



Research

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Animal behaviour

A simple explanation for the evolution of complex song syntax in Bengalese finches

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The songs of Bengalese finches (*Lonchura striata var. domestica*) have complex syntax and provide an opportunity to investigate how complex sequential behaviour emerges via the evolutionary process. In this study, we suggest that a simple mechanism, i.e. many-to-one mapping from internal states onto syllables, may underlie the emergence of apparent complex syllable sequences that have higher order history dependencies. We analysed the songs of Bengalese finches and of their wild ancestor, the white-rumped munia (*L. striata*), whose songs are more stereotypical and simpler compared with those of Bengalese finches. The many-to-one mapping mechanism sufficiently accounted for the differences in the complexity of song syllable sequences of these two strains.

1. Introduction

Birdsongs are of interest as a biological model of human language and its evolution [1]. Among songbirds, Bengalese finches (*Lonchura striata var. domestica*) have attracted considerable attention because their songs have complex sequencing rules (syntax) and therefore provide an opportunity to investigate how syntactical rules are formed [2]. By contrast, the songs of the white-rumped munia (*L. striata*), which are the wild ancestors of the Bengalese finch, are simple and have high linearity compared with Bengalese finch songs [3]. Thus, a comparison of the processes underlying the songs of these two strains might elucidate how the complex behavioural sequencing rule emerges via evolutionary processes.

We previously [4] demonstrated that there are significant higher order history dependencies in Bengalese finch songs, i.e. which syllable (song element) appear next depends on more than one previous syllables. We also demonstrated that a simple model with ‘many-to-one mapping’ from internal states to syllables, where the transition rule of internal states obeys a Markov process (the next state depends only on the current state and not on the preceding states), can generate apparently complex sequences with the higher order dependencies observed in Bengalese finch songs (also discussed in [5]). Here, many-to-one mapping means that more than one distinct state can produce the same syllable (the concept of the many-to-one mapping mechanism is illustrated in the electronic supplementary material, S1). In this study, we analysed Bengalese finch and white-rumped munia songs via many-to-one mapping representation and provide a simple explanation for the evolution of complex song syntax, which has higher order history dependencies.

2. Material and methods

(a) Subjects

The Bengalese finches were born and raised in colonies at the RIKEN Brain Science Institute. The white-rumped munias were captured in three areas in Taiwan: Huben,

Mataian and Taipei (for details, see [6]). Some of the finches were imported to Japan and housed at RIKEN, while others were kept in an indoor space in each captured area for recording. For both strains, we selected the individuals from which more than 20 bouts were recorded. The recording procedures for Bengalese finches are detailed in [4] and for white-rumped munias are detailed in [6]. All of the finches were older than 120 days at the time of recording. Because songs of Bengalese finches and white-rumped munias crystallize at 120 days post-hatching [2,7], the songs can be regarded as adult songs. Consequently, we analysed the undirected songs (songs in the absence of a female) of 43 adult male Bengalese finches and 44 adult male white-rumped munias.

(b) Song analysis

The Bengalese finch and white-rumped munia songs consist of acoustically continuous segments, termed syllables, that are separated by silent intervals. These songs were analysed by assigning a label to acoustically similar syllables based on visual inspection of the sonogram. Two expert annotators who were blind to the study aims annotated the songs. We used the syllable label sequence from one annotator for each bird. We confirmed the validity of the annotation skills of both annotators by evaluating the agreement of the annotations with the agreement of annotations made by other annotators. Both of our annotators yielded an average value of Fleiss's or Cohen's kappa greater than 0.82, which is considered 'almost perfect agreement'. This confirms the validity of the annotations of the two annotators (see [4] for details). Figure 1*a,b* (i) represent the sonograms (sound spectrograms) of representative songs for each strain, and the letters above the sonograms indicate the syllable labels. The total number of annotated syllables for each bird (after syllable repetition was collapsed into one syllable) was greater for Bengalese finches (mean = 1730.51) than for white-rumped munias (mean = 1391.59). We therefore reduced the song data of Bengalese finches (from latest recorded bouts to older bouts) to a mean of 1391.65 to equalize the average number of total syllables for both strains.

