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Birdsong production involves the simultaneous and precise control of a set of muscles that change the configuration and dynamics of the vocal organ. Although it has been reported that each one of the different muscles is primarily involved in the control of one acoustic feature, recent advances have shown that they act synergistically to achieve the dynamical state necessary for phonation. In this work, we present a set of criteria that allow the extraction of gating-related information from the electromyographic activity of the syringealis ventralis muscle, a muscle that has been shown to be involved in frequency modulation. Using dynamical models of the muscle and syringeal dynamics, we obtain a full reconstruction of the zebra finch song using only the activity of this muscle. *Published by AIP Publishing.* https://doi.org/10.1063/1.5024377

Complex behaviors require a precise and coordinated control of a set of muscles. One example is the production of sound in oscine birds, a biological model that has been used to study several issues, such as neural coding, learning, and motor control. In this work, we show that it is possible to extract information about the phonation intervals from the activity of a muscle that has been shown to be involved in frequency modulation. This allows us to create synthetic songs using only the activity of this one muscle. Even more, since it has been recently reported that this muscle shows spontaneous activation during sleep, the tools presented here would allow us to traduce this activity into sound, and "listen" to the bird's dreams.

I. INTRODUCTION

Birdsong is a complex behavior that requires the precise control of a set of muscles affecting the shape and configuration of the syrinx, the avian biomechanical device involved in phonation. Sound is produced when oscillating tissues, called labia, modulate the airflow driven through the syrinx by the respiratory system.[1] In the case of oscine birds, there are two pairs of labia, each one at the juncture of a bronchus and the trachea.

In this way, there are two time scales involved in the dynamics displayed by the vocal organ. There are fast labial oscillations (typically in the order of kHz), and slow modulations of the syringeal configuration, controlled by the muscles (typically a few oscillations per second). These slow modulations typically share their time scale with the dynamics of the respiratory muscles.

There is an easy and clear way to monitor the fast scale, since the labial oscillations modulate the airflow and therefore generate sound. The slower modulations, such as the force exerted by the muscles on the syrinx (or the syringeal

deformations induced by these forces), are more difficult to measure, particularly *in vivo* (measurements in preparations have been recently reported[2]). Historically, the envelope of the electromyographic activity (EMG) on one given muscle, corrected by some delay, has been used as a proxy for its tension. Recent modeling efforts,[3] based on biomechanical models of the muscle and labia, allow the translation of EMG data into slow parameter modulations, specifically the forces exerted on the labia, and their lengths.

The first attempts to elucidate the role played by the different muscles assumed that each one would be in charge mostly of a unique acoustic feature of the song.[4–6] It has been reported that some muscles are primarily involved in the gating of the sounds, while others participate mostly in the control of the fundamental frequency.[4,5] In particular, the *syringealis ventralis* (vS) muscle has been reported to be involved in frequency modulation. Since the vS muscle is attached directly to the *medial ventral cartilage* (MVC), which is embedded in the *medial labia*,[7] its contraction would affect the length (and therefore the tension) of the oscillating labia responsible for the modulation of the flow. Assuming that the tension affects the restitution constant of the tissue (thought as an elastic material), it is natural to expect a positive correlation between tension and fundamental frequency.

Yet, further work showed that muscles act synergistically to put the syrinx in the required dynamical state necessary for phonation,[8,9] and therefore it is reasonable to expect the different muscles to operate concurrently in each activity they might be involved with. In this way, even if specific muscles are principally involved in the modulation of specific acoustic features, they might still contribute to a variety of actions. In fact, it has been shown that the same muscle in charge of gating could affect the fundamental frequency of the vocalizations as well.[10] Could we expect the activity of the muscles mostly involved in frequency modulation to also carry information on the gating dynamics involved in birdsong production? In fact, in the process of validating the

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model relating EMG and tension,[3] it was observed that in some syllables, vS was clearly active **right before** onsets and **right after** offsets. This had been also suggested by Vicario in early experiments.[11] That leads to the conjecture that vS does have a role in gating as well, or at least shows concurrent activity with muscles responsible for the gating.

Here, we test the hypothesis that the activity of the vS muscle also contains gating related information, which can be used to predict when the bird is singing. In Sec. II, we present the experimental methods, in Sec. III, we introduce a set of criteria for determining silent periods using the activity of one syringeal muscle. In Sec. IV, we present a synthetic song obtained using these criteria together with biophysical models of the phonation previously discussed in the literature. Finally, in Sec. V, we discuss our results.

