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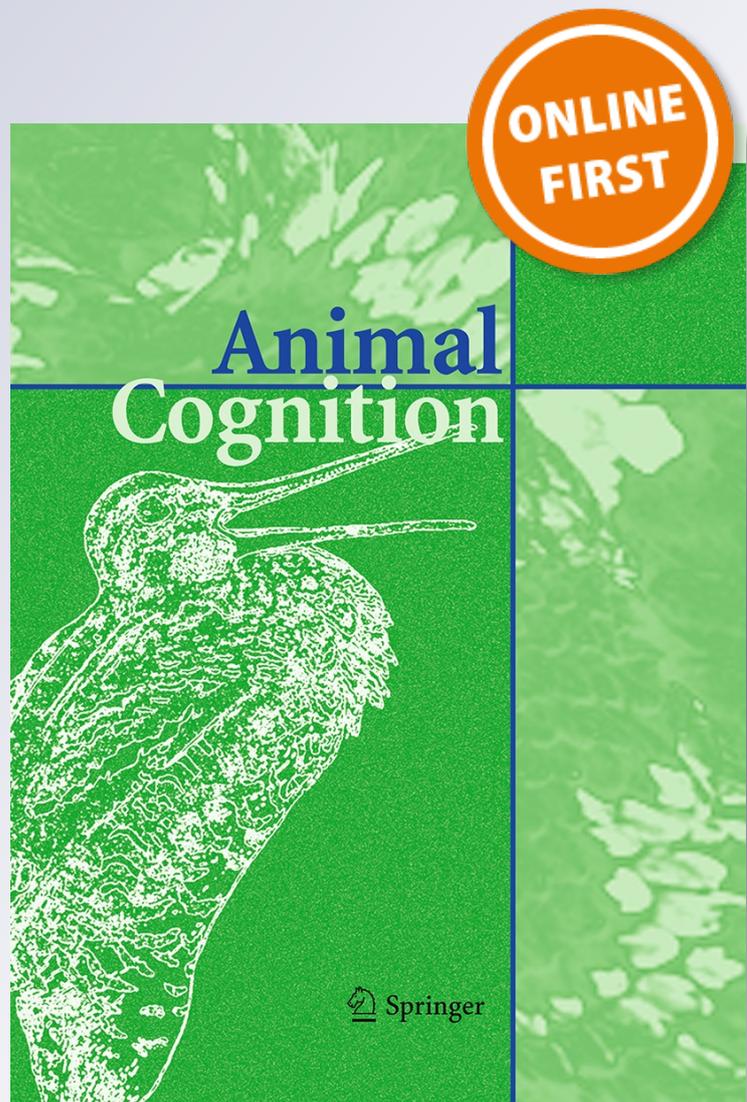
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‘Goats that stare at men’—revisited: do dwarf goats alter their behaviour in response to eye visibility and head direction of a human?

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Abstract Being able to recognise when one is being observed by someone else is thought to be adaptive during cooperative or competitive events. In particular for prey species, this ability should be of use in the context of predation. A previous study reported that goats (*Capra aegagrus hircus*) alter their behaviour according to the body and head orientation of a human experimenter. During a food anticipation task, an experimenter remained in a particular posture for 30 s before delivering a reward, and the goats’ active anticipation and standing alert behaviour were analysed. To further evaluate the specific mechanisms at work, we here present two additional test conditions. In particular, we investigated the effects of the eye visibility and head orientation of a human experimenter on the behaviour of the goats ($N = 7$). We found that the level of the subjects’ active anticipatory behaviour was highest in the conditions where the experimenter was directing his head and body towards the goat (‘Control’ and ‘Eyes closed’ conditions), but the anticipatory behaviour was significantly decreased when the body (‘Head only’) or the head and body of the experimenter were directed away from the subject (‘Back’ condition). For standing alert, we found no significant differences between the three

conditions in which the experimenter was directing his head towards the subject (‘Control’, ‘Eyes closed’ and ‘Head only’). This lack of differences in the expression of standing alert suggests that goats evaluate the direction of a human’s head as an important cue in their anticipatory behaviour. However, goats did not respond to the visibility of the experimenter’s eyes alone.

