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Object Permanence in the Dwarf Goat (*Capra aegagrus hircus*): Perseveration Errors and the Tracking of Complex Movements of Hidden Objects

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1 **Object permanence in the dwarf goat (*Capra aegagrus hircus*):**
2 **Perseveration errors and the tracking of complex movements of**
3 **hidden objects**

4

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31 **Abstract**

32

33 Object permanence is the notion that objects continue to exist even when they are out of an
34 observer's sight. In mammals, the highest stage of object permanence (Stage 6) has been
35 observed only in primates, whereas other species have shown difficulty in following once-
36 hidden objects, particularly when complex movements are involved. We conducted four
37 experiments to examine the ability of dwarf goats to mentally represent once-hidden objects.
38 In Experiment 1, we investigated whether dwarf goats are prone to commit the A-not-B or
39 perseveration error which is commonly used as a measure for self-control. Subjects here
40 continue to search for an object that was repeatedly hidden and successfully found at location
41 A in previous trials at that position, even if it has been hidden then in full sight at location B.
42 Experiments 2-4 investigated their ability to track the movements of hidden objects in a
43 crossed transposition task. Here, a reward was hidden in one of two hiding locations. After
44 baiting, both of the locations were changed in a crossed manner to see if the subjects were
45 able to follow the baited one and choose it at the new position. The setup of Experiments 2-4
46 varied to examine which strategies and modifications may influence the performance of the
47 subjects. The results of Experiment 1 suggest that dwarf goats only show a small prevalence
48 to commit the A-not-B error. In the transposition tasks, the goats showed little to moderate
49 success when both of the hiding locations were identical (Experiment 2 and 4) but a number
50 of goats solved the task when the two hiding locations varied in colour and shape (Experiment
51 3). Although other factors, such as the movement and the side of the baited cup influenced the
52 goats' decision making, the results provide the first evidence that dwarf goats might be able to
53 keep track of hidden objects that cross paths during transposition by encoding visual feature
54 cues.

55

56 **Keywords:** physical cognition; object permanence; transpositions; dwarf goat

57 **Introduction**

58

59 Following the trajectory of a previously seen but now hidden object is highly adaptive; this
60 ability is called object permanence. Briefly, object permanence refers to the notion that
61 objects are perceived by subjects as separate entities that continue to exist even when they are
62 out of the sight of the observer (Piaget, 1954). In the Piagetian classification, there are six
63 stages within the sensorimotor period during which sensorimotor intelligence in infants
64 develops (Piaget 1954; see Table 1). Although some researchers disagree with the temporal
65 onset of specific stages in human development (Baillargeon and DeVos, 1991), the
66 progression in the specific stages can also be observed in non-human animals, e.g. birds
67 (Hoffmann et al., 2011; Pollok et al., 2000; Zucca et al., 2007). Success on single visible
68 displacements (i.e., an object that is transferred in full view to a single hiding place) indicates
69 Stage 4b of object permanence. However, subjects at this stage still commit the A-not-B or
70 perseveration error, that is, they continue to search for an object that was repeatedly hidden
71 and successfully found at location A in previous trials at this location, even if it has been
72 transferred to and hidden then in full sight at location B. At Stage 5a, the subjects overcome
73 this kind of error, being able to solve sequential visible displacements. At Stage 5b, subjects
74 can solve double visible (i.e., sequential visits of more than one location before the final
75 hiding in one trial) and single invisible displacement (i.e., an object is first hidden in a
76 particular box that is then transferred to a second fixed hiding location while the box was
77 removed), but they fail to solve sequential invisible displacement (i.e., an object is first hidden
78 in a particular box that is then transferred to a second randomly chosen hiding location).
79 Solving sequential invisible displacements marks the beginning of Stage 6a. Subjects at Stage
80 6b can solve double invisible displacement, meaning that they can mentally reconstruct the
81 movements of an unperceived object (Doré and Dumas, 1987). As these invisible
82 displacement tasks are prone to local and stimulus enhancement effects due to a sequential
83 presentation, rotation tasks and transposition tasks may be more reliable indicators for
84 whether animals can follow invisible displacements. In transposition tasks, an object is hidden
85 in one of two or more boxes that then switch position. According to studies on dogs and great
86 apes (Rooijackers et al., 2009), a crossed transposition task seems to be the most difficult one
87 to solve. Here, two boxes change position in a crossed movement.

