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Synthesizing avian dreams FREE

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ABSTRACT

During sleep, sporadically, it is possible to find neural patterns of activity in areas of the avian brain that are activated during the generation of the song. It has recently been found that in the vocal muscles of a sleeping bird, it is possible to detect activity patterns during these silent replays. In this work, we employ a dynamical systems model for song production in suboscine birds in order to translate the vocal muscles activity during sleep into synthetic songs. Besides allowing us to translate muscle activity into behavior, we argue that this approach poses the biomechanics as a unique window into the avian brain, with biophysical models as its probe.

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In this work, we present a novel method to decipher and interpret the neural activity patterns associated with bird songs during sleep. Our research reveals that thanks to the discovery of vocal muscles' activity during sleep, we can effectively translate these silent replays of neural activity into synthetic songs. Key to our approach is the utilization of a dynamical systems model for song production. By employing this model, we not only translate muscle activity into behavior but also propose that biomechanics serves as a unique window into the avian brain. Our biophysical models function as probes, shedding light on the intricate relationship between neural activity and song production.

I. INTRODUCTION

The phenomenon of nocturnal neuronal replay has been reported in different species and behaviors; see, for example, Refs. 1–3. The term replay refers to the appearance, during sleep, of neuronal activity patterns similar to those present during the execution of motor actions. In particular, these replays have been recorded in songbirds,¹ a group of approximately 4000 avian species in which learning plays a fundamental role in the acquisition of song.^{4,5} More specifically, replays have been found in brain areas involved in song generation and, therefore, the neural activation is related to motor

patterns controlling the respiration and the configuration of the vocal organ. In this way, among all the neural patterns recorded during sleep, there are some of them that can be defined as “song replays.” On the other hand, it is difficult to interpret the behavior associated with those neural patterns that differ from the diurnal one as the neural code for song generation has not been unveiled yet.

Recent studies may shed some light on this matter. It has been shown that the neural patterns that occur during sleep in the song system of zebra finches (*Taeniopygia guttata*) generate electrical activity in the muscles that control the configuration of the syrinx, the avian vocal organ.^{6,7} This result shows that the replay activity is distributed throughout the song system neural network. It is worth mentioning that one of the outputs of this neural network (the tracheosyringeal part of the hypoglossal nucleus nXIIIts) directly innervates the syringeal muscles, while the respiratory neural nuclei activate the respiratory muscles through indirect connections. A particularly interesting aspect of this result is that, although the neural code to convert a pattern of neural activity into behavior (song) is not currently known, there have been several advances in developing dynamical systems models to translate patterns of syringeal muscle activity into sound. Biomechanical models of birdsong production have been investigated in the past years, which are driven by physiological signals and are capable of synthesizing realistic song-like sounds.^{8–10} In this way, it is possible to use the recordings of

syringeal muscle activity during sleep as the input of a mathematical model of the avian vocal apparatus and synthesize songs.

These nocturnal muscle activity patterns have recently been found to occur in suboscine birds as well,¹¹ a set of species phylogenetically close to the oscine birds,¹² but which are believed not to require vocal learning to produce their species typical song.^{13,14} This result is surprising precisely because the consolidation of learning was a tempting explanation for the presence of nocturnal replay.^{15,16} In addition, the existence of muscle replay is a very useful result to investigate the activity of the central nervous system during sleep in sub-oscines, whose song-related neuronal architecture is much less known.^{17,18}

The translation of electrical activity in the vocal muscles of the suboscine vocal apparatus into song is possible, thanks to the recent report of a dynamical model of the suboscine vocal apparatus.¹⁹ In this work, we report the recordings of syringeal muscle activity during sleep in Great Kiskadees (*Pitangus sulphuratus*), a suboscine species, and use the dynamical model to synthesize the songs associated with them. In summary, we synthesize avian dreamed songs.

II. RESULTS

The Great Kiskadee song is composed of three syllables, with their typical “kis-ka-dee” sound giving the common name to the species. Sound is produced by the oscillation of two pairs of soft tissues in the syrinx,²⁰ called labia, when the airflow coming from the air sacs has enough energy to induce auto-sustained oscillations.²¹ In the case of Kiskadees, the fundamental frequency of the sound is mainly controlled by the respiratory system, via the air sac pressure.²² On the other hand, their most prominent syringeal muscle, the obliquus ventralis muscle²³ (OVM), has been shown to control and amplify an amplitude modulation present in the first syllable of their song.¹⁹ During the production of this syllable, the electromyographic (EMG) activity of the OVM is most prominent. It is highly stereotyped and consists of bursts with a characteristic frequency (160–180 Hz, see Fig. 1). Most notably, the characteristic amplitude modulation of this sound (which gives rise to a typical “harshness” in the sound), is controlled in the frequency by the activity of the OVM.

An example of a simultaneous measurement of sound and the OVM EMG activity during song production is presented in Fig. 1.

