

49 Key Issues and Future Directions: The Comparative Approach to Language

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Like humans, many animals use their voice to communicate. Like human speech and language, animals' vocalizations can inform others about identity (what species they are, female or male, which individual). Like humans, animals flirt and fight with their voice, negotiate and manipulate, and can beg or raise alarm. Unlike humans, many animals have a small repertoire of communication sounds, are less flexible in its use, and do not need to imitatively learn their vocalizations. Moreover, there is no evidence that animals can convey complex abstract content the way language can. So, since human language differs in some important ways from most animal vocal communication systems, why then should one be interested in comparisons? What can be learned from the study of other animal species? In this chapter we provide our perspective on some key issues in the comparative approach and identify promising and relevant areas for further study.

1. *Why Comparative Studies?*

As outlined in chapter 44 by Fitch, it is crucial to realize that while human language is unique to our species, it consists of a set of processes that are partly also evident in other animals. Recognizing the multicomponent nature of language invites questions about the nature, development, and evolution of the different constituent components. Comparative studies can help to disentangle the knot of mechanisms underlying human language into components. Widely shared mechanisms indicate that these are unlikely to have evolved specifically for, or in consort with, communication by language. Rather, these mechanisms might have served as evolutionary building blocks for language. Comparative studies may also reveal mechanisms that are derived in humans, that is, for which the human abilities differ from those of other species and the evolutionary origin may not be immediately obvious, for instance, the syntactic structure of language (see ten Cate & Petkov,

chapter 47). This invites studies as to what exactly it is that differentiates the human ability from that of other species, for instance, to what extent the learning of syntactical rules is based on general learning mechanisms that may also be present in other species, such as statistical learning (e.g., Santolin & Saffran, 2018). Also, studies on animals provide options for experimental approaches that for ethical or other reasons cannot be done on humans, such as manipulating the expression of *FoxP* genes (see chapter 46 by Scharff, Knörnschild, & Jarvis) or rearing individuals under highly controlled conditions to examine factors affecting vocal learning. Finally, comparative studies can address one of the most challenging questions in science: how human language evolved. Comparing the presence and absence of specific traits in various species, in relation to variation in their ecological and social environment, their cognitive abilities and life history traits may contribute to identifying which selective forces have given rise to separate traits as well as to their linkage. Such studies may provide hypotheses about the stepping stones and processes responsible for our evolution from prelinguistic to linguistic human beings. Altogether, comparative studies can shed light on the question whether the evolutionary emergence of language is the product of one big leap or of an accumulation of smaller steps.

2. *Comparative Studies: How?*

There are two approaches to comparative studies (see Fitch, chapter 44). One is to compare related species, originating from a common ancestor, for example, comparing humans with great apes or other primates. It is based on the principle that evolution of any trait in any species, no matter how complex, is in one way or another based on traits present in an ancestral species. The closer two species are related, the higher the chances that comparing them will make it possible to trace the origin of a trait and to identify in what way the ancestral

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trait has been modified to gain its current utility. This approach is exemplified in chapter 45 by Fischer and Hage. It focuses on primate vocalizations: their meaning, their link to internal emotional or motivational state, the degree of flexibility in usage and structure, and the plasticity in development. They also address the degree of volitional control that primates may have over their use of vocalizations and how this may be related to neural control mechanisms, such as the monkey homologue of the human Broca's area. However, to get from an ancestral primate vocal production system to the human one also required a series of steps such as the mapping of auditory input to vocal output; coordination of breathing, articulation, and voicing; and the integration between brain areas supporting symbolic and linguistic thought. Fischer and Hage (chapter 45) illustrate how comparative studies help to identify crucial components involved in, and steps toward, language.

The second approach to comparative studies does not focus on closely related species, but on species that share particular traits. Over the course of evolution, analogous traits may have emerged in species not closely related, as a result of adaptations to similar selection pressures, that is, by convergence. A clear example of such a trait, mentioned in several chapters, is the presence of vocal production learning—the ability to learn to produce new vocalizations based on those heard or in responses to social influences by other individuals. This ability is present in several groups of mammals and birds, in which it evolved independently. Comparing species having this ability with those who don't have it, or have it only to some degree, as well as comparing the nature of the learning mechanisms in different vocal learning species can provide a wealth of information on what factors may affect such learning processes, such as predispositions or social interactions between the learner and other individuals. It may also provide animal models to examine neurobiological mechanisms underlying such learning. Additionally, it can offer insights in the social or ecological factors that may have contributed to the evolution of vocal learning.