II. EXPERIMENTAL METHODS

EMG activity of the vS muscle and sound was recorded simultaneously in five adult zebra finches (*Taeniopygia guttata*) during song production (bird names: ZF-MCV, 411, 4185, GY63, and 217). Experiments were performed in accordance with a protocol approved by the University of Buenos Aires (FCEN-UBA) Institutional Animal Care and Use Committee (C.I.C.U.A.L.). The vS muscle was exposed via incisions on the skin between the clavicles and the interclavicular air sac. Pairs of bipolar electrodes were inserted in the muscle and attached using a drop of surgical adhesive.

The signal from the electrodes was analogically amplified ($\times 225$) and filtered (high-pass RC filter 150 Hz) before acquisition. The acquired EMG signals were further filtered using the "Remove Noise" filter of the free software Praat,[12] and were further processed for analysis by calculating their envelopes. These were computed as the 90th percentile of the rectified signal in windows of fixed length (10 ms), and were then normalized to the range 0–1.

Sounds are presented throughout this paper using spectrograms, in which the spectral content is represented as a function of time. The spectrogram of the recorded song of one of the birds (namely, ZF-MCV) is presented in Fig. 1(a), while the simultaneous EMG activity of the left vS muscle (in blue), together with its envelope (green line), is presented in Fig. 1(b).

III. FREQUENCY CONTROL AND GATING RELATED ACTIVITY IN THE SYRINGEALIS VENTRALIS MUSCLE

In a recent work, we proposed a dynamical model of the biomechanics of the vS muscle and the oscillating labia.[3] The model is driven by the vS EMG activity, which determines the slack length of the muscle. The difference between the actual length and the slack length determines the force the muscle exerts on the labia to which it is connected via the MVC. The oscillating frequency of the labia (and thus of the sound produced) is calculated using a string model, in which its tension is proportional to its length, and the frequency proportional to the square root of the tension. The model predicts the modulation dynamics of the song's fundamental frequency, but it

does not deal with the determination of when the sound will be produced. Besides stretching the labia, vS contraction might cause configuration changes related to the gating of the phonations, but such a mechanistic link has not been measured or predicted.

Yet, it has been reported that the vS muscle also presents bursts of activity before the onset and after the offset of some syllables.[3,11] Although their role at these instances might be that of preparing the muscle to achieve the necessary configuration for the posterior phonation, it is parsimonious to expect that these pre- and post-syllabic bursts should be at least concurrent with the gating activity initiating and preventing phonation. Is it possible to link vS activity patterns with gating patterns for sound generation? Without attempting a mechanistic interpretation, we developed a set of criteria meant to predict song intervals based on the EMG activity. In this way, we propose that vS activity does reveal information on gating of sound production.

Based on the simultaneous inspection of song and vS EMG in a set of 5 animals, we propose three criteria that the EMG should satisfy during silent intervals. In total, they involve the definition of six parameters that were determined for each bird.

The parameters emerge in the following way:

i. First, the EMG signal is segmented into intervals in which it is above a certain threshold (first parameter).

ii. We observe that "short" intervals of activity are usually associated with bursts of activity at the onsets or offsets of "short" syllables. During these intervals, the EMG signal is generally below threshold. On the other hand, "long" intervals are usually associated with the longer and more complex syllables. To differentiate "short" and "long" intervals of activity, we define a second parameter $\Delta T_{interval}$ which represents the minimum duration of a "long" activity interval. These long intervals are indicated in Fig. 1(b) by the grey rectangles.

iii. In the case of short activity intervals, we search for local maxima of the activity, and predict silence while the signal remains above a certain percentage ($\mathbf{\Delta}_{max}$, third parameter) of the maximum value. These local maxima are indicated in Fig. 1(b) with green triangles.

iv. During long intervals, we observe that it is the significant minima, which are associated with the on-off transitions. In this case, we search for local minima. Of these, we select the ones that are significantly smaller than the adjacent maxima. By significant we mean that the difference between the minimum and the adjacent maxima is greater than a certain value ($\mathbf{\Delta}_{max-min}$, fourth parameter). The position of the significant minima is represented by black vertical lines in Fig. 1(b).

v. We predict silence while the difference of the signal with the maxima remains higher than a certain percentage of the difference between the significant minimum and the maxima ($\mathbf{\Delta}_{min}$, fifth parameter).

