On Vocal Cultures and Traditions in Vertebrates—Culture, Learning, and Grammar in Animals

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ABSTRACT

This review delves into the latest research on culture, learning, and grammar in animals, providing definitions of these debated terms and drawing conclusions about their existence beyond human societies. It explores mechanisms such as social learning and cumulative culture. The core focus is on the vocal culture of vertebrates, defined as the vocal traditions of various geographically spread groups. Numerous examples support each statement, with marine mammals, particularly humpback whales, frequently highlighted as exemplars of highly developed vocal culture in vertebrates, prompting further hypotheses and new questions. Moreover, it draws parallels with human culture, encouraging an exploration of cultural development and inheritance in other animals to gain insights into the evolution of human culture. Finally, the review emphasizes the importance of this phenomenon for the protection and conservation of highly social animals.

Keywords: Vocal culture, Animal dialects, Cumulative cultural evolution, Social learning, Humpback whale songs

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Methodology

Criteria used for selecting studies for this review include standard generic steps toward literature screening and the final selection of the ones to be included.[1] Research questions and objectives were limited to the terms contained in the title, subtitle, and keywords. Publications were chosen based on their authenticity, relevance, and contribution to the field. Further criteria used for screening inclusion were pivotal works from the earliest research on the topic toward the new approaches and tendencies of the same researcher groups; moreover, the latest data in the field were reviewed to ensure an up-to-date and relevant review is assembled and a balanced stand is represented. Consequently, specific taxa and species were more or less represented in this review, depending on the research effort focusing on it. Databases such as ResearchGate, Google Scholar, ScienceDirect, and PubMed were exploited to collect works that were suitable for writing this review.

Introduction

The concept of culture in non-human animals (hereafter referred to as animals) is a matter of ongoing debate.[2] While the definition of culture varies, culture-like elements can be found in a wide range of species, supporting arguments on the one hand that invertebrates express cultural traits[3–6] while on the other hand that they are unique to humans.[7,8] However, recent scientific developments suggest that culture is indeed a phenomenon common to many animal species.[4,9–13] To encompass its various forms, Whitehead and Rendell provided a broad yet informative definition of culture as "information or behavior—shared within a community—which is acquired from conspecifics through some form of social learning."[14,15]

Since a term borrowed from anthropology, *the method of exclusion*[16] remained the most common method to establish if a practice in animals is considered a culture. This approach relies on mapping the practice over time and space, marking its presence in some social units but its absence in others, concluding it is a specificity of certain areas.[17] An important predictor is to be able to rule out any genetic or ecological factors that pre-determine the development of the behavior in question.[7] A commonly cited example of material culture in the literature is *tool use* in non-human animals and how this practice varies from one group to another (the style of crafting the tool or how it is used).[17–20] Recently published research on grooming practices in wild chimpanzees—the grooming handclaps—and how it varies between communities also explores how this non-material cultural practice is passed within a single community.[21] As much as these behaviors vary between social units, they can vary over time, going through evolutions of different intensities. Cultural evolutions, similar to biological ones, are driven by innovations, equivalent to mutations in biological evolution.[19] The cultural evolution of the humpback whale song is a popular example due to its uniqueness in the natural world and its intensity, temporal, and spatial scale.[22] Only a few bird species, such as the corn bunting,[22] village indigo birds,[23] and great tits,[24] exhibit similarly elaborate and ever-changing vocal skills. These skills are often reflected in lifelong learning abilities that shape local culture and its dynamics.

Chapter key points

- The concept of culture in non-human animals is a matter of ongoing debate.
- *The method of exclusion* is the most common method.
- Genetic or ecological factors that pre-determine the development of the behavior in question need to be ruled out.
- Cultural evolutions, similar to biological ones, are driven by innovations.

