

WellBeing International

WBI Studies Repository

1-2015

“Goats That Stare at Men” – Dwarf Goats Alter Their Behaviour in Response to Human Head Orientation But Do Not Spontaneously Use Head Direction as a Cue in a Food-Related Context

Christian Nawroth

Martin Luther Universitat Halle-Wittenberg

Eberhard von Borell

Martin Luther Universitat Halle-Wittenberg

Jan Langbein

Leibniz Institute for Farm Animal Biology

Follow this and additional works at: <https://www.wellbeingintlstudiesrepository.org/soccog>



Part of the [Animal Studies Commons](#), [Comparative Psychology Commons](#), and the [Other Animal Sciences Commons](#)

Recommended Citation

Nawroth, C., von Borell, E., & Langbein, J. (2015). 'Goats that stare at men': dwarf goats alter their behaviour in response to human head orientation, but do not spontaneously use head direction as a cue in a food-related context. *Animal cognition*, 18(1), 65-73.

This material is brought to you for free and open access by WellBeing International. It has been accepted for inclusion by an authorized administrator of the WBI Studies Repository. For more information, please contact wbisr-info@wellbeingintl.org.



1 **“Goats that stare at men” – Dwarf goats alter their behaviour in**
2 **response to human head orientation but do not spontaneously use**
3 **head direction as a cue in a food-related context**

4 Christian Nawroth¹, Eberhard von Borell¹, Jan Langbein*²

5 ¹*Department of Animal Husbandry & Ecology, Institute of Agricultural and Nutritional Sciences,*
6 *Martin-Luther-University, Halle, GER*

7 ²*Institute of Behavioural Physiology, Leibniz Institute for Farm Animal Biology, Dummerstorf,*
8 *GER*

9

10

11

12

13 **Corresponding author**

14 Jan Langbein

15 Institute of Behavioural Physiology

16 Leibniz Institute for Farm Animal Biology

17 Dummerstorf, GER

18 Phone: +49-38208-68814

19 Fax: +49-38208-68801

20 Email address: langbein@fhn-dummerstorf.de

21

22 **Abstract**

23

24 Recently, comparative research on the mechanisms and species-specific adaptive values of
25 attributing attentive states and using communicative cues has gained increased interest, particularly
26 in non-human primates, birds, and dogs. Here, we investigate these phenomena in a farm animal
27 species, the dwarf goat (*Capra aegagrus hircus*). In the first experiment, we investigated the effects
28 of different human head and body orientations, as well as human experimenter presence/absence, of
29 a human on the behaviour of goats in a food-anticipating paradigm. Over a 30-sec interval, the
30 experimenter engaged in one of four different postures or behaviours (head and body towards the
31 subject, head to the side, head and body away from the subject, or leaving the room) before
32 delivering a reward. We found that the level of subjects' active anticipatory behaviour was highest
33 in the control condition and decreased with a decreasing level of attention paid to the subject by the
34 experimenter. Additionally, goats 'stared' (i.e., stood alert) at the experimental setup for
35 significantly more time when the experimenter was present but paid less attention to the subject
36 ('Head' and 'Back' condition) than in the 'Control' and 'Out' conditions. In a second experiment,
37 the experimenter provided different human-given cues that indicated the location of a hidden food
38 reward in a two-way object choice task. Goats were able to use both 'Touch' and 'Point' cues to
39 infer the correct location of the reward but did not perform above the level expected by chance in
40 the 'Head only' condition. We conclude that goats are able to differentiate among different body
41 postures of a human, including head orientation; however, despite their success at using multiple
42 physical human cues, they fail to spontaneously use human head direction as a cue in a food-related
43 context.

44

45 **Keywords:** Dwarf goats; social cognition; food-anticipation paradigm; attentive states; human-given
46 cues

47

48 **Introduction**

49

50 Over the last decade, research on the attribution of attentive states and the use of communicative
51 cues has provided insight into the complex social lives of non-human animals, particularly primates,
52 birds, and dogs. In addition to comparative reasons, it is important to know to what extent non-
53 human individuals understand the perceptual and mental states of others and the context in which
54 this knowledge is used (Gómez 2005a; Rosati and Hare 2009; Davidson et al. 2014).

55 The ability to recognise different attentive states of con- or heterospecifics may yield
56 adaptive advantages in the contexts of predation, deception or cooperation; for example, individuals
57 may benefit from knowing if others are observing them. Two types of test paradigms are commonly
58 used to study the recognition of attentive states. The first is a choice paradigm in which a subject
59 must choose between two individuals that differ in their attentive state towards the subject to
60 receive a reward. Subjects can either avoid being observed by choosing the non-attentive person
61 (competitive context: Flombaum and Santos 2005; Sandel et al. 2011) or the person paying them
62 attention (communicative context: Povinelli and Eddy 1996; Gácsi et al. 2004; Bulloch et al. 2008;
63 Proops and McComb 2010; Botting et al. 2011; Bania and Stromberg 2013; Nawroth et al. 2013a) –
64 expecting to receive a food reward with less delay. The second is a food-requesting paradigm in
65 which the subject faces a human experimenter who engages in different attentive states before a
66 reward is delivered after some delay (Kaminski et al. 2004; Hattori et al. 2007; Tempelmann et al.
67 2011; Maille et al. 2012; Bourjade et al. 2014). The latter paradigm has been applied to primate
68 species, with the behavioural analysis focusing on specific behavioural patterns. These patterns may
69 include the amount and duration of trained begging gestures (Kaminski et al. 2004; Maille et al.
70 2012; Bourjade et al. 2014) , the extent of gazing or alternated gazes directed towards the
71 experimenter’s face (Hattori et al. 2007; Bourjade et al. 2014) and/or intentional attempts to regain
72 the attention of another subject (Bourjade et al. 2014), all depending on the attentive state of a
73 human experimenter. However, general behaviour patterns, such as anticipatory behaviour, have

74 been rarely examined.