88

89

90

91 **Table 1** Summary of the stages of object permanence (after de Blois et al., 1998)

Stage	Description
1 and 2	No search for hidden objects.
3	Subjects can retrieve a partly hidden object.
4a	Subjects can retrieve a totally hidden object if they initiated search before the object was completely hidden.
4b	Subjects can retrieve a totally hidden object, but they persist searching at a previously rewarded location even if they saw the object disappear at a new location (perseveration or A-not-B error).
5a	Subjects overcome the perseveration error, and they can find an object that was hidden at a different location on every trial.
5b	Subjects can find an object that was hidden at various locations within the same trial.
6a	Subjects can find an object that was invisibly hidden at a different location on every trial.
6b	Subjects can find an object that was invisibly hidden at various locations within the same trial.

92

93 To date, there is no evidence that non-primate mammals are able to keep track of
 94 hidden objects in crossed transposition movements (Albiach-Serrano et al., 2012; Bräuer et
 95 al., 2006; Doré et al., 1996; Jaakkola et al., 2010; Rooijakkers et al., 2009). However, the
 96 performance of dogs increased when they had to follow non-crossed transpositions (Doré et
 97 al., 1996; Rooijakkers et al., 2009) or when the baited container was rotated only 90° instead
 98 of 180° (Miller et al., 2009).

99

100 To extend the range of species that have been used in previous research, we conducted
 101 a series of experiments on object permanence using dwarf goats (*Capra aegagrus hircus*).
 102 Previous studies in dwarf goats have demonstrated the excellent capability of these goats in
 103 discriminating and categorising visual stimuli, even over an extended time period (Langbein
 104 et al., 2008; Meyer et al., 2012). However, to date, no studies have investigated the ability of
 105 these goats to represent hidden objects. Our aim was to investigate the extent to which dwarf
 106 goats are capable of tracking previously hidden objects, which is particularly important for
 107 applied ethology as knowledge about the cognitive capacities of livestock species can affect
 108 and improve the welfare of domestic animals in modern husbandry systems in the long term.
 Although object permanence has obvious advantages in various aspects for the non-

109 domesticated animals, the consequences of this capacity affect domesticated animals under
110 husbandry conditions as well. For example, the ability to follow the trajectory of hidden food
111 or herd members may increase the environmental predictability for the subject. This might
112 lead to a decrease of stress in husbandry management as the suddenness of an appearing
113 objects or individual may vanish.

114 We conducted a total of four experiments to investigate object permanence in the
115 dwarf goat. In the first experiment, we tested goats for their ability to overcome the A-not-B
116 error, which can be used as an indicator of self-control (MacLean et al., 2014). Committing
117 this error seems also to depend on the communicative context in which the task is presented.
118 Topal et al. (2009) found that human children and dogs, but not wolves, committed search
119 errors more frequently in an ostensive-communicative context compared with a non-
120 communicative context. This result indicates a shared sensitivity to human communicative
121 signals from convergent social evolution humans and dogs (Hare et al., 2002). After
122 experiencing a reward being repeatedly hidden in a previously rewarded location ('A'), the
123 reward was transferred to a new location ('B') in full view of the subject. In Experiment 2, the
124 subjects were presented with cross transpositions of hidden objects using identical covers.
125 Although solving crossed transposition tasks ought to require a Piagetian Stage 6 of object
126 permanence, little is known regarding how contextual modifications of the setup may
127 influence performance. For example, Doré et al. (1996) found that using different visual
128 feature cues did not affect performance in dogs and cats during different transposition tasks.
129 To determine whether distinct visual feature cues may influence performance in goats, we
130 presented subjects with cross transpositions of hidden objects using cups of different sizes and
131 colours in Experiment 3. Finally, Experiment 4 replicated Experiment 2 with some minor
132 procedural modifications to control for sensory cueing and to facilitate the decision-making
133 ability of the subjects. We only used cross transposition movements to avoid stimulus and
134 local enhancement effects that have been previously reported in other studies with goats. For
135 example, Nawroth et al. (2014) tested goats and sheep on their ability to use indirect visual
136 information. Here, goats significantly improved their performance after controlling for
137 stimulus enhancement effects and outperformed sheep in the use of indirect information. We
138 hypothesise that goats should show no or only a small prevalence to commit the A-not-B error
139 because their domestication history did not rely on special human-animal communication
140 skills as for dogs (Miklósi et al., 2003). Because this study is one of the first to investigate
141 object permanence, particularly transposition movements, in farm animals, we were interested

