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

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Chapter 3*

Zebra finches are able to learn prefixation and suffixation patterns

* This chapter is based on: Jiani Chen, Naomi Jansen & Carel ten Cate (submitted).

Abstract

Adding an affix to transform a word is common across the world languages, with the edges of words more likely to carry out such a function. However, detecting affixation patterns is also observed in learning tasks outside the domain of language, suggesting that the underlying mechanism from which affixation patterns have arisen may not be language- or even human-specific. We addressed whether a songbird, the zebra finch, is able to discriminate between, and generalize about, affixation patterns. Zebra finches were trained and tested in a Go/Nogo paradigm to discriminate artificial song element 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 as either a 'prefix' or a 'suffix'. After training, the birds were tested with novel stems, consisting of either rearranged familiar element types or of novel element types. The birds were able to generalize the affixation patterns to novel stems with both familiar and novel element types. Hence 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. affixation patterns. Remarkably, birds trained with suffixation as Go pattern showed clear evidence of using both prefix and suffix, while those trained with the prefix as the Go-stimulus used primarily the prefix. This may imply an interesting parallel to the asymmetry in the type of affixation preferred in human languages.

Introduction

Understanding how human language may have arisen is still one of science's greatest challenges. Hypotheses about its evolutionary origin are linked to debates about the properties that make it unique and those that are shared with other animals (Fitch, 2010; Hauser, Chomsky et al., 2002). Comparative studies in non-human animals may thus provide a window on how linguistic complexity may have arisen and what its precursors might have been. Such studies can be directed at related taxa, like apes and monkeys. Alternatively, one can examine the presence of 'linguistic abilities' in more distantly related groups in which relatively complex and structured vocalizations evolved independently, such as songbirds. Songbirds show striking cognitive, neural, and genetic similarities with humans in vocal perception, production and auditory-vocal learning (e.g. Berwick, Okanoya et al., 2011; Bolhuis, Okanoya et al., 2010; Doupe & Kuhl, 1999; Ohms, Gill et al., 2010; ten Cate & Okanoya, 2012). For this reason they are seen as excellent comparative models to explore mechanisms that might have been at the basis of language evolution (Bolhuis & Everaert, 2013). In the current study we also use a songbird species, the zebra finch, and examine whether it is able to discriminate between, as well as to generalize, 'affixation' patterns.

Among the components of language, one of the most notable aspects is morphological transformation. Over decades, studies of inflectional morphology have been at the center of important debates about the fundamental nature of cognitive processes (Endress & Hauser, 2011). Affixation in languages, like the English past tense, provides a crucial case in establishing the view of mental computation as rule-based manipulation of symbol systems (Marslen-Wilson & Tyler, 1998). The great majority of English verbs form their past tense by adding an -ed affix to an unchanged stem. Knowledge of affixation rules plays an important role in learning vocabulary and in language development (Kuczaj, 1977; Mochizuki & Aizawa, 2000; Nagy, Diakidoy et al., 1993). Adding an affix to transform a word occurs quite often across languages. Interestingly, the edges of the words are more likely to carry out the grammatical functions; an affix in the first position (prefix) or in the last one (suffix) is much more frequent than affixes in other positions (Endress & Hauser, 2011; Endress, Nespors et al., 2009). This bias is not only observed in languages. Learning in serial memory tasks also showed that the edge positions of a sequence can be recalled more accurately (Endress, Carden et al., 2010; Henson, 1998, 1999; Hitch, Burgess et al., 1996; Wright, Santiago et al., 1985). Also in artificial language learning, participants were found to generalize regularities reliably at the edges but not in the middle of acoustic sequences (Endress & Mehler, 2010; Endress, Scholl et al., 2005). These examples suggest that prefixation and suffixation patterns are relatively easy to learn and that the edge-based positional learning competence could be an example of what Endress, Nespors, et al., (2009) called "perceptual and memory primitives"; phylogenetically pre-existing cognitive mechanisms which constrain rule-based learning in language acquisition and guide language evolution. If so, it raises the question to which extent the edge-based positional learning competence is shared with non-human animals and whether they can learn affixation rules.

