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Horses feel emotions when they watch positive and negative horse– human interactions in a video and transpose what they saw to real life.

4

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13

14 Abstract

15 Animals can indirectly gather meaningful information about other individuals by eavesdropping on their third-party interactions. In particular, eavesdropping can be used to 16 17 indirectly attribute a negative or positive valence to an individual and to adjust one's future 18 behavior towards that individual. Few studies have focused on this ability in nonhuman animals, 19 especially in nonprimate species. Here, we investigated this ability for the first time in domestic 20 horses (Equus caballus) by projecting videos of positive and negative interactions between an 21 unknown human experimenter (a "positive" experimenter or a "negative" experimenter) and an 22 actor horse. The horses reacted emotionally while watching the videos, expressing behavioral 23 (facial expressions and contact-seeking behavior) and physiological (heart rate) cues of positive 24 emotions while watching the positive video and of negative emotions while watching the 25 negative video. This result shows that the horses perceived the content of the videos and 26 suggests an emotional contagion between the actor horse and the subjects. After the videos were 27 projected, the horses took a choice test, facing the positive and negative experimenters in real 28 life. The horses successfully used the interactions seen in the videos to discriminate between 29 the experimenters. They touched the negative experimenter significantly more, which seems counterintuitive but can be interpreted as an appeasement attempt, based on the existing
literature. This result suggests that horses can indirectly attribute a valence to a human
experimenter by eavesdropping on a previous third-party interaction with a conspecific.

33

34 Introduction

35 Social animals can indirectly gather meaningful information from other individuals by 36 eavesdropping on their third-party interactions (i.e., "social eavesdropping"; Bonnie and Earley 37 2007). This social eavesdropping has been observed in various species and contexts. For 38 instance, in the context mate choice, birds and fishes can eavesdrop on interactions to assess 39 the quality of a potential partner (Mennill et al. 2002; Ophir and Galef 2004; Valone 2007; 40 Aquiloni and Gherardi 2010; Kavaliers et al. 2017). Several species of birds, fishes and rodents 41 observe conflictual interactions to judge the relative quality and dominance rank of the 42 opponents (Peake et al. 2001; Earley and Dugatkin 2002; Höjesjö et al. 2007; Valone 2007; Lai 43 et al. 2014). Furthermore, social eavesdropping can also allow animals to attribute a negative or positive valence indirectly to unknown individuals by two different mechanisms. First, 44 45 individuals can observe the emotional reaction of a third-party person during an interaction with 46 a stranger to adjust their own behavior towards that stranger; this has, for instance, been studied 47 in dogs and human infants (Feinman and Lewis 1983; Murray et al. 2008; Freidin et al. 2013; 48 Duranton et al. 2016). Second, animals can also indirectly attribute a valence to unknown 49 individuals based on how the individuals behaved towards a third party and to use this 50 information to adjust their own behavior towards the individuals accordingly. This latter ability 51 has been investigated in a few non-human species, including great apes, capuchin and marmoset 52 monkeys, domestic dogs and reef fish (see Abdai and Miklósi 2016 for a review). Chimpanzees, 53 dogs and marmoset monkeys were, for instance, shown to prefer eating food offered by an 54 experimenter who previously gave food to a human beggar more than food offered by an 55 experimenter who refused to do so (Russell et al. 2008; Subiaul et al. 2008; Marshall-Pescini 56 et al. 2011; Kawai et al. 2014). Similarly, capuchin monkeys and dogs showed a preference for 57 an experimenter who had previously helped open a container to retrieve an object (of neutral 58 valence to the subject) compared to an unhelpful experimenter (Anderson et al. 2013; Chijiiwa 59 et al. 2015). A similar ability has also been studied in reef fish species in the context of 60 interspecific mutualism with the cleaner fish (Labroides dimidiatus): reef fish were shown to 61 eavesdrop on the interaction between these cleaner fishes and other third-party clients in order 62 to select cooperative partners (that remove the ectoparasites from clients' mouths and do not

cheat by eating the clients' mucus; Bshary and Grutter 2006). This underlies the importance of
carrying out studies in taxa other than dogs and primates in order to know how widespread this
ability to attribute a valence based on social eavesdropping is.

This valence attribution, often studied in the context of cooperation, has also been reported during interactions involving emotional content. Nitzschner et al. (2012) showed dogs an interaction between a conspecific and a "nice" experimenter—paying attention to and petting another dog—and an "ignoring" experimenter who ignored the other dog. As cooperation is a complex mechanism that implies high cognitive demands (Cheney 2011), this alternative paradigm can be particularly useful to study a broader range of species, especially species that are not known to cooperate.

73 In this study, we investigated for the first time whether domestic horses (Equus caballus) could 74 indirectly attribute a valence to a human by eavesdropping on an interspecific social interaction. 75 We used a paradigm based on emotional interactions, as the expression and processing of 76 emotions have been well described in this species. Horses can express emotions both vocally 77 (Briefer et al. 2017) and visually (by body posture and facial features; Lansade et al. 2018). 78 Typical facial expressions have been well described for both negative (Dalla Costa et al. 2014, 79 2017; Gleerup et al. 2015) and positive (Lansade et al. 2018) emotions. Horses can recognize 80 facial expressions related to emotions in both humans (Smith et al. 2016; Nakamura et al. 2018; 81 Trösch et al. 2019a) and conspecifics (Wathan et al. 2016) and adjust their behavioral response 82 accordingly, even in a future encounter a few hours later (Proops et al. 2018). Moreover, horses 83 are both highly sociable (Ringhofer et al. 2017) and share a close relationship with humans in 84 their daily lives. They are very attentive to humans and their behavior (e.g., Proops et al. 2009; 85 Proops and McComb 2010, 2012; Lampe and Andre 2012; Proops et al. 2013; Malavasi and Huber 2016; Ringhofer and Yamamoto 2016; Trösch et al. 2019b) and can learn socially from 86 87 a conspecific or a human demonstrator (Krueger et al. 2014; Rørvang et al. 2015; Schuetz et al. 88 2017). Hence, horses are good candidates for investigating whether they can also learn by 89 eavesdropping on interactions between a human and a third-party conspecific to attribute a 90 valence to the human.