Both types of comparative studies may thus provide insight into questions about mechanisms (what are components of the language faculty, how do they work) as well as about the evolution of these mechanisms (what was their origin, how did they become the way they are).

3. Key Issues

The various chapters in this part reflect the current topics of comparative studies. They also identify several key issues for further study. We provide a brief discussion of these issues.

3.1. VOCAL PRODUCTION LEARNING Vocal production learning is a major area of research. This has demonstrated that humans are not the only species that learns most of their vocalizations imitatively from conspecifics. The process has fascinating parallels between such distantly related groups as humans and three orders of birds, which extend to the level of genes involved in the process (see Scharff, Knörnschild, & Jarvis, chapter 46). The considerable research efforts focused on songbirds have made song learning the prime model for the study of vocal learning in nonhuman animals. It has given rise to several prominent theories about the behavioral and neurobiological mechanisms underlying vocal learning (see Scharff, Knörnschild, & Jarvis, chapter 46). However, there are other groups of vocal learners, such as cetaceans (whales and dolphins) and bats. In terms of what we know about the learning mechanisms involved, these groups are much less studied. This is partly a consequence of the logistic constraints: cetaceans cannot readily be studied under controlled laboratory conditions and subjected to rigid experiments. There is a danger that because the outcome of their vocal development is clearly affected by learning, the as yet unknown underlying learning mechanisms and factors affecting the process are too readily assumed to be similar to what is occurring in birds, relying heavily on imitative learning. This may be right, but it may well be that other types of learning are involved. For instance, the example of an elephant producing human words (Stoeger et al., 2012) is striking, but its development is unclear. Is the system involved here the same as the one used for producing conspecific vocalizations? Or might it be the outcome of a separate process, one of skilled operant conditioning in which a trainer has shaped a behavior, in this case one producing a sound, to become similar to a human speech sound? This cautionary note also applies to the cases of "limited vocal production learning" as summarized by Scharff, Knörnschild, and Jarvis (chapter 46). The undisputed observation that there is a graded scale with respect to the occurrence of vocal imitation as outcome of a developmental process need not imply that the underlying process is also one that differs only in degree. It might reflect the presence of different underlying mechanisms. There is still a lot to uncover and the variation in the degree of vocal imitation among both birds and mammals can be used to reveal variation in underlying learning mechanisms. This may provide new hypotheses about human vocal learning, which is not just due to imitation, but also shaped by predispositions and the rewarding responses and guidance by infant caretakers.

3.2. COMPREHENSION LEARNING, USAGE LEARNING, AND REFERENTIAL SIGNALING

Linking the hearing of a sound to a particular event or object (comprehension or recognition learning) and learning the appropriate usage of a vocalization (usage learning) are more common than production learning. This raises the question of how they interact and are coupled to production learning: have they become an integral part of the production learning system, or are they to some extent separate? This is another understudied area. For instance, while only juvenile male zebra finches show song production learning, adult males (who sing) and females (who do not sing) can both be readily trained to discriminate different songs (Kriengwatana, Spierings, & ten Cate, 2016). For males this occurs without impacting their own songs. Comprehension learning thus seems at least partly separate from production learning, but it is unclear to what extent.

Usage learning links the production of a vocalization to a specific context. One aspect of this process concerns the degree of voluntary control over the production of such vocalizations. This varies among species. The example of macaques (Fischer & Hage, chapter 45), which after long training became capable of using two different vocalizations depending on context, indicate that for these primates flexibility seems limited. Some bird species show more flexibility. Fork-tailed drongos, for instance, mimic the alarm calls of other species (a case of production learning) and can flexibly use these calls to target particular species (Flower, Gribble, & Ridley, 2014), most likely the result of experience—that is, by usage learning. In this way, the drongos scare other species away from food that they can subsequently eat themselves.

Both comprehension and usage learning are required for referential signaling. Various great apes are able to use gestures or icons to refer to different objects or actions (e.g., Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986). They clearly have the cognitive ability for referential communication, but there is no evidence that they link this to using particular vocalizations, let alone vocal production learning. This ability has, however, been demonstrated by some dolphins (Richards, Wolz, & Herman, 1984) and also by grey parrots. In particular one parrot, Alex, was able of vocally expressing labels for many objects and actions (e.g., Pepperberg, 1999). He also mastered more abstract concepts such as *same* and *different* as well as several other cognitively advanced abilities. Here also, the considerable investment in training effort and the logistic constraints on controlled experiments with dolphins, parrots, and corvids are prime factors that are challenging when studying these species. However, the

developmental processes underlying referential signaling and their linkage to production learning are topics of great relevance if we want to understand how their nexus as present in language emerged.

