

Budgerigars and zebra finches differ in how they generalize in an artificial grammar learning experiment

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The ability to abstract a regularity that underlies strings of sounds is a core mechanism of the language faculty but might not be specific to language learning or even to humans. It is unclear whether and to what extent nonhuman animals possess the ability to abstract regularities defining the relation among arbitrary auditory items in a string and to generalize this abstraction to strings of acoustically novel items. In this study we tested these abilities in a songbird (zebra finch) and a parrot species (budgerigar). Subjects were trained in a go/no-go design to discriminate between two sets of sound strings arranged in an *XYX* or an *XXY* structure. After this discrimination was acquired, each subject was tested with test strings that were structurally identical to the training strings but consisted of either new combinations of known elements or of novel elements belonging to other element categories. Both species learned to discriminate between the two stimulus sets. However, their responses to the test strings were strikingly different. Zebra finches categorized test stimuli with previously heard elements by the ordinal position that these elements occupied in the training strings, independent of string structure. In contrast, the budgerigars categorized both novel combinations of familiar elements as well as strings consisting of novel element types by their underlying structure. They thus abstracted the relation among items in the *XYX* and *XXY* structures, an ability similar to that shown by human infants and indicating a level of abstraction comparable to analogical reasoning.

artificial grammar learning | rule learning | auditory perception | songbirds | parrots

One of the critical features of language learning is the ability to abstract the grammatical structure from spoken language. Such abstraction allows humans to learn about regularities in their native language and to generalize these regularities to novel input. This ability is examined in a standardized way in artificial grammar learning experiments, in which humans are exposed to strings of meaningless sounds (e.g., arbitrary speech syllables) organized according to a specific grammatical structure. Several studies have shown that the ability to abstract the underlying structure from such stimuli is present in young infants (1–5) in both the acoustic and the visual domain (6–8). This domain generality and its presence at a very early age have given rise to the notion that this cognitive ability may have preceded language evolution and served as a basis for present-day linguistic complexity. If so, it raises the question to what extent this ability is confined to humans or also can be found in nonhuman animals. In this context, comparative studies on nonhuman animals are needed to reveal the level of abstraction they are able to achieve in artificial grammar learning tasks. This information might provide hypotheses about how and why the more complex human grammatical competences have arisen. The current study addresses whether two bird species, the zebra finch and the budgerigar, are able to abstract *XYX* and *XXY* grammatical structures consisting of auditory items.

By now, a number of studies on birds (9–16), rats (17–19), and primates (20–22) have used the artificial grammar paradigm to address animal abilities to learn about grammatical structures. Many of

these studies used a discrimination task in which the animal has to learn to distinguish two differently structured string sets which are related to differences in reinforcement. However, success in such discrimination learning does not necessarily indicate that the animals learned the underlying structure of the string sets. They might, for instance, have solved the discrimination task by rote memorization of the different strings without detecting any structural relation between them. The critical test, and the hallmark of abstraction as shown by humans, is whether the discrimination between differently structured string sets is maintained in a test in which the novel test strings share no observable physical (acoustical or visual) similarity to the training strings, but only a relational one (23–26), i.e., where the only way to classify the novel stimuli is by the structural similarity between the training and test strings. This ability to maintain the discrimination is nicely illustrated by the classic study by Marcus and colleagues (1), in which infants were familiarized with a series of examples of an *XYX* structure (with “X” and “Y” items being speech syllables, resulting in strings such as “ga-ti-ga” or “li-na-li”). After familiarization, the infants were tested with syllables from novel categories (i.e., different consonants and vowels) arranged according to the same structure (e.g., “wo-fi-wo” for the *XYX* structure) or a different structure (e.g., “wo-wo-fi,” the *XXY* structure). The X and Y items are all drawn from the same pool, and in principle the only cue for discriminating between the novel strings is the similarity or dissimilarity in the arrangement of the items. Whether this ability to discriminate artificial grammar strings by their structure alone is present in nonhuman animals is still an open question, as the experiments that have tested this ability in a variety of mammal species [rhesus monkeys (22), rats

Significance

Human language learning is based on learning abstract grammatical structures. Whether any nonhuman animal can detect such structures is a contentious issue. We tested zebra finches and budgerigars on whether experience with auditory strings with different grammatical structures resulted in learning these structures. Both species were able to distinguish the differently structured strings but did so very differently. Zebra finches attended to the ordinal positions of specific items in a string. In contrast, budgerigars detected the underlying structure and used this structure to classify correctly strings consisting of fully novel items. This ability to perceive the abstract relation between items is comparable to analogical reasoning, something long thought to be unique for humans and known from only a few species.

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(17)] and bird [Bengalese finch (13), zebra finch (9, 15, 16)] species do not provide unambiguous evidence for this ability. The rhesus monkeys (22), for instance, were first habituated to either XXY or XYY strings in which X and Y were various call types. The same call types were used in tests with structure-consistent or structure-inconsistent strings, albeit novel exemplars. The monkeys were not tested with novel call types, and hence the generalization of the response could be based on the auditory similarity between novel and familiar string types. Therefore physical (acoustic) similarity, not structural similarity, between training and test items might have guided the responses. The rats continued to discriminate the patterns when the tones were transposed to different frequencies, but it is disputed whether this reflects recognition of the abstract pattern, or recognition of the novel tone sequences as transpositions of familiar ones (27, but also see ref. 28).

