Review paper

How is communication learned, processed, and used across different species, and what are some ways to facilitate interspecies communication?

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Abstract
Language has long been considered an ability unique to humans. However, studies have begun to show complex languages with morphosyntax in other animals. Moreover, animals, especially those in symbiotic relationships, use and respond to other species' languages. This paper examines the evolution of communicative behaviors with hopes of better understanding language as a social behavior that is not unique to humans. First, some similarities and differences in how animals learn and interact with their language are surveyed, and compared to human infants. Next, the evolution of communication and biological structures relevant to vocal signals are discussed. Finally, some possibilities to facilitate interspecies communication are explored, ending with future directions. This paper challenges the assumption that language is unique to humans, with applications in improving animal welfare and initiating interspecies cooperation.

Keywords
Animal communication, Interspecies communication, Interspecies cooperation, Vocal learning, Communication evolution, Language, Innate communication, Social reinforcement learning, Brain computer interface, Chemosignals

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Introduction

Communication is any interaction between two (or more) animals that cause a behavioral change in the receiver(s) (1). Communication is diverse, and can be seen in many forms and modalities, such as electric pulses, as in electric fishes, gestures, as in non-human primates, or ultrasonic vocalizations, as in mice. Language is a type of communication system and may contain structures such as words, grammar, and semantic syntax (2). While communication often occurs intraspecifically (within the same species), there are cases where animals communicate with other species (heterospecifically), including animals with symbiotic relationships and those that form mixed-species aggregations. For instance, warthogs lie down in front of a group of mongooses to signal that they want their ticks removed (3). This type of communication is often called interspecific communication.

In general, acoustic communication and vocal learning have been well-studied in only a few species, including songbirds, mice, and humans (*Homo sapiens*). One reason is due to the legacy of the outdated belief that language is equal to spoken language. Sign language was not widely considered a true language until William Stokoe's 1960 paper documenting its structure and complexity, although it has existed as long as spoken language, or maybe prior to spoken language, as there is increasing evidence that gestures may have evolved first (4-5), suggesting the importance of studying diverse forms of languages.

A major cause of the gap in knowledge between human and non-human animal communication could be human-centric biases derived from the common belief that humans are the most intelligent animal with the most complex linguistic and social systems. However, non-human animals, such as dolphins, have been found to be intelligent, and many social insects form complex societies (6-7). Despite this, some believe that language and the complexity that led to its evolution are unique to humans (8). Yet the definitions of "smart", "language", and even "social complexity" have been based on human behaviors. These beliefs could lead to anthropomorphizing non-human animal behaviors, setting unrealistic expectations, and overlooking behavioral diversity across species. Thus, it is important to examine how different species learn, process and use their own languages, including examples of interspecies communication that could be facilitated between human and non-human animals to improve animal welfare and initiate interspecies collaboration.

This paper discusses how communication is learned, processed, and used across different species, and proposes some ways to facilitate interspecies communication. By focusing on vocal communication, a well-studied and accessible modality to facilitate interspecies communication between humans and non-human animals, and investigating vocal learning, it shows that many vocal signals could be learned, bringing hope to facilitating interspecies communication. Also, the neural biological structures suggest that any animals in complex social environments can form complex vocalizations, suggesting possibilities of facilitating interspecies communication between humans and other social animals. First, Section 1 compares how different animals learn and acquire languages, with a focus on vocal learning and social reinforcement learning. Next, Section 2 compares the biological structures with a discussion on the evolution of communication. Then, Section 3 provides some possible ways to facilitate interspecies communication, followed by future directions and concluding remarks in Section 4.

1.0 How do different species learn, acquire, and interact with communication cues?

1.1 Innate communication

The animal kingdom is full of diversity, not only in terms of communication but also in terms of social or parental care structures, ontogeny, and life categories. Some species are born altricial, underdeveloped, and relatively immobile, with immature perception systems at birth, such as human and oscine passerines. These species require parental care. Other species are precocial and only need limited to no parental care, such as Australian brushturkeys (*Alectura lathami*), which requires no parental care, and blue wildebeest (*Connochaetes taurinus*), which can stand within minutes after birth (9-10). Developmental pace varies as well. Within the parental care and social structure system, there is also great diversity, including biparental care, monogamy, polygamy, cooperative breeding, etc (11). In insects, fish, and anurans, most young are developed with no parental care, although some families have notable exceptions (e.g. poison dart frogs, cichlid fishes, Hymenoptera, etc). In contrast, species like Sockeye salmon (*Connochaetes taurinus)* die after spawning, lacking the opportunity to teach or care for their young. Nonetheless, although there is no post-natal or post-hatching care for many species, there may be learning opportunities before the emergence in the uterus or egg, termed prenatal learning. Many species, including birds, humans, and mice can show auditory learning during embryonic development prenatally (11). This diversity leads to inquiries about innate communication and the role of learning in the development of adult-typical communication.

