



HAL
open science

Cognition and the human–animal relationship: a review of the sociocognitive skills of domestic mammals toward humans

Plotine Jardat, Léa Lansade

► To cite this version:

Plotine Jardat, Léa Lansade. Cognition and the human–animal relationship: a review of the sociocognitive skills of domestic mammals toward humans. *Animal Cognition*, 2022, 25, pp.369-384. 10.1007/s10071-021-01557-6 . hal-03361795

HAL Id: hal-03361795

<https://hal.inrae.fr/hal-03361795>

Submitted on 22 Aug 2022

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.

Cognition and the human-animal relationship: a review of the sociocognitive skills of domestic mammals toward humans

Plotine Jardat ^{a,b,c,¶}, Léa Lansade^{a*}

Affiliations:

^aCNRS, IFCE, INRAE, University of Tours, PRC, F-37380 Nouzilly, France

^bDepartment of Biology, École Normale Supérieure de Lyon, University of Lyon, Lyon, France

^cEcole Nationale Vétérinaire d'Alfort (ENVA), Maisons-Alfort, France

*Corresponding author (ORCID iD: 0000-0002-4185-9714) - mail: lea.lansade@inrae.fr

[¶]ORCID iD: 0000-0003-0374-5588 – mail: plotine.jardat@gmail.com

Abstract:

In the past 20 years, research focusing on interspecific sociocognitive abilities of animals toward humans has been growing, allowing a better understanding of the interactions between humans and animals. This review focuses on five sociocognitive abilities of domestic mammals in relation to humans: discriminating and recognizing individual humans; perceiving human emotions; understanding our attentional states and goals; using referential communication (perceiving human signals or sending signals to humans); and engaging in social learning with humans (e.g., local enhancement, demonstration and social referencing). We focused on different species of domestic mammals for which literature on the subject is available, namely, dogs, cats, ferrets, horses, cattle, sheep, goats and pigs. The results show that some species have remarkable abilities to recognize us or to read and understand the emotions or signals sent by humans. For example, sheep and horses can recognize the face of their keeper in photographs, dogs can react to our smells of fear, and pigs can follow our pointing gestures. Nevertheless, the studies are unequally distributed across species: there are many studies in animals that live closely with humans, such as dogs, but little is known about livestock animals, such as cattle and pigs. However, on the basis of existing data, no obvious links have emerged between the cognitive abilities of animals toward humans and their ecological characteristics or the history and reasons for their domestication. This review encourages continuing and expanding this type of research to more abilities and species.

Key words: interspecific social cognition, emotions, interspecific interactions, referential communication, social learning

Declarations:

Funding: No funding was received to assist with the preparation of this manuscript.

Conflicts of interest: the authors have no conflicts of interest to declare that are relevant to the content of this article.

Author contributions: LL had the idea for this review, PJ performed the literature search and drafted the work and LL revised it.

Availability of data and material/Code availability/Ethics approval/Consent to participate/Consent for publication: Not applicable

43 **Introduction**

44 In the past 20 years, research focusing on interspecific sociocognitive abilities of animals toward
45 humans has been growing, allowing us to understand better the human-animal relationship.
46 Domestic animals are defined as species that “adapted to man and the captive environment, by
47 some combination of genetic changes occurring over generations and environmentally induced
48 developmental events reoccurring during each generation” (Price 1984). This encompasses a large
49 number of species, and here, we will focus on domestic mammals. These species belong to several
50 phylogenetic clades and have different types of relationships with humans, along with diverse
51 histories of domestication, ecologies and social characteristics. The time of their domestication
52 varies, dating from approximately 16 000 years ago (dogs: Galibert et al. 2011) to approximately
53 2000 years ago (ferrets: Bulloch and Tynes 2010). Their diets range from strictly carnivorous (e.g.,
54 cats) to strictly herbivorous (e.g., cattle) and include omnivorous diets (e.g., pigs). They can be
55 highly social, living in family groups within large herds (e.g., horses: Dierendonck 2005), or
56 facultatively social (cats: Vitale Shreve and Udell 2015). Some species were initially domesticated
57 for their help in hunting (e.g., dogs) and others as livestock (e.g., cows). Finally, while some live in
58 our homes and are a core part of families (e.g., dogs and cats), others generally live away from
59 human houses and interact directly with humans only a few times a day or less (e.g., cattle, pigs
60 and horses). However, they all share a long common history with us, from their selection to their
61 daily life. They all rely on us for their survival whether it is to provide them with food, a habitat or
62 protection against predators. This proximity with humans of several millennia could be linked to
63 particular sociocognitive abilities toward humans. But what exactly do domestic mammals perceive
64 and understand about humans and what allows them to interact with us?

65 We will focus on domestic mammal species for which literature on the subject is available, namely,
66 dogs, cats, ferret, horses, cattle, sheep, goats and pigs (Table 2). Studies exploring their ability to
67 discriminate and recognize individual humans and their emotions are reviewed, along with those
68 exploring their abilities to understand our intentional states and goals, to communicate with us and
69 to learn socially from us (Fig 1).

70

71 **Method**

72 A literature search was carried out in the Web of Science database from March to July 2021
73 (<https://www.webofscience.com>). The search was based on three concepts: (a) “domestic
74 mammals” and related terms, (b) “sociocognitive skills” and related terms, and (c) “humans” and
75 related terms (Table 1). Keywords within each concept were combined with “or”, meaning that at
76 least one of the keywords needed to be present in the titles of publications selected. The concepts
77 were combined with “and”, so that only publications with a title containing all three concepts were
78 selected. Three filters were applied to select relevant scientific domains and article types (Table
79 S1). The search yielded 297 publications whose titles, and if necessary abstracts, were then
80 screened for relevance. Studies were included if they tested the existence of a domestic mammal’s
81 sociocognitive skill related to humans. Studies examining the conditions (e.g., age and social
82 context) influencing the cognitive performance of animals were excluded, as well as studies on wild
83 species. Reviews were included if they provided a global view of sociocognitive skills toward
84 humans of one or several domestic mammals. We retained 53 publications with these criteria. A
85 complementary research in the References section of the selected articles yielded 55 more
86 publications. In the text, 30 more references (giving definitions or studies about intraspecific
87 sociocognitive abilities, for example) are cited in order to put the results in perspective.

88

89 **Results**

90 The results of the review are summarized in Table 2, which shows for each species of domestic
91 mammal the studies and reviews about sociocognitive skills toward humans for which results are
92 available.

93 **Discussion**

94 **Discriminating and recognizing individual humans**

95 A first question concerns the ability of domestic mammals to discriminate between different
96 humans based on different types of sensory cues. Cattle and pigs can be trained to choose one of
97 two live handlers (that they could see and smell), and visual cues such as body height or color of

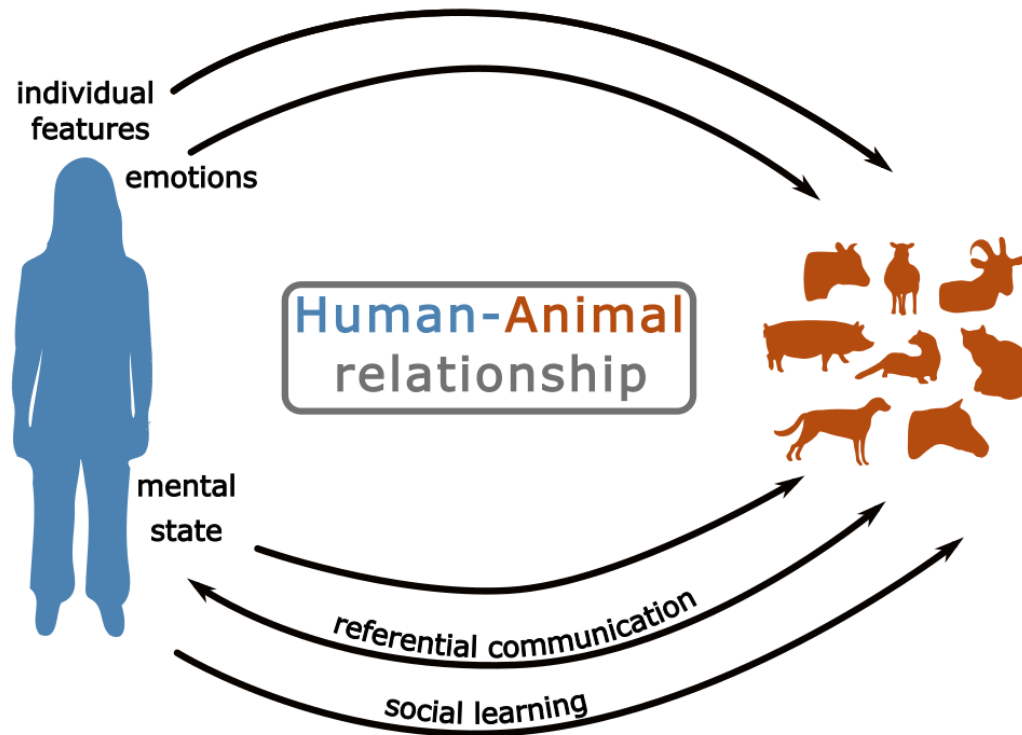


Fig 1 Summary of the sociocognitive abilities of domestic mammals toward humans reviewed in this paper

98 clothes seem particularly informative for them (pigs: Koba and Tanida 1999, 2001; cows: Rybarczyk
 99 et al. 2001). Dogs, horses, and sheep were able to distinguish individual humans based on visual
 100 cues only. These species either reacted differently to photographs of novel faces compared to
 101 familiar faces (dogs: Racca et al. 2010) or chose specific individuals in binary choice tests
 102 presenting two different photographs (horses: Stone 2010; Lansade et al. 2020a; sheep: Knolle et
 103 al. 2017). Auditory cues can also be used by horses to distinguish between different people (d’Ingeo
 104 et al. 2019). Lastly, olfactory cues were shown to be used by dogs to distinguish individuals, even
 105 in the case of identical twins who lived in the same environment (Pinc et al. 2011).

