



From simple behavioural tests to EEG measurements: Studying linguistic competence in dogs

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ABSTRACT

This critical review examines non-human manifestations of linguistic competence and its precursors, with a focus on findings from studies on domestic dogs (*Canis familiaris*). Previous research – including both theoretical reviews and empirical studies – has widely demonstrated that the domestic dog serves as an ideal natural model for studying a broad range of cognitive and behavioural traits shared with humans. Studies also indicate that dogs can interpret human communication cues in a remarkably child-like manner; they possess functionally human-analogous, voice-sensitive cortical regions and show specific neural responses to speech. Moreover, some dogs show evidence of learning word-object associations in ways unprecedented among nonhuman species. Together, these findings strongly support the translational value of dog-human comparisons for exploring the evolution of skills related to faculties of language and suggest that dogs may serve as models for studying natural variability in children's world learning abilities.

1. Introduction

The ontogenetic emergence and phylogenetic evolution of human language – a cognitive ability unique to our species – have long been central to comparative research. Decades ago, Sebeok in his seminal paper published in *Science* (Sebeok, 1965) argued that animal communication systems could be studied using concepts from linguistics, such as competence and performance. Since then, ongoing debates have focused on the continuity between various aspects of human language and animal communication systems, as well as on the possible existence of precursors to human language (e.g. Zuberbühler, 2015; Birchenall, 2016). Recent studies indicate that some important hallmarks of linguistic competence can evolve across different clades of animals. For example, even Japanese tits exhibit linguistic capabilities such as referentiality and compositionality (Suzuki, 2021). Additionally, audience awareness (i.e. signaller sensitivity to the audience) has also been observed in different species (see Coppinger et al., 2017, for a review). However, while nonhuman species may show some linguistic skills, human language is grounded in a range of uniquely human abilities, which are only present in rudimentary forms, even in our closest relatives, the non-human primates.

An intriguing question regarding potential parallels between human

language and animal communication systems is the extent to which animals can benefit from understanding aspects of human linguistic communication. A key term in exploring this question is *communicative competence* which refers to the abilities, that both signallers ('speakers') and receivers ('listeners') need to communicate effectively across various social contexts (Lillis, 2006). Although the manifestations of such social competence in interspecific (human-animal) contexts remain widely debated, communication between humans and nonhuman animals is gaining increasing interest in the field of comparative social cognition. In line with this, growing evidence suggests that many species – including higher mammals and birds – engage in complex communicative interactions with humans (see Hurn, 2024 for a review).

When studying animal understanding of human verbal communication, the central question is whether non-human receivers can perceive the unique features of linguistic communication that make it qualitatively distinct from animal communication systems. Specifically, these features are (i) *referential quality* – the capacity for a one-to-one semantic referential mapping; (ii) *the intentional nature of communicative acts* – the ability to infer that the message content is intentionally signalled by the communicator; and (iii) *the generalizability of linguistic signals* – the receiver's expectation that the validity of shared knowledge extends beyond the immediate context and applies to other situations.

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Apart from the capacity to use and understand symbols, taking the direction of translating these theoretical considerations into a more practical approach, the extent of ‘vocabulary’ and the recognition of ‘syntax’ are two essential aspects in studying how animals understand human linguistic communication. The first concerns an animal’s capacity to develop relevant responsiveness to human verbal signals (words). Word learning studies focus on three basic questions: whether subjects (i) can isolate word forms within different auditory inputs (ii) can develop associations between words and their referents, and (iii) can map meanings onto objects, agents or actions (e.g. [Pepperberg et al., 2000](#)). Studies on sensitivity to syntax, however, focus on assessing an animal’s understanding of the additional information encoded in the grammatical relationships of verbal signals (e.g. [Suzuki, Zuberbühler, 2019](#)).

2. Why dogs?

It is increasingly accepted that moving beyond traditional direct phylogenetic comparisons between humans and great apes – and instead focusing on convergent cases of linguistic capabilities in animals phylogenetically distant from humans – offers potential for deeper insights into the origins and evolution of linguistic abilities. Recent support for the domestic dog as a promising candidate for such comparative approaches comes from both theoretical reviews (e.g. [Miklósi Topál, 2012; 2013](#)) and research articles (e.g. [Topál et al., 2009; Bunford et al., 2020](#)) which show that dogs share a broad range of cognitive and behavioural traits with humans. Dogs demonstrate remarkable, infant-like social competence in their communicative skills, enabling them to perceive certain aspects of the intentional and referential nature of human communication. However, these interactions generally occur without the recognition of the generalizability of knowledge shared by their human partners. In the following paragraphs, we review the characteristics of dogs’ communicative competence that make them well-suited for engaging in communicative interactions with humans.