Innate communication is any communicative behavior an animal requires no learning to perform. In contrast, learned signals are those which are acquired at some point during development and which an animal will not produce unless exposed to the behavior either actively (i.e. teaching) or passively (i.e. observation). Currently, most animals that do not show vocal learning or other forms of learning regarding communication are categorized as having innate communication. Innate communication is widespread and has been shown in fish, birds, rodents, humans, and non-human primates. For instance, studies using cyprinid fishes (*Codoma ornata*) have analyzed recordings of behaviors and sound trials of sexually matured offsprings raised in isolation. The result showed subjects producing stereotypical acoustic signals and courtship behaviors in the appropriate context similar to their parents despite being raised in isolation, suggesting the ability to produce communication is innate in this type of fish (12). It remains unknown how fish know to produce innate signals, and whether these behaviors are encoded in genes. In addition, more studies are needed to explore whether or not dialects, or variations in communication, exist within the same fish species and other animals with primarily innate signals. However, there has been research investigating the neural mechanisms underlying innate vocalizations. Triggered by emotional states, innate vocalizations, such as some alarm calls in chickadees and ultrasonic vocalizations in mice, can be linked to brain stem activities and the periaqueductal grey (PAG) area in rodents and birds (14-13). Since PAG also regulates behaviors, including respiratory, defensive, and sexual, it could help to coordinate different behaviors with vocalizations (13).

Even animals exhibiting learned communication, such as songbirds and humans, still have ‘ancestral circuitry’ for innate signals (14). As much as scientists credit humans for having sophisticated language, humans have innate communication as well, including involuntary responses to stimuli such as tickle-induced laughter, or certain emotional expressions, such as crying due to sadness, which also could be linked to PAG, similar to birds and rodents (13). Since these signals can still be produced when deaf, and therefore unable to hear examples of the behavior, it suggests that they are innate (13, 15). They can also be traced along the phylogenetic tree, as similar innate communications are found in non-human primates (16).

1.2 Vocal learning

In addition to innate signals, complex vocal learners, such as humans, are born with the innate brain plasticity to learn languages, including brain pathways to finely control and enable the production of complex vocal language (13). Yet, though animals can be born with the biological structures that allow for complex communication, they still need to learn to acquire sophisticated communication. For example, young male zebra finches without a father fail to learn species-typical songs (17). This is where vocal learning plays a role.

Vocal learning is defined as learning to produce vocalizations by imitating the sounds of others. Unlike the more common auditory learning, which is learning to recognize and distinguish sounds, vocal learning is rare in non-human animals and even non-human primates. There are three types of vocal learning: usage learning, production learning, and vocal comprehension learning. Vocal usage learning is when an animal learns to use a sound in an appropriate context. The sound itself could be innate. For example, a baby vervet monkey learning to apply an innate alarm call to a specific predator would show vocal usage learning (18). Vocal production learning is when an animal learns to make a new sound but does not necessarily learn what context it should be used. For example, pet birds mimicking random utterances would be vocal production learning (19). Sometimes both production and usage learning could occur simultaneously when an animal learns to make a new sound and uses it in a new context, such as when a baby animal learns to produce a new alarm call and apply it to a predator (20). Vocal comprehension learning is when a response or meaning to a vocalization is learned, independent of the ability to produce the vocalization themselves. There are many examples of vocal comprehension learning in non-human animals such as dogs learning the meaning of English words, the association of the word 'sit' with the action of sitting down (21), for example, but obviously unable to produce them. Koko the gorilla has also been shown to understand more English words than the amount of sign language she can produce (22-23).

Vocal learning has been well-studied in humans and songbirds. It is thought to be an ability unique to only a handful of animals, including pinnipeds, cetaceans, bats, elephants, passerine birds, hummingbirds, and parrots (24-25). Those animals are sophisticated vocal learners, which means animals that typically produce complex signals, require auditory feedback, show vocal imitation, and may exhibit social reinforcement vocal learning by adapting and modifying communication according to social experience. However, recent research has shown more animal species that possess some degree of vocal learning, including mice (26), goats (27), non-human primates (28-29), and musk ducks (*Biziura lobata*) (30), leading to the 'Continuum Hypothesis' proposed by Arriage and colleagues (2012) which separates species into non-learner, limited vocal learner, moderate vocal learning, complex vocal learner, and high vocal learner (23). For instance, recent studies have suggested that mice show some similarities to songbirds and have vocal learning but at a limited level. Mice have similar activity in the forebrain motor cortex and striatum when singing compared to humans and songbirds. They also require vocal feedback and could change their song according to others, one characteristic of vocal learning and vocal mimicry (26). Similarly, baby macaques raised by heterospecific macaque parents have been shown to use vocalizations of their parental species instead of their own (29). This method, cross-fostering, as shown in Japanese macaques (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*), could indicate that their vocalizations are learned through vocal learning instead of innate vocalizations coded in genes, suggesting a preference for signal familiarity. However, it is unclear how different Japanese and rhesus macaque vocalizations are.