Keywords Dwarf goats · Eye visibility · Food anticipation paradigm · Head orientation · Social cognition

Introduction

The ability to recognise different attentive states of con- or heterospecifics may prove to be adaptive not only during cooperative or competitive events but also in the context of predation; for example, individuals of prey species, such as goats, may benefit from knowing whether they are being observed by others. Providing different test situations in which the body and head orientation of two humans were altered, Bulloch et al. (2008) showed that chimpanzees prefer to approach an attentive compared to a non-attentive person. The same paradigm has been used in studying attention recognition in several other primate (Botting et al. 2011; Bania and Stromberg 2012) and non-primate species (Gácsi et al. 2004; Proops and McComb 2010; Udell et al. 2011; Proops et al. 2013). For example, Proops and McComb (2010) showed that horses prefer to approach a person who is directing his/her head and body towards the subject, but they choose indifferently between two experimenters who are directing either only the head or only the body towards the subject. The results indicate that the horses were prone to approach the head and/or the body of an experimenter, independent of his/her attentive state and

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thus may have only reacted to a formerly rewarded cue (body and face oriented towards the subject) without having an understanding about the other individual's focus of attention. An additional concern is the amount of training and the general ontogeny the tested subject experienced, either during training sessions or during their lifetime. For instance, subjects may preferably approach a human who is looking towards them because they are used to getting a reward from humans who are looking at them directly. This issue has raised a considerable controversy about the impact of ontogeny and domestication on, e.g., dog's behaviour in socio-cognitive tasks (Roberts and Macpherson 2011; Udell et al. 2011; Virányi and Range 2011). Another test paradigm, mostly used with primates, is a food-requesting paradigm in which a test subject faces one human experimenter who engages in different postures towards the subject before a delayed reward will be delivered (Kaminski et al. 2004; Hattori et al. 2007; Tempelmann et al. 2011; Maille et al. 2012; Bourjade et al. 2014). The behavioural analysis in this paradigm focuses on the amount and duration of trained begging gestures (Kaminski et al. 2004; Maille et al. 2012; Bourjade et al. 2014), the extent of gazing or alternated gazes directed towards the experimenter (Hattori et al. 2007; Bourjade et al. 2014) and/or intentional attempts to regain the experimenter's attention (Bourjade et al. 2014), all depending on the attentive state of a human experimenter.

Nawroth et al. (2015a) have shown that dwarf goats tailor their anticipatory behaviour in a food anticipation task depending on the presence or absence of an experimenter in general and his head and body orientation in particular, thus interpreting the posture of the experimenter as an indicator of reward delivery. In that study, an experimenter remained for 30 s in a particular posture before delivering a reward to the tested subject, and the goats' active anticipation and standing alert behaviour were analysed. The authors found that the level of the subjects' active anticipatory behaviour was highest when the experimenter was looking in the direction of the test subject and decreased with a decreasing level of attention paid to the subject by the experimenter. Additionally, goats 'stared' (i.e. stood alert) at the experimental set-up/the experimenter for significantly more time when he was present but had his head and/or body directed away from the subject. However, it was not clear whether simple conditioned responses were responsible for the change in behaviour as described above (Proops and McComb 2010). For example, subjects may have learned in training trials that a certain posture of the experimenter (head and body oriented towards subject) will yield a reward. In test trials, postural differences may have simply led to a decreased expectation of reward delivery in test conditions that did not partially or fully mirror the position of the experimenter

in the instantly rewarded training trials. Thus, subjects may lack the ability to differentiate between the attentional states of others. One possible way to distinguish both interpretations is to test whether very subtle (e.g. eyes open or not) or irrelevant cues (body instead of head turned away) affect the behaviour of the test subjects.

Using the same food anticipation paradigm as Nawroth et al. (2015a), we wanted to evaluate whether such more subtle postural changes may affect the behaviour of the goats. If the goats are able to take into account the role of the eyes during the process of attention, anticipatory behaviour should be higher when the experimenter is looking at the subject compared to the condition where his eyes are closed. In contrast, we would expect a higher level of standing alert when the possibility of an immediate reward delivery is not certain; for example, when the experimenter is not focusing on the subject ('Eyes closed' and 'Back'). If the presence of the head alone was a salient cue used for evaluating the experimenter's orientation towards the goat, we would expect anticipatory behaviour and standing alert to be similarly high in the conditions where the experimenter is orienting his head towards the subject.

Animals, materials and methods

Ethics statement

All procedures involving animal handling and treatment were approved by the Committee for Animal Use and Care of the Ministry of Agriculture, Environment and Consumer Protection of the federal state of Mecklenburg-Vorpommern, Germany (Ref. Nr. 7221.3-2-005/14). Housing facilities met the German welfare requirements for farm animals.

