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SHORT COMMUNICATION

Gibbons (*Hylobates pileatus*, *H. moloch*, *H. lar, Symphalangus syndactylus*) follow human gaze, but do not take the visual perspective of others

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Abstract We investigated four gibbon species of two different genera (*Hylobates pileatus*, *H. moloch*, *H. lar*, *Symphalangus syndactylus*) in terms of their looking behavior in response to a human who either looked up or looked at the gibbon. Comparing those two conditions, gibbons as a group looked up more when the human was looking up, but they also performed more looks in other directions and thus generally looked more in this condition. Unlike great apes, gibbons did not respond differently between conditions when only the first look on every trial was considered. Furthermore, they did not perform double looks up to check where the human was looking and also did not habituate to the human's looks up. This suggests that gibbons co-orient with human gaze, but unlike great apes, they do not take the visual perspective of others.

Keywords Gibbons · Gaze-following · Social cognition · *Hylobates* · *Symphalangus*

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Introduction

One of the most basic social cognitive skills is gaze-following (Butterworth and Jarrett 1991) or 'looking in the direction that others are looking' (Rosati and Hare 2009). By following other individuals' gaze, one can gain valuable information about relevant events in the environment, for example, predators or food sources (McNelis and Boatright-Horowitz 1998). Gaze-following is widespread in the animal kingdom and has been reported for a variety of nonhuman primate species ranging from New World and Old World monkeys to great apes (Rosati and Hare 2009), but also other mammals like dogs (Miklósi et al. 1998) and goats (Kaminski et al. 2005), several bird species (Bugnyar et al. 2004), and even reptiles (Wilkinson et al. 2010). However, although many species share this skill, the underlying cognitive mechanisms and the corresponding functions may vary (Kehmeier et al. 2011). In its simpler form, gaze-following into distant space or visual co-orientation is an automatic, reflexive shift of gaze in response to another individual gazing to search for anything interesting along this line of sight, with the main function to detect predators (Gómez 2005). There is, however, a second, cognitively more complex variety, including gaze-following around a barrier or geometrical gaze-following, which requires the adjustment of the gaze-follower's current location, since the barrier blocks the direct line of sight (Gómez 2005). As opposed to reflexive anti-predator behavior, this second type of gaze-following requires an understanding of the visual perspective of another individual and thus what others can and cannot see, which might be an effective socio-cognitive strategy for species that live in complex social groups (Hare et al. 2001). The recent review by Rosati and Hare (2009) summarizes a large body of research on gaze-following in both monkeys and great apes, but also demonstrates that almost nothing is known about gibbons or lesser apes in this regard. The current study will try to close this gap.

Gibbons are an interesting group to study, since they are closely related with both monkeys and the great apes (Groves 2001), but as opposed to the majority of primate species, they live in monogamous pairs with their offspring and thus in small, stable family groups (Kleiman 1977). Because of this lack of social complexity, it is suggested that gibbons possess rather limited communicative and cognitive skills (Chivers 1976). Although so far little attention has been paid to gibbons, the very few existing studies have in general reported rather limited cognitive abilities (Abordo 1976; Suddendorf and Collier-Baker 2009). However, studies often suffer from the lack of motivation on the part of the gibbons, inappropriate design of the testing apparatus (Beck 1967), or from very small sample sizes. For example, a recent study reporting some evidence for gaze-following in gibbons tested only two pileated gibbons (Horton and Caldwell 2006). Both individuals were hand-raised, and although it was found that they followed the gaze of both conspecifics and humans, it might be the case that enculturation has strongly affected their behavior (Itakura and Tanaka 1998). Therefore, it is currently not clear whether the lack of studies demonstrating sophisticated cognitive skills in gibbons is caused by the difficulty of testing large sample sizes using appropriate designs or whether their often poor performance can be explained by their social organization and the resulting limited competition about resources within their groups (Humphrey 1976). Thus, gibbons are an important group to further our understanding about how socio-cognitive skills in general and gaze-following behavior in particular interact with variable social organizations and the related demands. If gaze-following abilities are largely driven by the demands of a certain social organization on an individual, gibbons should show less sophisticated gaze-following skills than any of their primate relatives with more complex social systems.

Therefore, in the current study, we tested gibbons of four species of two genera to investigate whether they follow the gaze direction of a human experimenter to a position in space. To enable a comparison with the four great ape species, we applied the method used by Call et al. (1998) and Bräuer et al. (2005). If gibbons are able to co-orient and therefore to follow human gaze, they should look up more when a human who is feeding them looks up than when the human simply looks at the gibbon. If they not only co-orient but actually understand that gaze is about something specific in the environment, they should look up repeatedly (double looks) to check where the human is gazing at, and the frequency of looks up should decrease over time as a result of habituation to the human's gazing at the ceiling (Bräuer et al. 2005).