Studies of sequential memorization in general have shown that the edge(s) of a sequence can be recalled better in birds and monkeys (Comins & Gentner, 2010; Endress, Carden et al., 2010; Orlov, Yakovlev et al., 2000; Terrace, Son et al., 2003; Wright, Santiago et al., 1985). In an artificial language learning experiment Endress et al. (2010) showed that chimpanzees also encode the edges of sequences better than the other positions in the sequences, similar to adult humans in the same experiment. Such experiments suggest that animals might also have the ability to recognize and learn affixation patterns, and in a pioneering study (Endress, Cahill et al., 2009), cotton-top tamarin monkeys were exposed to a set of human speech syllables ('stems') that were either preceded or followed by the affix syllable 'shoy'. When subsequently presented with novel stems, the tamarins discriminated between words starting with shoy as a 'prefix' and those that end with the same syllable as a 'suffix', demonstrating that they generalized the underlying affixation rule. Up to now, there is no evidence of such an ability from other animal species. Given the above mentioned similarities between songbirds and humans in vocal processing and also because birds show evidence of at least some, albeit simple, rule learning when trained and tested with strings of elements that are artificially structured according to different algorithms (e.g. Gentner, Fenn et al., 2006; Seki, Suzuki et al., 2013; van Heijningen, Chen et al., 2013; van Heijningen, de Visser et al., 2009), they are promising candidates to examine the presence of affixation learning as a more wide spread cognitive ability that is not specific to language nor to humans.

In the current study, we trained and tested zebra finches in a Go/Nogo paradigm to discriminate sequences constructed to resemble prefixation and suffixation patterns. In doing so, we concentrated on the edges of the sequences, in line with the studies that identified those as being the most salient parts of sequences and also the ones being used most for affixation in languages. We do not want to claim that such an experiment demonstrates the presence of the full formal notion of affixations in a non-human animal. What it can show is whether birds have the competence to detect surface transformations similar to different affixation patterns (prefix and suffix) and link these to different 'meanings' – in this case either a food reward or a mild punishment. The linkage of each affixation pattern to a different reward is also an advantage of using a Go/NoGo paradigm over a habituation paradigm as used in the tamarin study (Endress, Cahill et al., 2009). The habituation paradigm can tell whether animals spontaneously detect a change in a pattern, but detecting such a change is not linked to any consequence. The Go/Nogo not only tests whether the animals detect a difference, but also whether they can link this to a difference in consequences, analogous to human infants that have to learn over time how different affixations alter word meanings.. We also examine whether zebra finches can learn both prefixation and suffixation patterns equally well, or have a bias to be more sensitive to one over the other, as has been suggested for human languages (Cutler, Hawkins et al., 1985; Dryer, 2005; St Clair, Monaghan et al., 2009). We show that the zebra finches are able to learn both regularities. Remarkably, birds that had been trained with prefixation as Go pattern used predominantly the prefix to make their discrimination while birds trained with suffixation as Go pattern used both prefix and suffix.

Material and method

Subject and apparatus

Twelve zebra finches (6 males and 6 females) from the Leiden University breeding colony were trained and tested individually in sound attenuated chambers. None of the birds had previous experience with any kind of experiment. Six birds participated in Experiment 1; all 12 participated in Experiment 2. The experiment was conducted by using the Go/Nogo paradigm in an operant conditioning cage described earlier (van Heijningen, Chen et al., 2013). A fluorescent tube on the top of the box emitted daylight spectrum light on a 13.5 L: 10.5 D schedule. Sounds were played through a loudspeaker, attached above the box, at approximately 70 dB. Subjects gained access to food for 10 seconds after they responded to positive sound playback (Go stimuli). Conversely, if subjects responded to negative sound playback (Nogo stimuli), the light of the chamber was switched off for 15 second to indicate the error.

Stimuli

The ‘words’ used in this study consisted of artificially edited sequences consisting of four song elements. These elements were obtained from natural zebra finch songs (undirected songs) originating from our zebra finch song database. Seven elements, ‘flat,’ ‘stack,’ ‘trill,’ ‘downslide,’ ‘high,’ ‘curve,’ and ‘noisy’ (see Fig 1 for examples), were selected based on optimal discriminability. They were ramped and RMS equalized.

