

Response facilitation in the four great apes: is there a role for empathy?

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Abstract Contagious yawning is a form of response facilitation found in humans and other primates in which observing a model yawning enhances the chance that the observer will also yawn. Because contagious yawning seems to be more easily triggered when models are conspecifics or have a strong social bond with the observer, it has been proposed that contagious yawning is linked to empathy. A possible way to test this hypothesis is to analyze whether individuals' responses differ when they observe models yawning or performing different involuntary (i.e., nose wiping, scratching) and voluntary (i.e., hand closing, wrist shaking) actions that are not linked to empathy. In this study, we tested the four great ape species with two different setups by exposing them to a human experimenter repeatedly performing these actions online, and video-recorded conspecifics repeatedly performing these actions on a screen. We examined which behaviors were subject to response facilitation, whether response facilitation was triggered by both human models and video-recorded conspecifics, and whether all species showed evidence of response facilitation. Our results showed that chimpanzees yawned significantly more when and shortly

after watching videos of conspecifics (but not humans) yawning than in control conditions, and they did not do so as a response to increased levels of anxiety. For all other behaviors, no species produced more target actions when being exposed to either model than under control conditions. Moreover, the individuals that were more “reactive” when watching yawning videos were not more reactive when exposed to other actions. Since, at least in chimpanzees, (1) subjects only showed response facilitation when they were exposed to yawning and (2) only if models were conspecifics, it appears that contagious yawning is triggered by unique mechanisms and might be linked to empathy.

Keywords Contagious yawning · Chimpanzees · Great apes · Empathy · Response facilitation

Introduction

Response facilitation happens when observing a model performing an action increases the likelihood that the observer will also perform the same action (Byrne 1994). Although some authors prefer to refer to contagion when the target action is reflexive or involuntary, as in yawning (Zentall 2003), the more general term “response facilitation” is usually preferred, as for most actions it is not possible to exactly know whether the target action is reflexive or has been learned (e.g., Hoppitt et al. 2007). There are many examples of response facilitation across animal taxa. Synchronous courtship behavior and synchronized predator evasion in flocks and herds have been explained in terms of response facilitation (Armstrong 1951; Nuechterlein and Storer 1982). More recently, response facilitation has also been postulated as a more

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likely mechanism than imitation and social learning in some situations (e.g., Hoppitt et al. 2007).

One of the most basic examples of response facilitation is yawning. In 40–60 % of adult humans, yawning is easily triggered by seeing, reading or thinking about another individual yawning (Provine 1986, 2005; Platek et al. 2003). On the basis of experimental evidence, several authors have proposed that contagious yawning is linked to the ability to share others' emotions and engage in successful social interactions; in other words, it is linked to empathy (Preston and de Waal 2002; Platek et al. 2003; Singer 2006; Senju et al. 2007; but see Provine 1986; Nahab et al. 2009). In particular, both empathy and contagious yawning may rely on a perception–action mechanism in which perceiving one behavior would lead the subject to activate shared representations and involuntarily re-enact the observed behavior (Platek et al. 2003). For example, humans showing higher levels of response facilitation to yawning stimuli also score higher in questionnaires evaluating empathy, self-recognition, and theory of mind (Platek et al. 2003). Moreover, presumed emotional closeness between individuals best predicts yawning contagion in humans (Norscia and Palagi 2011).

Yawning is common across vertebrates, and yawning contagion has been shown in species other than humans (e.g., Anderson et al. 2004). Chimpanzees (*Pan troglodytes*), for example, yawn more when watching videos in which conspecifics are yawning than in control videos in which conspecifics are not yawning (Anderson et al. 2004; Campbell and de Waal 2011). Chimpanzees even show contagious yawning in response to 3D-animated chimpanzee yawns (Campbell et al. 2009). In gelada baboons (*Theropithecus gelada*) and bonobos (*Pan paniscus*), yawning is contagious and more frequent when subject and model have a stronger social bond, suggesting that contagious yawning might also be linked to empathy in nonhuman primates (Palagi et al. 2009; Demuru and Palagi 2012). Contagious yawning has also been documented in stump-tailed macaques (*Macaca arctoides*), although yawning responses elicited by unfamiliar video-recorded monkeys yawning were accompanied by self-scratching, suggesting that yawning was rather triggered by increased anxiety (Paukner and Anderson 2006). Finally, dogs may also show contagious yawning when watching videos of humans or conspecifics yawning (Joly-Mascheroni et al. 2008), although these findings are controversial (Harr et al. 2009; O'Hara and Reeve 2010).