75 Although the ability to recognise another individual is observing one has adaptive
76 advantages, the ability to follow the gaze of others may also be crucial to survival in some
77 circumstances. At least three different mechanisms can be classified: Gaze following, geometrical
78 gaze following and shared attention. Gaze following is defined as the co-orientation of one's own
79 gaze direction into distant space with that of another individual (Tomasello et al. 1998; Kaminski et
80 al. 2005; Wilkinson et al. 2010; Loretto et al. 2010). However, a learned association or a simple
81 behavioural response cannot be excluded as explanatory factors. In turn, geometric gaze following
82 enables a subject to follow the gaze of a con- or hetero-specific around barriers, which requires
83 taking the visual perspective of the other individual (Bugnyar et al. 2004; Bräuer et al. 2005; Range
84 and Virányi 2011). Another mechanism of co-orienting with another individual's gaze direction is to
85 share attention with the other individual towards the focal object. This latter mechanism is
86 commonly investigated using a so-called object choice task. Here, a subject chooses between two or
87 more containers, one of which covers a hidden food reward. Typically, a human experimenter
88 administers a communicative cue (e.g. pointing or gazing) towards the food-containing container,
89 and the tested subject is free to choose one (for a review see Miklósi and Soproni 2006). For
90 example, dogs have been shown to be exceptionally skilled at comprehending human-given cues
91 such as different forms of pointing gestures or gaze direction (Hare et al. 2002; Hare and Tomasello
92 2005; but see Udell et al. 2008). Other domesticated species, such as goats (Kaminski et al. 2005)
93 and horses (Maros et al. 2008; Proops et al. 2010), appear to be able to make use of some pointing
94 gestures comprehended by dogs, but fail to utilise gaze cues of a human experimenter to find a
95 reward. In addition, some non-domesticated species have been found capable of following human-
96 given cues, including gaze direction (e.g., grey parrots: Giret et al. 2009; rooks: Schmidt et al. 2011;
97 seals: Scheumann and Call 2004).

98 In previous research, Kaminski and colleagues (2005) showed that goats can follow the gaze
99 of conspecifics into distant space. They also showed that goats fail to use the head direction of a

100 human to find hidden food in an object-choice task, despite their success in using pointing and
101 touch cues. This negative result may reflect the incapacity of goats to use head direction as a
102 communicative cue. However, this result could also be due to methodological issues, for example,
103 an out-of-focus or out-of-sight cue (Mulcahy and Hedge 2012; Nawroth et al. 2014b).

104 In this study, we analysed the behaviour of subjects presented with hidden food with 1) no
105 need to use the orientation of the experimenter's head or body to infer the location of the reward
106 (Experiment 1) and 2) the need to interpret the physical cues, body or head orientation to infer the
107 location of the reward(Experiment 2). In the first experiment with dwarf goats, we employed an
108 experimental design similar to the food-requesting paradigm that has been primarily used with
109 primates (Kaminski et al. 2004; Tempelmann et al. 2011; Maille et al. 2012; Bourjade et al. 2014).
110 As the goats were not trained to exhibit specific begging behaviour, we refer to our paradigm as a
111 food-anticipation paradigm, according to the measured behavioural parameters. We analysed the
112 behaviour goats' exhibited towards the experimenter and the experimental setup in response to
113 different head and body postures as well as the presence and absence of the experimenter over a 30-
114 sec period. Because subjects had not been trained to produce begging gestures, we focused on more
115 general behavioural patterns; specifically, different types of anticipatory behaviour . Anticipatory
116 behaviour was described by Craig (1918) as arousal with goal-directed activity that occurs during
117 the appetitive phase, during which the actual reward is not yet available and/or visible. One of the
118 main characteristics of anticipation is enhanced attention which is reported to be characterised by
119 increases in activity and exploratory behaviour alternating with phases of standing alert and
120 watching (Bolles 1968; Hooks et al. 1994; Hansen and Jeppesen 2006; Zimmerman et al. 2011;
121 Imfeld-Mueller and Hillmann 2012; Moe et al. 2012). Importantly, anticipation requires the ability
122 to internally represent expectations of a forthcoming reward during the appetitive phase (Spruijt et
123 al. 2001). We therefore predicted that the time subjects spent spend engaging in anticipation
124 behaviours would depend on their perceived likelihood of reward delivery. In general, when the
125 experimenter is present and looking at the subject, anticipatory behaviour should be higher than

126 when the experimenter is absent and therefore unable to deliver the reward. In contrast, we would
127 expect a higher level of standing alert, although not full arousal, i.e., close watching and
128 observation of the experimental setup, when the possibility of immediate reward delivery is likely
129 but not certain; e.g., when the experimenter is present but not focused on the subject. Immediately
130 following, we conducted a second experiment in which we administered different human-given
131 cues to the subjects to find a hidden food reward using a very similar object-choice paradigm to
132 that used by Kaminski and colleagues (2005), with some modifications. We hypothesised that goats
133 should be able to use physical cues, such as pointing or touching, due to local enhancement or
134 learning effects. These effects are absent when only head direction is available as a communicative
135 cue. Therefore, goats should perform at a level equal to chance at sharing attention with other
136 individuals when only head cues are available, as there is no strong adaptive need for this ability
137 due to goats' abundantly distributed, natural food sources.

138

139 **Materials & Methods**

140

141 **Ethics statement**

142

143 All procedures involving animal handling and treatment were approved by the
144 Committee for Animal Use and Care of the Ministry of Agriculture, Environment and
145 Consumer Protection of the federal state of Mecklenburg-Vorpommern, Germany (Ref. Nr. 7221.3-
146 2.1-014/13). Housing facilities met the German welfare requirements for farm animals.

