



HAL
open science

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

Miléna Trösch, Sophie Pellon, Florent Cuzol, Céline Parias, Raymond Nowak,
Ludovic Calandreau, Léa Lansade

► To cite this version:

Miléna Trösch, Sophie Pellon, Florent Cuzol, Céline Parias, Raymond Nowak, et al.. Horses feel emotions when they watch positive and negative horse–human interactions in a video and transpose what they saw to real life. *Animal Cognition*, 2020, 23 (4), pp.643 - 653. 10.1007/s10071-020-01369-0 . hal-03038684

HAL Id: hal-03038684

<https://hal.science/hal-03038684>

Submitted on 3 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

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

4
5 Miléna Trösch^{a*} (milena.trosch@gmail.com), Sophie Pellon^a (pellon.sophie@gmail.com),
6 Florent Cuzol^a (florent.cuzol@gmail.com), Céline Parias^a (celine.parias@inrae.fr), Raymond
7 Nowak^a (raymond.nowak@inrae.fr), Ludovic Calandreau^a (ludovic.calandreau@inrae.fr), Léa
8 Lansade^a (lea.lansade@inrae.fr).

9 * corresponding author

10 ^a INRAE, PRC, CNRS, IFCE, Université de Tours, 37380 Nouzilly, France.

11 **Keywords:** *Equus caballus*, Social cognition, Social eavesdropping, Human-animal
12 relationship, Emotional contagion

13

14 **Abstract**

15 Animals can indirectly gather meaningful information about other individuals by
16 eavesdropping on their third-party interactions. In particular, eavesdropping can be used to
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

30 counterintuitive but can be interpreted as an appeasement attempt, based on the existing
31 literature. This result suggests that horses can indirectly attribute a valence to a human
32 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
44 or positive valence indirectly to unknown individuals by two different mechanisms. First,
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; Chijiwa
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

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

66 This valence attribution, often studied in the context of cooperation, has also been reported
67 during interactions involving emotional content. Nitzschner et al. (2012) showed dogs an
68 interaction between a conspecific and a “nice” experimenter—paying attention to and petting
69 another dog—and an “ignoring” experimenter who ignored the other dog. As cooperation is a
70 complex mechanism that implies high cognitive demands (Cheney 2011), this alternative
71 paradigm can be particularly useful to study a broader range of species, especially species that
72 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; Glerup 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
86 Huber 2016; Ringhofer and Yamamoto 2016; Trösch et al. 2019b) and can learn socially from
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.

91 To examine this, we showed the horses two kinds of interactions between an experimenter and
92 an unfamiliar “actor” horse: a positive interaction (a grooming session) and a negative
93 interaction (an unpleasant veterinary act). These scenes were presented to the horse through
94 silent videos projected in real size in front of each horse, and we investigated whether they
95 could perceive the emotional content of these scenes through behavioral and physiological
96 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

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

130 performing a veterinary act on the horse: touching her ears to administer an ointment and
131 applying a spray towards her head. We used a small air spray, which was completely hidden in
132 the experimenter's hand, so that it was invisible on the video. In that case, the actor horse
133 expressed fearful reactions by jolting and trying to run away from the experimenter (four times
134 in each video). She adopted a typical facial expression of negative emotions (Table S1):
135 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
142 any positive or negative emotions) in both videos, and the videos were later checked
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

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

157

158 **Set up and procedure**

159 The entire experiment took place in a large, familiar stall (3.5 x 4.5 m; Fig. 1). The videos were
160 projected onto a large white screen (2 x 2 m) by a DLP projector Acer P6200S. During the
161 video projection, the horse was attached in front of the screen by two loose leading reins (one
162 on each side of the horse). Moreover, an assistant stood next to the horse during the projection
163 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.