106 A second question concerns the ability of these species to recognize specific humans, an ability
 107 that implies both discrimination between individuals and the matching of an individual’s features to
 108 one’s memory of that particular individual (Tibbetts and Dale 2007). Dogs, horses and sheep could
 109 recognize their owner or handler from visual cues. For example, dogs chose their owner over a
 110 stranger when their faces were presented live through a hole or in pictures, either spontaneously

111 (live and pictures) or after training (live; Huber et al. 2013; Mongillo et al. 2017; from pictures:
112 Eatherington et al. 2020). After being trained to always choose a familiar picture over a novel one,
113 horses and sheep could spontaneously recognize a picture of their handler (Lansade et al. 2020a;
114 Knolle et al. 2017). Regarding auditory cues, cats were shown to distinguish their owner's voice
115 from that of a stranger's in a habituation-dishabituation protocol (Saito and Shinozuka 2013).

116 Faces are the main cue studied regarding the cognitive abilities mentioned above. Therefore,
117 researchers have attempted to determine which parts or characteristics of faces are used by
118 animals to differentiate and recognize them. A straightforward hypothesis is that they could use
119 simple cues such as hair color. However, dogs did not seem to distinguish human faces presented
120 upside down (although simple cues as hair color remained similar; Racca et al. 2010), and sheep
121 and horses still recognized the photograph of a familiar face when it was in black and white, from
122 a different angle or with a different hairstyle (Knolle et al. 2017; Lansade et al. 2020b). Therefore,
123 it seems that these animals may be using a holistic process to recognize human faces.

124 While the studies cited above investigated discrimination and recognition based on a single
125 modality (visual or auditory for example), cross-modal paradigms allow us to investigate whether
126 animals have multimodal mental representations of individual humans (that is, a mental
127 representation consisting of several types of features). In this way, dogs, cats and horses presented
128 with vocal and visual representations of humans (a voice and a portrait) had different reactions, for
129 example, looking longer at the picture, when the two stimuli were incongruent (i.e., the voice did
130 not correspond to the portrait) compared to when they were congruent (dogs: Adachi et al. 2007;
131 horses: Proops and McComb 2012; Lampe and Andre 2012; cats: Takagi et al. 2019).

132 Moreover, horses seem to perform this task with a left brain hemispheric specialization: they
133 correctly matched stimuli across modalities only when the visual stimulus was presented in their
134 right visual hemifield (Proops and McComb 2012).

135 In addition, this cross-modal representation of specific humans may also carry an emotional value
136 associated with the individual, as dogs and horses seem to react to a voice or odor of a human in
137 accordance with the valence of interactions they had previously experienced with that person
138 (horses: d'Ingeo et al. 2019; dogs: Siniscalchi et al. 2018b).

139 Overall, three capacities of increasing complexity have been revealed concomitantly in dogs, cats
140 and horses, namely, discriminating and recognizing individual humans and having cross-modal
141 representations of them. However, there are a lack of studies in cattle, goats, sheep, pigs and
142 ferrets regarding these skills. It should be noted that cattle, along with sheep, were shown to
143 recognize conspecific individuals on photographs (cattle: Coulon et al. 2009; sheep: Kendrick et al.
144 2001). Therefore, despite the failure of cattle to recognize human faces alone in experiments
145 carried out two decades ago (Rybarczyk et al. 2001), the use of newly available technologies (for
146 example, screens), such as those used with sheep or horses, could provide new insight into these
147 interspecific abilities in these species. Conversely, pigs appear unable to discriminate photographs
148 of conspecifics (Gieling et al. 2012), but there too, it could be interesting to test them in other
149 paradigms. Moreover, many of the studies reviewed examined discrimination and recognition of
150 humans from a visual perspective, which may not be an important modality in the animals studied.
151 It would be interesting in future studies to test other sensory cues such as olfactory or auditory cues
152 and compare the animals' discrimination and recognition performances based on these.

153

154 **Perceiving human emotions**

155 Distinct cognitive abilities have also been investigated regarding the perception of human
156 emotions by domestic mammals: can they discriminate our emotional expressions, do they prefer
157 some of our emotions to others, do they have a mental representation of our emotions, and how
158 do they react to them?

159 The ability to discriminate our emotional expressions through different sensory cues has been
160 explored in horses, dogs, cows, and. Horses followed an experimenter's gaze less if they were
161 expressing disgust compared to a neutral expression (Baba et al. 2019). Horses looked at pictures
162 of smiling humans differently than those of angry humans (Smith et al. 2016) and dogs could
163 differentiate the former from blank expressions after training (Nagasawa et al. 2011). Sniffing sweat
164 collected from humans watching a frightening film rather than a pleasing film caused horses to
165 make different head and ear movements (Sabiniewicz et al. 2020), and it led dogs to interact less
166 with a stranger (D'Aniello et al. 2018) and to use their nostrils in a different way (Siniscalchi et al.

167 2016). Similarly, cows spent more time smelling odors collected from students after an exam than
168 after a normal class (Destrez et al. 2021). Lastly, dogs were shown to be more likely to stop an
169 ongoing meal after hearing human voices expressing anger rather than happiness (Siniscalchi et
170 al. 2018a).

171 Other studies have explored the preference that domestic mammals can have for one human
172 emotion over another. In cats, the subjects spent more time in contact with their owner expressing
173 happiness than anger and more positive behaviors were observed (Galvan and Vonk 2016). Goats
174 preferred to initially interact with happy faces when left to move freely in an arena around which
175 were hung pictures of an unfamiliar human expressing happiness or anger (Nawroth et al. 2018).

176 Whether domestic mammals have a multimodal mental representation of human emotions has
177 also been explored in cross-modal paradigms. When simultaneously presented with pictures of two
178 different human emotions (e.g., happiness and anger) and a vocalization corresponding to one of
179 the emotions, dogs, cats and horses looked longer at one picture than the other, showing that they
180 can match vocal and visual cues of human emotions. Dogs and cats looked longer at the picture
181 that was congruent with the sound, while horses looked longer at the incongruent one (dogs:
182 Albuquerque et al. 2016; cats: Quaranta et al. 2020; horses: Nakamura et al. 2018; Trösch et al.
183 2019a). Further studies are necessary to understand whether these divergences depend on the
184 species or on the experimental conditions (such as familiarity and emotional content of the stimuli).

185 Interestingly, the species that have been examined also showed a brain hemisphere
186 specialization associated with our emotions: when perceiving emotions, horses, dogs and goats
187 tend to preferentially use either their right or left ear, eye or nostril, depending on its valence (Smith
188 et al. 2016; Siniscalchi et al. 2016, 2018a, c). However, this is not consistent for an emotion across
189 modalities and species; for example, a left hemisphere bias was observed with happy faces in
190 horses and goats and happy vocalizations in dogs, but happy faces were associated with a right
191 hemisphere bias in dogs (Smith et al. 2016; Nawroth et al. 2018; Siniscalchi et al. 2018c, a). In
192 domestic mammals, as well as in humans, different models have been proposed to describe the
193 hemispheric lateralization of emotion perception. The most recent results suggest that the right
194 hemisphere dominates for the perception of negative or arousing emotions while the left
195 hemisphere is favored when perceiving positive or familiar emotions (Gainotti 2019; Siniscalchi et

196 al. 2021). Therefore, the differences in hemisphere biases among domestic mammals when
197 perceiving human emotions could be explained by a discordance, for some animals, between the
198 valence of the emotion expressed and the way it is perceived (for example dogs could perceive
199 happy human faces negatively; Siniscalchi et al. 2021).

200 In addition to discriminating our emotions, dogs, cats and horses demonstrate behavioral and
201 physiological reactions when confronted with them. Dogs approached a human more if the latter
202 was pretending to cry rather than talking or humming (Custance and Mayer 2012). The sight of an
203 angry human picture compared with a happy picture led dogs to lick their mouth more (Albuquerque
204 et al. 2018) and it led horses to move less and look longer at the subject of the photograph when
205 encountered at a later time (Proops et al. 2018). Angry faces also caused horses' hearts to beat
206 faster (Smith et al. 2016), while in dogs, the difference between subjects' baseline and test heart
207 rates differed for each of the six human emotions they were shown in pictures (Siniscalchi et al.
208 2018c). Auditory cues have also been shown to elicit different behavioral and physiological
209 responses: when hearing a vocal expression of anger rather than happiness, horses oriented both
210 their ears forward for longer (Smith et al. 2018) and held a vigilant posture with their heart rates
211 attaining a higher maximum (Trösch et al. 2019a), while cats showed more stress-related behaviors
212 (Quaranta et al. 2020). In an experiment, dogs' heart rates also increased more compared to their
213 baseline, and they were more reactive and resumed an interrupted meal less frequently when they
214 heard anger rather than happiness, fear or sadness (Siniscalchi et al. 2018a); while in another
215 experiment they were more reactive when hearing a human crying rather than laughing (Huber et
216 al. 2017).

217 On the whole, when seeing fear or hearing anger expressed by humans, these animal reactions
218 resembled those observed when they experience negative emotions themselves (e.g., vigilant
219 attitude and elevated heart rate; Lansade et al. 2008), suggesting that the animals could be affected
220 by our emotional states. This would correspond in cognitive terms to emotional contagion, a
221 primitive form of empathy (defined as the capacity to be affected by and share the emotions of
222 other individuals; Preston and de Waal 2002); however, these reactions could also be the result of
223 the animals being afraid of the sound they heard or the expression they saw.

224 To summarize, the perception of human emotions has been explored mostly in dogs, cats and

225 horses, and it has been shown that these species differentiate our emotions, recognize them cross-
226 modally and react to them accordingly. The experiments have generally focused on a few emotions
227 (mostly happiness or joy compared to anger or fear), and these promising results encourage us to
228 test more kinds of emotions (e.g., sadness, anger, disgust, and surprise; Siniscalchi et al. 2018c,
229 a; Baba et al. 2019) and to implement these protocols in other species. Moreover, many
230 experiments used pictures of human emotional faces, but it seems that for dogs, our bodies could
231 be more important than our faces when perceiving our emotions (Correia-Caeiro et al. 2021), so
232 that in future experiments exploring the perception of human emotions by domestic mammals it
233 might be interesting to use pictures or films of whole bodies.

234

235 **Understanding humans' attentional state and goals**

236 In addition to perceiving individual humans and their emotions, we can wonder whether domestic
237 mammals can detect when we are attentive to them or to objects and whether they can understand
238 the goals of our actions when we interact with them.