Methods

Subjects

We tested 24 individuals from four different species including ten siamangs (*Symphalangus syndactylus*), eight pileated gibbons (*Hylobates pileatus*), four silvery gibbons (*H. moloch*), and two white-handed gibbons (*H. lar*), representing two genera (*Symphalangus:* $N = 10$, *Hylobates*: $N = 14$). The gibbons were housed in different zoos across Europe and lived in species-appropriate groups (Table 1). All were mother-reared except the four wild-born individuals whose rearing history is largely unknown. Ages ranged from three to 35 years with the majority being adult individuals (>6 years, Geissmann 1991).

Procedure

Depending on the housing conditions, subjects were tested either in their indoor or outdoor enclosures (Table 1). Since individuals were not used to being separated from their group, we ensured that the remaining group members did not influence the performance of the subject. Gibbons were tested at a mesh window (groups 3, 5, 7, 8, and 12), or in a separate room (4), which restrained other individuals than the subject from interacting with the human. Testing only started when the subject was not interacting with another group member and was located in front of the experimenter, who stood in front of the subject feeding desired food. The experimenter then suddenly stopped, while holding food in her hand followed by one of two conditions: In the *Experimental Condition*, the experimenter suddenly raised her head to look at the ceiling or up in the sky. In the *Control Condition*, she looked at the subject. Trials lasted 10 s in each condition, after which the experimenter continued feeding the subject until the next trial started. Subjects received six experimental and six control trials, making 12 trials altogether. If possible, all trials were completed within one session conducted on a single day. Order of conditions was counterbalanced and semi-randomized with the stipulation that the same condition could not appear in more than two consecutive trials. If the subject refused to participate, trials were completed the next day. All trials were videotaped and subsequently analyzed.

Coding

For each trial, we coded how often the subject looked either up or in another direction. *Look up* consisted of the subjects raising their head looking upwards above them. We also analyzed two further variants of *looks up*, namely *initial looks up* and *double looks up*. *Initial look up* was coded if the very first look at the beginning of each trial

Table 1 Genus, species, location, and individual characteristics of the gibbons

Genus	Species	Location	Testing area[a]	Group	Name	Age	Sex	Place of birth
Symphalangus	Siamang	Howletts Wild Animal Park	Out	1	Bulli	32	F	Captivity
		Howletts Wild Animal Park	Out	1	Xhabu	9	M	Captivity
		Howletts Wild Animal Park	Out	1	Xhali	7	F	Captivity
		Howletts Wild Animal Park	Out	2	Kuku-Gog	15	F	Captivity
		Marwell's Zoo	In	3	Luang	23	M	Captivity
		Marwell's Zoo	In	3	Simone	23	F	Captivity
		Marwell's Zoo	In	3	Hale Bob	11	M	Captivity
		Marwell's Zoo	In	3	Rosh	7	M	Captivity
		Zuerich Zoo	In	4	Ina	18	F	Wild
		Zuerich Zoo	In	4	Daw	5	F	Captivity
Hylobates	Pileated gibbon	Zuerich Zoo	In	5	Iba	34	F	Wild
		Zuerich Zoo	In	5	Emas	4	M	Captivity
		Zuerich Zoo	In	6	Khmer	24	M	Captivity
		Zuerich Zoo	In	6	Willow	21	F	Captivity
		Zuerich Zoo	In	6	Djantung	5	M	Captivity
		Zuerich Zoo	In	7	Yindhra	10	F	Captivity
		Zuerich Zoo	In	8	Banyar	7	M	Captivity
		Zuerich Zoo	In	8	Chamoa	6	M	Captivity
	Silvery gibbon	Howletts Wild Animal Park	Out	9	Marlene	24	F	Wild
		Howletts Wild Animal Park	Out	9	Imran	24	M	Wild
		Howletts Wild Animal Park	Out	10	Ujung	13	M	Captivity
		Howletts Wild Animal Park	Out	11	Reggat	7	F	Captivity
	White-handed gibbon	Vienna Zoo	In	12	Sipura	20	F	Captivity
		Vienna Zoo	In	12	Semera	3	F	Captivity

[a] *In,* indoor area; *out,* outdoor area

was a *look up* and not in another direction. *Double looks up* were coded when an individual looked up, then looked at the experimenter again, and looked up again with no more than 2 s and no *other looks* separating the two looks up (Call et al. 1998). *Other look* included all other gazing behaviors apart from looking up, such as downward, to either right or left, and behind. Looks—either up or in other directions—were only counted when the subject's head and gaze were oriented toward the human before the head movement started. If the head returned to this position afterward, the start of a new look was coded. Movements of the eyes alone were not considered, given the difficulties in detecting those subtle movements reliably.