Social Learning and Vocal Culture

When discussing culture, (social) learning is at the heart of the subject-cultural transmission of behaviors.[2] Schuppli and van Schaik, in their 2019 publication,[17] claim that all of the definitions of animal culture (mentioned in their paper) agree that the

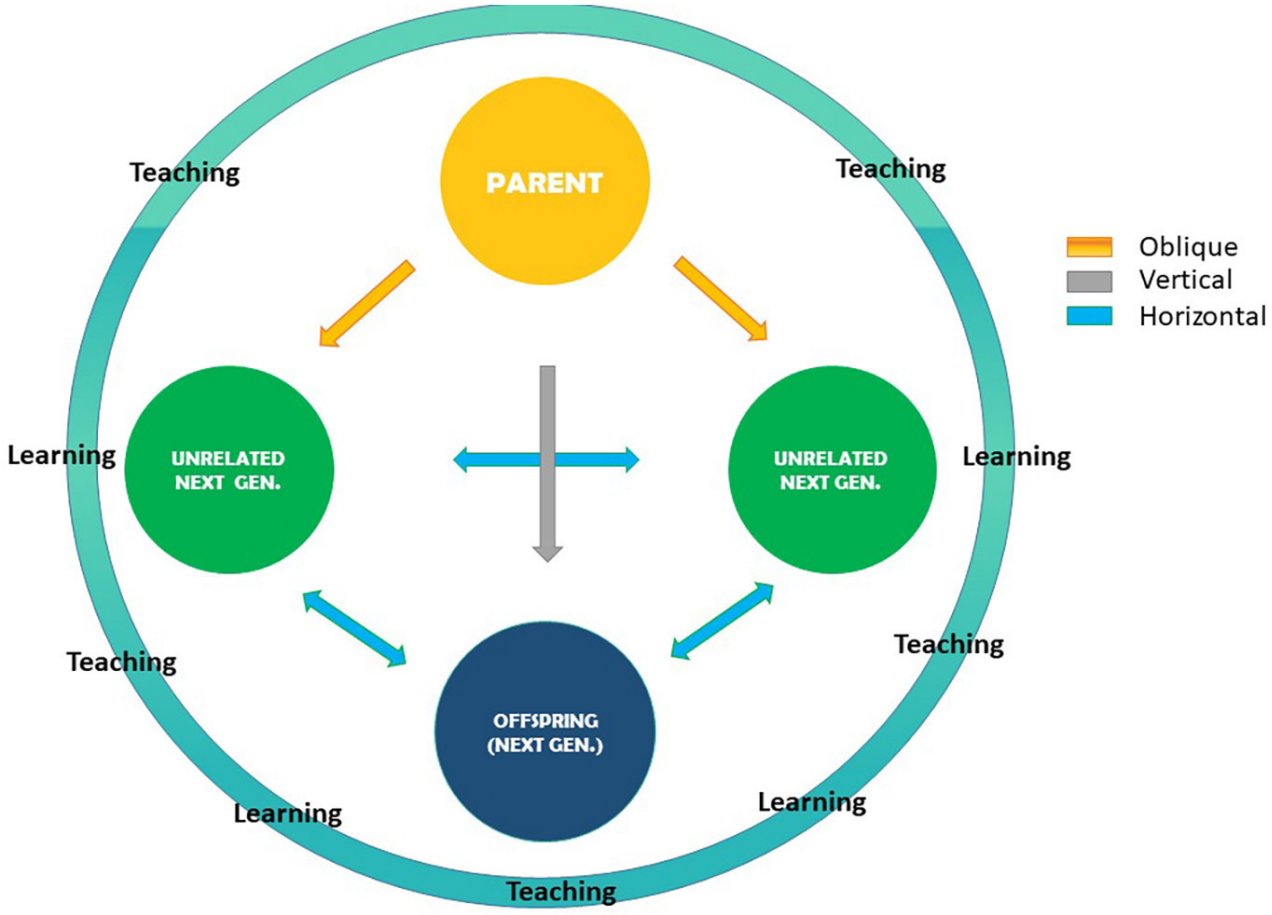

Fig 1 | Social learning- possible pathways

essence of culture lies in the skills and knowledge acquired through social learning, regardless of the specific method of social learning used. Social learning can occur in three ways: vertically (where knowledge is transferred from parents to their offspring), obliquely (where knowledge is passed to an indirect descendant or an unrelated member of the next generation), and horizontally (where knowledge is shared among peers) (Figure 1).[15,25] Learning in this social context can be obtained through active tutoring of one individual to another, called "teaching,"[26] or by simply observing others.[27–29] Under "observing," we can also include the active notion of "listening". This is how, we believe, vocal culture is cultivated in animals.[30]

Vocal culture is prevalent in animal societies, from species-specific vocalizations of cicadas[31] to clan-specific codas of sperm whales.[32,33] Vocal culture can, thus, be considered as any other form of culture–an element that a group uses to identify itself and create a blueprint within which it functions.