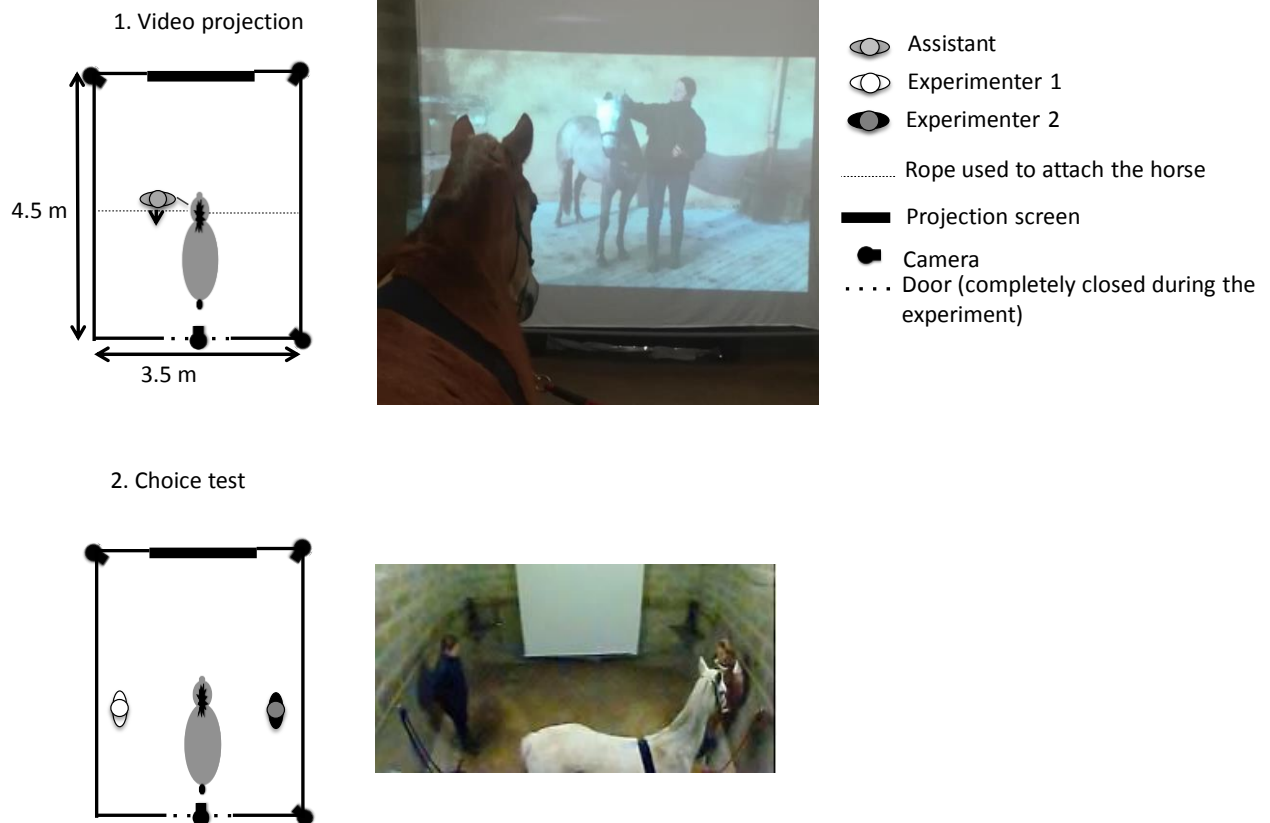
179 2. Projection of the negative and positive videos in random order.

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:

198 The control condition was realized with 23 new horses who were different from the ones used
199 in the test condition. The familiarization and projection of the negative and positive videos were
200 similar as in the test condition except that, in all videos, the horse and experimenters were
201 replaced by moving ovals. No choice test was carried out after the video projection.
202



203
204 **Fig. 1** Schematic representation and pictures of the video projection and the choice test

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:

212 1. Facial expression. Facial expressions were measured using the variables described in
213 Lansade et al. 2018: 1) the time spent with both ears oriented backward or forward; 2) the time
214 spent with the neck high, medium or low; and 3) the time spent with the whites of the eyes
215 visible (as we did not observe any half-closed eyes, we did not include the time spent with the
216 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
218 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 the
221 leading reins or the assistant.

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

226 4. Time spent facing the videos. We considered the horses as being attentive to the video when
227 they directly faced the video (the angle between their head and the center of the screen was $<$
228 15°) or when the angle was between 10° and 45° but at least one ear was oriented towards the
229 video (Proops et al. 2009; Lampe and Andre 2012; Proops and McComb 2012; Smith et al.
230 2018).