Subjects, housing and general procedure

Nine female Nigerian dwarf goats (*Capra aegagrus hircus*), aged 4–5.5 years, participated in the experiment. The goats were group-housed at the Leibniz Institute for Farm Animal Biology. The pen contained straw bedding and was equipped with an automatic waterer, a hayrack and a wooden rack for climbing. The goats had ad libitum access to hay. The subjects were not food-restricted before testing. The subjects were tested daily from 9:00 to 12:00 and 14:00 to 17:00 in May 2014. For training and testing, individual goats were physically and visually separated from their pen mates in an adjacent compartment next to their home pen (150 × 125 cm). The experimenter sat in another adjacent compartment separated from the test animal by a grating, allowing subjects to put their snout

through the gaps between the bars. A sliding board (60 × 25 cm) was placed on a small table at a height of approximately 35 cm in front of the grating. In the training and test trials, one dark brown bowl (diameter 14 cm) was placed on the board. A dark brown cup (diameter 11 cm; height 10 cm) was used to cover the reward in the bowl. The distance between the bowl and the subject was approximately 30 cm (see Fig. 1). The goats had previously participated in a study using the same paradigm (Nawroth et al. 2015a), as well as in various choice tasks (Nawroth et al. 2014, 2015b), and were therefore familiar with the general procedure.

Experimental procedure

One training session was conducted the day before testing began. The male experimenter put a food reward (a piece of uncooked pasta)—visible to the goat—in a bowl that was placed in the middle of the sliding board and covered the reward with a cup. The experimenter then pushed the board forward. After the subject put its snout through the middle gap in the grating, the experimenter uncovered the reward and gave it to the subject. This was repeated ten times for each subject. After the training trials, all individuals were familiar with the procedure and reliably chose the bowl when the board was pushed forward. The procedure used in the test trials was similar, except that after the experimenter had baited the cup, the subjects were required to wait 30 s to receive the reward. During this time, the experimenter engaged in one of the four conditions (Fig. 2a–d):

Control: the experimenter sat motionless with his head and body oriented towards the subject

Eyes closed: the experimenter sat motionless as in Control, but with his eyes closed

Head only: the experimenter sat motionless with his body oriented laterally to the goat to the right side and his head oriented towards the subject

Back: the experimenter sat motionless with his back towards the subject

Before each test trial, subjects received an additional training trial for motivational reasons. In total, subjects received four sessions containing 16 trials each (two test trials for each condition and eight training trials); therefore, there were a total of eight test trials per condition. The conditions were presented pseudorandomly, with the restriction that the same condition was never presented twice in a row.

Data coding and statistical analysis

The goats' behaviour was video-recorded (Panasonic WV-CP500, Tamron 13 VG2811ASIR-SQ lens, EverFocus EDRHD-4H4 HDcctv Hybrid DVR). We used the videos to calculate the total amount of time the subject was standing in front of the grating and oriented towards it during the 30-s delay of each trial (assuming that the subject was paying attention to the experimenter and/or the experimental set-up) and engaged in (a) active anticipatory behaviour (i.e. nervous tripping while repeatedly putting their snout through the bars) and (b) standing alert (i.e. standing motionless with an extended neck, observing the experimental set-up). For behavioural coding, we used The Observer 10.1 (Noldus Information Technology, Wageningen, Netherlands). Both behaviours were modelled using linear mixed models (PROC Mixed, SAS[®] 9.2,