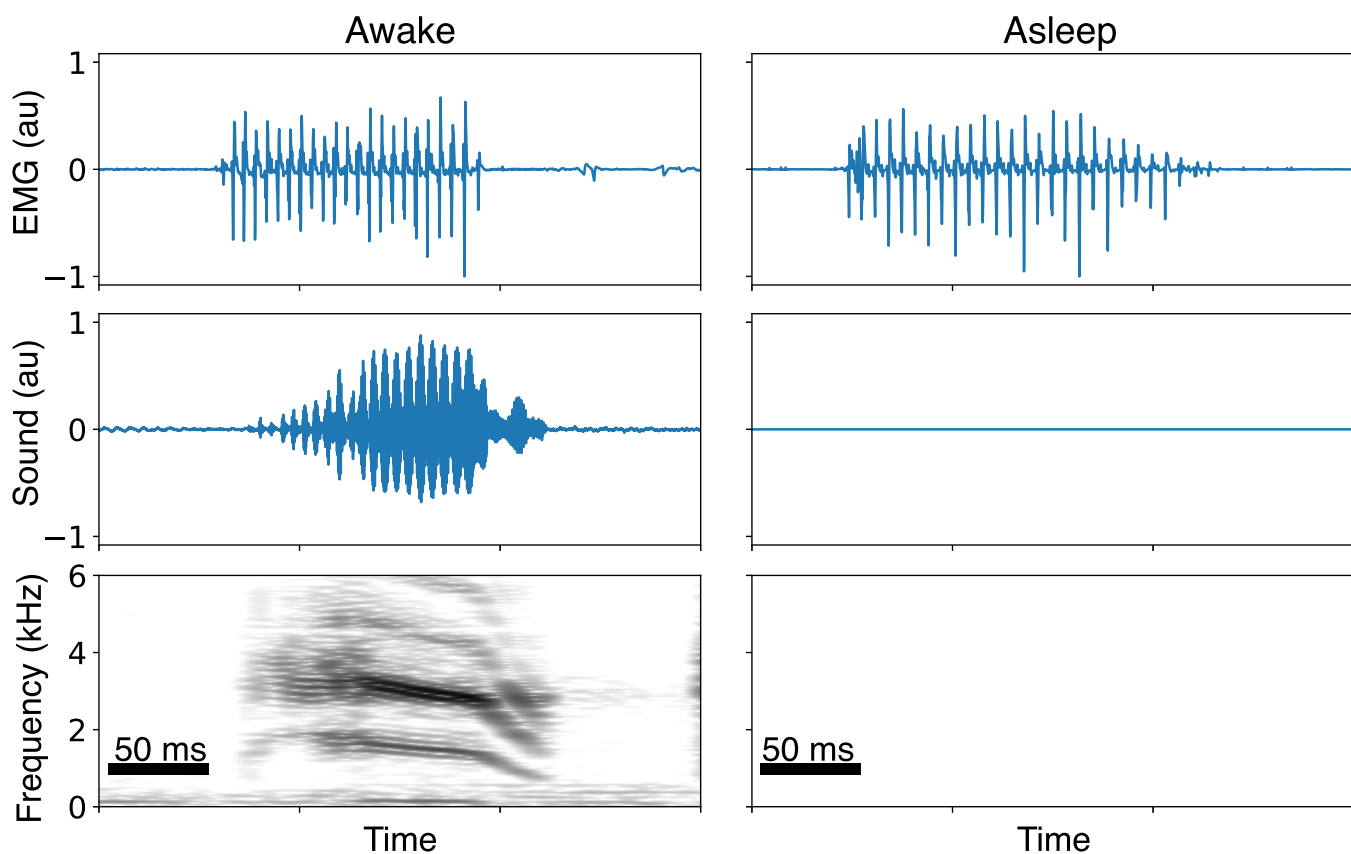


FIG. 1. Simultaneous measurement of the electromyographic (EMG) activity of the syringeal obliquus ventralis muscle (OVM) and sound during daytime song production (left) and during sleep (right) in Kiskadees. The top panel displays the EMG activity, the middle panel shows the measured sound, and the bottom panel shows the spectrogram of the sound.

In this species, patterns of song-like activation of the syringeal muscles occur spontaneously during sleep. An example of such activity is presented in Fig. 1, right panel. These patterns of burst-like activity are qualitatively similar to those produced during song (burst-like activation, with a well-defined characteristic frequency and a duration between 50 and 150 ms). However, their duration is more variable than that of song-related activity, and the bursting frequency is significantly reduced (for detailed descriptions and quantifications, see Ref. 11).

Since the respiratory rhythm is not altered during sleep, the high-energy airflow needed to start auto-sustained oscillations in the labia and generate sound is not produced and, thus, no sound is uttered while the OVM muscle is activated. Based on the known role of this muscle in the process of phonation, we propose to use a dynamical model of the phonation mechanism in order to translate this song-like activity observed during sleep into sound.