To examine this, we showed the horses two kinds of interactions between an experimenter and an unfamiliar "actor" horse: a positive interaction (a grooming session) and a negative interaction (an unpleasant veterinary act). These scenes were presented to the horse through silent videos projected in real size in front of each horse, and we investigated whether they could perceive the emotional content of these scenes through behavioral and physiological measurements. Then, the horses met the two experimenters in real life in a choice test. Our 97 hypotheses were the following: 1) Horses would express more positive emotions when 98 watching the positive scene and more negative emotions in front of the negative scene. A 99 control condition in which the tested horse observed the same videos but with the human and 100 horse actors replaced by moving ovals allowed us to check that the horses were not simply 101 reacting to a difference in movements between the two videos. 2) The horses would 102 discriminate between the positive and negative experimenters during the choice test by seeking 103 more contact with one of them.

104

105 Materials and methods

106 Subjects and husbandry

107 Forty-seven female adult Welsh ponies (mean age \pm SE = 8.47 \pm 0.61) were used for this study. 108 Twenty-four of them were included in the test condition, and 23 were included in the control 109 condition. These horses were bred and had lived all their lives at the experimental unit (PAO, 110 doi: 112 10.15454/1.5573896321728955E12) of the French National Institute for Agricultural 111 Research (INRA, Nouzilly, France). They were familiar with humans and being handled. 112 During the experiment, the horses were housed indoors on straw bedding in groups. They were 113 fed with straw and hay, with access to water ad libitum. None of the horses had been involved 114 in a similar experiment before.

115

116 Ethical note

117 Our protocol was submitted to the Val de Loire Ethical Committee (CEEA VdL, France) and 118 received a positive recommendation. Horses did not undergo any invasive procedure during the 119 experiment. Horses lived in groups, went to an outside paddock on a daily basis, and were not 120 food-deprived.

121

122 Videos

123 -Test condition

The experiment consisted of consecutively projecting two silent videos (one positive video and one negative one), each 30 s long, to a horse (Fig. S1). The positive video showed an experimenter grooming an "actor" horse. In this case, the actor horse expressed positive emotions (Table S1) through a typical facial expression that has been described before (Lansade et al. 2018): ears oriented backwards, low neck, lips extended and moving in a grooming attempt. The negative video showed a second experimenter (different from the first one)

performing a veterinary act on the horse: touching her ears to administer an ointment and applying a spray towards her head. We used a small air spray, which was completely hidden in the experimenter's hand, so that it was invisible on the video. In that case, the actor horse expressed fearful reactions by jolting and trying to run away from the experimenter (four times in each video). She adopted a typical facial expression of negative emotions (Table S1): elevated neck and eyes wide open with the sclera visible (Lansade et al. 2018).

136 The two experimenters (both women) and the actor horse were unfamiliar to the horses prior to 137 this experiment. Each experimenter wore a specific color of clothes (light brown for one of 138 them and dark blue for the other) and could be either positive or negative depending on the 139 horse tested: the role the two experimenters and the order of the videos were counterbalanced 140 between the horses. The videos were recorded beforehand and in the same location. 141 Importantly, the experimenters were asked to keep a neutral facial expression (not expressing any positive or negative emotions) in both videos, and the videos were later checked 142 143 independently by three people and edited to delete the scenes in which this was not the case. 144 The videos consisted in several short scenes following one another. The number and the 145 duration of these scenes were identical in all videos: two scenes of 10 s, followed by three 146 scenes of 2 s and then one last scene of 4 s. Moreover, all the videos were checked to ensure 147 that the experimenters' face was entirely visible during at least 60% of the video.

148

149 -Control condition

In the control condition, the videos used during the test were edited so that the experimenters and the horse were replaced by two ovals with the same surface area and colored with the main color of the experimenter and the actor horse as appropriate. The videos were edited semiautomatically using the image editing and analysis software ImageJ and Fiji (Schindelin et al. 2012; Rueden et al. 2017). These ovals followed the movement pattern of the horse and the experimenter and copied the variations in their surface area (which was recalculated every 25 ms).

157

158 Set up and procedure

The entire experiment took place in a large, familiar stall (3.5 x 4.5 m; Fig. 1). The videos were projected onto a large white screen (2 x 2 m) by a DLP projector Acer P6200S. During the video projection, the horse was attached in front of the screen by two loose leading reins (one on each side of the horse). Moreover, an assistant stood next to the horse during the projection for security reasons in case the horse became distressed or risked hurting itself during the course

164 of the equipment (which never occurred during our study). The assistant had his or her back to 165 the screen, was looking on the ground, and did not know which video was being projected in 166 order to avoid unintentional social cueing.

167

168 The horses were tested individually in the following manner:

169 - Test condition:

170 The test condition was realized with 24 horses.

171 1. Familiarization: The horses were familiarized with the experimental set up, video projection 172 and device used to measure their heart rate (cf. "Coding and statistical analyses"). 173 Familiarization consisted of at least 3 sessions of 10 minutes each, with one session per day, 174 typically on three consecutive days. More sessions were added if necessary until the horse could 175 be secured and stayed still while in front of a video with a heart rate lower than 80 bpm during 176 a period of more than 30 s. The videos used were specific to this familiarization and showed an 177 unknown horse walking and running in a sand paddock. The test took place in the afternoon on 178 the same day as the last familiarization session.

179 2. Projection of the negative and positive videos in random order.

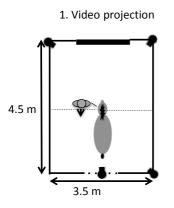
180 3. Choice test: At the end of the video projection, both experimenters, wearing the same clothes 181 as in the videos, entered the stall at the same time and placed themselves on either side of the 182 horse, facing the horse. The assistant gave each of the experimenters the two extremities of a 183 string passing by the halter of the horse, so that the horse was held in the middle of the stall 184 while the assistant was leaving (Fig. S2). The experimenters held the strings at 1m from the 185 horse and did not interact directly with her (they did not touch the horse and were looking at 186 the ground). When the assistant had left the stall and closed the door, he gave a signal to the 187 experimenters. At this signal, both experimenters released one extremity of the string at the 188 same time, let the other extremity slide by the halter and wrapped the string in their hand, so 189 that the horse was let free. The choice test then began. The test duration was 75 s, during which 190 the experimenters tried to attract the horse for 15 s (by looking at the horse, holding out a hand 191 towards the horse and calling it by doing a clicking sound with their mouths) and then stood 192 still with their hands behind their back and watching the ground for 60 s. Importantly, the 193 experimenters and the assistant did not know which videos the horse had seen before the choice 194 test and were thus blind to which experimenter played the role of the positive or the negative 195 experimenter.

