MEASURING LONG CONTEXT DEPENDENCY IN BIRDSONG USING AN ARTIFICIAL NEURAL NETWORK WITH A LONG-LASTING WORKING MEMORY

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ABSTRACT

The production of grammatically and semantically appropriate human language requires reference to non-trivially long history of past utterance, which is referred to as the *context dependency* of human language. Similarly, it is of particular interest to biologists how much effect past behavioral records of individual animals have on their future behavioral decisions. In particular, birdsong serves a representative case to study context dependency in sequential signals produced by animals. Previous studies have suggested that the songs of Bengalese finches (*Lonchura striata* var. *domestica*) exhibited a long dependency on previous outputs, while their estimates were upper-bounded by methodological limitations at that time. This study newly estimated the context dependency in Bengalese finch's song in a more scalable manner using a neural network-based language model, Transformer, whose accessible context length reaches 900 tokens and is thus nearly free from model limitations, unlike the methods adopted in previous studies. A quantitative comparison with a parallel analysis of English sentences revealed that context dependency in Bengalese finch song is much shorter than that in human language but is comparable to human language syntax that excludes semantic factors of dependency. Our findings are in accordance with the previous generalization reported in related studies that birdsong is more homologous to human language syntax than the entire human language, including semantics. Thus, this study supports the hypothesis that human language modules, such as syntax and semantics, evolved from different precursors that are shared with other animals.

Keywords birdsong, context dependency, Bengalese finch, language modeling, discrete variational autoencoder, unsupervised clustering, individual normalization

Significance Statement

- We investigated context dependency in over 10-hour recordings of Bengalese finch songs using a neural network-based language model.
- We proposed an end-to-end unsupervised clustering method of song elements (syllables) into statistically optimal categories.
- Context dependency in the birdsong is shorter than that in English sentences but comparable with the dependency in English syntax excluding semantic factors.

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1 Introduction

Making behavioral decisions based on past information is a crucial to how humans and animals live (Friston, 2003, 2010; Friston and Stephan, 2007). This underscores the biological inquiry into how much effect past events have on animal behaviors. These past records are not only limited to observations of the environment and other individuals but also include each individual's behavioral history. A typical example is human language production where the appropriate choice of words to utter depends on previously uttered words/sentences. For example, we can tell whether *was* or *were* is the grammatical option after *The photographs that were taken in the cafe and sent to Mary* ___ only if we keep track of the previous words for a sufficient length, at least up to *photographs*, and successfully recognize the two close nouns (*cafe* and *station*) as modifiers rather than the main subject. Similarly, semantically plausible words are selected based on the topic of preceding sentences, as exemplified by the appropriateness of *warship* over *canoe* after "missile" and "navy" are used in the same speech/document. This dependence on the production history is called *context dependency* and is considered a characteristic property of human languages (Harris, 1945; Chomsky, 1957; Larson, 2017; Khandelwal et al., 2018; Dai et al., 2019). Birdsongs, in particular, songs by Bengalese finches (*Lonchura striata* var. *domestica*), serve as a representative case study of context dependency in sequential signals produced by non-human animals. Their songs are sound sequences that consist of brief vocal elements called *syllables* (Hosino and Okanoya, 2000; Okanoya, 2004). Previous studies have suggested that birdsongs exhibit non-trivially long dependency on previous outputs (Katahira et al., 2011; Warren et al., 2012; Markowitz et al., 2013). Complex sequential patterns of syllables have been discussed in comparison with human language syntax from the viewpoint of formal linguistics (Okanoya, 2004; Berwick et al., 2011, 2012; Berwick and Chomsky, 2016). Neurological studies have also revealed homological network structures in the vocal production, recognition, and learning of songbirds and humans (Kuypers, 1958; Wild et al., 1997; Prather et al., 2008). Assessing whether birdsongs exhibit long context dependency similar to human language is an important comparative study that several previous studies have addressed using computational methods. Katahira et al. (2011) found that Bengalese finch songs are dependent on more than just one previously uttered syllable. Similarly, Markowitz et al. (2013) report that canary songs exhibit a dependency on the last six chunks of syllables. However, the reported lengths of context dependency were measured using a limited language model—Markov/n-gram model—that was only able to access a few recent syllables in the context by design (at most two in Katahira et al. and seven in Markowitz et al.). Thus, it is unclear if those numbers were real dependency lengths in the birdsongs or merely model limitations. Moreover, the use of a limited language model is problematic for comparative studies because human languages are not modeled precisely by a Markov process (Chomsky, 1956; Rabin and Scott, 1959).

Powerful language models are now available owing to recent advancements in machine learning, particularly in artificial neural networks (Vaswani et al., 2017; Devlin et al., 2018; Dai et al., 2019). These neural language models are flexible, can be fit to birdsong data, and importantly, can potentially refer to 200–900 syllables from the past when the data include such long dependency (Khandelwal et al., 2018; Dai et al., 2019). In the present study, we assessed a detailed estimate of context dependency length in the songs of Bengalese finches using the Transformer language model, which can exploit the longest context among currently available models and has state-of-the-art architecture in today's natural language processing (Vaswani et al., 2017; Devlin et al., 2018; Dai et al., 2019). We also performed the same dependency analysis on English sentences as a baseline for human language data. On one hand, we found that context dependency in Bengalese finch's song is much shorter than in English sentences. On the other hand, we found that the context dependency in the birdsong is slightly longer than and more comparable to the dependency in English syntax, where each word in the sentence is replaced with its grammatical category—such as NOUN and VERB—and semantic information included in the word is removed. These findings corroborate previous generalizations in comparative studies that birdsongs are more homologous to human language syntax than the entirety of human language including semantics (Berwick et al., 2011; Gibson and Tallerman, 2012; Miyagawa et al., 2013) and provide a new piece of evidence for the hypothesis that human language modules, such as syntax and semantics, evolved from different precursors that are shared with other animals (e.g., birdsongs and alarm calls respectively; Okanoya, 2007; Okanoya and Merker, 2007; Miyagawa et al., 2013, 2014; Nóbrega and Miyagawa, 2015).

The adopted analysis of context dependency is straightforward. First, we trained the Transformer language model on sequences of Bengalese finch syllables such that the model predicted upcoming syllables based on previously uttered ones. The trained model can be seen as a simulator of birdsong syntax, whose accessible context can be controlled by researchers, unlike real birds. Second, we measured the difference in predictive performance of the trained model working on full contexts and truncated contexts as depicted in Figure 1b. Intuitively, this difference became smaller as the truncated context got longer and contained more information. We found the maximum length of the truncated contexts where the prediction difference was above a canonical threshold. This length, the effective context length (Khandelwal et al., 2018; Dai et al., 2019), is our estimate of the context dependency in Bengalese finch songs.