2.1. Understanding ‘referentiality’

Referential signals are used by the signaller to draw the attention of the receiver to the target of interest (object, person, location, etc.). The responsiveness to referential signals – initially thought to be uniquely human – has been extensively investigated in various animal species. Not only primates (e.g. [Liebal, Slocombe and Waller, 2022](#)) but also some bird species (see [Smith, 2017](#)) and bottlenose dolphins ([King and Janik, 2013](#)) have been shown to produce and respond to functionally referential signals, mainly in the auditory domain. Importantly, true referentiality in the human sense has been questioned in these instances due to concerns about context-specificity and stimulus-independence ([Wheeler and Fischer, 2012](#)). However, other studies have provided evidence of comprehension of context-independent specific referential cues in the visual domain, such as directional gestures. Elephants ([Smet and Byrne, 2013](#)), seals ([Scheumann and Call, 2004](#)), and dolphins ([Herman et al., 1999](#)) have been found to comprehend the referential nature of human pointing. Moreover, some species have demonstrated the ability not only to comprehend but also to produce such signals ([Pika and Bugnyar, 2011; Vail, Manica and Bshary, 2013](#)).

Dogs have also been shown to interpret human directional gestures, including gaze direction ([Hare and Tomasello, 1999; Agnetta, Hare and Tomasello, 2000; Téglás et al., 2012; Met, Miklósi and Lakatos., 2014](#)) and various forms of pointing ([Soproni et al., 2002](#)). An intriguing aspect of dogs’ responsiveness to human gestural communication is their ability to utilize such signals spontaneously, and flexibly ([Duranton, Range and Virányi, 2017; Kaminski Schulz and Tomasello, 2012; Tauzin et al., 2015a; Téglás et al., 2012; Bray et al., 2020; Hare et al., 2010; MacLean et al., 2017; Udell, Giglio and Wynne, 2008; Wobber and Hare, 2009](#)) and from an early age ([Riedel et al., 2008; Bhattacharjee et al., 2017; Gácsi et al., 2009; Salomons et al., 2021](#)). Dogs’ performance in

such situations is comparable to that of 2-year-old children ([Lakatos et al., 2009; Hare and Tomasello, 2005](#)). Both infants and dogs exhibit a strong dependence on interpreting gestures in their daily interactions. For infants, gesture comprehension serves as a fundamental aspect of communicative development, whereas in dogs, it predicts success in training for service and detection tasks ([Lazarowski et al., 2019; MacLean and Hare, 2018; Tomasello, 2019](#)). Moreover, family dogs, unlike other domesticated animals kept as family pets, such as miniature pigs ([Pérez Fraga et al., 2023](#)), have been observed exhibiting attention-getting behaviours when faced with unsolvable problems. In such situations, they use gaze alternation and their body positioning as functionally referential and intentional communicative signals ([Miklósi et al., 2000; Gaunet and Deputte, 2011](#)). Furthermore, like infants ([Csibra, 2010; Behne, Carpenter and Tomasello, 2005](#)), dogs perform better at following human pointing gestures when these gestures are preceded by ostensive signals ([Kaminski, Schulz and Tomasello, 2012; Tauzin et al., 2015a](#)).

2.2. The intentional nature of human communication

Ostensive signals are specific tools used to express the intentional nature of human communication, which refers to the deliberate and purposeful actions taken by individuals to convey information. These include both verbal and non-verbal cues, such as gestures, facial expressions and eye contact. In brief, ostensive signals indicate an intention to communicate and are used to initiate and maintain interactions ([Tomasello et al., 2005](#)). Like responsiveness to referential signals, ostensive communication was initially thought to be a uniquely human trait, relying on metacognitive abilities that enable the open-ended and flexible nature of human communication ([Heintz and Scott-Phillips, 2023](#)). Humans are highly efficient receivers of ostension from an early age; for example, six-month-old infants have been shown to follow human gaze when presented in an ostensive manner ([Senju and Csibra, 2008](#)). According to [Csibra and Gergely \(2009\)](#), ostensive communication biases infants’ interpretation of others’ directional cues in at least three ways: by increasing attention, by creating a referential expectation, and by inducing a genericity bias (i.e. the tendency to interpret conveyed information as general knowledge).

Domestic dogs have evolved alongside humans for at least 15,000 years ([Larson et al., 2012](#)) and have more recently been artificially selected for cooperative and communicative abilities. As such, it is reasonable to assume that responsiveness to ostensive signals may be an adaptive trait ([Topál et al., 2009](#)). Indeed, research has shown that ostensive communication toward family dogs increases their chances of success in tasks such as socially demonstrated detours ([Pongrácz et al., 2004](#)), gaze following ([Duranton, Range and Virányi, 2017; Téglás et al., 2012](#)) and comprehension of pointing gestures ([Tauzin et al., 2015a](#)).

These findings suggest that, like human infants, family dogs are able to selectively comprehend ostensive communication. However, the question of whether this reflects truly increased referential expectation or merely heightened attentiveness remains open for further investigation. While some argue that the ability to follow human ostension develops through life experience, recent findings suggest that this ability, similarly to human children, emerges very early in life ([Byosiére et al., 2023](#)), making the experience-based interpretation less probable.

2.3. Generalizability of shared knowledge

Studies on the development of human communication suggest that signals indicating the intention to communicate – ostensive signals – trigger a learning predisposition in infants, facilitating their acquisition of knowledge through the observation of adult demonstrations ([Csibra and Gergely, 2009](#)). Infants tend to assume that the information presented by an adult, when accompanied by ostensive signals, applies also to other contexts. Research ([Topál et al., 2008](#)) demonstrates that this predisposition can explain the perseverative search error observed in

young infants during the A-not-B object search task (Wellman et al., 1986). In this two-way choice paradigm infants observe the hiding of the target object, and search for it under container A three times, and although observing the fourth hiding under container B, keep searching under container A (i.e. commit a perseverative error). The strong association found between the ostensive-communicative context of the hiding actions and the perseverative search error provides support for the "natural pedagogy" hypothesis (Csibra and Gergely, 2009). This hypothesis suggests that the perseverative error arises primarily from a pragmatic misinterpretation of the experimenter's hiding actions, which are perceived as a communicative teaching demonstration, leading to the assumption that the knowledge should be generalized to other contexts.

