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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-03361795v1

Submitted on 22 Aug 2022

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

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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

Introduction

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

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

Method

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

Results

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

Discussion

Discriminating and recognizing individual humans

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

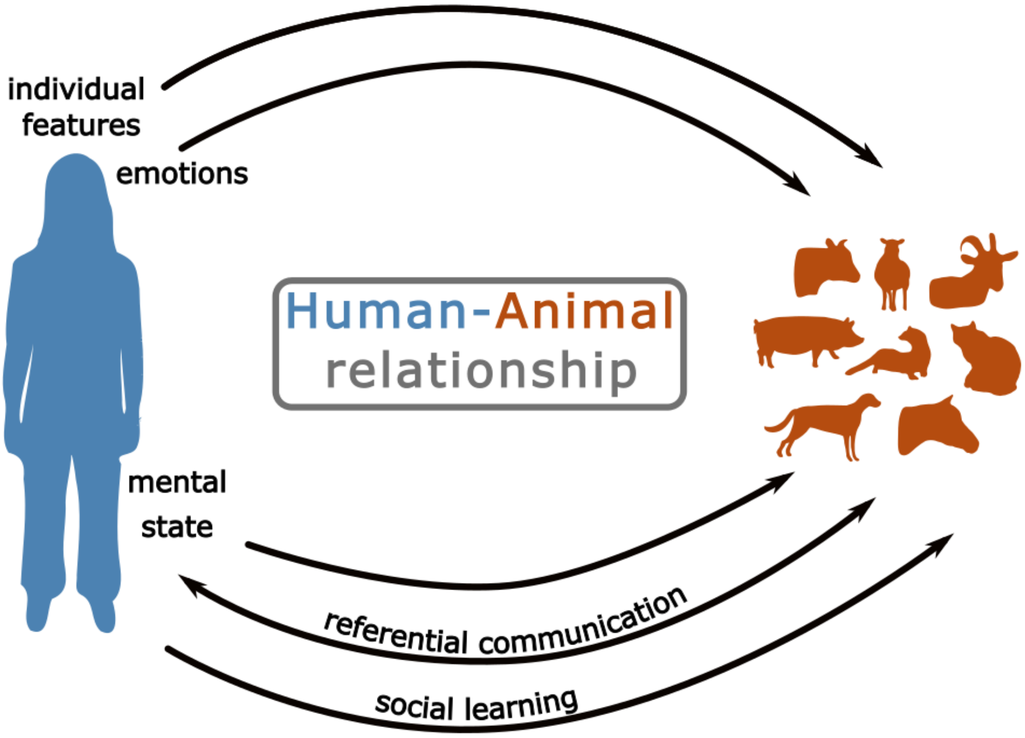

Fig 1 Summary of the sociocognitive abilities of domestic mammals toward humans reviewed in this paper

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

A second question concerns the ability of these species to recognize specific humans, an ability that implies both discrimination between individuals and the matching of an individual's features to one's memory of that particular individual (Tibbetts and Dale 2007). Dogs, horses and sheep could recognize their owner or handler from visual cues. For example, dogs chose their owner over a stranger when their faces were presented live through a hole or in pictures, either spontaneously (live and pictures) or after training (live; Huber et al. 2013; Mongillo et al. 2017; from pictures: Eatherington et al. 2020). After being trained to always choose a familiar picture over a novel one, horses and sheep could spontaneously recognize a picture of their handler (Lansade et al. 2020a; Knolle et al. 2017). Regarding auditory cues, cats were shown to distinguish their owner's voice from that of a stranger's in a habituation-dishabituation protocol (Saito and Shinozuka 2013).

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

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

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

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

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

Perceiving human emotions

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

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

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

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

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

Interestingly, the species that have been examined also showed a brain hemisphere specialization associated with our emotions: when perceiving emotions, horses, dogs and goats tend to preferentially use either their right or left ear, eye or nostril, depending on its valence (Smith et al. 2016; Siniscalchi et al. 2016, 2018a, c). However, this is not consistent for an emotion across modalities and species; for example, a left hemisphere bias was observed with happy faces in horses and goats and happy vocalizations in dogs, but happy faces were associated with a right hemisphere bias in dogs (Smith et al. 2016; Nawroth et al. 2018; Siniscalchi et al. 2018c, a). In domestic mammals, as well as in humans, different models have been proposed to describe the hemispheric lateralization of emotion perception. The most recent results suggest that the right hemisphere dominates for the perception of negative or arousing emotions while the left hemisphere is favored when perceiving positive or familiar emotions (Gainotti 2019; Siniscalchi et al. 2021). Therefore, the differences in hemisphere biases among domestic mammals when perceiving human emotions could be explained by a discordance, for some animals, between the valence of the emotion expressed and the way it is perceived (for example dogs could perceive happy human faces negatively; Siniscalchi et al. 2021).

