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

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## Chapter 4\*

# **Artificial grammar learning in zebra finches and human adults: $XYX$ vs $XXY$**

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\* This chapter is based on: Jiani Chen, Danielle van Rossum & Carel ten Cate (in press). Artificial grammar learning in zebra finches and human adults:  $XYX$  vs  $XXY$ . *Animal Cognition*

## **Abstract**

Abstracting syntactic rules is critical to human language learning. It is debated whether this ability, already present in young infants, is human- and language-specific or can also be found in non-human animals, indicating it may arise from more general cognitive mechanisms. Current studies are often ambiguous and few have directly compared rule learning by humans and non-human animals. 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. Some birds also discriminated novel stimuli when these were composed of familiar element types, but none of the birds generalized the discrimination to novel element types. We conclude that zebra finches show evidence of simple rule abstraction related to positional learning, suggesting stimulus bound generalization, but found no evidence for a more abstract rule generalization. This differed from the human adults, who categorized novel stimuli consisting of novel element types into different groups according to their structure. The limited abilities for rule abstraction in zebra finches, may indicate what the precursors of more complex abstraction as found in humans may have been like.

## **Introduction**

Humans exposed to a string of meaningless speech items (e.g. CV-syllables) arranged according to a specific algorithm, are generally well able to detect the underlying rule (Reber, 1967, 1990). Such syntactic rule abstracting is considered a hallmark of human linguistic abilities (Hauser, Chomsky et al., 2002; Marcus, Vijayan et al., 1999; Pinker, 1991). However, the ability for rule abstraction is also shown when the items are non-speech stimuli, like musical tones and other non-linguistic sounds (Endress, 2010; Gebhart, Newport et al., 2009; Saffran, Johnson et al., 1999, but see Creel, Newport et al., 2004) or pictures (Saffran, Pollak et al., 2007). Findings like this raise the question whether rule abstraction mechanisms are specific to language or more domain general (Folia, Udden et al., 2010; Gomez & Gerken, 2000). They also raise the question whether the ability for rule abstraction from structured acoustic input is specific to humans or shared with other species, providing a general cognitive basis for the evolution of human syntactical abilities. Various animal species have demonstrated an ability for abstraction in different contexts, such as for the concept of same vs different, which has been demonstrated in species ranging from bees (Giurfa, Zhang et al., 2001) to pigeons (Katz & Wright, 2006) and monkeys (Wright, Rivera et al., 2003). Against this background several studies have addressed the abilities of various non-human animals to detect and generalize regularities in acoustic string structures. Such a task requires the animals to first detect the structure of individual strings and next to notice the abstract similarity between different strings. In this respect it is similar to discrimination learning based on second order relationships, a task that chimpanzees, but not monkeys, can do using visual stimuli (Thompson & Oden, 2000).

Like humans, animals can be exposed to strings of meaningless sound and next be tested with strings consisting of novel items and/or novel arrangements of items. The responses to such novel stimuli allow conclusions about whether the subjects have been able to detect the underlying algorithm. Various experiments have used this paradigm to examine rule detection in primates (Endress, Carden et al., 2010; Fitch & Hauser, 2004; Hauser & Glynn, 2009; Hauser, Newport et al., 2001; Newport, Hauser et al., 2004); rats (de la Mora & Toro, 2013; Murphy, Mondragon et al., 2008; Toro & Trobalon, 2005); and birds (Gentner, Fenn et al., 2006; Herbranson & Shimp, 2003, 2008; Stobbe, Westphal-Fitch et al., 2012; Seki, Suzuki et al., 2013; van Heijningen, Chen et al., 2013; van Heijningen, de Visser et al., 2009; Comins & Gentner, 2014; Comins & Gentner, 2013; Yamazaki, Suzuki et al., 2012). However, the degree to which animals can detect and generalize rules to novel items – the hallmark of rule abstraction – is by no means clear, as the results of several studies can be explained by simpler mechanisms such as, e.g., phonetic generalization to novel strings or items (Beckers, Bolhuis et al., 2012; Corballis, 2007, 2009; Fitch & Friederici, 2012; Seki, Suzuki et al., 2013; ten Cate & Okanoya, 2012; van Heijningen, de Visser et al., 2009). Hence, there is a need for comparative studies, addressing similarities and differences in how humans and animals cope with extracting, processing and generalizing specific types of input.

In the current study we compare the abilities of zebra finches and human adults to detect the difference between an XYX and a XXY structure, where X and Y denote arbitrary items. In a classic study, Marcus, Vijayan et al. (1999) showed that 7-month old infants

habituated to *XXY* or *XYY* speech stimuli (such as ‘gatiga’ or ‘gatiti’, X and Y being different syllables) could extract the underlying regularity and apply it to novel stimuli composed of new syllables. The infants could also distinguish *XXY* from *XYY* strings. A subsequent study showed even 5-month old infants to have such ability, provided that they are trained and tested with congruent combinations of vocal and visual stimuli (Frank, Slemmer et al., 2009). Although the mechanisms that underlie the infants’ ability for generalization evoked much discussion (e.g. Altmann & Dienes, 1999; Eimas, 1999; Marcus, Vijayan et al., 1999; Negishi, 1999; Seidenberg, 1999), the observation that the infants are able to discriminate between stimuli with different structures and generalizing this to novel items without basing on the physical sameness of items is broadly accepted. As regards the abilities of non-human animals to detect and generalize such structures, the results are ambiguous. The first study to address this (Hauser, Weiss et al., 2002) suggested that tamarins could resolve the task, but this study has been retracted. Later on, Hauser and Glynn (2009) suggested that rhesus monkeys could discriminate *XYY* from *XXY* when X and Y were rhesus monkey calls. However, the strings used to test for rule learning were composed of the same call types as the ones used for training, i.e. they concerned within-category generalization, which, as demonstrated in other studies (e.g. Gentner et al. 2006; van Heijningen et al. 2009) several species are able to do. However, such findings leave the question for between-category generalization of the rule to truly novel items unanswered. Other studies have examined whether rats could extract and distinguish the grammar rules. Toro and Trobalon (2005) failed to find evidence for discriminating *XXY* from *XYY*, with X and Y being human speech stimuli, although recently de la Mora and Toro (2013) showed rats to be able to distinguish *XXY* from *XYZ* sequences. Using a different experimental design Murphy, Mondragon et al. (2008) claimed that rats could distinguish *XXY* from *XYY* and *XXY*. However, since the stimuli of this experiment were composed by using pure tones, it has been questioned whether this transfer is really based on extracting the underlying abstract rule by the rats or whether they generalized based on the tonal contour (Corballis, 2009; but see Mondragon, Murphy et al., 2009). So, the studies on mammals do not yet provide a conclusive answer to whether animals can abstract the rules underlying similarly structured auditory strings.

In our study we use a songbird, the zebra finch, to address this question. Songbirds are phylogenetically very distant from humans. Yet, their natural songs show many similarities to speech and language, making them of special interest for examining rule learning abilities. In contrast to many other species, including primates, songbirds have complex, learned, vocalizations consisting of strings of phonetically different elements (‘notes’). While the acoustic features of these elements may vary between individuals of a species, different individuals structure their element strings according to species specific sequencing rules. In addition, birdsong researchers have discovered remarkable neural and genetic parallels between the processes involved in the production, perception, and development of language and birdsong (e.g. Berwick, Okanoya et al., 2011; Bolhuis, Okanoya et al., 2010; Doupe & Kuhl, 1999; Ohms, Escudero et al., 2012). These similarities raise the question whether songbirds also share more advanced cognitive abilities involved in language processing, in particular in the area of rule abstraction. Establishing to what extent the rule abstraction capabilities in songbirds match (or differ from) those of humans will help to understand the relation between these capabilities and

the presence and evolution of vocal complexity, even though the similarities might be based on parallel evolution rather than reflecting a shared ancestral state.