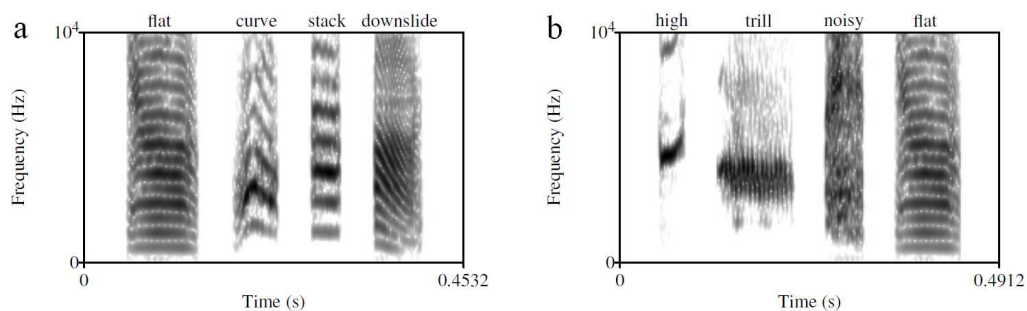


Fig. 1 Spectrograms of stimuli GABC for two different birds (a and b).

Two types of regularities, prefixation and suffixation, were used to construct the stimuli (Table 1). The ‘stems’ of the training stimuli were triplets constructed from three different element types ‘A, B and C’ in different combinations. Each element type occurred in every possible slot over the triplets. A fourth element type ‘G’ was only used as either a ‘prefix’ or a ‘suffix’. To eliminate pseudo effects due to an arbitrary parameter of the sounds, the element assignments were shuffled for the subjects, for instance, element ‘A’ could be ‘curve’ for one bird and ‘trill’ for another bird (Fig. 1). In Experiment 1, birds were first trained with three Go and three Nogo stimuli, each consisting of different combinations of an A, B and C element, and either preceded or followed by the affix (‘G’). The test stimuli of Experiment 1 were constructed by rearranging the element combinations of the stems. In Experiment 2, the training set included

the stimuli for the training as well as those for testing that had been used in Experiment 1. Testing occurred with stimuli in which the stems were formed by the novel element types ‘D, E, and F’, which never occurred in the training phase.

For each stimulus, 40 ms of silence was inserted between consecutive elements and 50 ms of silence was added at the start and the end to avoid acoustic distortions during playback. The training stimuli followed either a prefixation or a suffixation pattern. For half of the birds, the G-prefix predicted Go stimuli and the G-suffix the Nogo stimuli (Table 1, Condition 1), and vice versa for the other half of the birds (Table 1, Condition 2). The test stimuli were constructed by adding the G-suffix or –prefix to novel stems.

Procedure

To familiarize the birds with the Go/Nogo task, they were first trained to discriminate a natural song (Go stimulus) from a pure tone (Nogo stimulus). When their responses reached the training criterion (>75% response to Go stimuli and <25% response to Nogo stimuli) for at least two consecutive days, they were switched to the next phase of training, in which the experimental stimuli were presented.

Experiment 1

This experiment tested whether the birds were able to generalize the affixation patterns of the training stimuli when these were presented in combination with novel stems composed with familiar elements. Six birds (Group 1) were trained with three pairs of stimuli and subsequently tested with another three pairs of stimuli constructed from familiar element types but in novel combinations (Table 1). The tests started after the birds reached the training criterion to every training stimulus for at least three consecutive days.

In the tests, test stimuli were not reinforced to avoid additional learning. Every test contained 40 presentations of each test stimulus. However, to prevent extinction of the pecking behavior, only 20% of all stimulus presentations were test stimuli. The other 80% of stimulus presentations consisted of the reinforced training stimuli.

Table 1 Stimuli of Experiment 1 and 2

Condition	Experiment 1 (Group 1)			Experiment 2 (Group 1 & 2)			
	Training		Test	Training			
1	Go	Nogo	Test	Go	Nogo	Test 1	Test 2
2	Nogo	Go		Nogo	Go		
Stimulus	GABC	ABCG	GACB	GABC	ABCG	GDEF	
	GBCA	BCAG	GBAC	GBCA	BCAG	GEFD	
	GCAB	CABG	GCBA	GCAB	CABG	GFDE	ABC
			ACBG	GACB	ACBG	DEFG	DEF
			BACG	GBAC	BACG	EFDG	
			CBAG	GCBA	CBAG	FDEG	

Subjects in Experiment 1 were trained with 6 stimuli and tested with newly arranged ‘stems’ consisting of familiar element types. Subjects in Experiment 2 were trained with 12 stimuli and tested with new ‘stems’ consisting of novel element types. In Condition 1 the prefixation pattern predicted Go stimuli while the suffixation predicted the Nogo stimuli and vice versa for Condition 2.

