Linguistic birds : exploring cognitive abilities in zebra finches by using artificial grammars

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Chapter 1

General Introduction

Among animals, all kinds of senses are used for communication. There are chemical communication systems, systems mediated by behavioral displays (e.g. facial expressions and gestures), vocal communication systems, and so on. Among all communication systems, human language is the most complex one known to date. Understanding the evolution of the language faculty is one of the greatest scientific challenges; one that has given and still gives rise to hot debates (Hauser, Chomsky et al., 2002; Hauser, Yang et al., 2014; Jackendoff & Pinker, 2005) . The origin of language is difficult to track since there are neither fossils nor clearly identifiable, biologically heritable entities that directly link to such behavior. Comparative studies exploring the linguistic capacities in nonhuman animals provide an alternative perspective for understanding the evolution of language, while at the same time revealing more about the cognitive capacities of animals. Although the specific functioning of the communication system of each species is unique, studying what is and is not shared between different species can help us to identify what might have been at the evolutionary basis for a complex trait like human language or what might have been the selection pressures that have led to different evolutionary trajectories.

The aim of this thesis is to shed light on whether some capacities that are considered linked to, or characteristic for, language are shared between humans and nonhuman animals, which may help to understand the basic cognitive abilities from which the evolution of human language may have arisen. I start with comparing human language with other communication systems to illustrate how distinct language is and to make clear that, in order to understand the cognitive mechanisms that might have been at the basis for the evolution of the language faculty, one should not restrict oneself to examining the communication systems of other animals. I suggest that a possibly better way to study the evolutionary basis of language is to study the broader cognitive abilities of nonhuman animals and map these abilities to human linguistic capacities to check which are and which are not shared. This is the core theme of this thesis.

Human language and other communication systems

Language is highly structured and hierarchically organized. Language users must therefore possess a certain level of cognitive skills or capacities that allow them to comprehend language by decomposing the hierarchically structured units. Over the years, the question which aspects of human language are also found in non-human animal communication systems has been hotly debated (see Hauser, Yang et al., 2014 for a recent example). Humans have tried for decades to teach language to our closest primate relatives, but without much success (Bolhuis & Wynne, 2009). This indicates that some components that are important to language may not be available to our relatives. One key prerequisite tied to language is vocal imitation (Fitch, 2000), which enables learners to obtain the correct sounds and structures of their language from other individuals. Our primate cousins show almost no evidence of vocal imitation (Whiten & Ham, 1992). For example, monkeys produce basically all their species-typical call types even when they were reared in isolated conditions (Arbib, Liebal et al., 2008). A cross-fostering study showed that rhesus and Japanese macaques cross-fostered to each other produced limited changes in their species-specific vocalizations when compared with the control individuals that were raised by conspecifics (Owren, Dieter et al., 1993). Also, few studies show vocal dialects in primates, suggesting the lack of vocal imitation among nonhuman primates (Hauser, Chomsky et al., 2002).

Different from our primate cousins, distantly related species such as some marine mammals, bats and songbirds were found to have greater vocal learning abilities (Boughman, 1998; Janik & Slater, 1997; Janik & Slater, 1998; Knörnschild, Nagy et al., 2010; Wilbrecht & Nottebohm, 2003). Vocal learning in songbirds is especially well studied and striking parallels have been found between song learning and speech acquisition. Songbirds and humans both learn their vocalizations in early life, and the sensory-motor systems for vocal acquisition in songbirds and humans share notable similarities (Bolhuis, Okanoya et al., 2010; Doupe & Kuhl, 1999). Both human language and birdsong are also hierarchically organized, following certain syntactic constraints. However, the nature of the syntactic constraints is generally considered as the core difference between language and any non-human animal communication system known to date (Hauser, Chomsky et al., 2002). Unlike human language, bird songs can be considered as a regular language (characterized by finite-state machines, which are computational models that consist of a finite number of states and the transition functions between these states). In contrast, human languages demonstrate the ability of recursion, which is the possibility to infinitely embed syntactical structures inside an existing structure, and consequently has the features of a context-free language, allowing an infinite range of expressions (Berwick, Okanoya et al., 2011; Hauser, Chomsky et al., 2002). Recursive constructs such as a^nb^n (the bird the cat chased flew, a_1 = the bird, a_2 = the cat, b_2 = chased and b_1 = flew) occur in many human languages and rely on nested dependencies. To detect whether an animal can produce a context-free pattern, one needs to demonstrate that the animal can correctly pair the a(s) and the b(s) (Berwick, Okanoya et al., 2011). Dependency, especially the nonadjacent ones (such as illustrated in the sentence above, in which a_1 and b_1 have a nonadjacent dependency involving event knowledge) is suggested to be important and critical characteristic of human language (Everaert & Huybregts, 2013), and no evidence to date has shown the existence of nonadjacent dependencies in the communication system of any other animal.