Some studies have addressed rule abstraction in several songbird species, but, as in mammals, have so far not provided clear answers to the question of their ability for such abstraction (reviewed by ten Cate & Okanoya, 2012). With respect to the ability of songbirds to distinguish XYX from XXY and XYY strings, a first study was done by van Heijningen, Chen et al. (2013). In that study we examined the ability of zebra finches to discriminate such strings, using a ‘Go-NoGo’ design. We showed that zebra finches could discriminate two ‘Go’ stimuli with an XYX structure (ABA and BAB, with A and B indicating two different song elements) from four ‘NoGo’ stimuli (AAB, BBA, ABB and BAA). Using non-reinforced probe sounds having different structures, we demonstrated that the distinction was most likely based on detecting whether or not the stimulus strings contained AA or BB repetitions, rather than using a more complex abstract rule such as comparing the first and last items of strings, as suggested by Marcus, Vijayan et al. (1999). Even though the generalization to novel items was very limited (present in one bird out of eight), this finding indicates a sensitivity to repetition that is also present in humans (Endress, Dehaene-Lambertz et al., 2007; Gervain, Macagno et al., 2008; Kovács & Mehler, 2009) and may hint at a primitive rule-like regularity that may constitute a basis for the evolution of a higher level of abstraction (Endress, Nespor et al., 2009). However, the limited evidence for abstraction in our experiment might be due to the training in which only A and B elements were used to create XYX, XXY and XYY strings, precluding the birds from forming a more abstract representation of the string structure. Hence the results leave open the question whether any non-human animals can detect an abstract rule from training with a more extensive set of examples. In the current study we trained zebra finches to discriminate larger sets of XYX from XXY strings and examined whether they generalized the distinction to strings consisting of novel items (Experiments 1a and 1b).

As the operant paradigm differs from the habituation paradigm as used in the studies in human infants and monkeys, which has advantages and disadvantages (ten Cate & Okanoya, 2012), we also tested human adults with the same stimuli in a comparable operant design as used for the zebra finches (Experiments 2a and 2b) to allow a more direct comparison of zebra finches and humans.

## **Rule learning in zebra finches - Experiment 1a**

### **Material and Method**

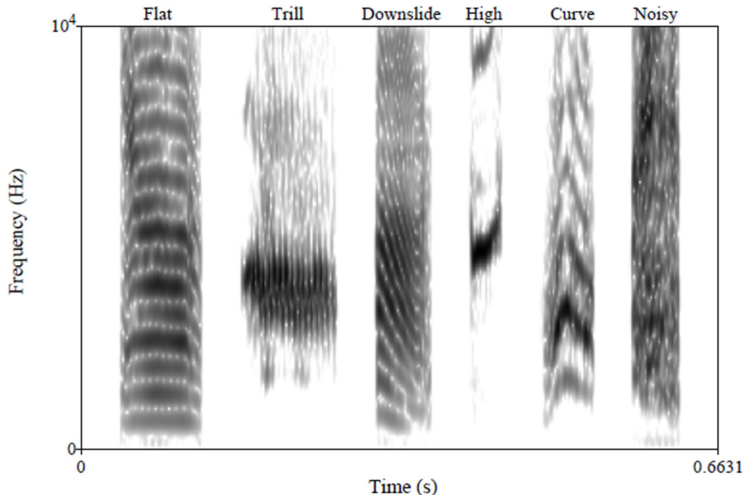
#### **Subjects and apparatus**

Six zebra finches (3 males and 3 females), which were all naïve to any experimental setup, were individually trained and tested in operant conditioning cages [70 (l) × 30 (d) × 45 (h) cm] in sound attenuated chambers using a Go/No-go paradigm. Each cage was made of wire mesh with a plywood back wall. The back wall contained a food hatch and two red pecking keys, each containing a red LED. A fluorescent tube on the top of the cage emitted daylight spectrum light on a 13.5 L: 10.5 D schedule (except for a penalty during which the light was switched off temporarily). In the training and test periods, the first pecking key was illuminated

with a red LED. A peck on the first key resulted in a sound stimulus and also activated the second key, indicated by switching on the LED of this key. Depending on the sound stimulus, a peck on the second key resulted in a food reward or a mild punishment of darkness (see procedure below; for more detailed description about the apparatus, see van Heijningen, Chen et al., 2013).

### Stimuli

Stimuli were constructed from zebra finch song elements originating from our zebra finch song database, consisting of undirected song. Natural zebra finch song consists of a series of 4-12 elements, which are sung in a relatively fixed sequence. These elements can be considered the natural units of production and perception in zebra finch songs (ten Cate, Lachlan et al., 2013). At the species level, song elements can be categorized into around eight different types and there are no strong constraints to the position of each element within the song (Lachlan, Verhagen et al., 2010). There is no indication that single elements or element combination carry any meaning and hence these elements seem suited to construct artificial meaningless strings. Based on optimal discriminability, six element types were selected ('flat,' 'trill,' 'downslide,' 'high,' 'curve,' and 'noisy', see Fig. 1). They were ramped and the RMS values of different song elements were equalized in PRAAT (version 5.1.15, [www.praat.org](http://www.praat.org)).



**Fig. 1** Spectrograms of the six element types.

Stimuli were constructed following *YXY* and *XXY* patterns. The *YXY* corpus contained triplets such as *ABA*, *BCB*, *CDC*, *DAD*, *EFE* etc. (A, B, C, D, E, F representing specific different song elements), and the *XXY* corpus contained triplets such as *AAB*, *BBC*, *CCD*, *DDA*, *EEF* etc (Table 1). Elements A, B, C and D were used to compose training stimuli. Another two elements E and F served as test elements and were not presented in the training phases. *YXY* stimuli were always presented as Go stimuli and *XXY* as Nogo stimuli during

training (in an earlier experiment, using a somewhat different grammar we obtained no evidence that it mattered which stimulus was the Go and which the Nogo, van Heijningen, de Visser et al., 2009). Forty ms of silence was inserted between consecutive elements of the various element sequences, which is comparable to the pauses that separate song elements in natural songs. To eliminate pseudo effect of an arbitrary parameter of the sounds, the element assignment was shuffled for the subjects, for instance, an ABA triplet could be ‘flat-downslide-flat’ for one bird and ‘high-trill-high’ for another bird.

**Table 1** Training and test stimuli of Experiment 1a

Phase	Training stimuli		control	Test stimuli (non-reinforced)		
	Go (XYX)	NoGo (XXY)		XYX	XXY	XYX
1	ABA	AAB	ABA AAB	BAB	BBA	
	ACA	AAC		BCB	BBC	
	ADA	AAD		BDB	BBD	
2	BAB	BBA	BAB BBA	CAC	CCA	
	BCB	BBC		CBC	CCB	
	BDB	BBD		CDC	CCD	
3	CAC	CCA	CAC CCA	DAD	DDA	
	CBC	CCB		DBD	DDB	
	CDC	CCD		DCD	DDC	
4	DAD	DDA	DAD DDA	ABA	AAB	
	DBD	DDB		ADA	AAD	
	DCD	DDC		BCB	BBC	
5	ABA	AAB	ABA AAB	EFE	EEF	FEE
	ADA	AAD		FEF	FFE	EFF
	BCB	BBC				
	CAC	CCA				
	CDC	CCD				
	DAD	DDA				

Phases 1-4 consist of 6 training stimuli and phase 5 consists of 12 training stimuli, selected from the 4 preceding training phases. Each letter indicates a different song element. Control test stimuli were identical to the training stimuli but not reinforced. The other test stimuli were different from training stimuli and not reinforced either.

## Procedure

The zebra finches were first trained to discriminate a natural zebra finch song (Go stimulus) from a pure tone (Nogo stimulus). Pecking on the first key initiated a playback of either a song or a tone. The birds gained access to food for 10s as reward when they pecked the second key after hearing a Go stimulus. Inversely, when they pecked the second key after hearing a Nogo stimulus, they received a mild punishment with the light extinguishing for 15s.

After the responses of the birds to the song and tone reached training criterion (>75% response to Go stimuli and <25% response to Nogo stimuli) for at least two full consecutive days, the training began, using the XYX stimuli as Go and the XXY stimuli as NoGo stimuli. This experiment contained 5 successive phases, each of which used a different set of training and test stimuli (Table 1).

When the birds reached training criterion for at least three full consecutive days, they entered a test phase. In test phases, test stimuli were not reinforced to avoid additional learning. They were presented in only 20% of all stimulus presentations to prevent extinction of the pecking behavior. The other 80% of stimulus presentations consisted of the reinforced stimuli used during the training phases. Every test contained 40 presentations of each test stimulus. Control test stimuli identical to the training stimuli (but not reinforced) were added to control for the effect of non-reinforcement. After finishing the test of phase 1, the test stimuli became the training stimuli for the next training phase. Testing for this phase started when the learning criterion had been reached again. When the birds finished the 4th training, they were tested with 6 pairs of stimuli (including control stimuli) selected from the 4 preceding training phases (see Table 1) to address whether they combined the information of the preceding phases. We next trained the birds with these 6 pairs of stimuli to enhance the learning of *XYX* and *XXY* rules. After this, a final test consisted of stimuli composed of new element types (E and F, Table 1). This test included an additional *XXY* structures (*EFF* and *FEE*) to examine whether this was discriminated from the *XYX* and *XXY* structures.

