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**Title:** Linguistic birds: exploring cognitive abilities in zebra finches by using artificial grammars  
**Issue Date:** 2014-10-16
Chapter 6

Summary and conclusion
Language is considered a key component that distinguishes humans from other animals. However, since the 19th century, researchers started to realize that some features related to language and language learning were shared with other animals. The debates on to what extent the language faculty is shared with nonhuman animals has boosted an increasing number of cognitive studies with animals. This thesis contributes to such cognitive research by examining whether learning abilities that are considered important in human language learning are also present in zebra finches. This can indicate that these processes may have a domain general origin and, during evolution, may have been co-opted for language.

Chapter 2 addressed the question: what mechanisms are involved in learning a sequence of vocal items in zebra finches. In this study, the birds were trained with sequences differing in transitional and positional information and subsequently tested with novel strings containing positional and transitional similarities with the training strings. When tested with two strings that shared more transitional than positional information with the training strings, birds were more likely to use transitional than positional information to recognize the test stimuli. When the test stimuli contained more positional similarity with one training stimulus and more transitional similarity with the other training stimulus, preferences for using positional or transitional information were both found in different birds, which suggested that both encoding mechanisms were involved in the discrimination. Unlike a previous study on sequential learning in a songbird, the starling (Comins & Gentner, 2010), which suggested that songbirds had a learning bias for positional information in the encoding of sequences, the results of this chapter suggested that the zebra finches are able to bias their sequential coding strategy depending on what might be most profitable given the context.

This study also showed that zebra finches were able to discriminate segments of the training strings according to their chaining regularities, even though the length of segments was much shorter than that of the training strings. A fundamental process during language acquisition is to segment words from fluent speech. Humans can accomplish this task by paying attention to transitional cues in continuous speech. The ability of zebra finch to employ transitional cues indicates that some similarities might be shared between the cognitive mechanisms of this bird species and humans.

Chapter 3 addressed whether zebra finches are able to discriminate between, and generalize, affixation patterns. Zebra finches were trained to discriminate artificial sequences resembling prefixed and suffixed ‘words’. The ‘stems’ of the ‘words’, consisted of different combinations of a triplet of song elements, to which a fourth element was added that acted as either a prefix or a suffix. Six zebra finches received the prefixed words as Go stimuli and the suffixed ones as Nogo stimuli, for another six birds the conditions were reversed. The birds were first trained with a set of affixed stems and subsequently tested with novel stems, which were composed either by rearranging the training stems (familiar element types) or by using novel element types.

The results show that the birds were able to generalize the affixation patterns to novel stems, with both familiar element types and novel element types. It indicates that the discrimination resulting from the training was not based on memorization of individual stimuli,
but on a shared property among Go or Nogo stimuli, i.e. their affixation patterns. We found that
the birds were able to learn both regularities. Remarkably, it seemed that using the suffix as a
cue was much weakened when birds trained with prefixation as the Go pattern. On the other
hand, birds were trained with suffixation as the Go pattern showed clear evidence of using both
prefix and suffix. This may imply an interesting parallel to the asymmetry in the type of
affixation preferred in human languages.

Chapter 4 deals with a controversial topic that is recently getting a lot of attention.
Discovering structured rules is a hallmark of human linguistic abilities. To demonstrate the
acquisition of abstract rules, successful categorization should not depend on the physical
similarity of strings of items that are all structured according to the same algorithm, but should
also be possible when the items of the individual strings bear no acoustic, but only structural
similarity to each other. Currently, few studies have addressed the question whether the animals
are able to generalize structures without relying on the physical similarities between stimuli as
humans do.

In a series of discrimination experiments, we presented zebra finches and human adults
with comparable training and tests with the same artificial stimuli consisting of XYX and XXY
structures, in which X and Y were zebra finches song elements. Zebra finches readily
discriminated the training stimuli. They showed evidence of simple rule abstraction related to
positional learning. Some birds also discriminated novel stimuli when these were composed of
familiar element types, but none of the birds generalized the patterns to novel element types.
These findings suggest that zebra finches may be able to a stimulus bound generalization, but we
found no evidence for a more abstract rule generalization. This differed from the human adults,
who readily categorized test stimuli consisting of novel element types into different groups
according to their structure. The limited abilities for rule abstraction in zebra finches may
indicate that the precursor of more complex abstractions is a stimulus bound rule learning
mechanism (that might have become more abstract under pressure of the growing lexicon in
human language).