Altogether, the comparison between communication in humans and nonhumans tells us that human language is highly distinctive, and that the spontaneous usage of some features in human language (such as recursion and nonadjacent dependency) are not found in the communication systems of nonhuman animals. But does this mean that the linguistic mechanisms underlying these features are as distinctive as one might think? In other words, is it possible that these features, although not shown in non-human animal communication, can still be recognized by domain-general cognitive mechanisms not specific to language? It is possible that the cognitive mechanisms that allow the detection of these features evolved for different purposes in nonhuman animals and thus are not obvious in their communication systems. This idea is supported by the presence of some advanced cognitive capacities that are not reflected in the communicative content of nonhuman animals. For example, animals are able to anticipate future (Correia, Dickinson et al., 2007; McKenzie, Cherman et al., 2004; Mulcahy & Call, 2006; Raby, Alexis et al., 2007), but there is no evidence showing that this capacity is reflected in their communications (they do not “talk” about things and events that are not here and now). Evidence of such abilities that are not reflected in communication also comes from studies of artificial language learning. Animals are able to perceive and generalize some types of grammatical structures not present in their communication signals (Ravignani, Sonnweber et al., 2013; Saffran, Hauser et al., 2008).

What to compare

Some capacities required for language learning and comprehension may have evolved from domain-general cognitive mechanisms (Endress, Cahill et al., 2009; Endress, Carden et al., 2010; Endress, Dehaene-Lambertz et al., 2007; Endress, Nespor et al., 2009). Therefore, comparing human language with communication systems of other animals may not be the best way to get insight in the type of mechanisms that may have shaped the evolution of language. A better approach might therefore be to compare the presence and nature of cognitive capacities that are relevant to language learning. These cognitive capacities refer to what an animal can learn and not to what can be seen in the communication system of this animal. A capacity may not be ‘expressed’ in certain domains, but may be present in others. If such capacity is found to be shared by different species, it may have been at the basis of the evolution of the higher complexity as present in the structure of language. Therefore, study of shared capacities, no matter whether they are present in the communication systems of other animals or not, might help us to identify which underlying mechanisms are homologous, which are convergent and which are unique to different species.

This thesis reflects the line of thought presented above by exploring the presence of several cognitive abilities in a non-human animal, the zebra finch. Considering that the most important and possibly most unique (Hauser, Chomsky et al., 2002), feature of language is the computational mechanism that processes syntactical structures, this thesis concentrates on the nature of several learning abilities underlying linguistic structures, in particular some that currently attract considerable attention– namely, sequential learning and rule learning. The study species used to address the topic is the zebra finch, a model species for comparative studies on vocal learning. Birdsong and human speech share notable similarities (Berwick, Okanoya et al., 2011; Wilbrecht & Nottebohm, 2003) and there are striking parallels between the ways in which infants and young birds learn their vocalizations (Doupe & Kuhl, 1999). Zebra finches, as a model species, have been studied extensively, and notable similarities between these birds and humans have been found in studies in various areas. Zebra finches show functional similarities with human auditory and motor cortices in their pallial ‘song’ regions (Jarvis, Güntürkün et al., 2005). Studies on the molecular genetics of vocal learning showed that the forkhead box protein P2 (FOXP2) gene, which is crucial to language acquisition, also plays a key role in song learning in zebra finches (Fisher & Scharff, 2009). Moreover, behavioral studies suggested that zebra finches shared some similarities with humans in using cues for perceiving speech sounds (Ohms, Escudero et al., 2012; Ohms, Gill et al., 2010; Spierings & ten Cate, 2014). Such similarities between humans and zebra finches make these birds of special interest for examining cognitive capacities that link to language processing.

Thesis outline

This thesis consists of the present introduction and 4 chapters consisting of empirical studies, addressing questions from the domains of sequential learning and rule generalization.

Sequential learning

Components of communication systems, such as behavioral displays and sounds, are arranged in sequences. Also verbal language, the most complex system of communication, consists of sequences of speech sounds. The capacity to learn and encode sequences is basic to language learning and is expected to be constrained by sequential memory. A sequence can be memorized by using the positional information of the items. That is, encoding the items with their positions in the sequence(Henson, 1998). Phenomena like serial order intrusion errors suggest such a positioned encoding mechanism, which is supported by evidence from serial recall experiments (Endress, Cahill et al., 2009; Endress, Carden et al., 2010; Hitch , Fastame et al., 2005). Positional encoding also gained considerable support from studies in nonhuman animals. Studies of serial recall in primates and birds suggested that nonhuman animals rely mostly on positional information when memorizing sequences (Comins & Gentner, 2010; Endress, Carden et al., 2010; Orlov, Amit et al., 2006; Orlov, Yakovlev et al., 2000; Terrace, Son et al., 2003). However, studies on statistical learning showed that humans and monkeys were also sensitive to associations between items (Aslin, Saffran et al., 1998; Hauser, Newport et al., 2001; Kelly & Martin, 1994; Saffran, Aslin et al., 1996; Saffran, Johnson et al., 1999). In these studies, learners were good at using chaining-like mechanisms based on transitional probabilities between subsequent items in a string. This suggested that transitional information between the items may also play an important role in sequential learning. So far, the only study explicitly testing how birds (starlings) process sequential information (Comins & Gentner, 2010) suggested that they relied heavily on positional information, raising the question whether songbirds can also use transitional information. In **chapter 2** we examine this question by conducting an experiment with artificial language stimuli containing both positional and transitional information.