There are some similarities and differences in vocal learning across animal species. Both humans and songbirds such as zebra finches' capacity for sensorimotor learning (when vocalization starts) are better early in development. Both also go through a transitional "babbling" phase where the vocalizations initially are immature and do not resemble adult communication, but eventually match the tutor (31-32). However, humans, and some species of songbirds and parrots, generally have open-ended vocal learning, which means having the ability to learn vocalization even after adulthood. Compared to humans, there is a variety of complexity in terms of syntax, whether birds carry on vocal production learning in adulthood, and which sex shows vocal learning (33). Although vocal learning in songbirds research has been historically male-centered (22), female songbirds sing and exhibit vocal learning in many species (34-35).

In sum, vocal learning is a rare ability in non-human animals and non-human primates, involving three types: vocal usage learning, vocal production learning, and vocal comprehension learning. While historically studied only in a few species, recent research has revealed vocal learning in other species, and there are some similarities and differences in vocal learning across species.

1.3 Social reinforcement learning

As any type of communication, including acoustic communication, is a tool used to live in social groups, learning how to adjust appropriate responses and vocalizations based on the reactions of others is crucial. This type of learning is social learning, and it plays an important role in vocal learning. For example, a male bird may choose to perform a song or courtship behavior according to the female bird's response (17). On the other hand, reinforcement learning refers to 'operant' behaviors learned through either positive or negative reinforcement. For instance, think of training a dog (*Canis lupus familiaris*) to do tricks, when the dog successfully completes the trick, a positive reinforcement or treat is given. Therefore, the dog is more likely to complete the trick next time. Social learning and reinforcement learning aid each other by producing social reinforcement learning which means, learning to behave in one way over another based on the social outcomes (36). Research in social reinforcement learning via social learning has been done in some non-human animals, including zebra finches, marmoset monkeys, and bats.

Studies in zebra finches, a sophisticated vocal learner, have shown that female feedback on immature male songs leads to better songs as young male birds sing more frequently and are more motivated to sing (17). This motivation comes from the dopamine released from the dopaminergic connections in the ventral tegmental area (VTA) in the striatum each time the female gives positive feedback for an attractive song, which also has a connection with Area X, part of the song system. Hormones, such as arginine vasotocin, a type of nonapeptide present in all non-mammal vertebrates, are also involved in social motivation for song learning (17, 37).

Similarly, studies in marmoset monkeys, which are classified as limited vocal learners, have shown that when twins are raised differently, one exposed to more contingent adult feedback calls and one with less feedback, showed that the twin who was exposed to more feedback developed mature calls faster (38). This suggests social reinforcement learning can enhance vocal production learning. When compared to human infants and songbirds, marmoset monkeys also show similar FOXP2 (a forkhead box gene) expression in cortico-striatal circuits that are thought to be related to speech and language impairments (39). A possible evolutionary correlation of social reinforcement learning in altricial species such as monkeys, and humans is the development of more mature calls as a way to attract caretakers (38).

Another example of social learning is pup-directed speech in bats, which is used to seek maternal care. “Motherese”, (also called pup, chick, or infant-directed speech, depending on the animal) is a form of socially influenced vocal feedback in which the vocalizations are slower and higher pitched than adult-directed vocalizations (40). Although parental care is restricted to females, both female and male greater sac-winged bats (*Saccopteryx bilineata*) have been shown to produce pup-directed vocalizations, which differ from adult-directed vocalizations in this way. Males have used pup-directed calls as a response to pup’s isolated calls (40). Parents also adjust their response to the call according to the pup’s calls.

In short, zebra finches, marmoset monkeys, and greater sac-winged bats have all been shown to modify their vocalizations according to social feedback, and as a result, get better at producing vocalizations with social reinforcement learning.