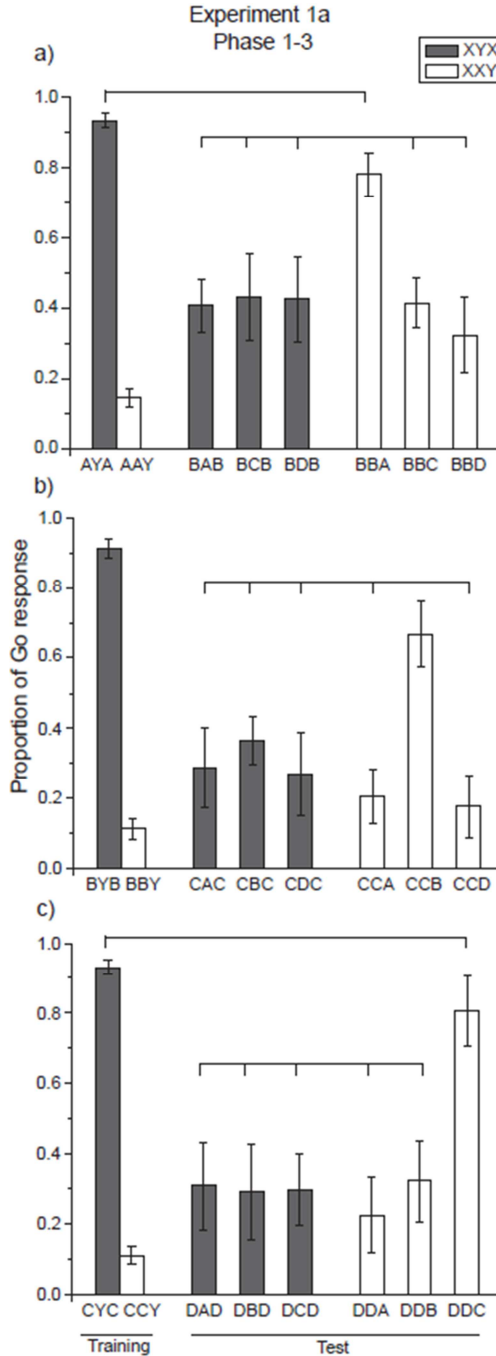
Some birds had a persistent lower response proportions to one or more stimuli during the final training phase. However, if the overall Discrimination Ratio (DR, calculated as the percentage response to Go stimuli divided by the sum of the percentage response to Go stimuli and the percentage response to Nogo stimuli) was  $> 0.75$  for at least three consecutive days, the bird entered the test phase.

#### Performance evaluation

To examine whether the birds transferred the discrimination learned during the training to the test stimuli, we calculated the DR for the *XYX* and *XXY* test stimuli. A DR higher than 0.50 indicated positive discrimination. We used Wilcoxon signed ranks test to examine the differences in responses to *XYX* and *XXY* strings. Simultaneous Testing Procedures (STP) based on G-tests were applied to detect how the birds categorized different test stimuli and to examine the performances of individual birds (Gabriel, 1966; Sokal & Rohlf, 1995; A Williams correction was calculated when numbers were lower than 5;  $G$  value  $> X^2$  critical value means  $P < 0.05$  and vice versa).

### Results

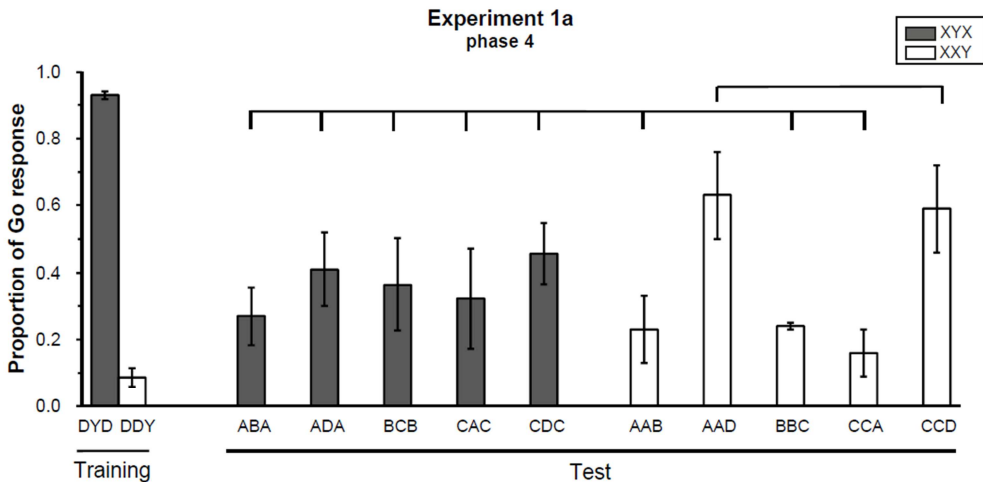
All birds reached criterion during training, but the training trials varied between different training phases. From training 1 to 5, birds took  $3418 \pm 692.47$ ,  $3262 \pm 594.77$ ,  $4066 \pm 1071.71$ ,  $2345 \pm 431.88$  and  $3895 \pm 359.80$  (Mean  $\pm$  SEM,  $n = 6$ ) trials respectively to reach training criterion.



**Fig. 2** Mean ( $\pm$ SEM,  $n = 6$ ) proportion of Go responses to the training and test stimuli in the a) first b) second and c) third phase of Experiment 1a. Y in the training stimuli refers to the three elements that can occupy this position, e.g. AYA includes ABA, ACA and ADA (see Table 1). The bars in the Test –section refer to the proportion of ‘Go’ responses to the different test stimuli. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 14.07) to different stimuli sets. Test stimuli that end with A in test phase 1 (Fig. 2a), B in test phase 2 (Fig. 2b) and C in test phase 3 (Fig. 2c) get more responses in comparison with the other test stimuli in the same test phase.

During all the tests, the responses to the positive control stimuli and the positive training sets showed no significant differences nor did the responses to the negative control stimuli and their negative training sets (all  $P > 0.05$ ). This indicates that the non-reinforcement condition did not have an impact on the performances of the birds. Therefore, we compared the responses to the test stimuli with the average responses to the positive and the negative training stimuli.

The results of test phase 1 showed that proportions of responses to BAB, BCB, BDB, BBC and BBD were all between the proportions of the Go and Nogo stimuli (XYX and XXY stimuli of training). They were all in the same homogenous group (no significant difference from each other,  $G = 1.20 < X^2$  critical value 14.07,  $df = 4$ , Fig 2a). The exception is provided by test stimulus ending with A (BBA), which is being treated as a Go stimulus (ABA, ACA and ADA,  $G = 10.19$ ,  $df = 1$ ,  $X^2$  critical value = 14.07, Fig 2a). This pattern is repeated in the test phases after the second and third training, where again all test stimuli form a homogenous group (all  $G < X^2$  critical value 14.07,  $df = 4$ ) while there is one stimulus (ending with B: CCB and ending with C: DDC, in test 2 and 3 respectively) with a score close to the Go stimuli (stimuli BAB, BCB and BDB in training 2 and stimuli CAC, CBC and CDC in training 3, both  $G < X^2$  critical value 14.07,  $df = 1$ , Fig 2b,c).

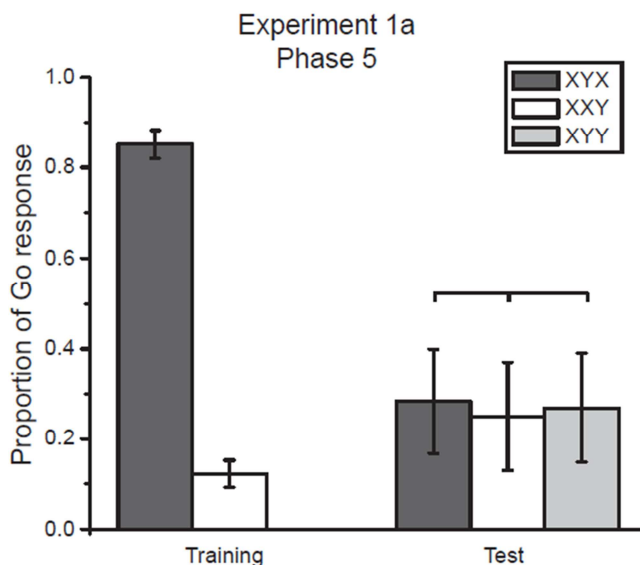


**Fig. 3** Mean ( $\pm$ SEM,  $n = 6$ ) proportion of Go responses to the training and test stimuli in phase 4 of Experiment 1a. Test stimuli consisted of familiar elements known from the training. Y in the training stimuli refers to the elements A, B and C, for which the values were averaged. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 19.68) to different stimuli sets.