231 - Choice test

232 During the choice test, we observed whether the horse touched each experimenter and how
233 many times each experimenter was touched. Indeed, physical contacts with the muzzle has been
234 described as an attention seeking behavior in horses (Malavasi and Huber 2016; Ringhofer and
235 Yamamoto 2016; Trösch et al. 2019b). The touches were usually brief, but if those were longer
236 than three seconds, it was taken into account by counting a new occurrence every three seconds
237 (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:

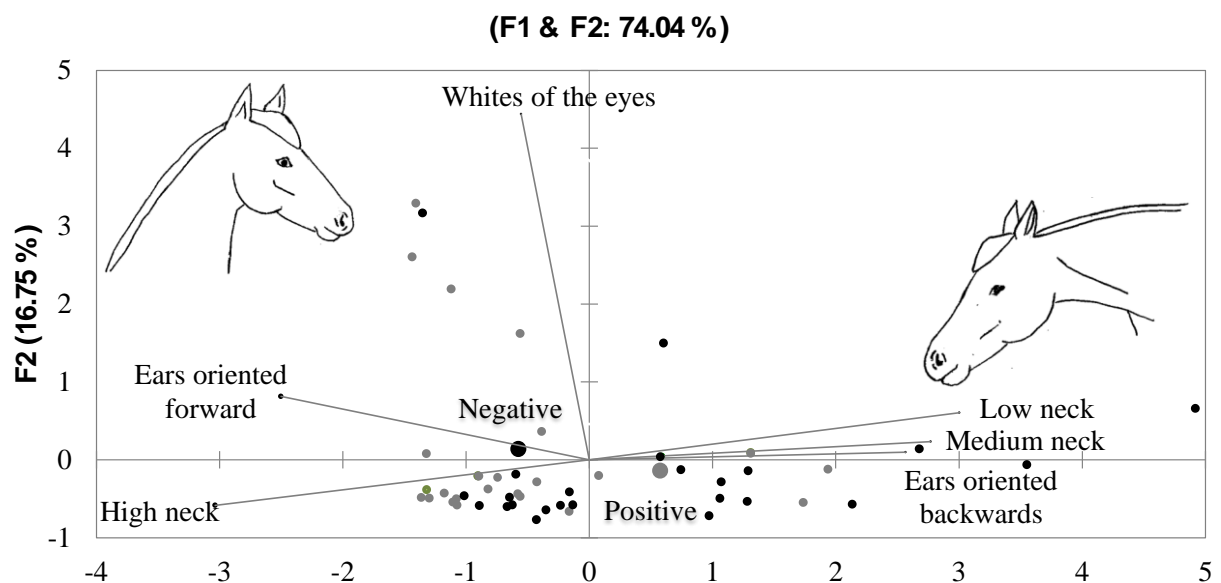
271 Facial expression was described by a PCA. The first factor of the PCA explained 57.30% of the
272 total variability (Fig. 2; Table 1). It opposed two different facial expressions: “ears oriented
273 forward”, “high neck”, and, to a lesser extent, “whites of the eyes” were negatively correlated
274 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
276 videos: horses presented significantly lower values when they watched the negative video than
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
 280 while watching the negative video than while watching the positive video ($V = 215$, $P = 0.065$).

281 **Table 1** Correlations between the variables included in the PCA and the first two factors for the test condition

	F1 (57.30%)	F2 (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

282



283

284 **Fig. 2** Facial expression recorded during the test condition as described by the PCA. The gray points represent the
 285 reactions towards the negative video and the black points represent the reactions towards the positive video. A
 286 Wilcoxon test showed that these two reactions differed significantly on the F1 axis. The large points represent the
 287 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.

