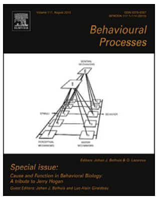
Behavioural Processes 117 (2015) 29–34

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Zebra finches can use positional and transitional cues to distinguish vocal element strings

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ARTICLE INFO

Article history:
Available online 11 September 2014

Keywords:
Chaining
Positional learning
Sequential learning
Song
Transitional learning
Zebra finch

ABSTRACT

Learning sequences is of great importance to humans and non-human animals. Many motor and mental actions, such as singing in birds and speech processing in humans, rely on sequential learning. At least two mechanisms are considered to be involved in such learning. The chaining theory proposes that learning of sequences relies on memorizing the transitions between adjacent items, while the positional theory suggests that learners encode the items according to their ordinal position in the sequence. Positional learning is assumed to dominate sequential learning. However, human infants exposed to a string of speech sounds can learn transitional (chaining) cues. So far, it is not clear whether birds, an increasingly important model for examining vocal processing, can do this. In this study we use a Go–Nogo design to examine whether zebra finches can use transitional cues to distinguish artificially constructed strings of song elements. Zebra finches were trained with sequences differing in transitional and positional information and next tested with novel strings sharing positional and transitional similarities with the training strings. The results show that they can attend to both transitional and positional cues and that their sequential coding strategies can be biased toward transitional cues depending on the learning context.

This article is part of a Special Issue entitled: In Honor of Jerry Hogan.

1. Introduction

Sequential learning, i.e. learning about the order in which events occur, is of prominent importance in the lives of humans. It enables activities ranging from the production of action sequences to the processing of language. Different theories have been proposed with respect to the cognitive mechanisms involved in sequence learning. One of these, the 'chaining' theory, assumes that a sequence of acts or items is remembered by pair-wise association of adjacent elements of a sequence (Henson, 1998): the sequence ABCDE is remembered by A triggering the representation of B, which in turn triggers C, etc. An alternative theory is that elements are encoded by their ordinal position in relation to the beginning or the end of the sequences: ABCDE is remembered by linking element A to position 1, element B to position 2, etc. (Henson, 1998). Over the years, most evidence is in favor of the positional theory. For example, most chaining models encounter difficulties in dealing with repeated items where two or more responses share the same cue (Henson, 1998, 2001). They also have a problem in handling erroneous responses, which leads to a cascade of subsequent errors (Henson, 1998, 2001). In contrast, the positional theory does not have problems with repeated items nor with erroneous responses. Serial recall experiments in humans have provided support for positional coding (Chiara Fastame et al., 2003; Endress et al., 2009; Henson, 2001), e.g. the phenomenon of serial order intrusion errors, in which an item of one string gets inserted in another one. Such insertions tend to occur at the same ordinal position in the new string as the position they occupied in the original string, suggesting the coding of the item's position (Chiara Fastame et al., 2003).

Chaining and positional theories also have a long history in studies of sequence learning in non-human animals (Comins and Gentner, 2010). Animals can also memorize a sequence of events and reproduce ordered lists of artificial items (Orlov et al., 2000, 2006; Terrace, 1987, 1993; Terrace et al., 2003). Again, the positional theory has gained considerable support from studies on species ranging from apes to birds (Comins and Gentner, 2010; Conway and Christiansen, 2001; Endress et al., 2010; Orlov et al., 2000, 2006; Scarf and Colombo, 2010; Terrace et al., 2003). For instance, starlings could learn to differentiate a string with vocal

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http://dx.doi.org/10.1016/j.beproc.2014.09.004
0376-6357/

elements in fixed positions from randomly ordered strings. However, when absolute position cues were removed but sequential information left intact, recognition failed (Comins and Gentner, 2010). This finding is of relevance in the context of comparative research on a particular type of sequence learning, in which vocal elements follow each other with different transitional probabilities. When 8-month-old human infants are exposed to a string of speech syllables consisting of combinations of frequently co-occurring elements, for which there is no cue to their relative position other than the transitional probability they use this information to identify trisyllabic nonsense ‘words’ from such strings (Saffran et al., 1996). Hence, in this context young infants are capable of statistical learning, a chaining-like mechanism based on transitional probabilities, that may aid them in natural language learning (Conway and Christiansen, 2001). Cotton-top tamarins, tested in a similar design as human infants, also were sensitive to the transitional information in strings, suggesting that this mechanism may be domain-general and present in animals (Hauser et al., 2001, see also Kelly and Martin, 1994). This makes it of particular interest to know whether songbirds, which are excellent model species for comparative studies on vocal processing (Bolhuis and Everaert, 2013; ten Cate, 2014), are also able to distinguish strings based on transitional cues of the constituent items.