A. Model description in singing birds

We use a previously published model of the phonation mechanism and consider the existence of two coupled sound sources.^{9,19,24} The key aspects of the model are depicted in Fig. 2. The model reads

$$\dot{x}_i = y_i, \tag{1}$$

$$\dot{y}_i = \alpha \gamma^2 + \beta_i \gamma x_i - \gamma^2 x_i^3 - \gamma x_i^2 y_i + \gamma^2 x_i^2 - \gamma x_i y_i - \gamma^2 a(x_i - x_k), \tag{2}$$

with x_i being the position of the i labia ($i = 1, 2$, and $k \neq i$), α being a parameter representing the air sac pressure, β_i being a parameter representing the muscle activity, γ being a time scale, and a being the coupling between the two sources. This model represents the normal form of a biophysical model of the vocal production mechanism and has been shown to produce realistic synthetic songs using physiological recordings as input.^{8,25,26} Its capability to reproduce

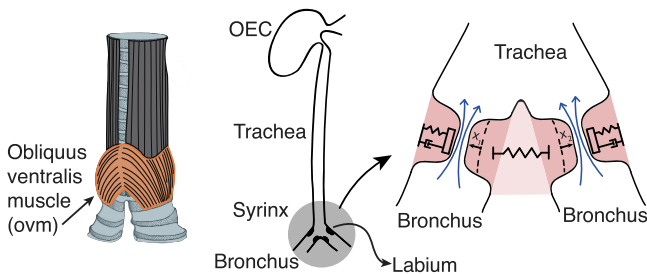


FIG. 2. Schematics of the Kiskadee vocal apparatus and model. Schematics of a ventral view of the Kiskadee syrinx, trachea, and bronchi (left panel). The oblique ventralis muscle (OVM) is shown in orange. The right panel shows the schematics of the vocal system: the syrinx is located at the juncture of the trachea and the bronchi and has two pairs of labia, the oscillating tissue. The airflow is modulated by the oscillations of the labia and travels through the trachea and a resonating cavity, called oro-esophageal cavity (OEC). Each pair of labia is modeled as a nonlinear oscillator, with a nonlinear restitution and dissipation (represented in the diagram as springs and pistons, respectively), and a coupling between them. The variables of the model, x_1 and x_2 , represent the medial position of each of the labia.

not only the fundamental frequency but also the spectral content of birdsong has made it a unique tool to study the song system.^{7,8,10} Note that most of the mathematical parameters of the model can be related to physiological parameters that can be obtained or inferred from recordings.

The oscillations of the labia, represented by the solution of this system, are responsible for the modulation of the airflow through the syrinx. The pressure fluctuations at the base of the trachea are driven by both sound sources and travel through the trachea, which can be modeled as an open-ended tube connected to a cavity, called oro-esophageal cavity (OEC).^{27,28} This pressure can then be computed as

$$P_b(t) = (y_1(t) + y_2(t)) - rP_b(t - 2\tau), \tag{3}$$

with r being the reflection coefficient at the juncture of the trachea and the OEC and τ being the time necessary for the fluctuation to travel through the trachea ($\tau = \frac{L}{c}$ with L being the length of the trachea and c being the speed of sound); $y_1(t) + y_2(t)$ are obtained from Eqs. (1) and (2). The transmitted pressure to the OEC is then

$$P_T(t) = (1 - r)P_b(t - \tau). \tag{4}$$

This cavity can be modeled as a Helmholtz resonator,^{29,30} where the displacement of the gas, z , follows the following differential equations:

$$\dot{z} = w, \tag{5}$$

$$\dot{w} = -\gamma_h^2 \omega_h^2 z - 2r_h \gamma_h w - \gamma_h^2 P_T, \tag{6}$$

with γ_h being a time constant, r_h being a damping factor, and ω_h being a characteristic frequency of the cavity.^{27,29} The complete song production model is, therefore, described by Eqs. (1)–(6). The input of this model is the parameters (α , β_i), with its final output, the time trace $z(t)$, representing the synthetic sound produced. Briefly, the sound source is modeled with Eqs. (1) and (2), generating a sound wave that is passively filtered by a tube [Eqs. (3) and (4)] and a Helmholtz resonator [Eqs. (5) and (6)]. The beak filtering properties can be neglected.

In the case of Kiskadees, which modulates the fundamental frequency of the vocalizations and controls the gating using the air sac pressure (controlled by the respiratory muscles), we considered the β_i parameter as a constant value modulated harmonically at the EMG frequency (see Sec. V). We then obtained a time trace of α (parameter related to pressure), compatible with experimental measurements and capable of reproducing the fundamental frequency evolution of a typical Kiskadee syllable (see detailed description in Sec. V). Keeping in mind that our goal is to translate EMG activity produced during sleep into sound, we propose a method to obtain this trace without explicitly using pressure measurements (which are not informative during sleep as they follow quiet breathing).

B. Using the dynamical model to translate vocal muscle activity into sound

To extend this procedure for the nighttime patterns, we rely on the highly stereotyped nature of the Kiskadee song. First, since no deviations from the breathing pressure patterns are observed during sleep, we propose to use the previously described pressure gesture $\alpha(t)$. However, since the duration of the activity during sleep is

significantly more variable, the duration of the pressure gesture was adjusted accordingly. The first challenge is then to infer the appropriate duration of the pressure gesture, given the measured EMG pattern during sleep.

