Review

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Sound sequences in birdsong: how much do birds really care?

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The complex and melodic nature of many birds' songs has raised interest in potential parallels between avian vocal sequences and human speech. The similarities between birdsong and speech in production and learning are well established, but surprisingly little is known about how birds perceive song sequences. One popular laboratory songbird, the zebra finch (*Taeniopygia guttata*), has recently attracted attention as an avian model for human speech, in part because the male learns to produce the individual elements in its song motif in a fixed sequence. But psychoacoustic evidence shows that adult zebra finches are relatively insensitive to the sequential features of song syllables. Instead, zebra finches and other birds seem to be exquisitely sensitive to the acoustic details of individual syllables to a degree that is beyond human hearing capacity. Based on these findings, we present a finite-state model of zebra finch perception of song syllable sequences and discuss the rich informational capacity of their vocal system. Furthermore, we highlight the abilities of budgerigars (*Melopsittacus undulatus*), a parrot species, to hear sequential features better than zebra finches and suggest that neurophysiological investigations comparing these species could prove fruitful for uncovering neural mechanisms for auditory sequence perception in human speech.

This article is part of the theme issue ‘What can animal communication teach us about human language?’

1. Introduction: birdsong as a model for human speech and language

Musings about the parallels between birdsong and human speech can be traced back thousands of years. Aristotle (350 BCE) in his ‘*History of animals*’, remarked on the ability of young songbirds to modify and improve their songs through instruction from their parents [1]. Modern research has confirmed that, like humans, some birds (namely, songbirds, parrots and hummingbirds) learn complex vocal patterns early in life, often during a sensitive period, and then produce species-specific vocal repertoires throughout adulthood [2–6]. There is also great diversity in the acoustic characteristics of birdsong across species and considerable variation in when and how birds learn their songs, providing a wealth of opportunity for rich comparative research [4,7,8]. At one extreme, there are some avian species, like the zebra finch (*Taeniopygia guttata*), that learn one song motif in the few weeks to a month or so after hatching and produce song consisting of repetitions of that motif without much variation throughout adulthood [9]. At the other extreme, there are species, such as the budgerigar (*Melopsittacus undulatus*), a psittacine, and the European starling (*Sturnus vulgaris*), a songbird, and many others that learn song in the sensitive period for song learning, but retain a high degree of vocal plasticity in learning and production throughout life, paralleling the open-endedness of vocal learning in humans [10–12]. Comparative research on vocal learning birds has led to the

discovery of convergent neural mechanisms controlling vocal learning and production in birds and humans [2,5,13–16] and a detailed understanding of the actions of neurotransmitters and hormonal modulators on vocal production and the underlying circuitry [17–20].

Recently, birdsong and its melodic patterns have attracted the interdisciplinary interest of biologists, psychologists and linguists probing whether avian vocal sequences rival the complexity of human language. The issue falls within the general problem of processing serial information, which has a long history. Lashley [21] was one of the first to ask how the brain represents serial behaviours, like birdsong or human speech. Associative chain theories posited that these behaviours are the result of each action or impulse simply leading to another. Lashley argued that associative chains are inadequate because serial behaviours are not organized according to the intrinsic associations between movements. For instance, the words 'right' and 'tire' are produced by the same vocal gestures but in reverse order. If movements were locked in associative chains, then only one of those words could be produced. From a perception perspective, the inadequacy of chains can be seen in the interpretation of a word like 'inexplicably' which must be processed according to its hierarchical nested structure [[in-[explic-able]]-ly], since [explic-able] must be put together before the preceding syllable [in-] can modify it [22]. Birdsong does not appear to have hierarchical structure, as Chomsky & Berwick argue [23], since there are no cases of birds embedding song motifs or phrases inside other song motifs or phrases, as we do in language. For instance, the sentence [The starling [the cats want] was tired] contains the phrase [the cats want] embedded within the phrase [The starling was tired] [24]. Rather, the dependences among elements in birdsong can be described by linear rather than hierarchical relationships, which may mean that associative chain theories are indeed sufficient for capturing how birds perceive sequences. While this suggests that birdsong is probably not a good model for human syntax perception, linear order is nevertheless important for human phonological processing and word recognition. Thus, avian perception of vocal sequences could still serve as a useful model for human speech perception [25–27].