Rule generalization

Language is a rule- or structure-mediated system, therefore rule abstraction is considered to be a hallmark of human linguistic abilities (Hauser, Chomsky et al., 2002; Marcus, Vijayan et al., 1999; Pinker, 1991). Rule learning abilities of animals have been tested in various species and findings from these tests suggest that some rule learning capacities are shared between human and other animals. The subsequent chapters of this thesis address rule learning abilities that have so far not, or hardly, been explored for non-human animals.

Edge-based rule learning

Endress, Nespor et al. (2009) proposed that rule abstraction involving language learning might have been complemented and constrained by a toolbox of ‘perceptual or memory primitives’. One of these primitives is related to edge-based positional regularities, in which rule generalizations are constrained by the edge positions. Edge-based positional regularities such as English regular past tense (-ed added to words, such as learned, recognized etc.) provides a strong case for establishing the view of mental computation as rule-based manipulation of symbol systems (Marslen-Wilson & Tyler, 1998). Tracking the edges of a sequence is not a phenomenon only found in humans. Evidence from a non-human primate study (Endress, Cahill et al., 2009) suggested an evolutionary precursor to human language affixation. In that study, cotton-top tamarin monkeys were shown to be able to discriminate between artificial words that start with a 'prefix' syllable and those that end with the same syllable as a 'suffix'. Up to now, there is no evidence from any other animal species suggesting an ability to learn patterns similar to the (surface) transformations of human affixation. In **chapter 3,** we trained and tested zebra finches to discriminate sequences constructed to resemble prefixation and suffixation patterns to further investigate this learning ability in nonhuman animals,

'Algebraic' rule learning

Studies exploring generalizations of more sophisticated rules, such as 'algebraic' rules and the learning of recursive structures are at the core of debates about the uniqueness of the faculty of language. An algebraic rule is defined as an "open-ended" abstract relationship for which we can substitute arbitrary items (Marcus, Vijayan et al., 1999). In a study of human infants, Marcus, Vijayan et al. (1999) exposed 7-months old infants to XYX or XYY speech stimuli (X and Y being consonant-vowel syllables) and showed that infants could abstract the underlying regularities and apply them to novel stimuli consisting of new syllables. This 'algebraic' generalization by the young infants inspired researchers to explore the presence of such an ability in nonhuman animals. By using similar designs, tests have been performed with monkeys, rats and birds (Hauser & Glynn, 2009; Murphy, Mondragon et al., 2008; Seki, Suzuki et al., 2013; Toro & Trobalon, 2005; van Heijningen, Chen et al., 2013). These animals were found to be able to discriminate different artificial structures. However, the question of whether or not these animals generalized the structures without relying on the physical similarities between stimuli still remains disputable (ten Cate & Okanoya, 2012). Therefore, **chapter 4** deals with this the question by addressing whether zebra finches show the ability of learning and generalizing 'algebraic' rules similar to those present in human infants.

Nonadjacent dependencies

Learning natural human languages is not just about generalizing simple and linear structures. A simple sentence like 'A fish swims' is not as simple as three words being put together linearly. In this sentence, a morpheme 's' was added spanning the intervening materials ('fish' and 'swim') to agree with the single number 'A'. Linguists have suggested that such nonadjacent dependencies might 'define' human language when compared to animal vocal communication (Everaert & Huybregts, 2013). Although nonadjacent dependencies are not easy to acquire, even for humans, there is some evidence suggesting that non-human primates are aware of nonadjacent dependencies between sounds (Newport, Hauser et al., 2004; Ravignani, Sonnweber et al., 2013). But experiments involving nonadjacent dependencies that have been done so far were all in primates and the dependencies between elements in these studies all occurred at the edges. In **chapter 5**,we trained and tested zebra finches with an artificial language consisting of different nonadjacent grammars to address the question whether or not they can learn nonadjacent dependencies and can even learn such dependencies when dependent items occur at arbitrary positions of sequences.

Finally, a summary of the results is given in the last chapter (**6**: **summary and conclusion**), which discusses the most important findings of this thesis.

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