In test 4, the responses to different test stimuli were not based on XYX and XXY structures (responses to ABA, ADA, BCB, CAC, CDC, AAB, BBC and CCA were all in the same homogeneous group,  $G = 13.56 < X^2$  critical value 19.68,  $df = 7$ , Fig 3), which indicates that the birds did not combine what they had learned in the 4 preceding training phases. Among the responses to the separate test stimuli, responses to AAD and CCD were higher, to which,

like the positive training set, had a D element in the final position (no significant difference from each other,  $G = 0.21$ ,  $X^2$  critical value = 19.68,  $df = 1$ ).

A final test (Test 5), this time with song elements E and F (not used in any of the previous stimuli) was given after a training with the 6 stimulus pairs from the 4th test (Table 1). Again the responses to the *XYX* and *XXY* test stimuli were not significantly different ( $Z = -1.214$ ,  $P = 0.225$ ,  $n=6$ ). In addition, the responses to the test stimuli of the *XYX*, *XXY* and *XXY* structures were all in the same homogenous group ( $G = 0.24 < X^2$  critical value 9.49,  $df = 2$ ), which was significantly different from the responses to the training stimuli (Fig 4).



**Fig. 4** Mean ( $\pm$ SEM,  $n = 6$ ) proportion of Go responses to training and test stimuli in phase 5 of Experiment 1a. Test stimuli consisted of novel elements not present in training. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 9.49) to different stimuli sets.

## Discussion

The results of the training demonstrate that zebra finches are able to discriminate strings in which the same elements are arranged in different sequences. However, the results of the first four tests suggest that the birds did not use the underlying *XYX* and *XXY* structures of the strings to guide their discrimination. Nevertheless, they differentiated among the test strings in a systematic way. The deviant test stimuli that were being treated more similar to *XYX* training stimuli in tests 1, 2, 3 and 4 were always the test stimuli that shared their final element with the *XYX* training stimuli (test 1: BBA - element A; test 2: CCB - element B; test 3: DDC - element C; test 4: AAD, CCD – element D). The most likely explanation is that the birds learned to use the final elements of the *XYX* strings to discriminate ‘good’ and ‘bad’ sounds, demonstrating a stimulus bound generalization. Attending to this final element can also explain the other results of test 4. Although the set contained stimuli that were very well discriminated in

earlier phases, in each subsequent training phase the birds had to relearn which final element was associated with obtaining the food reward. E.g. the final A element that indicated a 'Go' stimulus in phase 1 became a 'NoGo' stimulus in training phase 2, which is likely to have been at the expense of the earlier discrimination. To prevent the birds from using this regularity, we gave them the extended training set in phase 5. Every position of the song sequences of the training stimuli could be occupied by any of the four element types (A, B, C and D, see Table 1). Therefore the birds now had to use another strategy to discriminate between the positive and negative stimuli, such as paying attention to the abstract structure of the strings or rote memorization of individual stimuli. If the birds used abstract rules to make the distinction they were expected to respond to novel songs with novel element types according to the overall structures of the stimuli. In addition, if they could detect the *XYX* and *XXY* rules they might also notice that a *XYY* rule was different. However, the results of test 5 showed no difference in responding to the three stimulus structures. We conclude that the birds failed to detect the underlying structures of the stimuli and most likely relied on having learned particular elements in relation to their position (phase 1-4), or memorized the individual training strings (phase 5) to discriminate the training sets.

### **Rule learning in zebra finches - Experiment 1b**

It is possible that the training procedure of Experiment 1a biased the birds' learning process away from rule learning and towards tracking final elements. This may also have hampered rule learning in phase 5. Experiment 1b aimed at avoiding such a bias. To this end, a new group of naïve zebra finches was trained by immediately starting with the stimuli used in phase 5 of the previous experiment.

### **Material and Method**

#### Subjects and apparatus

Eight zebra finches (4 males and 4 females) were trained and tested in this experiment. The experimental conditions were identical to phase 5 of Experiment 1a.

#### Stimuli

Stimuli from the fifth training phase of the Experiment 1a were used as training stimuli in this experiment. After training, birds were switched to two successive test phases. Similar to test phase 5 of Experiment 1a, the first test contained novel stimuli with novel element types; for the second test the stimuli were constructed by re-arranging familiar element types (Table 2). This test was added to explore whether the discrimination shown in the training was maintained when familiar elements were combined in novel combinations.

#### Procedure

The procedure and criteria of performance were identical to Experiment 1a.

#### Performance evaluation

The statistical methods were the same as for Experiment 1a.

**Table 2** Training and test stimuli of Experiment 1b

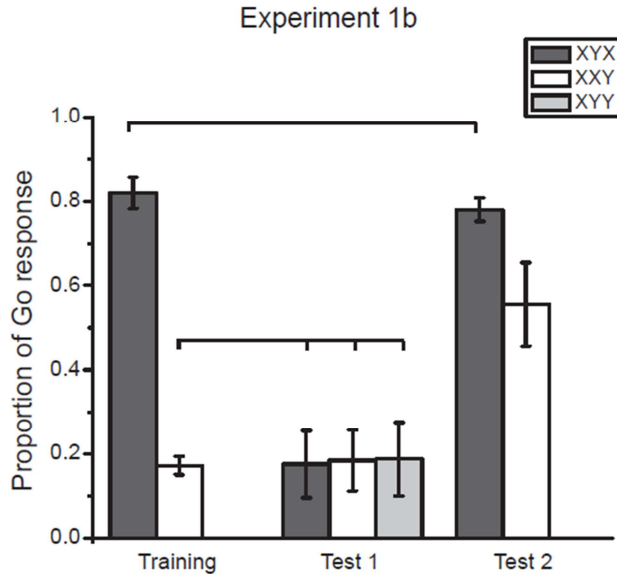
Training stimuli			Test stimuli (non-reinforced)			
Go (XYX)	NoGo (XXY)		control	XYX	XXY	XYX
ABA	AAB	1		EFE	EEF	FEE
ADA	AAD			FEF	FFE	EFF
BCB	BBC	2	ABA			
CAC	CCA		AAB			
CDC	CCD			BAB	BBA	
DAD	DDA			CBC	CCB	
				ACA	AAC	
				DCD	DDC	

Letters indicate different song elements. See Legend of Table 1 for further explanation

## Results

Seven out of eight birds learned to discriminate between the two sets of the training stimuli ( $10494 \pm 1289.96$  Mean  $\pm$  SEM trials were required until they reached training criterion,  $n = 7$ ). The responses to the control stimuli and their training sets again showed no significant differences (all  $p > 0.05$ ), which indicates that here also the non-reinforcement condition had no impact on the responses.

The results of Test 1 of this experiment showed that birds did not discriminate between the XYX, XXY and XYY test stimuli constructed from the novel elements E and F. The responses to all three test stimuli were in the same homogeneous group with those to negative training stimuli ( $G = 0.21$ ,  $df = 3$ ,  $X^2$  critical value = 12.59) and significantly different from those to the positive training stimuli ( $G = 688.35$ ,  $df = 4$ ,  $X^2$  critical value = 12.59, Fig 5). However in the second test, with familiar items in novel positions, the responses to XYX and XXY were significantly different ( $G = 18.56$ ,  $df = 1$ ,  $X^2$  critical value = 12.59). The responses to XYX stimuli in Test 2 were similar to XYX stimuli in training ( $G = 1.23$ ,  $df = 1$ ,  $X^2$  critical value = 12.59), whereas the responses to XXY structure in Test 2 were significantly different from those to other structures (all  $G > 12.59$ ). When analysed at the individual level, the DRs between these two sets of stimuli were high in two birds (0.88 and 0.70). The responses of these two birds to the XYX test stimuli were significantly different from the responses to the XXY test stimuli (all  $G > X^2$  critical value of 7.851, see Fig 6a for an example). Another two birds had lower DRs of 0.58 and 0.54, but the responses to the XYX and the XXY test stimuli also differed significantly (all  $G > X^2$  critical value of 7.851). Finally, three birds showed no clear patterns in discriminating between the test stimuli (DRs =  $0.50 \pm 0.01$  SEM,  $n = 3$ , all  $G < X^2$  critical value of 7.851, see Fig 6b for an example).