To construct a model that uses many-to-one mapping from latent states to syllables, we first conducted a hypothesis test for each syllable to determine whether the occurrence of the tested syllable is affected by the preceding syllable. In particular, we chose a non-repeated syllable that had both more than one preceding syllable and more than one subsequent syllable. We restricted the analysis to non-repeated syllables because we were not interested in the statistics of syllable repetition. We then tested whether the probability of transition from the syllable depends on the preceding syllable by performing a χ^2 -test for goodness of fit between the probability distributions, ignoring the preceding syllables and those conditioned on the most frequent preceding syllable. We interpreted the syllable as having second-order history dependency if $p < 0.05/n$, where n denotes the number of candidate syllables (the Bonferroni correction). Next, we split the syllables into distinct states depending on the preceding states. The resulting model is called the partially observable Markov model (POMM) [5], because the state transition obeys a Markov process and the states are partially observable due to the many-to-one mapping from the states to the output (syllable).

To evaluate the randomness or unpredictability of syllable sequences and states in the POMM, we calculated the conditional entropy [8], defined by

$$H(X|Y) = - \sum_x p(x) \sum_{\substack{y \\ y \neq x}} p(y|x) \log p(y|x),$$

where x denotes the previous syllable/state, y denotes the current syllable/state, and the summations are taken over all existing syllables/states except for the case $x = y$. Repeated syllables were collapsed into single syllable labels to eliminate the

influence of syllable repetition, which spuriously increases entropy. We used empirical probabilities for the probabilities $p(x)$ and $p(y|x)$.

3. Results

First, we confirmed previous reports that the syllable sequencing rules in Bengalese finch songs are more complex (less stereotyped) than those of white-rumped munia songs. The conditional entropy of the syllable sequence of Bengalese finches was significantly larger (figure 2*a*; $t_{85} = 2.761$, $p < 0.01$, unpaired t -test) compared with that of white-rumped munias, confirming this claim. The individual values of entropy are given in the electronic supplementary material, S2.

We then compared the statistical properties of Bengalese finch songs and white-rumped munia songs via the many-to-one mapping representation. The many-to-one mapping from states to syllables is a parsimonious explanation of the higher order history dependencies observed in Bengalese finch songs [4,5]. Thus, if there are no higher order history dependencies, there is no need for many-to-one mapping. Of the 43 Bengalese finches, we found more than one branching point (syllable) with significant second-order history dependency in 22 birds, of which 10 birds had one, six birds had two, five birds had three and one bird had four branching point(s) with significant higher order dependencies. Of the 44 white-rumped munias, 13 birds had at least one significant second-order dependency, of which 10 birds had one and three birds had two such branching point(s). These results suggest that the extent to which the birds have higher order history dependencies are greater in Bengalese finches compared with white-rumped munias. We then constructed the POMM by dividing the syllables with significant higher order dependencies into distinct states depending on the preceding syllables. For example, the syllable 'c' in figure 2*a* was divided into states $c(\leftarrow b)$ and $c(\leftarrow e)$ depending on the preceding syllables (b or e). From the transition diagram in which the first-order Markov process was assumed, it may seem that the transition from syllable 'c' to 'f' or 'd' is highly stochastic. However, with the POMM, we can observe the tendency that if 'b' is the preceding syllable, 'c' is followed by the syllables 'd'; if 'e' is the preceding syllable, 'c' is followed by the syllable 'f' almost deterministically. This reduces the entropy from 0.83 to 0.32. The song of the white-rumped munia in figure 1*b* did not have any higher order history dependency, and thus the Markov model and the POMM were identical and gave the same entropy value (=0.65).

Figure 2*b* compares the entropy of the state transition of the POMM for the two strains. In contrast to the entropy of syllable sequences (figure 2*a*), the significant difference between the two strains vanishes, and the mean values were almost identical ($t_{85} = 0.267$, $p = 0.79$). This result suggests that the many-to-one mapping from states to syllables, which can produce the higher order history dependencies in syllable sequences, is sufficient to account for the differences in complexity between the songs of Bengalese finches and white-rumped munias.