Although there are several actions other than yawning which subjects can copy from conspecifics, to our knowledge no study has so far compared primates' response when subjects are exposed to several different target actions. This comparison can be informative to understand whether different mechanisms trigger response facilitation of yawning as compared to other behaviors, i.e., whether

contagious yawning might be linked to empathic skills while other behaviors are not. Apart from yawning, for example, individuals can copy other conspecifics' behaviors that are already present in the subject's repertoire, such as nose wiping (i.e., quickly touching the nose with the hand), scratching (i.e., rubbing the skin with the fingers), hand closing (i.e., making a fist with the fingers and then opening it again), and wrist shaking (i.e., quickly rotating the hand around the wrist). These behaviors are all typically present in the behavioral repertoire of great apes (see Nishida et al. 1999), but only contagious yawning has been linked to empathy (see above); nose wiping and scratching can be involuntary actions like yawning (e.g., Leavens et al. 2001), but they have never been linked to empathy; hand closing and wrist shaking are more under voluntary control than the other actions (Napier 1980) and have also never been linked to empathy. If different mechanisms trigger response facilitation to different target actions, subjects should respond differently in the different situations. In particular, subjects might show response facilitation whenever they are exposed to involuntary actions, or only when they are exposed to yawning.

In this study, we tested the four great ape species (*Pan troglodytes*, *Pan paniscus*, *Pongo abelii*, *Gorilla gorilla*) with two different setups aimed at assessing the propensity of individuals to spontaneously reproduce the following target actions: yawning, nose wiping, scratching, hand closing, and wrist shaking. Unlike previous studies (e.g., Anderson et al. 2004; Campbell et al. 2009), we did not have a condition involving the mouth in addition to yawning, but included several target actions involving other body parts. We did this because our main goal was not to assess whether individuals produced yawning upon seeing it, which had already been established by previous studies; instead, our main goal was to assess response facilitation more broadly (i.e., we did not only address how yawning varied under different conditions but also how other behaviors varied under different conditions).

As a model, we used a human experimenter repeatedly performing several actions online, and video-recorded conspecifics repeatedly performing several actions on a screen. We used both online and video-recorded models because subjects might attend differently to videos and live models, possibly showing stronger reactivity in the mirror-neuron system when observing live motor acts (Jarvelainen et al. 2001). All models were familiar to the subjects, as unfamiliar models might hinder response facilitation (e.g., Harr et al. 2009; Campbell and de Waal 2011). Our aim was to examine (1) which behaviors are subject to response facilitation, (2) whether response facilitation is triggered by both human models and video-recorded conspecifics, and (3) whether all species show evidence of response facilitation.

Methods

Subjects

We tested 14 chimpanzees (*Pan troglodytes*), 4 bonobos (*Pan paniscus*), 5 gorillas (*Gorilla gorilla*), and 4 orangutans (*Pongo abelii*) housed at the Wolfgang Köhler Primate Research Centre in Leipzig Zoo, Germany. The subjects were of both sexes and of various ages. They were all housed in groups with their conspecifics in enclosures with outdoor and indoor areas. Apart from two wild-born gorillas, all the other subjects were born in captivity. Before and during this study, subjects were not deprived of food or water at any time. All subjects were used to being isolated in testing rooms and were tested by the same experimenter, who was familiar to them.

Materials and procedure

Subjects were individually tested with two setups. In the first setup (the human setup), subjects received two different conditions. In the baseline condition, the experimenter sat in front of the subject and fed her an assortment of small rewards for 3 min, independently of any action performed by the subject. In the experimental condition, the same procedure was followed and the same amount of food was given to the subject; however, the experimenter also repeatedly engaged in one specific action while feeding the subject, once every approximately 15 s. This action could be yawning, nose wiping, scratching, hand closing, or wrist shaking. Each subject received two sessions for each of the five actions, each composed of two experimental conditions alternated with two baseline conditions, one starting with the baseline and the other with the experimental condition. Half of the subjects started with the baseline and half with the experimental condition, and the same action was always performed within the same session.