147

148 **Subjects, housing and general procedure**

149

150 Eleven female Nigerian dwarf goats (*Capra aegagrus hircus*), aged 3-4.5 years, participated in both
151 experiments. Goats were group-housed at the Leibniz Institute for Farm Animal Biology. The pen
152 contained straw bedding and was equipped with an automatic waterer, a hayrack, a round feeder for
153 delivering commercial concentrate and a wooden rack for climbing. The goats had ad libitum access
154 to hay, and concentrate was offered twice daily at 300 g/d/animal. Subjects were not food restricted
155 before testing. The subjects were tested daily from 9:00-12:00 and 14:00-17:00 in April 2013. For
156 training and testing, individual goats were physically and visually separated from their pen-mates in
157 an adjacent compartment next to their home pen (150 cm x 125 cm). The experimenter sat in
158 another adjacent compartment separated from the test animal by a grate, allowing subjects to insert
159 their snouts through the bars. A sliding board (60 cm x 25 cm) was placed on a small table at a
160 height of approximately 35 cm in front of the grate. In the test and motivation trials, one or two dark
161 brown bowls (diameter: 14 cm), depending on the experiment, were placed on the board. Dark
162 brown cups (diameter: 11 cm; height: 10 cm) covered the bowls. The distance between the bowls
163 and the subject was approximately 30 cm. Goats had previously participated in a study (Nawroth et
164 al. 2014a) of a similar test design (i.e., an object-choice task) and were therefore familiar with the

165 general procedure; that they had to place their snout through the bars to indicate their choice and to
166 receive a reward.

167

168 **Experiment 1**

169

170 One training session was conducted the day before testing began. The experimenter put a food
171 reward (a piece of pasta) – visible for the goat - in a bowl that was placed in the middle of the
172 sliding board and covered it with a cup. The experimenter then pushed the board forward. After the
173 subject snouted through the middle gap of the grate, the experimenter uncovered the reward and
174 gave it to the subject. This was repeated ten times for each subject. After the training trials, all
175 individuals were familiar with the procedure and reliably chose the bowl when the board was
176 pushed forward. The procedure used in the test trials was similar, except that after the experimenter
177 had baited the cup, the subjects had to wait 30 seconds to receive the reward. During this time, the
178 experimenter engaged in one of four conditions (Figure 1 a-d):

179

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

181 Head: the experimenter sat motionless with his head oriented to the right

182 Back: the experimenter sat motionless with his back to the subject

183 Out: the experimenter left the test pen

184

185 Before each test trial, subjects received a training trial for motivational reasons. Subjects received a
186 total of four sessions of sixteen trials (two test trials for each condition and eight training trials) and
187 therefore a total of eight trials per condition. Conditions were presented pseudorandomly with the
188 restriction that the same condition was never presented twice in a row.

189



190
 191 Figure 1 I. Conditions in Experiment 1 a) Control b) Head c) Back d) Out II. Conditions in
 192 Experiment 2 e) Touch f) Point g) Gaze h) Control

193

194 **Data coding and statistical analysis**

195

196 Goat behaviour was video-recorded (Panasonic WV-CP500, Tamron 13VG2811ASIR-SQ lens,
197 EverFocus EDRHD-4H4 HDcctv Hybrid DVR). For Experiment 1, we used the videos to record the
198 total amount of time the subject was oriented towards the grate during the 30-sec delay of each trial
199 (assuming that the subject was paying attention to the experimenter and/or the experimental setup)
200 and engaged in a) active anticipatory behaviour (i.e., nervous tripping near the grate while
201 repeatedly snouting through the bars; see supplementary material, video S1) and b) standing alert
202 (i.e., standing motionless with an extended neck near the grate, observing the experimental setup;
203 see supplementary material, video S2). For behavioural coding, we used The Observer 10.1 (Noldus
204 Information Technology, Wageningen, Netherlands). Both behaviours were modelled using linear
205 mixed models (PROC Mixed, SAS® 9.2) to analyse the effects of ‘condition’, ‘half’ (i.e., first or
206 second half of trials per condition) and their interaction. Each animal was defined as the subject for
207 the repeated statement and was included with all fixed factors in both models. Least square means
208 (LSM) and their standard errors (SE) were calculated. For pairwise comparisons (post-hoc
209 analysis), adjustments for repeated testing were applied (Tukey–Kramer corrections). Additionally,
210 we scored the number of vocalization of all individuals across conditions.

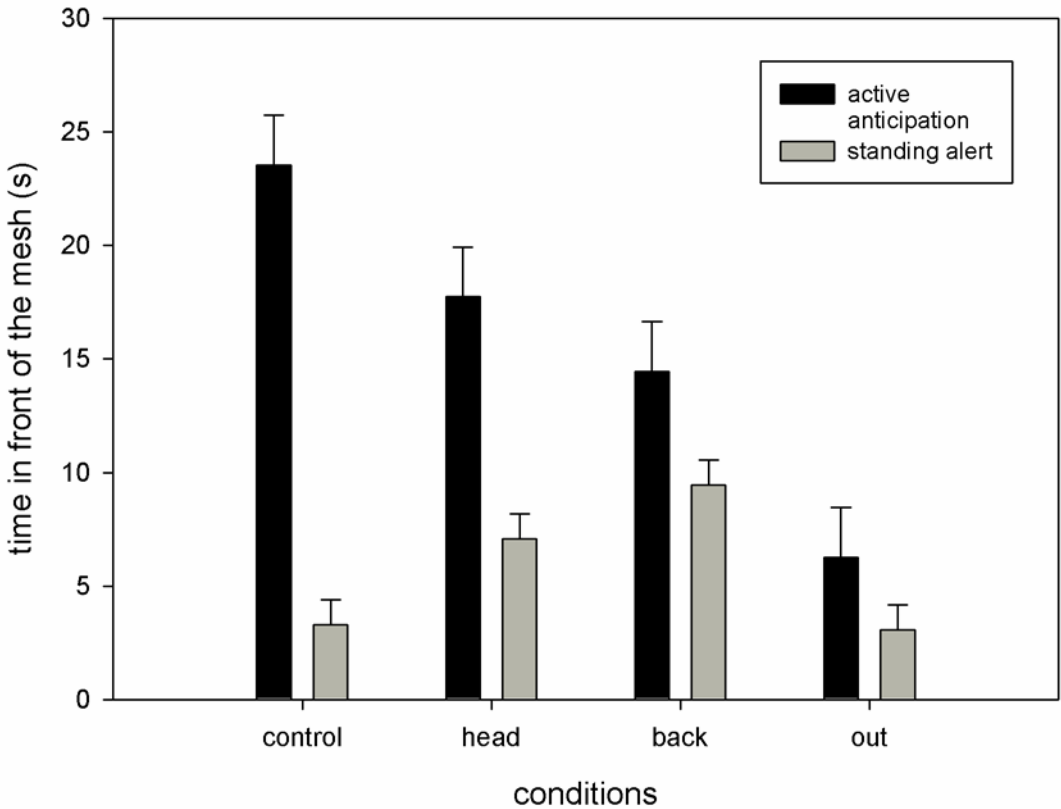
211

212 **Results**

213

214 In Experiment 1, two subjects interfered with the setup (kicking at the sliding board) during the test
215 trials and were therefore excluded. We found a significant effect of ‘condition’ (Figure 2; $F_{3,272} =$
216 86.79 ; $P < 0.001$), but not of either ‘half’ ($F_{1,272} = 1.44$; $P = 0.23$) or the interaction between the
217 two variables ($F_{1,272} = 1.94$; $P = 0.12$), on active anticipatory behaviour. Post-hoc analysis revealed
218 that active anticipatory behaviour decreased across the conditions with decreasing attention of the