Dogs have also been shown to exhibit functionally similar sensitivity to human ostensive-referential signals. To investigate the functional nature of dogs' sensitivity to these cues, the A-not-B object search paradigm, previously shown to induce perseverative search errors in human infants due to communicative cues (Topál et al., 2008), was used. The results revealed that, like infants, dogs commit perseverative search errors when the hiding events are presented in a communicative context. This suggests that social competence, including a predisposition to learn from human communication, is shared by both dogs and infants. The robust A-not-B error in dogs, which is absent in extensively socialized wolves, is believed to result from selective processes during domestication that enhanced sensitivity to human cues (Miklósi et al., 2003; Gácsi et al., 2009). However, the fact that the perseverative error is committed by dogs only in a communicative context does not necessarily imply the same interpretation as in human infants. Instead, evidence suggests that dogs' responses to human communication are driven by a desire to comply with the expectations that their human partner seemingly expresses through ostensive communication, even when this leads to inefficient or incorrect responses in a particular task situation (Pongrácz et al., 2004; Prato-Previde, Marshall-Pescini and Valsecchi, 2008; Erdőhegyi et al., 2007). The fact that perseverative errors in dogs are context-dependent, while in children they are independent of context, highlights important differences between dogs and human infants in terms of their interpretive processes. These findings seem to reveal a behavioural analogy between dogs and human infants. The A-not-B error often viewed as a mistake, may reflect advanced social competence in both dogs and infants. However, dogs appear to anchor communication to the specific situation and communicator (Topál et al., 2009).

3. How do dogs understand human linguistic communication?

3.1. Word learning, word comprehension in dogs

There is a huge discrepancy between behavioural experiment-based evidence on word comprehension of dogs and evidence from owner reports (Pongrácz et al., 2001; Reeve and Jacques, 2022). Moreover, owners' opinion on how well their dogs understand the human language spoken to them covers a wide range from "dogs only comprehend the tone of voice and context" to "they understand language similarly to a 3–4-year-old human infant". Most recently some owners even claim that their dogs use word buttons adequately to express what is on their mind, with some of these claims also corroborated by scientific investigations (Bastos, Evenson, et al., 2024; Bastos, Houghton, et al., 2024). One might be inclined to dismiss owners' opinions as biased, given that their claims have not yet been corroborated by behavioural studies (Kőszegi et al., 2023; Ramos and Mills, 2019), were it not for the growing body of evidence from non-invasive neuroscientific studies (e.g. Andics et al., 2016; Bunford et al., 2017; Kis et al., 2014) suggesting that dogs' word comprehension involves more than just the 'tone of voice' associated with certain contexts. Among others, dogs have been shown to possess functionally human-analogue voice-sensitive regions (Andics et al., 2014), abilities in the neural representation of lexical information

(Andics et al., 2016; Gábor et al., 2020), and segmentation of human speech (Boros et al., 2021) (for detailed discussion see Section 4.) So, considering the above, the question remains: How well do typical family dogs comprehend human language?

3.1.1. Word-referent Relationships, and word comprehension considering the level of correspondence

Understanding that words (i.e. specific verbal cues) refer to specific objects in the environment – referential understanding – is believed to be based on the formation of mental representations in humans. Mental representations are hypothetical internal cognitive symbols that represent external reality or even concepts. While in human studies, individuals' mental representations are relatively straightforward to study due to linguistic competence, the study of mental representations in non-verbal (non-human) animals has been quite a challenge. While case studies suggesting a referential understanding of object words have been accumulating (Herman, Richards and Wolz, 1984; Kaminski, Call and Fischer, 2004; Pepperberg, 2006; Pilley and Reid, 2011; Savage-Rumbaugh et al., 1986), behaviour-based evidence has generally been inconclusive partly due to possible issues of correspondence (Fitch, 2020). Correspondence here refers to the close similarity or equivalence of the mental representations of individuals. The *level of correspondence* may vary with complexity even between humans but is very difficult to assess in non-human animals. For example, if I say "tennis ball" to my dog and the dog subsequently brings me the tennis ball, this may appear to be evidence of a good correspondence between human and canine mental representations, supporting the case for referential understanding. However, we have good reason to suspect that the mental representation evoked in a dog by the phrase "tennis ball" does not correspond to the representation held by its human partner. It is well possible that hearing this verbal cue is connected not only to a specific object but also to toys generally, or to a place (Tauzin et al., 2015a), where toys usually can be found or an action of retrieving a toy, even the praise or reward I usually give upon receiving a toy, etc. Moreover, what if my dog does not bring me the tennis ball? Does this imply a lack of mental representation and/or an inability to form a referential understanding of the word? Or simply a lazy dog? We had little or no means to study mental representations and level of correspondence before the implementation of non-invasive in vitro neuroscientific assessments became possible (e.g. Boros et al., 2024).