Surprisingly, results from field studies are equivocal on how meaningful or salient sequential features in birdsong are for adult birds. A number of species vary sequential patterns of both the elements within a song and the song types within a song bout based on social context. Male house finches, for instance, increase the number of transitions from introductory syllables to main song syllables when counter-singing with other males [28]. Playback studies also show that some species are sensitive to manipulations of sequence. Swamp sparrows, for example, differentially respond when notes in their trills are rearranged [29]. A sequential rule of alternating pitch is important for species recognition in European robins [30]. California thrashers respond differently when their song phrases are presented in random sequences rather than naturally ordered sequences, though this result could be due to an absence of repeated phrases over short time scales in the random playback [31]. By contrast, there are other species for which sequence in song does not seem to matter. For instance, violating a sequential regularity of paired notes in the song of indigo buntings does not affect species recognition [30]. In the overwhelming majority of species, sensitivity to sequential features in song has not been tested in field studies and

most studies have not exhaustively explored the sequential rules birds could be using.

Field studies have produced more evidence for the importance of sequence in the perception of calls than in song. The calls of most songbird species are simpler in structure than song, are often innate (but see [32,33] for review and discussion of call learning), and serve a diverse set of functions including signalling food, maintaining contact and coordinating flight [33,34]. Recent playback studies have shown that differences in call sequence elicit different behavioural responses in the Japanese great tit and the southern pied babbler [35,36]. For example, Japanese great tits scan the surroundings and approach in response to calls ordered ABC-D, i.e. alarm calls followed by a recruitment call, but not to ones ordered D-ABC [35]. The birds are sensitive to this sequential rule even when exposed to synthetic playback where D is replaced with a heterospecific call of similar function [37]. While the researchers claim that this constitutes a form of compositional syntax (see Suzuki *et al.* [38] in this issue for discussion), Bolhuis *et al.* [39] argue that this system involves compound meanings rather than human language-like compositionality. Either way, the birds show sensitivity to some sequential information—the transition from ABC to D. But in the large majority of species, the importance of sequence in calls is uncertain or equivocal. In yellow-naped Amazon parrots, for instance, violations of normal sequential patterns in the duet calls of mated pairs only have minor behavioural effects [40]. In Carolina chickadees, interestingly, birds respond differently when typical sequences of their calls are violated in the autumn/winter but not in the spring [41]. In contrast to sequential properties, there is strong evidence that birds use the acoustic features of individual calls to extract important biological information [42,43].

Until recently, the sensitivity to complex acoustic sequences in birds has not been tested rigorously in the laboratory except for the dramatic effects of deafening on vocal learning and the subsequent production and maintenance of species-specific vocal behaviour in adulthood [11,44,45]. This gap in knowledge has occurred despite the fact that we know how important specialized perceptual sensitivities are for human speech learning and production [46]. In part, this is because auditory perception is inherently more difficult to study in birds compared with recording and analysing vocalizations. As the human and avian auditory systems are quite different in many respects, one can worry whether complex sounds are perceived differently by birds and humans [47–49]. Yet, there are a wealth of data from laboratory studies showing very similar perceptual experiences for birds and humans in perceiving pitch cues, many temporal cues and even speech sounds [50–53]. Since researchers in the laboratory have only recently begun exploring how birds listen to sequences (for review, see [54]), it is not yet clear how the melodies in birdsong that are salient to us sound to the birds.

The zebra finch, in particular, has become the favourite for tackling questions in the laboratory about parallels between birdsong communication and human language. Zebra finches are useful subjects because they are inexpensive and easy to house and breed in captivity. They also have an extremely short period of vocal development [9,55–57]. Importantly, each male learns to produce a fixed sequence of syllables within a motif that remains largely invariant throughout adulthood, suggesting this sequence might

convey biologically important information. Studies of song development also show that juvenile zebra finches build a full song sequence over time by learning the pairwise transitions between elements [58,59]. This is *prima facie* evidence that, at a basic level early in life, these birds perceive sequential information from a series of complex sounds and have the motor and sensory machinery to maintain a precise vocal sequence throughout adulthood [9,55,60]. Zebra finch song, in contrast to the whistled song of many songbirds [2], is also strongly harmonic—reminiscent of the formant quality of human speech, providing another rationale for comparative study. There are now enough comparative laboratory experiments on the perception of complex acoustic sequences in zebra finches that a much clearer picture is emerging of potential parallels with human speech perception. Surprisingly, the recent results raise the question of whether the apparent parallels we so commonly observe between human speech and melodic birdsong have led to misconceptions about what birds are really listening to in their songs.