239 The discrimination of human attentional states was explored in young pigs, which tended to
240 choose an attentive human over an inattentive human (at least when the pigs chose non-
241 impulsively; Nawroth et al. 2013). In addition, several species have been shown not only to
242 discriminate human attentional states but also to modify their behavior based on those states.
243 When a human experimenter was attentive rather than inattentive to the animals, cats spent more
244 time with the experimenter (Vitale and Udell 2019; Humphrey et al. 2020), and dogs modified their
245 facial expressions (Kaminski et al. 2017), displayed more attention-seeking behaviors (such as
246 whining or whimpering, Ohkita et al. 2016) and were more likely to play together (Mehrkam and
247 Wynne 2021). In similar situations, dogs and goats preferred to beg from the attentive experimenter
248 (Gácsi et al. 2004; Nawroth and McElligott 2017), dogs and horses were more likely to obey orders
249 or directions from that experimenter (dogs: Call et al. 2003; Bräuer et al. 2004; Virányi et al. 2004;
250 Schwab and Huber 2006; Kaminski et al. 2012, horses: Sankey et al. 2011), and sheep increased
251 their level of activity and glancing behavior (Beausoleil et al. 2006). Furthermore, horses seem able
252 to interpret humans' attentional states toward objects: they begged for food from a human who had

253 been facing a bucket when it was being filled for a different amount of time than one who had their
254 back to this process (Ringhofer and Yamamoto 2017; Trösch et al. 2019b).

255 Eye contact appears to be a determining cue to perceive humans' attentional state. For several
256 species, the animals' aforementioned behaviors differed when the experimenter was looking at the
257 animals in the eyes rather than looking away (sheep: Beausoleil et al. 2006; horses: Sankey et al.
258 2011; dogs: Kaminski et al. 2012; cats: Humphrey et al. 2020). However, it can be concluded only
259 that body and possibly head orientation were used for that purpose in goats, based on existing
260 studies (Nawroth and McElligott 2017).

261 In addition to reacting to our attentional state, we can wonder whether domestic mammals
262 understand the goal of our gestures toward them. In a study with goats, subjects showed more
263 anticipatory behaviors in front of an inaccessible reward when the human was attentive rather than
264 inattentive to them, suggesting that they may be capable of detecting the intention of the
265 experimenter to give them the reward or not (Nawroth et al. 2016c). To investigate further this issue,
266 the "unwilling versus unable" paradigm, classically used in primates (Call et al. 2004), was used in
267 horses: subjects were presented with an inaccessible reward, either because the experimenter
268 deliberately put it away or because the experimenter could not give it to the horse due to a physical
269 barrier or a fake show of clumsiness. The subjects showed significantly more interest when the
270 experimenter was willing but unable to give the treat than when he was unwilling to do so. Thus,
271 horses seem to interpret human gestures as goal-directed (Trösch et al. 2020a).

272 The ability of domestic mammals to perceive our goals can also be explored by observing their
273 responsiveness to ostensive cues. These are signals given specifically to attract the animals'
274 attention and initiate an interaction and can therefore help to determine whether the animals
275 perceive that we are speaking to and interacting with them. One example is, making calling noises
276 and calling their name, ostensive cues that cats seem sensitive to: subjects followed an
277 experimenter's gaze sooner and were more influenced by an experimenter producing such cues
278 rather than when they made other noises or read a poem (Pongrácz et al. 2019; Pongrácz and
279 Onofer 2020). Similarly, dogs were influenced by an experimenter calling their name and making
280 eye contact (Kis et al. 2012). Another example of ostensive cues is pet-directed speech, a type of
281 speech used specifically by humans to talk to animals, which is similar to the speech used to talk

282 to babies. Dogs and horses seem sensitive to this type of speech. Dogs were more attentive when
283 hearing humans talking in pet-directed speech (Jeannin et al. 2017) and they spent more time close
284 to a speaker broadcasting this type of speech than one broadcasting standard vocalization (called
285 adult-directed speech; Benjamin and Slocombe 2018). Horses performed better in a pointing task
286 and were more relaxed during grooming when the experimenter used pet-directed speech than
287 adult-directed speech (Lansade et al. 2021). However, these ostensive cues could also simply work
288 by attracting the animals' attention, without them being conscious that we are trying to communicate
289 with them intentionally.

290 Overall, sensitivity to humans' attentional states has been revealed in most of the species of
291 interest (with the exception of cattle and ferrets to date), and the animals' understanding of our
292 goals has been indirectly reported in dogs and cats (ostensive cues) and more directly reported in
293 horses ("unwilling vs unable" protocol; Trösch et al. 2020a).

294

295 **Referential communication with humans**

296 Referential communication is the exchange of referential signals that provide information about
297 environmental events (Evans 1997). For it to happen between humans and animals, the two parties
298 need to be able to give and receive information to and from each other.

299 **Perceiving human signals**

300 Many studies have focused on the ability of domestic mammals to understand human pointing
301 gestures, in which a human indicates the location of a food reward that the animal can obtain (for
302 reviews see Miklósi and Soproni 2006; Krause et al. 2018). The basic movement used is stretching
303 an arm at approximately 45° from the body, and pointing a finger. These gestures have been
304 investigated in dogs, cats, horses, ferrets, pigs and goats, showing that each species follows them
305 to various degrees (dogs and cats: Miklósi et al. 2005; ferrets: Hernádi et al. 2012; goats: Nawroth
306 et al. 2020; pigs: Nawroth et al. 2014), although in horses, the results have been more inconsistent
307 (Maros et al. 2008; Proops et al. 2010; Lansade et al. 2021). Dogs seem to be the most flexible
308 species. They can follow a cross pointing cue (right arm pointing to the left for example; Soproni et
309 al. 2002; Miklósi et al. 2005), which goats can also follow (Nawroth et al. 2020). Asymmetric pointing

310 cues (with the experimenter closer to the wrong choice) were also effective with dogs but not goats
311 or pigs, which raises the question of whether these last two species use the pointing cues as local
312 enhancement (see below) rather than referential cues (Nawroth et al. 2014, 2020). Other body
313 parts have also been tested in some species: dogs, cats and pigs were shown to follow head
314 orientation (dogs: Ittyerah and Gaunet 2009; cats: Pongrácz et al. 2019; pigs: Nawroth et al. 2014).
315 Body orientation was followed by pigs (Nawroth et al. 2014) but not horses (Proops et al. 2010),
316 and dogs could also follow a pointed leg or a bow (Udell et al. 2008; Lakatos et al. 2009). Dogs are
317 also the species for which most studies have been published, with experiments exploring the
318 influence of social, emotional and other types of factors on this capacity (for literature review, see
319 Krause et al. 2018). For example they were shown to modulate their answer to pointing gestures
320 in accordance with the reliability of a pointer (based on a previous experience with this person;
321 Pelgrim et al. 2021).

322 Other referential cues can also be taught to dogs. They can use vocal referential cues and learn
323 to fetch a particular object after learning the word associated with it (Kaminski et al. 2004). However,
324 when receiving contradictory information, for example, a vocal order to fetch one of two objects
325 while pointing to the other object, the majority of dogs preferred to follow the gestures, suggesting
326 that they focused more on visual than acoustic information when interacting with humans (D’Aniello
327 et al. 2016). Another type of referential cue that can be used with dogs is replicas: in an experiment,
328 dogs successfully fetched different objects that were presented to them as life-sized or miniature
329 replicas (Kaminski et al. 2009).

330 **Sending signals to humans**

331 Several studies have shown that certain species produce behaviors in the presence of humans
332 that could be interpreted as communication signals intended for us. Horses display very specific
333 facial expressions in response to being groomed by a human (Lansade et al. 2018), although
334 further research is needed to determine whether these expressions are intended for humans. Cats
335 have been shown to produce different purrs in different contexts that include humans (the acoustic
336 spectrum of purrs used in soliciting contexts has different characteristics than those used in non-
337 soliciting contexts; McComb et al. 2009). In dogs and horses, some behaviors are modulated by
338 humans’ mental states. For example, dogs modify their facial expression according to our

339 attentional state (Kaminski et al. 2012), and display different gestural and vocal signals based on
340 our response (Siniscalchi et al. 2018b). Similarly, horses seem to communicate with humans as
341 they solicited (with touches from the muzzle) and looked at an experimenter differently depending
342 on whether the experimenter had witnessed the hiding process of an inaccessible food reward
343 (Ringhofer and Yamamoto 2017; Trösch et al. 2019b). Moreover, studies focusing on referential
344 communicative behaviors from animals to humans have shown that horses, dogs and goats use
345 gaze alternation when presented with an inaccessible food reward: they looked back and forth
346 between the reward and the experimenter, which is a behavior that could be interpreted as an
347 attempt to attract the human's attention to the reward. The animals modulated this behavior based
348 on the experimenter's attentional state, which suggests that humans were the target of the behavior
349 (dogs: Miklósi et al. 2005; horses: Malavasi and Huber 2016; goats: Nawroth et al. 2016b). In a
350 comparative study, cats were shown to produce fewer gaze alternations than dogs (Miklósi et al.
351 2005), but changes in this behavior based on human attentional states remain unexplored. Pigs
352 also seem to produce human-oriented behaviours, although not more in the presence of an
353 inaccessible food reward than an accessible one (Gerencsér et al. 2019; Pérez Fraga et al. 2021).
354 It is a valid possibility that all these signals are expressed intentionally with the aim of
355 communicating with humans, but to reach such conclusions, several more criteria need to be
356 validated as defined by Townsend et al. (2017). For example, it should be demonstrated that the
357 animals monitor their audience and adapt their behavior to its reactions. These criteria have been
358 validated in dogs, showing that they use various gestures like gaze alternations, but also other
359 movements, as referential signals. These gestures seem to be used particularly to request desired
360 actions or objects from humans (Kaminski et al. 2011; Worsley and O'Hara 2018).

361

362 In essence, the understanding of referential communication signals (mostly pointing) from
363 humans has been revealed in dogs, cats, ferrets, goats, pigs and, in certain contexts, horses, while
364 the production of such signals (or at least behaviors regulated by human attentional states) has
365 been observed in dogs, cats, horses and goats, leaving the examination of these abilities in cattle
366 and sheep open for future research.

367

368 **Social Learning from humans**

369 Social learning takes place when an individual uses information from another individual to learn
370 something (Heyes 1994). This can happen in an interspecific manner, between an animal and a
371 human, and can take different forms.