2.0 Communication-related biological structures and the evolution of complex communication

Overall, across animal species that display vocal learning, it appears as though forebrain structures are important for vocal learning, while motor control structures are necessary for fine-tuning vocal production (35). However, the exact brain structures do not appear to be homologous but rather have likely convergently evolved, as distantly related animals such as songbirds and humans are both regarded to be sophisticated vocal learners with extensive vocalizations despite the fact that birds evolved from theropod dinosaurs and mammals from synapsids, which diverged around some 300 million years ago (41). (For more details on specific vocal learning related structures, see Table 1)

Table 1: Comparative neurobiology table of seven vocal learning animals and a non-vocal learning control

Animal	Vocalization structures	General areas related to vocalizations	Brain areas related to vocal learning and production	Brain areas related to auditory processing
Aves (birds)				
Parrot (33, 42)	syrinx	MMSt, NAO, MOc, AAC, lAM	HV; HVo; NAO; LPOm; LAN; LAHV; NLC; AAC; DMm; DM	CMHV; NCM; PC; ACM; MLD
Hummingbird (33, 43-44)	syrinx	VAS; VAN; VLN; VA; VMN; VMM	VMH, VAP; VAM	CM; NCM; CSt; Ai; NDC; MLD
Songbird (33, 44-47)	syrinx	Area X; MAN; MOc-like; HV*; RA; NIF; Av	nXIIts; DM	CM; CSt; NCM; MLD; L2
Cowbird* (48)	syrinx	NA	anterior forebrain pathway with basal ganglia relay; posterior pathway, HV* and RA	NA
Primates				
Human (44)	larynx	NA	aSt; ACC; aSMA; DLPFC; aT; Broca; FMC; PAG; Am	Wernicke
Marmoset monkey (39, 13)	larynx	NA	PFC; PMC	A1; CM*
Non-primate mammal				
Bats (49-50)	larynx	NA	PAG; ACC; PLA	FAF; CN; NACT; SG; SC; AC; IC; SOC; NLL; MGB; CP
Control* (48, 14)	NA	RVL, Brainstem, Midbrain	NA	NA

1. HV* The articles (33, 48) used HVC but did not define it. However, other articles mention it as the telencephalic sensorimotor nucleus (51) thought to be hyperstriatum ventrale (39), which is the same as HV. To eliminate confusion, abbreviations with the same meaning such as HVC and HV are changed to have the same abbreviation.
2. Cowbirds* is a brood parasite
3. Control* is a general animal, not referring to a specific order
4. A1; CM* It is unclear whether the above findings indicate innate or learned vocal signal processing (39)
5. CM* The article (39) defined it as the central-medial belt, however, another article defined it as the Caudal mesopallium (33).
6. Above are some examples of neurobiological structures but not all

What might have led mammals and birds to converge on similar neural pathways for vocal learning and why might they evolve complex, learned communication in the first place? Previous theories that explain the evolution of language include the "social complexity hypothesis", which suggests that an increase in vocal complexity is caused by an increase in social group complexity. According to this theory, organisms with bigger, more complex social groups would have more complex vocalizations (52). Although this paper focuses on vocal communication, ants with sophisticated pheromone communication could correlate with this theory as they have complex social groups too. Another previous theory is the "Machiavellian intelligence hypothesis", also known as the "social brain hypothesis" (53). This theory suggests a positive correlation between the size and complexity of brains and the size and complexity of social groups, meaning larger brains evolved to adjust to larger, more complex social groups. In addition, neurobiological structures behind vocal learning seem to link to fine motor controls that allow the production of new vocalizations. The "Kuypers-Jürgens hypothesis", which suggests a direct control of the laryngeal motor cortex for laryngeal motor neurons, may support this (54). These theories suggest that language is a tool for socialization as a more complex social environment leads to biological changes and more complex language. Language possibly evolved to satisfy the need to communicate in their social environments, which suggests that any species living in a complex social environment would need to have complex communications as an accommodation.

3.0 What are some ways to facilitate interspecies communication?

Symbiotic relationships are long-term, close interactions between two species. It could benefit both parties, as in mutualism, harm one party, and benefit the other, as in parasitism, or benefit one party but not affect the other, as in commensalism.

Interspecies communication has been observed in many symbiotic species, especially species engaged in mutualism. For example, goby fish and pistol shrimp are in a roommate relationship, living in the same burrow that the shrimp maintains (55). The goby fish would warn the pistol shrimp regarding danger by flicking its tail while the shrimp communicates about its existence by touching the fish with its antennae. Likewise, with mostly similar prey and predators, dwarf mongooses (*Helogale parvula*) forage with hornbill species *Tockus deckeni* and *T. flavirostris* where hornbills benefits by gaining easier prey access while allowing mongooses to reduce vigilance time, enabling safer and more efficient foraging (56). The hornbills and mongooses will wait for each other and avoid foraging alone with the hornbill usually communicating the start of forage with a "chivvying" behavior and the alpha female mongoose signaling a "moving out" call for their group and the bird to start foraging.