Within the broader framework of vocal culture, we can distinguish *vocal traditions* as specific elements. The general term "traditions," borrowed from anthropology, explains specific practices and rituals that are stable and consistent over time and passed down from generation to generation within a culture.[34] In the context of vocal culture, we can add a layer of defining vocal traditions as vocal specificities of an organizational level smaller than the species—ecotype (orcas), clans (sperm whales), troops (monkeys). These vocal traditions, within-species variation, usually vary with the geographic distribution of the groups and serve various purposes, such as maintaining group cohesion, signaling danger, mate selection, or coordinating activities.[35,36] By integrating the concept of vocal traditions, we can ultimately understand this phenomenon as *dialects*.[37–39]

In the context of birds, the term "vocal dialects" is commonly used to describe variations in song patterns, pitch, tone, and melody among different populations of the same species.[40,41] These dialects are similar to regional accents in human speech and can vary greatly based on geographic location.[41,42] Dialects, or vocal geographic variations,[42] appear to be a by-product of physical isolation within populations, where vocal communication diverges alongside other local adaptations.[15,41] This divergence often correlates with genetic differentiation.[43] Dialects reflect the relatedness between different local populations of the same species, with more interacting populations sharing more of their vocal repertoire.[43] As methodology evolves (for instance, through the use of AI) and acoustic analysis techniques advance, we increasingly uncover the commonality of dialects in animal vocal culture. By now, alongside our extensive knowledge of dialects in singing birds,[44] researchers

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have concluded that dialects exist in naked mole rats,[45] crows,[40] parrots,[46] common marmosets,[47] wild chimpanzees,[48] bats,[49] elephant seals,[50] orcas,[43] sperm whales,[32] humpback whales...[22]

In her chapter in Exploring Animal Behavior Through Sound,[41,51] Rebecca Dunlop discusses how dialects can function as early indicators of genetic differentiation. Similar to physical boundaries that can separate populations from mixing, dialects are a specified cultural boundary that does the same. It is an open question whether genetic differentiation is a consequence of dialect differences or a cause. Deecke and colleagues[43] further suggested that dialects help maintain the cohesion and integrity of matrilineal groups. This is relevant for orcas and sperm whales, which are matrilineal-connected species. Interestingly, in humpback whales, only maternal care toward offspring is reported, but only males sing.[52–54] As a species, they are not particularly social, unlike sperm whales and orcas. Given the specificity of the dialect phenomenon in only a few whale species, it is likely that cultural transmission plays a more significant role than genetic mechanisms.[43] Ultimately, this distinction contributes to the overall species' vocal culture.