2. Comparative perception of differences in sound sequences

In testing humans on the acoustic sequences of speech, we might ask whether one sequence of five to six speech syllables or words is different from another sequence presented seconds to minutes later in which the same sounds are presented but in a different order [61,62]. For humans, solving this task engages a number of higher-order perceptual and cognitive mechanisms normally used in language processing, including segmentation of the sounds, comparing them with representations stored in short-term and long-term memory, accessing meanings associated with them and representing the transitions and structural relationships among the speech sounds [63]. Recent laboratory investigations of how zebra finches perceive sequences of their vocalizations are modelled after this kind of classification task. For instance, Braaten *et al.* [64] trained both adult and juvenile zebra finches to ‘Go’ (i.e. respond) to a normal conspecific song motif and to ‘NoGo’ (i.e. not respond) to a reversed version of the song motif. After learning to classify sounds in this way, the birds were tested with probe stimuli that were either order-reversed (i.e. syllables presented in a reversed order) or syllable-reversed (i.e. syllables all reversed but presented in the correct order). Both juveniles and adults responded predominantly with a ‘Go’ response to the order-reversed motif, meaning that song with the syllables produced in the order-reversed sequence still sounded more like a normal song than expected. By contrast, song motifs with each syllable reversed, but produced in the correct sequence, were responded to much less frequently. In other words, it was changes to syllable structure, but not syllable sequence, that caused a salient change from the normal song motif. Interestingly, with considerably more training, the birds did learn to withhold responses to order-reversed motifs, showing that it was possible to acquire sensitivity to syllable sequence, although the learning was slower than for syllable reversals.

A more recent study, by Spierings & ten Cate [65], used an artificial grammar learning approach to ask how zebra finches classify sequences of syllables. After training, the birds could successfully categorize zebra finch syllables as fitting into an *XXY* or *XXY* structure. But when probed with structurally identical strings consisting of familiar or novel items, the

birds could only categorize test items correctly to the degree that they shared sequential features with the training strings, i.e. shared bigrams or positional cues [66]. This means that the zebra finches were sensitive to some sequential information through explicit training in the classification paradigm, but that they did not learn the abstract sequential relationships among the sounds. Thus, the birds do not exhibit anything like the human capacity to process hierarchically structured sequences [67].

But this does not mean that zebra finches do not have sensitivity to linear sequences of similar complexity to those in human speech. Some phonological patterns in human language involve dependencies among elements that are not immediately adjacent [68]. A study showed that, after progressive training, zebra finches could learn non-adjacent dependencies between song elements, i.e. that a sequence starting with A must end with B [69]. Other recent work testing sequence perception paralleling human speech has shown some sensitivity in zebra finches to prosodic cues, affixation-like patterns, rhythmic patterns and the acoustic context of syllables [70–73]. For instance, Knowles *et al.* [73] showed that zebra finches can differentiate song sequences similarly to the way we perceive competing words, distinguishing between sequences that share an affix like ‘captain’ and ‘captive’ based on when the sounds start to diverge (i.e. after the shared prefix ‘cap’). But taken together, the overall impression from these studies is that, even when using their own species-specific vocalizations, adult zebra finches are extremely limited in perceiving sequential features.