Second, the timing of EMG and phonation must be inferred for the case of sleep activation, when only the EMG song-like pattern is measured. That is, it is necessary to correctly align $\alpha(t)$ with the EMG activity. We propose to estimate the timing and duration of the phonation interval from activity observed during singing.

For a set of 95 instances of song from 2 birds, we calculated the sound duration, EMG modulation frequency, EMG duration, EMG frequency, and EMG onset time (relative to phonation) of the first syllable. The Pearson correlation between these variables is presented in the left panel of Fig. 3. This shows a compact representation of all the calculated values, avoiding auto-correlations and repetitions. The high correlation between the EMG duration and sound duration (correlation coefficient of 0.80) shows that the sound duration can be estimated from the EMG duration. In the middle panel of Fig. 3, we show the relationship between these two variables (red and blue dots indicate different individuals), together with a linear fit, computed with an ordinary least squares implementation included in the statistical package “statmodels” in Python. The blue band around the fitting curve indicates the two sigma (95%) confidence region. We propose to use this linear fit to calculate the sound duration for EMG patterns measured during sleep. Once this value is calculated from the EMG duration, the pressure patterns were adjusted in duration via a linear stretching or compression to this duration. On the other hand, the EMG onset time does not present a high correlation with any of the measurable variables. The most parsimonious strategy is then to sample its value from its distribution (presented in the left panel of Fig. 3). This procedure allows us to drive the model using the EMG data observed during sleep.

The result of this procedure is presented in Fig. 4, where we show the synthetic sound generated for both awake singing and sleep

patterns of activity. Note that in the Kiskadee song, the presence of low-frequency modulations in the sound amplitude imparts a rough tonality to the sound.¹⁹ Consequently, the lower average modulation frequencies observed in the replays recorded during sleep result in sounds that are rougher compared to those generated when the bird is awake.

We generated the synthetic syllables by employing the duration and frequency modulation parameters derived from 95 EMG activity files recorded simultaneously with song execution. Similarly, synthetic songs were created using frequency modulation and duration parameters, computed from the EMG activity duration as previously described, based on 103 records of EMG activity patterns measured during sleep. For each synthesis, we computed the spectrum using the fast Fourier transform (FFT) of the signal. The spectrum computation for the audio file was executed through a Python implementation. Applying the fast Fourier transform (FFT) to the audio data allowed us to obtain its frequency domain representation. The resulting spectrum was truncated to retain only the first half, as it is symmetrical. We computed the magnitude values of the frequency components and performed normalization with respect to the length of the audio data. Subsequently, the power spectrum was derived by squaring the magnitude values.

Subsequently, we computed 4465 Pearson correlation values between the spectra corresponding to the synthesis with song parameters (Fig. 5, left panel) and 5253 correlations between the spectra of the syntheses with sleep parameters (Fig. 5, middle panel). The distributions were compared using the Z-test, resulting in $Z = 4.51$ (indicating a significant difference). This finding aligns with our earlier work, where we observed significantly distinct values in the durations of activity patterns and modulation frequencies for awake and asleep birds.¹¹ In Ref. 11, it was observed that in sleeping birds, the replay activity patterns exhibited a broader range of durations when compared to those recorded in singing birds. Additionally, the average modulation frequency identified in

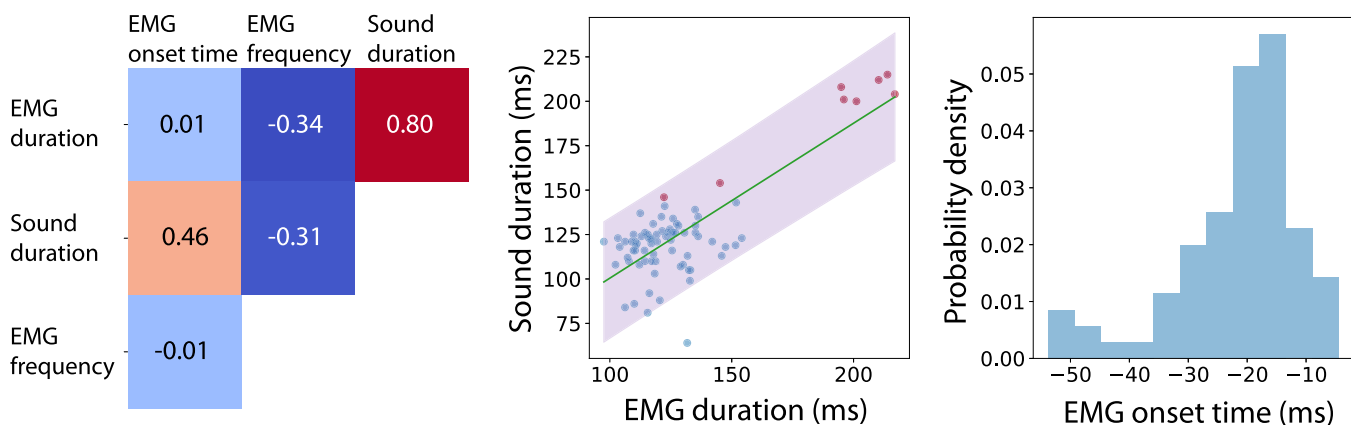


FIG. 3. Analysis of the relationship between OVM EMG activity and sound characteristics ($N = 95$ vocalizations from two different birds). Correlations between a set of relevant features (left panel): EMG duration, EMG onset time, EMG frequency, and sound duration. Each block shows the Pearson correlation value between two features avoiding auto-correlations and repetitions. Linear regression of sound duration and OVM EMG activity duration (green line, 95% confidence interval represented as the shaded region) (middle panel). The different colors indicate different birds. Probability distribution of EMG onset time, relative to sound onset time (left panel).