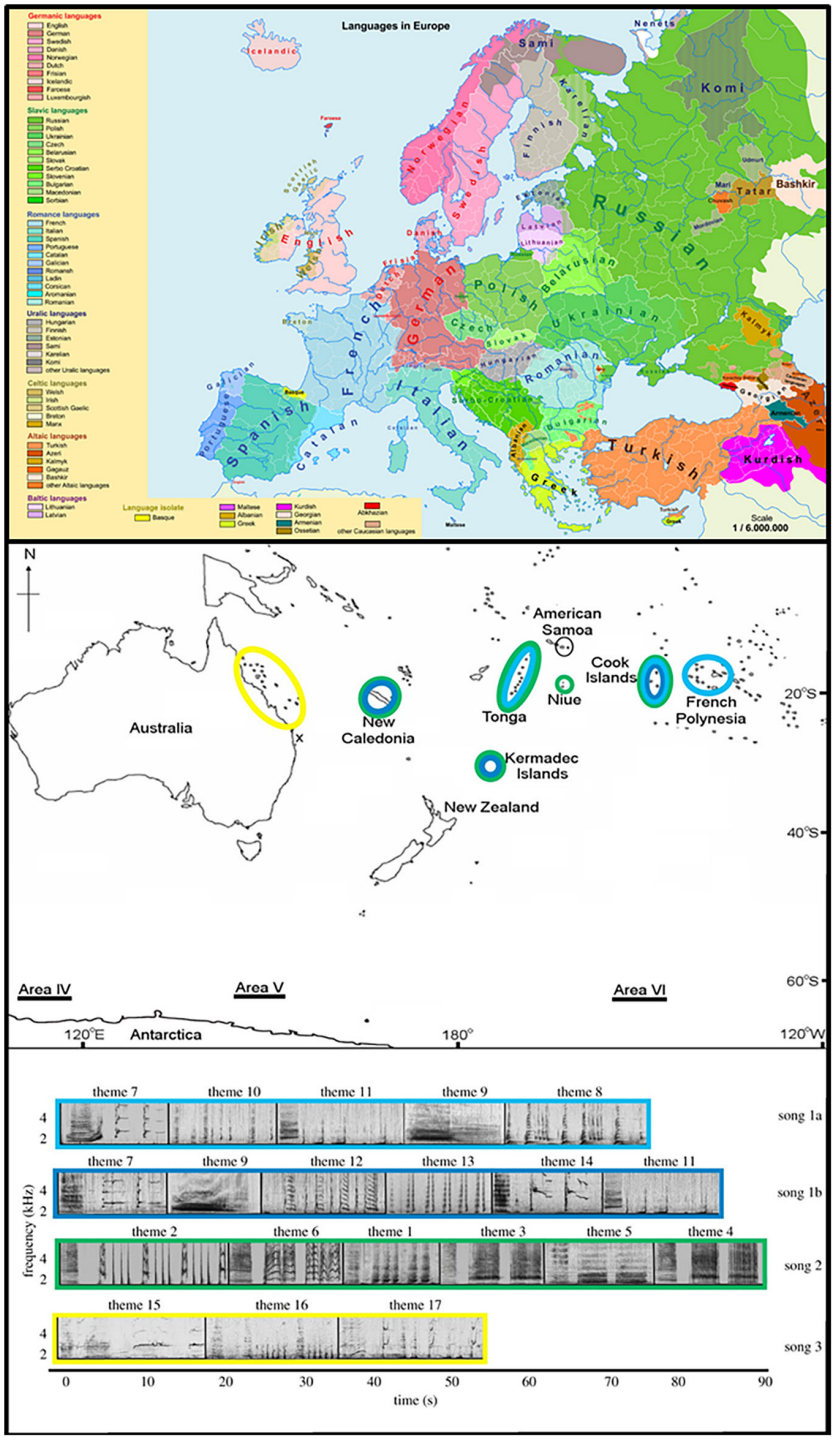

Fig 2 | In the top figure, a map of Europe is presented, with different colors labeling areas where languages of the same family are spoken (Languages of Europe.svg: The original uploader ArdadN at English Wikipedia.Later version(s) by Ervidervi, Komita at en.wikipedia. derivative work: Hayden120, CC BY-SA 3.0 https://creativecommons.org/licenses/by-sa/3.0›, via Wikimedia Commons). On the bottom, a map of the Southwestern Pacific is presented, showing different humpback whale song types sung in the same season, along with corresponding spectrograms (retrieved from Owen et al., 2019)[87]

Chapter key points

- Vocal culture is very present in animal societies.
- The essence of culture lies in the skills and knowledge acquired through social learning.
- Within vocal culture, we can distinguish vocal traditions and dialects.
- Dialects, or vocal geographic variations, are similar to regional accents in human speech.
- Dialects can function as early indicators of genetic differentiation.
- Cultural transmission is probably more significant than genetic mechanisms to maintain group cohesion.

Cumulative Cultural Evolution (CCE)

As defined by Tomasello in 1993, "Cumulative cultural evolution is the gradual accumulation of cultural modifications."[8,55,56] Initially, it was believed only humans have cultures. Further, it was discussed that animals might have cultures as well, but they mostly lack cultural evolution. Finally, we now understand that cultural evolution, together with the accumulation of these changes over generations (CCE), is a phenomenon widespread across the animal kingdom.

