Starlings recognize simple dependency patterns

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Long-distance dependencies between elements are an important aspect of human language. There is some experimental evidence that animals, including songbirds, are capable of learning to recognize and generalize dependency patterns in nonlinguistic auditory or visual sequences. Here we present the results of an experiment following up on the important work of Gentner et al. (2006) and Abe & Watanabe (2011), who determined that songbirds were capable of learning to recognize some types of center-embedded patterns in auditory sequences. We tested the ability of three starlings to learn to recognize and generalize another type of simple center-embedded pattern, of the form A-B-A, and we report on one bird's successful performance. These results, like those of previous experiments, suggest that the ability of animals to learn particular dependency patterns shows individual variation.

1. Introduction: Sequence learning by animals and its significance

One of the major debates in language evolution has centered around the question of whether particular aspects of the language faculty, such as long-distance dependencies, are unique to human language and cognition. This question of uniqueness may be addressed by testing the ability of animals to recognize analogous patterns in nonlinguistic sequences (Fitch & Friederici 2012).

Long-distance dependencies are of particular interest because they are a prerequisite to recursive center-embedding, i.e. the nesting of one dependency within another of the same type (Rogers & Pullum 2006, Rohrmeier et al. 2015), and therefore are related to the vital and controversial issue of recursion (Hauser et al. 2002). Dependencies in language, e.g. between a subject and a verb, are determined by meaning, but in nonlinguistic sequences, a dependency may consist of two identical or similar elements (Gebhart et al. 2009, Dedhe et al. 2023), or a pair of elements that consistently co-occur (de Vries 2008). Two simple forms of nonlinguistic sequences with long-distance dependencies are the form AⁿBⁿ (e.g. AABB, AAABBB), in which the A and B elements can be analyzed as forming embedded "bracket" pairs, and the form *ABA*, in which the A's are matched elements and the B a string of one or more different intervening elements. Some animals, particularly passerine birds, have demonstrated the ability to recognize and generalize auditory sequences of these types, and even more complex sequences with multiple center-embedded dependencies. This

paper reports on a new experiment concerning the ability of European starlings to recognize and generalize an auditory pattern of the form ABA. Starlings are of particular interest because of their complex songs and vocal learning abilities, and are excellent problem solvers (Audet et al. 2023).

Previous experiments have demonstrated the ability of starlings and other songbirds, as well as nonhuman primates (Jiang et al. 2018, Ferrigno et al. 2020), to recognize dependency patterns, though the interpretation of the results is not always clear. Gentner et al. (2006) found that some European starlings could learn to distinguish sequences of the form AⁿBⁿ from strings not matching the pattern (e.g. ABAB, AABBB). However, it is uncertain whether such sequences are most accurately analyzed as exhibiting center-embedded dependencies between A and B elements (Rogers and Pullum 2011: 339); they may also be recognized by a count-and-match process. Therefore, it remains uncertain whether these results actually demonstrate an ability to track dependencies between elements. Similarly, Van Heijningen et al. (2009) showed that zebra finches could learn to recognize AⁿBⁿ patterns in sequences of motifs from their songs. However, most of their birds did not succeed at this task, and further probe tests suggested that the one bird that succeeded was using simpler processes to solve the task, e.g. the presence of adjacent identical motifs.

In another follow-up to Gentner et al. (2006), Abe and Watanabe (2011) demonstrated that Bengalese finches were able to learn both simple dependency patterns and more complex center-embedded patterns. In their first experiment, the finches were familiarized with auditory sequences that contained a single long-distance dependency. In a second experiment, the birds were successfully trained to recognize patterns with multiple center-embedded dependencies, e.g. ABCBA, ABCDCBA. The birds learned to recognize these sequence types consistently, distinguish them from other sequence types, and generalize to new sequences following the same patterns. However, Beckers et al. (2012) argued that the finches could have accomplished the task in the second experiment by memorizing substrings, rather than generalizing the abstract center-embedded pattern. Still, the results of Abe & Watanabe's (2011) prior experiment, in which birds recognized long-distance dependencies, are robust and intriguing, since these single dependencies are a necessary precondition for deeper center-embedding patterns. Here, we report on an auditory task with starlings which tested their ability to recognize A-B-A patterns.

2. The current experiment

The present experiment attempted to test whether European starlings could learn to distinguish simple dependency patterns of the A-B-A form from patterns with the same elements in a different order (A-A-B). These patterns unambiguously display center-embedding, i.e. a B element between two matching A's, but they may also be amenable to other forms of pattern recognition, e.g. the presence or absence of adjacent identical elements. Once a bird had learned to classify multiple sequences following this pattern, we used probe stimuli to determine whether it was truly generalizing the A-B-A pattern or using other cues.