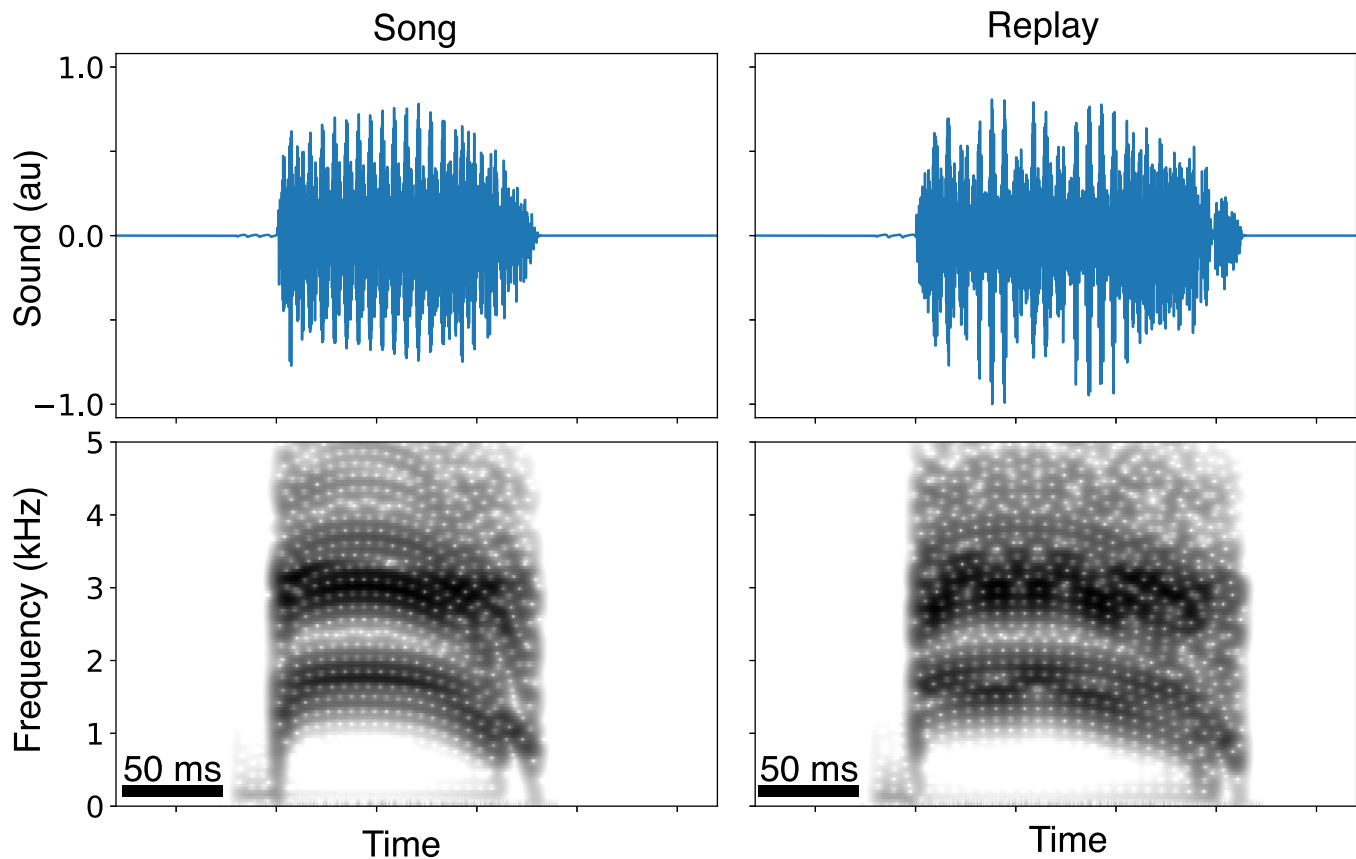


FIG. 4. Synthetic sounds produced by the model driven by EMG produced during daytime singing (left panel) and by EMG observed during sleep (right panel). The parameters used for these simulations were $(\gamma, a, r, L, c) = (10000, 0.0025, 0.4, 0.1m, 350 \frac{m}{s})$. The tracheal length was estimated at 10 cm (approximately three times the value used for a zebra finch,⁸ a bird three times smaller), and $c = 350 \frac{m}{s}$ stands for the speed of sound. The parameter γ in the normal form is a time scale factor.²⁹ The reflection coefficient at the end of the trachea was fixed at 0.4, a value low enough that ensures that the Helmholtz frequency ω_h predominates as the main resonance of the upper tract filter.²⁹ The chosen coupling constant between the two sound sources, denoted as $a = 0.0025$ ($a \ll 1$), aligns with findings in,¹⁹ which showed that muscle denervation results in a significant decrease, though not elimination, of slow modulations in sound amplitude.

sleeping birds was approximately 20 Hz lower than that recorded in their singing counterparts. Finally, we calculated the correlations between the spectra of the sleep and song syntheses (Fig. 5, right panel). When comparing this distribution with the correlation values obtained from syntheses with parameters from singing birds, a highly significant difference emerged ($Z = 12.6$).