The concept of CCE in animals has provided insights into the culture and cognition of non-human animals, although, as culture itself, was considered a hallmark of humans.[8,55,56] New studies, on the contrary, give us a rich contingent of examples of CCE in animals, including birds, such as crows and pigeons, known for their behavior and tool use,[57,58] and primates like macaques, chimpanzees, and baboons, noted for their social interactions and ecological skills.[59–61] Vocalizations in some species of songbirds[62] and cetaceans[63] also reflect CCE.

We can argue that birds and whales have the most elaborate vocal cultures within the animal kingdom, next to us humans.[22] In line with the extensive research input in bird bioacoustics and a habit of comparing human vocalization to that of birds, it actually makes much more sense to look into whale acoustics when seeking answers about human language and vocal display evolution because of the same mammal brain used to produce the information and process it.[64]

In their recent paper, by unveiling the sperm whale phonetic alphabet, Sharma and colleagues concluded that "the sperm whale communication system is, in principle, capable of representing a large space of possible meanings, using, similar mechanisms to those employed by human sound production and representation systems (e.g., speech, text, Morse code, and musical notation)."[64] In a similar manner, in this review, we can conclude, backed up by Hersh, Ravignani, and Whitehead,[65] that whales are the next frontier for research on human language evolution.

Comparing birds to whales is logical due to their similar vocal abilities and cultural tendencies. Bird vocalizations are much better studied than those of whales, providing a useful comparison. In birds, learning is categorized into two types: open- and closed-ended learning.[66] Closed-ended learners acquire one or several songs within the first year of life, which they use for the rest of their lives. Open-ended learners can acquire new song types beyond the first year of life, continuing to learn new songs beyond the most plastic years of brain development. However, some bird species complicate this strict division. For example, great tits (*Parus major*) take several years to start acquiring different song types.[24] If not observed carefully, these species might seem like closed-ended learners, only to prove otherwise after a few years. This also depends on the number of inspected animals, as it takes only one to prove a species to be open-ended learners, while it takes many more to prove the opposite.[67,68]

Similarly, for now, we can consider humpback whales to be open-ended learners, as no records exist of the same song being used again after it was outdated.[22] However, could this be just a matter of the sampling effort we have for this species? Unlike great tits, it may turn out that humpback whales are closed-ended learners, reaching the peak of their learning abilities when older. Moreover, there could be differences between different breeding stocks.[15] Just as they practice singing different songs, different mechanisms of song modifications (evolutions, referring to mild changes over seasons;[69] and revolutions, referring to intense, complete song replacements[70]) seem to govern their vocal culture. Notably, song revolutions have so far been registered only in the Southern Hemisphere,[70–73] named "Southern Hemisphere Cultural Exchange (SHCE)."[73] One specificity connected to this social difference between the geographic locations of humpback populations—Northern and Southern Hemisphere—could also potentially be reflected in the CCE phenomenon.[7,14,54–62] Recent studies have highlighted humpback whales due to the unique characteristics of their songs.[22] Male humpback whale vocalizations are considered to represent an elaborate oral culture. This culture is maintained within breeding stocks through stock-specific songs, typically shared only with conspecifics of the same stock.[74] Occasionally, song revolutions occur, where songs are passed to neighboring stocks, representing cultural transmission.[16,75–77] Beyond rare song revolutions, there is evidence of song flow from one stock to another.[72,78,79] This natural process of song dynamics can be seen as cultural exchange (transmission).[80–83] Another element of CCE[2] exchange can exist between different populations of the same species, like in the above example, but also between different species – so-called co-cultures.[84]

In the case of mixing differences between Northern and Southern Hemisphere populations, as mentioned, Northern Hemisphere whales do not experience song revolutions,[73] and so the song is only slightly modified from season to season, leading to solidified cultural accumulation of the Northern Hemisphere. On the contrary, Southern Hemisphere whales, with their song revolutions, seem to erase this type of accumulation in their vocal displays, leading to the absence of this cultural phenomenon in Southern Hemisphere populations (in part, described by the loss of song complexity with each revolution[85]). There is a possibility that this strategy can also be considered an example of CCE. To quote Whiten, "(CCE can) instead act to select against and possibly eliminate some cultural entity—one can make an analogy between such changes and the organic selection that led to the loss of limbs in snakes, for example."[2] In conclusion, we are yet to discover if we can consider Southern Hemisphere humpback whales' ability to adopt completely new songs on a population level as a part of their specific vocal tradition.[15]