4. Discussion

In this study, we first confirmed that the syllable sequence of the Bengalese finch song is complex and unpredictable

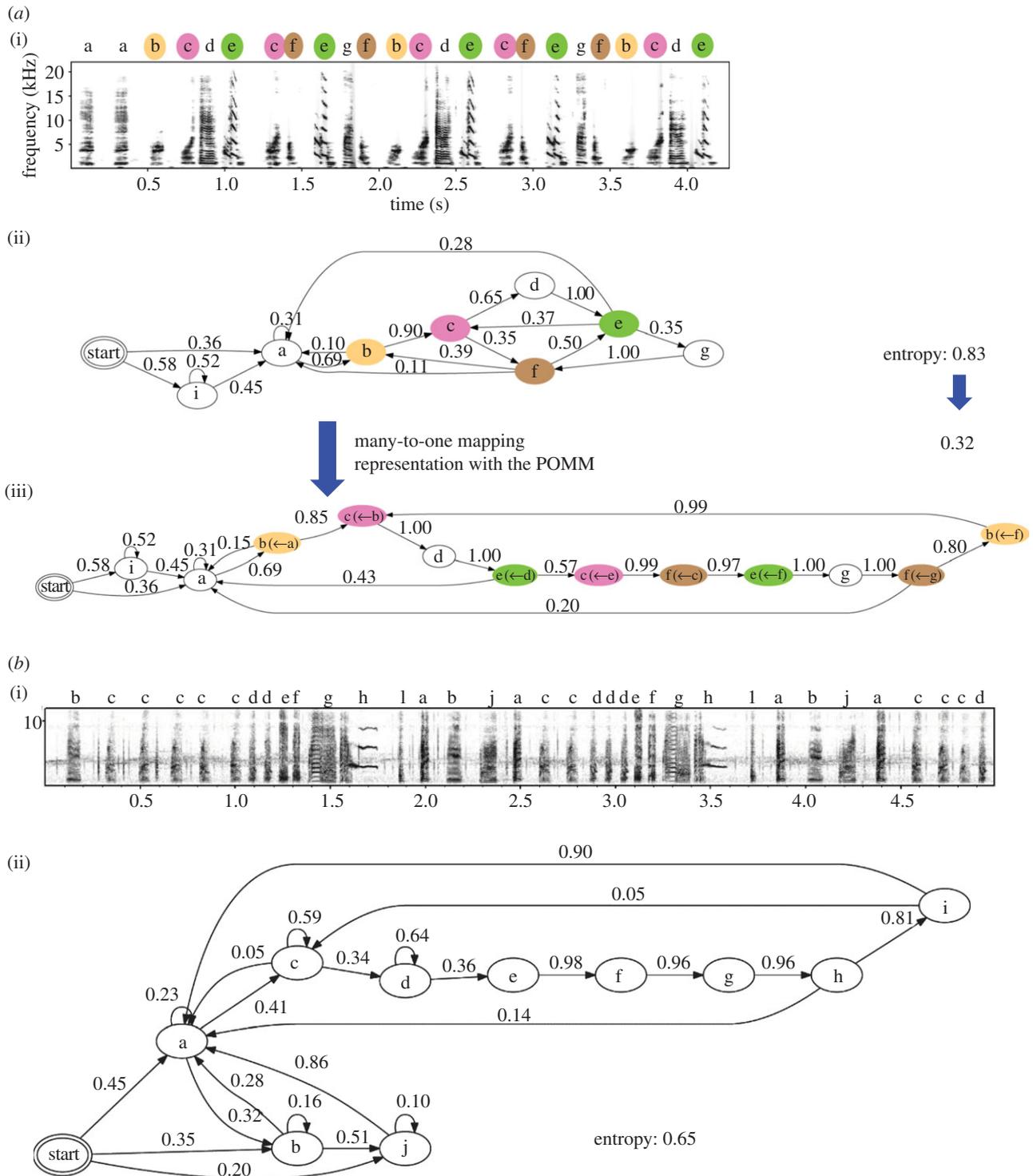


Figure 1. Examples of Bengalese finch and white-rumped munia songs. (a) (i) sonogram of a Bengalese finch song with syllable labels. (ii) Markov model representation of syllable sequences. The ellipses represent one syllable, and the arrows with values represent transitional probabilities. Rare transitions with probabilities < 0.01 were omitted. (iii) POMM representation of the aforementioned sequences. Syllables that have significant higher order dependency on the preceding syllables are divided into distinct states depending on the preceding syllables. The entropy of state transition is shown for each model. (b) An example of a white-rumped munia song. (ii) For this song, the Markov model and POMM are identical because no significant history dependency was found.

compared with its wild ancestor, the white-rumped munia. Here, the complexity was measured by the entropy of the syllable sequences, assuming a first-order Markov model. However, we found that the difference in entropy between the two strains disappeared when they were compared with the state sequence of the POMM, in which the states were mapped onto syllables with a 'many-to-one' mapping. The many-to-one mapping model was reported to reproduce

several characteristics of Bengalese finch songs, suggesting the sufficiency of the model [5]. The white-rumped munia songs tend to lack the higher order history dependency, and thus the many-to-one mapping was less necessary. Given that the entropy of the state sequence of the POMM did not differ between the two strains, it is reasonable to conclude that the syntactical complexity of Bengalese finch songs emerges from more common use of many-to-one mapping

