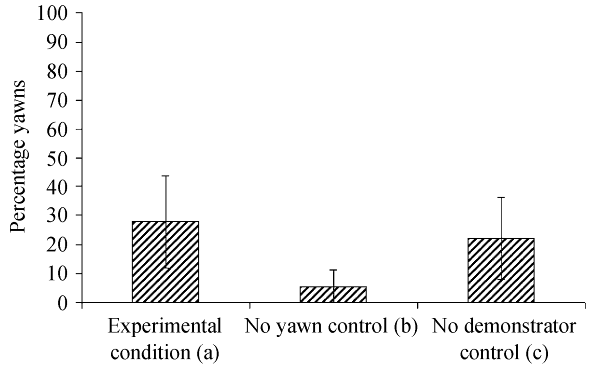

Fig. 2 Experiment 1. The total percentage of yawns of all subjects in (bar a) the experimental condition in which the tortoises observed the demonstrator perform a single conditioned yawn (bar b) the no yawn control condition in which the demonstrator was present but did not perform the conditioned yawn and (bar c) the no demonstrator control condition in which the stimulus was presented but the demonstrator was not there

The whiskers on all bars represent standard error.

2.3 Experiment 3

Fig. 4 presents the percentage of yawns observed in each condition. A Friedman's test revealed that there was no difference in the tortoises behavior between conditions (χ^2= 0.55, *df* = 2, *P* = 0.78). Examination of the individual data (Table 2) revealed that four of the six tortoises responded in this experiment, however, not a single animal responded more in the real yawn condition than in the two control conditions.

3 Discussion

The results of the three experiments presented in this paper suggest that the red-footed tortoise does not yawn in response to observing a conspecific yawn. Experiment 1 examined whether tortoises would yawn more when observing a conspecific perform a conditioned yawn than in other control conditions. They did not. The results revealed that there was no overall difference in responding across conditions suggesting that tortoises do not possess the ability to yawn contagiously. This

Table 1 The size, sex and the number of trials in which each tortoise yawned in each condition of Experiment 1

Tortoise	Size (cm)	Sex	Experimental Condition	No Yawn Control	No Demonstrator Control
Moses	14	Female	0	0	0
Aldous	17	Male	1	0	2
Wilhelmina	16.2	Female	3	1	2
Quinn	10.5	Unknown	1	0	0
Esme	11	Unknown	0	0	0
Molly	11	Unknown	0	0	0

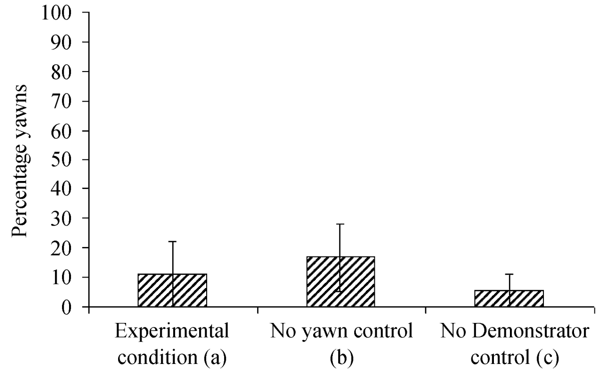

Fig. 3 Experiment 2. The total percentage of yawns of all subjects in (bar a) the experimental condition in which the tortoises observed the demonstrator perform six to nine conditioned yawns per animal conditioned yawns (bar b) the no yawn control condition in which the demonstrator was present but did not perform the conditioned yawn and (bar c) the no demonstrator control condition in which the stimulus was presented but the demonstrator was not there
The whiskers on all bars represent standard error.

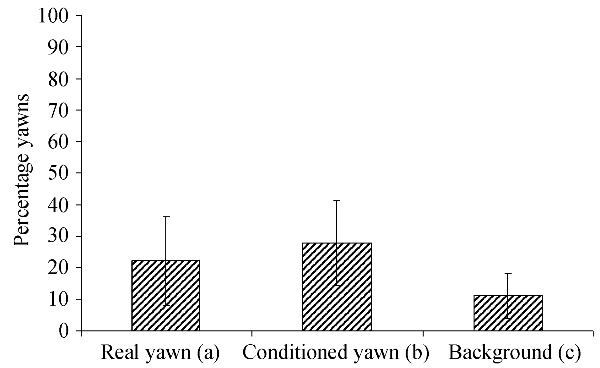

Fig. 4 Experiment 3. The total percentage of yawns of all subjects in (bar a) The experimental condition in which the tortoises observed a video containing six real yawns (bar b) the conditioned yawn control condition in which the tortoises watched video containing six conditioned yawns and (bar c) the background control condition in which the video background from each of the clips was played
The whiskers on all bars represent standard error.