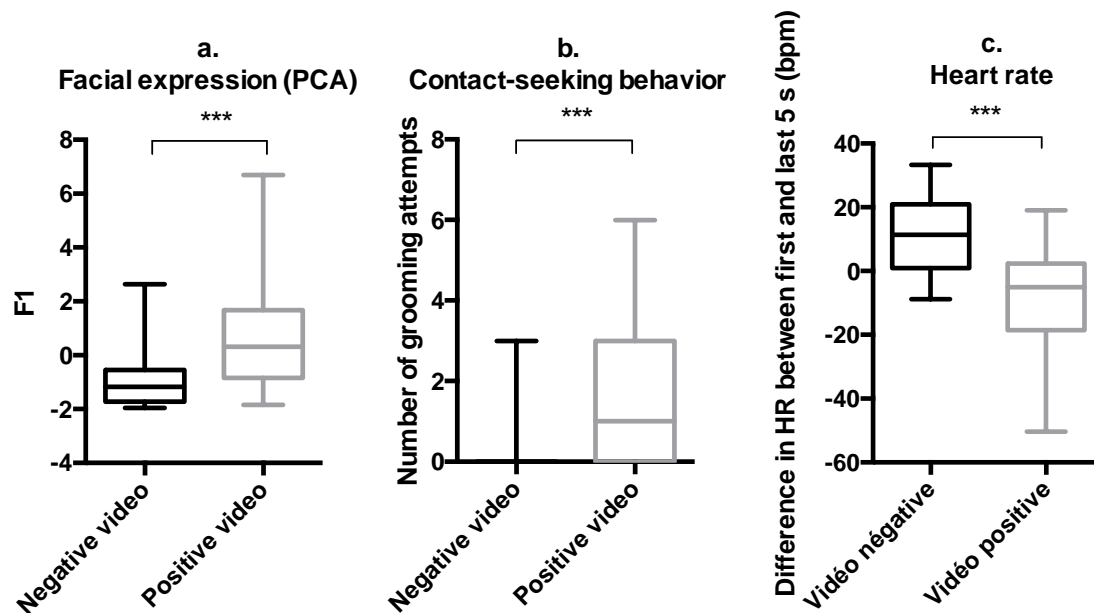
290 The difference in mean heart rate between the first and last 5 s of the video ($W = 408$, $P < 0.001$;
 291 Fig. 3) was significantly higher for the negative video than for the positive video. This
 292 difference significantly differed from zero for both videos (negative: $V = 227$, $p < 0.001$;
 293 positive: $V = 57$, $p = 0.023$). It was positive for the negative video, meaning that the heart rate

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

304

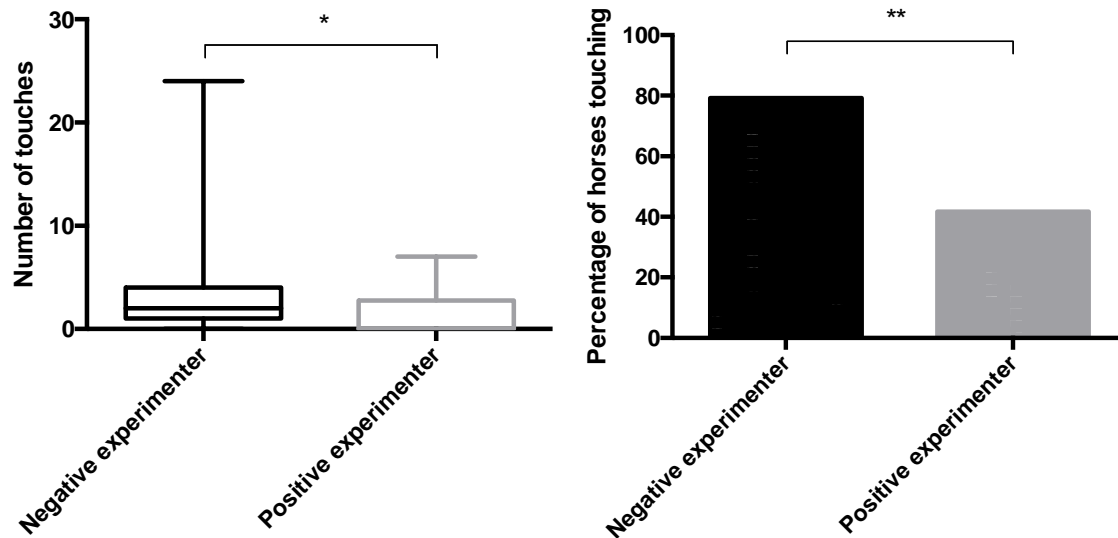
305 - Control condition:

306 The first two factors of the PCA characterizing the facial expression explained 62.79% of the
 307 total variability and are described in Table S2. None of these factors enabled significant
 308 differentiation between the two videos ($F1: V= 138$, $P= 0.988$; $F2: V= 162$, $P= 0.482$; Fig. S3).
 309 None of the other variables differed significantly between the two videos (Table S3): number
 310 of grooming attempts ($W= 241$, $P= 0.483$); variation in heart rate between the beginning and
 311 end of the video ($W= 325$, $P= 0.187$); time spent paying attention to the videos ($W= 336$, $P=$
 312 0.112).