Experiment 2

This experiment tested whether the zebra finches could generalize the affixation patterns to stems constructed from novel element types. It also addressed whether the discrimination shown in training and test was dependent on the presence of prefix only, suffix only, or both. A total of 12 birds were used. Six of these had previously been used in Experiment 1, another six had not been trained and tested before. The six pairs of Go and NoGo training and test stimuli in Experiment 1 were combined and used as training stimuli (Table 1). After the responses of the birds to every stimulus of the training reached criterion for at least three days, the first test started. Test 1 examined the response to new stimuli with novel stems that constructed with novel element types. The second test was given after Test 1, consisting of the ABC and DEF stems without any affix. If the birds learned both prefixation and suffixation patterns, we expected them to respond to these ‘stem-only’ stimuli at an intermediate level compared to their responses to the ‘affix-versions’. As Experiment 1, the percentages of stimulus presentations with training and test were 80:20 and the test stimuli were not reinforced.

Results

Experiment 1

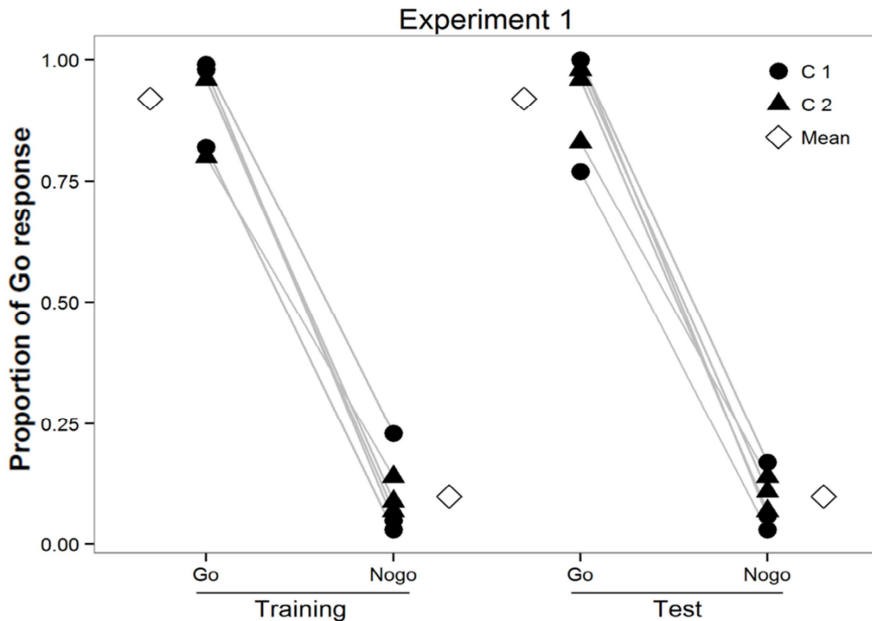


Fig. 2 Performances of individual birds of Experiment 1. All birds discriminated between prefix and suffix stimuli, both in the training and in the test, and irrespective whether the Go-stimulus was a prefix (Condition 1 (C1)) or a suffix (Condition 2 (C2)). Mean response ratios (proportion of responses to the ‘Go’ stimulus) of all birds are showed as well. Both training and test stimuli were constructed with element type A, B, and C (in different sequences), using G as affix. Test stimuli were not reinforced; ‘Go’ and ‘Nogo’ indicate test stimuli that are structurally similar to Go and Nogo training stimuli.

All birds ($n=6$) reached training criterion. All birds distinguished non-reinforced test stimuli with different structures as well as they discriminated the reinforced stimuli (Fig. 2). The responding ratios in the test were 0.92 ± 0.04 SEM to the Go pattern and 0.10 ± 0.02 SEM to the Nogo pattern. The Discrimination Ratio (DR, calculated as the percentage response to Go stimuli divided by the sum of the percentage response to Go stimuli and the percentage response to Nogo stimuli) for individual birds were all higher than 0.5 (DR = 0.908 ± 0.018 SEM), which indicates positive discrimination (Wilcoxon Signed-rank test $Z = -2.201$, $p = 0.028$). There was no significant difference between training condition 1 and condition 2 (responses to the Go pattern: $U = 3.0$, $p = 0.700$; responses to the Nogo pattern: $U = 3.0$, $p = 0.700$, Mann-Whitney U test).