III. TRILLS

The great Kiskadees exhibit a distinct vocalization pattern in the context of territorial disputes. This behavior is part of a multimodal display that involves the extension of a crest of feathers on the head. The vocalization consists of a sequence of short syllables generated at a rate between 10 and 20 Hz, commonly referred to as a “trill.” Analyzing muscular activity patterns during sleep reveals consistent activity patterns corresponding to these vocalizations:

sequences of brief activation patterns occurring at a rate between 15 and 20 Hz.¹¹

Interestingly, each of these patterns exhibits a modulation of approximately 150 Hz, akin to the modulations observed in EMG activity recordings during the typical “song” syllables. Therefore, we generated a synthetic sound file using the same model employed for synthesizing natural song syllables, based on one of these EMG activity patterns. In the illustrated example, the trill comprised 16 short syllables, each generated with the duration and modulation of the corresponding EMG pattern segment. Subsequently, these syllables were sequentially spliced, with each syllable initiated at the onset of the corresponding EMG pattern. The synthetic trill is depicted in Fig. 6. Remarkably, during the recording of these “trill” activity patterns, the sleeping bird exhibits the same crest extension observed during trill execution in territorial disputes (see supplemental material in Ref. 11).

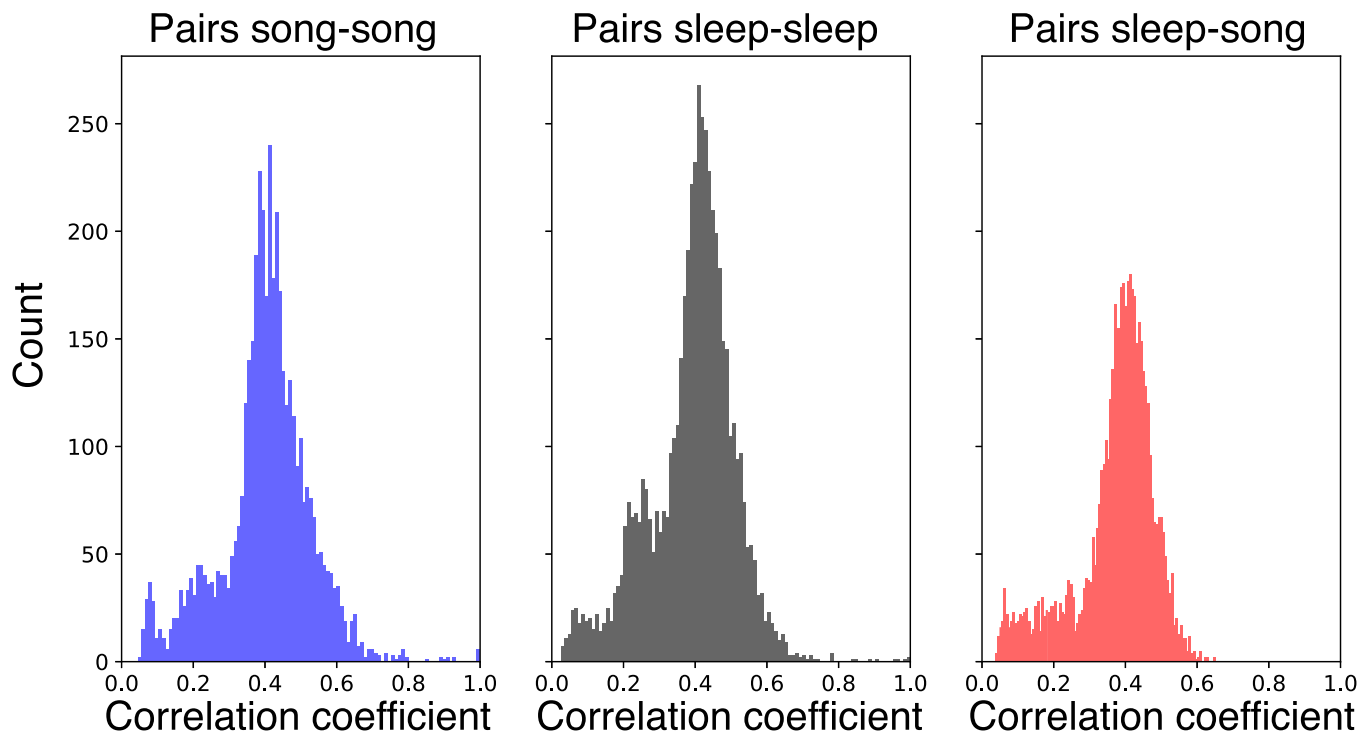


FIG. 5. Correlations for synthetic sounds generated from EMG recordings during singing and sleeping. The Pearson correlation coefficients are calculated from pairs of spectra of synthetic sounds with song parameters (left panel), sounds with sleep parameters (middle panel), and pairs of sleep and song parameters (right panels).