The ability of animals to detect grammatical structures has also been tested using an artificial grammar in which several training items belonging to two different categories (A and B) were arranged either as an $(AB)^n$ or an A^nB^n grammar. A series of experiments on tamarins (21), starlings (12), and pigeons and keas (14) demonstrated that all species discriminated among the training sets. However, in order to show what these species learned about the grammatical structure, they were tested with strings consisting of novel items belonging to the same categories as the training items. The tamarins were trained and tested with the A and B items being male and female voices (21); for the starlings, the A and B items were warble and rattle song syllables (12); and for the pigeons and keas, the A and B items were visual tiles showing either a circle or small squares (14). Such test strings could thus always be classified by attending to the acoustic or visual category identity of the training and test items. Only one experiment, in zebra finches, tested whether any species could transfer discrimination between $(AB)^n$ and A^nB^n strings to similarly structured strings consisting of items belonging to novel categories C and D (16). Like the other species, zebra finches could discriminate correctly between test strings with novel items belonging to A and B categories, but most birds failed to discriminate the two string types when they consisted of C and D element types. There was one notable exception of a bird that did transfer the discrimination to strings with the novel element types. Zebra finches also have been tested using the XYX vs. XXY or XYY grammars discussed above (9, 15, 16). As in previous studies, they had no difficulty in discriminating between the training strings, but when tested with novel combinations of familiar elements or strings with novel element types their responses varied. Some individuals ignored novel stimuli, whilst others generalized based on acoustical similarities between the training and test stimuli (9, 15). Thus, there seems a range in acoustic string discrimination strategies among zebra finches, but there is no clear evidence that they can abstract the underlying structure.

To conclude, the various experiments discussed above either did not address whether nonhuman animals can generalize to novel strings having only a structural similarity to the training strings or have not provided unambiguous evidence that they can do so (24, 26). Therefore, it is still an open question whether they can show the same abstraction shown by infants in the study of Marcus et al. and others (1, 2). Addressing this question is important, not only in the context of grammar learning experiments but also for understanding animal cognition more generally. This type of abstraction is a cognitively advanced ability, comparable to a relational or analogical match-to-sample task as examined in studies on visual pattern abstraction. In a normal match-to-sample task, animals can obtain a reward by choosing from two alternatives the object that matches the one shown previously. However, in a relational match-to-sample task an animal is trained with pairs of stimuli bearing a particular relation to each other, for instance being either the same as (e.g., AA, BB) or different from (e.g., AB) each other. Next they are tested with

pairs of novel items that do not share a physical resemblance with the training stimuli, but do share the same underlying structure, such as CC or CD. Such a task thus requires the matching of relations between relations (29–33). Similarly, learning to identify correct sequences of novel auditory items, such as an XYX or XXY structure, requires that the animal first detects that the relation between the X and Y items differs in the XYX and XXY samples and next abstracts this relation to novel samples.

In the current study, we also used the artificial grammar-learning paradigm with XYX and XXY stimuli. One species we used is the zebra finch. Like humans, zebra finches are vocal learners. Their songs consist of ordered, rapidly produced elements. They are a widely used model species for comparative studies on speech and language (34) as well as for auditory learning (26). In addition, we used budgerigars, a representative of another vocal-learning clade, the parrots. Budgerigars are vocal learners with more vocal variation than zebra finches and an open-ended learning capacity. This parrot species produces long and flexible warble songs that vary both in the sequential structure as well as in the shape and duration of elements (35, 36). Even with this strong variation, budgerigars are able to detect minor changes in familiar songs (37). Budgerigars also are frequently used in studies on auditory learning. Although zebra finches and budgerigars have similar hearing abilities, a comparative study showed that budgerigars are better at identifying acoustic stimuli (38). Thus far, budgerigars have not been tested in an artificial grammar learning task, making it of interest to compare them to zebra finches. A comparison of species belonging to these two distinct clades also is of interest because the previously mentioned studies comparing another parrot species, the kea, with pigeons (also a different clade) revealed that these species used very different strategies to distinguish between two string sets consisting of different visual patterns (14, 39). All keas showed the same consistent strategy, but the pigeons showed no consistent pattern at either the species or individual level (39). As mentioned above, previous experiments on zebra finches showed a considerable variety in strategies in distinguishing auditory strings (9, 15, 16) and, as parrots have not yet been tested in an auditory artificial grammar paradigm, our experiment may reveal whether here too the parrot species behaves differently.

Both zebra finches and budgerigars were first trained in a go/no-go paradigm to discriminate between five XYX and five XXY triplets. These triplets consisted of zebra finch song elements or, in an additional zebra finch experiment, artificial sounds (Fig. S1). After reaching the criterion for reliable discrimination of the training stimuli (*Methods*), all birds received six different sets of test stimuli, henceforth described as tests 1–6. Test 1 consisted of triplets also used during the training, but now without reinforcement, providing the control condition. The stimuli used in tests 2–5 consisted of items that also occurred in the training stimuli but were arranged in new combinations. Test 6 consisted of triplets involving items that had not been used for the training stimuli. These different tests give rise to different predictions about how the test stimuli should be classified, depending on what the subject learned during training. If the birds use rote memorization of the individual stimuli, all novel stimuli should be considered as more or less equal, irrespective of their structure. On the other hand, if the birds learn to discriminate between the stimuli based on their structure (XYX or XXY), they should classify all test stimuli according to this structure. Finally, if the birds categorize the test triplets according to their physical similarity with the training triplets, there should be variation among the responses over the various tests, because these similarities differ in the different triplet combinations. The results show striking species-specific learning strategies. The zebra finches categorized the test triplets based on their similarity to the training triplets, i.e., they used the similarity in the ordinal position of the items in the training and the test strings to discriminate the test

strings. They did not discriminate among the new triplets. Budgerigars, on the other hand, generalized the discrimination learned in the training strings to new arrangements of familiar sounds and, in an additional experiment, transferred that discrimination to novel items. Therefore they learned the underlying structures of the training strings, thus demonstrating a level of abstraction rarely observed among nonhuman animals.