One possible explanation for the difference between zebra finches and humans in sequence perception is that the classification tasks above were perhaps too difficult for animals. In a classification task, subjects must form long-term memory representations of ‘Go’ sounds and compare them with incoming stimuli. Perhaps a more straightforward discrimination test that focuses on simpler sensory processing would provide some insight into the nature of the performance differences between birds and humans. The rich history of research in human sensory psychology, especially that dealing with short- and long-term auditory memory [63,74], illustrates the value of approaches that minimize the role of higher-order mechanisms and instead focus on early sensory discrimination and echoic memory processes, which last for only a few seconds [75]. In the study reviewed below, we employ such an approach and ask the simple question: Can birds discriminate the difference between two acoustic sequences that occur in rapid succession? If birds and humans perform similarly on such a task, it would suggest that species differences at higher cognitive levels are responsible for species differences in classification tasks. If, on the other hand, birds and humans respond differently on this type of task, it would suggest that the failure of birds may be due to more elementary sensory processing mechanisms rather than the elaborate cognitive and memory processes involved in human speech perception.

3. Discrimination of syllable sequence versus syllable fine structure: a direct comparison

In the discrimination task described below, the bird is trained to peck a key while listening to a repeating background sound (i.e. the standard) in order to elicit either a different sound (i.e. a target trial) or the same sound (i.e. a sham

1. Peck observation (obs) key to change repeating background sound.

Short inter-stimulus interval allows focus on sensory discrimination.

2. Peck report (rep) key if change (i.e. presentation of the target) is detected.

Figure 1. Schematic of a discrimination task used to test sequence perception in zebra finches. The short interval between the sounds being discriminated means that the task relies more on elementary sensory processing than higher-order cognitive mechanisms. (Online version in colour.)

trial). The bird is trained to ‘Go’ (i.e. peck a different key) when it detects a difference between the background and the target sound, which are usually separated by only a few hundred milliseconds [76]. As the birds are trained to respond to a difference between two sounds rather than to classify two sounds, solving the task makes less of a demand on higher-order cognitive mechanisms. A simplified schematic of the trial events is shown in figure 1.

Lawson *et al.* [77] used this discrimination task to compare directly, within the same test session, a zebra finch’s ability to hear changes in syllable fine structure versus changes in syllable sequence in natural song motifs. In this test, the birds heard a background sound, consisting of repetitions of a natural zebra finch motif, and were tested on their ability to discriminate various targets that involved either syllable reversals or a shuffling of the syllable sequences within a 100-trial test session (figure 2). Zebra finches were exceedingly good at discriminating reversals of single syllables in a motif but quite poor at discriminating changes in syllable order in the motif. Canaries and Bengalese finches, whose species-specific vocalizations are quite different from those of zebra finches, were tested on the same zebra finch stimuli and performed like the zebra finches. Budgerigars, on the other hand, performed equally well on motifs with syllables shuffled and motifs with syllables reversed (figure 3).

These comparative findings are surprising in several ways. First, even in a cognitively simple task, zebra finches still show a remarkable insensitivity to changes in syllable order in their natural motifs. Recall that male zebra finches learn to produce these sequences from tutors with a high degree of precision early in life [9]. Second, two other songbird species, canaries and Bengalese finches, behave like zebra finches and are equally insensitive on this sequential task. Canaries are seasonal learners whose song exhibits long-range sequential regularities [78]. Bengalese finches, though closed-ended learners, have a song that is

Figure 2. Examples of stimuli used to test the relative salience of changes to syllable structure and syllable sequence in zebra finch song motifs. Modified from [77]. (Online version in colour.)

considerably more variable and sequentially complex than zebra finches [79]. In sum, all three songbirds, tested in exactly the same way, discriminate syllable reversals well but have trouble with changes in syllable sequences. Taken together, this provides a compelling case that syllable sequence may be unimportant for these songbirds, though further tests are needed using species-specific vocalizations. Interestingly, from casual listening to these same complex stimuli, humans generally hear changes in syllable order but are quite insensitive to syllable reversals—just the opposite of the songbirds. The fact that the budgerigar, a

Figure 3. Performance (hit rate (%) for targets) by different species of vocal learning birds on discriminating target zebra finch song motifs containing either syllable reversals or syllable shuffles. Redrawn from [77], including data from Bengalese finches tested using the same stimuli and methods.

psittacine, was much better than the songbirds at discriminating changes in syllable order in zebra finch motifs suggests the value of more comparative studies.