196

197 - Control condition:

The control condition was realized with 23 new horses who were different from the ones used in the test condition. The familiarization and projection of the negative and positive videos were similar as in the test condition except that, in all videos, the horse and experimenters were replaced by moving ovals. No choice test was carried out after the video projection.

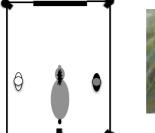






Assistant
 Experimenter 1
 Experimenter 2
 Rope used to attach the horse
 Projection screen
 Camera
 Door (completely closed during the experiment)

2. Choice test





203

204 Fig. 1 Schematic representation and pictures of the video projection and the choice test

205

206 Coding and statistical analyses

207 The behavior of the horses was recorded with a camera during the video projection and the

208 choice test and analyzed later using BORIS software (v. 6.0.6; Friard and Gamba 2016).

- 209
- 210 Video projection
- 211 Four types of measures were analyzed:

1. Facial expression. Facial expressions were measured using the variables described in Lansade et al. 2018: 1) the time spent with both ears oriented backward or forward; 2) the time spent with the neck high, medium or low; and 3) the time spent with the whites of the eyes visible (as we did not observe any half-closed eyes, we did not include the time spent with the eyes wide open in the analyses since it would have been the exact opposite of the time with the

217 whites of the eyes visible). We only included in the analysis the variables that were expressed

by the animals and visible enough on the video recordings to be analyzed without ambiguity

219 (see Table 1 for the complete list).

220 2. Number of grooming attempts. The number of times the horse extended her lips to nibble theleading reins or the assistant.

3. Variation in heart rate between the beginning and end of the video. The heart rate of the
horses was measured during the video projection using a heart monitor system (Polar Equine
RS800CX Science, Polar Oy, Finland). The difference in mean heart rate during the first and
last 5 s of each video was calculated.

4. Time spent facing the videos. We considered the horses as being attentive to the video when
they directly faced the video (the angle between their head and the center of the screen was <
15°) or when the angle was between 10° and 45° but at least one ear was oriented towards the
video (Proops et al. 2009; Lampe and Andre 2012; Proops and McComb 2012; Smith et al.
2018).

231 - Choice test

During the choice test, we observed whether the horse touched each experimenter and how many times each experimenter was touched. Indeed, physical contacts with the muzzle has been described as an attention seeking behavior in horses (Malavasi and Huber 2016; Ringhofer and Yamamoto 2016; Trösch et al. 2019b). The touches were usually brief, but if those were longer than three seconds, it was taken into account by counting a new occurrence every three seconds (examples of this procedure: Lansade et al. 2018; Trösch et al. 2019b).

238

239 Data were analyzed by a coder who was blind to whether the video watched by the horse was 240 positive or negative. Moreover, facial expressions and time facing the videos were analyzed by 241 two coders since these components can be relatively ambiguous to record. The arithmetic means 242 of the values coded by the two coders were used for the statistical analyses. Interobserver 243 reliabilities were calculated: ears oriented forward (ICC= 0.96, lower bound= 0.94), ears 244 oriented backward (ICC= 0.93, lower bound= 0.90); low neck (ICC= 0.93, lower bound= 0.90); 245 medium neck (ICC= 0.98, lower bound= 0.98); high neck (ICC= 0.99, lower bound= 0.98); 246 whites of the eyes visible (ICC= 1, lower bound= 1); time spent paying attention to the video 247 (ICC= 0.95, lower bound= 0.92). The values obtained are all considered to represent excellent 248 reliability (Koo and Li, 2016).

249

250 Statistics were performed with Xlstat software (Addinsoft, Paris, France) for the analysis of 251 facial expression and with R 3.0.2 (R Core Team 2013) for all the other analyses. The 252 significance threshold was fixed at 0.05. To cope with our limited sample size, we used 253 nonparametric statistical tests. All of the tests we used were two-tailed. To reduce the number 254 of two-by-two comparisons and to be able to consider facial expression as a whole (cf. Lansade 255 et al. 2018), facial expressions were characterized using a principal component analysis (PCA) 256 based on Spearman correlations. A Wilcoxon signed-rank test for paired samples was then 257 performed to test whether the two first factors of the PCA of each subject differed while 258 watching the negative and the positive videos. We used a Wilcoxon signed-rank test for paired 259 samples to test whether the horses expressed each of the variables described above differently 260 when watching the two videos (both in the test and the control conditions) and whether they 261 touched one experimenter more than the other in the choice test. We used a Wilcoxon signed-262 rank test to test whether the variation in heart rate differed significantly from zero during the 263 negative and positive videos. We used McNemar's test to investigate whether horses were more 264 likely to touch one of the experimenters throughout the total duration of the test (75 s), as our 265 data were binary. Supplementary statistical analyses comparing the results for each variable 266 between the test and the control condition are presented in Online Resource 1.

267

268 **Results**

269 Video projection

270 - Test condition:

271 Facial expression was described by a PCA. The first factor of the PCA explained 57.30% of the 272 total variability (Fig. 2; Table 1). It opposed two different facial expressions: "ears oriented 273 forward", "high neck", and, to a lesser extent, "whites of the eyes" were negatively correlated 274 with factor 1, while "ears oriented backwards", "low neck" and "medium neck" were positively 275 correlated (Table 1). The scores of the horses on factor 1 differed significantly between the two videos: horses presented significantly lower values when they watched the negative video than 276 277 when they watched the positive video (V= 33, P< 0.001; Fig. 2). Factor 2 represented 16.75% 278 of the variability and was mainly correlated with the variable "whites of the eyes" (Table 1).