Results and Discussion: Zebra Finches and Budgerigars

Results: Zebra Finches. When trained with zebra finch song stimuli, the zebra finches learned to discriminate between the two sets of training triplets correctly in, on average, 13,850 trials ($SD = 8,124$). During the test phase, they correctly discriminated between the XYX and the XXY triplets of test 1 (training triplets; $P = 0.014$) and test 2 (new combination; $P = 0.015$; see *SI Test Stimuli* for stimulus composition and terminology). They did not show discrimination between the XYX and XXY triplets in test 3 (new combination and one new position; $P = 0.99$), test 4 (new combination and two new positions; $P = 0.092$), or test 6 (new elements, $P = 0.201$). Surprisingly, in test 5 (new combination and three new positions) the birds did discriminate between the XYX and XXY structures, but they responded more often to the triplets in the no-go structure than to the triplets in the go structure ($P = 0.008$). For example, if a bird had been trained to respond when it heard an XXY structure, it would now go more often after hearing an XYX -structured triplet (Fig. 1A). There was no effect of sex of the bird ($F = 2.8$, $P = 0.15$), or whether the go structure during

training was XYX or XXY ($F = 0.33$, $P = 0.58$), or whether the bird had experience with the go/no-go paradigm in a previous experiment ($F = 1.95$, $P = 0.21$).

The responses of individual zebra finches varied in the different tests (Fig. 1B). All zebra finches correctly discriminated between the go and no-go stimuli (all test scores fell outside the 95% confidence interval of a binomial distribution, indicated by green dots in Fig. 1B) only in test 1. The other tests showed more variation among the individual birds. In test 3, in particular, one bird responded more to the stimuli with a no-go structure than to the stimuli with the go structure (indicated by a red dot in Fig. 1B), and one zebra finch discriminated the stimuli correctly. None of the other subjects deviated from chance level (black dots in Fig. 1B). When two elements of the triplet were in a position similar to the opposite training structure (test 5), three birds discriminated the stimuli by responding more to the no-go structures. In test 6 none of the birds differed from chance level. Despite this individual variation, Kendall's τ_b test showed a systematic decrease of the test score over tests 2–5 ($\tau = -0.623$, $P < 0.001$).

A second group of zebra finches trained on triplets consisting of artificial sounds showed similar results (Fig. 1C). They learned to discriminate the training triplets in 13,238 trials ($SD = 3,482$). Again, they discriminated correctly only in tests 1 and 2 (test 1, $P < 0.01$; test 2, $P < 0.01$). No significant discrimination was seen in tests 3, 4, and 6 (test 3, $P = 0.7$; test 4, $P = 0.17$; test 6, $P = 0.1$). As in the previous group, these zebra finches also discriminated significantly between the XYX and XXY triplets in test 5 by