The excellent discrimination of syllable structure by zebra finches is perhaps not unexpected in that zebra finches, particularly, and birds, in general, excel in the discrimination of temporal fine structure of complex sounds, well beyond the abilities of humans (and perhaps other mammals) tested on the equivalent tasks [80–84]. These results raise the possibility that much more information might be transmitted in the fine structure of complex birdsong syllables than has previously been suspected from an analysis by traditional spectra and sonograms or from human perceptual reports. Indeed, while zebra finches produce song syllables in a repetitive fixed sequence, there is some acoustic variation among renditions of a motif within a song bout [60]. If it is shown that birds can discriminate acoustic differences in the performance of the same natural syllable across renditions of the bird's motif, this would suggest that birds may enjoy a far richer communication system than previously envisioned: one that primarily uses syllable structure rather than syllable sequence to communicate biologically relevant information [84].

The limited sensitivity to syllable sequence relative to the remarkable sensitivity to syllable structure in adult zebra finches is both puzzling and intriguing given that these birds obviously learn these sequences early in life. One possibility is that, during song development, zebra finches do not attend to the sequential patterns of whole motifs, but instead focus on learning the spectro-temporal features of smaller chunks of motifs [58,85]. Thus, instead of storing individual elements and the transition probabilities between them, the birds may be encoding chunks of sounds (i.e. strings of consecutive elements) that they eventually produce in a crystallized sequential structure. But if this capability also exists in adulthood, birds should be sensitive to some motif sequence manipulations, such as at chunk boundaries, as adults. Another possibility is that the learned sequential patterns in zebra finch motifs are due to a combination of innate predispositions, involving a mechanism like an auditory template, coupled with some vocal learning and improvisation. For instance, James & Sakata [86] tutored naive juvenile zebra finches with randomized sequences of syllables and

found that the birds converged on certain sequential patterns. Zebra finch song across wild and captive individuals also shows a hint of sequential regularities across populations, though in general motifs seem to be random sequences of syllables [87]. So, perhaps only a very simple computational mechanism for sequence perception is necessary for song learning and maintenance in zebra finches. Or, if a more complex mechanism is involved, perhaps it is available for only a few weeks after hatching and then is no longer fully accessible from auditory input in adult zebra finches. This conclusion is somewhat tempered by the fact that Braaten *et al.* [64] showed no differences in juvenile and adult sequence perception of syllables. Another possibility is that the auditory mechanisms involved in learning to produce a song sequence in juvenile males are different from those involved in song perception. Female zebra finches, of course, do not learn to produce songs, but can perceive sequence differences in classification tasks and can even learn to do so faster than males [88]. This suggests that male and female zebra finches may share a neural substrate for extracting sequential features, which is at least partly distinct from the mechanisms in juvenile males for learning to produce song sequences.

But the allure of potential parallels between zebra finch song and human speech may be distracting from the more obvious hypothesis that the learning and processing of syllable structure seems to be the dominant mechanism in zebra finch song communication. Recent findings from song tutoring experiments are tantalizing in this regard. Lipkind *et al.* [89] manipulated the tutor songs juveniles were exposed to and analysed how the birds adjusted their songs to match the new templates. They found that the birds copied changes in syllable structure even if it caused errors in sequence, showing that they prioritize efficient learning of syllable structure at the expense of syllable sequence. These results align with the Braaten *et al.* [64] notion that zebra finches are more sensitive to syllable structure than syllable sequences during juvenile song learning. But none of these findings should distract from the fact that the zebra finch does provide an invaluable opportunity to examine the relationship between physiological mechanisms for processing syllable structure and syllable sequences and any

changes in those mechanisms that occur over development as the sensitive period for song learning ends.

4. Proposed model of zebra finch song sequence perception

A number of recent efforts have attempted to model birdsong and other animal vocalizations using the formal language hierarchy, also known as the Chomsky hierarchy (for review, see [24,90]). The formal language hierarchy captures the nested levels of complexity of all logically possible patterns and describes the computational machinery necessary to recognize strings of a formal language. Human syntactic patterns require at least context-free machinery, meaning the capacity is needed to store symbols in a memory stack from which the symbol can later be popped off and compared with an incoming element [25,90]. Human phonological patterns, on the other hand, all fit within the regular languages and can be recognized using finite-state automata (FSAs), a type of machine that only knows its current state and the transition rules that connect pairs of states [91]. Berwick *et al.* [24] argue that all birdsong patterns can be described using regular languages, meaning that the context-free machinery necessary for human syntax is not required for recognizing the patterns of birdsong. From the studies reviewed above, zebra finch song production and recognition clearly do not require more than finite-state computational power.