313

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).



319
 320 **Fig. 4** Number of touches and percentage of horses that touched each experimenter. Significance was tested by a Wilcoxon
 321 signed-rank test for paired samples for the number of touches and with a McNemar's test for the percentage of horses touching
 322 an experimenter: * $P < 0.05$, ** $P < 0.01$. $n = 24$ individuals

323
 324 **Discussion**

325 In accordance with our hypothesis, our results show that the horses reacted differently when
 326 watching a positive video (with an experimenter grooming a horse) and a negative video (with
 327 an experimenter performing an unpleasant veterinary act) and that the information observed in
 328 these videos later influenced their behavior towards the two experimenters in a choice test in
 329 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

340 that precisely followed their displacement and variations in surface area. The horses did not
341 react differently when watching the two videos in this control condition. This suggests that the
342 horses actually perceived and reacted to the content of the videos in the test condition. We can
343 also notice that the emotional response of the horses during the control condition was
344 intermediate between the positive and the negative video of the test condition: they did not
345 attempt to groom the experimenter as they did during the positive video of the test and their
346 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; Špinka
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

374 to the experimenters' facial expressions as we controlled both experimenters' facial expressions
375 in the videos. In any case, our results show that the horses perceived the valence of the
376 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).

404 Furthermore, the horses might have responded to the choice test based on the experimenters'
405 behavior seen on video, either by using the behavior in itself (e.g., the experimenters'
406 gestures)—independently of the actor horse—or by interpreting this behavior as part of the
407 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.

418 In all cases, our results suggest that horses are capable of social learning by eavesdropping on
419 the behavior of others (McGregor 1993). This is coherent with the results of previous studies
420 in horses that showed that they could attribute a valence to humans based on the previous
421 interactions they had had together (Henry et al. 2005; Sankey et al. 2010). Our study goes one
422 step further, as the horses attributed a valence based on indirect cues only—by observing a
423 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
438 aspects, such as depth and perspective. Previous studies have shown that horses can recognize
439 persons they have seen in pictures (e.g., Proops et al. 2018; Stone 2009), our results show that
440 this extends to videos as well. To recognize the experimenters, our subjects might have used
441 the experimenters' face, body features or the color of their clothes. Hence, our findings are

442 particularly interesting for further studies, as video projection can be a very useful tool for
443 behavioral studies, e.g., to study animals' understanding of emotions or of specific
444 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'Équitation; 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 were
476 conducted.

477 **Acknowledgements**

478 We thank Fabrice Reigner and his team for allowing us to use the animals and facilities and for
479 their assistance in taking care of the horses. Our research was financially supported by the IFCE
480 (Institut Français du Cheval et de l'Équitation).

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
- 486 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](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
- 499 Briefer EF (2018) Vocal contagion of emotions in non-human animals. *Proc R Soc B Biol*
500 *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*

- 506 108:10902–10909. doi: 10.1073/pnas.1100291108
- 507 Chijiwa 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–
531 952. doi: 10.1098/rspb.2002.1973
- 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:

- 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
546 by previous exposure to the same stressor. *Anim. Cogn.* 19, 501–511.
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
554 behaviour of foals toward humans. *Appl Anim Behav Sci* 93:341–362. doi:
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
563 reciprocity. *Biol Lett* 10: 20140058. doi: 10.1098/rsbl.2014.0058
- 564 Keeling LJ, Jonare L, Lanneborn L (2009) Investigating horse-human interactions: The
565 effect of a nervous human. *Vet J* 181:70–71. doi: 10.1016/j.tvjl.2009.03.013
- 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-](https://doi.org/10.1016/S0168-1591(97)00129-9)
568 [1591\(97\)00129-9](https://doi.org/10.1016/S0168-1591(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
580 horses (*Equus caballus*). *Anim Cogn* 15:623–630. doi: 10.1007/s10071-012-0490-1
- 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 (*Equus caballus*). *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 (*Equus caballus*) 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 (*Equus caballus*). *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*

- 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) ImageJ2: ImageJ 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
676 others: A review of public information use. *Behav Ecol Sociobiol* 62:1–14. doi:
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