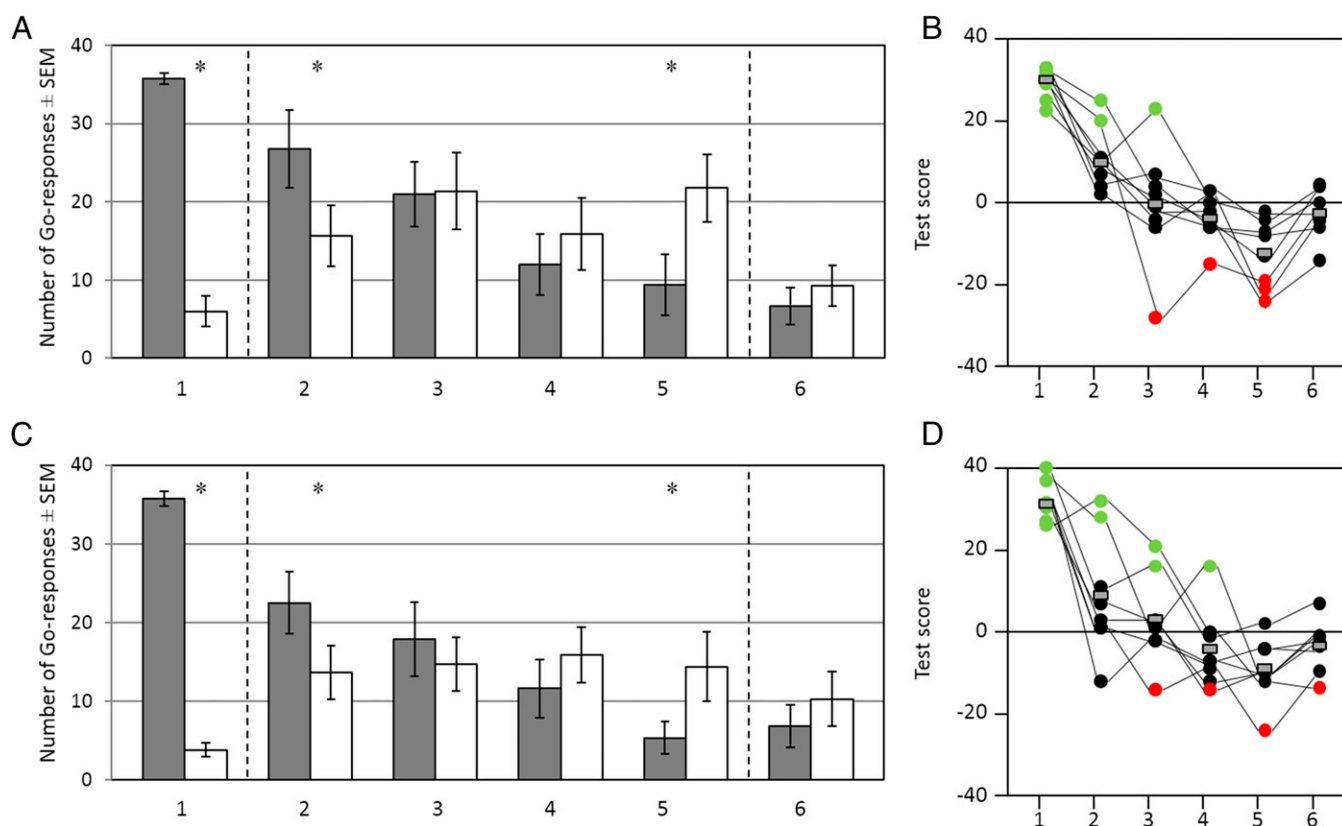


Fig. 1. (A) Average proportional responses ($\pm SEM$) in tests 1–6 to the two different structures of the test items for the zebra finches that heard zebra finch song elements. The gray bars indicate the responses to stimuli with a structure similar to the go stimuli. The white bars indicate the responses to the stimuli with the no-go structure. (B) The test scores of the individual zebra finches that heard zebra finch song elements. A green dot indicates a correct discrimination between the XYX and XXY triplets. Black dots indicate no difference between the responses to XYX and XXY triplets. Red dots indicate a reversed response, in which the structure that was trained as no-go received more responses than the go-structure. Gray blocks show the average responses of the group. (C) Average proportional responses ($\pm SEM$) of the zebra finches that heard artificial sounds. (D) The test scores of the individual zebra finches that heard artificial sounds. Group averages are shown by gray blocks. Asterisks in A and C indicate significant differences in response to the XYX and XXY structures.

responding more to the no-go items ($P = 0.01$). Again, there was no effect of sex ($P = 0.91$) or of the structure of the go stimuli ($P = 0.78$).

The individual responses of the zebra finches to the artificial stimuli also are very comparable to those of the zebra finches hearing zebra finch song elements. All zebra finches responded more to the go structure than to the no-go structure only in test 1. Again, the greatest variation is shown in test 3, in which two individuals made a correct discrimination and one bird discriminated incorrectly. In test 4, also, one individual made the correct discrimination, and one individual responded more to the no-go structure than to the go structure. These individuals did not discriminate in tests 3 or 5. In test 5, one individual responded more to the test stimulus having the no-go structure. In test 6, the generalization test, one of the zebra finches discriminated between the XYX and XXY triplets incorrectly. As in the previous experiment, these birds also showed a systematic decline in responses to the go-type stimuli over tests 2–5 ($\tau = -0.454$, $P = 0.001$).

Discussion: Zebra Finches. The zebra finches learned to discriminate between the XYX and XXY patterns of both zebra finch song elements and artificial sounds. When the birds heard triplets consisting of novel items, their response rates dropped, and they did not discriminate between the XYX and XXY structures. However, their responses to new combinations of training elements differentiated according to the positional similarities between test and training items. They maintained the correct discrimination between XYX and XXY only in test 2, in which the test strings showed a greater positional similarity to the training strings of the same structure than to the other structure. When the similarities in the positions of elements of the test triplets shifted toward a greater similarity to the triplets of the no-go structure, the zebra finches responded more often to those test triplets. There is a clear overall pattern from responding more to the go structure toward responding more to the no-go structure with increased positional similarity of the test triplets to the no-go training triplets. These results indicate that the zebra finches learned the positions of the elements in the various training stimuli and responded to the test strings based on the similarity in item positions.

Results: Budgerigars. The budgerigars were subjected to two consecutive experiments. The first experiment (“mixed test”) was a replication of the first zebra finch experiment. The second experiment was a transfer task. After training in the second experiment, the birds were not tested, but the training strings were instantly replaced by novel strings consisting of zebra finch song elements of categories not heard previously. Transfer tests are commonly used to assess whether animals are able to transfer a learned distinction to novel stimuli. With no familiar sounds presented after the transfer, we tested whether the budgerigars were incapable of generalization based on structural similarities or were able to make such generalizations but did not show this ability in the mixed test.

Mixed Test. Like the zebra finches, the budgerigars learned to discriminate between the XYX and XXY triplets during training (mean trials, $7,816 \pm 4,845$). In contrast to the zebra finches, the budgerigars consistently discriminated between the test strings with familiar items according to their structural similarity to the training strings (test 1, $P = 0.031$; test 2, $P = 0.035$; test 3, $P = 0.041$; test 4, $P = 0.035$; test 5, $P = 0.043$). In test 6, generalization to novel elements, the budgerigars responded hardly at all and did not discriminate between test strings ($P = 0.31$) (Fig. 2A). Here, also, there was no effect of sex of the bird ($t = -6.01$, $P = 0.31$) or of the go structure during training ($t = -5.37$, $P = 0.24$).

The majority of the individual budgerigars followed the pattern seen at the group level (Fig. 2B). All birds discriminated between the stimuli in test 1, and at least one-half of the birds made a significantly correct discrimination in tests 2–5. In test 6

none of the birds discriminated between the test triplets. One bird showed a consistently high correct discrimination in tests 1–5, but its performance also dropped to the chance level in test 6. Nevertheless, the figure shows that if a bird did respond in test 6, that response was more often to a string with the grammatically correct structure. There was no significant relation between the test score and the test number over tests 2–5 ($\tau = -0.096$, $P = 0.55$), indicating that the budgerigars’ responses are not affected by the similarity in item positions in the training and test strings.