- 279 The scores on factor 2 tended to differ between the two videos: the horses tended to score higher
- while watching the negative video than while watching the positive video (V = 215, P = 0.065).
- **Table 1** Correlations between the variables included in the PCA and the first two factors for the test condition

| | F1 | F2 |
|-------------------------|----------|----------|
| | (57.30%) | (16.75%) |
| High neck | -0.900 | -0.128 |
| Medium neck | 0.822 | 0.051 |
| Low neck | 0.891 | 0.132 |
| Ears oriented forwards | -0.742 | 0.177 |
| Ears oriented backwards | 0.761 | 0.021 |
| Whites of the eyes | -0.164 | 0.968 |

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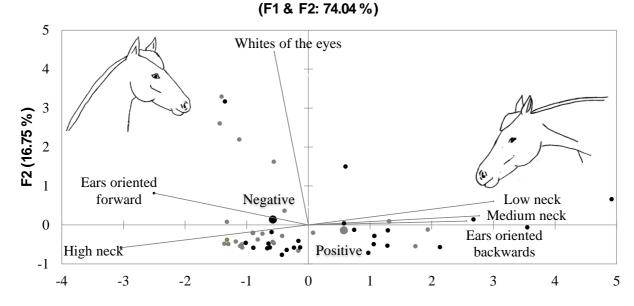


Fig. 2 Facial expression recorded during the test condition as described by the PCA. The gray points represent the reactions towards the negative video and the black points represent the reactions towards the positive video. A Wilcoxon test showed that these two reactions differed significantly on the F1 axis. The large points represent the barycenter for each video (Negative = negative video; Positive = positive video)

288 The number of grooming attempts was significantly higher (W= 131, P< 0.001; Fig. 3) while

289 watching the positive video than while watching the negative video.

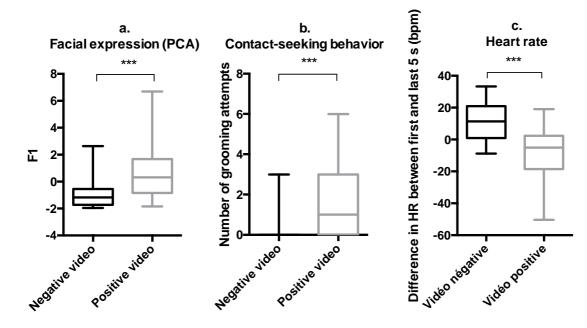
290 The difference in mean heart rate between the first and last 5 s of the video (W = 408, P < 0.001;

Fig. 3) was significantly higher for the negative video than for the positive video. This

292 difference significantly differed from zero for both videos (negative: V= 227, p< 0.001;

positive: V=57, p=0.023). It was positive for the negative video, meaning that the heart rate

- increased while the horse watched the negative video, and was negative for the positive video,
- 295 meaning that the heart rate decreased while the horse watched the positive video.
- 296 The time spent facing the videos did not significantly differ between the videos (W= 324, P=
- 297 0.282).
- 298
- 299



300

301
302Fig. 3 a. First factor of the PCA representing the facial expression, b. number of grooming attempts and c. difference in mean
heart rate between the first and last 5 s of the video during the negative and the positive videos in the test condition. Significance
was tested by a Wilcoxon test for paired samples: *** P < 0.001. n = 24 individuals</th>

304

305 - Control condition:

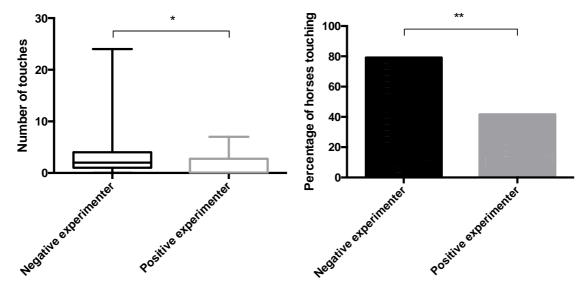
The first two factors of the PCA characterizing the facial expression explained 62.79% of the total variability and are described in Table S2. None of these factors enabled significant differentiation between the two videos (F1: V= 138, P= 0.988; F2: V= 162, P= 0.482; Fig. S3). None of the other variables differed significantly between the two videos (Table S3): number of grooming attempts (W= 241, P= 0.483); variation in heart rate between the beginning and end of the video (W= 325, P= 0.187); time spent paying attention to the videos (W= 336, P= 0.112).

314 Choice test

315 The horses touched the negative experimenter significantly more frequently than they did the

316 positive experimenter (W= 384, P= 0.042; Fig. 4). They were also more likely to touch the

- 317 negative experimenter at least once when we considered the data as binary (McNemar's chi-
- 318 squared= 7.11, df= 1, P= 0.008; Fig. 4).



320
321
322Fig. 4 Number of touches and percentage of horses that touched each experimenter. Significance was tested by a Wilcoxon
signed-rank test for paired samples for the number of touches and with a McNemar's test for the percentage of horses touching
an experimenter: * P < 0.05, ** P < 0.01. n = 24 individuals

323

319

324 **Discussion**

In accordance with our hypothesis, our results show that the horses reacted differently when watching a positive video (with an experimenter grooming a horse) and a negative video (with an experimenter performing an unpleasant veterinary act) and that the information observed in these videos later influenced their behavior towards the two experimenters in a choice test in real life.

330

331 Horses perceived and reacted to the emotional content of the videos

332 In our study, the horses reacted coherently with the type of information contained in the video 333 they were watching: they showed clear positive facial expressions during the positive video and 334 clear negative facial expressions during the negative video; they sought contact almost 335 exclusively during the positive videos; their heart rate decreased during the positive video while 336 it increased during the negative video. In a control condition, we verified that these differences 337 were not merely due to the fact that there was more movement in the negative video (as the 338 actor horse tried to get away from the unpleasant stimulus) compared to the positive video. 339 Indeed, in the control videos, the horse and the experimenter were replaced with moving ovals

that precisely followed their displacement and variations in surface area. The horses did not react differently when watching the two videos in this control condition. This suggests that the horses actually perceived and reacted to the content of the videos in the test condition. We can also notice that the emotional response of the horses during the control condition was intermediate between the positive and the negative video of the test condition: they did not attempt to groom the experimenter as they did during the positive video of the test and their heart rate increased less than during the negative video of the test (Online Resource 1).