In the second setup (the video set-up), for each species we prepared an approximately 3 min video in which familiar conspecifics of the same social group performed one specific action ten times. This action could be yawning, nose wiping, or scratching. Hand closing and wrist shaking actions were not included in this setup given the difficulty involved in finding good examples of these actions by conspecifics to prepare the videos. Each video was displayed on a 35-cm-screen computer monitor in a continuous loop for the whole duration of the exposure period. Each subject received two sessions for each of the three actions, each composed of three different phases: the 3 min before the video was displayed, the 3 min during which the video was displayed, and the 3 min after the video was displayed. In both setups, the order in which the actions

were presented across sessions was alternated and counterbalanced across subjects.

Scoring and data analysis

We videotaped all the trials and later scored the subjects' behaviors from the videotapes. In each setup, phase, and condition, and for each of the corresponding actions, we coded the number of times each subject performed yawning, nose wiping, hand closing, and wrist shaking, and the seconds each subject spent scratching. A second observer coded 20 % of all the trials to assess the interobserver reliability of all the subjects' behaviors (Spearman's correlation: $\rho = 0.67$, $p < 0.001$).

In the human setup, for each subject, action, and condition, data from the two administered sessions were pooled together. Because the homogeneity of variance assumption was violated, for each action we used nonparametric Wilcoxon tests to compare the amount/duration of target actions performed in the experimental condition to that performed in the baseline condition for all species together and then separately for each species with $N \geq 5$ (i.e., chimpanzees and gorillas).

In the video setup, data from the two administered sessions were pooled together for each subject, action, and phase. For each action we used Friedman tests to analyze whether the amount/duration of target actions performed by subjects varied across phases. When the results of the Friedman test were significant, Wilcoxon tests were used for pair-wise comparisons (Cohen and Cohen 1983). Because some possible instances of contagious yawning have been linked to increased anxiety (Paukner and Anderson 2006), in the yawning condition we also used Friedman tests to compare the duration of scratching behavior (which is a common indicator of anxiety in primates: Maestriperi et al. 1992; Schino et al. 1996; Baker and Aureli 1997) across phases. In this way, we could examine whether the variation of yawning across phases mirrored differences in the level of anxiety experienced by the subject. Analyses were performed for chimpanzees and gorillas, and then repeated for all species together.

Finally, for each action we used the difference between the amount/duration of target actions performed in the experimental condition/video and post-video phase and that performed in the baseline condition/pre-video phase to calculate individual "reactivity" to the different target actions. We pooled data for all species together and used Spearman's correlations to analyze whether individuals that were more "reactive" in one setup or with one action were also more reactive in the other setup or with other actions. All tests were exact and two-tailed with the α level set at 0.05. Only significant results are reported.

Results

Human setup

Yawning and hand closing were never elicited as the target action, neither in the experimental nor in the baseline condition. For the other three behaviors, no species differed in the amount/duration of the target action between the baseline and the experimental condition (Fig. 1a–c). These results held when pooling together all four species.

Video setup

Chimpanzees showed a significant difference in yawning across phases when yawning was the target action ($\chi^2 = 9.0$, $df = 2$, $n = 14$, $p = 0.005$; Fig. 2a). In particular, chimpanzees yawned significantly more when the video was displayed and after the video was displayed than before the video was displayed (in both cases, $n = 6$,

$T = 21$, $p = 0.031$). Moreover, chimpanzees did not scratch differentially across phases when yawning was the target action ($\chi^2 = 2.415$, $df = 2$, $n = 14$, $p = 0.299$). No other species showed differences when the target action was yawning. For the other four behaviors, no species differed in the amount/duration of the target action across phases, even when pooling together the data of the four species (Fig. 2b, c).

Reactivity

We did not find significant correlations in individual reactivity for the same target action between the human and video setups. Similarly, no correlation was found between any two actions in the human setup. However, in the video setup, we found that individuals were more reactive when yawning was the target action, and they were significantly less reactive when nose wiping was the target action ($N = 27$, $\rho = -0.402$, $p = 0.038$).