Transfer task. All birds learned to discriminate between the go and no-go items during the first training phase and reached the discrimination criterion faster than in the previous experiment (mean \pm SD mixed test = $7,816 \pm 4,845$; mean \pm SD transfer task = $6,483 \pm 4,491$; $P < 0.01$). Of the six budgerigars, five retained their discrimination after the transfer to new song elements (Fig. 3) as shown by their discrimination ratios (correct go responses/all go responses) for the transfer sets. Transfer set 1 consisted of the first responses to each of the 12 XYX and 12 XXY stimuli, transfer set 2 consisted of all responses to the second time the subjects heard the stimuli, and so forth. The five budgerigars discriminated the two stimulus structures significantly above chance level for the first transfer set and remained above chance for all subsequent sets (individual budgerigar P2: all $P < 0.04$; budgerigar P4: all $P < 0.001$; budgerigar P8: all $P < 0.02$; budgerigar P9: all $P < 0.01$; and budgerigar P11: all $P < 0.01$). One individual did not perform better than chance after the transfer, although he also learned to discriminate between the training items by the fifth time he encountered the stimuli (budgerigar P7: test set 1–4, all $P > 0.19$; set 5, $P < 0.01$) (Fig. 3).

Discussion: Budgerigars. The budgerigars successfully categorized triplets in the mixed test by their structure as long as the items in these triplets were familiar. They hardly responded to triplets consisting of new items and showed no significant difference in response to those triplets. When they did respond, however, they responded more toward triplets that were similar in structure to the go stimuli. Their correct categorization of triplets in which all items were in new positions shows that they generalized based on the structure of the training triplets. If they had not generalized the structure, their responses would have been at chance level; if they had generalized based on positional similarities between training and test items, their responses would have been more similar to those of the zebra finches.

The low number of responses to the stimuli with new items in test 6 might reflect a weakness of the test procedure of the go/no-go task that has been noted before (9, 15, 16, 40). Because only the go training stimuli (consisting of familiar items) provided a reward, the budgerigars might quickly have learned to ignore any stimulus containing novel items. However, although they ignored the strings consisting of novel items in the mixed test, they nevertheless noted the structure of these strings, because, averaged over the first encounters with the novel training strings of the transfer task, five of the six budgerigars immediately discriminated correctly between XYX and XXY triplets. These responses demonstrate an immediate generalization of the structural information provided by the training stimuli.

General Discussion

Our results show that in the same learning task zebra finches used positional information to discriminate between string sets, whereas budgerigars used the grammatical structure underlying the training strings to categorize new strings. The abstraction shown by the budgerigars requires learning the relations between items in a string. The budgerigars first had to learn that the relation between the items differed in the XYX - and the XXY -structured triplets and then had to link these differences to their actions and to the received feedback. When hearing unfamiliar sounds, they needed to perceive the relations between these new

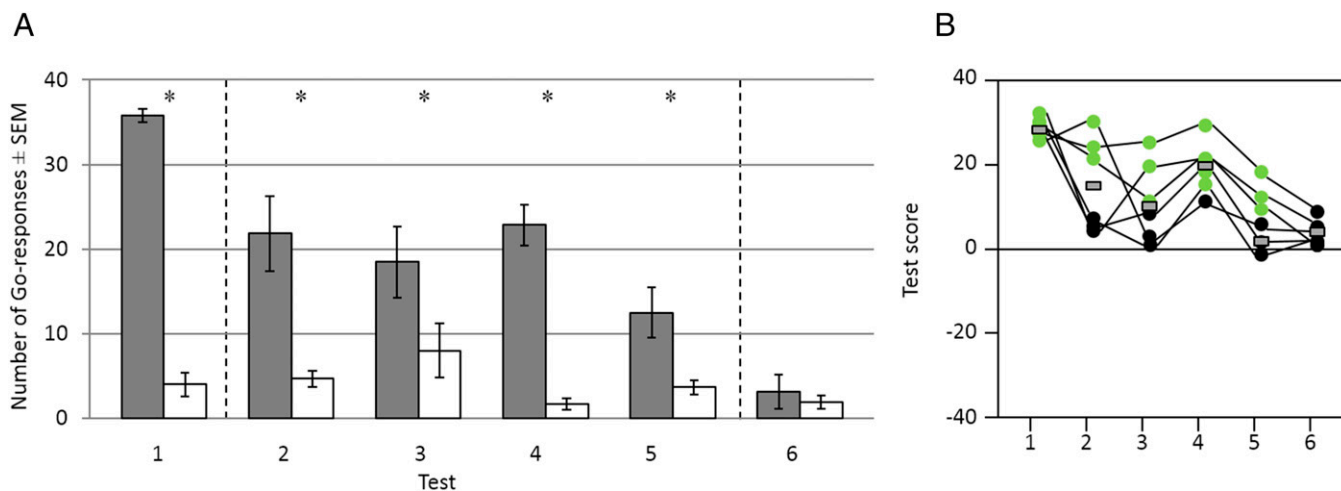


Fig. 2. (A) The average proportion of responses of the budgerigars in the different tests. The gray bars indicate the responses to stimuli with a structure similar to the go stimuli. The white bars indicate the responses to stimuli with the “no-go” structure. Asterisks indicate significant differences in response to the XYX and XXY structures. (B) The test scores of the individual budgerigars. A green dot indicates a correct discrimination between the XYX and XXY triplets. Black dots indicate no difference between the responses to XYX and XXY triplets. Gray blocks show the average test score of the group with the same color coding.

items and compare these relations to the structural relations between the training items to give the appropriate response. Nonhuman species’ ability for such abstraction has been debated and, until now, had not been clearly shown (see Introduction and ref. 24). Several studies have shown that animals can discriminate between artificially constructed sound strings (e.g., 8–10, 12, 14, 15). However, this discrimination usually is based on attending to specific, familiar sound features, like repetitions of items belonging to a familiar category (9, 15, 16).