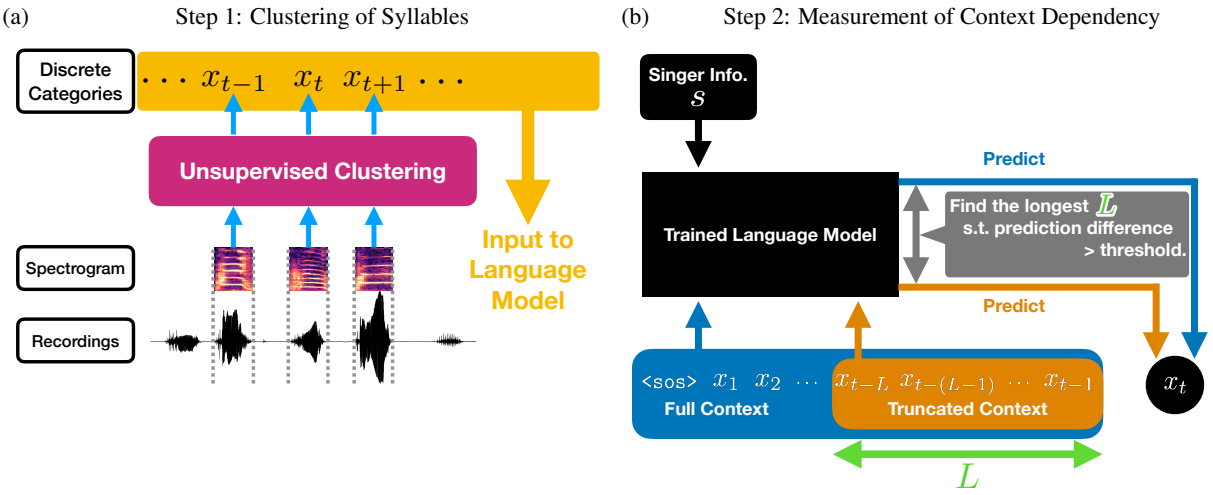

Figure 1: Schematic diagram of the proposed analysis, consisting of two steps. (a) Clustering of Bengalese finch syllables. The recordings were transformed into spectra and categorized by an unsupervised, end-to-end clustering system. The resulting sequences of discrete syllable categories were used as inputs to the language model. (b) Assessment of context dependency in the birdsong. The Transformer language model was fit to the birdsong data and its predictive performance was tested on the full and truncated contexts. The effective context length is the maximum length L of the truncated context such that the prediction difference is greater than an arbitrary threshold ($= 1\%$ in perplexity by convention).

The syntactic analysis of animal songs is typically performed on sequences of discretely categorized syllables (Payne and McVay, 1971; Seyfarth et al., 1980; Hosino and Okanoya, 2000; Kojima, 2003; Suzuki et al., 2006; Kakishita et al., 2007; Markowitz et al., 2013; Kershenbaum et al., 2014, 2016; Sainburg et al., 2019a, but see Katahira et al., 2011; Morita and Koda, 2019; Sainburg et al., 2019b for categorization-free approaches). The present study also followed this approach and represented each syllable with a discrete category (Figure 1a). This was useful for comparison with English text data in the analysis of context dependency. The syllable categories were discovered by a novel end-to-end clustering method that automatically classified segmented recordings—with variable duration—into an unspecified number of statistically optimal, individual-invariant categories.

2 Results

2.1 Clustering of Syllables

The context dependency analysis adopted herein was performed on sequences of discrete symbols such as human language sentences represented by sequences of text words. Thus, we needed a discrete representation of the syllables of Bengalese finches. The classical approach to this discretization task is based on visual and/or auditory inspection of human experts (Hosino and Okanoya, 2000; Okanoya, 2004; Kakishita et al., 2007; Katahira et al., 2011; Kershenbaum et al., 2014; Tachibana et al., 2014). More recently, several researchers explored fully unsupervised classification of animal vocalization (i.e., getting completely rid of the manual classification) based on acoustic features extracted by artificial neural networks called *variational autoencoders* (VAEs; Kingma and Welling, 2014; Coffey et al., 2019; Goffinet et al., 2019; Sainburg et al., 2019b). The present study extended this latter approach and proposed an end-to-end unsupervised clustering method named the *ABCD-VAE* (whose first four letters stand for the Attention-Based Categorical sampling with the Dirichlet prior). The proposed method automatically classifies segmented recordings—with variable duration—into an unspecified number of statistically optimal categories. It also allowed us to exploit the speaker-normalization technique developed for unsupervised learning of human language from speech recordings (van den Oord et al., 2017; Chorowski et al., 2019; Dunbar et al., 2019; Tjandra et al., 2019), yielding syllable classification modulo individual variation.

A high-level description of the clustering system is as follows. We trained a RNN to "hear" a syllable in its entirety (*encoding*) and reproduce it as precisely as possible (*decoding*). To accomplish this task, the RNN must store the information about the entire syllable in its internal state—represented by a fixed-dimensional vector, analogous to a fixed number of neurons exhibiting certain activation patterns in the real brain—when it transitions from the encoding phase to the decoding phase. Thus, this internal state of the RNN can be used as a fixed-dimensional representation of