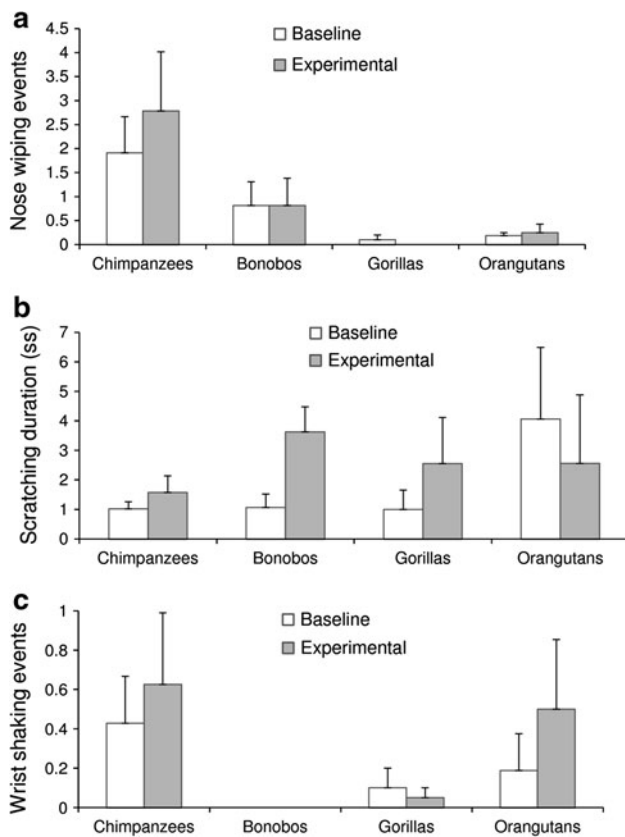


Fig. 1 For each species, mean (+SE) **a** number of nose wiping events when nose wiping was the target action, **b** duration of scratching when scratching was the target action, and **c** wrist shaking events when wrist shaking was the target action as performed by subjects in the baseline and in the experimental condition of the two administered sessions of the human setup. There were no significant differences in the amount/duration of the target action between the baseline and the experimental condition

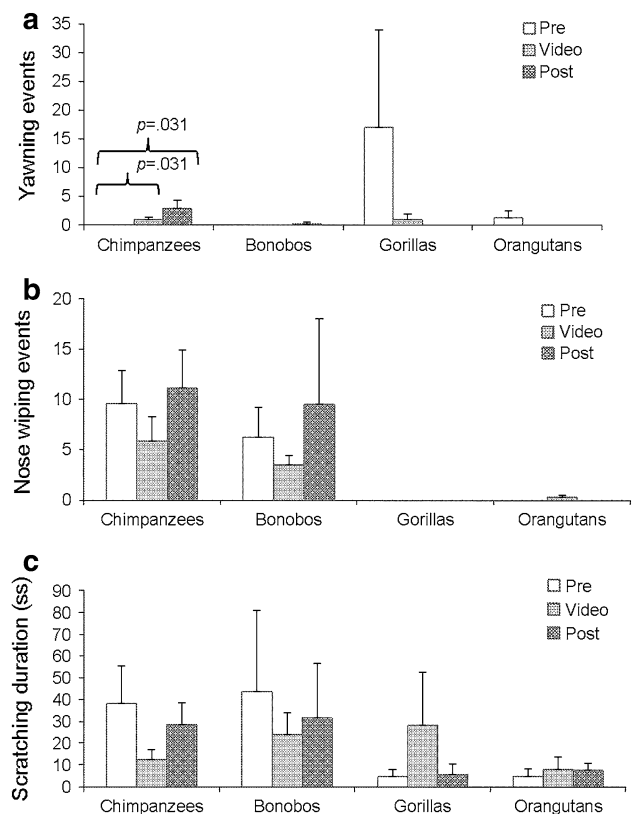


Fig. 2 For each species, mean (+SE) **a** number of yawning events when yawning was the target action, **b** nose wiping events when nose wiping was the target action, and **c** duration of scratching when scratching was the target action as performed by subjects in the pre-video, in the video, and in the post-video phases of the two administered sessions of the video setup. Significant differences in the amount/duration of the target action between phases are reported

Discussion

Chimpanzees yawned significantly more when watching videos of conspecifics yawning and shortly after they had watched such videos, as compared to before they watched the videos. In contrast, their scratching behavior did not change across phases of the yawning video. For all the other behaviors of the human and video setups, no species produced more target actions when being exposed to the model. Finally, the individuals that were more “reactive” to yawning in the video setup were significantly less reactive to nose wiping in the same setup. No other correlations within and across setups were found.