The results of the budgerigars were obtained by using a different experimental paradigm (go/no-go) from the one most commonly used in infant studies (familiarization). Nevertheless, the abstraction shown by the budgerigars seems comparable to that observed by Marcus et al. (1) in human infants at the age of 7 mo (1), who were able to learn structures such as XYX vs.

XXY. However, as noted for rule learning in humans (e.g., refs. 41–43), sets of strings can be discriminated in many ways, ranging from rote memorization of the different strings to using the abstract structure underlying a set. Similarly, the training stimuli used in our present experiment allowed discrimination based on structure (XYX vs. XXY, or every other diagnostic form, such as a repetition of X) as well as discrimination based on memorization of element positions. Interestingly, infants do not always discriminate XYX and XXY strings based on their structure but also may use positional information that is present in training strings. Gerken (41) presented two groups of infants with different subsets of triplets from the stimuli of Marcus et al. (1). One group heard four XXY triplets in which both the X and the Y syllable were different in each triplet. The second group heard a subset of four triplets in which the Y syllable was constant (always “di”). Infants in the first

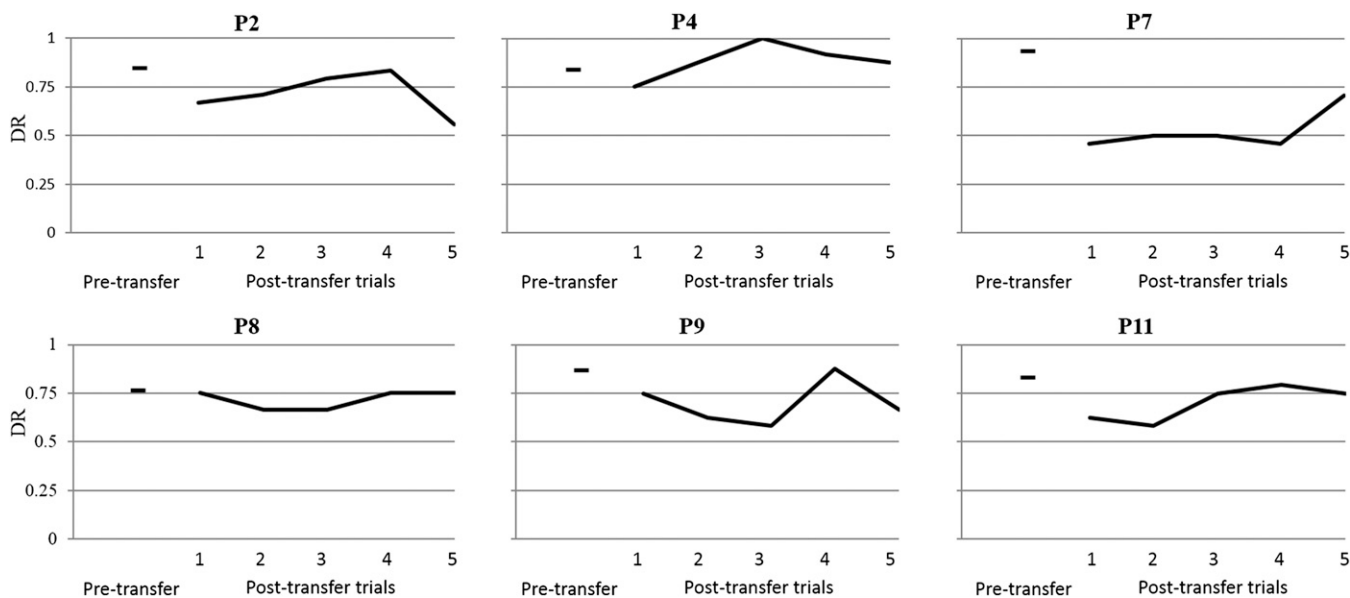


Fig. 3. The discrimination ratio per set of test trials (each set consists of 12 different go and 12 different no-go triplets) per individual. The short line indicates the average discrimination ratio (DR) of the last 100 trials of the training. The line shows the responses to the first five trial sets (1–5) after being transferred to new stimuli. Five of six budgerigars discriminated above chance level immediately after the transfer.

group generalized the structure of the triplets to novel exemplars, but infants in the second group generalized only to novel exemplars with the di syllable in the final position. Thus, depending on the type of information presented during familiarization, infants attended either to the grammatical structure or to the ordinal position of specific items in the triplets. In our experiment, in which the training stimuli could be discriminated either on structure or on item positions, the zebra finches are clearly biased to memorize the ordinal positions of familiar elements, while the budgerigars attended to the underlying structures. The behavior of the two species thus reflects two different strategies, both of which are present in human infants.