Experiment 2

Test 1

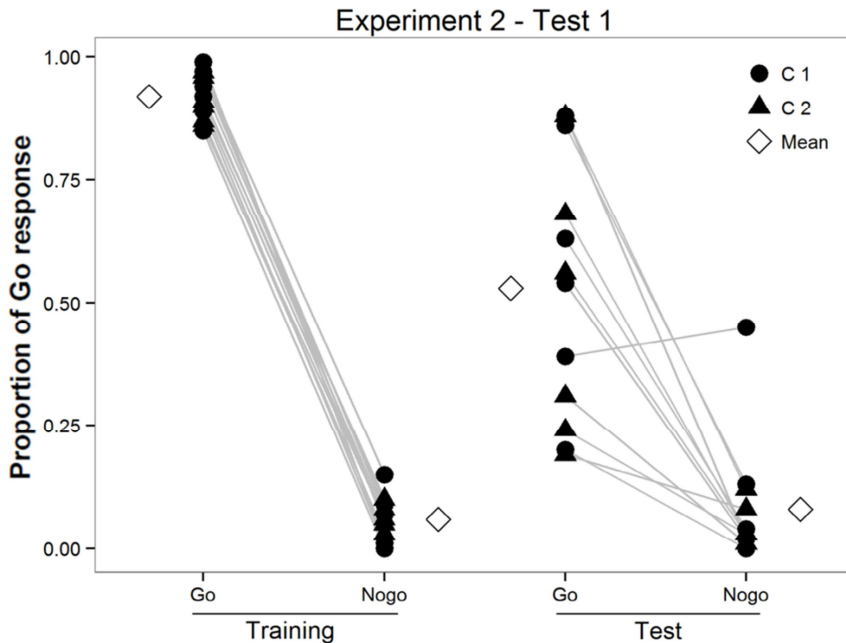


Fig. 3 Displayed are the performances of individual birds in Experiment 2, Test 1. Eleven birds discriminated between prefix and suffix stimuli in the test irrespective whether the Go-stimulus was a prefix (Condition 1 (C1)) or a suffix (Condition 2 (C2)). Mean response ratios of all birds are shown as well. Training stems were constructed with element type A, B, and C while test stems were constructed with element types D, E and F. Element G was used as the affix both in training and test. Test stimuli were not reinforced; 'Go' and 'Nogo' indicate test stimuli that are structurally similar to Go and Nogo training stimuli.

All birds ($n = 12$) learned to discriminate the Go and Nogo stimuli in the training. In Test 1, there was no significant difference between different training conditions (responses to the Go pattern: $U = 14.50$, $p = 0.589$; responses to the Nogo pattern: $U = 18.0$, $p = 1.0$, Mann-Whitney U test). The different training groups (Group 1 versus Group 2) also showed no significant difference (responses to the Go pattern: $U = 13.50$, $p = 0.485$; responses to the Nogo

pattern: $U = 15.50$, $p = 0.699$, Mann-Whitney U test). Therefore, the two groups were pooled. The responding ratios to the test stimuli with affixation patterns similar to Go training stimuli differed significantly from those to test stimuli with affixation patterns similar to the Nogo training stimuli (0.53 ± 0.08 SEM and 0.08 ± 0.04 SEM respectively, Fig 3. $Z = -2.934$, $p = 0.003$, Wilcoxon signed-rank). Eleven birds showed high DR in the test (0.92 ± 0.02 SEM). Only one out of 12 birds did not generalize the Go and Nogo patterns to the test stimuli (DR = 0.47).

Test 2

While the previous tests showed no differences in response patterns between the two training conditions, this test did. Therefore, data from the two training conditions are presented separately. Page's trend test for ordered alternatives (Page, 1963; Siegel & Castellan, 1981) was applied to detect whether the responses to test stimuli were ordered according to their affixes, testing the hypothesis that the responses to stimuli without an affix are expected to be in between those with a prefix or suffix

Condition 1 – Go: prefix

Responses to the stimulus without affix (ABC and DEF) were compared with their 'affix-versions' (GABC and ABCG; GDEF and DEFG). The one bird that did not generalize the Go and Nogo response to stimuli with novel element types was excluded from the test involving the DEF stem.