142 in whether the performance of the goats will match those of dogs and cats in previous studies
143 (Doré et al., 1996; Rooijakkers et al., 2009).

144

145 **Methods**

146

147 **Ethics statement**

148

149 All of the procedures involving animal handling and treatment were approved by the
150 Committee for Animal Use and Care of the Ministry of Agriculture, Environment and
151 Consumer Protection of the federal state of Mecklenburg-Vorpommern, Germany (Ref. Nr.
152 7221.3-2-005/14).

153

154 **Subjects, housing and general procedure**

155

156 Ten female Nigerian dwarf goats (*Capra aegagrus hircus*), aged 4-5.5 years, participated in
157 all of the experiments. The goats were group-housed at the Leibniz Institute for Farm Animal
158 Biology. The pen contained straw bedding and was equipped with an automatic waterer, a
159 hayrack and a wooden rack for climbing. The goats had *ad libitum* access to hay. The subjects
160 were not food restricted before testing and were tested from 9:00-11:00 and 14:00-16:00 in
161 May 2014. For training and testing, individual goats were physically and visually separated
162 from their pen-mates in an adjacent compartment next to their home pen (150 cm x 125 cm).
163 The experimenter sat in another adjacent compartment that was separate from the test animal
164 by a grating, allowing subjects to insert their snouts through the bars. A sliding board (60 cm
165 x 25 cm) was placed on a small table at a height of approximately 35 cm in front of the
166 grating (see ESM Videos 1-4). In the test and motivation trials, two (Experiment 2-4, see
167 Figure 1) to three cups (Experiment 1) were placed on the board. The distance between the
168 cups and the subject was approximately 30 cm. The goats had previously participated in
169 different studies on exclusion performance (Nawroth et al., 2014) and were therefore familiar
170 with the general procedure; the goats had to place their snout through the bars to indicate their
171 choice and to receive a reward. None of the previous experiments involved the transposition
172 of hidden objects (i.e., food rewards).

173



174

175 **Figure 1** Depiction of the test setup in Experiment 2.

176

177 **Experiment 1: A-not-B task**

178

179 In the training and test trials, we presented subjects with three identical plates (dark brown: Ø
180 14 cm) with corresponding cups (dark brown: Ø 11 cm). Before a session, three motivation
181 trials were conducted to ensure motivation and to make subjects understand that they can
182 choose any of the three locations. Here, all three of the plates with the corresponding cups
183 behind them were present. In each trial, the experimenter baited only one of the plates with a
184 reward (an uncooked piece of pasta) in full view of the subject and pushed the sliding board
185 towards the grating, allowing the subjects to make a choice. Each of the three plates was
186 baited once in the three motivation trials without covering the plates and subjects were
187 rewarded as soon as they chose the baited location. In the following training trials, the reward
188 was always put on the left (6 subjects) or right plate (6 subjects) on the sliding board, and all
189 of the plates were covered with the corresponding cup. The experimenter covered the left and
190 the right plate first. Immediately after, he covered the plate in the middle. The experimenter
191 now pushed the sliding board towards the grating, allowing the subjects to make a choice. If a
192 subject chose the correct location three times in a row, a test trial was conducted. The subjects
193 received a maximum of six training trials to reach this criterion. A test trial was similar to the
194 training trials except that, after initial baiting, the experimenter uncovered the baited location
195 and moved the reward in full view of the subject to the plate on the other side of the sliding
196 board (left to right or right to left). The reward was covered again and the experimenter
197 pushed the sliding board towards the grating, allowing the subjects to make a choice. Each

198 subject therefore received one test session consisting of three to six training trials and one test
199 trial. The initial reward position was randomised across subjects.