Fig. 1 Depiction of the test set-up during the 'Head only' condition

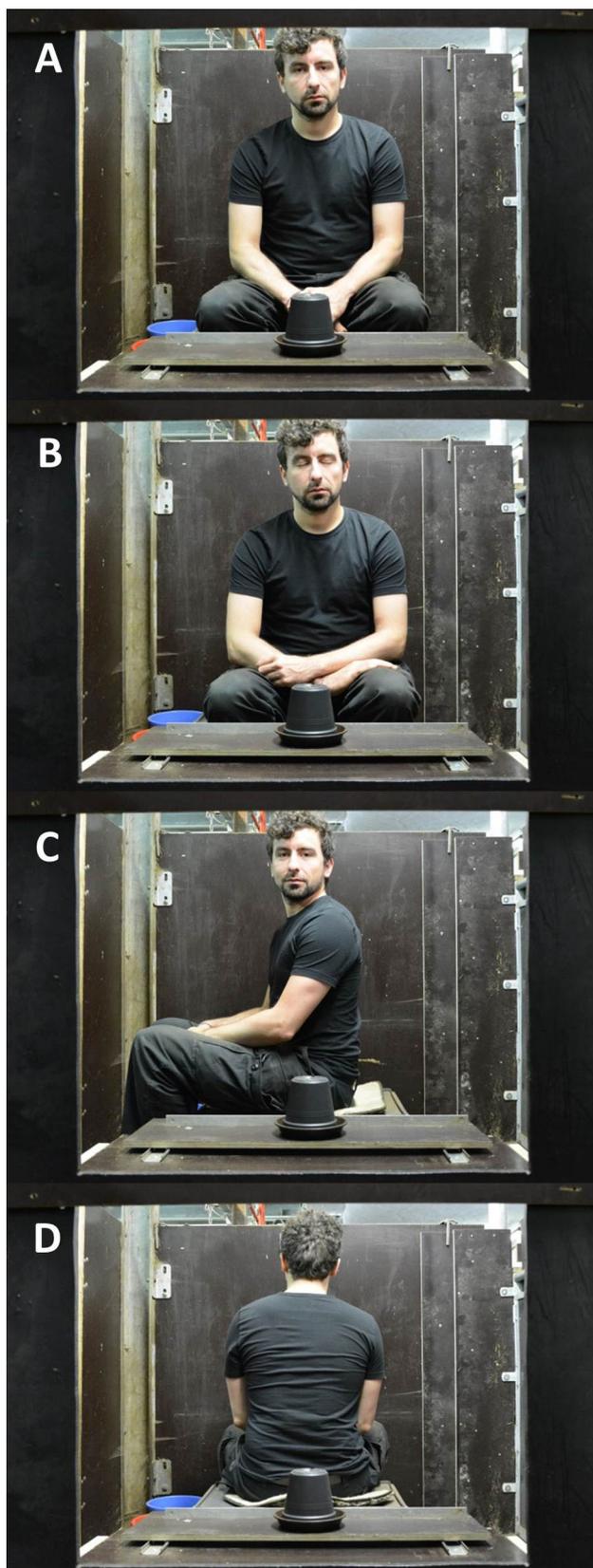


Fig. 2 Four different test conditions: **a** Control. **b** Eyes closed. **c** Head only. **d** Back

Cary, USA) to analyse the effects of ‘condition’, ‘half’ (i.e. first or second half of trials per condition) and their interaction. Each animal was defined as the subject for the repeated statement and was included with all fixed factors in both models. Least square means (LSM) and their standard errors (SE) were calculated. For pairwise comparisons (post hoc analysis), adjustments for repeated testing were applied (Tukey–Kramer corrections).

Results

Two subjects interfered with the set-up (kicking at the sliding board) during the test trials and were therefore excluded. Thus, a total of seven subjects were included in the analysis. We found a significant effect of ‘condition’ ($F_{3,42} = 12.39$; $P < 0.001$; see Fig. 3), but not of either ‘half’ ($F_{1,42} = 0.55$; $P = 0.46$) or the interaction between the two variables ($F_{3,42} = 0.06$; $P = 0.98$), on active anticipatory behaviour. The post hoc analysis revealed that the active anticipatory behaviour was significantly higher when the experimenter was directing his head and body towards the subject compared to the condition where he was turning his back towards it (‘Control’ and ‘Eyes closed’ compared to ‘Back’; post hoc analysis; all $P < 0.05$). In addition, active anticipatory behaviour was higher in the ‘Eyes closed’ compared to the ‘Head only’ condition ($P < 0.05$). There was no difference between the ‘Control’ and ‘Eyes closed’ condition ($P > 0.05$). For standing alert, we found an effect of ‘condition’ ($F_{3,42} = 6.80$; $P < 0.001$; see Fig. 3) but not of either ‘half’ ($F_{1,42} = 0.48$; $P = 0.49$) or the interaction between