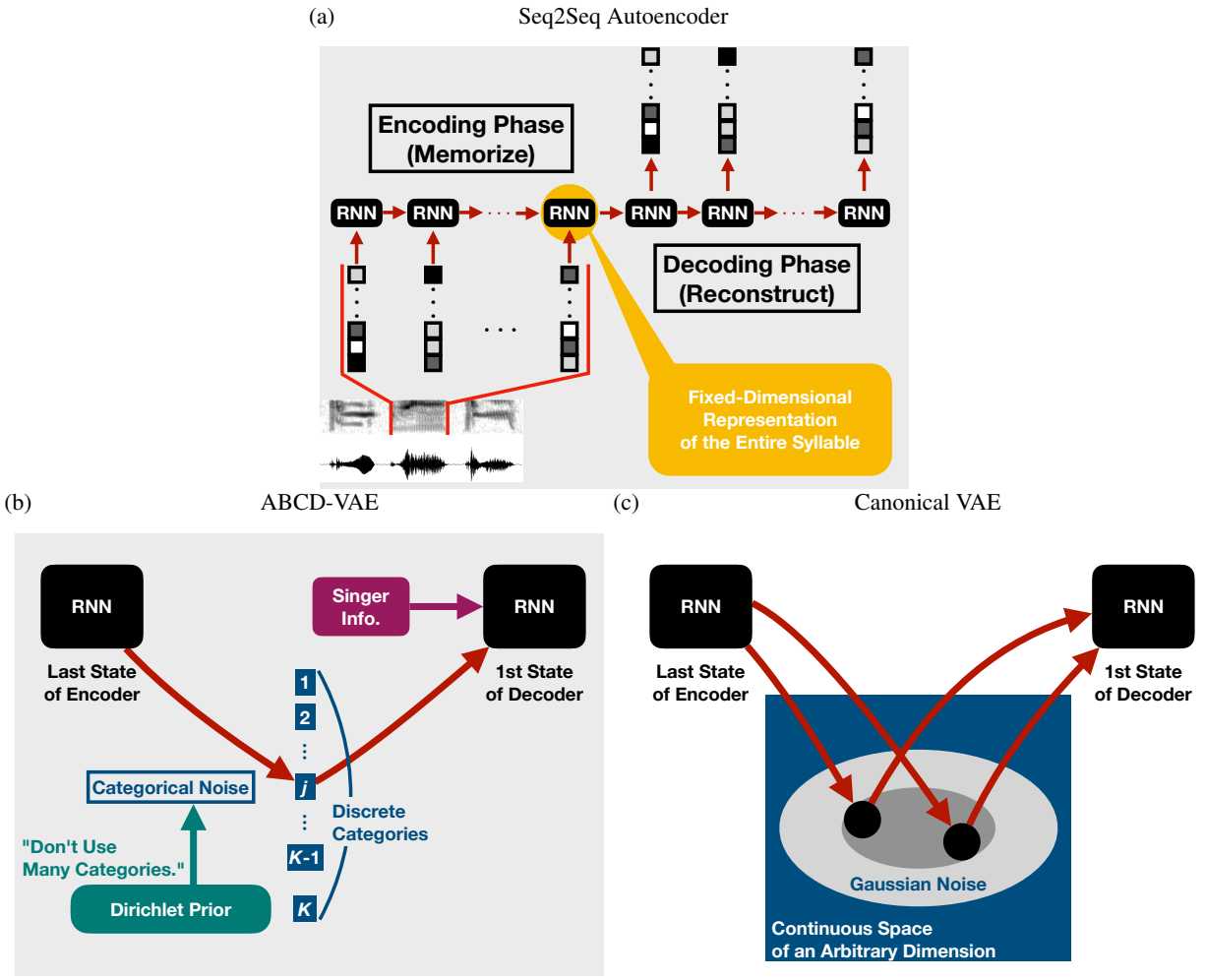

Figure 2: Schematic diagram of the proposed clustering method (combination of a and b, highlighted in light gray). (a) The high-level structure of the sequence-to-sequence (seq2seq) autoencoder. It was trained to first read syllable spectra frame by frame and then reconstruct them as precisely as possible. A fixed-dimensional representation of entire input syllables was obtained in the middle between the encoder and the decoder. (b) The ABCD-VAE that encoded syllables into discrete categories between the encoder and the decoder. A statistically optimal number of categories were detected under an arbitrarily specified upper bound thanks to the Dirichlet prior (Bishop, 2006; O'Donnell, 2015; Little, 2019). The identity of the syllable-uttering individual was informed by the decoder besides the syllable categories. Therefore, individual-specific patterns need not have been encoded in the discrete syllable representation (Jang et al., 2017; van den Oord et al., 2017; Chorowski et al., 2019). (c) The canonical VAE with the Gaussian noise. It was also inserted between the encoder and the decoder and used to increase the interpretability of the continuous-valued features.

the syllables. We also installed a discretization module between the encoder and the decoder, and thereby obtained syllable classifications (Figure 2b). This discretization is the major difference from the previous VAE studies on animal voices that extracted continuous-valued features from the middle point (using a Gaussian noise, Figure 2c). Moreover, the proposed method automatically detects the statistically optimal number of syllable categories (under an arbitrary upper bound, which we set at 128; owing to the Dirichlet prior; Bishop, 2006; O'Donnell, 2015; Little, 2019) and works in a non-parametric manner compared to the previous end-to-end classification (Jang et al., 2017; van den Oord et al., 2017; Chorowski et al., 2019; Tjandra et al., 2019).

Syllables collected from 18 adult male finches were analyzed ($465,310$ syllables in total) and 39 categories—shared across the individuals—were detected (Figure 3a). The predicted classification captured major spectral patterns (Figure 3b, e). It ignored individual variations and other minor differences visible in the syllable embeddings obtained via the canonical continuous-valued VAE (Figure 3d). The unsupervised classification was mostly consistent with manual annotations assigned by a human expert (Figure 3c; Tachibana et al., 2014).

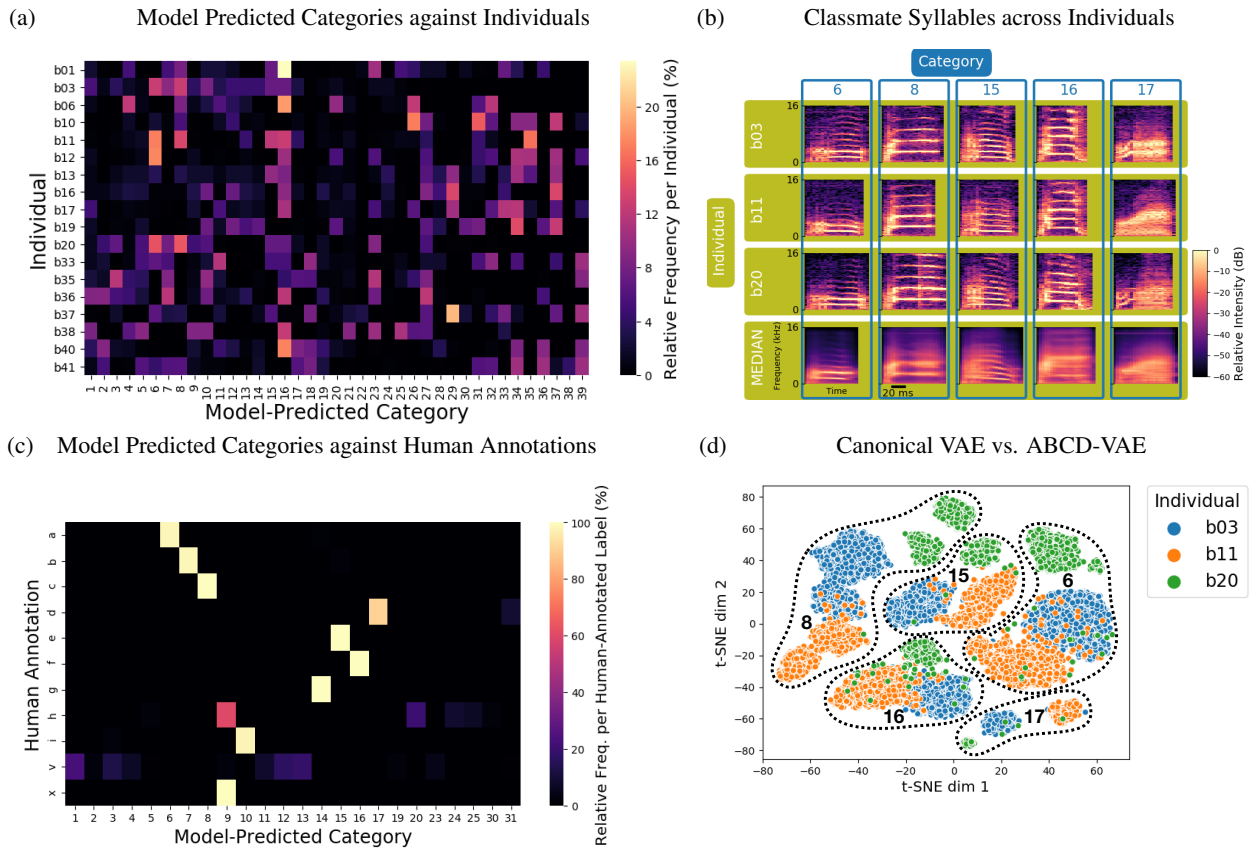

Figure 3: Clustering results of Bengalese finch syllables based on the ABCD-VAE. (a) Relative frequency of syllable categories (columns) per individual (rows). The category indices were renumbered for better visualization because the original values were arbitrarily picked from 128 possible integers and were not contiguous. (b) Syllable spectrograms and their classification across individuals. Syllables in each of the first to third rows (yellow box) were sampled from the same individual. Each column (blue frame) corresponds to the syllable categories assigned by the ABCD-VAE. The bottom row provides the median spectrogram of each category over all the 39 individuals. The examples had the greatest classification probability (> 0.999) among the syllables of the same individual and category. (c) Relative frequency of syllable categories (columns) per label manually annotated by a human expert (Tachibana et al., 2014). Only data from a single individual (b03) were presented because the manual annotations were not shared across individuals. (d) Comparison between syllable embeddings by the canonical continuous-valued VAE with the Gaussian noise (scatter points) and classification by the ABCD-VAE (grouped by the dotted lines). The continuous representation originally had 16 dimensions and was embedded into the 2-dimensional space by t-SNE (van der Maaten and Hinton, 2008). The continuous embeddings included notable individual variations represented by colors, whereas the ABCD-VAE classification ignored these individual variations.