347

348 Their emotional reactions while watching the videos in the test might have been caused by two 349 different types of cues (nonexclusively). First, they might have used the emotions of the actor 350 horse in the videos. Our results could thus be explained by an emotional contagion between the 351 actor horse and the horse watching the video. Emotional contagion is the reflex-like trigger of 352 one's emotion caused by observing this emotion in another individual (Hatfield et al. 1993; 353 Boissy et al. 1998; de Waal 2007, 2012). This effect carries important functions for group 354 living, such as the synchronization of behaviors and the consolidation of social bonds by sharing 355 positive emotions, and reacting appropriately to an unperceived or unknown stimulus (e.g., 356 reacting quickly to the arrival of a predator that only one member of the group has seen; Spinka 357 2012). Emotional contagion has been shown in various species (for a review: de Waal 2007; 358 Špinka 2012; Briefer 2018), including farm animals: some evidence has been found among 359 sheep (e.g., Yonezawa et al. 2017), pigs (e.g., Goumon and Špinka, 2016; Reimert et al., 2014), 360 chickens (Edgar et al. 2011) and cattle (Boissy et al., 1998). Previous studies on horses have 361 showed a transmission of emotions in negative contexts (e.g., Christensen et al. 2008; Keeling 362 et al. 2009; Rørvang et al. 2015; Rørvang and Christensen 2018) but never in positive contexts. 363 Our study suggests the emotional contagion of positive valence as well. Indeed, the horses not 364 only reacted less negatively while watching the positive video, they also presented a facial 365 expression associated with positive emotions (Lansade et al. 2018) and a behavioral response 366 typical of this type of positive interaction, as they attempted to groom the assistant. Mutual 367 grooming is an important affiliative behavior in horses (Arnold and Grassia 1982; Kimura 1998; 368 Heitor et al. 2006) and when a human grooms a horse, the horse tends to reciprocate the 369 grooming with humans (McGreevy et al. 2009). Second, the horses might have reacted to the 370 valence of the experimenters' behaviors during the interaction with the actor horse (i.e., 371 grooming the actor horse or performing unpleasant veterinary acts). Importantly, the spray used 372 in the negative video was completely hidden inside the experimenter's hand so that the horse 373 watching the video did not simply react to the vision of a scary object. Nor did the horses react to the experimenters' facial expressions as we controlled both experimenters' facial expressions
in the videos. In any case, our results show that the horses perceived the valence of the
interactions seen in the videos and that perception induced a consistent emotional response.

377

378 Horses discriminated between the two experimenters in the choice test

379 During the choice test, the horses behaved differently with the experimenters based on the 380 previously observed interaction between the experimenters and the actor horse. However, 381 contrary to a more intuitive hypothesis, horses touched the negative experimenter more than 382 they did the positive experimenter. One possible explanation is that the horses interpreted the 383 negative video as a conflict between the horse and the negative experimenter. Hence, the horses 384 might have touched the negative experimenter as an appeasement behavior. Indeed, during the 385 postconflict periods, friendly contacts between a third-party horse and group mates previously 386 involved in a conflict have been described in horses (Cozzi et al. 2010). Similar results have 387 also been found in bonobos in a cooperation paradigm (Krupenye and Hare 2018). Indeed, the 388 bonobos preferred the negative experimenter, who tried to steal a stuffed toy from the neutral 389 experimenter, more than the positive experimenter, who helped the neutral experimenter 390 retrieve the toy. The authors proposed that the negative experimenter might have appeared more 391 dominant than the positive one, which would explain the bonobos' preference, as they also 392 showed an attraction to dominant individuals in the same study. It would thus be interesting in 393 further studies to test whether a similar phenomenon could explain the behavior of the horses 394 towards the negative experimenter.

395 To discriminate between the experimenters, the horses might have adjusted their behavior 396 towards the experimenters based on the emotional state expressed by the actor horse during the 397 interactions seen on video: the horses eavesdropped on the emotional state of a third-party horse 398 involved in a social interaction with a human experimenter, thereby attributing a positive or 399 negative valence to that specific experimenter; they remembered the information and used it to 400 adjust their later behavior towards this experimenter. This type of eavesdropping has, for 401 instance, been shown in human infants and in dogs: they adapt their behavior with a stranger 402 depending on their mother's/owner's emotional reaction towards the stranger (Feinman and 403 Lewis 1983; Murray et al. 2008; Freidin et al. 2013; Duranton et al. 2016).

Furthermore, the horses might have responded to the choice test based on the experimenters' behavior seen on video, either by using the behavior in itself (e.g., the experimenters' gestures)—independently of the actor horse—or by interpreting this behavior as part of the interaction (e.g., an experimenter grooming a horse and an experimenter performing veterinary

408 acts). In the latter circumstance, they would have attributed a positive or negative valence to 409 each experimenter based on the behavior the experimenter demonstrated during the interaction 410 with the actor horse and then adjusted their own behavior in the choice test based on the 411 experimenters' valence. This might be related to the ability of "social evaluation" described in 412 the context of cooperation as the ability to attribute a value to a behavioral pattern demonstrated 413 during a third-party social interaction, associate this behavior with a specific individual and use 414 this information to adjust one's behavior towards this individual (Abdai and Miklósi, 2016). 415 Again, the horses could not have reacted to the human facial expressions in the videos (as it 416 was shown in Proops et al. 2018) because we made sure that both experimenters kept a neutral 417 facial expression.

In all cases, our results suggest that horses are capable of social learning by eavesdropping on the behavior of others (McGregor 1993). This is coherent with the results of previous studies in horses that showed that they could attribute a valence to humans based on the previous interactions they had had together (Henry et al. 2005; Sankey et al. 2010). Our study goes one step further, as the horses attributed a valence based on indirect cues only—by observing a third-party interaction.

424

425 Video projection was validated as a tool to study horse behavior

426 The horses presented a high interest for the videos, facing them for almost the entire duration 427 of the video projection in both the test and the control conditions (Table S3). They faced even 428 more the videos in the test condition – showing an interaction between an experimenter and a 429 horse- than in the control condition -showing moving ovals that had no particular meaning for 430 them (Online Resource 1). This confirms that they perceived the content of the videos. 431 Furthermore, they reacted accordingly to the content of the test videos: reacting negatively to 432 the negative video and positively to the positive video. The horses also discriminated between 433 the positive and negative experimenters they saw in the videos when meeting them for the first 434 time in real life. This implies that the horses recognized the experimenters they saw in 2D when 435 confronted with these experimenters in real life during the choice test. This is particularly 436 impressive because there is a loss of information in 2D videos compared to reality (Fagot 437 2000):, e.g., the horses did not have access to olfactory or auditory cues, nor to some visual aspects, such as depth and perspective. Previous studies have shown that horses can recognize 438 439 persons they have seen in pictures (e.g., Proops et al. 2018; Stone 2009), our results show that this extends to videos as well. To recognize the experimenters, our subjects might have used 440 441 the experimenters' face, body features or the color of their clothes. Hence, our findings are

particularly interesting for further studies, as video projection can be a very useful tool for
behavioral studies, e.g., to study animals' understanding of emotions or of specific
communication gestures.