200

201 *Data scoring and analysis*

202 All of the test trials were coded live and videotaped (see ESM Video 1). A “correct” choice
203 was scored if the subject chose the baited cup by snouting through the bars. For group data in
204 the test trial, a binomial test was conducted.

205

206 **Results**

207

208 Nine subjects reached the criterion after three trials. One subject did not reach the criterion
209 after six training trials and was excluded from the test trial. In the test trials, six subjects chose
210 the location where the reward was actually hidden (‘B’) ($p = 0.04$, one-sided), whereas one
211 subject chose the location that was previously rewarded (‘A’). Two subjects chose the cup
212 that was positioned in the middle.

213

214 **Experiment 2: crossed transposition**

215

216 Experiment 2 was conducted approximately four hours after Experiment 1. Before each test
217 session, two training trials were conducted to ensure motivation. Here, only one of the two
218 cups was present and was either positioned on the left or right side of the board. E baited the
219 cup in full view of the subject and pushed the sliding board towards the grating, allowing the
220 subjects to make a choice. In the test trials, we presented subjects with a transposition in
221 which two identical cups (brown; Ø 9 cm) crossed paths. A reward (an uncooked piece of
222 pasta) was put on either the left or right side of the sliding board for 2 seconds before it was
223 covered with the corresponding cup. After baiting, E simultaneously moved the left cup to the
224 right side and the right cup to the left side of the board so that the cups crossed their path in
225 the middle. After the transposition, E waited for 2 seconds until he pushed the sliding board
226 towards the grating, allowing the subjects to make a choice. The baited cup could either cross
227 path towards or away from the subject compared with the unrewarded cup. Each subject
228 received only one test session consisting of twelve test trials. The reward position and cross
229 direction (towards or away) were randomised throughout the test session.

230

231 *Data scoring and analysis*

232 All the test trials were coded live and videotaped. A “correct” choice was scored if the subject
233 chose the baited cup by snouting through the bars (see ESM Video 2). All of the choices
234 could be classified unambiguously as correct or incorrect; therefore, we did not calculate the
235 inter-observer reliability. To test against the chance level (50%), we used one-sample t-tests.
236 To analyse the impact of the first six vs. the last six trials of a test session, the cross direction
237 (left cup crossed towards or away from the experimenter) and the baited side (left or right
238 location seen from the experimenter) on performance, a generalised linear mixed model
239 (PROC GLIMMIX, SAS® 9.2, SAS Institute Inc., Cary, NC, USA) with a binary distribution
240 (0 and 1) and a logit link function was used. For individual data, a binomial test was
241 conducted. If a subject chose the correct cup ten or more times out of twelve trials, this
242 individual performance was counted as significant ($p = 0.039$, two-tailed) compared with the
243 chance level (50%).

244

245 **Results**

246 The subjects as a group showed no preference for the baited cup or the position where the
247 reward was last seen ($t_9 = 1.309$; $p = 0.223$, see Figure 2). We found no change in
248 performance when comparing the first vs. the second half of the trials (mean first: $0.612 \pm$
249 0.074 ; mean second: 0.528 ± 0.076 ; $F_{1, 76.0} = 0.61$; $p = 0.436$). The subjects’ performance was
250 better when the hidden reward was moved to the right side compared with the left (mean left:
251 0.429 ± 0.073 ; mean right: 0.702 ± 0.067 ; $F_{1, 73.8} = 6.83$; $p = 0.01$). The performance did not
252 depend on the movement of the cups during transposition, i.e., if the position of the baited cup
253 during crossing was the one towards or away from the test subject (mean towards: $0.548 \pm$
254 0.076 ; mean away: 0.593 ± 0.075 ; $F_{1, 76.0} = 0.18$; $p = 0.67$). On an individual level, one subject
255 performed significantly better than expected by random chance (50%; see Table 2).