Although there is a consensus on the existence of mental representations and referential understanding in humans, claims of referentiality in animals often meet considerable scepticism. These critical views stem from the so-called associationist account of animal communication, the core idea of which is that animal communication is primarily based on learned associations between signals and responses. This view suggests that animals communicate through a system of conditioned responses where signals (such as sounds or gestures) become associated with specific outcomes or behaviours. Similarly to the debate on mentalization (or Theory of Mind) in non-humans (Halina, 2015), it is often the case with studies of referential communication in animals, that on the behaviour level, associationist explanations are also plausible. The pressure to rule these out often presents a great challenge. Fortunately, the mentalist account, which argues that animal communication involves an understanding of mental states, and relies on mental representations that can be recalled, manipulated and represented, is gaining acceptance in animal cognition research (Fitch, 2020), as neuroscientific investigations emerge in support of this view. Reflecting on the aforementioned example, some may argue that my dog bringing me the tennis ball upon hearing "tennis ball" is simply a conditioned response (verbal cue to response) and does not necessarily imply the existence of a mental representation or referential understanding, however, such an explanation is likely to be too simplistic in light of recent findings. A recent EEG study on dogs using the event-related potential (ERP) methodology demonstrated that, upon hearing an object's name, dogs form an expectation based on the mental representation evoked by the word,

linking the word and object in a referential manner (Boros et al., 2024 – see below for more details of this study).

3.1.2. Significance of object-related actions and the context

As briefly mentioned above, the argument that animals, in our case family dogs, form mental representations and exhibit referential understanding of certain words does not imply that these representations are identical, or even comparable to those of a human. According to owners' accounts and various studies, dogs' ability to comprehend speech is influenced by various factors such as gestural cues (Tempelmann, Kaminski and Tomasello, 2014), context (Gaunet and Deputte, 2011) and also related actions (Ramos and Ades, 2012). Controlled behaviour studies often fail to demonstrate dogs' comprehension of object labels beyond a limited set of items. These results could be interpreted as a lack of knowledge but may also stem from the performance-based nature of these measures. Additionally, stimulus words in such studies are typically presented "stripped" of context, gestures, or related actions – elements that might be integral to the mental representation formed. Thus, the word alone may be insufficient to evoke the intended representation. The finding that family dogs learn action labels more readily than object labels (Ramos and Mills, 2019) further supports this notion. Coupling actions with object labels may facilitate dogs' learning and improve their performance in behavioural experiments, potentially aligning more closely with neural evidence.

3.1.3. Individual differences, intraspecies variability

The question of word comprehension in family dogs is further complicated by recent findings of significant interspecies variation in the ability to learn object names (Fugazza et al., 2021). While the average family dog is capable of understanding only a few object names at most (Kőszegi et al., 2023; Ramos and Mills, 2019), some exceptional dogs exhibit remarkably fast and efficient learning abilities (Fugazza, Andics, et al., 2021), acquiring a vocabulary of up to hundreds of object names – usually toys (Fugazza, Dror, et al., 2021; Pilley and Reid, 2011). Importantly these exceptional dogs can retain object names for years (Dror et al., 2024). This striking intraspecies variability presents a valuable opportunity for research into the genetic and environmental factors underlying exceptional word-learning abilities. It also offers an opportunity to explore the underlying mechanisms. The emergence of word (object name) learning competence in dogs may serve as a model system for investigating the early evolution of human linguistic competence.

3.2. The role of prosody in communicative interactions

Prosody refers to a large group of features beyond syllables in speech that have a huge impact on the establishment of the phonological and lexical representation of spoken words (for a review see Dahlan, 2015). Here we use the term acoustic prosody to refer to features such as pitch, intonation, rhythm and intensity. In contrast, visual prosody pertains to the facial and bodily signals that accompany speech. Parallel to lexical content, we also adjust prosodic features to reflect our emotional states and intentions as well as to accommodate the audiences' needs and capabilities (e.g. Spinelli, Fasolo and Mesman, 2017).

When communicating with partners who have limited or developing language knowledge, we tend to exaggerate prosodic elements that enhance clarity and capture or maintain attention (for a review see Dominey and Dodane, 2004). A well-known example of such speech style is infant-directed speech (IDS), often referred to as motherese. IDS is characterized by heightened and more variable pitch, slower tempo, vowel hyperarticulation and several specific facial expressions and gestures that are uncommon or absent in adult-directed speech (ADS, for a review see Soderstrom, 2007). There is ample evidence that several prosodic features of natural IDS play a crucial role in language acquisition and are essential for healthy language development (for a review see Golinkoff et al., 2015). For instance, when caregivers produce

vowels and consonants for infants, they often exaggerate the acoustic differences between these sounds compared to adult-directed speech. This phenomenon, known as hyperarticulation, creates greater perceptual space between utterances, making it easier for infants to distinguish and form vowel and consonant categories (e.g. Fernald, 2000). Other acoustic prosodic features, such as heightened overall pitch and specific pitch contours, aid language acquisition by engaging infants and maintaining their attention during social interactions (e.g. Fernald and Kuhl 1987;). Besides the typical infant-directed acoustic prosodic features, people tend to use specific facial expressions, movements and gestures when addressing infants (e.g. Brand et al., 2002; Chong et al., 2003). However, while the role of infant-directed acoustic prosodic features in language acquisition is well documented, the contribution of visual prosodic characteristics to language development remains largely unexplored.