The test showed a significant decline in responses from GABC, ABC to ABCG ($L = 81.5$, $n = 6$, $p < 0.05$, Fig. 4a). However, most birds showed little or no differentiation between ABC and ABCG. Only one bird showed a clear intermediate response to ABC. A similar responding pattern was observed in the test with novel elements. Again a significant decline was found in responses to GDEF, DEF and DEFG ($L = 68.5$, $n = 5$, $p < 0.05$, Fig. 4b). However, the responses to the 'stem-only' stimuli were more similar to the responses to suffixed stimuli.

Condition 2 – Go: suffix

In Condition 2, the training stimuli of the Go pattern ended with a suffix while the Nogo pattern started with a prefix. The data were analyzed in the same way as those obtained for Condition 1.

The responses to stimuli decreased gradually from the Go pattern, the 'stem-only' pattern to the Nogo pattern, whether these consisted of familiar or novel element combinations. The declining trend was shown most clearly in the test with DEF stem (test with ABC stem: $L = 83$, $n = 6$, $p < 0.05$, Fig. 4c; test with DEF stem: $L = 84$, $n = 6$, $p < 0.05$, Fig. 4d).

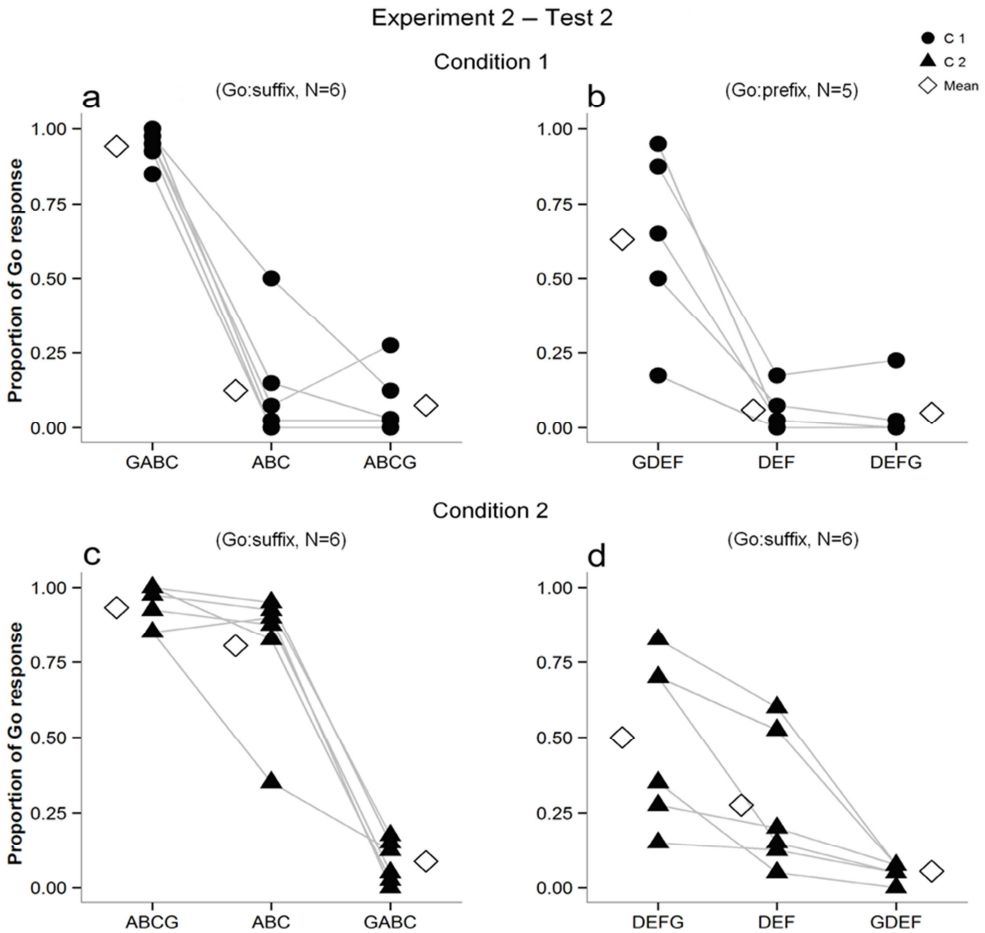


Fig. 4 Displayed are the performances of individual birds in Experiment 2, Test 2. (a) Responses to stimuli with familiar stems in Condition 1 (C1). (b) Responses to stimuli with novel stems in Condition 1. (c) Responses to stimuli with familiar stems in Condition 2 (C2). (d) Responses to stimuli with novel stems in Condition 2. Mean response ratios of all birds are shown as well.