372 **Local enhancement**

373 A few studies have shown that the attention of dogs, horses or goats is influenced by spatial cues
374 provided by a human, a phenomenon called local enhancement (Thorpe 1956). For dogs, when a
375 toy was hidden in front of them in one of five hiding places, the places where they looked for the
376 toy depended on the movements the experimenter had made around the hiding places before and
377 after the baiting, which showed that the animals' attention, indicated by their searching, had been
378 influenced by the spatial cues provided by the human (Péter et al. 2016). Dogs were also more
379 likely to fetch a ball from a box by touching the handle than the other parts of the box if they had
380 seen their owner use the handle (Kubinyi et al. 2003). Regarding horses, when offered the
381 possibility to choose one of three buckets in which food had been placed in front of them, their
382 behavior was also influenced by the position of the experimenter, suggesting that they were using
383 local enhancement in this task (Krueger et al. 2011). Moreover, in several experiments, horses
384 which had seen a human activate a switch to obtain food hidden in a box performed better in
385 reproducing this action than a group that had not seen this demonstration (Schuetz et al. 2017;
386 Bernauer et al. 2020). However, in another study exploring horses' ability to reproduce a human's
387 movements to obtain food, the animals which had seen the human make the right movements did
388 not perform better than those which had not (Rørvang et al. 2020). It is possible that these different
389 findings resulted from differences in experimental conditions. Thus, under certain conditions horses
390 and dogs seem able to use spatial information associated with humans to solve problems. In the
391 same way, the attention of dogs and goats seemed to be attracted by the movements of humans:
392 subjects moved around a detour apparatus and reached a bait more quickly if they had seen a
393 human taking the detour than if they had not (Pongrácz et al. 2001; Nawroth et al. 2016a), but this
394 was not the case for horses in a similar experiment (Burla et al. 2018).

395 **Demonstration**

396 Another form of social learning is the ability to reproduce a movement demonstrated by another
397 individual (Heyes 1994). In dogs and cats, demonstration has been studied in the context of the
398 “do as I do” order, whereby an animal learns to reproduce object-directed movements previously
399 performed by its owner (the reproduced movement having a similar function, e.g., a dog removes
400 a lid from a box with its mouth after the owner remove it with their hand). Dogs seem able to
401 reproduce familiar and novel actions in a very flexible manner (for example, the demonstration and
402 reproduction could be separated by several minutes and by some distractions and they could be
403 conducted in different places; Topál et al. 2006; Fugazza and Miklósi 2014). A recent experiment
404 suggests that cats could also be able to reproduce the movements of a human demonstrator
405 (Fugazza et al. 2020). However, more experiments need to be conducted to assess further the
406 ability of these species to truly reproduce our movements and to differentiate it from local
407 enhancement (Rørvang et al. 2018).

408 **Social referencing**

409 Social referencing is defined as the ability to receive and use another individual’s interpretation
410 of a situation to form one’s own understanding of that situation (Feinman 1982). In this way, dogs,
411 cats and horses have been shown to adapt their behavior toward a novel object or person (for
412 example, changing the time spent close to it) based on the way they see a familiar human acting
413 toward it (for example, whether or not they touch it) or to the intonation of their voice or the emotions
414 displayed in its presence (dog: Merola et al. 2012a, b; Duranton et al. 2016 ; cat: Merola et al. 2015;
415 horse: Schrimpf et al. 2020).

416 Certain species have also been shown to perform social referencing of humans after observing
417 third party interactions: horses and dogs were shown (at least in some contexts) to behave
418 differently with an experimenter depending on the way this experimenter had interacted with a third
419 party (horses: Trösch et al. 2019b; dogs: Chijiwa et al. 2015; Anderson et al. 2017; Silver et al.
420 2021), which showed that the animals could attribute a reputation to humans. Conversely, in cats
421 no such differences were noted in an experiment similar to that used with dogs (Chijiwa et al.
422 2021).

423 Overall, the ability to learn socially from humans by local enhancement, social referencing and
424 possibly demonstration has been shown in dogs, cats, horses and goats, while to our knowledge,

425 it remains unexplored in cattle, sheep, ferrets and pigs. In the latter, the ability to follow an informed
426 conspecific to find hidden food has been demonstrated (Held et al. 2000), encouraging us to
427 explore their ability to use information given by humans in similar situations.

428

429 **Conclusion**

430 In summary, various interspecific sociocognitive abilities toward humans have recently been
431 explored in some domestic mammals, namely, dogs, cats, ferrets, horses, cattle, sheep, goats and
432 pigs (Fig. 1). However, at present, we are far from knowing all the cognitive abilities in question in
433 all the species mentioned within this review, and some species have been studied far less than
434 others (for example, cattle or ferrets compared to dogs; see Table 2).

435 When reviewing this literature, no group or tendency regarding the sociocognitive abilities of
436 domestic mammals toward humans could be identified (Table 2). In contrast, the results from
437 existing studies on livestock species (such as sheep) are similar to those from studies on species
438 that typically develop individual relationships with humans, such as horses (compare Knolle et al.
439 2017 to Lansade et al. 2020a for an example of face recognition in sheep and horses). This
440 suggests that the abilities of these species could differ less than assumed, which encourages
441 further investigations to enrich our current knowledge on all species and to help avoid the
442 mistreatment of animals that can result from underestimating their mental abilities (Nawroth et al.
443 2019). Moreover, certain cognitive abilities such as the perception of intentions, which used to be
444 seen as specific to humans, are now being described in domestic mammals such as horses (Trösch
445 et al. 2020a), and in the future these explorations could also be conducted in other farm animals.
446 In addition, although this review was restricted to domestic mammals, it should be noted that such
447 cognitive capacities have now also been described in domestic birds (for example McMillan et al.
448 2015).

449 Further research is also needed to investigate sociocognitive capacities toward humans in some
450 domestic mammal species which have not been investigated in this domain (e.g., donkeys and
451 rabbits). Wild species living close to humans as pets (e.g., sugar gliders) or on farms (e.g., deer)
452 could also benefit from studies to determine how much they understand humans and how they can

453 interact with them. Moreover, exploring the sociocognitive skills of these species (living close to
454 humans but not artificially selected) could help to understand the respective roles of environmental
455 factors and genetic changes in the development of these cognitive abilities toward humans (for
456 reviews on dogs, see Hare et al. 2002 and Udell et al. 2010).

457 More broadly, reviewing the literature on sociocognitive skills of wild mammals toward humans
458 could help compare domestic and non-domesticated species, and launch a reflection on the causal
459 links between domestication and the sociocognitive skills of mammals toward humans. Indeed,
460 domestication is thought to be the reason for high sociocognitive skills at least in dogs (McKinley
461 and Sambrook 2000; Hare et al. 2002). However, it is also possible that, on the contrary, the wild
462 species that domestic mammals originate from were chosen for their particular sociocognitive skills
463 toward humans. Finally, it is also possible that these high sociocognitive skills toward humans are
464 not a prerogative of domestic animals and are also present in some wild species but they have not
465 been investigated because of the scarcity of their interactions with us. Similarly, for each species
466 reviewing their intraspecific sociocognitive skills and comparing them to those toward humans could
467 help us understand the specificities of their relationship with humans and to determine what the
468 focus of future research should be (for example, in a given species, a sociocognitive skill that is
469 present toward conspecifics is more likely to be present toward humans than one that is not present
470 toward conspecifics).

471 The present review did not discuss the protocols of the studies, but it should be noted that in a
472 number of experiments, humans were present to restrain the animal or to serve as a stimulus, and
473 thus subtle unintentional cues could have been given, which would constitute a bias (also known
474 as the 'clever Hans' effect). Given the sensitivity of these species to human cues, it is necessary to
475 develop protocols that limit bias from experimenter cues as much as possible. For instance, this
476 can be achieved by insuring that handlers are blind to the experimental condition, as in D'Aniello
477 et al. (2018) or Proops et al. (2018), or by using innovative technologies, as in Lansade et al.
478 (2020a), where horses were interacting only with a touchscreen that was automatically controlled
479 by a computer. Indeed, overestimating (as well as underestimating) a species' cognitive abilities
480 can have consequences not only in terms of scientific conclusions but also in terms of welfare
481 (Rørvang et al. 2018).

482 Overall, the study of the sociocognitive abilities of domestic mammals toward humans seems to
483 be in its early stages, and more species need to be thoroughly examined to reach a better and
484 more comprehensive understanding of the human-animal relationship.

485

486 **Declarations:**

487 **Funding:** No funding was received to assist with the preparation of this manuscript.

488 **Conflicts of interest:** the authors have no conflicts of interest to declare that are relevant to the
489 content of this article.

490 **Author contributions:** LL had the idea for this review, PJ performed the literature search and
491 drafted the work and LL revised it.

492 **Availability of data and material/Code availability/Ethics approval/Consent to**
493 **participate/Consent for publication:** Not applicable

494

495 **References**

496 Adachi I, Kuwahata H, Fujita K (2007) Dogs recall their owner's face upon hearing the owner's voice.

497 *Anim Cogn* 10:17–21. <https://doi.org/10.1007/s10071-006-0025-8>

498 Albuquerque N, Guo K, Wilkinson A, et al (2016) Dogs recognize dog and human emotions. *Biol Lett*

499 12:20150883. <https://doi.org/10.1098/rsbl.2015.0883>

500 Albuquerque N, Guo K, Wilkinson A, et al (2018) Mouth-licking by dogs as a response to emotional

501 stimuli. *Behav Processes* 146:42–45. <https://doi.org/10.1016/j.beproc.2017.11.006>

502 Anderson JR, Bucher B, Chijiwa H, et al (2017) Third-party social evaluations of humans by monkeys

503 and dogs. *Neurosci. Biobehav. Rev.* 82:95–109

504 Baba C, Kawai M, Takimoto-Inose A (2019) Are horses (*Equus caballus*) sensitive to human emotional

505 cues? *Animals* 9:630. <https://doi.org/10.3390/ani9090630>

506 Beausoleil NJ, Stafford KJ, Mellor DJ (2006) Does direct human eye contact function as a warning cue

507 for domestic sheep (*Ovis aries*)? *J Comp Psychol* 120:269–279. <https://doi.org/10.1037/0735->