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

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

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

Understanding humans' attentional state and goals

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

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

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

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

The ability of domestic mammals to perceive our goals can also be explored by observing their responsiveness to ostensive cues. These are signals given specifically to attract the animals' attention and initiate an interaction and can therefore help to determine whether the animals perceive that we are speaking to and interacting with them. One example is, making calling noises and calling their name, ostensive cues that cats seem sensitive to: subjects followed an experimenter's gaze sooner and were more influenced by an experimenter producing such cues rather than when they made other noises or read a poem (Pongrácz et al. 2019; Pongrácz and Onofer 2020). Similarly, dogs were influenced by an experimenter calling their name and making eye contact (Kis et al. 2012). Another example of ostensive cues is pet-directed speech, a type of speech used specifically by humans to talk to animals, which is similar to the speech used to talk to babies. Dogs and horses seem sensitive to this type of speech. Dogs were more attentive when hearing humans talking in pet-directed speech (Jeannin et al. 2017) and they spent more time close to a speaker broadcasting this type of speech than one broadcasting standard vocalization (called adult-directed speech; Benjamin and Slocombe 2018). Horses performed better in a pointing task and were more relaxed during grooming when the experimenter used pet-directed speech than adult-directed speech (Lansade et al. 2021). However, these ostensive cues could also simply work by attracting the animals' attention, without them being conscious that we are trying to communicate with them intentionally.

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

Referential communication with humans

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

Perceiving human signals

Many studies have focused on the ability of domestic mammals to understand human pointing gestures, in which a human indicates the location of a food reward that the animal can obtain (for reviews see Miklósi and Soproni 2006; Krause et al. 2018). The basic movement used is stretching an arm at approximately 45° from the body, and pointing a finger. These gestures have been investigated in dogs, cats, horses, ferrets, pigs and goats, showing that each species follows them to various degrees (dogs and cats: Miklósi et al. 2005; ferrets: Hernádi et al. 2012; goats: Nawroth et al. 2020; pigs: Nawroth et al. 2014), although in horses, the results have been more inconsistent (Maros et al. 2008; Proops et al. 2010; Lansade et al. 2021). Dogs seem to be the most flexible species. They can follow a cross pointing cue (right arm pointing to the left for example; Soproni et al. 2002; Miklósi et al. 2005), which goats can also follow (Nawroth et al. 2020). Asymmetric pointing cues (with the experimenter closer to the wrong choice) were also effective with dogs but not goats or pigs, which raises the question of whether these last two species use the pointing cues as local enhancement (see below) rather than referential cues (Nawroth et al. 2014, 2020). Other body parts have also been tested in some species: dogs, cats and pigs were shown to follow head orientation (dogs: Ittyerah and Gaunet 2009; cats: Pongrácz et al. 2019; pigs: Nawroth et al. 2014). Body orientation was followed by pigs (Nawroth et al. 2014) but not horses (Proops et al. 2010), and dogs could also follow a pointed leg or a bow (Udell et al. 2008; Lakatos et al. 2009). Dogs are also the species for which most studies have been published, with experiments exploring the influence of social, emotional and other types of factors on this capacity (for literature review, see Krause et al. 2018). For example they were shown to modulate their answer to pointing gestures in accordance with the reliability of a pointer (based on a previous experience with this person; Pelgrim et al. 2021).