As in previous studies, chimpanzees yawned more when and after watching videos of conspecifics yawning than under control conditions (Anderson et al. 2004; Campbell and de Waal 2010). Chimpanzees did not yawn more as a response to enhanced levels of anxiety, as their scratching behavior did not significantly vary across phases of the yawning videos (in contrast to stump-tailed macaques: Paukner and Anderson 2006). Interestingly, yawning was the only behavior that elicited response facilitation. However, response facilitation only occurred in the video setup, suggesting that contagious yawning in chimpanzees is more easily triggered by conspecifics yawning than by human experimenters yawning, despite conspecifics in our study being video-recorded and video-recorded conspecifics tending to elicit weaker reactivity in the mirror-neuron system than live conspecifics (Jarvelainen et al. 2001). This is in line with contagious yawning in animals having so far only been triggered by watching conspecifics or mirror-images yawning (Anderson et al. 2004; Paukner and Anderson 2006; Palagi et al. 2009; Campbell and de Waal 2011; Demuru and Palagi 2012). If empathy underlies contagious yawning, contagious yawning should be triggered more frequently by familiar conspecifics living in the same social group rather than by human models, since the former have a stronger bond with the tested subjects (see Campbell and de Waal 2011). Dogs might be the only exception to this pattern, as they have shown contagious yawning when exposed to a human model (Joly-Mascheroni et al. 2008), but these findings are controversial (Harr et al. 2009; O’Hara and Reeve 2010).

Importantly, no action other than yawning elicited response facilitation. This result supports the hypothesis that contagious yawning might be triggered by mechanisms other than those eliciting response facilitation of other behaviors, even when these behaviors are involuntary. In addition, individuals that showed more response facilitation to yawning were those that showed *less* response facilitation to another involuntary target action such as nose wiping, confirming that reactivity to other involuntary actions might depend on different mechanisms than those

triggering contagious yawning (Platek et al. 2003; Anderson et al. 2004; Campbell and de Waal 2011; Norscia and Palagi 2011). For example, it has been proposed that contagious yawning is a simple form of response facilitation that does not require empathic skills and thus also occurs in vertebrates that lack empathy (e.g., Yoon and Tennie 2010). However, the only study, to our knowledge, which tested yawning in species other than mammals showed that contagious yawning was never elicited in red-footed tortoises (*Geochelone carbonaria*) under different conditions, leading the authors to conclude that contagious yawning may involve more complex social processes than mere response facilitation (Wilkinson et al. 2011).

The three great ape species other than chimpanzees showed no effect upon watching either type of model performing target actions, including yawning. It might be speculated that chimpanzees better activate shared representations to re-enact observed behaviors, thus showing more reactivity to contagious yawning as compared to the other great apes. If empathy is really linked to contagious behavior, however, the fact that all great apes possess the cognitive skills usually considered to be prerequisites for the understanding of others’ mental states, such as perspective taking and mirror self-recognition (e.g., Gallup et al. 2003; Brauer et al. 2005), would suggest that all great apes should be responsive to contagious behavior. It is indeed conceivable that our small sample size, together with important interindividual differences in terms of reactivity to the target actions (e.g., Anderson et al. 2004), might be responsible for our results. Future studies with larger sample sizes are clearly needed to confirm our findings.

To conclude, our study provided evidence for differences in response facilitation depending on the target action and species. In particular, our study found response facilitation only when chimpanzees watched conspecifics yawn, but not when humans yawned, or when conspecifics performed other actions. These findings support the view that mechanisms triggering contagious yawning may be different from those involved in other behaviors, and that contagious yawning may involve more complex social processes than mere response facilitation, such as empathic skills.

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