219 experimenter towards the goats (all $P < 0.02$). For standing alert, we found an effect of ‘condition’
 220 (Figure 2; $F_{3,272} = 16.87$; $P < 0.001$), but not of either ‘half’ ($F_{7,272} = 1.30$; $P = 0.256$) or the
 221 interaction between the two variables ($F_{7,272} = 1.15$; $P = 0.33$). Subjects were significantly less
 222 likely to stand alert in the ‘Control’ and ‘Out’ conditions than in the ‘Head’ and ‘Back’ conditions
 223 (post-hoc analysis; all $P < 0.01$). Only two subjects vocalized during the test trials. One of these
 224 rarely vocalised in any condition (Control: 1; Head: 0, Back: 0; Out: 2). Vocalisation of the second
 225 subject increased across the conditions with decreasing attention of the experimenter towards the
 226 subject (Control: 3, Head: 10, Back: 17; Out: 36).
 227



228 Figure 2
 229

229 Results of Experiment 1. Graph shows the amount of time subjects engaged in active anticipatory
 230 behaviour (grey bars) and standing alert (white bars) during the 30-sec interval of each trial (LSM \pm
 231 SE).
 232

233

234 **Experiment 2**

235

236 Two bowls were placed 35 cm apart on the sliding board; the experimenter remained in the same
237 position as in Experiment 1. At the beginning of each test session, individuals received two training
238 trials in which the experimenter baited either the left or the right cup - in full view of the subject.
239 This was performed to ensure that the goats recognised that only one cup was baited. In the test
240 trials, the experimenter baited one of the cups out view of the subject and then placed both cups on
241 the sliding board. He then administered one of the following four conditions (Figure 1 e-h):

242

243 Touch: the experimenter touched the baited cup for three seconds

244 Point: the experimenter pointed at the baited cup for three seconds

245 Head only: the experimenter oriented his head towards the baited cup for three seconds

246 Control: the experimenter remained motionless for three seconds

247

248 After each condition, the experimenter pushed the board toward the grate and the individual was
249 permitted to make a choice. Subjects received six sessions of 14 trials (four trials for each test
250 condition and two trials for the control condition in each session), for a total of 24 trials per test
251 condition and twelve trials for the control condition. We reduced the number of trials in the control
252 condition to avoid potential side biases as reported in the study of Kaminski and colleagues (2005).
253 We reasoned that the lack of information provided by the experimenter in this condition was likely
254 to encourage subjects to follow arbitrary decision rules (such as “always chose left when no
255 information is available”) that would therefore facilitate side preferences. Left and right bowls were
256 baited pseudorandomly with the restriction that no side was baited more than twice consecutively.

257

258

259 **Data coding and statistical analysis**

260

261 Goat behaviour was video-recorded (Panasonic WV-CP500, Tamron 13VG2811ASIR-SQ lens,
262 EverFocus EDRHD-4H4 HDcctv Hybrid DVR). For Experiment 2, the trials were scored live. A
263 “correct” choice was scored if the subject chose the baited cup. The effects of ‘condition’, ‘half’ and
264 their interaction on performance (correct and incorrect choices) were modelled using a generalised
265 linear mixed model (PROC GLIMMIX, SAS® 9.2, SAS Institute Inc., Cary, NC, USA) with a
266 binary distribution (0 and 1) and a logit link function. This procedure can accommodate unbalanced
267 data; in our study, test conditions were presented over 24 trials, and the control condition was
268 presented over 12 trials. Each animal was identified as the subject for the repeated statement and
269 was included with all fixed factors in both models. Least square means (LSM) and their standard
270 errors (SE) were calculated. For pair wise comparisons, post-hoc analysis with adjustments for
271 repeated testing was applied (Tukey–Kramer corrections). For individual data on performance,
272 binomial tests were conducted. If the subjects chose correctly in 18 or more of the 24 trials in a
273 given condition, it was considered as significant ($P = 0.023$, two-tailed).

274

275 **Results**

276

277

278 We found a significant effect of the interaction of ‘half’ and ‘condition’ on performance (Figure 3;
279 $F_{3,80} = 3.93$; $P = 0.011$). Post-hoc analysis revealed that subjects performed significantly better in
280 the ‘Touch’ and ‘Point’ conditions than in the ‘Control’ condition in the first half of trials (all $P <$
281 0.01) and significantly better in the ‘Touch’ and ‘Point’ conditions than the ‘Head only’ and
282 ‘Control’ conditions in the second half of trials (all $P < 0.01$). We found no significant difference in
283 performance between ‘Head only’ and ‘Control’ or between ‘Point’ and ‘Touch’. The factor ‘half’
284 had an effect on performance in only the ‘Point’ condition ($P = 0.04$). Goats exhibited slightly
285 improved performance in this condition across sessions. On an individual level, six subjects
286 performed above the level expected by chance in the ‘Touch’ condition and ten subjects performed
287 better than expected by chance in the ‘Point’ condition (see Table 1). No subject exceeded the
288 chance level in either the ‘Head only’ or ‘Control’ conditions.

289

290

291

292

293

294

295

296

297

298

299

300

301 Table 1 Results of Experiment 2. Numbers indicate the percentage of correct choices for each
 302 condition- Individual performances exceeding chance level are in bold (binomial test; $P < 0.05$).