3.3. CULTURAL EVOLUTION Another aspect of vocal production learning concerns its consequences. In humans, the transfer of language from one generation to the next has given rise to the emergence of the multitude of different languages as a consequence of this process of cultural transmission. This process is not specific to humans. Regional vocal differentiation among members of the same species also occurs in songbirds (e.g., white crowned sparrows; Baker, 1975) and sea mammals (e.g., humpback whales; Garland et al., 2011). The variation among and within species can be studied to assess the impact of social or geographical factors affecting the formation, disappearance, or changes of dialects and language diversity.

3.4. SPEECH PRODUCTION AND PERCEPTION Over the years, many of the features that were once considered specialized adaptations to the production and perception of speech have been detected in other animal species. The permanently descended larynx in humans, for instance, was thought to be a uniquely human trait linked to the evolution of the ability to produce speech sounds by vocal tract filtering (Lieberman, Klatt, & Wilson, 1969). It certainly is a derived trait when humans are compared with great apes. However, a descended larynx also exists in other species, suggesting that it evolved by selection for producing low-frequency formants, driven by selection to simulate the presence of a larger animal to a receiver (e.g., Charlton & Reby, 2016). Also, many species, including several bird species (see chapter 48 by Kriengwatana & Beckers) are able to produce vocal variation by controlled and flexible filtering of harmonic spectra originating from a vibrating sound source. Comparative studies thus indicate a scenario in which the descended larynx of humans evolved for other reasons and only later became of use for producing speech sounds. Another comparative study (Fitch, Marthur, de Boer, & Ghazanfar, 2016) showed that the vocal tract of macaques is capable of producing a large range of vowel-like sounds, in contrast to what was thought in the past (Lieberman et al., 1969). So, a variety of studies indicate that a source-filter mechanism and the morphology of the sound producing system, and with this the ability to produce a wide range of sounds, are not uniquely human. This shifts the emphasis for studying what is special on human speech production to the way the system is being used, that is, its neural control (Fitch, 2018): what distinguishes the abilities of humans and

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nonhuman primates in this respect (see Fischer & Hage, chapter 45)?

Also for speech perception, comparative studies demonstrated that several features once thought special for human speech perception exist in other species, as outlined by Kriengwatana and Beckers (chapter 48). This ranges from the phenomenon of categorical perception to that of speaker normalization. The fact that other species with vocalizations that deviate strongly from speech sounds show comparable phenomena to humans when tested with human speech sounds indicates that even quite advanced perceptual mechanisms assumed to be human-specific may be shared among vertebrate species. This supports theories that speech perception is utilizing more general cognitive processes (e.g., Burgering, ten Cate, & Vroomen, 2018). It also questions theories postulating that the ability to recognize speech sounds is linked to being able to produce them (see Kriengwatana & Beckers, chapter 48). Nevertheless, there are likely to be species-specific specializations in human speech perception, as there are in other animal species for perception of species-specific vocalizations. There is a need for more detailed comparative studies to unravel the nature and interaction of shared and specialized mechanisms involved in speech perception, as well as on how experience affects the development of such mechanisms. This latter question requires experiments in which the exposure to various sounds is controlled, for which animal studies will be of particular relevance. Comparative studies are also required to examine whether and how the ability and constraints of animals to perceive certain speech parameters is related to the presence and relevance of particular features of their own vocalizations. So, studies on the cognitive and neural mechanisms that animals use to process human speech sounds and species-specific vocalizations may provide model systems to inform new theories of speech perception, its development and interaction with more general auditory mechanisms, as well as on the evolutionary origin of the speech perception mechanisms.