2.1. Methods

2.1.1. Subjects and stimuli

Data were collected from three wild-caught adult starlings. All stimuli were artificially concatenated sequences of 3 or 4 motifs from recorded starling songs (as in Gentner et al. 2006), each 800-1000ms long, separated by 200ms silences.

In the first phase of the task, the bird was trained to distinguish two specific sequences of motifs: A-B-A and A-A-B, i.e. a sequence with a non-adjacent dependency between the two identical elements, and one in which those elements were adjacent. Subsequent phases added new training strings; the types of stimuli used at each phase, and the subjects' performance, are detailed below.

2.1.2. Experimental setup and trials

Each bird was housed individually in an acoustically isolated operant conditioning chamber, with a feeding apparatus activated by performing trials. The bird was able to initiate trials at any time by inserting its beak into the central peck-port. After doing this, the bird heard a stimulus and was required to respond within a two-second window. The stimuli were coded as either go-right or go-left, and pecking the correct port for a given stimulus type resulted in a food reward. Test trials added in the testing phases (see Section 2.2) were initiated the same way as normal trials, i.e. by the bird pecking the central port. These trials employed random reinforcement; whether the bird's response was correct or incorrect, a reward would be given 50% of the time. A session (used to measure the birds' performance over time) was defined as a block of 100 normal trials, plus 100 test trials in the testing phases; all stimuli were presented in random order. Performance in a session was measured as percentage of correct responses on all normal trials, disregarding trials in which the bird did not respond within two seconds. Performance on test trials was analyzed separately and compared to normal trial performance, as discussed below.

2.2. Results by phase

2.2.1 Training 1-2: ABA and AAB strings

In the first training phase (Training 1), the bird was trained to distinguish two strings using the trial structure detailed above: ABA (go left) and AAB (go right). Once the bird was performing stably above chance (10 consecutive sessions above 65%) on these two strings, the additional sequences BAB and BBA were introduced to the set of stimuli (Training 2). Once performance was stable above chance (20 sessions above 65%) on all four strings, the first testing phase began. Table 1 lists the training and testing phases, and the strings introduced in each phase. The strings introduced in subsequent phases, and the bird's performance, are described in following subsections.

Two of the three subjects, Birds 1 and 3, were not successful on the first phase of the task; i.e. performance on the first four trained strings was not significantly greater than chance after 300 sessions. However, Bird 2 displayed above-chance performance at 200 sessions and was therefore advanced to the testing phases. From here on we will track the performance of Bird 2.

Table 1: Training and test stimuli for each phase of task

Phase	Left	Right
Training 1	ABA	AAB
Training 2	ABA BAB	AAB BBA
Testing 1	ABA BAB + CDC DCD	AAB BBA + CCD DDC
Training 3	ABA BAB CDC DCD	AAB BBA CCD DDC
Testing 2	ABA BAB CDC DCD + EFE FEF	AAB BBA CCD DDC + EEF FFE
Training 4	ABA BAB CDC DCD EFE FEF	AAB BBA CCD DDC EEF FFE
Testing 3	ABA BAB CDC DCD EFE FEF + $ABBA\ CBBC$	AAB BBA CCD DDC EEF FFE + ABBC CBBA
Testing 4	ABA BAB CDC DCD EFE FEF + AAA BBB CCC DDD EEE FFF	AAB BBA CCD DDC EEF FFE
Testing 5	ABA BAB CDC DCD EFE FEF	AAB BBA CCD DDC EEF FFE + ABC DEF

2.2.2 Testing 1-2 and Training 3-4: Generalization of the ABA/AAB pattern

In testing phases 1 and 2, two successive sets of test strings were introduced which followed the same ABA/AAB pattern but with new motifs (see Table 1). In each test phase, the new test strings were randomly reinforced (as defined in Section 2.1.2), in order to evaluate whether the bird was generalizing the pattern it had learned to new strings. In the following training phases (3 and 4), the test strings for the prior test phase were reinforced. When performance on all training strings was stably above chance (at least 10 sessions above 65%), the next test phase commenced, and so on. In contrast to the 200 sessions it took to learn the original pattern, Bird 2 immediately generalized to new strings within the ABA/AAB paradigm, i.e. in each test stage, performance on the introduced test strings was significantly above chance (i.e. 65% or higher for 10 sessions) and did not differ significantly from performance on previously learned strings (Testing 1: t(52) = 1.36, p = 0.178; Testing 2: t(9) = 0.861, t(9) = 0.41. Once the bird's performance was stable on all these strings, we moved on to testing two

hypotheses for which criteria it was using. While persistent correct performance might be taken to indicate learning and generalization of a simple ABA embedded pattern, this is not the only possibility. Correct performance on the 12 learned strings could be accounted for by an alternative rule: recognition of strings containing an adjacent pair of identical motifs (e.g. BB). We tested these two hypotheses with three sets of test strings that fulfilled both criteria, or neither, in order to infer what criterion the bird was using to classify strings.