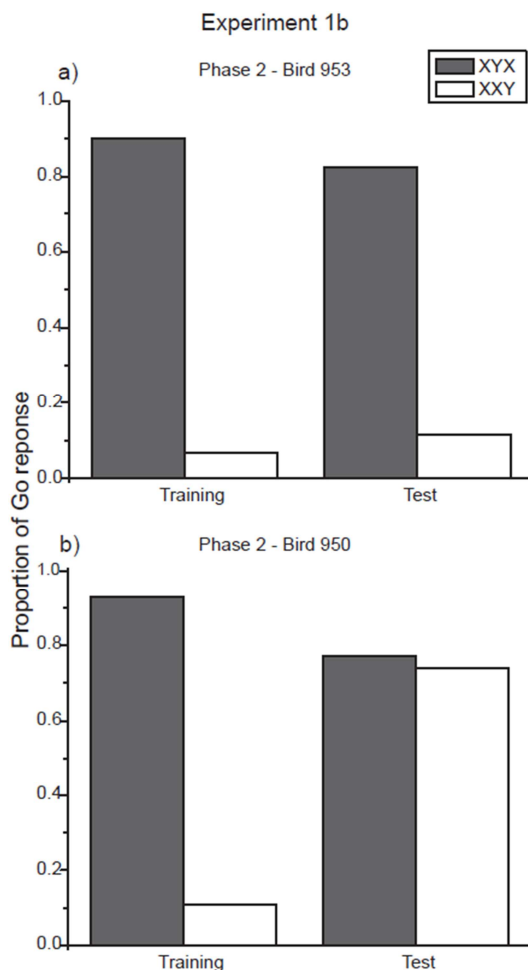


**Fig. 5** Mean ( $\pm$ SEM,  $n = 7$ ) proportion of Go responses to training and test stimuli. Stimuli in Test 1 consisted of novel elements not present in training. Stimuli in Test 2 consisted of familiar elements from training but with novel combinations. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 12.59) to different stimuli sets.

## Discussion

As in Experiment 1a, the zebra finches were able to simultaneously discriminate a large set of different stimuli. Nevertheless, here also the birds did not generalize the discrimination to novel element types not covered in the training sets. It indicates a lack of abstract rule learning, similar to the results in Experiment 1a. However, results of the second test showed that, when novel stimuli consisted of re-arranging familiar elements from the training sets, some birds were able to discriminate between different structures. While the equal response to the XXY training and test stimuli as shown by bird 953 (Fig. 6a) might be because they share the bigrams present in the first two elements, this does not explain the high response that this and the other individuals showed towards to the test stimuli with the XYX structure, which do not share bigrams in identical positions to the XYX training stimuli. Note that in fact the XYX test stimuli in this experiment share the final bigrams with the XXY training stimuli (e.g. AB, BC) and the other way around. If the birds were classifying the test stimuli according to the final bigrams, they would have classified XYX test stimuli as XXY and the other way around. However, those birds that did discriminate in the test classified them according to their XYX or XXY structure, hence opposite to the position of the final bigrams. Although these results may indicate that the birds detected, and hence abstracted, the XYX structure when familiar items were used, an alternative, simpler explanation that can not yet be excluded relates to the initial bigrams of the test stimuli. The birds may have been using a rule like: if it starts with AA, BB, CC or DD treat the stimulus as a NoGo stimulus; if these specific bigrams are not present, treat stimuli as a Go stimulus. Attention to repetitions was also demonstrated in an earlier study on zebra finches

using similar stimuli (van Heijningen, Chen et al., 2013), as well as in a recent study on Bengalese finches (Seki, Suzuki et al., 2013). Such a rule would be an example of a stimulus bound generalization (see general discussion).



**Fig. 6** Individual differences in Go responses to the training and test stimuli in phase 2 of Experiment 1b. a) Bird 953 showed clear pattern of discriminating both training and test stimuli. b) Bird 950 showed no significant discrimination among the test stimuli although it was able to discriminate the training stimuli. Test stimuli were composed with familiar elements known from the training stimuli, but in novel combinations.

### Rule learning in humans - Experiment 2a

Experiment 1 demonstrated that zebra finches discriminate the various training sets by concentrating on the presence and position of particular elements, rather than generalizing on the *XYX* or *XXY* patterns. This is unlike the pattern shown by human infants (Marcus, Vijayan et al., 1999). While a limitation on rule learning abilities in birds might be a reason for this difference, another one might be the methodology. Infants were tested using a habituation paradigm, while the current experiment used a Go-NoGo discrimination task. To examine this

issue, Experiment 2 (a and b) subjected adult human participants to the same training and tests as used for the zebra finch Experiments 1a and 1b respectively, except that a categorizing setup was used instead of the Go/No-go.

Experiment 2a was a shortened version of Experiment 1a. It started off with a training and test using the same stimuli as in phase 1 of Experiment 1a, but as a pilot experiment showed that humans already discriminated the stimulus sets used in test phase 1 we decided to present all test stimuli immediately after an individual finished training phase 1, without any further training.

## Material and Method

### Subjects and apparatus

Twenty six native speakers of Dutch (15 males and 11 females) with mean age of 22.12  $\pm$  0.51 SEM (range 19 to 30) were asked to participate. None of them had experience with this kind of experiment. The experiment took place in a quiet area, where participants sat in front of a laptop with a headphone playing sounds at a standardized volume of 40 dB. A custom-designed program (in Processing 1.5.1) controlled training and testing of the participants. At the start of the experiment, the computer screen showed an instruction asking the participants to click on the mouse to trigger a sound playback. After the sound playback a red and a green box were shown. The participants were instructed to categorize the sounds that they heard by clicking one of the boxes, but received no further instructions. They had to discover that a click on the green box after hearing a *XYX* stimulus or on the red box after hearing a *XXY* stimulus resulted in being ‘rewarded’ with a picture of a smiling face. If they clicked on the green box after hearing an *XXY* stimulus or on the red box after hearing an *XYX* stimulus, they were ‘punished’ with a picture of a sad face. Participants had to respond within 5s, otherwise a neutral face was presented and the answer was considered incorrect.

**Table 3** Training and test stimuli of Experiment 2a

Training stimuli		Test stimuli (non-reinforced)			
Go ( <i>XYX</i> )	NoGo ( <i>XXY</i> )	control	<i>XYX</i>	<i>XXY</i>	<i>XYX</i>
		1	<i>BAB</i> <i>BCB</i> <i>BDB</i>	<i>BBA</i> <i>BBC</i> <i>BBD</i>	
<i>ABA</i> <i>ACA</i> <i>ADA</i>	<i>AAB</i> <i>AAC</i> <i>AAD</i>	<i>ABA</i> <i>AAB</i>	<i>EFE</i> <i>FEF</i>	<i>EEF</i> <i>FFE</i>	<i>FEE</i> <i>EFF</i>
		2			

Letters indicate different song elements. See legend of Table 1 for further explanation.

### Stimuli

The human participants were tested with the same zebra finch song elements and element sequences as used for the zebra finches. However, we increased the interval between the elements to 100 instead of 40 ms, as birds are capable of more precise temporal resolution for complex sounds than human (Dooling, Leek et al., 2002) and our pilot experiment indicated that with the 40 ms interval humans had problems with detecting that the stimuli consisted of three

elements. Table 3 shows the stimulus compositions used in this experiment. As in the zebra finch experiment, we shuffled the element assignment for the participants to avoid coincidental effects caused by particular elements or element combinations.

### Procedure

Participants were first trained to categorize the training stimuli. In a first training session they would hear 24 sound sequences (3 *XYX* and 3 *XXY* stimuli each played 4 times). If their responses to the stimuli reached criterion (correct categorization of the two structures each higher than 75%), they would go over to the test phase. If they did not reach criterion performance they would hear another series of 24 sequences. After reaching the training criterion, the participants would see an instruction (in Dutch), saying: ‘Het volgende deel van de test gaat nu beginnen. Je krijgt nu geen feedback’ (The next phase of the test will now start. You will not receive feedback). In the two test phases (phase 2 started right after phase 1), each stimulus was played two times, including two control stimuli that were identical to the training stimuli.

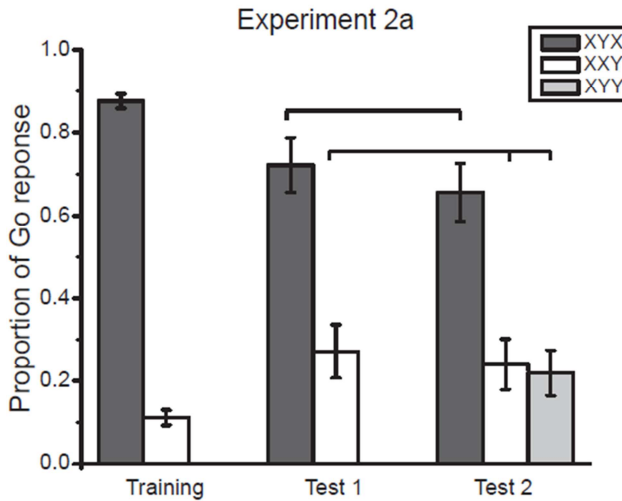
### Performance evaluation

In this experiment, participants categorized stimuli according to their structure. Therefore, in order to compare the results directly with the zebra finch experiments, the correct responses to *XYX* stimuli were treated as Go responses to Go stimuli and the incorrect responses to *XXY* stimuli were treated as Go responses to Nogo stimuli. The performance in the final training sessions was compared with that of the tests. In this experiment, the total number of test stimuli per individual participant was relatively low, so we analyzed the data at group level. STP based on G-tests was applied to detect how the participants categorized different stimuli.