A point worth considering, though, is that most characterizations of birdsong using the formal language hierarchy do not make a distinction between the patterns birds produce and the patterns they perceive. Previous studies have described the finite-state structure of zebra finch song from a production perspective and have provided evidence that they learn these sequential regularities from their fathers [92]. But, we propose another FSA for zebra finch perception of song sequences (figure 4). The model proposes that zebra finches encode three kinds of information: (i) what the first syllable is; (ii) what the last syllable is; and, (iii) a bag of syllables in the song. Studies, using both classification and discrimination tasks with zebra finches, indicate that sequential changes affecting the first and last syllables are especially salient [77,93,94]. This is consistent with evidence for the initial and final elements being special in human speech perception [63]. Past work shows that zebra finches are also sensitive to repeated syllables [94], suggesting that the FSA is limited to accessing each syllable in the bag once. But the syllables in the bag can be accessed in any order, meaning that the FSA would accept both ABCDE and ACDBE, for instance, as valid strings.

It is important to note that some classification tasks have shown that zebra finches can use sequence information beyond the identities of the first and last syllables (for example, Chen & ten Cate [93]). One possibility is that explicit training in a classification paradigm can cause zebra finches to memorize bigrams and longer strings and/or represent positional information about middle syllables. Future tests of the same birds using the same stimuli in both classification and discrimination paradigms could help resolve this issue.

While the model in figure 4 entails that only a limited set of information can be encoded in the sequences of zebra finch song, the birds could be communicating a very large amount of information by manipulating the temporal fine structure

Figure 4. Finite-state automaton modelling zebra finch song perception. '0' is the initial state, '2' is the final state and state '1' is a loop where syllables can be generated/recognized in any order. The model captures three things the birds represent: (i) what the first syllable is; (ii) what the last syllable is; and (iii) a bag of syllables in the song.

and other acoustic features of individual syllables. As the birds can hear changes to fine structure that go well beyond human capabilities [80], it is reasonable to think that the birds take advantage of this acoustic channel for communicating biological information, such as about individual identity and motivational state, both in learned song and in their complex system of calls [84,95]. Birds may also communicate some information about individual identity through the invariant properties of syllable sequence in a motif, and then layer detailed information about motivational state, emotion, physical condition, etc. in the content of individual syllables. Thus, it is possible that zebra finch vocal communication, though architecturally different from human language, is similar in informational capacity. Yet there is no evidence that birds are using song to refer to information external to the singer, which is a key attribute of abstract symbols [8]. Future studies in the laboratory and field investigating the functions of syllable-level details in zebra finch song, such as in playback experiments and preference tests, are needed to identify what, if any, information is encoded in these sounds.

Despite the strong evidence presented here for limits in sequence perception in several songbird species, not all birds are as limited. Budgerigars, for example, do quite well on sequence discrimination and comparisons between such species may be fruitful for uncovering what neural mechanisms allow some brains to process auditory sequences better than others. Budgerigars stand in contrast to the zebra finch in that they are very open and flexible vocal learners in regard to both their calls and their warble song [11,96]. Their complex and learned warble song has a quantifiable sequential structure that can be described as a fifth-order Markov sequence, meaning that the probability of a warble element type occurring depends on the previous five elements [97,98]. Tu & Dooling [97] tested the abilities of budgerigars, canaries and zebra finches to detect insertions of single warble elements out of order in long, natural sequences of this species-specific warble. Budgerigars were able to detect these insertions at a level well above chance, while canaries and zebra finches performed at chance level. When budgerigars were tested on detecting single elements inserted in randomized sequences of warble elements, their performance fell to chance, suggesting that natural warble has rules that the birds can use to discriminate changes in sequence.