Table 2 The number of trials in which each tortoise yawned in each condition of Experiment 3

Tortoise	Real Yawn	Conditioned Yawn	Background
Moses	0	1	1
Aldous	2	2	0
Wilhelmina	0	0	0
Quinn	0	0	0
Esme	0	0	1
Molly	2	2	0

suggests that contagious yawning may not be the result of a fixed action pattern for which the releaser stimulus is a yawn (Provine, 1986; Yoon and Tennie, 2010) but rather supports the idea that higher level mechanisms such as nonconscious mimicry (Yoon and Tennie 2010) or empathy (Anderson et al., 2004; Paukner and Anderson, 2006; Palagi et al., 2009; Joly-Mascheroni et al., 2008) may control this behavior. However, examination of the individual data revealed an overall low level of responding. Interestingly, of the three animals that did respond two responded more in the yawn condition than in the control conditions. This suggests that the tortoises may have the ability to yawn when they observe a conspecific yawning but it is possible that a single conditioned yawn per trial was not enough to evoke convincing evidence of contagious yawning in this species. The majority of research in this area has used multiple yawns (up to 19, Jolie-Mascheroni et al., 2008) as stimuli. It is therefore plausible that, under experimental conditions, multiple yawns are necessary for contagious yawning to occur.

Experiment 2 thus examined whether contagious yawning would be observed if the demonstrator performed multiple conditioned yawns. The results revealed that this was not the case. The tortoises were equally as likely to respond in the control conditions as they were in the experimental conditions. The combined results of Experiment 1 and 2 suggest that the tortoises do not yawn after observing a conspecific yawn. Again, the data contradict the hypothesis that contagious yawning is the result of a fixed action pattern (Provine, 1986; Yoon and Tennie, 2010) and suggests that higher processes such as empathy may be involved (Anderson et al., 2004; Anderson and Matsuzawa, 2006; Paukner and Anderson, 2006; Palagi et al., 2009; Joly-Mascheroni et al., 2008) or nonconscious mimicry (Yoon and Tennie 2010).

Experiment 3 examined the possibility that the lack of differential responding observed in the first two experiments was because the conditioned yawn did not appear as a yawn to the tortoises. The results revealed that the animals appeared to respond more in both the yawn and the conditioned yawn conditions than when they were presented with the background control. However, this apparent difference was not close to reaching statistical significance. Thus, the findings of Experiment 3 support those of Experiments 1 and 2 which together reveal that the red-footed tortoise does not yawn in response to observing a conspecific yawn. It is possible that the tortoises did not perceive the video stimuli as a real tortoise and that the experimental stimulus (the conditioned yawn) with which the tortoises were presented may have lacked some elements which, though not apparent to humans, were essential for contagious yawning to take place. For example, the demonstrator was trained to express a simulated yawn by opening its mouth wide and turning its head up. However, a yawn also involves the movement of air and this is something which was not simulated in either our conditioned yawn experiments or in the video playback. It is possible that a real yawn is necessary to stimulate the observer tortoise. Yet, video stimuli have successfully stimulated yawns in a variety of species (Anderson et al., 2004; Paukner and Anderson, 2006) and video stimuli have produced appropriate responses to social stimuli in the red-footed tortoise (Wilkinson et al., unpublished data). However, the use of video stimuli to elicit behavior in animals is controversial because it is not clear what the animals perceive on the screen. This may account for the differences seen between Joly-Macheroni et al.'s (2008) study in which dogs observed a real-life human demonstrator yawning and that of Harr et al. (2009) in which the yawns were presented as video stimuli. Little work has directly investigated picture-object recognition in reptiles. However, there is evidence that reptiles, including the red-footed tortoise, respond to video stimuli of conspecifics as if they were the real animals (e.g. Ord and Evans, 2002; Ord et al., 2002; Van Dyk and Evans, 2008; Wilkinson et al., unpublished data).

Overall, our findings are more consistent with the suggestion that tortoises do not yawn in a contagious manner and thus suggest that contagious yawning is not simply the result of a fixed action pattern and releaser stimulus, as if this mechanism controlled the behavior it would be predicted that contagious yawning would be present in all vertebrates that yawn. We suggest that contagious yawning may be controlled through social processes such as nonconscious mimicry or empathy, neither of which would have predicted the presence of contagious yawning in the red-footed tortoise. This finding indirectly suggests that, rather than increasing arousal, yawning may be a form of communication that evolved to synchronize group behavior (Daquin et al., 2001). However, the type of information that it might communicate or behavior that it might promote remains unclear. Numerous researchers have suggested that contagious yawning may be an indicator of empathy; however, results in experiments with humans have been equivocal (Platek et al., 2003; Schurmann et al., 2005). The findings of this study suggest that contagious yawning may be controlled by higher level social processes as it is believed that tortoises do not possess nonconscious mimicry or empathy. However, the current data do not allow us to determine whether contagious yawning is a result of nonconscious mimicry or empathy. The nonconscious mimicry hypothesis predicts the presence of contagious yawning in species in which perception and action rely on common neural representations we therefore might expect to observe it in animals living in complex social groups. The empathy hypothesis predicts that we would expect to see little evidence of contagious yawning outside the higher primates and (possibly) domesticated dogs, species believed to be capable of empathy (Joly-Mascheroni et al., 2008). Further research is needed to determine which of these social processes may be involved in controlling yawning.

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