### Results

Twenty four participants finished the training and the test; two participants quit after being unable to reach the training criterion. The participants needed on average  $74 \pm 15.95$  SEM ( $n = 24$ ) trials to reach criterion.

Fig. 7 shows the results of the test. The participants discriminated the *XYX* and *XXY* structures quite well during the final training session. Although they showed some decrease in discrimination with the test stimuli, the responses to the *XYX* structure and to the *XXY* structure were significantly different for both tests using familiar elements (BAB, etc.  $G = 60.86$ ,  $df = 1$ ,  $X^2$  critical value = 12.59) and unfamiliar elements (EFE, etc.  $G = 34.82$ ,  $df = 1$ ,  $X^2$  critical value = 12.59). However, the responses to the *XXY* and *XXY* structures showed no significant difference ( $G = 0.12$ ,  $df = 1$ ,  $X^2$  critical value = 12.59).



**Fig 7** Mean ( $\pm$ SEM,  $n = 24$ ) proportion of Go responses in the training (last section) and tests in Experiment 2a. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 12.59) to different stimuli sets.

## Discussion

Unlike the zebra finches, the human participants generalized the discrimination to the test stimuli, no matter whether these were composed of familiar elements that they heard during training or of novel elements that they had never encountered before. So, even with a very limited training set, humans already generalized the underlying pattern, rather than using the individual sounds to discriminate the stimuli. In the second test, the responses to XXY and XYY structures were not significantly different, indicating that presence, but not position, of the repeated elements might have been used for the discrimination. Indeed, when the participants were asked what pattern they had detected in the stimuli, most mentioned that they paid attention to the presence or absence of repeated elements to discriminate the stimuli.

### Rule learning in humans - Experiment 2b

This experiment used the same training and test sequences as used in Experiment 1b.

## Material and Method

### Subjects and apparatus

Another twenty six native Dutch speakers (15 males and 11 females), with a mean age of  $22.15 \pm 0.5$  SEM (range 19 to 30) and no experience with this kind of experiment, participated in this experiment. The training and testing conditions were identical to Experiment 2a.

## Stimuli

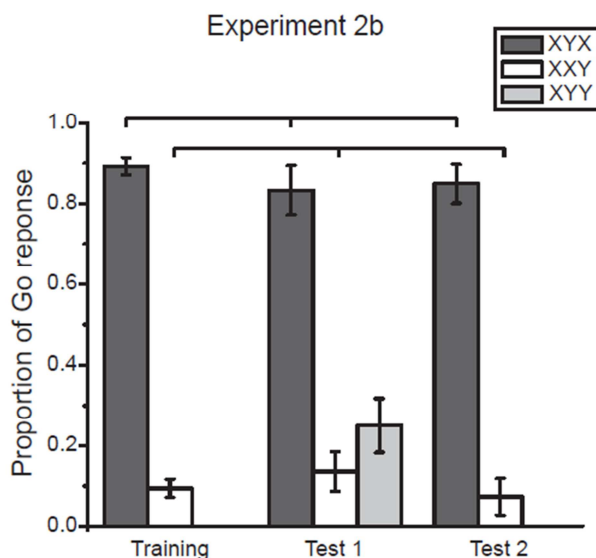
The stimuli for this part of experiment were composed in the same way as those in Experiment 1b, but, as in Experiment 2a, using a 100 ms instead of a 40 ms pause in between the elements. There was one training phase with 6 pairs of stimuli and two test phases with 3 and 4 pairs of stimuli respectively, identical to the layout of Experiment 1b (Table 2). Element assignments for the participants were shuffled.

## Procedure

The procedure was identical to Experiment 2a except that different training and test stimuli were used (see Table 2).

## Performance evaluation

The same statistical methods as for Experiment 2a were used in this experiment.



**Fig. 8** Mean ( $\pm$ SEM,  $n = 24$ ) proportion of Go responses in the training (last section) and tests in Experiment 2b. Lines above the bars indicate homogenous responses (no significant differences,  $X^2$  critical value of 12.59) to different stimuli sets.

## Results

Two out of 26 participants did not finish the experiment due to the failure during training. The other 24 participants reached criterion performance after on average  $89 \pm 11.42$  (Mean  $\pm$  SEM) trials. As shown in Fig 8, participants showed no significant differences in responding to the *XYX* stimuli in the last section of training and *XYX* stimuli presented in the both tests ( $G = 3.10$ ,  $df = 2$ ,  $X^2$  critical value = 12.59). Also the responses to *XXY* stimuli did not differ between training and tests ( $G = 2.80$ ,  $df = 2$ ,  $X^2$  critical value = 12.59). However, the

responses to the XYY stimuli belonged to neither this XYX group ( $G = 154.35$ ,  $df = 3$ ,  $X^2$  critical value = 12.59) nor to the XXY group ( $G = 18.84$ ,  $df = 3$ ,  $X^2$  critical value = 12.59).

## Discussion

Again, the human participants discriminated novel XYX from novel XXY strings. Compared with the performance of Experiment 2a, participants had higher accuracies in categorizing the stimuli according to their structure. In addition, participants categorized the XYY stimuli different from the other ones, although they categorized XYY stimuli more like XXY stimuli than like XYX stimuli. This outcome shows that the participants not only used the element repetitions as criterion to categorize the stimuli, but also attended to the position of the repeated elements. Again, this was confirmed by the comments of the participants after the experiment.

## General discussion

Our results demonstrate that birds and humans show different levels of generalization. The results of Experiment 1 demonstrate that zebra finches are able to categorize element strings according to their structure, i.e. they pay attention to the sequence and position of elements, confirming results obtained in earlier studies in this species (van Heijningen, Chen et al., 2013; van Heijningen, de Visser et al., 2009), as well as in Bengalese finches (Seki, Suzuki et al., 2013). This ability to discriminate between XYX and XXY strings is not based on rote memorization of individual strings. If so, they would treat all test stimuli as equally novel. Rather, the birds showed a generalization in which they used familiar and indicative elements (the identity -A, B, C or D- of the final element in the XYX stimuli in the phases 1-4 of Experiment 1a) or element bigrams (AA, BB, CC, DD in Experiment 1b) to classify novel stimuli. This generalization is stimulus bound in the sense that the birds can track a regularity in a surface feature, and only generalize to strings with the indicative elements in the same position as in the training strings and not to strings composed from novel elements. These results show a striking similarity to those obtained in an experiment by Gerken (2006) on 9-months old human infants. Infants exposed to a XYX or XXY strings of consonant-vowel (CV) items in which they could use the presence or absence of a particular CV item in a specific position (i.e. the Y-item was the same for all training stimuli, but the X varied) generalized to novel strings that had the same Y-item in the same position as in the training stimuli. They did not generalize to novel items having the same abstract structure, but in which both X and Y were novel. It was only when the infants were trained with several different strings in which both X and Y differed between the strings (e.g. ABA, CDC, etc.) that they were able to generalize to novel items. A later study (Gerken, 2010) showed that even a limited exposure to such strings was sufficient to induce the generalization. It is here that the results of the infants and zebra finches diverge: zebra finches trained with a set of stimuli that share their abstract structure only (Experiment 1b) did not generalize to novel stimuli and hence did not detect the underlying pattern. The birds in our Experiment 1a and the infants in the experiment described by Gerken (2006) were exposed to input that can be described at at least two levels. One is the more abstract level based on the string structure (XYX or XXY), another is a simpler one that is restricted to learning that a particular element has a particular position in the strings. Given that the zebra finches in our

experiments failed on learning the more abstract structure even though the training strings in Experiment 1b are suitable for learning such a pattern, suggests that we have, at least in this experiment, reached a limit on the abilities for generalization in zebra finches. Whether this demonstrates an absolute barrier or whether such generalization might be induced by training with a larger, more varied training set remains to be investigated. The methodology might also restrict the learning of a more complex generalization. As in most comparison studies between humans and other animals (e.g. Stobbe et al. 2012), the human subjects in our experiment required far fewer trials than zebra finches. This might have affected what type of regularities have been learned Peña, Bonatti et al. (2002). In the Go/Nogo paradigm, the animals require extensive training, which might focus attention towards the familiar elements or bias rote memorization.