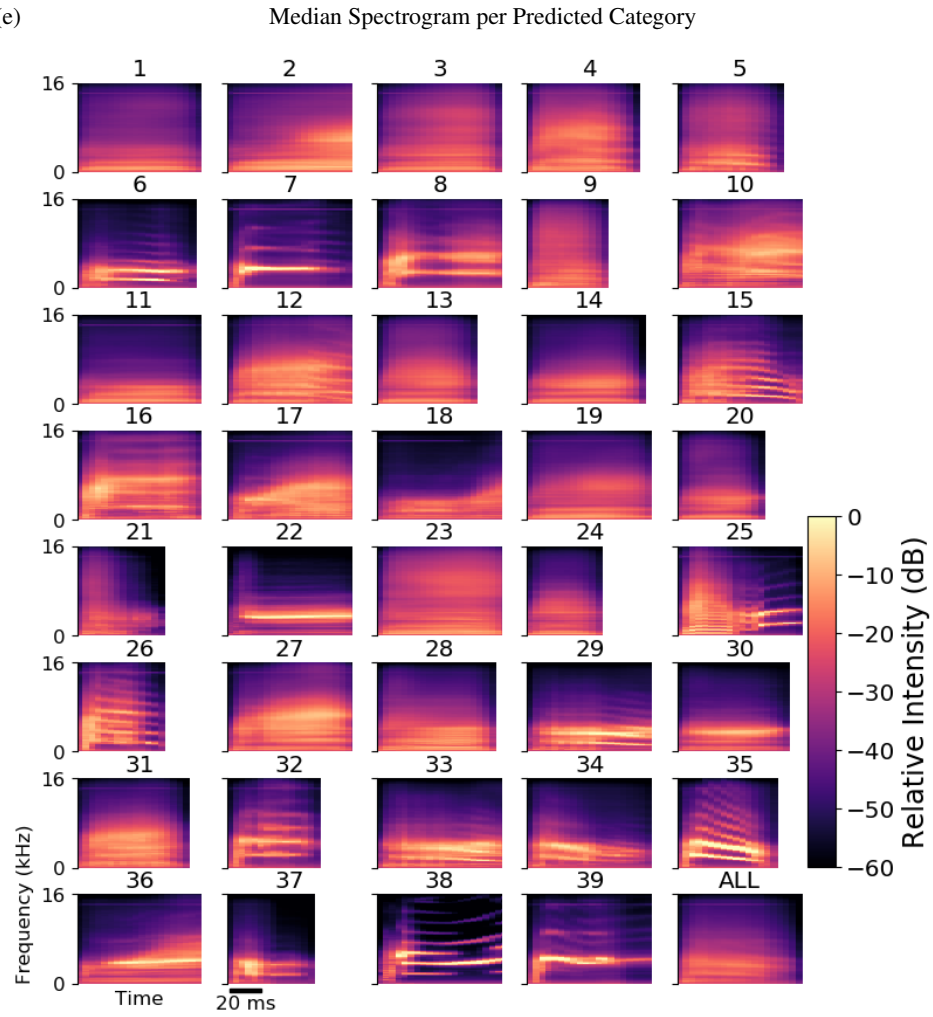

Figure 3 (cont.): (e) Median spectrogram of each syllable category predicted by the ABCD-VAE.

2.2 Context Dependency

The classification results in the previous subsection yielded sequences of discretely represented syllables called *bouts* ($9,139$ sequences in total). Our objective is to assess context dependency in these bouts. We measured the context dependency via the Transformer language model trained on $9,039$ bouts. The remaining 100 bouts were used to score its predictive performance from which the dependency was calculated. The model predictions were provided in the form of the log conditional probability of the test syllables given the preceding ones in the same bout: i.e., $\log \mathbb{P}(x_t \mid x_1, \dots)$. We compared the model predictions conditioned on the full context $(x_1, \dots, x_{t-1})$ and the truncated context $(x_{t-L}, \dots, x_{t-1})$ and found the *statistically* effective context length (SECL) defined by the maximum length of the truncated context wherein the mean prediction difference between the two contexts was significantly greater than the canonical 1% threshold in perplexity (at 0.05 level of significance estimated from 10,000 bootstrapped samples; Khandelwal et al., 2018).

In addition to the Bengalese finch bouts, we performed the same analysis on two types of English sentences for comparison ($12,327$ training sentences and $2,006$ test sentences; Silveira et al., 2014). One of them represented the words by their lemma. The other English data reduced the words to the part-of-speech (PoS) categories such as NOUN and VERB (cf. Perfors et al., 2011). This PoS representation removed semantic information from the English sentences; thus, the reported context dependencies were free of semantic factors such as words (at distance) encoding the topic of the sentences (e.g., "missile" and "warship" may co-occur in military documents and be stochastically dependent on each other without a grammatical relation such as subject and object).

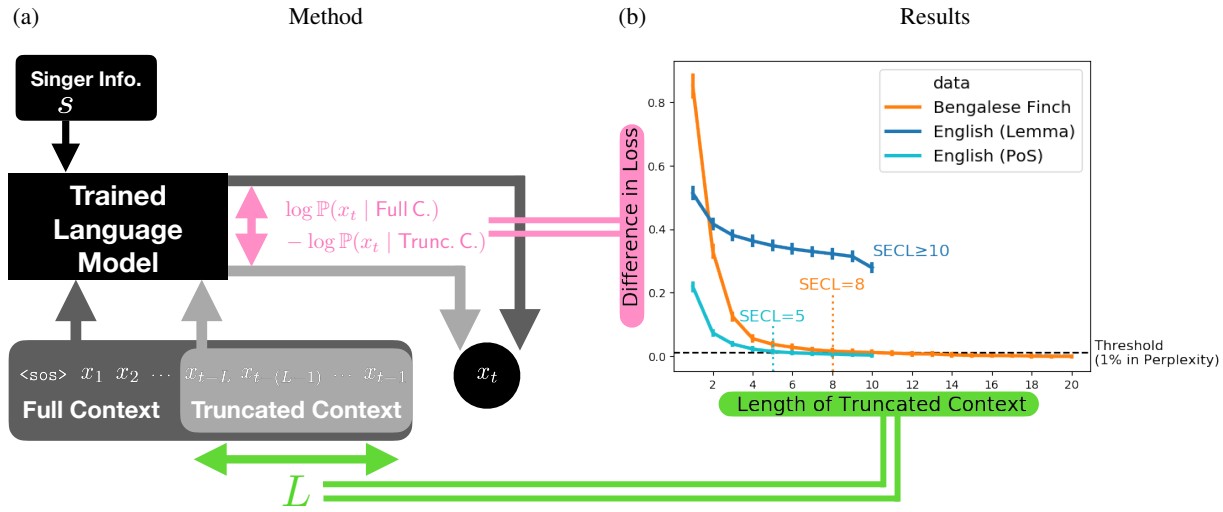

Figure 4: The differences in the mean loss (negative log probability) between the truncated- and full-context predictions. The x-axis corresponds to the length of the truncated context. The error bars show the 90% confidence intervals estimated from 10,000 bootstrapped samples. The loss difference is statistically significant if the lower side of the intervals are above the threshold indicated by the horizontal dashed line.