3.2.1. Prosodic characteristics of dog-directed speech

The prosody used when addressing dogs and infants shares many similarities. Both are characterized by heightened pitch, a wider pitch range, shorter utterances and more frequent happy facial expressions compared to adult-directed speech (e.g. Hirsh-Pasek and Treiman, 1980; Gergely et al., 2023). This resemblance is not surprising when considering the communicative cues that elicit social responsiveness from dogs and infants. Both are highly attentive and show a behavioural and neural preference for high-pitched voice (e.g. Trainor and Zacharias, 1998; Jeannin et al., 2017). Both rely on ostensive-communicative cues (see Section 2.2 for details) to engage in social interactions (e.g. Senju and Csibra, 2008; Téglás et al., 2012). Moreover, both dogs and infants show a preference for human faces displaying positive expressions over those with negative emotional cues (e.g. Kim and Johnson, 2013; Müller et al., 2015).

In addition to the similarities, there are at least two significant differences between dog- and infant-directed prosody. First, hyperarticulation appears to be absent in dog-directed speech, which may suggest that speakers do not intend to teach language to canine partners (e.g. Burnham et al., 2002). The second notable difference lies in the facial prosodic features of the two speech styles. Speakers tend to use less intense and less frequent facial expressions when addressing dogs compared to infants and even adults (Gergely et al., 2023; Koós-Hutás et al., 2024a). Interestingly, and in line with previous studies, speakers still employ exaggerated acoustic prosody with dogs, suggesting that the two modalities may serve different – and likely species-specific – functions during social interactions with dogs and humans (Koós-Hutás et al., 2024b).

3.2.2. Language tutoring versus attention-getting features of prosody

In a recent comparative study, Koós-Hutás and co-workers examined the acoustic and facial prosody of female and male speakers in different situations, including object label tutoring and attention-getting scenarios, directed at their own 6–18-month-old infant, family dog, and spouse (Koós-Hutás et al., 2024a, 2024b). This design allowed the researchers to investigate which prosodic features contributed to attention-getting versus language tutoring functions. Previous research has shown that large pitch contours in infant-directed speech (manifesting as a wider pitch range) can facilitate word segmentation, thereby aiding language acquisition (e.g., Trainor and Desjardins, 2002). In contrast, it has been shown that a higher overall pitch, which is crucial for attention-getting, not only fails to facilitate but also impedes word segmentation (e.g., Trainor and Desjardins, 2002). When uttering an object label to be taught to their infants, speakers used both attention-getting features (i.e. higher overall pitch) and language learning aids (i.e. wider pitch range and longer utterances) in their prosody. Interestingly, when speaking to their dogs, speakers used only the attention-getting tool, while when addressing their spouses, they used only one language learning aid: longer utterances (Koós-Hutás et al., 2024b). These results further support the notion that, when

talking to dogs, speakers do not aim to teach language but instead use acoustic tools to engage their canine partners in social interactions.

4. Neurocognitive aspects of linguistic competence in dogs

Recent advances in the field of canine neuro-cognition have allowed for the development of fully non-invasive methods to gather brain activity data related to dogs' social cognition (Bunford et al., 2017). Such advances are crucial in the field of canine linguistic competence where there is a dissociation between production and understanding, much like in the case of preverbal infants (Kuhl, 2010). In a recent systematic review of the effects of sleep on memory and word learning in infancy (Belia et al., 2023), authors surveyed the available sixteen articles on the associations between sleep and the memory processes involved in word learning in infancy and found positive associations between sleep and word learning in fifteen cases.

Canine polysomnography (PSG) is a fully non-invasive method (Kis et al., 2014), that allows for the recording of dogs' EEG activity during sleep. Relative EEG spectrum (derived from the absolute power spectral density for each frequency bin) is extracted for the different sleep stages: drowsiness, non-REM, and REM. In addition, sleep spindles (transient oscillations in the sigma range, characteristic of non-REM sleep) can also be quantified. Canine PSG can be used to test the effect of word learning or similar situations on dogs' brain activity as well as to see how individual differences in linguistic competence or test performance relate to variation in brain activity.

Another EEG-based non-invasive technology is the event-related potential (ERP) method (Törnqvist et al., 2013). An ERP is the measured brain response directly resulting from the dogs' specific sensory event. Canine ERP can be used to test the potentially differential processing of various linguistic stimuli, with the method's specific strength being its high temporal resolution. On the other hand, functional magnetic resonance imaging (fMRI) is used for its good spatial resolution to locate stimuli-related activity (blood-oxygen-level-dependent signal) in specific regions of the brain. The canine fMRI is fully non-invasive, but requires intensive training, as dogs must remain motionless for several minutes during the procedure (Andics et al., 2014). Canine fMRI (as well as canine EPR studies) can be used to test the processing of various linguistic stimuli and brain data might be correlated with dogs' behavioural measures recorded in a separate session.