508 7036.120.3.269

509 Benjamin A, Slocombe K (2018) 'Who's a good boy?!' Dogs prefer naturalistic dog-directed speech.
510 Anim Cogn 21:353–364. <https://doi.org/10.1007/s10071-018-1172-4>

511 Bernauer K, Kollross H, Schuetz A, et al (2020) How do horses (*Equus caballus*) learn from observing
512 human action? Anim Cogn 23:. <https://doi.org/10.1007/s10071-019-01310-0>

513 Bräuer J, Call J, Tomasello M (2004) Visual perspective taking in dogs (*Canis familiaris*) in the
514 presence of barriers. Appl Anim Behav Sci 88:299–317.
515 <https://doi.org/10.1016/j.applanim.2004.03.004>

516 Bulloch MJ, Tynes V V. (2010) Ferrets. In: Behaviour of Exotic Pets, Wiley-Blac. pp 59–68

517 Burla JB, Siegwart J, Nawroth C (2018) Human demonstration does not facilitate the performance of
518 horses (*Equus caballus*) in a spatial problem-solving task. Animals 8:96.
519 <https://doi.org/10.3390/ani8060096>

520 Call J, Bräuer J, Kaminski J, Tomasello M (2003) Domestic Dogs (*Canis familiaris*) Are Sensitive to
521 the Attentional State of Humans. <https://doi.org/10.1037/0735-7036.117.3.257>

522 Call J, Hare B, Carpenter M, Tomasello M (2004) "Unwilling" versus "unable": chimpanzees'
523 understanding of human intentional action. Dev Sci 7:488–498. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2004.00368.x)
524 [7687.2004.00368.x](https://doi.org/10.1111/j.1467-7687.2004.00368.x)

525 Chijiwa H, Kuroshima H, Hori Y, et al (2015) Dogs avoid people who behave negatively to their owner:
526 Third-party affective evaluation. Anim Behav 106:123–127.
527 <https://doi.org/10.1016/j.anbehav.2015.05.018>

528 Chijiwa H, Takagi S, Arahori M, et al (2021) Cats (*Felis catus*) Show No Avoidance of People Who
529 Behave Negatively to Their Owner. Anim Behav Cogn 8:23–35.
530 <https://doi.org/10.26451/abc.08.01.03.2021>

531 Correia-Caeiro C, Guo K, Mills D (2021) Bodily emotional expressions are a primary source of
532 information for dogs, but not for humans. Anim Cogn 3:267–279. [https://doi.org/10.1007/s10071-](https://doi.org/10.1007/s10071-021-01471-x)
533 [021-01471-x](https://doi.org/10.1007/s10071-021-01471-x)

534 Coulon M, Deputte BL, Heyman Y, Baudoin C (2009) Individual recognition in domestic cattle (*Bos*
535 *taurus*): Evidence from 2D-images of heads from different breeds. PLoS One 4:e4441.
536 <https://doi.org/10.1371/journal.pone.0004441>

537 Custance D, Mayer J (2012) Empathic-like responding by domestic dogs (*Canis familiaris*) to distress

538 in humans: An exploratory study. *Anim Cogn* 15:851–859. <https://doi.org/10.1007/s10071-012->
539 0510-1

540 D’Aniello B, Scandurra A, Alterisio A, et al (2016) The importance of gestural communication: a study
541 of human–dog communication using incongruent information. *Anim Cogn* 19:1231–1235.
542 <https://doi.org/10.1007/s10071-016-1010-5>

543 D’Aniello B, Semin GR, Alterisio A, et al (2018) Interspecies transmission of emotional information via
544 chemosignals: from humans to dogs (*Canis lupus familiaris*). *Anim Cogn* 21:67–78.
545 <https://doi.org/10.1007/s10071-017-1139-x>

546 d’Ingeo S, Quaranta A, Siniscalchi M, et al (2019) Horses associate individual human voices with the
547 valence of past interactions: a behavioural and electrophysiological study. *Sci Rep* 9:11568.
548 <https://doi.org/10.1038/s41598-019-47960-5>

549 De Waal FBM (2008) Putting the altruism back into altruism: The evolution of empathy. *Annu Rev*
550 *Psychol* 59:279–300. <https://doi.org/10.1146/annurev.psych.59.103006.093625>

551 Destrez A, Costes-Thiré M, Viart AS, et al (2021) Male mice and cows perceive human emotional
552 chemosignals: a preliminary study. *Anim Cogn* 1–10. <https://doi.org/10.1007/s10071-021-01511->
553 6

554 Dierendonck MC vo. (2005) The importance of social relationships in horses. Utrecht University

555 Duranton C, Bedossa T, Gaunet F (2016) When facing an unfamiliar person, pet dogs present social
556 referencing based on their owners’ direction of movement alone. *Anim Behav* 113:147–156.
557 <https://doi.org/10.1016/j.anbehav.2016.01.004>

558 Eatherington CJ, Mongillo P, Lööke M, Marinelli L (2020) Dogs (*Canis familiaris*) recognise our faces
559 in photographs: implications for existing and future research. *Anim Cogn* 23:711–719.
560 <https://doi.org/10.1007/s10071-020-01382-3>

561 Evans CS (1997) Referential Signals. Springer, Boston, MA, pp 99–143

562 Feinman S (1982) Social Referencing in Infancy. *Merrill Palmer Q* 28:445–470

563 Fugazza C, Miklósi Á (2014) Deferred imitation and declarative memory in domestic dogs. *Anim Cogn*
564 17:237–247. <https://doi.org/10.1007/s10071-013-0656-5>

565 Fugazza C, Sommese A, Pogány Á, Miklósi Á (2020) Did we find a copycat? Do as I Do in a domestic
566 cat (*Felis catus*). *Anim Cogn* 1:121–131. <https://doi.org/10.1007/s10071-020-01428-6>

567 Gácsi M, Miklód Á, Varga O, et al (2004) Are readers of our face readers of our minds? Dogs (*Canis*
568 *familiaris*) show situation-dependent recognition of human's attention. *Anim Cogn* 24:144–153.
569 <https://doi.org/10.1007/s10071-003-0205-8>

570 Gainotti G (2019) A historical review of investigations on laterality of emotions in the human brain. *J*
571 *Hist Neurosci* 28:23–41. <https://doi.org/10.1080/0964704X.2018.1524683>

572 Galibert F, Quignon P, Hitte C, André C (2011) Toward understanding dog evolutionary and
573 domestication history. *Comptes Rendus - Biol* 334:190–196.
574 <https://doi.org/10.1016/j.crvi.2010.12.011>

575 Galvan M, Vonk J (2016) Man's other best friend: domestic cats (*F. silvestris catus*) and their
576 discrimination of human emotion cues. *Anim Cogn* 19:193–205. [https://doi.org/10.1007/s10071-](https://doi.org/10.1007/s10071-015-0927-4)
577 [015-0927-4](https://doi.org/10.1007/s10071-015-0927-4)

578 Gerencsér L, Pérez Fraga P, Lovas M, et al (2019) Comparing interspecific socio-communicative skills
579 of socialized juvenile dogs and miniature pigs. *Anim Cogn* 22:917–929.
580 <https://doi.org/10.1007/S10071-019-01284-Z>

581 Gieling ET, Musschenga MA, Nordquist RE, van der Staay FJ (2012) Juvenile pigs use simple
582 geometric 2D shapes but not portrait photographs of conspecifics as visual discriminative stimuli.
583 *Appl Anim Behav Sci* 142:142–153. <https://doi.org/10.1016/j.applanim.2012.10.018>

584 Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs.
585 *Science (80-)* 298:1634–1636. <https://doi.org/10.1126/science.1072702>

586 Held S, Mendl M, Devereux C, Byrne RW (2000) Social tactics of pigs in a competitive foraging task:
587 The “informed forager” paradigm. *Anim Behav* 59:569–576.
588 <https://doi.org/10.1006/anbe.1999.1322>

589 Hernádi A, Kis A, Turcsán B, Topál J (2012) Man's underground best friend: Domestic ferrets, unlike
590 the wild forms, show evidence of dog-like social-cognitive skills. *PLoS One* 7:e43267.
591 <https://doi.org/10.1371/journal.pone.0043267>

592 Heyes CM (1994) Social learning in animals: Categories and mechanisms. *Biol Rev Camb Philos Soc*
593 69:207–231. <https://doi.org/10.1111/j.1469-185x.1994.tb01506.x>

594 Huber A, Barber ALA, Faragó T, et al (2017) Investigating emotional contagion in dogs (*Canis*
595 *familiaris*) to emotional sounds of humans and conspecifics. *Anim Cogn* 20:703–715.

596 <https://doi.org/10.1007/s10071-017-1092-8>

597 Huber L, Racca A, Scaf B, et al (2013) Discrimination of familiar human faces in dogs (*Canis*
598 *familiaris*). *Learn Motiv* 44:258–269. <https://doi.org/10.1016/j.lmot.2013.04.005>

599 Humphrey T, Proops L, Forman J, et al (2020) The role of cat eye narrowing movements in cat–
600 human communication. *Sci Rep* 10:16503. <https://doi.org/10.1038/s41598-020-73426-0>

601 Ittyerah M, Gaunet F (2009) The response of guide dogs and pet dogs (*canis familiaris*) to cues of
602 human referential communication (pointing and gaze). *Anim Cogn* 12:257–265.
603 <https://doi.org/10.1007/s10071-008-0188-6>

604 Jeannin S, Gilbert C, Amy M, Leboucher G (2017) Pet-directed speech draws adult dogs' attention
605 more efficiently than Adult-directed speech. *Sci Rep* 7:4980. [https://doi.org/10.1038/s41598-017-](https://doi.org/10.1038/s41598-017-04671-z)
606 [04671-z](https://doi.org/10.1038/s41598-017-04671-z)

607 Kaminski J, Call J, Fischer J (2004) Word learning in a domestic dog: Evidence for “fast mapping.”
608 *Science* (80-) 304:1682–1683. <https://doi.org/10.1126/science.1097859>

609 Kaminski J, Hynds J, Morris P, Waller BM (2017) Human attention affects facial expressions in
610 domestic dogs. *Sci Rep* 7:12914. <https://doi.org/10.1038/s41598-017-12781-x>

611 Kaminski J, Neumann M, Bräuer J, et al (2011) Dogs, *Canis familiaris*, communicate with humans to
612 request but not to inform. *Anim Behav* 82:651–658.
613 <https://doi.org/10.1016/j.anbehav.2011.06.015>

614 Kaminski J, Schulz L, Tomasello M (2012) How dogs know when communication is intended for them.
615 *Dev Sci* 15:222–232. <https://doi.org/10.1111/j.1467-7687.2011.01120.x>

616 Kaminski J, Tempelmann S, Call J, Tomasello M (2009) Domestic dogs comprehend human
617 communication with iconic signs. *Dev Sci* 12:831–837. [https://doi.org/10.1111/J.1467-](https://doi.org/10.1111/J.1467-7687.2009.00815.X)
618 [7687.2009.00815.X](https://doi.org/10.1111/J.1467-7687.2009.00815.X)

619 Kendrick KM, Da Costa AP, Leigh AE, et al (2001) Sheep don't forget a face. *Nature* 414:165–166.
620 <https://doi.org/10.1038/35102669>

621 Kis A, Topál J, Gácsi M, et al (2012) Does the A-not-B error in adult pet dogs indicate sensitivity to
622 human communication? *Anim Cogn* 15:737–743. <https://doi.org/10.1007/s10071-012-0481-2>

623 Knolle F, Goncalves RP, Jennifer Morton A (2017) Sheep recognize familiar and unfamiliar human
624 faces from two-dimensional images. *R Soc Open Sci* 4:171228.