Discussion

The results of Experiment 1 showed that the birds perfectly generalized the discrimination obtained during the training to test stimuli that shared the affixes with the training stimuli, but had a novel stem constructed from familiar element types. It shows 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. This shared property could be having either a G-suffix or G-prefix. However, the result can also be obtained if the birds paid attention to whether the stimuli either started or ended with an A, B or C element. Also, if the birds use the G-element, they can achieve discrimination by attending to either the suffix position only, the prefix position only, or both. Experiment 2 addressed these questions. Test 1 shows that discrimination is maintained even when the affixations are connected to stems consisting of novel element types. So, while the somewhat lower response to test stimuli that were structurally

similar to the Go-training stimuli indicates some effect of the stem, the discrimination can only be due to presence and position of the affix: the G-element.

The results of the second test of Experiment 2 demonstrate that birds paid attention to both the prefix and suffix. However, the birds trained with suffixed sequences as Go stimuli responded to the 'stem-only' stimuli at a more intermediate level than the birds trained with the prefix as the Go-stimulus. This effect was less strong when the stem was ABC. Though the stimulus ABC was not affixed, it overlapped with the first part of the suffixed version used as training stimulus, and birds may have used this as an additional cue to discriminate the stimuli. The test with novel element types excluded the use of such a cue and demonstrated that at least one group attended very clearly to both prefix and suffix (Fig. 4d). The results of the two conditions together suggest that the zebra finches primarily make their judgments when listening to the beginning of the stimuli.

All birds were trained with exactly the same stimuli but the Go and Nogo associations were opposite for the two groups. Birds trained with prefixes as Go-stimuli responded strongest to stimuli starting with a 'G', whereas birds trained with the suffix as a Go-stimulus showed clear evidence of using both affixes. It suggests that the responses are guided both by a tendency to pay more attention to the first part of a sequence as well as paying attention to a shared feature of a stimulus set. For several songbird species there is evidence that different parts of the song may differ in their information content (e.g. Elfstrom, 1990; Kreutzer, Vallet et al., 1992; Leader, Wright et al., 2000; Lengagne, Aubin et al., 2000; Mundinger, 1975; Nelson & Poesel, 2007) and, depending on the context, either the beginning or end of songs seems most important to convey particular information. The asymmetry in attending to prefix and suffix as shown by the zebra finches may have a similar background. Interestingly, this may imply a parallel process to word recognition in human. In human linguistic studies, it has been suggested that there is a preference for suffixation in natural languages (Bybee, Pagliuca et al., 1990; Cutler, Hawkins et al., 1985; Dryer, 2005). Among the various hypotheses offered to explain the suffixation preference is the idea that suffix does not present a problem for making word recognition more difficult while prefix does (Dryer, 2005). It has been proposed that the beginning of a word is its most psychologically salient part (Clark, 1991) and it is important for spoken word activation (Marslen-Wilson, 1987; Rodd, 2004). In the prefixed word, the processing of the stem does not precede the affix, so it is not easy to do an on-line exploitation of the information of the whole word (Kandel, Spinelli et al., 2012). The suffixation preference in language is proposed to be driven by a cognitive mechanism that is not specific to language (Hupp, Sloutsky et al., 2009) and our results suggests it may even be by a mechanism not specific to humans.

So, we conclude that our results provide the first evidence in a non-primate of learning a rule that, at least in its surface pattern, is similar to a linguistic affixation pattern: birds can identify that the presence of a specific vocal unit at one or the other edge of a string is linked to different 'meanings' and can generalize this knowledge to novel strings. As songbirds are phylogenetically quite distant from humans, our findings are unlikely to indicate a shared ancestral trait but might be the result of independent evolution. Also for this reason, the similarity should not be taken as evidence that the competence is formally fully similar to that of

humans using affixations. As outlined by Berwick et al. (2011), there is quite a gap between the syntactic structures birds use or can detect and those present in human languages. However, our experiment indicates a processing competence that may also have been present in pre-linguistic humans and acted as a domain-general perceptual and memory primitive (Endress et al. 2009) that has been co-opted for the evolution of a linguistic phenomenon.

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