4.1. Canine sleep EEG in the context of word learning and linguistic competence

4.1.1. EEG evidence of sleep-driven memory consolidation in a word learning task – the neurally detectable effect of learning new words

Memory consolidation evidence was found related to word learning (Kis et al., 2017) using non-invasive polysomnography. Dogs on one occasion participated in a command learning task, where they had to learn novel words associated with previously known commands (Sit! and Lay down!). On another occasion (either before or after command learning) a control task was administered, where dogs carried out the same Sit and Lay down actions, but using the previously known commands without learning new words. On both occasions the behavioural tests were followed by a polysomnography recording, which showed that dogs' brain activity (sleep EEG spectrum) differed between the word learning versus the control occasion: during non-REM sleep slow wave delta (1–4 Hz) activity increased, while alpha (8–12 Hz) activity decreased; during REM sleep theta activity increased. A follow-up study on the same dataset (Iotchev et al., 2017) further demonstrated that, after word-learning sessions (compared to the control condition), sleep spindle density also increased as well.

4.1.2. Sleep EEG correlates of word learning efficiency

Behavioural data (Kis et al., 2017) showed that dogs' performance in

the above-described word learning task significantly improved after the 3-hour-long sleeping session (polysomnography recording) compared to the pre-sleep baseline. Furthermore, individual differences in learning gain (performance improvement compared to baseline) were related to the dogs' sleep EEG spectrum: decreased REM sleep delta (1–4 Hz) as well as increased REM sleep beta (12–30 Hz) power co-varied with better learning acquisition in the word learning task. The same word learning task (associating new commands with previously known actions) was also used in an experiment (Reicher et al., 2024) where dogs participated in both a controlling and a permissive training style session. These sessions differed in the rewarding of correct actions (food reward only with no praise vs. food reward combined with verbal and physical reinforcement) as well as in the reaction to incorrect actions (scolding the dog using a firm but not threatening voice vs. calling the dog with a high-pitched voice and encouraging it). Such differences in training styles did not have a main effect on dogs' test performance, nor on their post-sleep re-test performance. Similarly, no effect of training style on sleep EEG spectrum was found. Sleep spindles were also found to be associated with post-sleep learning in the word-learning tasks. Higher sleep spindle density co-varied with better learning gains both in the dataset of Kis et al., 2017 (Iotchev et al., 2017) as well as in the supportive condition of Reicher et al., 2024 (Iotchev et al., 2020).

4.1.3. Novel approaches to potentially study (and aid) linguistic competence (and word learning)

Sleep deprivation: Sleep deprivation, defined as inadequate sleep duration or quality, disrupts cognitive functions essential for learning, such as attention, working memory, and executive function. Several studies have demonstrated that both acute and chronic sleep deprivation negatively impact the ability to learn and recall new words. For instance, sleep-deprived individuals exhibit reduced accuracy and slower reaction times in word-learning tasks compared to those who are well-rested (Drummond, 2000). Sleep deprivation can be induced through Total Sleep Deprivation (TSD) where participants are kept awake continuously for a set period, typically ranging from 24 to 72 hours or Partial Sleep Deprivation (PSD) where participants are allowed to sleep 4–6 hours per night. PSD can also be achieved through selective stage deprivation in which participants are awakened during specific sleep stages such as REM or slow-wave sleep. PSD is a more ecologically valid method compared to TSD as it better mimics real-world scenarios of chronic sleep restriction (Van Dongen et al., 2003). Sleep deprivation protocols can be combined with neuroimaging techniques to investigate their effects on brain function. Neuroimaging studies have shown that sleep-deprived individuals exhibit reduced activation in brain regions associated with memory encoding, such as the hippocampus and pre-frontal cortex (Yoo et al., 2007). This reduced activation suggests that sleep deprivation impairs the neural mechanisms required for effective word learning.

There is evidence that selective sleep deprivation can be conducted with family dogs in a fully non-invasive manner. In a REM deprivation study, even a 3-hour-long disturbed afternoon sleep led to alterations in a post-sleep emotion recognition task (Bolló et al., 2020). In future studies, applying this validated protocol – which is easily, non-invasively and cost-effectively applicable – could provide insights into how sleep deprivation affects command learning-related memory consolidation in dogs. Such studies could offer new perspectives on how dogs acquire their unique ability to participate in the human communicative system.

Targeted Memory Reactivation (TMR): Targeted Memory Reactivation (TMR) is an emerging technique in cognitive neuroscience that aims to enhance memory consolidation by triggering specific memory traces during sleep. TMR involves presenting cues (usually sounds or odours) that are associated with learning experiences while an individual is in a specific sleep stage, typically SWS. After a learning experience, during SWS, the hippocampus spontaneously replays newly encoded information, which strengthens synaptic connections in the

neocortex, facilitating long-term memory storage (Diekelmann and Born, 2010). TMR leverages this natural process by externally cueing the brain during SWS to reactivate specific memories and enhance synaptic connections.