256

257 **Experiment 3: crossed transposition with different visual feature cues**

258

259 Experiment 3 was conducted the day after Experiment 2. Before each test session, two
260 training trials were conducted. In contrast to Experiment 2, two cups differing in colour and
261 size were used for the transposition task (dark brown: \varnothing 11 cm; white, \varnothing 9 cm). The general
262 setup of Experiment 3 differed slightly from that of Experiment 2 in three ways: 1. The
263 movement of the cups on the sliding board in Experiment 2 produced some sound and seemed
264 to distract several of the subjects. Therefore, the cups were positioned upside-down on the
265 board and the reward was placed into one of the cups in full view of the subject. 2. E baited

266 the cup with his contralateral hand, but performed the transposition movement with his
267 ipsilateral hand to avoid potential cueing for a particular hand. 3. In addition, a piece of pasta
268 was taped inside both of the cups to avoid olfactory cues. All of the other conditions were the
269 same as those in Experiment 2.

270

271 *Data scoring and analysis*

272 The impact of the identity of the baited cup (smaller white cup or bigger brown cup) on
273 subjects' performance was added as additional factor to the generalised linear mixed model.
274 All other data scoring and analyses were the same as those in Experiment 2 (see ESM Video
275 3).

276

277 **Results**

278 One subject had to be excluded due to a lack of motivation at the beginning of the test session.
279 The subjects as a group significantly preferred the baited cup ($t_8 = 3.885$; $p = 0.005$, see
280 Figure 2). We found no change in performance when comparing the first half against the
281 second half of the trials (mean first: 0.674 ± 0.079 ; mean second: 0.780 ± 0.067 ; $F_{1,75.38} =$
282 1.14 ; $p = 0.29$). In addition, the performance of the subjects did not depend on the side (mean
283 left: 0.686 ± 0.071 ; mean right: 0.770 ± 0.078 ; $F_{1,58.4} = 0.60$; $p = 0.442$) or movement of the
284 baited cup during transposition (mean towards: 0.796 ± 0.072 ; mean away: 0.650 ± 0.074 ; $F_{1,57.9} =$
285 1.86 ; $p = 0.177$). However, the subjects' performance was better when the bigger, brown
286 cup was baited rather than the smaller, white cup (mean large brown cup: 0.879 ± 0.050 ;
287 mean small white cup: 0.501 ± 0.075 ; $F_{1,70.1} = 12.03$; $p = 0.0009$). On an individual level,
288 three subjects performed significantly better than expected by random chance (50%, see Table
289 2).

290

291 **Experiment 4: crossed transposition with modifications and controls**

292

293 Experiment 4 was conducted approximately 1 week after Experiment 3. Before each test
294 session, two training trials were conducted as described for Experiment 2. The setup was
295 identical to that of Experiment 3, except that we abstained from the delay after cup
296 movement, and both of the cups were identical in shape and colour (dark brown coloured, Ø:
297 11 cm), thus replicating Experiment 2 with several procedural modifications. All of the other
298 conditions were the same as those in Experiment 3.

299

300 *Data scoring and analysis*

301 Data scoring and analysis were the same as in Experiment 2 (see ESM Video 4).

302

303 **Results**

304 The subjects as a group significantly preferred the baited cup ($t_9 = 2.689$; $p = 0.025$, see
305 Figure 2). We found no change in performance when comparing the first and second halves of

306 the trials (mean first: 0.622 ± 0.089 ; mean second: 0.675 ± 0.085 ; $F_{1, 74.4} = 0.19$; $p = 0.66$).