Some animals take advantage of environmental “cues" by eavesdropping on heterospecific communications, such as squirrels eavesdropping on robins’ alarm calls to access danger levels (57), male tungara frogs (*Engystomops pustulosus*) responding to heterospecific frog calls for predation (58), and ant-following birds eavesdropping on other ant-following bird species to find army ants for prey (59), which could be a learned behavior based on ecological experience, suggesting the possibility for other species to learn eavesdropping behavior. Some species, such as flycatcher birds, *Lanio versicolor*, and *Thamnomanes schistogynus*, even exploit other birds’ eavesdropping behavior on their alarm calls by using “alarm call deception” to access prey abandoned by disturbed birds (60). However, as those “cues” are not intended for the eavesdropping species, this behavior is not communication, suggesting the importance for interspecies communication research to move beyond alarm calls and whether they can be used and perceived in mixed species assemblages. Since ways to facilitate interspecies communication are currently a gap in research, this section discusses previous attempts, recent brain-brain communication related topics and proposes two solutions, chemosignal communication and facilitating symbiotic relationships.

3.1 Teaching non-human animals human languages

Early attempts to communicate with non-human animals include the iconic Clever Hans effect, where the animal was not learning about human language but instead analyzing social cues to guess the answer without neither understanding the question nor the answer. Scaffolding, where the teacher encourages students to explore possible answers independently instead of directly providing the answer, might have helped social learning but could lead to unintended responses in the case of Clever Hans (61). Other failed attempts include the classic behaviorist learning theory, where the animal does not comprehend anything but is rather reacting due to the conditioning effect where an automatic behavior is associated with a stimulus due to reinforcement (62).

Some progress in teaching non-human animals human communication includes using a Model/Rival Technique (63), where another individual serves as an exemplar and a rival for the “trainer” attention to compete with the learner (61). As shown in Alex the parrot and Kenzi the bonobo’s training with the Model/Rival Technique, the results were successful because the learning material is made feasible and beneficial, with the intend to teach the significance behind words to the learner, therefore, easier to learn. Another example of successful interspecies communication between humans and non-human animals is Koko the gorilla. Koko learned at least 2000 spoken English words and 1000 signs (64). She showed auditory learning, imitative learning, and vocal comprehension learning, (as gorillas lack the larynx to produce vocalizations). She is also known to communicate and show a variety of emotions (65).

It is unclear whether animal infants with interspecific parents can gain interspecies communication, such as feral children. There are some tales and cases of possible interspecies communication in feral children raised by heterospecific animals but it is not well-studied (66-67). It is unclear whether or not having heterospecific parents would lead to the development of an intermediate communication between the language of the two species if there is direct communication and whether or not the parent and child would be able to communicate and understand each other.

3.2 Brain-brain communication:

It's unknown if similar neural circuitry between species with complex communication could be taken advantage of for more direct communication, but brain-brain interface may allow direct control of non-human animals with human brain signals. With this technology, humans can "cooperate" with non-human animals, such as using beetles instead of dogs to find buried people after earthquakes (68). In another case, the company KAIST used brain-computer interface (BCI) as a stimulation device to control turtles' instinct behaviors with human thought via a non-invasive method (69). However, the "cooperating" animal is not doing so out of its own wish, and there does not seem to be communication between the human and the nonhuman animal. Despite its many applications, it is unclear how the non-human animals perceive being controlled and more research is needed to show the non-human animal's narrative of this borderline enslavement idea. It is also unclear if non-human animals can control human behavior with their brainwaves, but it is highly likely.

Another similar technology is the animal computer interaction (ACI), where humans attempt to interact and communicate with non-human animals through play (70). This technology usually involves humans and a technology intermediate connected to a non-human animal which allows humans to playfully interact with the animal. For example, children at a hospital could watch a dog play with the robot ball they control (71). However, the same ethical concerns apply to this technology because the non-human animal does not seem to interact with the device as much as its human counterparts and could not express its preferences for what type of games, how it wants to play, when, etc.

It is also possible to transmit information directly through brain-brain communication, the direct transmission of information between two organisms through their brains, by receiving weak magnetic fields because areas related to social recognition in the frontal lobe produce electromagnetic fields that could transmit emotional and cognitive information to another brain, enabling a new form of social interaction (72). For example, in Egyptian fruit bats (*Rousettus aegyptiacus*), there were neuronal correlates where local field potentials and spiking activity increased simultaneously in the brains of socially interacting individuals which varied with the degree of interactions, suggesting synchronized brain activity that could be used to coordinate complex social interactions, although the mechanism facilitating this synchrony remains unknown (73).