The SECL of the Bengalese finch song was eight (the orange line in Figure 4). In other words, the restriction on the available context to the one to eight preceding syllables decreased the mean predictive probability from the full-context baseline by a significantly greater amount than the threshold. However, the difference became marginal when nine or more syllables were included in the truncated context. On one hand, this is under the SECL of the English lemma data, which was ten or greater (the dark blue line, achieved the upper bound). On the other hand, the English SECL decreased to five when we represented the words by the PoS tags and removed the semantic factors (the light blue line). Hence, the context dependency in Bengalese finch songs is more comparable to that in the English syntax than in the full English including semantics.

3 Discussion

This study assessed the context dependency in Bengalese finch's song to investigate how long individual birds must remember their previous vocal outputs to generate well-formed song bouts. We addressed this question by fitting a state-of-the-art language model, Transformer, to the bouts, and evaluating the decline in the model's performance upon truncation of the context. We also proposed an end-to-end clustering method of Bengalese finch syllables, the ABCD-VAE, to obtain discrete inputs for the language model. In the section below, we discuss the results of this syllable clustering (§3.1) and then move to consider context dependency (§3.2).

3.1 Clustering of Syllables

The clustering of syllables into discrete categories played an essential role in our analysis of context dependency in Bengalese finch songs, particularly for the comparison to human language in text. Various studies have observed how fundamental the classification of voice elements is to animal vocalization (Payne and McVay, 1971; Seyfarth et al., 1980; Hosino and Okanoya, 2000; Kojima, 2003; Suzuki et al., 2006; Kakishita et al., 2007; Markowitz et al., 2013; Kershenbaum et al., 2016; Sainburg et al., 2019a, but see Katahira et al., 2011; Morita and Koda, 2019; Sainburg et al., 2019b for categorization-free approaches).

Our syllable clustering is based on the AVCD-VAE and features the following advantages over previous approaches. First, the ABCD-VAE works in a completely unsupervised fashion. The system finds the statistically optimal classification of syllables instead of generalizing manual labeling of syllables by human annotators (as opposed to Tachibana et al., 2014). Thus, the obtained results are more objective and reproducible (cf. Janik, 1999). Second, the ABCD-VAE detects the statistically optimal number of syllable categories rather than pushing syllables into a pre-specified number of classes (as opposed to Jang et al., 2017; van den Oord et al., 2017; Chorowski et al., 2019). This update is of particular importance when we know little about the ground truth classification—as in the cases of animal song studies—and need a more non-parametric analysis. Third, the ABCD-VAE adopted the speaker-normalization technique used for human

speech analysis and finds individual-invariant categories of syllables (van den Oord et al., 2017; Chorowski et al., 2019; Tjandra et al., 2019). Finally, the end-to-end clustering by the ABCD-VAE is more optimal than the previous two-step approach—acoustic feature extraction followed by clustering—because the feature extractors are not optimized for clustering and the clustering algorithms are often blind to the optimization objective of the feature extractors (Coffey et al., 2019; Goffinet et al., 2019; Sainburg et al., 2019b). Chorowski et al. (2019) also showed that a similar end-to-end clustering is better at finding speaker-invariant categories in human speech than the two-step approach.

It should be noted that the classical manual classification of animal voice was often based on *visual* inspection on the waveforms and/or spectrograms rather than auditory inspection (Payne and McVay, 1971; Katahira et al., 2011; Tachibana et al., 2014). Similarly, previous VAE analyses of animal voice often used a convolutional neural network that processed spectrograms as images of a fixed size (Coffey et al., 2019; Goffinet et al., 2019). By contrast, the present study adopted a RNN (specifically, a version called the long short-term memory, abbreviated as LSTM Hochreiter and Schmidhuber, 1997) to process syllable spectra frame by frame as time series data. Owing to the lack of ground truth as well as empirical limitations on experimental validation, it is difficult to adjudicate on the best neural network architecture for auto-encoding Bengalese finch syllables and other animals' voice. Nevertheless, RNN deserves close attention as a neural/cognitive model of vocal learning. There is a version of RNN called *reservoir computer* that has been developed to model computations in cortical microcircuits (Maass et al., 2002; Natschläger et al., 2003; Jaeger and Haas, 2004). Future studies may replace the LSTM in the ABCD-VAE with a reservoir computer to build a more biologically plausible model of vocal learning (cf. Dehaene et al., 1987). Similarly, we may filter some frequency bands in the input sound spectra to simulate the auditory perception of the target animal (cf. the Mel-frequency cepstral coefficients, MFCCs, are used in human speech analysis; Chung et al., 2016; Chorowski et al., 2019; Tjandra et al., 2019), and/or adopt more anatomically/bio-acoustically realistic articulatory systems for the decoder module (cf. Wang et al., 2020, implemented the source-filter model of vocalization based on an artificial neural network). Such Embodied VAEs would allow constructive investigation of vocal learning beyond mere acoustic analysis.

A visual inspection of classification results shows that the ABCD-VAE can discover individual-invariant categories of the Bengalese finch syllables (Figure 3). This speaker-normalization effect is remarkable because the syllables exhibit notable individual variations in the continuous feature space mapped into by the canonical VAE and cross-individual clustering is difficult there (see Figure 3d and the supporting information S1.4; Coffey et al., 2019; Goffinet et al., 2019; Sainburg et al., 2019b). Previous studies on Bengalese finch and other songbirds often assigned distinct sets of categories to syllables of different individuals, presumably because of similar individual variations in the feature space they adopted (Katahira et al., 2011; Markowitz et al., 2013; Tachibana et al., 2014; Kershenbaum et al., 2016; Sainburg et al., 2019b).

The end-to-end classification by the ABCD-VAE can be applied to a broad range of studies on animal vocalization, including cases where sequential organization of voice units is not at issue. The limitations of the proposed method are the prerequisite for appropriate voice segmentation as it operates on predefined time series of sound spectra, and a single category is assigned to each time series. Although birdsongs often exhibit clear pauses and researchers use them to define syllable boundaries, appropriate voice segmentation is not necessarily clear for other animals (Kershenbaum et al., 2016; Sainburg et al., 2019b), including human speech (Chiu et al., 2017; Dunbar et al., 2017, 2019; Rao et al., 2017). A possible solution to this problem (in accordance with our end-to-end clustering) is to categorize sounds frame by frame (e.g., by spectrum and MFCC) and merge contiguous classmate frames to define a syllable-like span (Chorowski et al., 2019; Tjandra et al., 2019).