625 <https://doi.org/10.1098/rsos.171228>

626 Koba Y, Tanida H (2001) How do miniature pigs discriminate between people? Discrimination between
627 people wearing coveralls of the same colour. *Appl Anim Behav Sci* 73:45–58.
628 [https://doi.org/10.1016/S0168-1591\(01\)00106-X](https://doi.org/10.1016/S0168-1591(01)00106-X)

629 Koba Y, Tanida H (1999) How do miniature pigs discriminate between people? The effect of
630 exchanging cues between a non-handler and their familiar handler on discrimination. *Appl Anim*
631 *Behav Sci* 61:239–252. [https://doi.org/10.1016/S0168-1591\(98\)00192-0](https://doi.org/10.1016/S0168-1591(98)00192-0)

632 Krause MA, Udell MAR, Leavens DA, Skopos L (2018) Animal pointing: Changing trends and findings
633 from 30 years of research. *J Comp Psychol* 132:326–345. <https://doi.org/10.1037/com0000125>

634 Krueger K, Flauger B, Farmer K, Maros K (2011) Horses (*Equus caballus*) use human local
635 enhancement cues and adjust to human attention. *Anim Cogn* 14:187–201.
636 <https://doi.org/10.1007/s10071-010-0352-7>

637 Kubinyi E, Miklósi Á, Topál J, Csányi V (2003) Dogs (*Canis familiaris*) Learn from their Owners via
638 Observation in a Manipulation Task. *J Comp Psychol* 117:156–165. [https://doi.org/10.1037/0735-](https://doi.org/10.1037/0735-7036.117.2.156)
639 [7036.117.2.156](https://doi.org/10.1037/0735-7036.117.2.156)

640 Lakatos G, Soproni K, Dóka A, Miklósi Á (2009) A comparative approach to dogs' (*Canis familiaris*)
641 and human infants' comprehension of various forms of pointing gestures. *Anim Cogn* 12:621–
642 631. <https://doi.org/10.1007/s10071-009-0221-4>

643 Lampe JF, Andre J (2012) Cross-modal recognition of human individuals in domestic horses (*Equus*
644 *caballus*). *Anim Cogn* 15:623–630. <https://doi.org/10.1007/s10071-012-0490-1>

645 Lansade L, Bouissou MF, Erhard HW (2008) Fearfulness in horses: A temperament trait stable across
646 time and situations. *Appl Anim Behav Sci* 115:182–200.
647 <https://doi.org/10.1016/j.applanim.2008.06.011>

648 Lansade L, Colson V, Parias C, et al (2020a) Female horses spontaneously identify a photograph of
649 their keeper, last seen six months previously. *Sci Rep* 10:6302. [https://doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-020-62940-w)
650 [020-62940-w](https://doi.org/10.1038/s41598-020-62940-w)

651 Lansade L, Colson V, Parias C, et al (2020b) Human Face Recognition in Horses: Data in Favor of a
652 Holistic Process. *Front Psychol* 11:2311. <https://doi.org/10.3389/fpsyg.2020.575808>

653 Lansade L, Nowak R, Lainé AL, et al (2018) Facial expression and oxytocin as possible markers of

654 positive emotions in horses. *Sci Rep* 8:14680. <https://doi.org/10.1038/s41598-018-32993-z>

655 Lansade L, Trösch M, Parias C, et al (2021) Horses are sensitive to baby talk : Pet-directed speech
656 facilitates communication with humans in a pointing task and during grooming. *Anim Cogn*.
657 <https://doi.org/10.1007/s10071-021-01487-3>

658 Malavasi R, Huber L (2016) Evidence of heterospecific referential communication from domestic
659 horses (*Equus caballus*) to humans. *Anim Cogn* 19:899–909. [https://doi.org/10.1007/s10071-](https://doi.org/10.1007/s10071-016-0987-0)
660 [016-0987-0](https://doi.org/10.1007/s10071-016-0987-0)

661 Maros K, Gácsi M, Miklósi Á (2008) Comprehension of human pointing gestures in horses (*Equus*
662 *caballus*). *Anim Cogn* 11:457–466. <https://doi.org/10.1007/s10071-008-0136-5>

663 McComb K, Taylor AM, Wilson C, Charlton BD (2009) The cry embedded within the purr. *Curr Biol*
664 19:R507–R508. <https://doi.org/10.1016/j.cub.2009.05.033>

665 McKinley J, Sambrook TD (2000) Use of human-given cues by domestic dogs (*Canis familiaris*) and
666 horses (*Equus caballus*). *Anim Cogn* 3:13–22. <https://doi.org/10.1007/s100710050046>

667 McMillan N, Hahn AH, Spetch ML, Sturdy CB (2015) Avian cognition: examples of sophisticated
668 capabilities in space and song. *Wiley Interdiscip Rev Cogn Sci* 6:285–297.
669 <https://doi.org/10.1002/wcs.1346>

670 Mehrkam LR, Wynne CDL (2021) Owner attention facilitates social play in dog–dog dyads (*Canis*
671 *lupus familiaris*): evidence for an interspecific audience effect. *Anim Cogn* 24:341–352.
672 <https://doi.org/10.1007/s10071-021-01481-9>

673 Merola I, Lazzaroni M, Marshall-Pescini S, Prato-Previde E (2015) Social referencing and cat–human
674 communication. *Anim Cogn* 18:639–648. <https://doi.org/10.1007/s10071-014-0832-2>

675 Merola I, Prato-Previde E, Marshall-Pescini S (2012a) Social referencing in dog-owner dyads? *Anim*
676 *Cogn* 15:175–185. <https://doi.org/10.1007/s10071-011-0443-0>

677 Merola I, Prato-Previde E, Marshall-Pescini S (2012b) Dogs’ Social Referencing towards Owners and
678 Strangers. *PLoS One* 7:e47653. <https://doi.org/10.1371/journal.pone.0047653>

679 Miklósi Á, Pongrácz P, Lakatos G, et al (2005) A comparative study of the use of visual communicative
680 signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and
681 humans. *J Comp Psychol* 119:179–186. <https://doi.org/10.1037/0735-7036.119.2.179>

682 Miklósi Á, Soproni K (2006) A comparative analysis of animals’ understanding of the human pointing

683 gesture. *Anim Cogn* 9:81–93. <https://doi.org/10.1007/s10071-005-0008-1>

684 Mongillo P, Scandurra A, Kramer RSS, Marinelli L (2017) Recognition of human faces by dogs (*Canis*
685 *familiaris*) requires visibility of head contour. *Anim Cogn* 20:881–890.
686 <https://doi.org/10.1007/s10071-017-1108-4>

687 Munksgaard L, De Passillé AM, Rushen J, Ladewig J (1999) Dairy cows use of colour cues to
688 discriminate between people. *Appl Anim Behav Sci* 65:1–11. [https://doi.org/10.1016/S0168-](https://doi.org/10.1016/S0168-1591(99)00055-6)
689 [1591\(99\)00055-6](https://doi.org/10.1016/S0168-1591(99)00055-6)

690 Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from
691 blank expressions. *Anim Cogn* 14:525–533. <https://doi.org/10.1007/s10071-011-0386-5>

692 Nakamura K, Takimoto-Inose A, Hasegawa T (2018) Cross-modal perception of human emotion in
693 domestic horses (*Equus caballus*). *Sci Rep* 8:8660. <https://doi.org/10.1038/s41598-018-26892-6>

694 Nawroth C, Albuquerque N, Savalli C, et al (2018) Goats prefer positive human emotional facial
695 expressions. *R Soc Open Sci* 5:180491. <https://doi.org/10.1098/rsos.180491>

696 Nawroth C, Baciadonna L, McElligott AG (2016a) Goats learn socially from humans in a spatial
697 problem-solving task. *Anim Behav* 121:123–129. <https://doi.org/10.1016/j.anbehav.2016.09.004>

698 Nawroth C, Brett JM, McElligott AG (2016b) Goats display audience-dependent human-directed
699 gazing behaviour in a problem-solving task. *Biol Lett* 12:20160283.
700 <https://doi.org/10.1098/rsbl.2016.0283>

701 Nawroth C, Ebersbach M, von Borell E (2013) Are juvenile domestic pigs (*Sus scrofa domestica*)
702 sensitive to the attentive states of humans?-The impact of impulsivity on choice behaviour.
703 *Behav Processes* 96:53–58. <https://doi.org/10.1016/j.beproc.2013.03.002>

704 Nawroth C, Ebersbach M, von Borell E (2014) Juvenile domestic pigs (*Sus scrofa domestica*) use
705 human-given cues in an object choice task. *Anim Cogn* 17:701–713.
706 <https://doi.org/10.1007/s10071-013-0702-3>

707 Nawroth C, Langbein J, Coulon M, et al (2019) Farm animal cognition-linking behavior, welfare and
708 ethics. *Front Vet Sci* 6:24. <https://doi.org/10.3389/fvets.2019.00024>