In this study, we trained zebra finches to discriminate between strings with identical numbers and types of items, but in which the position of, as well as the transitional probabilities between the items differ. Zebra finches are extensively studied as a comparative model for linguistic processing, ranging from studies on the molecular and neural mechanisms of vocal learning (Bolhuis et al., 2010), up to the processing of speech sounds (Ohms et al., 2010) and artificial grammar learning (van Heijningen et al., 2009, 2013). That zebra finches can learn sequences of song elements is well established in the context of song learning, where young birds copy songs from song tutors. They may do so by learning chunks of elements (ten Cate and Slater, 1991; Williams and Staples, 1992), but this observation provides no insight in the mechanism involved. A recent study (Lipkind et al., 2013) showed that zebra finches might copy element sequences by first concentrating on bigrams, which may indicate the use of a chaining-like mechanism during song learning. However, adult zebra finches can also learn to discriminate strings of elements in which an odd element is embedded either early or late in a series of identical elements (Verzijden et al., 2007) – a task that can be solved by positional learning, but not by chaining. So, such circumstantial evidence suggests that zebra finches can use both positional and chaining mechanisms to memorize element sequences, but thus far no study tested this explicitly.

In the current experiment, zebra finches could use both transitional and positional information to discriminate two strings consisting of song elements arranged in different patterns. Given that positional learning is the most likely strategy for sequential learning, we designed our experiments in such a way that solving the task by using transitional information would be encouraged. After a discrimination training on these strings, we tested the bird’s sequential coding strategies by giving probe tests with novel sequences that contained different degrees of chaining and positional information. The results show that zebra finches used both types of information.

2. Materials and methods

2.1. Subject and apparatus

Eight zebra finches (4 males and 4 females, age: 226 d ± 15 SEM) were individually housed in operant conditioning cages (70 cm × 30 cm × 45 cm) in sound attenuated chambers. The cages were made of wire mesh with a plywood back wall that contained a food hatch and two red pecking sensors. Each sensor contained a red LED that indicated the activated stage of the sensor. Five perches were mounted between the back and front side of the cage to enable hopping behavior. The sensors and the food hatch could be reached from the middle perch. The birds remained in the operant conditioning cages until they completed the training and tests. They were kept on a 10.5–13.5 dark–light schedule (similar to the dark–light condition of the breeding colony in which they were housed previously). Drinking water and cuttlebone were available ad libitum during the whole period of the experiments. The food intake was measured daily to keep track of a sufficient food intake. The study was conducted according to Association for the Study of Animal Behaviour guidelines on animal experimentation as well as to the Dutch law on animal experimentation, and approved by the Leiden University Committee for animal experimentation (DEC) (permit no. 12180).

Acoustic stimuli were delivered from a loudspeaker located above the cage and were calibrated to a pressure level of 70 dB. A custom-designed controller controlled the pecking sensors, food hatch, chamber light, auditory stimuli presentation and also registered the responses of a subject.

Table 1
Training and test stimuli in Experiment 1.

Experiment 1	Set A		Set B	
Training	Go	abcdefabefcdab	Nogo	abdfcedfabceab
Test	A1	abe**fc**dabcdefab	B1	abcedfce**ab**dfab
	A2	abe**fc**de**fabc**dab	B2	abcedfabdf**ce**ab

Letters indicate different song elements. Underlined: elements in identical positions to the Go-string; bold: elements in identical position to the Nogo string.

2.2. Stimuli

Stimuli were constructed from ramped and RMS equalized zebra finch song elements. Song elements were arranged in a linear way with 40 ms pause inserting in between two adjacent elements, which is comparable to the duration of pauses between elements in natural zebra finch songs. The duration of all stimuli was less than 1.6 s (see Fig. 1 for an example). Natural zebra finch songs consist of a series of song elements that may differ in type or order among different males (Zann and Bamford, 1996). There is no indication that single elements or element combinations carry specific meanings and hence these elements are suitable for constructing artificial strings. We selected six element types, based on optimal discriminability, from our zebra finch song database. To eliminate pseudo effects due to any arbitrary parameter of the song elements, the assignments of the element types were shuffled for each subject. For instance, a string ‘abcdef’ has different combinations of element types for different individuals.

Song elements were assigned to different ordinal positions to construct stimuli. Besides differences between the stimuli in the position of elements, the chaining regularities also differed between different sets of sequences. ‘Set A’ stimuli always contained ‘cd’ and ‘ef’ bigrams while ‘Set B’ stimuli always contained ‘df’ and ‘ce’ bigrams (Tables 1 and 3). In order to encourage the birds to take the full string structure into account when memorizing the strings, all training sequences started and ended with an ‘ab’ bigram. This made it more difficult to differentiate between the strings by just attending to the very first or the final elements of the strings.

2.3. Procedure

To familiarize the birds with the Go/Nogo task, they were first trained to discriminate a natural song (Go stimulus) from a pure