Further evidence for the ability of budgerigars to perceive sequences comes from the study by Spierings & ten Cate [65] reviewed above. In that study, zebra finches could only use positional information about elements they were trained on to classify sequences as fitting into an XXY or YYX structure. Budgerigars, on the other hand, maintained their classification when tested on novel stimuli that did not share acoustic similarities with the training stimuli, showing that they are able to use the abstract relations between elements to distinguish sequences.

Perhaps budgerigar perception of sequences could be modelled with an FSA similar to the proposed one for zebra finches but with an added sensitivity to open bigrams—this is pairwise order information—at any distance. For instance, CAT has the open bigrams CA, AT and CT. This class of finite-state patterns is important in vowel and sibilant harmony in human phonology [91]. The ability to represent open bigrams would give an animal greater sensitivity to when sequence ABCDE is changed to ADBCE because open bigram BD is violated along with contiguous transitions AB, CD and DE, providing a redundant set of cues. While an FSA with sensitivity to open bigrams may account for the abilities of budgerigars reported in Lawson *et al.* [77], it is difficult to capture the abstract rule learning shown in Spierings & ten Cate [65] using such a model. An intriguing possibility is to model the behaviour using a push-down automaton with a single memory slot (as described in Idsardi [99] in this issue). In this way, the budgerigar auditory system may be able to store an incoming sound and then compare it with the next sound, similarly to how we keep track of past words when processing the following words of a sentence. Importantly, neuroanatomical differences between songbirds and parrots associated with vocal learning ability have already been identified [100]. Whether such differences exist in the central auditory systems of birds that differ in sequence perception abilities has yet to be investigated but could help in identifying the neural basis of computational mechanisms important for human speech perception, like the representation of open bigrams or push-down automata.

5. Perception of vocal sequences in other songbirds

This paper has focused on the processing of syllable sequences by zebra finches because these birds have become such a popular animal model for human speech and language, with the hopes of probing the evolutionary roots of syntax [54]. While several other songbirds tested in the same paradigm behave like zebra finches, it would be surprising if all songbirds do. There are thousands of species of birds that rely on auditory information to learn their species-specific song. Perhaps species with flexible repertoires that exhibit vocal learning throughout life, such as the mockingbird and European starling, might also show the ability to discriminate changes in sequences of complex acoustic signals. Past work has shown that European starlings can classify conspecific songs based on the sequential order of motifs and can learn abstract patterning rules, though claims that they can learn recursive patterns can be explained by simpler rules [101–106]. More species would have to be tested to determine whether there is a relationship between open-ended learning and sequence perception. But it is certainly possible that the rich variation in song

learning abilities across species is mirrored in an equally rich variation in perceptual abilities and computational mechanisms across species.

6. Conclusion

We have reviewed the evidence of how birds perceive sequential features of their songs with a focus on the zebra finch and using laboratory approaches. Because of the increasing popularity of zebra finches as an animal model of vocal learning and communication, there are now enough data from various approaches in the field and the laboratory that a stronger and more refined picture is emerging on the differences between bird acoustic communication and human speech and language. The evidence suggests surprisingly that at least some avian species are not encoding much information in the sequential patterns of their songs and that none of the species tested approaches the level of human capability. On the other hand, the exquisite sensitivity to the acoustic details of song syllables in zebra finches and other birds also suggests that birdsong is much richer in transmitting information about the state of the singer than we could ever imagine since we are not able to hear much of what is conveyed at the level of acoustic fine structure.

Nevertheless, vocal learning birds provide enormously valuable and unique animal models for human speech and language. They can serve as a vast resource for understanding how the brain processes learned vocal signals, for investigating how evolutionary forces shape the acoustic features used in vocal communication, for studying the dynamics of how information is shared in pairs and large groups, and, most importantly, for understanding the neurobiological mechanisms supporting the development and maintenance of learned vocal communication systems [8]. The zebra finch, in particular, remains a particularly useful model species in neurophysiological studies of vocal–motor learning [107–109].

Ethics. The work was conducted with permission of the University of Maryland IACUC, protocol 1191420-7.

Data accessibility. This article has no additional data.

Authors' contributions. A.R.F. collected and analysed the behavioural data on Bengalese finches and drafted the manuscript; W.J.I. carried out the FSA modelling and critically revised the manuscript; G.F.B. critically revised the manuscript; R.J.D. helped draft and critically revise the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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