	Touch	Point	Gaze	Control
Subject	24 trials	24 trials	24 trials	12 trials
2	91.67	83.33	50.00	66.67
3	95.83	91.67	58.33	25.00
4	66.67	87.50	66.67	25.00
5	62.50	58.33	50.00	58.33
6	58.33	79.17	37.50	58.33
7	83.33	79.17	50.00	50.00
8	83.33	91.67	37.50	41.67
9	66.67	87.50	45.83	16.67
33	79.17	79.17	54.17	58.33
44	70.83	87.50	54.17	41.67
55	87.50	100.00	41.67	66.67
Mean	76.89	84.09	49.62	46.21
SEM	3.78	3.22	2.66	5.31

303

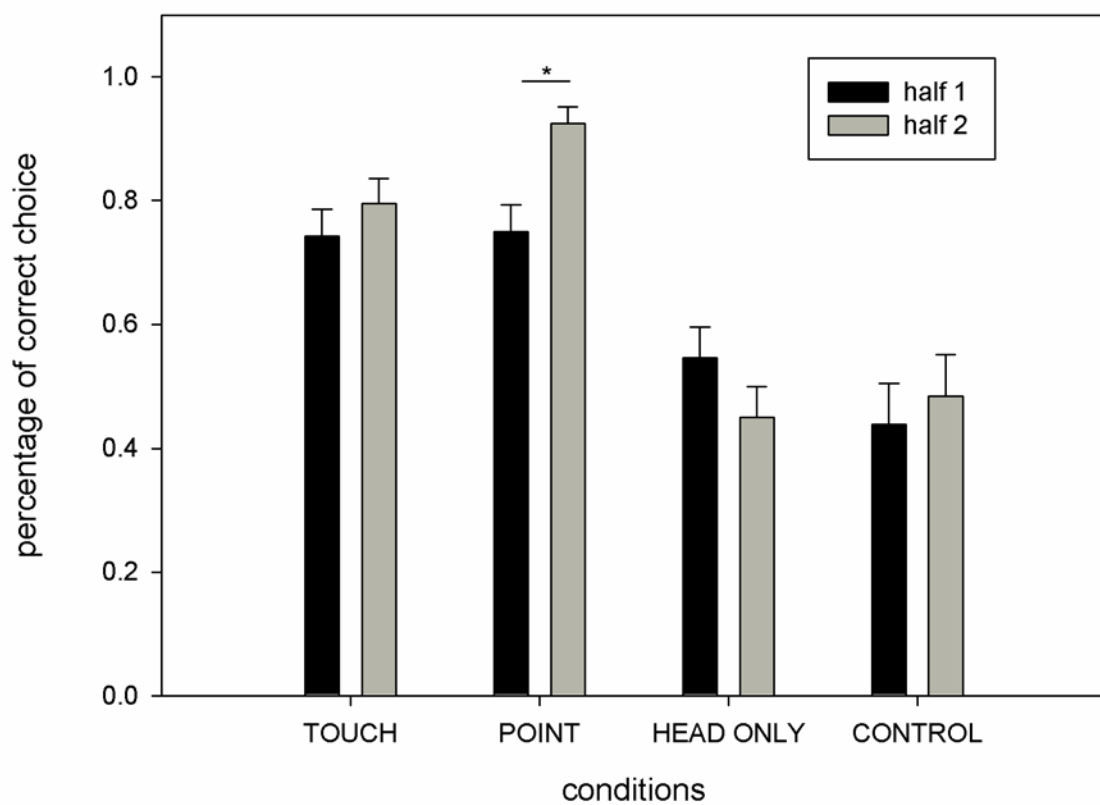


Figure 3

Results of Experiment 2. Graph shows the relative performance of subjects in locating a hidden food reward after administering different human-given cues (LSM \pm SE). Asterisk indicates significant differences between the first and second half of trials.

310 **Discussion**

311

312 In Experiment 1, we observed a steady decrease in the active anticipatory behaviour of goats
313 between the ‘Control’ condition to the ‘Out’ condition. Anticipatory behaviour depends not only on
314 the past or present experience but also on predictions and expectations about the future (Butz et al.
315 2003). In the present study, in addition to indicating a subject’s sensitivity to the reward, different
316 levels of active anticipation in the subjects suggest differences in their perceptions and processing
317 the various head and body postures of the human experimenter, that latter of which suggest different
318 levels of attention towards the subject. In contrast, goats stood alert for significantly more time
319 when the experimenter was present but not paying attention to the subject (‘Head’ and ‘Back’
320 conditions) relative to the ‘Control’ and ‘Out’ conditions. These results indicate that the subjects
321 tailored their behaviour according to the presence or absence of the experimenter in general and the
322 head and body orientation of the experimenter in particular as a means for reward delivery.

323 In Experiment 2, goats correctly used ‘Touch’ and ‘Point’ cues to infer the location of the
324 reward but did not perform better than expected by chance in the ‘Head only’ and ‘Control’
325 conditions. These results therefore mirror those of Kaminski and colleagues (2005). However, in
326 contrast to Kaminski and colleagues (2005), in which the development of a strong side bias was
327 indicated, goat performance in the ‘Point’ condition increased significantly over time in the present
328 study – indicating that subjects learned to use this gesture to find the hidden reward. As suggested
329 by the data from within individuals, no side bias was evident in the other test conditions, indicating
330 that our subjects’ performance at the chance level in the ‘Head only’ condition was not due to
331 development of a strong side bias, as reported in Kaminski et al. (2005). In contrast to ‘Head only’
332 cues, ‘Point’ and ‘Touch’ cues involve local and stimulus enhancement effects of the experimenter.
333 As the goats were unable to use cues lacking local enhancement (i.e., head cues), this suggests that
334 they likely do not understand the head direction as a cue (at least innately and without extensive
335 training; see below). This is one of few studies of how non-human animals perceive the head and

body orientation and communicative cues of humans, using a nearly identical setup in both experiments (but see von Bayern and Emery 2009); it is also one of the first to test non-primate mammals with a design similar to the food-requesting paradigm used previously with great apes and monkeys (but see Gaunet and Deputte 2011).