Chapter key points

- CCE is the gradual accumulation of cultural modifications.
- Birds and whales have the most elaborate vocal cultures within the animal kingdom, next to us humans.
- Whales are the next frontier for the research on human language evolution.
- Social differences between the geographic locations of humpback populations—Northern and Southern Hemisphere—are reflected in CCE; song dynamics can be seen as cultural exchange.
- CCE exchange can exist between different populations of the same species and between different species, called "co-cultures."

Mechanisms of Change

Beyond the existence of evolutionary and revolutionary song changes, we are not yet aware of the mechanisms under which these changes occur. One hypothesis is that each breeding stock, or perhaps each hemisphere, has its own set of rules or "grammar" for compiling songs or other vocalizations. Grammar would be a predefined structure of how vocalization should be designed within species, depending on their geographical location.[86] Although they are same in structure, we now know that the similarity between songs—on a smaller scale (specific sounds used to compile the song)—of different breeding stocks somewhat depends on their physical proximity. As Darling noted in his recent publication, geographic distance is not a predictor but a factor for song similarity.[22,87] Although humpback whales are unique in periodically revolutionizing their oral culture, the similarity or dissimilarity of their cultures depends on physical distance

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and the mutual influence of neighboring stocks (while revolutions change the sound content, their rough general organization is always blueprinted). This parallels with human language, where similar processes occur. In human language evolution, geographical proximity is an important factor in the relatedness of languages. Additionally, there are several language families in human culture, each comprising distinctive languages that function under similar grammatical rules. These language families, now spread over large areas, were once spoken in regions of close proximity (Figure 2).[87]

A similar concept is observed in the other parts of the animal kingdom, particularly among marine mammals, with the twist of active initiation to approximate vocalizations (so-called vocal contextual learning). For instance, there are reports of orcas adapting their vocalizations to those of bottlenose dolphins with whom they were in contact in captivity.[88] This phenomenon is also observed in wild animals, in multispecies groups of Odontocetes.[89]

What seems not to be affected by geography or any other parameter whatsoever, is the organization of whale song structure.[73] Orca vocalizations vary in call pitch between ecotypes of Northeast Pacific, yet, the types of calls they use are the same;[90] humpback whale song varies between populations and seasons, being under constant modification, and yet, these changes are always made to follow a specific song structure;[91] just last year, we have learned about the phonetic alphabet of sperm whale codas, and how different clans use them, varying their clan–specific vocalizations;[63] similarly, more than whales, other vertebrates also use structured vocalization—Diana monkeys are noted to use variations of their basic call types, its acoustic structures, and by combining, to expand their general vocal repertoire;[92] putty-nosed monkeys rely on call–sequence for the meaning, not just separate calls;[93] bird song structure encompass one species, but is applicable to the entire class—as phonological syntax.[94]

Chapter key points

- The mechanisms behind evolutionary and revolutionary song changes in animals are not yet fully understood.
- Each humpback whale breeding stock or hemisphere may have its own set of rules or "grammar" for compiling songs or vocalizations, independent of geographical location.
- The similarity between songs of different breeding stocks depends on their physical proximity, although geographic distance is a factor, not a predictor, for song similarity.
- Humpback whales periodically revolutionize their oral culture, but the similarity or dissimilarity of their cultures depends on physical distance and mutual influence of neighboring stocks.
- The organization of whale song structure is not affected by geography or other parameters, and changes in whale songs follow a specific structure.
- Similar processes occur in human language evolution, where geographical proximity is important for the relatedness of languages, and language families function under similar grammatical rules.
- Marine mammals, such as orcas, can adapt their vocalizations to those of other species they are in contact with, demonstrating vocal contextual learning.
- Other vertebrates, such as Diana monkeys and putty-nosed monkeys, also use structured vocalizations and call sequences to expand their vocal repertoire and convey meaning.