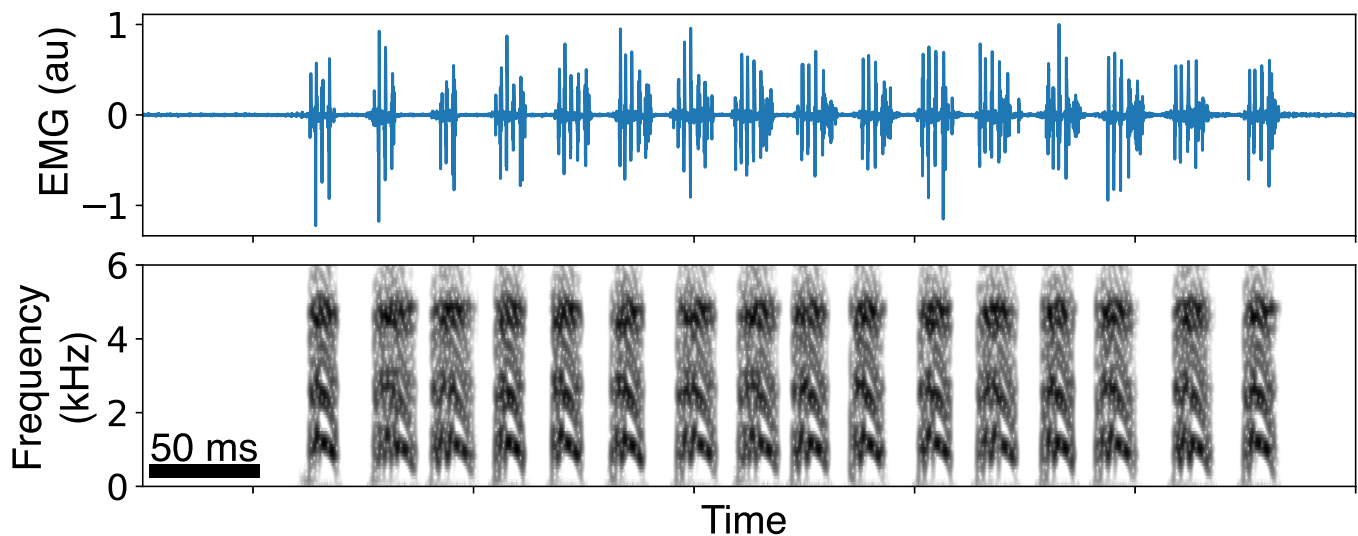


FIG. 6. Trill EMG activity recorded during sleep and synthetic sounds generated by the dynamical model. The trill is a different type of vocalization generated by the Kiskadee in territorial disputes. The EMG activity recorded in the OVM muscle during sleep exhibits the characteristic modulation of the trill. The synthetic sounds were generated using the same set of parameters as in Fig. 4.

IV. DISCUSSION

Replays of behavior-related neural activity during sleep have been shown to occur in different species, including rodents and oscine birds. In oscine birds, while sleep is known to be necessary for song development,^{31,32} the specific role of these replays is still under discussion.

In oscine birds, it has been shown that, while the pressure gesture needed to produce song is inhibited during sleep, these events of neural replay descend to the syringeal muscles, which contract (as if attempting to produce sound) during sleep.⁶ These patterns of muscle activation during sleep can be triggered by sensory cues (song playback) or even emerge spontaneously.

The fact that these patterns can be measured at the syringeal muscles of suboscines, species where we have recently shown that patterns of song-like activation occur spontaneously during night sleep, provides an important clue to unveil the role of replays. Since they are usually considered non-learners, and the lack of dialects in the Kiskadees songs supports this hypothesis for this specific species, the occurrence of “song replays” may suggest the existence of an underlying neural structure, which predates the evolution of learning.¹¹ It also provides a unique tool to study the suboscine song system. In suboscines, there is little knowledge of the neural structures related to song production. While some areas have been shown to be similar to those of the oscine song system,¹⁸ they seem to lack the highly developed telencephalic nuclei of the oscines. Hence, studying replays by inspecting the electrical activity of different brain areas could be challenging.

On the other hand, the lack of a neural code to translate the neural activity into behavior has limited the understanding of replays, even in species where the song system is well described. Despite having neural recordings correlated with song, it is yet not possible to interpret in terms of behavior those nocturnal neural patterns that depart from what the bird generates while singing. In this work, we argue that biomechanics can provide a unique advantage to progress in this direction. First, the EMG activity recorded in the syringeal muscles represents the integrated output of the central nervous system. That is, a great part of the translation has already been done by the system itself. In addition, we have a more complete understanding of the physical mechanisms by which these instructions are translated by the muscles into specific properties³³ (such as labial tension) and how these affect the behavioral output.