From an evolutionary perspective, the ability to detect those individuals that are paying one attention is crucial in intra- (e.g., deception) and inter-specific encounters (e.g., predator avoidance). For goats, as a prey species, this ability may be particularly useful in inter-species encounters (see positive results of Experiment 1). The ability to co-orient one's own gaze into distant space with that of others, as shown by Kaminski and colleagues (2005), is likely an adaptation for predator detection as well. In contrast, using the gaze cues of con- or hetero-specifics that are directed towards food sources may be useful in cooperative and/or competitive contexts. Because food sources for goats are likely abundantly distributed, there is likely no strong adaptive need to share attention with other individuals on particular food sources (see negative results of Experiment 2). These results support the findings of previous research (Baciadonna et al. 2013; Briefer et al. 2014) which showed that goats favoured personal over social information in a foraging task. For horses, which similarly rely on abundant, widely distributed food sources, no evidence for the use of head cues in an object choice task has been found (Proops et al. 2010; Proops et al. 2013), although they can differentiate among different head and body postures of humans (Proops and McComb 2010; Proops et al. 2013), similar to the goats of the current study. In contrast, species such as dogs (McKinley and Sambrook 2000; Soproni et al. 2001; Hare et al. 2002) and pigs (Nawroth et al. 2014b), which rely more heavily on patchily distributed food sources, have been shown to use head cues in object choice tasks. Other candidate species for testing the effect of species-specific foraging ecology on the use of head direction as communicative cue in a food-related context are sheep and cattle, which both rely on abundant distributed food sources. No studies using object choice tasks in these species are yet available.

While trained begging behaviour or communicative gestures have been used to evaluate

362 changes in the behaviour of non-human primates in response to different human attentive states
363 (Povinelli and Eddy 1996; Maille et al. 2012; Bourjade et al. 2014), spontaneous anticipatory
364 behaviour may be a more informative measure for other non-human animals, especially non-
365 primates. Thus, anticipatory behaviour may serve as an additional parameter for assessing not only
366 the animal's sensitivity to a reward but also how it perceives the different head and body postures of
367 a human. The observed anticipatory behaviour in Experiment 1 may have involved some
368 understanding of the level of attention the experimenter was paying to the subject during the
369 different test conditions. A higher level of the experimenter's attention may indicate a higher
370 probability of reward delivery, which in turn could increase the active anticipatory behaviour of the
371 test subject. In contrast, a lower level of attention by the experimenter while he is present may
372 indicate a reduced probability of a reward delivery, leading to a subsequent decrease in arousal and
373 increase in the time standing alert. Another, more parsimonious, explanation may be that the
374 behavioural differences between the test conditions and the control condition may reflect a
375 decreased expectation of reward delivery in the test trials that partially or fully did not mirror the
376 position of the experimenter in the instantly rewarded training trials (Gómez 2005b). Goats likely
377 learned that the posture of the experimenter in the training trials (body and head oriented towards
378 subject), together with the cup covering the reward, signalled an immediately impending food
379 delivery. This visual cue was largely absent when the experimenter left the room and differed more
380 ('Body' condition) or less ('Head' condition) from the 'Control' condition when the experimenter
381 was present. Interestingly, we found no differences in the time spent in active anticipatory
382 behaviour or standing alert between the first and second half of sessions, indicating that no learning
383 took place during the test sessions.

384 In a study of domestic fowl, the time spent standing alert was slightly greater when subjects
385 anticipated a learned positive outcome, rather than a neutral or negative one, following an acoustic
386 cue (Zimmerman et al. 2011). In our study, subjects only experienced positive outcomes but varied
387 substantially in their extent of standing alert, potentially indicating high sensitivity toward the head

388 and body orientation of other subjects. We suggest that this particular behaviour should also be
389 considered in future behavioural studies. For example, this behavioural measure could be included
390 in expectation-of-violation paradigms in non-primate mammals (Müller et al. 2011; Proops and
391 McComb 2012) in which context-dependent variation in anticipatory behaviour is expected and
392 parameters such as 'looking time' are difficult to measure due to the lateral eye position of
393 ruminants..The pattern of recorded vocalisations (at least for one subject) in Experiment 1 may
394 indicate attempts to attract the experimenter's attention (Kaminski et al. 2004; Bourjade et al.
395 2014). However, in light of the lower level of anticipatory behaviour exhibited toward the
396 experimenter, the most likely explanation for the increase in vocalization rate may have been an
397 increase in frustration/distress in the subject. Unfortunately, due to the low number of vocalising
398 individuals, no meaningful analysis was possible. Moreover, no other visual or auditory behavioural
399 indicators of attempts to draw the attention of the experimenter were observed (Bourjade et al.
400 2014). The results of Experiment 1 suggest that the subjects acknowledged the presence and absence
401 of the experimenter in general and his head and body orientation in particular as indicators of
402 reward delivery. Future studies should investigate the cognitive mechanisms underlying these
403 discriminatory abilities by focusing on their functional properties under similar test conditions
404 (Flombaum and Santos 2005; von Bayern and Emery 2009). Although we found neither an
405 indication of the subjects' spontaneous use of head direction nor an increase in their performance
406 over time in the 'Head only' condition in Experiment 2, we cannot exclude the possibility that an
407 increase in the number of trials or a more salient presentation of this cue could lead to success, at
408 least in some individuals (Giret et al. 2009; Schmidt et al. 2011). However, an increase in
409 performance over repeated trials would likely be the result of a conditioned response rather than
410 comprehension of the communicative cue.

411 We conclude that goats can differentiate among the different body postures of a human,
412 including head orientation, and that they can use various physical human cues. However, they fail to
413 spontaneously use human head direction as a cue in a food-related context.

415 **Acknowledgments**

416

417 We would like to thank Katrin Siebert for data coding, Gerd Nürnberg for statistical advice, and
418 Dieter Sehland and Heinz Deike for excellent technical assistance.

