LIMITATIONS IN AVIAN PERCEPTION OF VOCAL SEQUENCES: IMPLICATIONS FOR LANGUAGE EVOLUTION

ADAM R. FISHBEIN[*1], NORA H. PRIOR[1], GREGORY F. BALL[1] and ROBERT J. DOOLING[1]

[*]Corresponding Author: afishbei@umd.edu

[1]Department of Psychology, Neuroscience and Cognitive Science Program, University of Maryland, College Park, USA

Birdsong and human speech have strong parallels: both consist of learned acoustic elements produced in sequences (Bolhuis, Okanoya, & Scharff, 2010; Doupe & Kuhl, 1999). In speech, sequences are fundamentally important in the perception of phonological and syntactic patterns. In birdsong, the production of sequences has been well-described, but the importance of these sequences in perception is uncertain or equivocal for most species. Here, we summarize the results of several studies which show limitations in avian perception of sequences and a greater importance of the acoustic details of individual elements. We also highlight greater sequence sensitivity in the budgerigar (Melopsittacus undulatus), a psittacine, compared to the zebra finch (Taeniopygia guttata), a songbird, illustrating how a careful species comparison might be useful for studying human language evolution.

In our studies, birds were trained through operant conditioning to perform a psychophysical discrimination task. The bird pecks a key (the observation key) while listening to a repeating sound (the background stimulus) in order to elicit either a different sound (a target stimulus) or the same sound (a sham trial). If the bird pecks another key (the report key) when the target sound is presented, then it is rewarded with millet from a food hopper.

In study 1, three songbird species (zebra finch, canary, and Bengalese finch) were tested along with a psittacine (budgerigar) (Lawson, Fishbein, Prior, Dooling, & Ball, 2018). In this study, we used a zebra finch song motif (consisting of 3-8 elements or "syllables") as the background, while the targets involved either song elements temporally reversed or song elements shuffled out of their natural sequence. The results showed that all the species tested were very sensitive

to reversals of individual elements, but that budgerigars were much better than the songbirds at hearing changes to sequence. The zebra finches' relative lack of sensitivity to the sequence of elements in conspecific motifs is surprising given that these birds learn to produce their song elements in a fixed sequence early in life and maintain the sequence throughout life.

Budgerigar song, called "warble," consists of a rambling, jazz-like structure. Previous work has shown that the birds are sensitive to violations in the sequential order of natural song (Tu & Dooling, 2012), but it is not clear what sort of rules they can use: (1) rules about the transitions between particular sounds or (2) rules about the abstract relationships among elements. In study 2, budgerigars were tested on their ability to discriminate changes to a sequential pattern of conspecific song elements, AAB, i.e. same-same-different. In experiment 1, budgerigars, unlike humans, primarily used transition rules to detect violations of the AAB pattern, rather than abstract structure. In experiment 2, the stimuli were presented so that transition rules were no longer reliable cues, and the birds showed the ability to use abstract structure but only of the first two elements.

During song bouts, zebra finches sing many renditions of their motifs, which have the same sequential structure but differ in fine-grained acoustic details. This dimension of their song has been largely overlooked by researchers, as the sequential structure of their song is more striking to casual human listeners and was assumed to be a salient song feature for zebra finches. In study 3, zebra finches were tested on their ability to discriminate the subtle acoustic differences that occur among renditions of the same song syllables by the same individual. We show that zebra finches are very sensitive to subtle acoustic variation in renditions of natural song motifs which is in striking contrast to their insensitivity to sequence changes in study 1.

Together these experiments highlight the limitations birds have in perceiving sequence information, which is in striking contrast to human language perception. Birdsong may be an architecturally different communication system than human language – where information in birdsong is primarily conveyed in the acoustic details of vocal elements with the sequential patterns of those elements having at best secondary importance. Yet, the species differences between zebra finches and budgerigars in sequence perception observed here and in other work (Spierings & Ten Cate, 2016) offer an important opportunity for comparative neurobiological studies. Explaining how budgerigar brains are better able to process acoustic sequences than songbird brains could provide clues as to why human brains are better adapted for sequence processing than those of other primates.

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