3.3 Chemosignals and emotion contingency

Albeit vocal communication is a very common means of communication for humans, there are other types of communication that could be important for facilitating interspecies communication such as through chemosignals. Universal across different species, chemosignals produced through the body's secretions, such as sweat, and remain in the form of odors, is the oldest type of sense (e.g. before the audition, etc.). It has been proposed that there might be a distinctive chemical signal for each emotion (75).

Chemosignals are known to communicate different emotional states such as fear and happiness subconsciously intraspecifically, including communicating mate capability and kin in humans (75). Chemisignals could possibly lead to emotional contingency, which is studied in rats, dogs, and zebra finches (74). They are contagious across conspecifics, regardless of familiarity, and are also contagious interspecifically (75). Experiments in dogs have shown their ability to sync or experience the emotions experienced by humans when presented with human odors secreted under different emotional states. For instance, dogs could respond with the same emotions to body odors of humans in states of happiness and fear (75), similar to the response in human-to-human experiments, although it is unclear whether or not this is a learned behavior. There is usually a change in heart rate and emotional response according to the scent (76). A similar reaction is recorded in horses (77).

Due to chemosignals' power in communication, being able to decode and synthesize chemosignals could be a solution to facilitating interspecies communication. For instance, emotion detecting sensors could be implemented in livestock farms to assess animals' state of well-being, improving animal welfare. In addition, synthesized chemosignals related to territory marking or warning could be put around human properties to notify wildlife, avoiding human-wildlife conflicts that could be prevented through communication. Moreover, many common animals, including ants and dogs, are shown to detect cancer by using smell to detect volatile organic compounds (VOC) (78-79). As these animals are common in households, facilitating interspecies communication with them would help with early cancer detection.

Interspecies communication could also be facilitated in other communication modalities including gestures. For example, fish which are believed to only have innate communication can learn and perform tricks (80), which could be adapted into a form of gestural communication. It is highly possible that fish can learn and communicate with humans through gestures, although they lack biological structures similar to the larynx that allow speech.

3.4 Facilitating symbiotic relationships

Human-wildlife interspecies cooperation in the form of mutualism exists in many species. For instance, honey hunters in sub-Saharan Africa cooperate with honeyguide species to locate bee nests, dolphins help herd fish toward fishers, orcas increase the accessibility of whales for whaling crews, etc (81). These corporations lead to benefits such as greater survival, efficiency, food, and safety for both humans and the cooperating species. For example, cooperating with honeyguides increases the chance of locating bee nests by five times and offer beeswax, an important food source that would otherwise be a limited and stung risky opportunity for honeyguides (82); while human dolphin cooperation allows a three to seven times increase in catches and increases dolphins' foraging success rates (83). Similarly, orcas are offered the whale tongue, their favorite part, after a successful harvest for humans due to their collaboration (84); and wolves helped with chasing prey while humans aided with killing prey, offsetting each other's weakness with their strength (83).

Since human-wildlife cooperation often involves localized vocal signals and the behaviors and signals are often acquired through learning, passing down through generations of fishermen and dolphins, for example, these interspecies collaborations could be a learned behavior that could be facilitated (83).

There are many benefits of human-wildlife interspecies cooperation that greatly extend survival and financial benefits (as humans often rely financially on hunting with increased efficiency from the other animals' help due to their interspecies cooperation). Cooperation could be an enjoyable experience that strengthens social bonds for both species (85-86, 83). Furthermore, harvesting wildlife resources by cooperating with other animals also leads to smaller ecological impacts, such as reducing bycatch in human-dolphin cooperation and assisting forest regulation in human-honeyguide cooperation (83), making it a more sustainable method, which is even more important given the current environmental state. However, human-wildlife cooperation is threatened in many aspects. For instance, the intentional murder of dolphins and orcas by humans has led to pods moving away (83). Thus, mutual respect for wildlife is key for maintaining and establishing interspecies cooperation. Many indigenous communities have existed in harmony and mutual respect with nature, such as viewing wildlife as their teachers and taking lessons from the way wolves hunt by driving prey off into cliffs (87-88). Perhaps, giving more attention to indigenous values would help take away anthropogenic views that hinder the establishment of human-wildlife symbiotic relationships.