419

420 **References**

421

- 422 Baciadonna L, McElligott AG, Briefer EF (2013) Goats favour personal over social information in
 423 an experimental foraging task. *PeerJ* 1:e172. doi: 10.7717/peerj.172
- 424 Bania AE, Stromberg EE (2013) The effect of body orientation on judgments of human visual
 425 attention in western lowland gorillas (*Gorilla gorilla gorilla*). *J Comp Psychol* 127:82–90. doi:
 426 10.1037/a0027261
- 427 Von Bayern AMP, Emery NJ (2009) Jackdaws respond to human attentional states and
 428 communicative cues in different contexts. *Curr Biol* 19:602–6. doi: 10.1016/j.cub.2009.02.062
- 429 Bolles RC (1968) Anticipatory general activity in thirsty rats. *J Comp Phys Psych* 65:511–513.
- 430 Botting JL, Wiper ML, Anderson JR (2011) Brown (*Eulemur fulvus*) and Ring-Tailed Lemurs
 431 (*Lemur catta*) Use Human Head Orientation as a Cue to Gaze Direction in a Food Choice
 432 Task. *Folia Primatol* 82:165–176. doi: 10.1159/000333142
- 433 Bourjade M, Meguerditchian A, Maille A, et al. (2014) Olive baboons, *Papio anubis*, adjust their
 434 visual and auditory intentional gestures to the visual attention of others. *Anim Behav* 87:121–
 435 128. doi: 10.1016/j.anbehav.2013.10.019
- 436 Bräuer J, Call J, Tomasello M (2005) All great ape species follow gaze to distant locations and
 437 around barriers. *J Comp Psychol* 119:145–54. doi: 10.1037/0735-7036.119.2.145
- 438 Briefer EF, Haque S, Baciadonna L, McElligott AG (2014) Goats excel at learning and
 439 remembering a highly novel cognitive task. *Front Zool* 11:20. doi: 10.1186/1742-9994-11-20
- 440 Bugnyar T, Stöwe M, Heinrich B (2004) Ravens, *Corvus corax*, follow gaze direction of humans
 441 around obstacles. *Proc Biol Sci* 271:1331–6. doi: 10.1098/rspb.2004.2738
- 442 Bulloch MJ, Boysen ST, Furlong EE (2008) Visual attention and its relation to knowledge states in
 443 chimpanzees, *Pan troglodytes*. *Anim Behav* 76:1147–1155. doi:
 444 10.1016/j.anbehav.2008.01.033
- 445 Butz M V., Sigaud O, Gérard P (2003) Anticipatory Behavior: Exploiting Knowledge About the
 446 Future to Improve Current Behavior. *Anticip. Behav. Adapt. Learn. Syst. Found. Theor. Syst.*
 447 Springer, pp 1–10
- 448 Craig W (1918) Appetites and aversions as constituents of instincts. *Biol Bull* 34:91–107.
- 449 Davidson GL, Butler S, Fernández-Juricic E, et al. (2014) Gaze sensitivity: function and
 450 mechanisms from sensory and cognitive perspectives. *Anim Behav* 87:3–15. doi:
 451 10.1016/j.anbehav.2013.10.024
- 452 Flombaum JI, Santos LR (2005) Rhesus Monkeys Attribute Perceptions to Others. *Curr Biol*
 453 15:447–452. doi: 10.1016/j.cub.2004.12.076
- 454 Gácsi M, Miklosi A, Varga O, et al. (2004) Are readers of our face readers of our minds? Dogs
 455 (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim Cogn*
 456 7:144–153. doi: 10.1007/s10071-003-0205-8

- 457 Gaunet F, Deputte BL (2011) Functionally referential and intentional communication in the
458 domestic dog: effects of spatial and social contexts. *Anim Cogn* 14:849–60. doi:
459 10.1007/s10071-011-0418-1
- 460 Giret N, Miklósi Á, Kreutzer M, Bovet D (2009) Use of experimenter-given cues by African gray
461 parrots (*Psittacus erithacus*). *Anim Cogn* 12:1–10. doi: 10.1007/s10071-008-0163-2
- 462 Gómez J-C (2005a) Species comparative studies and cognitive development. *Trends Cogn Sci*
463 9:118–25. doi: 10.1016/j.tics.2005.01.004
- 464 Gómez J-C (2005b) Requesting gestures in captive monkeys and apes: Conditioned responses or
465 referential behaviours? *Gesture* 5:91–105. doi: 10.1075/gest.5.1.08gom
- 466 Hansen SW, Jeppesen LL (2006) Temperament, stereotypies and anticipatory behaviour as
467 measures of welfare in mink. *Appl Anim Behav Sci* 99:172–182. doi:
468 10.1016/j.applanim.2005.10.005
- 469 Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in
470 dogs. *Science* 298:1634–6. doi: 10.1126/science.1072702
- 471 Hare B, Tomasello M (2005) The emotional reactivity hypothesis and cognitive evolution. *Trends*
472 *Cogn Sci* 9:464–465. doi: 10.1016/j.tics.2005.08.010
- 473 Hattori Y, Kuroshima H, Fujita K (2007) I know you are not looking at me: capuchin monkeys’
474 (*Cebus apella*) sensitivity to human attentional states. *Anim Cogn* 10:141–148. doi:
475 10.1007/s10071-006-0049-0
- 476 Hooks MS, Jones GH, Juncos JL, et al. (1994) Individual differences in schedule-induced and
477 conditioned behaviours. *Behav Brain Res* 60:199–209.
- 478 Imfeld-Mueller S, Hillmann E (2012) Anticipation of a food ball increases short-term activity levels
479 in growing pigs. *Appl Anim Behav Sci* 137:23–29. doi: 10.1016/j.applanim.2012.01.012
- 480 Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors
481 controlling apes’ behavior from humans. *Anim Cogn* 7:216–23. doi: 10.1007/s10071-004-
482 0214-2
- 483 Kaminski J, Riedel J, Call J, Tomasello M (2005) Domestic goats, *Capra hircus*, follow gaze
484 direction and use social cues in an object choice task. *Anim Behav* 69:11–18. doi:
485 10.1016/j.anbehav.2004.05.008
- 486 Loretto M-C, Schloegl C, Bugnyar T (2010) Northern bald ibises follow others’ gaze into distant
487 space but not behind barriers. *Biol Lett* 6:14–7. doi: 10.1098/rsbl.2009.0510
- 488 Maille A, Engelhart L, Bourjade M, Blois-Heulin C (2012) To beg, or not to beg? That is the
489 question: mangabeys modify their production of requesting gestures in response to human’s
490 attentional states. *PLoS One* 7:e41197. doi: 10.1371/journal.pone.0041197
- 491 Maros K, Gácsi M, Miklósi Á (2008) Comprehension of human pointing gestures in horses (*Equus*
492 *caballus*). *Anim Cogn* 11:457–466. doi: 10.1007/s10071-008-0136-5
- 493 McKinley J, Sambrook TD (2000) Use of human-given cues by domestic dogs (*Canis familiaris*)
494 and horses (*Equus caballus*). *Anim Cogn* 3:13–22. doi: 10.1007/s100710050046
- 495 Miklósi A, Soproni K (2006) A comparative analysis of animals’ understanding of the human
496 pointing gesture. *Anim Cogn* 9:81–93. doi: 10.1007/s10071-005-0008-1