Although TMR is a valuable tool for accelerating memory consolidation and has several clinical implications (Schouten et al., 2017), the underlying mechanisms are still unknown. Human and rodent studies have explored various factors, such as sleep duration (Creery et al., 2015), delta power (Oudiette et al., 2013), changes in negative-to-positive slow oscillation slope (Rihm et al., 2014), theta power (Schreiner, Lehmann, and Rasch, 2015), as well as spindle power and density (Creery et al., 2015; Rihm et al., 2014) which were found to be positively correlated with the cueing benefits of TMR. However, other studies have failed to confirm these associations (Cox et al., 2014; Diekelmann et al., 2012).

The existing non-invasive polysomnographic method provides an opportunity to investigate the effects of TMR and its controversial underlying mechanisms in family dogs. To the best of our knowledge, there is currently no evidence of TMR being successfully applied to dogs. Future research should explore this possibility.

4.2. ERP evidence of linguistic competence in dogs

Voice and speech processing of awake family dogs has also been tested with the event-related potential (ERP) method. An early (200–300 ms) and a late (650–800 ms) difference was present in the ERPs for known instruction words versus phonetically dissimilar nonsense words; there were no differences between the ERPs for known versus phonetically similar nonsense words (Magyari et al., 2020).

Dogs were also found to show a differential ERP response depending on the species of the caller, demonstrated by a more positive ERP response to human vocalizations compared to dog vocalizations in a time window between 250 and 650 ms after stimulus onset; a later time window between 800 and 900 ms also revealed a valence-sensitive ERP response in interaction with the species of the caller (Bálint et al., 2022). The same procedure was repeated on sleeping dogs, and a species (between 250–450 and 600–800 ms after stimulus onset) and a species by valence interaction (between 550 and 650 ms after stimulus onset) effect was observed during drowsiness. A valence (750–850 ms after stimulus onset) and a species by valence interaction (between 200 and 300 ms and 450–650 ms after stimulus onset) effect were also observed during non-REM specific at the Cz electrode (Eleőd et al., 2023).

Dogs' ERPs for artificial words previously presented in a continuous speech stream with different distributional statistics revealed an early effect (220–470 ms) of transitional probability and a late component (590–790 ms) modulated by both word frequency and transitional probability (Boros et al., 2021). ERPs to objects primed with matching or mismatching object words showed a mismatch effect at a frontal electrode, with a latency (206–606 ms) comparable to the human N400; a greater difference for words that dogs knew better, according to owner reports, further supported a semantic interpretation of this effect (Boros et al., 2024).

4.3. Canine fMRI studies in the context of word learning and linguistic competence

Fifteen years ago, the first non-invasive functional MRI (Magnetic Resonance Imaging) study was published on unrestrained awake family dogs (Tóth et al., 2009). This pioneering training technique which taught dogs to lie motionless in an MRI scanner, later enabled researchers to conduct non-invasive functional MRI studies. Using this methodology, it has been showed that dogs and humans have functionally analogous voice-sensitive areas in their primary auditory cortices, share regions that respond more to conspecific vocalizations and both species process emotionally valenced vocal sounds in secondary auditory regions (Andics et al., 2014). Since then, numerous studies

Table 1

Summary of the main findings on linguistic competence in dogs.

Main concomitants of linguistic competence	Pros & cons of the human infant-like linguistic abilities of dogs - summary of research findings -		Selected supporting references
	PROS	CONS	
Attending to humans' attentional state	ability to distinguish between attentive and inattentive human partners		Kaminski et al. (2009, 2013)
	human-like susceptibility to the audience effect		Kiss et al., (2020); Marshall-Pescini et al., (2013)
		willingness to obey is unaffected by changes in human visual attention	Kiss and Topál, (2019)
Understanding referentiality	spontaneous and flexible use of human pointing and gaze direction early		Miklósi et al. (1998)
	developmental responsiveness to human directional gestures		Riedel et al., (2008); Salomons et al., (2021)
	understanding the referential nature of directional signals: pointing ¹ , looking ² , speech direction ³		¹ Lakatos et al., (2009); ² Virányi et al., (2004); ³ Langner et al., (2023)
	Selectively develop referential expectations based on human gaze cues.		Soproni et al. (2001)
	Preceding or accompanying human ostensive signals specifically enhance the referential interpretation of directional gestures in dogs		Kaminski et al. (2012); Téglás et al., (2012)
		Directional gestures are interpreted as imperatives rather than as signals to guide attention toward a specific referent.	Wobber and Hare, (2009)
		Pointing refers to a direction or location for dogs, rather than to a specific target.	Tauzin et al., (2015b)
		Referential understanding of human directional signals is limited to cooperative contexts.	Pettersson et al., (2011)
Responsiveness to ostensive signals (perceiving)	infant-like, early emerging preference for establishing eye		Virányi et al. (2008)

(continued on next page)

Table 1 (continued)