Domestication has also led to some symbiotic relationships and interspecies communication. For instance, cats (*Felis catus*) have been shown to use interspecies communication through meows with their humans. Adult cats have rarely been shown to use meows with other cats (89-90) but could have made their meow language that is different from other cat-human pairs to communicate with their human caretakers (91). However, it is unclear whether or not a change in caretaker or having different caretakers in the same household would impact cats' meow language. The way cats adapted to use meows is similar to the Nicaraguan sign language phenomenon where a group of deaf children invented their sign language to communicate (92). Thus, it could be inferred that any social animals have the urge and the ability to communicate with others, and this ability is not unique to humans, further suggesting the likelihood of establishing interspecies communication.

The emergence of symbiotic relationships could have possibly led to the emergence of interspecies communication, suggesting another solution to establishing interspecies communication. Facilitating those relationships could lead to many benefits, including friendship and a more sustainable harvest of animal products. Future collaborations could include working with animals of smaller sizes to find human remains after earthquakes more efficiently.

4.0 Future directions

4.1 Invertebrate communication: is having a brain necessary for complex communication?

Invertebrates without brains, such as starfish and sea cucumbers, can still communicate chemically through pheromones regarding aggregation and spawning (93-94). Thus, having a brain might not be necessary for communication, given the definition of communication is any interaction between two animals that causes a behavioral change, although certain types of communicative behaviors, such as vocalizations, may require specific brain and vocal structures. After all, brain, intelligence, and language may not equal each other.

4.2 Plants and microbes: symbiotic relationships and interspecies communication.

In addition to multicellular animals, plants, and microbes, including bacteria, fungi, and even viruses, are shown to have interspecies communication as well, sometimes with each other. Fungus and bacteria found in the human body are shown to have symbiotic relationships and interspecies interactions (95). Plants are also shown to have interspecies communication with bacteria and soil microbes (96). For instance, potential signaling factors, 12-hydroxystearic acid, for interspecies communication have been discovered in wheatgrass's microbial culture (97). Other methods of interspecies communication include releasing VOC from microbes, plants, and other organisms to communicate across kingdoms. As bacteria and fungi have a symbiotic relationship and play an important role in plant nutrient acquisition, VOC from bacteria and fungi closely affects plant health and growth (96).

Other cross-kingdom communication besides bacteria and plants includes plant and animal interactions. Many animals have symbiotic relationships with plants. Bees and flowers are classic examples, having interspecies communications through visual signals (98).

Bacteria use cell-cell interspecies communication by releasing chemical signaling molecules or autoinducers, which impacts biofilm and antibiotics production (99). Other than bacteria, viruses communicate interspecifically and intraspecifically as well. They use exosomes, vesicles that transport proteins and mRNA to other cells that can impact cell growth (100). Since viruses can also communicate, it is blurring the line between what is considered living and what is considered intelligent. Although unexplored, humans could possibly communicate with bacteria and viruses through decoding and synthesizing chemicals.

5.0 Conclusion

Existing research has used humans as a standard and tried to find clues in other animals that exhibit similar behaviors, which explains the big focus on spoken language and vocal learning (101). However, the animal kingdom is full of diversity that has yet to be explored, partially due to technological limits. For example, mice and songbirds have been studied extensively due to their easy accessibility and fit to the lab equipment. In contrast, ants might have a similar level of social complexity compared to humans and communicate through pheromones, which is not commonly regarded as language and is more difficult to study due to technology constraints and their small size (102). Also, dolphins, another highly intelligent and social animal that shows vocal production learning, are not well-studied in terms of their neurobiological structures for vocal learning because they are not as accessible as mice and there might be ethical problems with performing the same methods on them as mice. Due to the above reasons, vocal learning, especially vocal production learning, might not be as unique or important as we think, as most animals can learn to modify their behavior in other modalities. Because humans have evolved to have vocal cords for human language in the first place, and evolution has shaped different animals differently, human-centric biases should be avoided to explore the diversity of communicative behaviors, including those in other modalities. It would be more beneficial to look at the animal kingdom as a whole and each animal as a unique product that has evolved to maximize survival in its unique situation. Thus, trying to fit the behavior of one animal into another might not work, simply because it has evolved its own behaviors.