Analysis

For reliability purposes, a naïve coder, not aware of the hypothesis, coded 20 % (five individuals) of the original material. Observed agreement was 85 % with a kappa value of 0.74, which represents a good level of agreement (Fleiss 1981).

In addition to an ANOVA, we used nonparametric statistics (Wilcoxon, Mann–Whitney U) to analyze the gibbons' looking behavior across conditions, as the assumptions for an ANOVA were not perfectly met, and the sample size was rather small. Statistics were calculated using R 2.10.0 (2010) including the package "exactRankTests" (Hothorn and Hornik 2010). We examined differences between genera but not between the *Hylobates* species, because two species of *Hylobates* were only represented by a few individuals.

Results

We analyzed different phases of each trial and will present the results accordingly. First, we compared the frequencies of *initial looks up* between the two conditions and included the first *look up* of each trial in this analysis. Second, we examined the mean frequencies of all looks (*looks up* and *other looks*) occurring during the 10-s test period in the two conditions. Third, we compared the mean frequencies of *double looks up* between the two conditions to investigate whether gibbons repeatedly looked up to check where the human is gazing. Finally, we analyzed whether the frequency of *looks up* changed with the increasing number of trials, which would indicate that the gibbons habituated to the experimental condition over time.

Looking behavior

The comparison of the mean frequencies of *initial looks up* found no significant difference between conditions (experimental: $M = 0.18$, $SD = 0.19$; control: $M = 0.11$, $SD = 0.13$; exact Wilcoxon: $T^{+} = 70.5$, $N = 14$ (10 ties), $P = 0.270$), indicating that if only their very first look up is considered, gibbons do not look up more when the human was looking upwards compared to when she was looking at them.

We then analyzed the mean frequencies of all *looks up* and *other looks* and conducted an ANOVA with the within-subject factors condition (experimental vs. control) and gaze direction (*look up* vs. *other looks*) and the between-subject factors testing area (outside vs. inside) and genus (*Hylobates* vs. *Symphalangus*). There was a main effect of condition with gibbons looking more in the experimental condition compared to the control condition ($F_{(1,20)} = 11.51$, $P = 0.003$) and a main effect of gaze direction with gibbons looking more in other directions than looking up ($F_{(1,20)} = 105.11$, $P < 0.001$). There was also a main effect of the between-factor testing area with gibbons looking more inside than outside ($F_{(1,20)} = 7.57$, $P = 0.012$) and a main effect of the between-factor genus with *Hylobates* producing more looking behaviors than *Symphalangus* ($F_{(1,20)} = 4.64$, $P = 0.044$). No other factors or their interactions reached significance. In the next step, we used nonparametric statistics to analyze looking behaviors (*look ups* and *other looks*) separately.

We first looked at the frequency of all *looks up* over the duration of 10 s in each of the two conditions (Fig. 1). As a group, gibbons looked up significantly more in the experimental condition ($M = 0.45$, $SD = 0.33$) compared to the control condition ($M = 0.29$, $SD = 0.26$, exact Wilcoxon: $T^{+} = 137.5$, $N = 18$ (6 ties), $P = 0.021$). However, when genera were tested separately, mean frequencies of *looks up* did not differ between conditions for both *Symphalangus* (exact Wilcoxon: $T^{+} = 21$, $N = 7$ (3 ties), $P = 0.281$) and *Hylobates* (exact Wilcoxon: $T^{+} = 54.5$, $N = 11$ (3 ties), $P = 0.054$). The comparison of the two genera within each condition revealed that in the experimental condition, individuals of the genus *Hylobates* looked up significantly more often compared to *Symphalangus*, while in the control condition, the two genera did not differ from each other (Mann–Whitney U: experimental: $U = 29$, $P = 0.014$, $N_S = 10$, $N_H = 14$; control: $U = 40$, $P = 0.073$; $N_S = 10$, $N_H = 14$).

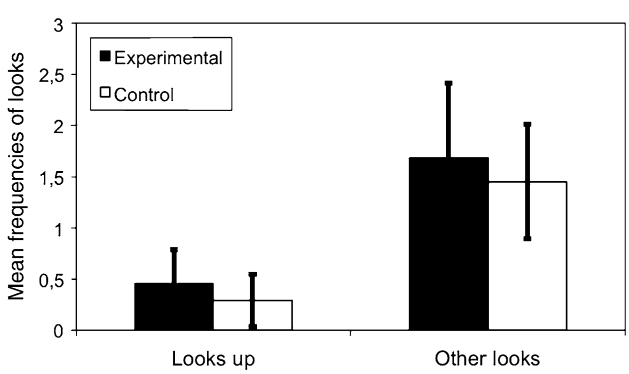

Fig. 1 Mean frequencies of *looks up* and *other looks* (±standard deviations) per trial (10 s) in the experimental and control conditions