- 497 Moe RO, Stubbsj  en SM, Bohlin J, et al. (2012) Peripheral temperature drop in response to
498 anticipation and consumption of a signaled palatable reward in laying hens (*Gallus*
499 *domesticus*). *Physiol Behav* 106:527–33. doi: 10.1016/j.physbeh.2012.03.032
- 500 Mulcahy NJ, Hedge V (2012) Are great apes tested with an abject object-choice task? *Anim Behav*
501 83:313–321. doi: 10.1016/j.anbehav.2011.11.019
- 502 M  ller C a, Mayer C, D  rrenberg S, et al. (2011) Female but not male dogs respond to a size
503 constancy violation. *Biol Lett* 7:689–91. doi: 10.1098/rsbl.2011.0287
- 504 Nawroth C, von Borell E, Langbein J (2014a) Exclusion Performance in Dwarf Goats (*Capra*
505 *aegagrus hircus*) and Sheep (*Ovis orientalis aries*). *PLoS One* 9:e93534. doi:
506 10.1371/journal.pone.0093534
- 507 Nawroth C, Ebersbach M, von Borell E (2013) Are juvenile domestic pigs (*Sus scrofa domestica*)
508 sensitive to the attentive states of humans? - The impact of impulsivity on choice behaviour.
509 *Behav Processes* 96:53–58. doi: 10.1016/j.beproc.2013.03.002
- 510 Nawroth C, Ebersbach M, von Borell E (2014b) Juvenile domestic pigs (*Sus scrofa domestica*) use
511 human-given cues in an object choice task. *Anim Cogn* 17:701–713. doi: 10.1007/s10071-013-
512 0702-3
- 513 Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. *Monogr Soc Res Child*
514 *Dev* 61:1–191.
- 515 Proops L, McComb K (2010) Attributing attention: the use of human-given cues by domestic horses
516 (*Equus caballus*). *Anim Cogn* 13:197–205. doi: 10.1007/s10071-009-0257-5
- 517 Proops L, McComb K (2012) Cross-modal individual recognition in domestic horses (*Equus*
518 *caballus*) extends to familiar humans. *Proc R Soc B Biol Sci* 279:3131–3138. doi:
519 10.1098/rspb.2012.0626
- 520 Proops L, Rayner J, Taylor AM, McComb K (2013) The Responses of Young Domestic Horses to
521 Human-Given Cues. *PLoS One* 8:e67000. doi: 10.1371/journal.pone.0067000
- 522 Proops L, Walton M, McComb K (2010) The use of human-given cues by domestic horses, *Equus*
523 *caballus*, during an object choice task. *Anim Behav* 79:1205–1209. doi:
524 10.1016/j.anbehav.2010.02.015
- 525 Range F, Vir  nyi Z (2011) Development of Gaze Following Abilities in Wolves (*Canis Lupus*).
526 *PLoS One* 6:e16888.
- 527 Rosati AG, Hare B (2009) Looking past the model species: diversity in gaze-following skills across
528 primates. *Curr Opin Neurobiol* 19:45–51. doi: 10.1016/j.conb.2009.03.002
- 529 Sandel AA, MacLean EL, Hare B (2011) Evidence from four lemur species that ringtailed lemur
530 social cognition converges with that of haplorhine primates. *Anim Behav* 81:925–931. doi:
531 10.1016/j.anbehav.2011.01.020
- 532 Scheumann M, Call J (2004) The use of experimenter-given cues by South African fur seals
533 (*Arctocephalus pusillus*). *Anim Cogn* 7:224–230. doi: 10.1007/s10071-004-0216-0
- 534 Schmidt J, Scheid C, Kotrschal K, et al. (2011) Gaze direction: A cue for hidden food in rooks
535 (*Corvus frugilegus*)? *Behav Processes* 88:88–93. doi: 10.1016/j.beproc.2011.08.002

- 536 Soproni K, Miklósi Á, Topál J, Csányi V (2001) Comprehension of human communicative signs in
537 pet dogs (*Canis familiaris*). *J Comp Psychol* 115:122–126.
- 538 Spruijt BM, Van den Bos R, Pijlman FTA (2001) A concept of welfare based on reward evaluating
539 mechanisms in the brain: Anticipatory behaviour as an indicator for the state of reward
540 systems. *Appl Anim Behav Sci* 72:145–171.
- 541 Tempelmann S, Kaminski J, Liebal K (2011) Focus on the essential: all great apes know when
542 others are being attentive. *Anim Cogn* 14:433–439. doi: 10.1007/s10071-011-0378-5
- 543 Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics.
544 *Anim Behav* 55:1063–1069.
- 545 Udell M a. R, Dorey NR, Wynne CDL (2008) Wolves outperform dogs in following human social
546 cues. *Anim Behav* 76:1767–1773. doi: 10.1016/j.anbehav.2008.07.028
- 547 Wilkinson A, Mandl I, Bugnyar T, Huber L (2010) Gaze following in the red-footed tortoise
548 (*Geochelone carbonaria*). *Anim Cogn* 13:765–769. doi: 10.1007/s10071-010-0320-2
- 549 Zimmerman PH, Buijs S a. F, Bolhuis JE, Keeling LJ (2011) Behaviour of domestic fowl in
550 anticipation of positive and negative stimuli. *Anim Behav* 81:569–577. doi:
551 10.1016/j.anbehav.2010.11.028
- 552