307 The performance of the subjects was better when the reward was moved to the right side

308 (mean left: 0.46 ± 0.09 ; mean right: 0.8 ± 0.067 ; $F_{1, 74.4} = 7.57$; $p = 0.0075$) and when the

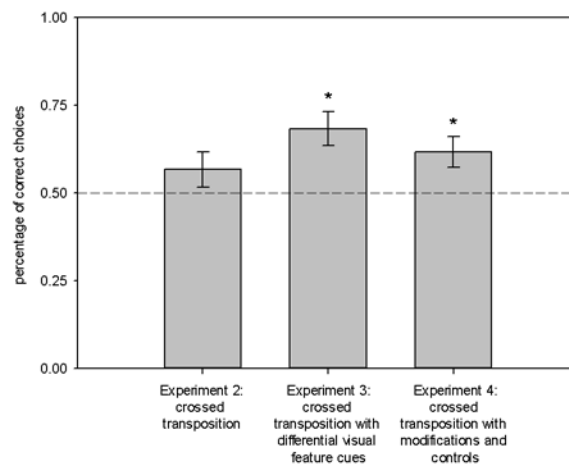
309 rewarded cup was moved towards the subject during the transposition (mean towards: $0.854 \pm$

310 0.055 ; mean away: 0.366 ± 0.080 ; $F_{1, 74.3} = 16.11$; $p = 0.0001$). On an individual level, none of

311 the subjects performed significantly better than expected by random chance (50%, see Table

312 2).

313



314

315 **Figure 2** Mean correct choices of Experiments 2, 3 and 4. The dashed line represents the

316 chance level; the error bars represent standard errors; * $p < 0.05$; one-sample t-test.

317

318

319

320

321

322

323

324 **Table 2** Individual results of Experiments 2, 3 and 4. Individual performances above chance
 325 level (10 or more correct trials out of 12; $p < 0.05$; binomial test; two-sided) are marked in
 326 bold.

Subject #	Experiment 2	Experiment 3	Experiment 4
13	6	6	9
14	7	6	8
15	6	10	6
16	7	10	8
17	4	7	4
18	8	7	6
19	4	-	7
20	9	10	9
22	10	9	8
24	7	9	9

327

328 Discussion

329

330 In Experiment 1, the subjects showed no tendency to commit the A-not-B error in their
 331 decision making process, thus reaching Stage 4b of object permanence according to this task.
 332 This good performance in resisting to commit the A-not-B-error can additionally be seen as
 333 an indicator of advanced self control (MacLean et al., 2014). Although perseveration errors
 334 were not prevalent, it would be of interest if the administration in terms of a communicative
 335 and ostensive context had an effect on performance, as for young children and dogs but not
 336 wolves (Topál et al., 2009). In the transposition tasks, the goats showed little to moderate
 337 success when both of the covering cups were identical (Experiment 2 and 4), but goats as a
 338 group and a number of individual goats solved the task when the two cups varied in colour
 339 and shape (Experiment 3). Intriguingly, none of the subjects showed a performance below
 340 chance level in all three transposition tasks, indicating that these goats are not as prone to the
 341 spatial search bias that was reported for dogs (Dumas, 1998). These results indicate that goats
 342 may be able to track the movement of hidden objects and thus reach Stage 6 of object
 343 permanence (Piaget, 1954).

344 Despite mentally keeping track of the hidden object, subjects could have used simpler
 345 rules of thumb to gain the reward. For example, the results of Experiments 2 and 4 are
 346 confounded by a side bias to the left (i.e., by choosing the baited cup at the right location seen
 347 from the experimenter's view) and by a choice of the cup that was crossed near them,
 348 respectively. As the choice of the cup that was crossed towards the subjects can be explained
 349 best by the more proximate and therefore salient movement of the cup, the observed side bias