709 Nawroth C, Martin ZM, McElligott AG (2020) Goats Follow Human Pointing Gestures in an Object
710 Choice Task. *Front Psychol* 11:1–6. <https://doi.org/10.3389/fpsyg.2020.00915>

711 Nawroth C, McElligott AG (2017) Human head orientation and eye visibility as indicators of attention

712 for goats (*Capra hircus*). PeerJ 5:e3073. <https://doi.org/10.7717/peerj.3073>

713 Nawroth C, von Borell E, Langbein J (2016c) 'Goats that stare at men'—revisited: do dwarf goats alter
714 their behaviour in response to eye visibility and head direction of a human? *Anim Cogn* 19:667–
715 672. <https://doi.org/10.1007/s10071-016-0957-6>

716 Ohkita M, Nagasawa M, Kazutaka M, Kikusui T (2016) Owners' direct gazes increase dogs' attention-
717 getting behaviors. *Behav Processes* 125:96–100.
718 <https://doi.org/10.1016/J.BEPROC.2016.02.013>

719 Pelgrim MH, Espinosa J, Tecwyn EC, et al (2021) What's the point? Domestic dogs' sensitivity to the
720 accuracy of human informants. *Anim Cogn* 24:281–297. [https://doi.org/10.1007/s10071-021-](https://doi.org/10.1007/s10071-021-01493-5)
721 [01493-5](https://doi.org/10.1007/s10071-021-01493-5)

722 Pérez Fraga P, Gerencsér L, Lovas M, et al (2021) Who turns to the human? Companion pigs' and
723 dogs' behaviour in the unsolvable task paradigm. *Anim Cogn* 24:33–40.
724 <https://doi.org/10.1007/s10071-020-01410-2>

725 Péter A, Topál J, Miklósi Á, Pongrácz P (2016) I saw where you have been-The topography of human
726 demonstration affects dogs' search patterns and perseverative errors. *Behav Processes* 125:51–
727 62. <https://doi.org/10.1016/j.beproc.2016.02.005>

728 Pinc L, Bartoš L, Reslová A, Kotrba R (2011) Dogs discriminate identical twins. *PLoS One* 6:4–7.
729 <https://doi.org/10.1371/journal.pone.0020704>

730 Pongrácz P, Miklósi Á, Kubinyi E, et al (2001) Social learning in dogs: The effect of a human
731 demonstrator on the performance of dogs in a detour task. *Anim Behav* 62:1109–1117.
732 <https://doi.org/10.1006/anbe.2001.1866>

733 Pongrácz P, Onofer DL (2020) Cats show an unexpected pattern of response to human ostensive
734 cues in a series of A-not-B error tests. *Anim Cogn* 23:681–689. [https://doi.org/10.1007/s10071-](https://doi.org/10.1007/s10071-020-01373-4)
735 [020-01373-4](https://doi.org/10.1007/s10071-020-01373-4)

736 Pongrácz P, Szapu JS, Faragó T (2019) Cats (*Felis silvestris catus*) read human gaze for referential
737 information. *Intelligence* 74:43–52. <https://doi.org/10.1016/j.intell.2018.11.001>

738 Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci* 25:1–
739 20. <https://doi.org/10.1017/S0140525X02000018>

740 Price EO (1984) Behavioral Aspects of Animal Domestication. *Q Rev Biol* 59:1–32.

741 <https://doi.org/10.1086/413673>

742 Proops L, Grounds K, Smith AV, McComb K (2018) Animals Remember Previous Facial Expressions
743 that Specific Humans Have Exhibited. *Curr Biol* 28:1428-1432.e4.
744 <https://doi.org/10.1016/j.cub.2018.03.035>

745 Proops L, McComb K (2012) Cross-modal individual recognition in domestic horses (*Equus caballus*)
746 extends to familiar humans. *Proc R Soc B Biol Sci* 279:3131–3138.
747 <https://doi.org/10.1098/rspb.2012.0626>

748 Proops L, Walton M, McComb K (2010) The use of human-given cues by domestic horses, *Equus*
749 *caballus*, during an object choice task. *Anim Behav* 79:1205–1209.
750 <https://doi.org/10.1016/j.anbehav.2010.02.015>

751 Quaranta A, D'Ingeo S, Amoruso R, Siniscalchi M (2020) Emotion recognition in cats. *Animals*
752 10:1107. <https://doi.org/10.3390/ani10071107>

753 Racca A, Amadei E, Ligout S, et al (2010) Discrimination of human and dog faces and inversion
754 responses in domestic dogs (*Canis familiaris*). *Anim Cogn* 13:525–533.
755 <https://doi.org/10.1007/s10071-009-0303-3>

756 Ringhofer M, Yamamoto S (2017) Domestic horses send signals to humans when they face with an
757 unsolvable task. *Anim Cogn* 20:397–405. <https://doi.org/10.1007/s10071-016-1056-4>

758 Rørvang MV, Nielsen TB, Christensen JW (2020) Horses failed to learn from humans by observation.
759 *Animals* 10:. <https://doi.org/10.3390/ani10020221>

760 Rørvang M V., Christensen JW, Ladewig J, McLean A (2018) Social learning in horses-fact or fiction?
761 *Front Vet Sci* 5:212. <https://doi.org/10.3389/fvets.2018.00212>

762 Rybarczyk P, Koba Y, Rushen J, et al (2001) Can cows discriminate people by their faces? *Appl Anim*
763 *Behav Sci* 74:175–189. [https://doi.org/10.1016/S0168-1591\(01\)00162-9](https://doi.org/10.1016/S0168-1591(01)00162-9)

764 Sabiniewicz A, Tarnowska K, Świątek R, et al (2020) Olfactory-based interspecific recognition of
765 human emotions: Horses (*Equus ferus caballus*) can recognize fear and happiness body odour
766 from humans (*Homo sapiens*). *Appl Anim Behav Sci* 230:105072.
767 <https://doi.org/10.1016/j.applanim.2020.105072>

768 Saito A, Shinozuka K (2013) Vocal recognition of owners by domestic cats (*Felis catus*). *Anim Cogn*
769 16:685–690. <https://doi.org/10.1007/s10071-013-0620-4>

770 Sankey C, Henry S, André N, et al (2011) Do horses have a concept of person? PLoS One 6:e18331.
771 <https://doi.org/10.1371/journal.pone.0018331>

772 Schrimpf A, Single MS, Nawroth C (2020) Social referencing in the domestic horse. *Animals* 10:164.
773 <https://doi.org/10.3390/ani10010164>

774 Schuetz A, Farmer K, Krueger K (2017) Social learning across species: horses (*Equus caballus*) learn
775 from humans by observation. *Anim Cogn* 20:567–573. [https://doi.org/10.1007/s10071-016-1060-](https://doi.org/10.1007/s10071-016-1060-8)
776 8

777 Schwab C, Huber L (2006) Obey or Not Obey? Dogs (*Canis familiaris*) Behave Differently in Response
778 to Attentional States of Their Owners. <https://doi.org/10.1037/0735-7036.120.3.169>

779 Silver ZA, Furlong EE, Johnston AM, Santos LR (2021) Training differences predict dogs' (*Canis lupus*
780 *familiaris*) preferences for prosocial others. *Anim Cogn* 24:75–83.
781 <https://doi.org/10.1007/s10071-020-01417-9>

782 Siniscalchi M, D'Ingeo S, Fornelli S, Quaranta A (2018a) Lateralized behavior and cardiac activity of
783 dogs in response to human emotional vocalizations. *Sci Rep* 8:77.
784 <https://doi.org/10.1038/s41598-017-18417-4>

785 Siniscalchi M, D'Ingeo S, Minunno M, Quaranta A (2018b) Communication in dogs. *Animals* 8:131.
786 <https://doi.org/10.3390/ani8080131>

787 Siniscalchi M, D'Ingeo S, Quaranta A (2016) The dog nose “KNOWS” fear: Asymmetric nostril use
788 during sniffing at canine and human emotional stimuli. *Behav Brain Res* 304:34–41.
789 <https://doi.org/10.1016/j.bbr.2016.02.011>

790 Siniscalchi M, D'Ingeo S, Quaranta A (2018c) Orienting asymmetries and physiological reactivity in
791 dogs' response to human emotional faces. *Learn Behav* 46:574–585.
792 <https://doi.org/10.3758/s13420-018-0325-2>

793 Siniscalchi M, D'Ingeo S, Quaranta A (2021) Lateralized emotional functioning in domestic animals.
794 *Appl Anim Behav Sci* 237:. <https://doi.org/10.1016/j.applanim.2021.105282>

795 Smith AV, Proops L, Grounds K, et al (2016) Functionally relevant responses to human facial
796 expressions of emotion in the domestic horse (*Equus caballus*). *Biol Lett* 12:20150907.
797 <https://doi.org/10.1098/rsbl.2015.0907>

798 Smith AV, Proops L, Grounds K, et al (2018) Domestic horses (*Equus caballus*) discriminate between

799 negative and positive human nonverbal vocalisations. *Sci Rep* 8:13052.
800 <https://doi.org/10.1038/s41598-018-30777-z>

801 Soproni K, Miklósi Á, Topál J, Csányi V (2002) Dogs' (*Canis familiaris*) responsiveness to human
802 pointing gestures. *J Comp Psychol* 116:27–34. <https://doi.org/10.1037/0735-7036.116.1.27>

803 Stone SM (2010) Human facial discrimination in horses: Can they tell us apart? *Anim Cogn* 13:51–61.
804 <https://doi.org/10.1007/s10071-009-0244-x>

805 Takagi S, Arahori M, Chijiwa H, et al (2019) Cats match voice and face: cross-modal representation of
806 humans in cats (*Felis catus*). *Anim Cogn* 22:901–906. [https://doi.org/10.1007/s10071-019-](https://doi.org/10.1007/s10071-019-01265-2)
807 [01265-2](https://doi.org/10.1007/s10071-019-01265-2)

808 Thorpe WH (1956) *Learning and Instinct in Animals*. Methuen, London

809 Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. *Trends Ecol Evol* 22:529–
810 537. <https://doi.org/10.1016/j.tree.2007.09.001>

811 Topál J, Byrne RW, Miklósi Á, Csányi V (2006) Reproducing human actions and action sequences:
812 “Do as I do!” in a dog. *Anim Cogn* 9:355–367. <https://doi.org/10.1007/s10071-006-0051-6>