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

Sending signals to humans

Several studies have shown that certain species produce behaviors in the presence of humans that could be interpreted as communication signals intended for us. Horses display very specific facial expressions in response to being groomed by a human (Lansade et al. 2018), although further research is needed to determine whether these expressions are intended for humans. Cats have been shown to produce different purrs in different contexts that include humans (the acoustic spectrum of purrs used in soliciting contexts has different characteristics than those used in non-soliciting contexts; McComb et al. 2009). In dogs and horses, some behaviors are modulated by humans' mental states. For example, dogs modify their facial expression according to our attentional state (Kaminski et al. 2012), and display different gestural and vocal signals based on our response (Siniscalchi et al. 2018b). Similarly, horses seem to communicate with humans as they solicited (with touches from the muzzle) and looked at an experimenter differently depending on whether the experimenter had witnessed the hiding process of an inaccessible food reward (Ringhofer and Yamamoto 2017; Trösch et al. 2019b). Moreover, studies focusing on referential communicative behaviors from animals to humans have shown that horses, dogs and goats use gaze alternation when presented with an inaccessible food reward: they looked back and forth between the reward and the experimenter, which is a behavior that could be interpreted as an attempt to attract the human's attention to the reward. The animals modulated this behavior based on the experimenter's attentional state, which suggests that humans were the target of the behavior (dogs: Miklósi et al. 2005; horses: Malavasi and Huber 2016; goats: Nawroth et al. 2016b). In a comparative study, cats were shown to produce fewer gaze alternations than dogs (Miklósi et al. 2005), but changes in this behavior based on human attentional states remain unexplored. Pigs also seem to produce human-oriented behaviours, although not more in the presence of an inaccessible food reward that an accessible one (Gerencsér et al. 2019; Pérez Fraga et al. 2021). It is a valid possibility that all these signals are expressed intentionally with the aim of communicating with humans, but to reach such conclusions, several more criteria need to be validated as defined by Townsend et al. (2017). For example, it should be demonstrated that the animals monitor their audience and adapt their behavior to its reactions. These criteria have been validated in dogs, showing that they use various gestures like gaze alternations, but also other movements, as referential signals. These gestures seem to be used particularly to request desired actions or objects from humans (Kaminski et al. 2011; Worsley and O'Hara 2018).

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

Social Learning from humans

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

Local enhancement

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

Demonstration

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

Social referencing

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

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

Overall, the ability to learn socially from humans by local enhancement, social referencing and possibly demonstration has been shown in dogs, cats, horses and goats, while to our knowledge, it remains unexplored in cattle, sheep, ferrets and pigs. In the latter, the ability to follow an informed conspecific to find hidden food has been demonstrated (Held et al. 2000), encouraging us to explore their ability to use information given by humans in similar situations.

Conclusion

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

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

Further research is also needed to investigate sociocognitive capacities toward humans in some domestic mammal species which have not been investigated in this domain (e.g., donkeys and rabbits). Wild species living close to humans as pets (e.g., sugar gliders) or on farms (e.g., deer) could also benefit from studies to determine how much they understand humans and how they can interact with them. Moreover, exploring the sociocognitive skills of these species (living close to humans but not artificially selected) could help to understand the respective roles of environmental factors and genetic changes in the development of these cognitive abilities toward humans (for reviews on dogs, see Hare et al. 2002 and Udell et al. 2010).

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

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

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

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

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Table 1: Comprehensive literature search terms

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 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

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

The review focused on species for which data are available.

	Dog	Cat	Horse	Ferret	Cattle	Sheep	Goat	Pig
Perception of human individuals								
Discrimination	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)
Recognition	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)		
Cross-modal representation	Adachi et al. (2007); Siniscalchi et al. (2018b)	Takagi et al. (2019)	Proops and Mccomb (2012); Lampe and Andre (2012)					
Perception of human emotions								
Discrimination	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)			
Preference		Galvan and Vonk (2016)					Nawroth et al. (2018)	
Cross-modal representation	Albuquerque et al. (2016)	Quaranta et al. (2020)	Nakamura et al. (2018); Trösch et al. (2019a)					
Behavioral and physiological responses	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								
Attentional states	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.

	Goals			Trösch et al. (2020a)				Nawroth et al. (2016c)	
	Sensitivity to ostensive cues	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									
	Understanding cues from humans	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)	Nawroth et al. (2014)
	Communication attempts	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)					
	Referential communication signals toward humans	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									
	Local enhancement	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)
	Use of demonstrations	Topál et al. (2006); Fugazza and Miklósi (2014)	Fugazza et al. (2020)						
	Social referencing	Merola et al. (2012a, b); Chijiiwa et al. (2015); Duranton et al. (2016); Anderson et al. (2017); Silver et al. (2021)	Merola et al. (2015); Chijiiwa et al. (2021)	Schrimpf et al. (2020); Trösch et al. (2019b)					

SUPPLEMENTARY INFORMATION

Table S1: Comprehensive literature search filters

Three filters were applied consecutively to refine the research. The listed categories and 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