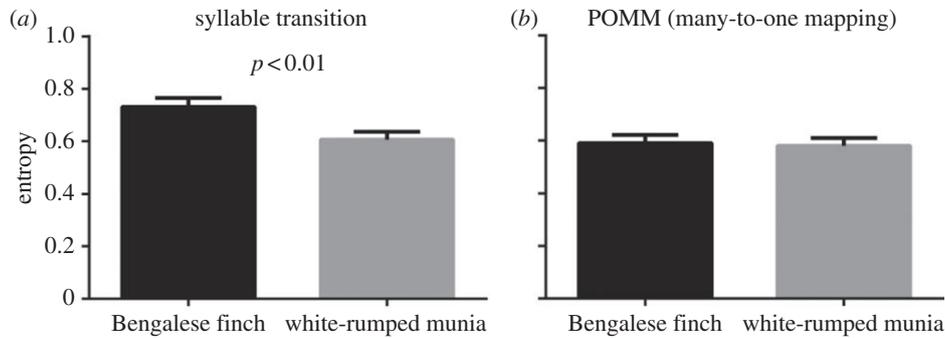


Figure 2. Comparison of the entropy of Bengalese finch and white-rumped munia songs. (a) Conditional entropy of syllable transition (for the Markov model). (b) Conditional entropy of the state transition in POMM. Error bars represent the s.e.m.

rather than from differences in the complexity of the state transition itself. Although there were significant differences between the two strains in the entropy of the syllable transition, there was also substantial overlap (see the electronic supplementary material, S2). The songs of some white-rumped munias were more complex than those of some Bengalese finches. The evolution of the complex song syntax of the Bengalese finch from that of the white-rumped munia should therefore be regarded as a gradual population-level change.

The POMM-like representation can be related to the songbird's brain structure. Primarily, two nuclei within the songbird brain are involved in generating songs: the HVC (proper name) and the robust nucleus of the archistriatum (RA). The HVC appears to encode sequential information, while the RA encodes the acoustic structure of individual song syllables [9]. The sequential pattern of birdsongs is considered to be generated by a sequential activity pattern of RA-projecting neurons in the HVC. If we regard a sequential activity pattern as 'states' in the POMM, the many-to-one mapping can be implemented for the synaptic connection from HVC neurons to RA neurons [4,10]. The main locus of the synaptic plasticity that enables birds to learn songs is the synaptic connection from the HVC to the RA [11]. Our scenario for the evolution of Bengalese finch song syntax suggests that the differences in song complexity between Bengalese finches and white-rumped munias lie in the structural differences in the HVC–RA connection and its plasticity mechanism. An alternative hypothesis regarding the neural implementation is that birds merely memorize the same syllable multiple times in various 'memory slots'. We can still confirm a many-to-one mapping (from different memory slots to an identical motor pattern) in this case. If this hypothesis is

true, however, there might not be any many-to-one anatomical connections. Therefore, our results do not provide conclusive evidence regarding the neural mechanism but rather offer a prediction concerning the proximate factor of bird song evolution. Understanding how the process by which many-to-one mapping in the syllable sequence of Bengalese finch songs occurs during the song learning process and comparing it to that of white-rumped munias will also provide valuable insight into how song syntax is acquired and how it evolved.

In addition to Bengalese finches, several species are capable of producing sequences with higher order history dependencies, including canaries [12], whales [13] and, of course, humans. However, Bengalese finches are unique because their wild ancestor, which has less higher order history dependencies, has been identified. Thus, these two strains provide an opportunity to study how the ability to generate complex sequences can emerge via evolution. This study provides new insights on the differences between the two strains by suggesting that the apparently complex sequence generation can emerge by a simple evolutionary change at the neural mechanistic level. The proposed principle is simple and can easily be implemented in a hierarchical control system. Hierarchical control is a common principle of neural motor systems. Our proposed system could therefore apply to other complex behaviours in a wide range of animal species.

All experimental procedures and housing conditions were approved by the Animal Care and Use Committee at RIKEN.

Data accessibility. Audio data of Bengalese finch and white-rumped munia songs have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.6pt8g>

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