813 Townsend SW, Koski SE, Byrne RW, et al (2017) Exorcising Grice’s ghost: an empirical approach to
814 studying intentional communication in animals. *Biol Rev* 92:1427–1433.
815 <https://doi.org/10.1111/brv.12289>

816 Trösch M, Bertin E, Calandreau L, et al (2020a) Unwilling or willing but unable: can horses interpret
817 human actions as goal directed? *Anim Cogn* 23:1035–1040. [https://doi.org/10.1007/s10071-020-](https://doi.org/10.1007/s10071-020-01396-x)
818 [01396-x](https://doi.org/10.1007/s10071-020-01396-x)

819 Trösch M, Cuzol F, Parias C, et al (2019a) Horses categorize human emotions cross-modally based
820 on facial expression and non-verbal vocalizations. *Animals* 9:862.
821 <https://doi.org/10.3390/ani9110862>

822 Trösch M, Pellon S, Cuzol F, et al (2020b) Horses feel emotions when they watch positive and
823 negative horse–human interactions in a video and transpose what they saw to real life. *Anim*
824 *Cogn* 23:643–653. <https://doi.org/10.1007/s10071-020-01369-0>

825 Trösch M, Ringhofer M, Yamamoto S, et al (2019b) Horses prefer to solicit a person who previously
826 observed a food-hiding process to access this food: A possible indication of attentional state
827 attribution. *Behav Processes* 166:103906. <https://doi.org/10.1016/j.beproc.2019.103906>

828 Udell MAR, Dorey NR, Wynne CDL (2010) What did domestication do to dogs? A new account of
829 dogs' sensitivity to human actions. *Biol Rev* 85:327–345. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.2009.00104.x)
830 [185X.2009.00104.x](https://doi.org/10.1111/j.1469-185X.2009.00104.x)

831 Udell MAR, Giglio RF, Wynne CDL (2008) Domestic Dogs (*Canis familiaris*) Use Human Gestures But
832 Not Nonhuman Tokens to Find Hidden Food. *J Comp Psychol* 122:84–93.
833 <https://doi.org/10.1037/0735-7036.122.1.84>

834 Virányi Z, Topál JÓ, Gácsi MÁ, et al (2004) Dogs respond appropriately to cues of humans' attentional
835 focus. *Behav Processes* 66:161–172. <https://doi.org/10.1016/j.beproc.2004.01.012>

836 Vitale KR, Udell MAR (2019) The quality of being sociable: The influence of human attentional state,
837 population, and human familiarity on domestic cat sociability. *Behav Processes* 158:11–17.
838 <https://doi.org/10.1016/j.beproc.2018.10.026>

839 Vitale Shreve KR, Udell MAR (2015) What's inside your cat's head? A review of cat (*Felis silvestris*
840 *catus*) cognition research past, present and future. *Anim Cogn* 18:1195–1206.
841 <https://doi.org/10.1007/s10071-015-0897-6>

842 Worsley HK, O'Hara SJ (2018) Cross-species referential signalling events in domestic dogs (*Canis*
843 *familiaris*). *Anim Cogn* 21:457–465. <https://doi.org/10.1007/s10071-018-1181-3>

844

845

846 **Table 1: Comprehensive literature search terms**

847 Items within each concept were combined with “or”, meaning that at least one of the keywords needed to be present in the titles of selected publications. The
 848 concepts were combined with “and”, so that only publications with a title containing all three concepts were selected.

Concept (a) domestic mammals	Concept (b) sociocognitive skills	Concept (c) humans
domestic mammal, companion animal, pet, dog, canis, canine, canid, cat, felis, feline, felid, horse, equus, equid, donkey, ferret, mustela, mustelid, rabbit, oryctolagus cuniculus, cobaye, guinea pig, cavia porcellus, mouse, mus musculus domesticus, rodent, rat, ratus norvegicus, mink, neogale vison, farm animal, livestock, cow, bos, bovine, cattle, yak, zebu, buffalo, bubalus, sheep, ovis, ovine, goat, capra, caprine, pig, sus, camel, camelus, camelid, alpaca, vicugna, llama, lama	cognition, social cognition, sociocognitive, learning, recognition, emotion, emotional, mental states, referential communication, cross-modal representation, attention, attentional, empathy, empathic, pet-directed speech, emotional contagion, sympathy, empathic perspective, social eavesdropping, social referencing, reputation, social evaluation, demonstration, imitation, social influences, stimulus reinforcement, local reinforcement, teach, point, pointing, ostensive cue, pet-directed speech, communicate, communication, communicating, gaze alternation	human, homo sapiens, caretaker, caregiver, keeper, groom, owner

849

850

851 **Table 2: Research papers and reviews on the sociocognitive abilities of domestic mammals toward humans**

852 The review focused on species for which data are available.

853

		Dog	Cat	Horse	Ferret	Cattle	Sheep	Goat	Pig
Perception of human individuals									
	<i>Discrimination</i>	Racca et al. (2010); Pinc et al. (2011)		Stone (2010); d'Ingeo et al. (2019); Lansade et al. (2020a)		Munksgaard et al. (1999); Rybarczyk et al. (2001)	Knolle et al. (2017)		Koba and Tanida (1999, 2001)
	<i>Recognition</i>	Huber et al. (2013); Mongillo et al. (2017); Eatherington et al. (2020)	Saito and Shinozuka (2013)	Lansade et al. (2020a, b)			Knolle et al. (2017)		
	<i>Cross-modal representation</i>	Adachi et al. (2007); Siniscalchi et al. (2018b)	Takagi et al. (2019)	Proops and McComb (2012); Lampe and Andre (2012)					
Perception of human emotions									
	<i>Discrimination</i>	Nagasawa et al. (2011); Siniscalchi et al. (2016, 2018a); D'Aniello et al. (2018); Correia-Caeiro et al. (2021)		Smith et al. (2016); Baba et al. (2019); Sabiniewicz et al. (2020)		Destrez et al. (2021)			
	<i>Preference</i>		Galvan and Vonk (2016)					Nawroth et al. (2018)	
	<i>Cross-modal representation</i>	Albuquerque et al. (2016)	Quaranta et al. (2020)	Nakamura et al. (2018); Trösch et al. (2019a)					
	<i>Behavioral and physiological responses</i>	Custance and Mayer (2012); Huber et al. (2017); Albuquerque et al. (2018); Siniscalchi et al. (2018a, 2018c)	Quaranta et al. (2020)	Smith et al. (2016, 2018); Proops et al. (2018); Trösch et al. (2019a)					
Understanding humans' attentional state and goals									
	<i>Attentional states</i>	Call et al. (2003); Bräuer et al. (2004); Gácsi et al. (2004); Virányi et al. (2004); Schwab and Huber (2006); Ohkita et al. (2016); Kaminski et al. (2012); Mehrkam and Wynne (2021);	Vitale and Udell (2019); Humphrey et al. (2020)	Sankey et al. (2011); Ringhofer and Yamamoto (2017); Trösch et al. (2019b)			Beausoleil et al. (2006)	Nawroth and McElligott (2017)	Nawroth et al. (2013)

Table 2 (continued): Research papers and reviews on the sociocognitive abilities of domestic mammals toward humans.

	<i>Goals</i>			Trösch et al. (2020a)			Nawroth et al. (2016c)
	<i>Sensitivity to ostensive cues</i>	Kis et al. (2012); Jeannin et al. (2017); Benjamin and Slocombe (2018)	Pongrácz et al. (2019); Pongrácz and Onofer (2020)	Lansade et al. (2021)			
Referential communication							
	<i>Understanding cues from humans</i>	Soproni et al. (2002); Kaminski et al. (2004); Miklósi et al. (2005); Miklósi and Soproni (2006); Udell et al. (2008); Ittyerah and Gaunet (2009); Kaminski et al. (2009); Lakatos et al. (2009); Udell et al. (2010); D'Aniello et al. (2016); Krause et al. (2018); Pelgrim et al. (2021)	Miklósi et al. (2005); Miklósi and Soproni (2006); Krause et al. (2018); Pongrácz et al. (2019)	Miklósi and Soproni (2006); Maros et al. (2008); Proops et al. (2010); Krause et al. (2018); Lansade et al. (2021)	Hernádi et al. (2012)		Miklósi and Soproni (2006); Nawroth et al. (2020)
	<i>Communication attempts</i>	Kaminski et al. (2012, 2017); Siniscalchi et al. (2018b)	McComb et al. (2009)	Lansade et al. (2018); Ringhofer and Yamamoto (2017); Trösch et al. (2019b)			
	<i>Referential communication signals toward humans</i>	Miklósi et al. (2005); Kaminski et al. (2011); Worsley and O'Hara (2018)	Miklósi et al. (2005)	Malavasi and Huber (2016)			Nawroth et al. (2016b); Gerencsér et al. (2019); Pérez Fraga et al. (2021)
Social learning							
	<i>Local enhancement</i>	Pongrácz et al. (2001); Kubinyi et al. (2003); Péter et al. (2016)		Krueger et al. (2011); Burla et al. (2018); Schuetz et al. (2017); Bernauer et al. (2020); Rørvang et al. (2020)			Nawroth et al. (2016a)
	<i>Use of demonstrations</i>	Topál et al. (2006); Fugazza and Miklósi (2014)	Fugazza et al. (2020)				
	<i>Social referencing</i>	Merola et al. (2012a, b); Chijiwa et al. (2015); Duranton et al. (2016); Anderson et al. (2017); Silver et al. (2021)	Merola et al. (2015); Chijiwa et al. (2021)	Schrimpf et al. (2020); Trösch et al. (2019b)			

855 **SUPPLEMENTARY INFORMATION**

856 **Table S1: Comprehensive literature search filters**

857 Three filters were applied consecutively to refine the research. The listed categories and
 858 document types were selected.

Web of Science categories (1)	Document types	Web of Science categories (2)
Behavioral Sciences or Neurosciences or Veterinary Sciences or Zoology or Agriculture Dairy Animal Science or Psychology Biological or Ecology or Evolutionary Biology or Communication or Psychology Developmental or Agronomy or Social Work or Agriculture Multidisciplinary	Early Access or Articles or Review Articles	Behavioral Sciences or Neurosciences or Veterinary Sciences or Zoology or Agriculture Dairy Animal Science or Psychology Biological or Psychology or Psychology

859

860