445

446 Conclusion and implications for horse management and welfare

447 Our study shows that horses react appropriately to the interactions between a horse and a human 448 seen on video: the horses expressed the same emotions as the actor horse seen in these videos 449 via their facial expressions, behavior and heart rate. These results might be explained by a 450 reaction to the valence of the experimenters' behavior during the interaction or by emotional 451 contagion. This emotional contagion would have occurred by visual means only and concerned 452 emotions of negative as well as positive valence. When meeting the real persons afterwards in 453 a choice test, the horses discriminated between them by touching the negative experimenter 454 more, which may be interpreted as an appeasement behavior. Our results suggest that horses 455 are capable of perceiving the valence of an interaction seen on video, of reacting emotionally 456 accordingly to this valence, and of social eavesdropping.

457 Our findings can have applied repercussions in terms of horse welfare and management. Indeed, 458 in the case of veterinary or farriery practices that are unpleasant, it might be better to conduct 459 them with no other horse watching; otherwise, the stress of the handled horse could spread to 460 the other horses through emotional contagion, and the other horses might attribute a negative 461 valence to the vet or farrier, potentially complicating future encounters with them. Finally, if 462 horses can attribute a valence to humans after seeing a positive or negative interaction with 463 another horse, we could also use this type of set up to test the valence of a specific interaction 464 for horses, e.g., handling or riding methods.

465

466 **Compliance with ethical standards**

467 **Disclosure of potential conflicts of interest**

468 This study was funded by IFCE (Institut Français du Cheval et de l'Equitation; grant:469 Cognition-équitation).

470 Conflict of interest: the authors declare that they have no conflicts of interest.

471

472 Ethical approval

473 All applicable international, national, and/or institutional guidelines for the care and use of 474 animals were followed. All procedures performed in studies involving animals were in 475 accordance with the ethical standards of the institution or practice at which the studies were476 conducted.

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- 481

482 **References**

- 483 Abdai J, Miklósi Á (2016) The origin of social evaluation, social eavesdropping,
- 484 reputation formation, image scoring or what you will. Front Psychol 7:1–13. doi:
- 485 10.3389/fpsyg.2016.01772
- Anderson JR, Kuroshima H, Takimoto A, Fujita K (2013) Third-party social evaluation of
- 487 humans by monkeys. Nat Commun 4:1561–1565. doi: 10.1038/ncomms2495
- 488 Aquiloni L, Gherardi F (2010) Crayfish females eavesdrop on fighting males and use
 489 smell and sight to recognize the identity of the winner. Anim Behav 79:265–269.
- 490 doi: 10.1016/j.anbehav.2009.09.024
- 491 Arnold, G.W., Grassia, A., 1982. Ethogram of agonistic behaviour for thoroughbred horses.
 492 Appl. Anim. Ethol. 8, 5–25. https://doi.org/10.1016/0304-3762(82)90129-8
- 493 Boissy A, Terlouw C, Le Neindre P (1998) Presence of cues from stressed conspecifics
- 494 increases reactivity to aversive events in cattle: Evidence for the existence of alarm
 495 substances in urine. Physiol Behav 63:489–495. doi: 10.1016/S0031-
- 496 9384(97)00466-6
- 497 Bonnie KE, Earley RL (2007) Expanding the scope for social information use. Anim
 498 Behav 74:171–181. doi: 10.1016/j.anbehav.2006.12.009
- Briefer EF (2018) Vocal contagion of emotions in non-human animals. Proc R Soc B Biol
 Sci 285:20172783. doi: 10.1098/rspb.2017.2783
- 501 Briefer EF, Mandel R, Maigrot AL, et al (2017) Perception of emotional valence in horse
 502 whinnies. Front Zool 14:1–12. doi: 10.1186/s12983-017-0193-1
- 503 Bshary R, Grutter AS (2006) Image scoring and cooperation in a cleaner fish mutualism.
 504 Nature 441:975–978. doi: 10.1038/nature04755
- 505 Cheney DL (2011) Extent and limits of cooperation in animals. Proc Natl Acad Sci

Animal Cognitionhttps://doi.org/10.1007/s10071-020-01396-x 506 108:10902-10909. doi: 10.1073/pnas.1100291108 507 Chijiiwa H, Kuroshima H, Hori Y, et al (2015) Dogs avoid people who behave negatively 508 to their owner: Third-party affective evaluation. Anim Behav 106:123–127. doi: 509 10.1016/j.anbehav.2015.05.018 510 Christensen JW, Malmkvist J, Nielsen BL, Keeling LJ (2008) Effects of a calm companion 511 on fear reactions in naïve test horses. Equine Vet J 40:46–50. doi: 512 10.2746/042516408X245171 513 Cozzi A, Sighieri C, Gazzano A, et al (2010) Post-conflict friendly reunion in a permanent 514 group of horses (*Equus caballus*). Behav Processes 85:185–190. doi: 515 10.1016/j.beproc.2010.07.007 516 Dalla Costa E, Bracci D, Dai F, et al (2017) Do Different Emotional States Affect the Horse 517 Grimace Scale Score? A Pilot Study. J Equine Vet Sci 54:114–117. doi: 518 10.1016/j.jevs.2017.03.221 519 Dalla Costa E, Minero M, Lebelt D, et al (2014) Development of the Horse Grimace Scale 520 (HGS) as a pain assessment tool in horses undergoing routine castration. PLoS One 521 9:1-10. doi: 10.1371/journal.pone.0092281 522 de Waal FBM (2012) The antiquity of empathy. Science 336:874–876. doi: 523 10.1126/science.1220999 524 de Waal FBM (2007) Putting the altruism back into altruism: The evolution of empathy. 525 Annu Rev Psychol 59:279–300. doi: 10.1146/annurev.psych.59.103006.093625 526 Duranton C, Bedossa T, Gaunet F (2016) When facing an unfamiliar person, pet dogs 527 present social referencing based on their owners' direction of movement alone. 528 Anim Behav 113:147-156. doi: 10.1016/j.anbehav.2016.01.004 529 Earley RL, Dugatkin LA (2002) Eavesdropping on visual cues in green swordtail 530 (Xiphophorus helleri) fights: A case for networking. Proc R Soc B Biol Sci 269:943-952. doi: 10.1098/rspb.2002.1973 531 532 Edgar JL, Lowe JC, Paul ES, Nicol CJ (2011) Avian maternal response to chick distress. 533 Proc R Soc B Biol Sci 278:3129–3134. doi: 10.1098/rspb.2010.2701 534 Fagot J (2000) Picture perception in animals. Psychology Press 535 Feinman S, Lewis M (1983) Social Referencing at Ten Months : A Second-Order Effect on 536 Infants' Responses to Strangers. Child Dev 54:878-887 537 Freidin E, Putrino N, D'Orazio M, Bentosela M (2013) Dogs' eavesdropping from people's 538 reactions in third party interactions. PLoS One 8:1–8. doi:

Animal Cognitionhttps://doi.org/10.1007/s10071-020-01396-x 539 10.1371/journal.pone.0079198 540 Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software 541 for video/audio coding and live observations. Methods Ecol Evol 7:1325–1330. doi: 542 10.1111/2041-210X.12584 543 Gleerup KB, Forkman B, Lindegaard C, Andersen PH (2015) An equine pain face. Vet 544 Anaesth Analg 42:103–114. doi: 10.1111/vaa.12212 545 Goumon, S., Špinka, M., 2016. Emotional contagion of distress in young pigs is potentiated by previous exposure to the same stressor. Anim. Cogn. 19, 501–511. 546 547 https://doi.org/10.1007/s10071-015-0950-5 548 Hatfield E, Cacioppo JT, Rapson RL (1993) Emotional contagion. Curr Dir Psychol Sci 549 2:96-99. doi: 10.1111/1467-8721.ep10770953 550 Heitor, F., do Mar Oom, M., Vicente, L., 2006. Social relationships in a herd of Sorraia 551 horses. Part II. Factors affecting affiliative relationships and sexual behaviours. Behav. 552 Processes 73, 231–239. https://doi.org/10.1016/j.beproc.2006.05.005 553 Henry S, Hemery D, Richard MA, Hausberger M (2005) Human-mare relationships and behaviour of foals toward humans. Appl Anim Behav Sci 93:341–362. doi: 554 555 10.1016/j.applanim.2005.01.008 556 Höjesjö J, Andersson P, Engman A, Johnsson JI (2007) Rapid bystander assessment of 557 intrinsic fighting ability: behavioural and heart rate responses in rainbow trout. 558 Anim Behav 74:1743–1751. doi: 10.1016/j.anbehav.2007.04.013 559 Kavaliers M, Matta R, Choleris E (2017) Mate-choice copying, social information 560 processing, and the roles of oxytocin. Neurosci Biobehav Rev 72:232–242. doi: 561 10.1016/j.neubiorev.2016.12.003 562 Kawai N, Yasue M, Banno T, Ichinohe N (2014) Marmoset monkeys evaluate third-party reciprocity. Biol Lett 10: 20140058. doi: 10.1098/rsbl.2014.0058 563 564 Keeling LJ, Jonare L, Lanneborn L (2009) Investigating horse-human interactions: The effect of a nervous human. Vet J 181:70-71. doi: 10.1016/j.tvjl.2009.03.013 565 566 Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-567 ranging horses. Appl. Anim. Behav. Sci. 59, 265–276. https://doi.org/10.1016/S0168-568 1591(97)00129-9 569 Koo TK, Li MY (2016) A Guideline of Selecting and Reporting Intraclass Correlation 570 Coefficients for Reliability Research. J Chiropr Med 15:155–63. doi: 571 10.1016/j.jcm.2016.02.012

572 Krueger K, Farmer K, Heinze J (2014) The effects of age, rank and neophobia on social 573 learning in horses. Anim Cogn 17:645-655. doi: 10.1007/s10071-013-0696-x 574 Krupenye C, Hare B (2018) Bonobos Prefer Individuals that Hinder Others over Those 575 that Help. Curr Biol 28:280-286.e5. doi: 10.1016/j.cub.2017.11.061 576 Lai WS, Yu WC, Liu CY, et al (2014) A new method for studying social eavesdropping 577 using male golden hamsters. Physiol Behav 128:202–211. doi: 578 10.1016/j.physbeh.2014.01.029 579 Lampe JF, Andre J (2012a) Cross-modal recognition of human individuals in domestic horses (Equus caballus). Anim Cogn 15:623-630. doi: 10.1007/s10071-012-0490-1 580 581 Lansade L, Nowak R, Lainé AL, et al (2018) Facial expression and oxytocin as possible 582 markers of positive emotions in horses. Sci Rep 8:1-11. doi: 10.1038/s41598-018-583 32993-z 584 Malavasi R, Huber L (2016) Evidence of heterospecific referential communication from 585 domestic horses (*Equus caballus*) to humans. Anim Cogn 19:899–909. doi: 586 10.1007/s10071-016-0987-0 587 Marshall-Pescini S, Passalacqua C, Ferrario A, et al (2011) Social eavesdropping in the 588 domestic dog. Anim Behav 81:1177-1183. doi: 10.1016/j.anbehav.2011.02.029 589 McGreevy PD, Oddie C, Burton FL, McLean AN (2009) The horse-human dyad: Can we 590 align horse training and handling activities with the equid social ethogram? Vet J 591 181:12-18. doi: 10.1016/j.tvjl.2009.03.005 592 McGregor PK (1993) Signalling in territorial systems: a context for individual 593 identification, ranging and eavesdropping. Philos Trans R Soc London Ser B Biol Sci 594 340:237-244. doi: 10.1098/rstb.1993.0063 595 Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in 596 songbirds. Science 296:873. doi: 10.1126/science.296.5569.873 597 Murray L, De Rosnay M, Pearson J, et al (2008) Intergenerational transmission of social 598 anxiety: The role of social referencing processes in infancy. Child Dev 79:1049-599 1064. doi: 10.1111/j.1467-8624.2008.01175.x 600 Nakamura K, Takimoto-Inose A, Hasegawa T (2018) Cross-modal perception of human 601 emotion in domestic horses (Equus caballus). Sci Rep 8:1-9. doi: 10.1038/s41598-602 018-26892-6 603 Nitzschner M, Melis AP, Kaminski J, Tomasello M (2012) Dogs (Canis familiaris) evaluate 604 humans on the basis of direct experiences only. PLoS One 7: e46880. doi:

| 605 | 10.1371/journal.pone.0046880 |
|-----|--|
| 606 | Ophir AG, Galef BG (2004) Sexual experience can affect use of public information in mate |
| 607 | choice. Anim Behav 68:1221–1227. doi: 10.1016/j.anbehav.2003.12.023 |
| 608 | Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2001) Male great tits eavesdrop on |
| 609 | simulated male-to-male vocal interactions. Proc R Soc B Biol Sci 268:1183–1187. |
| 610 | doi: 10.1098/rspb.2001.1648 |
| 611 | Proops L, Grounds K, Smith AV, McComb K (2018) Animals Remember Previous Facial |
| 612 | Expressions that Specific Humans Have Exhibited. Curr Biol 28:1428-1432.e4. doi: |
| 613 | 10.1016/j.cub.2018.03.035 |
| 614 | Proops L, McComb K (2010) Attributing attention: the use of human-given cues by |
| 615 | domestic horses (<i>Equus caballus</i>). Anim Cogn 13:197–205. doi: 10.1007/s10071- |
| | |
| 616 | 009-0257-5 |
| 617 | Proops L, McComb K (2012) Cross-modal individual recognition in domestic horses |
| 618 | (<i>Equus caballus</i>) extends to familiar humans. Proc R Soc B Biol Sci 279:3131–3138. |
| 619 | doi: 10.1098/rspb.2012.0626 |
| 620 | Proops L, McComb K, Reby D (2009) Cross-modal individual recognition in domestic |
| 621 | horses (<i>Equus caballus</i>). Proc Natl Acad Sci 106:947–951. doi: |
| 622 | 10.1073/pnas.0809127105 |
| 623 | Proops L, Rayner J, Taylor AM, McComb K (2013) The Responses of Young Domestic |
| 624 | Horses to Human-Given Cues. PLoS One 8:26–28. doi: |
| 625 | 10.1371/journal.pone.0067000 |
| 626 | Reimert, I., Bolhuis, J.E., Kemp, B., Rodenburg, T.B., 2014. Emotions on the loose: |
| 627 | emotional contagion and the role of oxytocin in pigs. Anim. Cogn. 18, 517–532. |
| 628 | https://doi.org/10.1007/s10071-014-0820-6 |
| 629 | Ringhofer M, Inoue S, Mendonça RS, et al (2017) Comparison of the social systems of |
| 630 | primates and feral horses: data from a newly established horse research site on |
| 631 | Serra D'Arga, northern Portugal. Primates 58:479–484. doi: 10.1007/s10329-017- |
| 632 | 0614-y |
| 633 | Ringhofer M, Yamamoto S (2016) Domestic horses send signals to humans when they |
| 634 | face with an unsolvable task. Anim Cogn 20:397–405. doi: 10.1007/s10071-017- |
| 635 | 1074-x |
| 636 | Rørvang MV, Ahrendt LP, Christensen JW (2015) A trained demonstrator has a calming |
| 637 | effect on naïve horses when crossing a novel surface. Appl Anim Behav Sci |

Animal Cognitionhttps://doi.org/10.1007/s10071-020-01396-x 638 171:117-120. doi: 10.1016/j.applanim.2015.08.008 639 Rørvang MV, Christensen JW (2018) Attenuation of fear through social transmission in 640 groups of same and differently aged horses. Appl Anim Behav Sci 209:41–46. doi: 641 10.1016/j.applanim.2018.10.003 642 Rueden CT, Schindelin J, Hiner MC, et al (2017) Image 2: Image for the next generation 643 of scientific image data. BMC Bioinformatics 18:1-26. doi: 10.1186/s12859-017-644 1934-z 645 Russell YI, Call J, Dunbar RIM (2008) Image scoring in great apes. Behav Processes 646 78:108-111. doi: 10.1016/j.beproc.2007.10.009 647 Sankey C, Richard-Yris MA, Henry S, et al (2010) Reinforcement as a mediator of the 648 perception of humans by horses (*Equus caballus*). Anim Cogn 13:753–764. doi: 649 10.1007/s10071-010-0326-9 650 Schindelin J, Arganda-Carreras I, Frise E, et al (2012) Fiji: An open-source platform for 651 biological-image analysis. Nat Methods 9:676-682. doi: 10.1038/nmeth.2019 652 Schuetz A, Farmer K, Krueger K (2017) Social learning across species: horses (Equus 653 *caballus*) learn from humans by observation. Anim Cogn 20:567–573. doi: 654 10.1007/s10071-016-1060-8 655 Smith AV, Proops L, Grounds K, et al (2016) Functionally relevant responses to human 656 facial expressions of emotion in the domestic horse (Equus caballus). Biol Lett 657 12:20150907. doi: 10.1098/rsbl.2016.0549 658 Smith AV, Proops L, Grounds K, et al (2018) Domestic horses (*Equus caballus*) 659 discriminate between negative and positive human nonverbal vocalisations. Sci Rep 660 8:1-8. doi: 10.1038/s41598-018-30777-z 661 Špinka M (2012) Social dimension of emotions and its implication for animal welfare. 662 Appl Anim Behav Sci 138:170-181. doi: 10.1016/j.applanim.2012.02.005 663 Stone SM (2009) Human facial discrimination in horses: Can they tell us apart? Anim 664 Cogn 13:51-61. doi: 10.1007/s10071-009-0244-x 665 Subiaul F, Vonk J, Okamoto-Barth S, Barth J (2008) Do chimpanzees learn reputation by 666 observation? Evidence from direct and indirect experience with generous and 667 selfish strangers. Anim Cogn 11:611-623. doi: 10.1007/s10071-008-0151-6 668 Trösch M, Cuzol F, Parias C, et al (2019a) Horses categorize human emotions cross-669 modally based on facial expression and non-verbal vocalizations. Animals 9: 862-670 872. doi: 10.3390/ani9110862

671 Trösch M, Ringhofer M, Yamamoto S, et al (2019b) Horses prefer to solicit a person who 672 previously observed a food-hiding process to access this food: A possible indication 673 of attentional state attribution. Behav Processes 166:103906. doi: 674 10.1016/j.beproc.2019.103906 675 Valone TJ (2007) From eavesdropping on performance to copying the behavior of others: A review of public information use. Behav Ecol Sociobiol 62:1–14. doi: 676 677 10.1007/s00265-007-0439-6 678 Wathan J, Proops L, Grounds K, McComb K (2016) Horses discriminate between facial 679 expressions of conspecifics. Sci Rep 6:1–11. doi: 10.1038/srep38322 680 Yonezawa T, Sato K, Uchida M, et al (2017) Presence of contagious yawning in sheep. 681 Anim Sci J 88:195–200. doi: 10.1111/asj.12681 682 683

Animal Cognitionhttps://doi.org/10.1007/s10071-020-01396-x