Language Acquisition Device (LAD)

Considering that in some species, populations never mix, yet still use the same rules to structure their vocalizations, it is reasonable to infer that the basis for this uniformity lies in genetics. One possible explanation could be the language acquisition theory, namely, the Language Acquisition Device (LAD), as proposed by Chomsky.[95] The LAD would be a hypothetical tool, biologically hardwired in the brain of all individuals, that enables humans to acquire and reproduce language (under all its complex and still not well– understood rules) with ease. This theory is interesting because it shows that every human infant can acquire any language in the first years of life, independent of differences between its maternal language and the one it is exposed to, with equal ease. Moreover, they can innately understand grammar and syntax.[96] This means that our brains understand some language structures and use them to learn a language, even though we are, for the most part, not consciously aware of what those structures are. Chomsky explains this by the theoretical existence of a "Universal Grammar," which gathers those "unfamiliar language rules," potentially governing all human languages.[15] Something rather similar was discovered by AI scientists in the past years, in the field of Natural Language Processing, with the invention of Cross-lingual word embedding. It is a method that represents words correlations, of different languages, in the same embedding space.[97] Using this approach, it was demonstrated unexpectedly high level of similarity between many world languages, even the ones not closely related.[97,98]

Still, in the discussion on the "Faculty of Language" and language evolution, it is urged to distinguish between language as a communication system and the hardwired system responsible for its computation, as these are completely different subjects, and thus, debates mixing the two cannot be of any use.[99] We are not aware of the mechanisms of animal auditory– vocal learning from peers, and more than that, the mechanisms or rules under which most of these vocalizations change, but the change is obviously happening in a specific way, facilitating all animals in the group to learn, reproduce, and maybe even participate in the process of sound evolution. Considering the requirements needed to stay updated (keeping track of every sound change and being able to reproduce it), it is hardly likely these processes are happening at random.[80] Interesting propositions on song acquisition and reproduction has been tested so far in humpback whale songs, one of them being a song partitioning

into a more convenient-to-remember-parts, used in so-called "song hybridization events".[100] These events occur in song-type substitution periods (revolutions) when there is a "hybrid" song, constructed of parts of a new and an old song.

Chapter key points

- The uniformity in vocalization rules across populations that never mix suggests a genetic basis.
- Chomsky's theory proposes that humans have a biologically hardwired tool in the brain, the LAD, which enables language acquisition and reproduction.
- Chomsky's concept of a "Universal Grammar" suggests that there are common language structures governing all human languages.
- AI scientists have discovered high levels of similarity between many world languages using cross-lingual word embedding.
- It is important to distinguish between language as a communication system and the hardwired system responsible for its computation.
- The mechanisms of animal auditory-vocal learning and the rules governing vocalization changes are not well understood, but changes occur in a specific way.
- Humpback whale songs undergo "song hybridization events" during song-type substitution periods, where parts of new and old songs are combined.

Conclusion

Vocal cultures and traditions in vertebrates are a research area of great potential, highlighting the intertwined influence of culture, learning, and communication. Across the animal kingdom, from birds to whales to monkeys, vocal traditions play a crucial role in mate selection, group cohesion, and identity. These vocal behaviors are not simply instinctual but are learned and transmitted through social learning pathways, whether by observing or through active learning/teaching by both parties involved. The ability to pass culture through generations accentuates the noticeable importance and specialization of communication systems in non-human animals, drawing an exciting parallel to human languages and grammar. The diversity and complexity of these vocal traditions highlight the adaptive significance of culture in the animal kingdom. By studying these behaviors, researchers gain valuable insights into the evolutionary foundations of communication and social structures. Moreover, understanding how animals learn and transmit vocalizations can inform conservation strategies, particularly for species whose survival depends on maintaining social cohesion and effective communication. Ultimately, the exploration of vocal cultures in vertebrates not only enriches our knowledge of animal behavior but also provides a deeper appreciation of the shared elements of culture and learning across species, emphasizing the continuity between human and animal communication.

To conclude, the value of these information further solidify the importance of species protection in its widest form, as by losing eve a few specimens, from a few localities can mean irretrievably loosing knowledge, traditions and adaptations built for an unmeasurable amount of time, which most likely, could never be repeated or copied.

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