Chapter 5 examined the ability of zebra finches to learn nonadjacent dependencies
between items in a string of vocal elements. The birds were trained and tested with an artificial
grammar consisting of different nonadjacent dependencies. Zebra finch song elements were
arranged in strings according to a particular grammar involving a non-adjacent dependency
between two items. In experiment 1 of this chapter, the two elements involved in the
dependency always occurred at the edges of sequences but the number and nature of intervening
elements varied, creating strings with varied length. One step further, experiment 2 tested the
ability of this songbird species to detect dependencies between elements that occurred at
arbitrary positions in the sequences.

Results from Experiment 1 showed that birds generalized nonadjacent dependencies
over varied distances. They were able to discriminate novel stimuli according to the relations
between non-adjacent items even when the intervening items were never heard by the subjects
before. Nonadjacent dependencies in human language do not always occur at the edges, they can
occur at arbitrary positions in speech sequences. In the second experiment, one zebra finch
learned to detect non-adjacent dependencies in different positions in the stimulus sequences. The results of this chapter suggest that the quite complex cognitive capacity to detect relationships between elements that are non-adjacent in a vocal sequence is present in zebra finches.

**Conclusion**

To conclude, this thesis showed that songbirds are not only able to encode sequences by using positional cues, but also to use transitional information between items for sequential encoding. The clear presence of using transitional information in the zebra finches is of particular interest from a comparative perspective. Transitional information has been shown in an experimental setting to be exploited by human infants in a fundamental process of language acquisition, in which words were segmented from continuous speech (Saffran, Aslin et al., 1996). In addition to previous findings from primates and rats (e.g. Hauser, Newport et al., 2001; Toro & Trobalon, 2005), birds now are also shown to be sensitive to transitional information, suggesting that such a cognitive skill is broadly present and may have been recruited for language learning from a more general domain. Our findings are by no means suggesting that positional cues are less important. On the contrary, we suggest that learning of the structure of a sequence might well be constrained by perceptual and memory primitives, such as seen in the learning of the edge-based positional regularities. Zebra finches in this thesis were shown to generalize edge-based positional patterns resembling the surface transformations of human prefixation and suffixation. This suggests that affixation patterns in human languages might have a prelinguistic origin, perhaps related to serial position learning and co-opted for use in language.

Of course, there are more sophisticated regularities that do not simply rely on the positions of items or linear transitions between items. To generalize a more abstract rule, one needs to make categorizations without basing this on the physical similarity between items. In this thesis, zebra finches were found to discriminate an XYX from an XXY structure with familiar stimuli only. Together with previous studies, which provided no strong evidence for such rule generalization (Hauser & Glynn, 2009; Murphy, Mondragon et al., 2008; Seki, Suzuki et al., 2013; Toro & Trobalon, 2005; van Heijningen, Chen et al., 2013, discussed in chapter 4), this divergence from what has been observed in humans suggests that the ability to generalize ‘algebraic’ rules might be unique to humans. However, more studies are still needed to make sure that the failure of finding this ability is not due to methodological factors. Finally, in this thesis, another more sophisticated regularity, that of detecting nonadjacent dependency relations between items, was shown to be present in the zebra finches. The birds were able to learn nonadjacent dependencies at varied distance and at arbitrary positions of sequences. This latter ability has not been demonstrated in any non-human animal study before and thus provides a new perspective on what animals can do and what is shared with humans.

Altogether, this thesis provides positive evidence for similarities between humans and songbirds in using transitional information, generalizing surface transformations of human affixation patterns and detecting nonadjacent dependencies. The presence of such similarities between species that shared a common ancestor some 300 million years ago may indicate that either such abilities are rooted in a deep past, or, more likely, that they evolved independently
and, in the case of zebra finches, unrelated to their use in natural vocal communication. Demonstrating these similarities in the highly constrained and simplified conditions in our experiments cannot result in the conclusion that ‘birds can do the same thing as humans’. However, they do demonstrate cognitive abilities that may also have been present in prelingual humans and that may have been evolutionary precursors co-opted for constructing the complex syntax processing machinery present in modern humans.
Reference