2.2.3. Testing 3: Disambiguating the learned pattern

This stage was intended to disambiguate which of two strategies the bird might have successfully used to classify the twelve trained strings, using four test strings that all contained two adjacent identical motifs: ABBA, CBBC, ABBC, and CBBA. Consistently classifying ABBA and CBBC as go-left, and the others as go-right, would mean that the bird was generalizing the first/last match rule. Conversely, going right on all strings containing a doubled motif would produce a pattern of largely "correct" performance on non-match strings and poor performance on the others; e.g. ABBA would be classified incorrectly as go-right while ABBC would be correctly placed in the same category. Performance on these stimuli, however, was around chance and did not consistently show either pattern. The bird's performance on these four strings was significantly lower than performance on the twelve learned strings at the time (t(49) = 2.37, p = 0.02). Neither of the hypothesized patterns (go left for first-last match, or go right for two adjacent identical motifs) clearly emerged for individual strings. The subsequent phases attempted to clarify further which strategy the bird was using.

2.2.4. Testing 4: Strings that fit both criteria

The intention of Testing 4 was to further clarify whether the bird was classifying strings by one of the two alternative strategies discussed previously. This was performed with strings that fit both criteria: three adjacent identical motifs, e.g. AAA, BBB. If the bird was using the first-last match criterion, AAA-type strings would be classified as go-left; if its criterion was two adjacent identical motifs, they would be classified as go-right. No significant difference was observed between performance on AAA-type strings and the learned ABA/AAB stimuli (t(18) = 0.17, p = .86). Over 10 sessions with these test strings, the bird tended toward going left at above chance rates, suggesting it was in fact generalizing the intended pattern.

2.2.4. Testing 5: Strings that fit neither criterion

While the bird's classification of AAA-type strings suggested it was successfully generalizing the first-last-match pattern, we probed it further using strings that exemplified neither pattern: strings like ABC with no repeat elements. If the bird was classifying strings based on first-last match, it would be expected to

categorize these strings as not representing this pattern (i.e. go right); on the other hand, if it was classifying strings based on adjacent identical elements, it would place them in the same category as the first-last match strings (i.e. left). In this case, the bird preferred to go left on these strings (t (19) = 6.7, p < 0.001). This suggests it may have been classifying them based on the absence of two adjacent identical elements, a feature for which it had been previously trained to go right. Alternatively, it may have been uncertain how to respond to these strings, as it had not previously heard any stimuli with no repeated elements.

2.3. Discussion and conclusion

Our results with the successful bird contribute to the evidence that avians can learn to recognize dependency patterns in auditory sequences. Once this bird learned the pattern exemplified by the initial four sequences (ABA / BAB vs. AAB / BBA), it immediately generalized to new sequences exemplifying the same patterns with different elements, demonstrating that it had not merely memorized the sequences it was first trained on but learned the relevant pattern.

However, the results of the later test phases are not entirely clear as to whether the successful bird was relying on a strategy involving dependencies rather than a more "local" strategy, i.e. listening for adjacent identical motifs. In the case of the strings ABBA and CBBC, and their non-match counterparts, the bird's performance did not show a very clear tendency toward classifying strings based either on two adjacent identical motifs, or on a match between first and last motif. The results from AAA-type strings were clear; the bird classified these as go-left, implying it had generalized the first-last pattern rather than the two adjacent motifs pattern, although they could also have been classified as go-right based on the presence of two adjacent identical motifs. Strings with three different motifs, e.g. ABC, were predominantly classified as go-left, suggesting a tendency to go right on strings with two adjacent identical motifs, and left otherwise. The bird may have been attentive to both patterns as criteria for classifying strings because it had been very extensively trained to distinguish ABA and AAB patterns, and may have had difficulty with the ABC-type strings because it had not previously been exposed to stimuli with no repeats. In general, however, the bird's responses on test strings suggest a correct generalization of the first-last-match pattern.

As in previous animal sequence-learning studies (e.g. Gentner et al. 2006, Van Heijningen et al. 2009, Jiang et al. 2018, Ferrigno et al. 2020, Liao et al. 2022), not all of the animal participants were equally successful at the basic task. In this case only one bird learned the pattern. Two birds out of the three initially tested did not achieve consistently higher than chance performance on the first four strings (ABA/BAB and AAB/BBA) after around 300 sessions. The bird that did succeed learned to generalize this pattern after extensive training. These results suggest that among starlings, as among other nonhuman species, ability on center-embedding pattern recognition tasks can vary greatly across individuals. This may reflect different aptitudes for particular patterns, or other cognitive factors.

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