In this work, we have shown that dynamical systems models of biomechanics can, in fact, translate these patterns of muscle activation into behavior. The use of physical models which capture the underlying dynamical mechanisms, allows us to extrapolate their region of validity, and extend it to try to understand how patterns that differ quantitatively from those produced during song production, are translated into sound. In this way, we were able to create physically plausible renditions of sound. The strategy proposed here can be generalized to other species: if there are uninhibited outputs of the central nervous system, dynamical models of the biomechanics can be used to translate these signals, which represent a global readout of the central nervous system, into behavior.

In other words, in this work, we have shown how physical models can be used to listen to what a bird is dreaming.

V. METHODS

A. Birds

Great Kiskadees were captured using mist nets in La Plata, Buenos Aires, Argentina, as described in the permit DI-331-2018-GCDEBA-DFYMAGP issued by the Buenos Aires Province. Birds were transported to the laboratory for experimentation and housed in acoustic chambers in a 14:10 h light cycle. Food and water were provided *ad libitum*. After the conclusion of the experiments, electrode removal, and full recovery from surgery, birds were released in the area where they had been captured. Experiments were conducted according to the regulation of the Institutional Animal Care and Use Committee of the University of Buenos Aires (CICUAL, Protocol No. 113, 2019).

B. Surgery

To measure the EMG activity of the obliquus ventralis muscle, custom made bipolar electrodes (25 μm diameter, stainless steel 304, heavy polyimide HML insulated, annealed, California Fine Wires Company) were implanted in the left side of the obliquus ventralis muscle as previously described.³⁴ The EMG signal was analogically filtered (150 Hz high-pass RC filter) and differentially amplified (by a factor of 225) by a custom-built electronic board, which was carried on a previously fitted backpack.

C. EMG and song recordings

After surgery, birds were housed in custom-built acoustic chambers. EMG and audio signals were acquired simultaneously at a 44 150 Hz sampling rate. Signals were digitized using a data acquisition device (DAQ, National Instruments USB-6212), connected to a PC, and using custom MATLAB scripts. Sound was recorded using a condenser microphone (Takstar SGC568) connected to an audio power amplifier (Behringer MIC100). EMG signals were digitally filtered, using a 150 Hz high-pass and a 3 kHz low-pass five-order Butterworth filters applied in turn.

D. Construction of physiological instructions (α , β_i)

We first synthesized 1s segments of sounds using $\beta_1 = \beta_2 = -0.061$ and α in the range $(-0.6, 0)$, for a one-source model. For each of this (α, β_i) , we calculated the fundamental frequency of the sound, computed as the location of the FFT maxima of $y(t)$. This range of parameters allowed us to produce sounds with frequencies in the range of 500–2000 Hz, which covers the typical range for the Kiskadee.

To produce a realistic sound, we then extracted the fundamental frequency time trace of a real Kiskadee syllable. Then, we estimated α , which produced the most similar frequency for each value and, thus, transformed the frequency time series into an α time series. Finally, the α time series was set to a proper value on silent periods [a value for which no oscillatory solutions exist in the dynamical system of Eqs. (1) and (2)],

$$\alpha(t) = \begin{cases} \alpha(f) & \text{if } t_s < t < t_e \\ 0.05 & \text{otherwise} \end{cases}, \quad (7)$$

where t_s stands for the start time of phonation, t_e stands for the ending time, and $\alpha(f)$ stands for the time trace previously obtained.

The EMG activity was introduced as a forcing of the β_i parameters. Based on the typical EMG activity, the most straightforward way to introduce this forcing is as a harmonic

variation in the β_i time trace. The parameters β_i were modified according to

$$\beta_i(t) \rightarrow \beta_i(t) + A \sin(2\pi ft), \quad (8)$$

with f being the EMG frequency (in Hz). The amplitude parameter of the forcing was defined as

$$A(t) = \begin{cases} 0.035 & \text{if } t'_s < t < t'_e \\ 0 & \text{otherwise} \end{cases}, \quad (9)$$

where t'_s and t'_e stand for the start and end time of the EMG activity.

As outlined in Ref. 19, the denervation of the OVM results in a notable reduction in sound amplitude modulations, although it does not entirely eliminate them. To accommodate for this residual effect, we employ the values $\beta_1 = -0.061$, $\beta_2 = -0.091$.

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AUTHOR DECLARATIONS

Conflict of Interest

The authors have no conflicts to disclose.

Author Contributions

Juan F. Döppler: Investigation (equal); Visualization (equal). **Melina Atencio:** Investigation (supporting). **Ana Amador:** Conceptualization (equal); Investigation (equal); Supervision (equal); Writing – original draft (equal). **Gabriel B. Mindlin:** Conceptualization (lead); Funding acquisition (lead); Investigation (lead); Writing – original draft (lead).

DATA AVAILABILITY

Data and codes that support the findings will be available at <https://zenodo.org/records/10719129>.

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