The positional learning observed in the zebra finches is a strategy commonly seen when animals are trained to discriminate between strings of visual or acoustic stimuli. Zebra finches are known to use the positional information in strings of song elements, although they also can use transitional information (44). Other animals also use positional information in auditory and nonauditory string-learning tasks. For instance, when pigeons are trained to respond to sequences with an A-B-C-D structure (the letters depicting different image categories), they respond more quickly when they see new strings in which the category items are in the original ordinal position than when they see strings in which the category items are switched (e.g., A-C-B-D) (45, 46). A similar mapping of items to positions in both string-discrimination and food-localization paradigms has been noted in several primate species (20, 47, 48). While the positional learning as observed in the zebra finches is thus not uncommon, the detailed memory for item positions that they demonstrate in the current experiment is impressive, as they kept track of item positions over a set of ten training strings.

Learning about abstract structures and relations, as shown by the budgerigars, is rare in the animal kingdom. The cognitive process underlying abstraction is considered a higher-order cognitive ability as it requires an individual to ignore the specific features of individual items and to attend to the global, structural features, in this case of the sound strings. This ability is analogous to the cognitive skills used in relational match-to-sample tasks. As described in the Introduction, success in these tasks is possible only when the subject attends to the relation between items (e.g., whether two items are the same or different). The subject must transfer the learned relations between familiar items to novel ones during testing (30–33), comparable to the requirements for success in our artificial grammar learning task. The ability to perform such a relational match-to-sample task long was thought to be unique for humans; it also has been demonstrated in some great ape species (30) and recently has been demonstrated in crows and amazon parrots (32, 33, but also see ref. 49), but so far only in the visual domain. Our findings suggest that the species that succeeded in a relational match-to-sample task, might also succeed in artificial grammar tasks such as the current one.

While our experiment reveals a clear species difference in the strategies used to discriminate the string sets, the cause of this difference is not clear. It is unlikely that the observed difference is due to the nature of the sound items. Zebra finches trained and tested with unfamiliar, nonsong stimuli also used the positional learning strategy, so the use of this strategy is not linked to the items being species-specific sounds. For the budgerigars, the zebra finch song elements were equally as unfamiliar as the artificial sounds were to the zebra finches. It is more likely that the difference in strategy is based on a species- or clade-specific difference. The two species have different singing styles: The budgerigars are open-ended vocal learners, whereas vocal learning in zebra finches is limited to a sensitive phase during development. Whether or how such differences might be responsible for the observed difference in discrimination is unclear. A likely alternative explanation may be that the budgerigars are more cognitively advanced in solving complex learning tasks or in abstraction in general. This explanation also may be supported by the previously mentioned

study by Dent et al. (38), which showed that budgerigars are better than zebra finches at identifying complex acoustic stimuli (although that study did not address the budgerigars' ability for abstraction). In our experiment, also, the budgerigars required fewer trials to reach the training criterion. Our findings thus confirm that different bird species trained and tested on the same stimulus sets can behave quite differently, as was observed for the keas and pigeons in a visual grammar learning task (39). In that study pigeons and keas both attended to local features of the training stimuli; the species differed in which features were used and the consistency with which a specific strategy was used among individuals. In the current study, the difference between species seems to be a more fundamental one, with both zebra finches and budgerigars being consistent within the species, but one attending to local features and the other to a higher-order regularity. It is obvious that further comparative work is needed to reveal the origin and scope of the cognitive differences between the various bird species. As noted above, both the parrot and the songbird clades contain cognitively advanced species (50, 51) and hence provide ample opportunity for such studies.

Conclusions

We have demonstrated the ability of a vocal learning avian species, the budgerigar, to learn about the abstract relations between items in an acoustic string. Our results indicate that the cognitive system necessary to detect grammatical regularities in sound strings is not unique to humans or to having language. Instead, it seems to be an ability that is uncommon throughout the animal kingdom, and may indicate a case of parallel evolution between humans and at least one nonhuman animal species.

Methods

This research was approved by the Leiden Committee for Animal Experimentation (application numbers 12214 and 12215).

Zebra Finches.

Subjects. Sixteen zebra finches [eight males, eight females, 202–482 d post hatching (dph)] from the breeding colony of Leiden University were used, equally divided between the two experiments. Six birds had been trained previously in a go/no-go paradigm but not in a comparable learning task, and the previous training had been with human speech sounds rather than song elements. Nevertheless, we factored this training as a potential effect in the analysis. Before the experiment, the zebra finches lived in single-sex groups on a 13.5-h/10.5-h light/dark schedule at 20–22 °C. Food, water, grit, and cuttlebone were available ad libitum.

Apparatus. All experiments were conducted in an operant conditioning cage (zebra finches: 70 cm long × 30 cm wide × 45 cm high; budgerigars: 70 cm long × 60 cm wide × 60 cm high). Each operant cage was in a separate sound-attenuated chamber and was illuminated by a fluorescent tube that emitted a daylight spectrum on a 13.5-h/10.5-h light/dark schedule. A speaker (Vifa 10BGS119/8) was located 1 m above the center of the cage. The cage walls were made from wire mesh except for the plywood back wall which supported two pecking keys with LED lights. A food hatch, easily accessible to the birds, was located between these two keys. Pecking the left key (sensor 1) elicited a stimulus and illuminated the LED light of the key on the right (sensor 2). Depending on the sound, the bird had to peck sensor 2 (the go response) or withhold its response (the no-go response). A correct pecking response resulted in access to food for 10 s, and an incorrect peck led to 15 s of darkness.