3.2 Context Dependency

According to our analysis of context dependency, Bengalese finches are expected to keep track of up to eight previously uttered syllables—not just one or two—during their singing. This is evidenced by the relatively poor performance of the song simulator conditioned on the truncated context of one to eight syllables compared to the full-context condition. Our findings add a new piece of evidence for long context dependency in Bengalese finch songs found in previous studies. Katahira et al. (2011) showed that there are at least two dependent context lengths. They compared the first order and second order Markov models, which can only access the one and two preceding syllable(s), respectively, and found significant differences between them. A similar analysis was performed on canary songs by Markowitz et al. (2013), with an extended Markovian order (up to seventh). The framework in these studies cannot scale up to assess longer context dependency owing to the empirical difficulty of training higher-order Markov models (Katz, 1987; Kneser and Ney, 1995; Bengio et al., 2001, 2003; Goldwater et al., 2006; Teh, 2006). By contrast, the present study exploited a state-of-the-art neural language model (Transformer) that can effectively combine information from much longer contexts than previous Markovian models and potentially refer up to 900 tokens (Dai et al., 2019). Thus, the dependency length reported in this study is not likely to be upper-bounded by the model limitations and provides a more precise estimation of the real dependency length in a birdsong than previous studies. The long context dependency in Bengalese

finch songs is also evidenced by experimental studies. Warren et al. (2012) reported that several pairs of syllable categories had different transitional probability depending on whether or not the same transition pattern occurred in the previous opportunity. In other words, $\mathbb{P}(B \mid AB \ldots A\_) \neq \mathbb{P}(B \mid AC \ldots A\_)$ where A, B, C are distinct syllable categories, the dots represent intervening syllables of an arbitrary length ($\not\ni A$), and the underline indicates the position of B whose probability is measured. They also found that the probability of such history-dependent transition patterns is harder to modify through reinforcement learning than that of more locally dependent transitions. These results are consistent with our findings. It often takes more than two transitions for syllables to recur (12.17 syllables on average with the SD of 11.30 according to our own bout data, excluding consecutive repetitions); therefore, the dependency on the previous occurrence cannot be captured by memorizing just one or two previously uttered syllable(s).

Our study also found that Bengalese finch songs are more comparable to human language syntax than to the entirety of human language including semantics. This was demonstrated by our analysis of English sentences represented by sequences of lemmas and PoS categories. While the lemma-represented English sentences exhibited long context dependency beyond ten words as reported in previous studies (Khandelwal et al., 2018; Dai et al., 2019), the dependency length decreased to five—below the Bengalese finch result—when the PoS representation was used and semantic information was removed from the sentences. The gap between the two versions of English suggests that the major factor of long-distance dependencies in human language is the semantics, not the syntax. This is consistent with previous studies reporting that human language syntax prefers shorter dependency (Gibson, 1998; Futrell et al., 2015). Moreover, comparative studies between birdsong and human language often argue the former's lack of semantic function (Berwick et al., 2011, 2012; Gibson and Tallerman, 2012; Miyagawa et al., 2013, 2014), without referential variations seen in alarm calls (Seyfarth et al., 1980; Ouattara et al., 2009; Suzuki et al., 2016). This claim led to the hypothesis that human language syntax and semantics evolved from different precursors—sequence-generating system, such as animal song, and information-carrying system such as alarm calls—which were integrated to shape the entirety of human language (Okanoya, 2007; Okanoya and Merker, 2007; Miyagawa et al., 2013, 2014; Nóbrega and Miyagawa, 2015). Our findings are in accordance with this view, providing a novel relative similarity between birdsong and human language syntax compared to the whole linguistic system. Note that this kind of direct comparative study of human language and animal song was not feasible until flexible language models based on neural networks became available.

The reported context dependency on eight previous syllables also has an implication for possible models of Bengalese finch syntax. Feasible models should be able to represent the long context efficiently. For example, the simplest and traditional model of the birdsong and voice sequences of other animals—including human language before the deep learning era—is the n-gram model, which exhaustively represents all the possible contexts of length $n-1$ as distinct conditions (Katz, 1987; Kneser and Ney, 1995; Hosino and Okanoya, 2000; Goldwater et al., 2006; Teh, 2006). This approach, however, requires an exponential number of contexts to be represented in the model. In the worst case, the number of possible contexts is $39^8 = 5,352,009,260,481$ when there are 39 syllable types and the context length is eight as detected in this study. Such an exhaustive representation is not only hard to store and learn—for both real birds and simulators—but also uninterpretable to researchers. Thus, a more efficient representation of the context syllables is required (cf. Morita and Koda, 2020). Katahira et al. (2011) assert that the song syntax of the Bengalese finch can be better described with a lower-order hidden Markov model (Rabiner, 1989; Beal et al., 2002, HMM;) than the n-gram model. Moreover, hierarchical language models used in computational linguistics (e.g., probabilistic context-free grammar) are known to allow a more compact description of human language (Perfors et al., 2011) and animal voice sequences (Morita and Koda, 2019) than sequential models like HMM. Another compression possibility is to represent consecutive repetitions of the same syllable categories differently from transitions between heterogeneous syllables (cf. Kershenbaum et al., 2014). This idea is essentially equivalent to the run length encoding of digital signals (e.g., `AAABBCDDEEEEE` can be represented as `3A2B1C2D5E` where the numbers count the repetitions of the following letter) and is effective for data including many repetitions like Bengalese finch's song. For the actual implementation in birds' brains, the long contexts can be represented in a distributed way (Nishikawa et al., 2008): Activation patterns of neuronal ensemble can encode a larger amount of information than the simple sum of information representable by individual neurons, as demonstrated by the achievements of artificial neural networks (Bengio et al., 2001, 2003; Ryeu et al., 2001; Tsuda, 2001; Maass et al., 2002; Jaeger and Haas, 2004; Nishikawa and Okanoya, 2006).

While this study discussed context dependency in the context of memory durability required for generating/processing birdsongs (cf. Katahira et al., 2011; Warren et al., 2012; Markowitz et al., 2013), there are different definitions of context dependency designed for different research purposes. Sainburg et al. (2019a) studied the *mutual information* between birdsong syllables—including Bengalese finch ones—appearing at each discrete distance. Following a study on human language by Lin and Tegmark (2017), Sainburg et al. analyzed patterns in the decay of mutual information to diagnose the generative model behind the birdsong data, instead of addressing the question about memory. Importantly, their mutual information analysis cannot replace our model-based analysis to assess the memory-oriented context dependency: Mutual information is a pairwise metric of probabilistic dependence between two tokens (e.g., words in human languages, syllables in birdsongs), and thus, everything in the middle is ignored. To see the problem, suppose