3.5. SYNTAX One of the hotly debated topics in language evolution concerns how syntax, as a core property of all languages, evolved. Did genetic changes around 100,000 years ago result in the emergence of computational abilities that made it possible to create hierarchically structured expressions (Berwick & Chomsky, 2016)? Or has there been a more gradual incremental evolution of such abilities, resulting from extending rule learning mechanisms shared with other species (e.g., Christiansen & Chater, 2015)? One reason that this debate is heated is due to a lack of knowledge on the presence of rule learning abilities in other species. Comparative

research follows two approaches to address this issue. One is to study the complexity of animal vocal structures. The song of songbirds is often used as reference in this context as their vocal complexity seems beyond that of many other animal vocalizations. However, although songbird songs can be complex, the few that have been studied in depth for syntax can be described by grammatical rules belonging to the bottom region of the hierarchy of grammar structures: a finite state grammar (Berwick, Okanoya, Beckers, & Bolhuis, 2011). Therefore it has been argued that nonhuman animals do not possess any meaningful linguistic computational abilities. This argument seems to be premature for at least three reasons. First, the actual number of species for which vocal structures have been examined in great detail is still limited—there may be more complexly structured animal vocalizations but we may simply not have come across them yet. Second, complex songs may not have evolved to convey complex structured messages, but rather to produce variability in vocal signals that may impress, or appeal to, conspecifics of own or the other sex. Such variability need not have led to evolution toward a hierarchically organized compositional vocal system. It may be no coincidence that where there are indications of a more combinatorial and compositional vocal system in animals this has been found in studies examining how different types of calls within a species are combined. Calls are more like referential signals than songs (e.g., different alarm calls may refer to different types of predators) and their combinations may produce combined meanings, which may be seen as first steps toward more complicated messages. This work is still in its early stages, with a few primate (Schlenker, Chemla, & Zuberbühler, 2016) and bird (Griesser, Wheatcroft, & Suzuki, 2018) species being studied. Examining species in which call variation and call exchanges form an important part of the intraspecific communication will be a profitable way forward to detect whether more complexly structured vocal communication systems exist. The third objection against using lack of vocal complexity as an argument that animals lack relevant computational abilities is that such abilities may be present but are not used in shaping vocalizations. In their daily life, animals may be confronted with situations that require sequential procedures (e.g., for food extraction) or analogical reasoning (transferring experience from one situation to another one). Such conditions may provide selection for more generally applicable computational abilities. Hence, to address the syntactic abilities of animals, they should be presented with tasks and tests that address these abilities. Ten Cate and Petkov (chapter 47) review these abilities. They show that many species are capable of learning sequential patterns such as

learning about adjacent and even nonadjacent dependencies and may be capable of statistical learning. Nevertheless, the currently available studies do not yet allow a firm conclusion about the presence of more complex, hierarchical, computational abilities. They may be present, but as animals may have solved tasks aimed at revealing such abilities by simpler ways, this issue is still in need of further study. As it is clear that there are species differences in computational abilities even among the limited number of species studied, expanding the current range of species is of importance to advance the field. This applies in particular to species like great parrots, as well as different corvid species. These are increasingly studied for their advanced skills in several cognitive domains, such as tool use (Auersperg, Szabo, von Bayern, & Kacelnik, 2012) or analogical reasoning (Smirnova, Zorina, Obozova, & Wasserman, 2015; Obozova, Smirnova, Zorina, & Wasserman, 2015), but studies of their linguistic abilities are still rare. Such studies will provide valuable insights into whether the learning mechanisms for learning about vocal structures and syntactic rules are special or originated from more domain general rule learning (Santolin & Saffran, 2018) or other cognitive mechanisms.

4. Conclusion

The chapters in this part, as well as the brief overview here highlight that comparative research related to speech and language nowadays covers a wide range of topics. While some studies initially may have started off from asking whether animals have the same abilities as humans, these studies are getting more bidirectional, with animal findings informing theories of the mechanisms underlying human linguistic abilities. At the same time, it has to be noted that comparative studies still cover only a modest variety of species, predominantly a limited number of primate and songbird species. While there certainly are merits to a focus on a few animal models for particular questions, this narrow range of species also presents a problem. When only few species are studied, it is tempting to generalize the outcome of those studies as indicating that “animals” can or cannot do certain things. But despite the fact that comparisons and generalizations among the species studied thus far are sometimes constrained by differences in experimental paradigms, it has also become increasingly clear that animal species can differ considerably in their abilities. Thus, one species’ capabilities or inabilities certainly should not be taken as being representative of all species. It calls for including a broader range of species in comparative studies, as well as for using more comparable experiments, to understand the causes for variation

in the “linguistic abilities” of nonhuman animals. Nevertheless, what can be noted is that while language as a whole is unique to humans, comparative studies have shown that what at first sight seemed major differences between humans and other species may not be as fundamental as once thought, and that many linguistic features may have been derived from precursors that are more widely spread among other species.

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