To demonstrate the acquisition of abstract rules, successful categorization should not depend on the physical similarity of items but should also be present when the exemplars bear no physical similarity to each other (Lea, 1984; Pearce, 2008). Human adults in our experiment and infants in the study by Marcus, Vijayan et al. (1999) were successful in categorizing novel strings into different groups according to their structures. This kind of task may require knowledge of a second-order relationship, in which the subjects need to detect the relationship between two other relationships (Thompson & Oden, 2000). Given an exemplar like ABA and a test stimulus like EFE, learners needed to know the relationships between individual elements within each sequence and the relationship between the two sequences to enable correct generalizing. Earlier studies showed that starlings (Comins & Gentner, 2013; Gentner, Fenn et al., 2006), zebra finches (van Heijningen, de Visser et al., 2009) and Bengalese finches (Seki, Suzuki et al., 2013) are all able to generalize a string structure to a novel string in which the individual items are replaced by novel ones from the same phonetic category. Of these species, zebra finches are the only ones that have been tested with the novel strings consisting of items belonging to novel categories and they fail in such a generalization. This failure might indicate that this ability, which is fundamental to syntactic abilities, is lacking or only marginally present, as is concluded from other studies on various non-human animals (Oden, Thompson et al., 1990; Thompson & Oden, 2000). However, a few individual birds in the current study succeeded in discriminating between stimulus strings that consisted of familiar element types but novel combinations, similar to what has been found in rhesus monkeys (Hauser & Glynn, 2009). While it cannot be excluded that this generalization was based on a rule like: ‘if the string contains AA, BB, CC or DD bigrams treat it as a NoGo-stimulus, if it does not, treat as a Go-stimulus’, it might also indicate that some abstract learning has occurred, but linked to the presence of familiar items (song elements).

Against the above background, the results of the human adults are of particular interest. In contrast to both birds and infants they readily generalized to novel strings even after training with a single set of XYX and XXY stimuli, although the stimulus set allowed also for learning the same regularity as the zebra finches (the final element of the XYX strings). The difference between adults and infants might be related to their experiences: human adults have been trained to master rule abstraction over their life. But even though humans thus show a broader generalization than the birds do, they still base their discrimination on applying a relatively

simple rule: presence or absence of repeated elements (XX) rather than on learning an XYX rule. Such a bias for learning about element repetitions is also shown in human infants (Gervain, Macagno et al., 2008; Kovács & Mehler, 2009). This might reflect a bias to use so-called perceptual or memory primitives (POMPs), as suggested by Endress, Nespore et al. (2009). Only after the more extensive training with more exemplars, as in Experiment 2b, did human adults also recognize that the structure is XXY and not XYX and hence applied a more extensive rule. Interestingly, den Bos and Poletiek (2010) using an artificial grammar task in which human adults could use either a grammar cue derived from example strings or a more local cue (a particular item in a fixed position in strings), also found their participants to focus on the local cue over the grammar one.

In the current study we found that zebra finches shared the same learning mode with human infants when they could use a stimulus bound generalization. However, while human adults succeeded in abstracting structural rules from the stimuli, abstracting in zebra finches seems constrained to the identity and position of specific diagnostic stimulus items.

To conclude, simple rule abstraction may be shared between humans and birds, but it remains to be investigated at which level of abstraction rule learning of non-human animals, whether mammals or birds, diverges from that of humans. Without implying that the abilities as observed in zebra finches are phylogenetically widespread or representative of other non-human species, the results do suggest a scenario in which the human ability to derive and apply a more general or complex underlying rule from experience with specific exemplars is something that might have arisen, both in ontogeny and during evolution, in a gradual progression from identifying individual stimuli, via stimulus bound generalization and recognizing patterns like repetitions towards more abstract patterns.

## References

- Altmann, G. T. M., & Dienes, Z. (1999). Rule Learning by Seven-Month-Old Infants and Neural Networks. *Science*, 284(5416), 875. doi: 10.1126/science.284.5416.875a
- Beckers, G. J., Bolhuis, J. J., Okanoya, K., & Berwick, R. C. (2012). Birdsong neurolinguistics: songbird context-free grammar claim is premature. *Neuroreport*, 23(3), 139-145. doi: 10.1097/WNR.0b013e32834f1765
- Berwick, R. C., Okanoya, K., Beckers, G. J., & Bolhuis, J. J. (2011). Songs to syntax: the linguistics of birdsong. *Trends in cognitive sciences*, 15(3), 113-121. doi: 10.1016/j.tics.2011.01.002
- Bolhuis, J. J., Okanoya, K., & Scharff, C. (2010). Twitter evolution: converging mechanisms in birdsong and human speech. *Nature Reviews Neuroscience*, 11(11), 747-759. doi: 10.1038/Nrn2931
- Comins, J. A., & Gentner, T. (2014). Auditory temporal pattern learning by songbirds using maximal stimulus diversity and minimal repetition. *Animal cognition*, 1-8. doi: 10.1007/s10071-014-0732-5
- Comins, J. A., & Gentner, T. Q. (2013). Perceptual categories enable pattern generalization in songbirds. *Cognition*, 128(2), 113-118. doi: 10.1016/j.cognition.2013.03.014
- Corballis, M. C. (2007). Recursion, language, and starlings. *Cognitive science*, 31(4), 697-704. doi: 10.1080/15326900701399947
- Corballis, M. C. (2009). Do rats learn rules? *Animal Behaviour*, 78(4), E1-E2. doi: 10.1016/j.anbehav.2009.05.001
- Creel, S. C., Newport, E. L., & Aslin, R. N. (2004). Distant melodies: statistical learning of nonadjacent dependencies in tone sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30(5), 1119-1130. doi: 10.1037/0278-7393.30.5.1119
- de la Mora, D. M., & Toro, J. M. (2013). Rule learning over consonants and vowels in a non-human animal. *Cognition*, 126(2), 307-312. doi: 10.1016/j.cognition.2012.09.015
- den Bos, E., & Poletiek, F. (2010). Structural selection in implicit learning of artificial grammars. *Psychological Research PRPF*, 74(2), 138-151. doi: 10.1007/s00426-009-0227-1
- Dooling, R. J., Leek, M. R., Gleich, O., & Dent, M. L. (2002). Auditory temporal resolution in birds: discrimination of harmonic complexes. *The Journal of the Acoustical Society of America*, 112(2), 748-759.
- Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: common themes and mechanisms. *Annual Review of Neuroscience*, 22, 567-631. doi: 10.1146/annurev.neuro.22.1.567
- Eimas, P. D. (1999). Do infants learn grammar with algebra or statistics? *Science*, 284(5413), 435-436; author reply 436-437.
- Endress, A. D. (2010). Learning melodies from non-adjacent tones. *Acta Psychologica*, 135(2), 182-190. doi: 10.1016/j.actpsy.2010.06.005
- Endress, A. D., Carden, S., Versace, E., & Hauser, M. D. (2010). The apes' edge: positional learning in chimpanzees and humans. *Animal cognition*, 13(3), 483-495. doi: 10.1007/s10071-009-0299-8
- Endress, A. D., Dehaene-Lambertz, G., & Mehler, J. (2007). Perceptual constraints and the learnability of simple grammars. *Cognition*, 105(3), 577-614. doi: 10.1016/j.cognition.2006.12.014
- Endress, A. D., Nespore, M., & Mehler, J. (2009). Perceptual and memory constraints on language acquisition. *Trends in cognitive sciences*, 13(8), 348-353. doi: 10.1016/j.tics.2009.05.005
- Fitch, W. T., & Friederici, A. D. (2012). Artificial grammar learning meets formal language theory: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1598), 1933-1955. doi: 10.1098/rstb.2012.0103
- Fitch, W. T., & Hauser, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science*, 303(5656), 377-380.
- Folia, V., Udden, J., de Vries, M., Forkstam, C., & Petersson, K. M. (2010). Artificial Language Learning in Adults and Children. *Language Learning*, 60, 188-220. doi: 10.1111/j.1467-9922.2010.00606.x
- Frank, M. C., Slemmer, J. A., Marcus, G. F., & Johnson, S. P. (2009). Information from multiple modalities helps 5-month-olds learn abstract rules. *Developmental science*, 12(4), 504-509. doi: 10.1111/j.1467-7687.2008.00794.x
- Gabriel, K. R. (1966). Simultaneous Test Procedures for Multiple Comparisons on Categorical Data. *Journal of the American Statistical Association*, 61(316), 1081-&. doi: 10.2307/2283202
- Gebhart, A. L., Newport, E. L., & Aslin, R. N. (2009). Statistical learning of adjacent and nonadjacent dependencies among nonlinguistic sounds. *Psychonomic bulletin & review*, 16(3), 486-490. doi: 10.3758/PBR.16.3.486
- Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature*, 440(7088), 1204-1207. doi: 10.1038/nature04675
- Gerken, L. (2006). Decisions, decisions: infant language learning when multiple generalizations are possible. *Cognition*, 98(3), B67-B74. doi: 10.1016/j.cognition.2005.03.003
- Gerken, L. (2010). Infants use rational decision criteria for choosing among models of their input. *Cognition*, 115(2), 362-366. doi: 10.1016/j.cognition.2010.01.006