Main concomitants of linguistic competence	Pros & cons of the human infant-like linguistic abilities of dogs - summary of research findings -		Selected supporting references
	PROS	CONS	
communicative intention)	contact with humans Ostensive signals facilitate responses to directional signals: gaze following ¹ , pointing ² Cues that signal the human's communicative intention increase chances of success in social learning situations ostensive-communicative signals induce a 'ready-to-obey' or 'ready-to-learn' attitude	which, however, is largely tied to the here-and-now	¹ Duranton, Range and Virányi, (2017), ² Tauzin et al., (2015a) Pongrácz et al., (2004) Topál et al., (2009)
Generalization of knowledge		no evidence of an infant-like bias to receive generic information about shared knowledge in ostensive communicative contexts	Topál et al., (2009)
Sensitivity to prosodic features of verbal addressing	shared acoustic features between dog- and infant-directed speech selective responsiveness in the non-primary auditory regions to both dog- and infant-directed speech prosody (fMRI) valence-sensitive behavioural and physiological ¹ as well as neural ² responses in the primary auditory regions (fMRI)		Hirsh-Pasek and Treiman (1982); Gergely et al. (2017) Gergely et al., (2023) ¹ Siniscalchi et al., (2018); ² Andics et al., (2014)
Word/speech comprehension	comprehensive vocabulary averages 30–90 words (owners' reports) separate neural processing of the reward value of words in terms of both meaning and intonation (fMRI)	Speech comprehension is influenced by various factors such as gestural cues ¹ , context ² , and related actions ³	Pongrácz et al., (2001); Reeve and Jacques, (2022) ¹ Tempelmann, Kaminski and Tomasello, (2014); ² Gaunet and Deputte, (2011); ³ Ramos and Ades, (2012) Andics et al., (2016)

Table 1 (continued)

Main concomitants of linguistic competence	Pros & cons of the human infant-like linguistic abilities of dogs - summary of research findings -		Selected supporting references
	PROS	CONS	
	Neural discrimination of know instructions from phonetically similar nonsense (EEG-ERP) Objects primed with matching or mismatching object words show a mismatch effect in EEG responses. neural sensitiveness to various aspects of human speech: speech naturalness and language familiarity ¹ ; word familiarity ² ; segmental and suprasegmental content ³		Magyari et al. (2020) Boros et al. (2024) ¹ Cuaya et al., (2022); ² Prichard et al., (2018); ³ Boros et al., (2020)
Label learning	remarkably fast and efficient abilities to learn object-label associations ¹ and retain them in memory for years ² acquiring a vocabulary of object names containing up to hundreds	The vast majority of family dogs are capable of understanding only a few object names at most.	¹ Fugazza et al., (2021)b; ² Dror et al., (2024) Fugazza, et al., 2021a; Pilley and Reid, (2011) Kőszegi et al., (2023); Ramos and Mills, (2019) Kis et al. (2017)
	Memory consolidation after a word learning task is facilitated by sleep and the process is detectable by EEG measurements. Sleep EEG correlates of word learning efficiency		Reicher et al. (2024); Iotchev et al., (2020)

have used such specifically trained family dogs, who can stay still in the scanner, to examine neural correlates of speech.

In a ground-breaking study, Andics and co-workers (2016) studied whether and how intonational and lexical cues in human speech are processed in dog brains. To do so, four types of speech stimuli were played to the dogs: praise words with praising intonation, praise words with neutral intonation, neutral words with praising intonation and neutral words with neutral intonation. This study had three major findings: (1) intonation is processed independently from word meaning in the primary auditory regions of dogs, (2) word meaning shows laterality and is processed independently from intonational cues, and (3)

dogs rely on both meaning and intonation when processing the reward value of words, as praising words with praising intonation evoke the greatest neural responses from primary reward areas in the dog brain.

Recent findings also show that dog brains are sensitive to various aspects of human speech such as speech naturalness (i.e. scrambled versus normal speech), language familiarity (native versus foreign language – Cuaya et al., 2022), word familiarity (Prichard et al., 2018), and both segmental (changes in speech sounds) and suprasegmental (changes in voice identity) content (Boros et al., 2020). Moreover, there is also evidence that dogs, similar to human infants, are sensitive to speech prosody that is directed at them (Gergely et al., 2023).

5. Conclusions and outlook

Despite the impressive body of research on domestic dogs' interspecies communicative and comprehensive linguistic competence, there are still a lot of open questions. One of the main challenges is the apparent discrepancy between evidence from neuroscientific studies (EEG, fMRI) and those coming from experiments measuring behaviour. Behavioural studies often fail to demonstrate that dogs have a comprehensive vocabulary beyond a handful of words (Reeve et al., 2022; Kőszegi et al., 2023), primarily consisting of action commands (Ramos and Mills, 2019). However, some exceptional dogs – though very few worldwide – have been documented to comprehend and respond adequately to object labels in the hundreds (Bloom, 2004; Pilley, 2011; Fugazza et al., 2021; Dror et al., 2023), acquiring new words rapidly (Fugazza et al., 2021), and retaining this knowledge for up to two years (Dror et al., 2024). This remarkable intraspecies variation in dogs' interspecies communication presents a valuable opportunity to model the early evolution of linguistic competence in a species that, although only distantly related to humans shares the same environment.

As detailed above, research findings from behavioural, physiological and brain imaging studies suggest that domestic dogs possess impressive linguistic capacities, such as lexical processing and even referential understanding (see Table 1 for the summary of main findings). However, it remains puzzling why family dogs often fail to demonstrate these capabilities in behaviour studies, particularly under laboratory conditions. To address this challenge, it would be necessary to adopt a more synergistic approach, to tackling existing methodological issues. This could ultimately lead to a clearer, more evolutionarily and ecologically valid framework for understanding canine linguistic competence.

Author statement

All authors contributed significantly in the literature search and the preparation of this critical review.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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