350 can have several explanations. Hemispheric lateralization can play a role in behavioural
351 responses especially in species with eyes placed laterally (Leliveld et al., 2013). Austin and
352 Rogers (2007) suggested for horses that the left eye is more reactive to visual stimuli. Farmer
353 et al. (2010) suggested that the left eye may be preferred in stimuli to which the horse needs to
354 respond quickly or give its greater attention at that moment. However, as the test
355 compartment was not symmetrically, slight changes in light intensity or structural differences
356 may have influenced the behaviour of the goats, too. Kaminski et al. (2005) also reported a
357 development of a side bias when they were testing goats in an object choice task, but do not
358 report if the direction of the side bias was consistent across subjects. Therefore, further
359 investigations are necessary to evaluate the underlying causes of this decision bias. In
360 addition, the subjects in Experiment 3 preferred the larger, brown cup compared with the
361 smaller, white one. This preference could either be the result of the more salient cue size or
362 due to the subjects' previous experience with similarly coloured cups (e.g., Experiments 1 and
363 2). Because adopting only one of these simpler strategies (e.g., always choosing the right side)
364 would have led to 50% success, only a combination of two or more of these simpler strategies
365 could have increased individual and group performance above chance level. In addition, it is
366 not clear whether these strategies either increased the performance of subjects that otherwise
367 would have persisted in choosing the location where they had last seen the reward or if they
368 actually hampered the performance of subjects that would have otherwise performed above
369 chance level in choosing the correct location after the transposition. Although subjects could
370 have also rapidly learned the contingencies of the transposition task, we found no indication
371 for learning in the single transposition experiments and across these experiments. These
372 results are surprising, because no other tested non-primate mammal has shown a similar
373 performance yet (Albiach-Serrano et al., 2012; Bräuer et al., 2006; Collier-Baker et al., 2004;
374 Doré et al., 1996; Jaakkola et al., 2010; Rooijackers et al., 2009). Other studies found no
375 positive performance when using three baiting locations in which only two out of three cups
376 were moved – decreasing the chance level to 33% (Doré et al., 1996; Jaakkola et al., 2010). In
377 addition, using different visual feature cues had no effect on performance in dogs or cats
378 (Doré et al., 1996). Other rules, such as always choosing the opposite side, are highly unlikely
379 because no learning within sessions took place and no initial tendency of goats to choose the
380 opposite side from where they last have seen the reward was observed, especially in
381 Experiment 1 and in the preceding motivation trials. However, we tested the same subjects in
382 every experiment and can therefore not rule out the possibility that goats may have learned
383 between test sessions. Although we did not control for subtle experimenter cues, there is

384 currently no evidence that goats are able to comprehend or learn to use the gaze direction of a
385 human experimenter (Kaminski et al., 2005; Nawroth et al., 2015). Indeed, a study by Schmitt
386 et al. (2014) in long-tailed macaques showed that the presence of the experimenter decreased
387 the performance of the subjects in an object choice task.

388 Fully developed object permanence may be useful in being up to date about the
389 positions of conspecifics (as suggested by Zucca et al., 2007) and mentally tracking the
390 movements of group members would allow animals foraging in dense vegetation to stay close
391 to their group members (Noë and Laporte, 2014). Because dogs as social animals may have
392 similar demands regarding group cohesion as do goats, our results are rather surprising. We
393 suggest that the lower performance in dogs compared with the goats in cross transposition
394 tasks is due rather to a stronger spatial search bias (Dumas, 1998) than to a general inability to
395 represent complex movements of hidden objects (Miller et al., 2009).

396 In husbandry systems, the resulting novelty or suddenness of the (re-)appearance of
397 particular objects and individuals can be a potential stressful event, eliciting physiological
398 responses of different degree (Désiré et al., 2002). For example, a study by Désiré et al.
399 (2004) showed that lambs responded to the suddenness of an appearing object with a startle
400 response coupled with an increase in heart rate. From an applied perspective, future studies
401 might address the question of how the development of object permanence affects animals'
402 well-being. For example, a full blown ability of object permanence may lead to a higher
403 predictability of the environment, especially for re-appearing objects or subjects that went out
404 of sight – which is common practice in production systems. Whether an increased
405 predictability elicits boredom or whether it reduces stress by reducing surprising events in the
406 environment needs to be evaluated in the future while physiological measures might
407 contribute to answer this question (e.g., von Borell et al., 2007).

408 Our results are in line with recent findings of unexpected cognitive capacities in the
409 physico-cognitive domain in this species (Briefer et al., 2014; Nawroth et al., 2014), leading
410 to the assumption that ungulates have a quite sophisticated perception of their physical
411 environment. This perception should be taken into consideration in the management and
412 design of husbandry environments, increasing animal welfare in the long term.

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