- Gervain, J., Macagno, F., Cogoi, S., Peña, M., & Mehler, J. (2008). The neonate brain detects speech structure. *Proceedings of the National Academy of Sciences*, *105*(37), 14222-14227. doi: 10.1073/pnas.0806530105
- Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concepts of 'sameness' and 'difference' in an insect. *Nature*, *410*(6831), 930-933. doi: 10.1038/35073582
- Gomez, R. L., & Gerken, L. (2000). Infant artificial language learning and language acquisition. *Trends in cognitive sciences*, *4*(5), 178-186.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: what is it, who has it, and how did it evolve? *Science*, *298*(5598), 1569-1579. doi: 10.1126/science.298.5598.1569
- Hauser, M. D., & Glynn, D. (2009). Can free-ranging rhesus monkeys (*Macaca mulatta*) extract artificially created rules comprised of natural vocalizations? *Journal of Comparative Psychology*, *123*(2), 161-167. doi: 10.1037/a0015584
- Hauser, M. D., Newport, E. L., & Aslin, R. N. (2001). Segmentation of the speech stream in a non-human primate: statistical learning in cotton-top tamarins. *Cognition*, *78*(3), B53-64.
- Hauser, M. D., Weiss, D., & Marcus, G. (2002). RETRACTED: Rule learning by cotton-top tamarins. *Cognition*, *86*(1), B15-B22.
- Herbranson, W. T., & Shimp, C. P. (2003). "Artificial grammar learning" in pigeons: a preliminary analysis. *Learning & behavior*, *31*(1), 98-106.
- Herbranson, W. T., & Shimp, C. P. (2008). Artificial grammar learning in pigeons. *Learning & behavior*, *36*(2), 116-137.
- Katz, J. S., & Wright, A. A. (2006). Same/different abstract-concept learning by pigeons. *Journal of experimental psychology. Animal behavior processes*, *32*(1), 80-86. doi: 10.1037/0097-7403.32.1.80
- Kovács, Á. M., & Mehler, J. (2009). Flexible Learning of Multiple Speech Structures in Bilingual Infants. *Science*, *325*(5940), 611-612. doi: 10.1126/science.1173947
- Lachlan, R. F., Verhagen, L., Peters, S., & ten Cate, C. (2010). Are there species-universal categories in bird song phonology and syntax? A comparative study of chaffinches (*Fringilla coelebs*), zebra finches (*Taenopygia guttata*), and swamp sparrows (*Melospiza georgiana*). *Journal of Comparative Psychology*, *124*(1), 92-108. doi: 10.1037/a0016996
- Lea, S. E. G. (1984). In what sense do pigeons learn concepts? In H. L. Roitblat, T. G. Bever & H. S. Terrace (Eds.), *Animal cognition* (pp. 263-276). Hillsdale, NJ: Erlbaum: Psychology Press.
- Marcus, G. F., Vijayan, S., Bandi Rao, S., & Vishton, P. M. (1999). Rule learning by seven-month-old infants. *Science*, *283*(5398), 77-80.
- Mondragon, E., Murphy, R. A., & Murphy, V. A. (2009). Rats do learn XYX rules. *Animal Behaviour*, *78*(4), E3-E4.
- Murphy, R. A., Mondragon, E., & Murphy, V. A. (2008). Rule learning by rats. *Science*, *319*(5871), 1849-1851. doi: 10.1126/science.1151564
- Negishi, M. (1999). Do infants learn grammar with algebra or statistics? *Science*, *284*(5413), 435; author reply 436-437.
- Newport, E. L., Hauser, M. D., Spaepen, G., & Aslin, R. N. (2004). Learning at a distance II. Statistical learning of non-adjacent dependencies in a non-human primate. *Cognitive Psychology*, *49*(2), 85-117. doi: 10.1016/j.cogpsych.2003.12.002
- Oden, D. L., Thompson, R. K. R., & Premack, D. (1990). Infant Chimpanzees Spontaneously Perceive Both Concrete and Abstract Same Different Relations. *Child Development*, *61*(3), 621-631. doi: 10.1111/j.1467-8624.1990.tb02807.x
- Ohms, V. R., Escudero, P., Lammers, K., & ten Cate, C. (2012). Zebra finches and Dutch adults exhibit the same cue weighting bias in vowel perception. *Animal cognition*, *15*(2), 155-161. doi: 10.1007/s10071-011-0441-2
- Pearce, J. M. (2008). *Animal Learning and Cognition*. New York: Psychology Press.
- Peña, M., Bonatti, L. L., Nespor, M., & Mehler, J. (2002). Signal-driven computations in speech processing. *Science*, *298*(5593), 604-607.
- Pinker, S. (1991). Rules of Language. *Science*, *253*(5019), 530-535. doi: 10.1126/science.1857983
- Reber, A. S. (1967). Implicit Learning of Artificial Grammars. *Journal of Verbal Learning and Verbal Behavior*, *6*(6), 855-863. doi: 10.1016/S0022-5371(67)80149-X
- Reber, A. S. (1990). On the Primacy of the Implicit - Comment. *Journal of Experimental Psychology: General*, *119*(3), 340-342. doi: 10.1037//0096-3445.119.3.340
- Saffran, J. R., Johnson, E. K., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*(1), 27-52.
- Saffran, J. R., Pollak, S. D., Seibel, R. L., & Shkolnik, A. (2007). Dog is a dog is a dog: infant rule learning is not specific to language. *Cognition*, *105*(3), 669-680. doi: 10.1016/j.cognition.2006.11.004
- Seidenberg, M. S. (1999). Do infants learn grammar with algebra or statistics? *Science*, *284*(5413), 434-435; author reply 436-437.

- Seki, Y., Suzuki, K., Osawa, A. M., & Okanoya, K. (2013). Songbirds and humans apply different strategies in a sound sequence discrimination task. *Frontiers in psychology*, *4*, 447. doi: 10.3389/fpsyg.2013.00447
- Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: the principles and practice of statistics in biological research*. New York: Freeman and Co.
- Stobbe, N., Westphal-Fitch, G., Aust, U., & Fitch, W. T. (2012). Visual artificial grammar learning: comparative research on humans, kea (*Nestor notabilis*) and pigeons (*Columba livia*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1598), 1995-2006. doi: 10.1098/rstb.2012.0096
- ten Cate, C., Lachlan, R., & Zuidema, W. (2013). Analyzing the structure of bird vocalizations and language: finding common ground. In J. J. Bolhuis & M. Everaerts (Eds.), *Birdsong, speech, and language* (pp. 243-260). Cambridge: The MIT press.
- ten Cate, C., & Okanoya, K. (2012). Revisiting the syntactic abilities of non-human animals: natural vocalizations and artificial grammar learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1598), 1984-1994. doi: 10.1098/rstb.2012.0055
- Thompson, R. K. R., & Oden, D. L. (2000). Categorical perception and conceptual judgments by nonhuman primates: The paleological monkey and the analogical ape. *Cognitive science*, *24*(3), 363-396. doi: 10.1207/s15516709cog2403\_2
- Toro, J. M., & Trobalon, J. B. (2005). Statistical computations over a speech stream in a rodent. *Perception & psychophysics*, *67*(5), 867-875.
- van Heijningen, C. A., Chen, J., van Laatum, I., van der Hulst, B., & ten Cate, C. (2013). Rule learning by zebra finches in an artificial grammar learning task: which rule? *Animal cognition*, *16*(2), 165-175. doi: 10.1007/s10071-012-0559-x
- van Heijningen, C. A., de Visser, J., Zuidema, W., & ten Cate, C. (2009). Simple rules can explain discrimination of putative recursive syntactic structures by a songbird species. *Proceedings of the National Academy of Sciences*, *106*(48), 20538-20543. doi: 10.1073/pnas.0908113106
- Wright, A. A., Rivera, J. J., Katz, J. S., & Bachevalier, J. (2003). Abstract-concept learning and list-memory processing by capuchin and rhesus monkeys. *Journal of experimental psychology. Animal behavior processes*, *29*(3), 184-198.
- Yamazaki, Y., Suzuki, K., Inada, M., Iriki, A., & Okanoya, K. (2012). Sequential learning and rule abstraction in Bengalese finches. *Animal cognition*, *15*(3), 369-377. doi: 10.1007/s10071-011-0462-x