vi. Finally, we conjecture that there is a minimum duration of phonation, corresponding to the shortest syllable of the bird's repertoire ($\mathbf{\Delta}t_{min}$, sixth parameter). In this way, we predict as silent periods, the intervals that
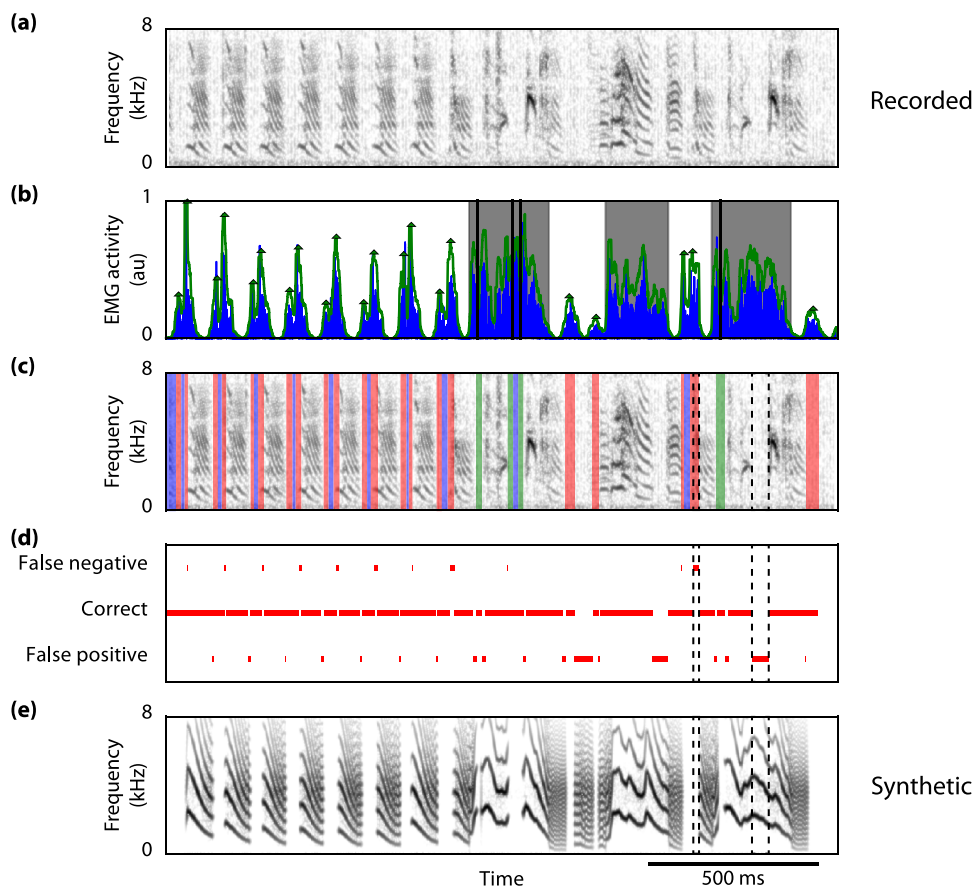
FIG. 1. Gating criteria and synthetic song. (a) Spectrogram of the recorded song. (b) Rectified EMG signal recorded from the vS muscle (blue) recorded simultaneously with the sound. Envelope of the EMG signal (green). Long intervals of activity above the threshold are outlined by grey rectangles. Significant minima in long intervals are indicated by black vertical lines, and maxima of activity in short intervals, with green triangles. (c) Spectrogram of the recorded song with predicted silent intervals defined by the criteria. Red rectangles: intervals corresponding to the first criterion (maxima in short intervals of activity). Green rectangles: intervals corresponding to the second criterion (significant minima in long intervals). Blue rectangles: intervals corresponding to the third criterion (minimum duration of phonation interval). (d) Performance of the criteria. False negatives represent intervals of sound that are predicted as silent, while false positives indicate silent periods that are predicted as sound intervals. (e) Spectrogram of the synthetic song obtained by applying the gating criteria.

(according to the other criteria) would correspond to phonating intervals but are shorter than this minimum duration.

We evaluated these criteria for the five different birds. In each case, we found that, by adjusting the parameters, it was possible to achieve a high prediction performance (accuracy of $76\% \pm 5\%$, over 70% in all cases). The results are summarized in Table I. The errors of the criteria are categorized into two classes. In false negatives ($5\% \pm 1\%$), the criteria predict a silent interval, while the bird is actually singing. In false positives ($19\% \pm 4\%$), we predict sound production, while the bird is silent.