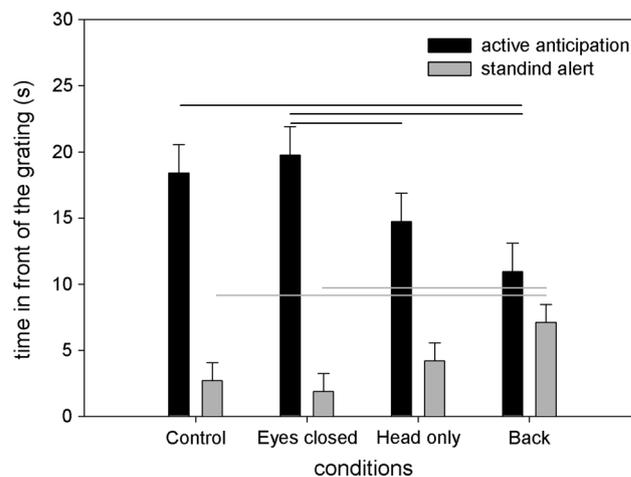


Fig. 3 The graph shows the amount of time subjects engaged in active anticipatory behaviour (black bars) and standing alert (grey bars) during the 30-s intervals in the different conditions (LSM \pm SE). Horizontal lines above the bars indicate significant differences between single conditions ($P < 0.05$)

the two variables ($F_{3,42} = 0.36$; $P = 0.78$). The subjects were significantly less likely to stand alert in conditions where the experimenter was directing his head and body towards the subject compared to the condition where he was turning his back towards it (i.e. 'Control' and 'Eyes closed' conditions compared to 'Back' condition; post hoc analysis; all $P < 0.05$). No other differences between conditions could be found ($P > 0.05$).

Discussion

In the current study, we investigated the effect of several different postures of a human experimenter on goats' anticipatory behaviour. We found that the level of the subjects' active anticipation was highest in the conditions where the experimenter was directing his head and body towards the goats, and active anticipation was significantly decreased when the head and body of the experimenter were directed away from the subject. In addition, active anticipatory behaviour differed between the 'Head only' and the 'Eyes closed', but not with the 'Control' condition. For standing alert, we found no significant differences between the three conditions in which the experimenter was directing his head towards the subject.

Nawroth (2015a) discussed the possibility that learning about the difference in the experimenter's head and body position in a test compared to training trials may offer a simple explanation for changes in the anticipatory behaviour of the goats (see also Proops and McComb 2010). Taking into account the general surface of the head and the body, merely turning the head is a less salient cue compared to turning the entire body. If goats only responded to the experimenter's posture with a conditioned response, this response should be decreased when the body of the experimenter is turned away compared to when only the head is turned. Nawroth et al. (2015a) found a significant difference in the active and passive anticipatory behaviour in the 'Control' condition compared to the test condition where only the head of the experimenter was turned away. In the current study, we found no significant change in standing alert behaviour when the experimenter was turning his body, but not his head ('Head only'), away from the subject compared to the 'Control' condition. However, a direct comparison between both conditions is necessary to make final conclusions.

For great apes, Kaminski et al. (2004) suggested that the visibility of the experimenter's face provides information about the human's attentional state, while body orientation provided information about the experimenter's general disposition to offer food and thus led to a

decreased begging rate when the body of the experimenter was turned away, irrespective of the head direction. As soon as the offering of the food was no longer restricted due to a specific body direction, the orientation of the face became the key factor (Tempelmann et al. 2011). It would be interesting to investigate whether goats that experience a human turning his/her back during training trials will exhibit the same behaviour in test trials as the goats in the current study and the one by Nawroth et al. (2015a).

In both active anticipation and standing alert behaviour, we did not find a behavioural difference between the 'Control' and the 'Eyes closed' condition. Previous experiments designed to explore animals' ability to read humans' eyes as a cue for a possible understanding of attentional states have produced mixed results for other species (Proops and McComb 2010; but see Hattori et al. 2010; Botting et al. 2011; Maille et al. 2012). We speculate that goats are less sensitive to information from the eyes as they have morphological features thought to conceal gaze direction, i.e., dark or no exposed sclera (Emery 2000), and due to the lateral position of their eyes, head and eyes are normally moved together (Davidson et al. 2014). Studies in different mammal and bird species have shown that their brain contains neurons that are selectively responsive to head or body orientation, simple facial features or even eye direction (see Emery 2000; Tate et al. 2006). This suggests a degree of hierarchical processing or hierarchical encoding of the direction of another's attention, which may explain the response of the goats towards the head and body orientation, but not the visibility of the eyes of a human. Additional controls—such as blinds that cover the mouth or the eyes of the experimenter—and additional validation through other test paradigms, e.g. choice tasks, either cooperative (Proops and McComb 2010) or competitive (Sandel et al. 2011), are also necessary to support our results.

We conclude that the lack of differences in the expression of standing alert during the conditions where the experimenter is facing towards the subject suggests that goats evaluate the direction of a human's head as an important cue in their anticipatory behaviour. However, goats did not respond to the visibility of the experimenter's eyes alone.

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