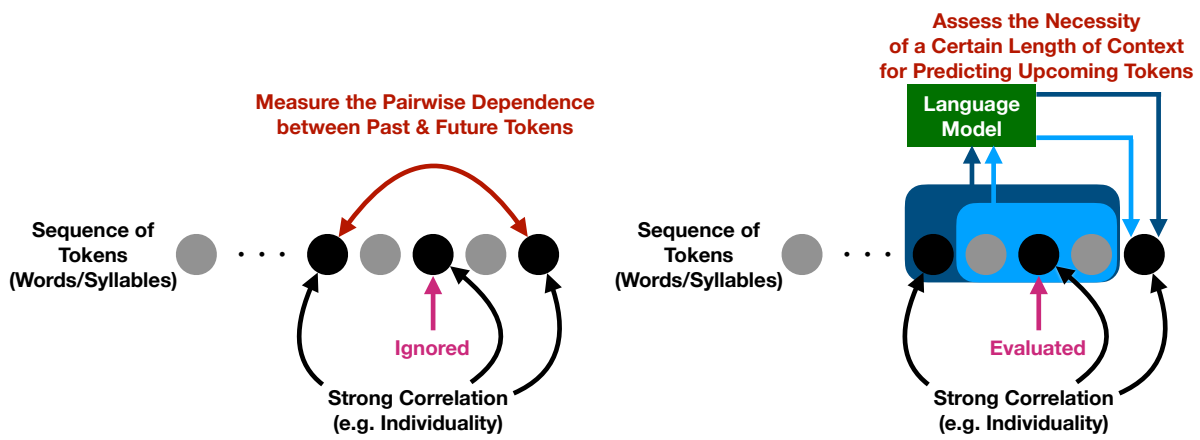

Figure 5: The analysis of context dependency based on the (a) mutual information and (b) language modeling.

that some tokens reflect the individuality of the speaker, as depicted in Figure 5a. (See the supporting information S3.1 for a more concrete, mathematical example of this problematic situation. S3.2 introduces other examples that demonstrate difficulties in the mutual information analysis.) Two occurrences of speaker-encoding tokens are dependent on each other regardless of their distance if the other tokens between the two are ignored, and this pairwise dependence is what mutual information accounts for. It should be clear now that such pairwise dependence does not necessarily match the agent-oriented concept of context dependency as the only thing relevant to the song recognition task (or speaker identification in this toy example) is the most recent occurrence of the correlating tokens. By contrast, our language modeling approach captured the agent-oriented concept of context dependency as desired. Dependency on a token in the past is detected if the prediction of upcoming tokens becomes notably more difficult by limiting the available context to the more recent tokens (Figure 5b; Khandelwal et al., 2018; Dai et al., 2019). In other words, reference to a token in the distant past is considered unnecessary if the same information (e.g., speaker identity) is available from more recent tokens. Therefore, the present study complements, rather than repeats/replaces, the mutual information analysis and findings from it.

We conclude the present paper by noting that the analysis of context dependency via neural language modeling is not limited to Bengalese finch's song. Since neural networks are universal approximators and potentially fit to any kind of data (Cybenko, 1989; Hornik, 1991; Jin et al., 1995; Maass et al., 2002; Lu et al., 2017), the same analytical method is applicable to other animals' voice sequences (Payne and McVay, 1971; Suzuki et al., 2006; Markowitz et al., 2013; Morita and Koda, 2019). Moreover, the analysis of context dependency can also be performed in principle on other sequential behavioral data besides vocalization, including dance (Frith and Beehler, 1998; Scholes, 2006, 2008) and gestures (van Lawick-Goodall, 1968; de Waal, 1988; Tanner and Byrne, 1996; Liebal et al., 2006). Hence, our method provides a crossmodal research paradigm for inquiry into the effect of past behavioral records on future decision making.

4 Materials & Methods

4.1 Recording and Segmentation of Bengalese Finch's Song

We used the same recordings of Bengalese finch songs that were originally reported in our earlier studies Tachibana et al. (2014, 2015). The data were collected from 18 adult males (>140 days after hatching), each isolated in a birdcage placed inside a soundproof chamber. The microphone (Audio-Technica PRO35) was installed above the birdcages. The output of the microphone was amplified using a mixer (Mackie 402-VLZ3) and digitized through an audio interface (Roland UA-1010/UA-55) at 16-bits with a sampling rate of 44.1 kHz. The recordings were then down-sampled to 32 kHz (see Tachibana et al. (2014, 2015) for more information about the recording).

Song syllables were segmented from the continuous recordings using the thresholding algorithm proposed in the previous studies (Tachibana et al., 2014, 2015). We defined a sequence of the syllables as a bout if every two adjacent syllables in the sequence were spaced at most 500 msec apart. These segmentation processes yielded 465,310 syllables and 9,139 bouts in total ($\approx$ 10.79 hours).

4.2 Clustering of Syllables

To perform an analysis parallel to the discrete human language data, we classified the segmented syllables into discrete categories in an unsupervised way. Specifically, we used an end-to-end clustering method, named the sequence-to-sequence ABCD-VAE, that combined (i) neural network-based extraction of syllable features and (ii) Bayesian classification, both of which worked in an unsupervised way (i.e., without top-down selection of acoustic features or manual classification of the syllables). This section provides an overview of our method, with a brief, high-level introduction to the two components. Interested readers are referred to S1 in the supporting information, where we provide more detailed information. One of the challenges to clustering syllables is their variable duration as many of the existing clustering methods require their input to be a fixed-dimensional vector. Thus, it is convenient to represent the syllables in such a format (but see Bellman and Kalaba, 1959; Levenshtein, 1966; Morita and O'Donnell, To appear, for alternative approaches). Previous studies on animal vocalization often used acoustic features like syllable duration, mean pitch, spectral entropy/shape (centroid, skewness, etc.), mean spectrum/cepstrum, and/or Mel-frequency cepstral coefficients at some representative points for the fixed-dimensional representation (Katahira et al., 2011; Tachibana et al., 2014; Mielke and Zuberbühler, 2013; Morita and Koda, 2019). In this study, we took a non-parametric approach based on a sequence-to-sequence (seq2seq) autoencoder (Bowman et al., 2016; Chung et al., 2016; Zhao et al., 2017; Sainburg et al., 2019b). The seq2seq autoencoder is a RNN that first reads the whole spectral sequence of an input syllable frame by frame (*encoding*. the spectral sequence was obtained by the short-term Fourier transform with the 8 msec Hanning window and 4 msec stride), and then reconstructs the input spectra (*decoding*; see the schematic diagram of the system provided in Figure 2a). Improving the precision of this reconstruction is the training objective of the seq2seq autoencoder. For successful reconstruction, the RNN must store the information about the entire syllable in its internal state—represented by a fixed-dimensional vector—when it transitions from the encoding phase to the decoding phase. And this internal state of the RNN served as the fixed-dimensional representation of the syllables. We implemented the encoder and decoder RNNs by the LSTM (Hochreiter and Schmidhuber, 1997, the encoder was bidirectional; Schuster and Paliwal, 1997).

One problem with the auto-encoded features of the syllables is that the encoder does not guarantee their interpretability. The only thing the encoder is required to do is push the information of the entire syllables into fixed-dimensional vectors, and the RNN decoder is so flexible that it can map two neighboring points in the feature space to completely different sounds. A widely adopted solution to this problem is to introduce Gaussian noise to the features, turning the network into the *variational* autoencoder (VAE, depicted in Figure 2c; Kingma and Welling, 2014; Bowman et al., 2016; Zhao et al., 2017, see also Coffey et al., 2019; Goffinet et al., 2019; Sainburg et al., 2019b for its applications to animal vocalization). Abstracting away from the mathematical details, the Gaussian noise prevents the encoder from representing two dissimilar syllables close to each other. Otherwise, the noisy representation of the two syllables will overlap and the decoder cannot reconstruct appropriate sounds for each.