The parameters defining the criteria were chosen for each bird after a systematic search leading to the maximization of the accuracy. In cases where different sets of parameters provided similar accuracies, we selected those that also minimized the percentage of false negatives. It is worth noticing that an alternative strategy could consist of minimizing the percentage of false positives. The parameters for each case are presented in Table II.

In Fig. 1, we show how these parameters are used to define the criteria met by the EMG activity for silent intervals,

for the case of bird ZF-MCV using the parameters presented in Table II. In Fig. 1(c), we represent the spectrogram of the song together with the predicted silent intervals. Red rectangles indicate intervals corresponding to the first criterion (short intervals, segments around significant maxima), green rectangles correspond to those defined by the second criterion (long intervals, on-off transitions associated with significant minima), and blue ones to the third criterion (minimum duration of phonation). In Fig. 1(d), we present the intervals corresponding to correct prediction, false positives, and false negatives for the bird ZF-MCV.

TABLE I. Accuracy of prediction of song intervals using the vS EMG signal for each of the birds analyzed.

Bird name	Accuracy(%)	False positive(%)	False negative(%)
ZF-MCV	84	13	3
411	78	18	5
4185	72	23	5
GY63	70	23	7
217	74	20	6

TABLE II. Values of the parameters defining the criteria for each of the birds analyzed.

Bird name	Threshold(au)	$\Delta T_{interval}$(s)	Δ_{max}	$\Delta_{max-min}$	Δt_{min}(s)	Δ_{min}
ZF-MCV	0.08	0.1	0.6	0.55	0.03	0.8
411	0.3	0.1	0.8	0.6	0.034	0.2
4185	0.12	0.1	0.5	0.5	0.034	0.5
GY63	0.009	0.12	0.5	0.1	0.04	0.25
217	0.01	0.1	0.5	0.2	0.03	0.4

IV. SONG SYNTHESIS

In a recent work, we presented and fitted a model that allows the fundamental frequency of song to be computed from the EMG activity of the vS muscle.[3] Here, we show that the activity of the vS muscle contains enough information to also estimate the time intervals when song is actually produced. In addition, it has been shown that song synthesis using a biomechanical model of the syringeal labial dynamics provides adequate renditions of zebra finch song,[10,13–17] even if the pressure gestures are represented as a stepwise function in the synthesis.[18] This is a non-trivial result, because playback of the synthetic song elicits a similar response in a highly specific neural nucleus of the song system, HVC (used as a proper name), to playback the bird's recorded song. Combining all these ingredients, we obtained a synthetic song using only the EMG activity of the vS muscle, for both estimating frequency modulation and gating activity. In previous work, we have already shown how to transform activity from muscle vS into frequency modulation. Now we show that the same muscle can be used to determine phonation intervals. The resulting synthetic song is presented in Fig. 1(e). In Figs. 1(c)–1(e), two dashed rectangles indicate intervals of false negative (the first one) and false positive (the second one). Notice that by inspecting the synthetic song, during false negative intervals, there is sound production in the real song, but not in the synthetic one. On the other hand, during false positive intervals there is synthetic sound, while the bird is actually silent.

In order to quantify the pertinence of the proposed criteria, we calculated the similarity between two synthetic songs. Both were generated with the labial tension predicted by the biophysical model of vS driven by EMG activity (see Ref. 3 for further details). In the first synthesis, we used an on-off proxy for the pressure defined by the onsets and offsets of the real song, that is, the phonation intervals of the synthetic song correspond exactly to the phonation intervals of the actual song. In the second synthesis, the phonation intervals were defined according to the criteria described above.