Most animals have innate communication, such as fish, birds, and mice, while some animals have complex communication that requires learning. For instance, complex vocal communications involve vocal learning, including vocal usage learning, vocal production learning, and vocal comprehension learning. Once thought of as a rare ability and only studied in a few species, recent research in vocal learning has expanded to other species, highlighting the importance of understanding different animals' communicative behaviors. Vocal learning is enhanced by social reinforcement learning, as shown in animals, including zebra finches, marmoset monkeys, and bats. Vocal learning-related structures are found in different animals, suggesting a convergent evolution due to language and communication serving as personal tools with complexity based on the social environment needs. When teaching non-human animal communication for use in human-animal interactions, it is important to make sure that the learning material is beneficial, and feasible, to the learner and confirms comprehension. Recent technological attempts at interspecies communication include BCI, and ACI emphasize human control of non-human animals over mutual communication. Thus, more collaborative approaches to facilitate interspecies communication include chemosignals and emotional contingency, possibly decoding and synthesizing chemicals to communicate with other animals, and establishing symbiotic relationships, which have survival, social, and ecological benefits. Future directions include invertebrate communication, plant-microbe interactions, and cross-kingdom communication, leading to questioning the causation between, brain, intelligence, and language.

Language and communication should not be defined based on one species's characteristics. It is important to investigate the diversity of communicative behaviors in the vast biodiversity with an open mind, especially in understudied species. Interspecies communication helps find a middle ground between species, improving animal welfare and initiating interspecies cooperation. Studying animal communication, including interspecies communication, provides insight into the evolution of communication while allowing a better understanding of animals' behavior and needs.

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Abbreviations

A1- primary auditory cortex
AAC- central nucleus of the anterior arcopallium or archistriatum, robust appearing nucleus within the arcopallium
AC- auditory cortex
ACC- anterior cingulate cortex
ACI- animal computer interaction
ACM- caudomedial archistriatum
Ai- Intermediate arcopallium
Am- Nucleus ambiguus
Area X- nucleus in the anterior striatum
aSMA- Anterior supplementary motor area
aSt- Anterior striatum
aT- Anterior thalamus
Av- avalanche nucleus, small nucleus near the latter in the mesopallium
BCI- brain-computer interface
CM- Caudal mesopallium
CMHV- caudal-medial hyperstriatum, ventrale
CN- cochlear nucleus
CP- cerebral peduncle
CSt- Caudal striatum
DLPFC- Dorsolateral prefrontal cortex
DM- dorsomedial nucleus of the intercollicular nucleus of midbrain
DMm- magnocellular nucleus of the dorsomedial thalamus, vocal nucleus of the anterior striatum
FAF- frontal auditory field, vocal nucleus of the anterior nidopallium
FMC- Face motor cortex
HV- hyperstriatum ventrale
HVo- oval nucleus of the anterior hyperstriatum ventrale
IAM- small nucleus near the latter in the mesopallium or lateral nucleus of the anterior mesopallium
IAN- lateral nucleus of the anterior neostriatum, small nucleus in the nidopallium
IC- inferior colliculus
L2- Field L2, the main ovoidalis thalamo-recipient zone, subfield of field L, the region in the caudal medial neostriatum or nidopallium
LAHV- lateral nucleus of the anterior hyperstriatum ventrale

LAN- lateral nucleus of the anterior neostriatum
LPOm- magnocellular nucleus of the parolfactory lobe
MAN- anterior nidopallium, magnocellular nucleus of anterior nidopallium
MGB- medial geniculate body
MLD- Mesencephalic lateral dorsal nucleus
MMSt- magnocellular nucleus of the anterior striatum
MOc- oval nucleus of the mesopallium complex in the anterior mesopallium
MOc-like- a structure similar to the oval nucleus of the mesopallium complex
NAO- oval nucleus of the anterior neostriatum or nidopallium
NCAT- nucleus of the central acoustic tract
NCM- caudomedial neostriatum or nidopallium
NDC- Caudal dorsal nidopallium
NIF- interfacial nucleus of the nidopallium
NLC- central nucleus of the lateral nidopallium or neostriatum, prominent nucleus that bulges from the nidopallium into the overlying ventricle
NLL- nucleus of the lateral lemniscus
nXIIts- Tracheosyringeal subdivision of the 12th nucleus
PAG- Periaqueductal gray
PC- caudal paleostriatum
PFC- prefrontal cortex
PLA- paralemniscal area
PMC- premotor cortex
RA- robust nucleus of the arcopallium or archistriatum
RVL- rostroventral lateral medulla
SG- suprageniculate body
SOC- superior olive complex
VA- vocal nucleus of the arcopallium, robust appearing nucleus within the arcopallium
VAM- vocal nucleus of the anterior mesopallium
VAN- anterior nidopallium
VAS- nucleus in the anterior striatum
VLN- vocal nucleus of the lateral nidopallium, prominent nucleus that bulges from the nidopallium into the overlying ventricle
VMM- small nucleus near the latter in the mesopallium
VMN- small nucleus in the nidopallium
VOC- volatile organic compounds
vPFC- ventral prefrontal cortex
VTA- Ventral tegmental area

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