Stimuli. The stimuli consisted of three sound items concatenated in triplets according to either an XYX or an XXY structure. One group of zebra finches received elements from natural zebra finch songs, which were ramped (3 ms) and rms (0.1) equalized in PRAAT (version 5356, freeware available at www.praat.org). The other group received artificially created sounds, such as a clap, a trumpet, white noise, or pure tones, also ramped and rms equalized. The frequency of these sounds was modified so that the peak frequencies fell within the hearing range of the zebra finches. Durations were adjusted to be in the same range as the zebra finch song elements. Triplets were created from either three zebra finch song elements or three artificial sounds, with 40 ms of silence between the sound items and 50 ms silence at the beginning and the end of the triplet. For each bird, 10 triplets were created for the training

phase; five of these triplets followed the XYX structure, and five triplets followed the XXY structure (Fig. S1 and Table S1). The test triplets were created in a fashion similar to the training triplets but consisted of new combinations of the elements and also novel elements not heard before (Table S2). We created six different types of test stimuli, which were presented to the birds in random order. Details of the composition of the test stimuli are provided in *SI Test Stimuli*.

Procedure. Before the experimental training phase, each bird was conditioned to become familiar with the go/no-go paradigm, using a conspecific song as the go stimulus and a pure tone as the no-go stimulus. When the birds reached our standard discrimination criterion of more than 75% correct responses to the go stimuli and fewer than 25% incorrect responses to the no-go stimuli on two consecutive days, they proceeded to the training phase. In the training phase all birds received five different go triplets and five no-go triplets (Table S1). For one-half of the birds, the triplets with an XYX structure were the go triplets; for the other birds the triplets with an XXY structure were the go triplets. When the birds reached our standard discrimination criterion for the five stimuli on average for three consecutive days, they were subjected to an accustoming phase before the test phase started. In this accustoming phase all stimuli occurred both with and without feedback at an 80–20% ratio. When the birds' performance returned to the criterion level (usually within 1 or 2 d), they proceeded to the test phase. During the test phase a peck on sensor 1 was followed by a training triplet in 80% of the cases, and the subsequent behavior of the bird was reinforced. In 20% of the cases the bird heard a test triplet after pecking sensor 1. In these cases the response of the subject was not reinforced. The test phase lasted until each test triplet appeared 40 times. All test triplets were mixed at random with the training triplets.

Analyses. The analyses were conducted on an individual level as well as on a group level. First, we calculated a test score for each bird for each test. This test score was calculated as the number of correct responses to the test triplets structured like the go training triplets minus the incorrect responses to the test triplets structured like the no-go training triplets consisting of the same elements (e.g., DCD versus DDC): test score = response to go triplet – response to no-go triplet. Because all birds were tested with 40 go and 40 no-go triplets for every test condition, their test scores could range from +40 to –40, with +40 being perfect discrimination and 0 being performance at chance level. The individual analyses were done with a binomial test with a Holm correction, in which this test score was measured against a binomial distribution with a success probability of 0.5. When the individual test score was within the 95% confidence interval of the binomial distribution, we report this result as having $P > 0.05$. The group analyses were done with a linear mixed model, based on the test scores. We tested for an effect of sex and go-item structure (XYX or XXY). To analyze the difference in response per test on a group level, we performed a paired Wilcoxon signed rank test between the number of responses to the test stimuli with the go structure and the number of responses to the test stimuli with the no-go structure. We examined whether there was a systematic change in the test scores over tests 2–5 using Kendall's τ_b test.

Budgerigars.

Subjects. Six budgerigars (two males, four females, 263–389 dph) were used in both the mixed test and the transfer experiments. They came from different breeders in the Netherlands and were individually housed on a 13.5-h/10.5-h light-dark schedule at 20–22 °C before the experiment. Food, water, grit, and cuttlebone were available ad libitum.

Stimuli. The mixed test was conducted with the same zebra finch song stimuli in the same configurations used for the zebra finches. However, we extended the pauses between consecutive elements to 100 ms, because a pilot experiment suggested that the budgerigars found it harder to discriminate the rapid succession of the zebra finch song elements.

Training stimuli for the transfer experiment were constructed from the zebra finch song elements heard by the budgerigars in the first experiment. With these eight elements we created a balanced set of eight XYX and eight XXY triplets (Table S3). Four new types of zebra finch song elements were used to create 12 XYX and 12 XXY stimuli for the second training phase (Table S4). These new elements had not been heard previously and were the same for all budgerigars.

Procedure. The mixed test was conducted in an identical fashion to the tests with the zebra finches. The procedure of the transfer test was as follows. Before the start of the training (between 203 and 404 d after the end of the previous experiment), the budgerigars were again conditioned in the go/no-go set-up. A warbled song from a budgerigar unknown to the subject birds served as the go stimulus, and a pure tone served as the no-go stimulus. When the birds reached the standard learning criterion on three consecutive days, they proceeded to the first training phase in which the birds were trained to discriminate between XYX and XXY triplets. Each individual bird received the same go-structure and reinforcement as during the previous experiment. This phase lasted until each individual bird reached the standard criterion for three consecutive days. The subject was next immediately transferred to a second training phase. In this second phase, the budgerigars were presented with 12 go and 12 no-go triplets, each of which consisted of novel elements. Reinforcement in this second training phase was identical to the first training phase of the experiment: food was available after a correct response and the lights switched off after an incorrect response. After 2,000 trials in the second training phase, the birds were returned to their home cages, regardless of their performance in this phase.

Analysis. The results from the mixed test were analyzed in a similar fashion as the zebra finch results. The results from the transfer test were calculated as discrimination ratios (correct go responses/all go responses). These ratios were analyzed for deviations from chance level with a generalized linear mixed model. Because the birds received reinforcement during both the first and the second training phase of the transfer test, only the data from the first five sets of trials after the transfer were used for the analysis.

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