The comparison of the mean frequencies of *other looks* across conditions revealed that, as a group, gibbons performed more *other looks* in the experimental condition ($M = 1.68$, $SD = 0.74$) compared to the control condition ($M = 1.45$, $SD = 0.56$, exact Wilcoxon: $T^{+} = 183.5$, $N = 21$ (3 ties), $P = 0.016$). Considering genera, we found no differences between *Hylobates* and *Symphalangus* (Mann–Whitney U: experimental: $U = 46.5$, $P = 0.175$; $N_S = 10$, $N_H = 14$; control: $U = 38.5$, $P = 0.065$; $N_S = 10$, $N_H = 14$). Those results indicate that gibbons also looked more often in other directions when the experimenter looked up compared to when the experimenter faced them, regardless of genus.

To investigate whether gibbons were more likely to perform *double looks* in the experimental condition—that is repeated looking upwards, which would indicate that they double check where the human is looking—we compared the frequencies of those *double looks up* between the experimental ($M = 0.06$, $SD = 0.12$) and the control conditions ($M = 0.02$, $SD = 0.056$), but found no significant difference between conditions (exact Wilcoxon: $T^{+} = 21$, $N = 7$ (17 ties), $P = 0.281$).

Habituation

To investigate whether the gibbons habituated over time to the human's gazing upwards in the experimental condition, we compared the mean number of *looks up* in the first block (trial 1–3) to the second block (trial 4–6). There was no difference between the two blocks indicating that the frequency of *looks up* did not decrease with increasing number of trials (exact Wilcoxon: $T^{+} = 110.5$, $N = 17$ (7 ties), $P = 0.109$).

Discussion

We found that, as a group, gibbons looked up more when the experimenter was looking up compared to when she was looking at the gibbons. This suggests that the gibbons followed the gaze of a human experimenter and therefore showed the skill of visually co-orienting with others, like other primate species (Rosati and Hare 2009). On the other hand, they also differed from other species, in particular from great apes, in several respects. First, when only initial looks where considered, gibbons did not respond differently across conditions, as has been found for great apes (Bräuer et al. 2005). Second, gibbons also performed more looks in other directions in the experimental condition compared to the control condition, suggesting that gibbons looked more in *all* directions when the human looked upwards. This suggests that watching the experimenter look up causes the gibbons to be generally more vigilant and to check the surroundings for relevant events. Interestingly, the gibbons also seemed to generally look more when they were in their inside compared to their outside enclosures. However, this occurred irrespective of the condition and therefore regardless of the looking behavior of the experimenter. Third, similar to findings in young chimpanzees (Tomasello et al. 2001), the gibbons did not habituate to the human's looking behavior over time. This suggests that gaze-following in both gibbons and young chimpanzees may be a rather simple, reflexive behavior, whereas gaze-following in adult chimpanzees is characterized by habituation and therefore may represent a more sophisticated behavior possibly based on a different cognitive mechanism (Gómez 2005). Most importantly, gibbons, unlike the great apes, did not perform more double looks up in the experimental condition, that is, they did not double check and therefore look up repeatedly to examine where the human is gazing (Bräuer et al. 2005).

Furthermore, our data raise the question whether there are differences between genera, since individuals of the genus *Hylobates* generally looked more compared to those of the genus *Symphalangus*. Currently, we cannot offer a good explanation for this difference between genera. However, it seems unlikely that this difference is due to the low performance of a particular population, since our sample contains siamangs of four groups from three different zoos.

In summary, the results of this study suggest that gaze-following skills of gibbons represent a reflexive co-orienting to the shift in somebody's gaze direction, not characterized by an understanding of the visual perspective of the human, and thus, their gaze-following skills seem much less sophisticated than those of great apes. We suggest that the lack of social complexity in those monogamous species is a possible explanation for this difference between gibbons and the other apes. For gibbons, there is no need to adapt for living in complex social groups, since there is only limited competition over recourses such as food or mating partners (Sandel et al. 2011). However, to test this hypothesis further, a systematic comparison of different species, including monkeys and apes, as a function of their social organization is essential. Furthermore, although gaze-following skills have been studied in a wide range of primate species, very different paradigms were used rendering a comparison of results impossible at this stage (Rosati and Hare 2009). In the current study, we only investigated the gibbons' behavior when looking into distant space, but to investigate in more detail whether gibbons show any gaze-following skills beyond visual co-orientation, future research should investigate gibbons' gazing behavior around barriers (Bräuer et al. 2005; Okamoto-Barth et al. 2007).

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