The Gaussian VAE represents the syllables as real-valued vectors of an arbitrary dimension, and researchers need to apply a clustering method to these vectors in order to obtain discrete categories. This two-step analysis has several problems:

i The VAE is not trained for the sake of clustering, and the entire distribution of the encoded features may not be friendly to existing clustering methods.

ii The encoded features often include individual differences and do not exhibit inter-individually clusterable distribution (see Figuref 3d and the supporting information S1.4).

To solve these problems, this study adopted the ABCD-VAE, which encoded data into discrete categories with a categorical noise under the Dirichlet prior, and performed end-to-end clustering of syllables within the VAE (Figure 2b). The ABCD-VAE married discrete autoencoding techniques (Jang et al., 2017; van den Oord et al., 2017; Chorowski et al., 2019) and the Bayesian clustering popular in computational linguistics and cognitive science (e.g., Anderson, 1990; Kurihara and Sato, 2004, 2006; Teh et al., 2006; Kemp et al., 2007; Goldwater et al., 2009; Feldman et al., 2013; Kamper et al., 2017; Morita and O'Donnell, To appear). It has the following advantages over the Gaussian VAE + independent clustering (whose indices, except iii, correspond to the problems with the Gaussian VAE listed above):

i Unlike the Gaussian VAE, the ABCD-VAE is optimized for clustering, aiming at optimal discrete encoding of the syllables.

ii The ABCD-VAE can exploit a speaker-normalization technique that has proven effective for discrete VAEs: The "Speaker Info." is fed directly to the decoder (Figure 2b), and thus individual-specific patterns need not be encoded in the discrete features (van den Oord et al., 2017; Chorowski et al., 2019; Tjandra et al., 2019, this is also the framework adopted in the ZeroSpeech 2019, a competition on unsupervised learning of spoken human languages; Dunbar et al., 2019).

Table 1: The size of the training and test data used in the neural language modeling of Bengalese finch songs and the English language. The "SECL" portion of the test syllables was used to estimate the SECL (see §4.4).

Data type	Usage	# of bouts/sentences	# of syllables/words	
			Total	SECL
Bengalese finch	Training	9,039	458,753	—
	Test	100	6,557	4,657
English	Training	12,327	179,456	—
	Test	2,006	21,759	8,833

iii Thanks to the Dirichlet prior, the ABCD-VAE can detect the optimal number of categories on its own (under an arbitrarily specified upper bound; Bishop, 2006; O'Donnell, 2015; Little, 2019). This is the major update from the previous discrete VAEs that eat up all the categories available (Jang et al., 2017; van den Oord et al., 2017; Chorowski et al., 2019).

Note that the ABCD-VAE can still measure the similarity/distance between two syllables by the cosine similarity of their latent representation immediately before the computation of the classification probability (i.e., logits; cf. Mikolov et al., 2013; Deng et al., 2018).

4.3 Language Modeling

After the clustering of the syllables, each bout, $\mathbf{x} := (x_1, \ldots, x_T)$, was represented as a sequence of discrete symbols, x_t. We performed the analysis of context dependency on these discrete data.

The analysis of context dependency made use of a neural language model based on the current state-of-the-art architecture, Transformer (Vaswani et al., 2017; Al-Rfou et al., 2018; Dai et al., 2019). We trained the language model on 9,039 bouts, containing 458,753 syllables (Table 1). These training data were defined by the complement of the 100 test bouts that were selected in the following way so that they were long enough (i) and at least one bout per individual singer was included (ii):

i The bouts containing 20 or more syllables were selected as the candidates.

ii For each of the 18 finches, one bout was uniformly randomly sampled among those uttered by that finch.

iii The other 82 bouts were uniformly randomly sampled from the remaining candidates.

The training objective was to estimate the probability of the whole bouts $\mathbf{x}$ conditioned on the information about the individual s uttering $\mathbf{x}$: That is, $\mathbb{P}(\mathbf{x} \mid s)$. Thanks to the background information s, the model did not need to infer the singer on its own. Hence, the estimated context dependency did not comprise the correlation among syllables with individuality, which would not count as a major factor especially from a generative point of view.

The joint probability, $\mathbb{P}(\mathbf{x} \mid s)$, was factorized as $\mathbb{P}(\mathbf{x} \mid s) = \prod_{t=1}^{T} \mathbb{P}(x_t \mid x_1, \ldots, x_{t-1}, s)$, and, the model took a form of the left-to-right processor, predicting each syllable x_t conditioned on the preceding context `<sos>`, $x_1, \ldots, x_{t-1}$, where `<sos>` stands for the special category marking the start of the bout. See the supporting information S2 for details on the model parameters and training procedure.

4.4 Measuring Context Dependencies

After training the language model, we estimated how much of the context $x_1, \ldots, x_{t-1}$ was used effectively for the model to predict the upcoming syllable x_t in the test data. Specifically, we wanted to know the longest length L of the truncated context $x_{t-L}, \ldots, x_{t-1}$ such that the prediction of x_t conditioned on the truncated context was worse (with at least 1% greater perplexity) than the prediction based on the full context (Figure 1b). This context length L is called the *effective context length* (ECL) of the trained language model (Khandelwal et al., 2018).

One potential problem with the ECL estimation using the Bengalese finch data was that the test data was much smaller in size than the human language corpora used in the previous study. In other words, the perplexity, from which the ECL was estimated, was more likely to be affected by sampling error. To obtain a more reliable result, we bootstrapped the test data (10,000 samples) and used the five percentile of the bootstrapped differences between the truncated and full context predictions. We call this bootstrapped version of ECL the *statistically effective context length* (SECL).

It is more appropriate to estimate the SECL by evaluating the same set of syllables across different lengths of the truncated contexts. Accordingly, only those that were preceded by 20 or more syllables (including <sos>) in the test bouts were used for the analysis (4.657 syllables in total, Table 1).

4.5 English Data

For comparison, we also estimated the SECL of the language model trained on English data. The data were constructed from the Universal Dependencies English Web Treebank (the training and test portions; Silveira et al., 2014). The database consists of textual English sentences and each word is annotated with the lemma and PoS category. We constructed two versions of training and test data using these lemma and PoS representations of the words: Words may exhibit correlation with one another due to their semantics (e.g., same topic) when they are coded as the lemma. By contrast, the PoS representation of words removes such semantic information, and allowed us to assess the purely syntactic dependencies among the words (cf. Perfors et al., 2011). Note that this semantics-free data may serve as a more appropriate baseline for the study of birdsongs, whose variation is considered not to encode different meanings (Okanoya, 2007; Okanoya and Merker, 2007; Berwick et al., 2011, 2012; Gibson and Tallerman, 2012; Miyagawa et al., 2013, 2014) unlike alarm calls (Seyfarth et al., 1980; Ouattara et al., 2009; Suzuki et al., 2016).

The words that were preceded by ten or more tokens (including <sos>) in the test data sentences were used to estimate the SECL. Accordingly, the upper bound on the SECL (=10) was lower than in the analysis of the Bengalese finch data (=20). The reason for the different settings is that the English sentences were shorter than the Bengalese finch bouts: The quartiles of the bout lengths were 22, 44, and 68, while those of the sentence lengths were 7, 14, and 22 (where both the training and test data were included).

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