With this comparison, we specifically test the hypothesis that vS activity is capable of providing accurate gating information. The method of comparison was the calculation of the similarity of the two synthetic songs, using the software "Sound Analysis Tools,"[19] running on Matlab. The computed accuracy for the case displayed in Fig. 1 was 81% and the similarity was 96%. The similarity plot is shown in Fig. 2.
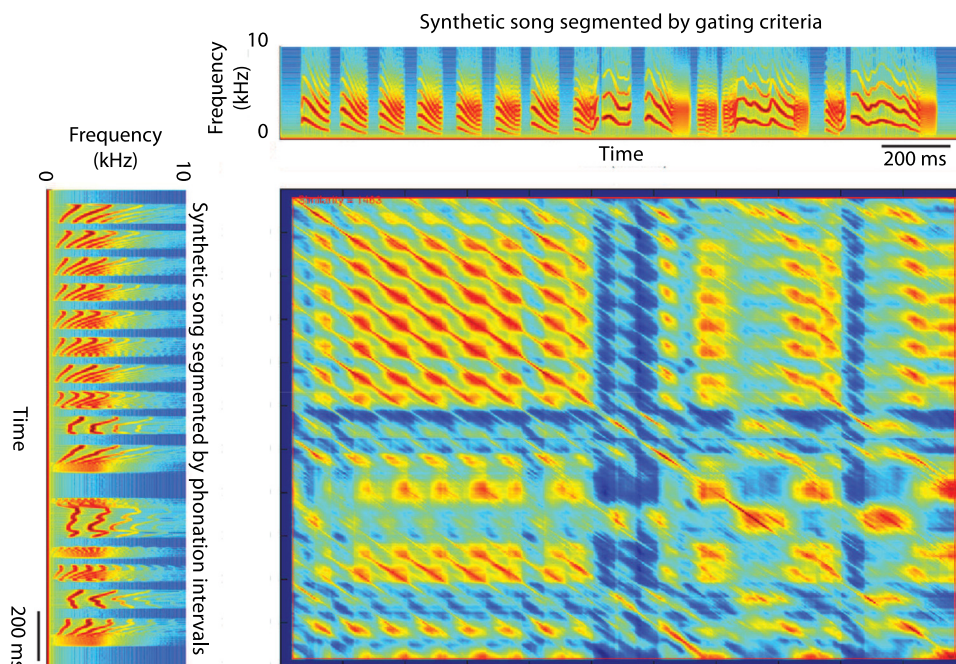

FIG. 2. Similarity plot for the two synthetic songs. Top: Synthetic song obtained by applying the gating criteria. Left: Synthetic song obtained by segmenting the song according to the actual sound onsets and offsets of the uttered song. Center: Similarity plot, red areas indicate sections of high similarity. Notice the high score of similarity across the diagonal. This plot was obtained using the software "Sound Analysis Tools" for Matlab.

The present synthesis is bound to be an approximation. There are many muscle pairs involved in the control of the oscine syrinx, and pressure has been shown to operate synergistically with the muscles in the control of the fundamental frequency.[20] Neither of these elements is considered here. Yet, we have shown that using only measurements of EMG from one of the two vS muscles it is possible to obtain a reasonable approximation of the song.

V. DISCUSSION

The first description of the functionality of the different syringeal muscles is evolving into a synergistic one, where the activity of individual muscles is correlated with different acoustical features.[8,9] Furthermore, the synergistic interaction between muscles operates in non-trivial ways. One of the vS control features might be the activation bursts at the onset of downsweep syllables. The activity patterns of vS have been shown to affect frequency modulation, but they occur also concurrently with gating and may be needed to move the medial labium during this activity.

Here, we show that the activity of the vS muscle contains gating related information *in an operational (as opposed to mechanistic) way*: a set of *ad hoc* criteria allows one to determine, from EMG, the phonating intervals with a success rate above 70%. We developed a set of simple criteria that were sufficient and consistent to accurately predict sound production intervals in a set of data from five different birds. The criteria perform remarkably well in the short simple syllables, in which the vS is mostly silent during phonation. This novel result was observed in all the zebra finch songs analyzed. The smooth downsweep modulation observed in these syllables might be the result of a relaxing labial tension after being tightened by a sudden vS activity burst.

It is evident that some of the gating information is missing, especially in the more complex syllables. It is likely that, in these cases, the action of different muscles is required to either generate more complex movement of the medial labium or move the lateral labium to facilitate sound onset and offset. It is known that other syringeal muscles, such as the *syringealis dorsalis* (dS), *trachoebronchialis ventralis* (vTB), and *tracheobronchialis dorsalis* (dTB), play active roles in gating of sound in zebra finch song, and incorporating their activity therefore could help improve the gating prediction.

Even with these limitations, the gating information obtained via these criteria enabled us to do a full reconstruction of the song using the activity of only one muscle. This might be particularly important since recently it has been shown that replay in sleeping birds is expressed at the level of the syringeal muscles.[21] The techniques described in this work would allow us then to translate these patterns into song, opening the door to study the behavioral correlates of brain activity during sleep. In other words, we are developing the tools that will allow us to "listen" to birds dreaming about song.

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