When Does Song Begin? Exploring Preparatory Features of Song Respiration

Nguyen, M. N., Arnold, R. L., Magee, A. R., Zacharias, F., Williams, A. M., & Cooper, B. G.

Psychology Department, Texas Christian University, Fort Worth, TX 76129

INTRODUCTION

Human language is an action wherein one plans for, produces, and terminates sound production. Errors in motor planning for initiation and cessation of speech lead to vocal dysfluency. Motor control of respiration is critical for the myoelastic aerodynamic mechanism of sound generation that is used by humans and many other vocalizing animals. Developing our understanding of how the forebrain directly modulates brainstem respiratory circuitry to produce sound is essential for understanding language initiation. Songbirds are an animal model for speech production in humans because of the similarities between song learning and production and language acquisition and speech production. Zebra finches (*Taeniopygia guttata*) sing a learned song that is composed of a stereotyped syllable sequence (motif), and the motif is preceded by a variable number of introductory notes (1-7 notes). It has been argued that introductory notes are a preparatory motor behavior that facilitates the production of the upcoming song. Here we explore whether the respiratory patterns producing introductory notes are a form of song motor preparation by comparing similarity in respiratory patterns during the introductory note sequence compared to the first song syllable. Our goal was to determine whether the introductory note respiratory cycle (inspiration followed by expiration) sequence becomes increasingly similar to the first song respiratory cycle. We postulated that if introductory notes are preparatory in nature, then the birds should produce increasingly similar motor gestures to the song motor pattern. These results will shed light on whether or not introductory notes are preparatory for song. Our broader goal is to understand the neural control of motor preparation, therefore these results will be foundational for future studies aimed at exploring the neural circuits necessary for preparing to sing.

METHODS

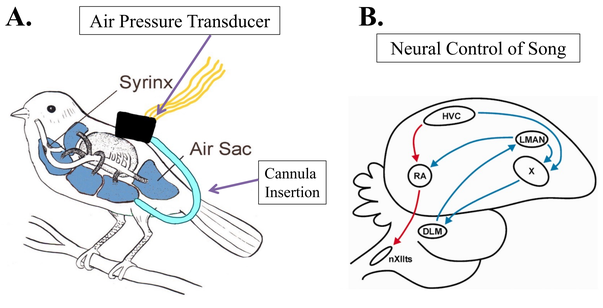

Fig. 1 – Methods and Procedures

A) Subsyringeal air pressure was recorded from six zebra finches in the presence of a female and while in isolation.

- Each bird was accustomed to holding the pressure transducer on its back, held in place by a Velcro elastic band. A counter-weighted balance arm was used to offset the weight of the pressure transducer and accompanying wires to facilitate free movement.
- The cannula was inserted into an anterior thoracic air sac, allowing for measurement of air pressure changes inside the air sac by connecting the free end of the cannula to a piezo-resistive pressure transducer.

B) The neural control of song is similar to the neural system necessary for language production. HVC (proper name) is thought to be necessary for song initiation, and RA (nucleus robustus of the arcopallium) control brainstem areas necessary for motor control of song.

Are introductory notes a form of song motor preparation or motor practice?

1. Respiratory analyses of the zebra finch introductory notes

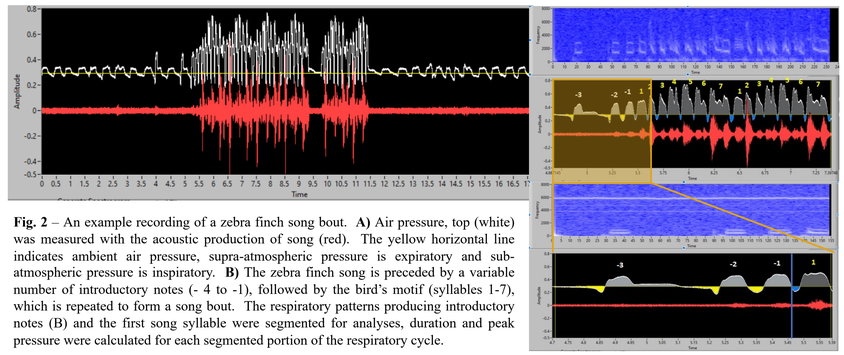

Fig. 2 – An example recording of a zebra finch song bout. **A)** Air pressure, top (white) was measured with the acoustic production of song (red). The yellow horizontal line indicates ambient air pressure, supra-atmospheric pressure is expiratory and sub-atmospheric pressure is inspiratory. **B)** The zebra finch song is preceded by a variable number of introductory notes (- 4 to -1), followed by the bird's motif (syllables 1-7), which is repeated to form a song bout. The respiratory patterns producing introductory notes (B) and the first song syllable were segmented for analyses, duration and peak pressure were calculated for each segmented portion of the respiratory cycle.

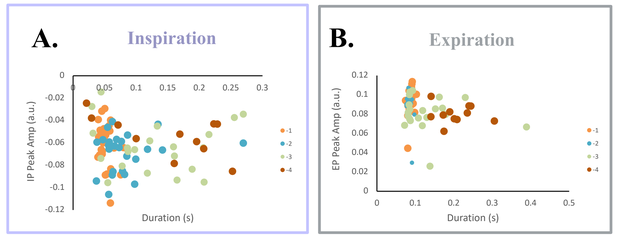

Fig. 3 – Example data analysis for each bird for all recorded songs. **A)** Left: Each data point corresponds to the duration and peak negative pressure (MB, inspiration). **B)** The vocal portion of the introductory note is generated by an expiratory pulse (EP, expiration) of air. The peak amplitude and duration for each measured EP is displayed.

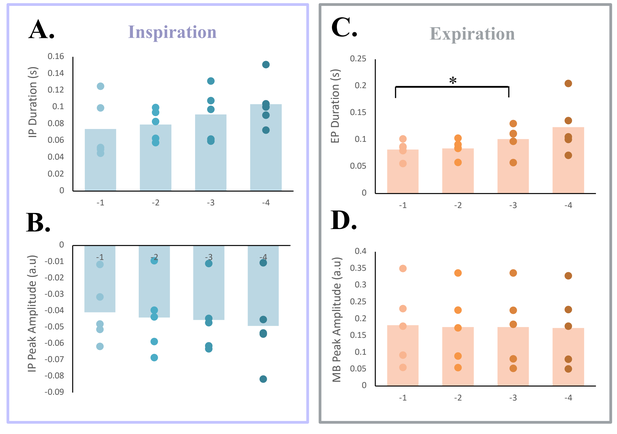

Fig. 4 – Group averages and individual animal changes (N = 5) in respiratory patterns during the production of introductory notes. **A)** The average duration for each introductory note is shown with the dots corresponding to individual animals. Three animals show a decrease in MB duration and two animals decrease and then increase in duration. MB peak amplitude does not change significantly across the sequence of introductory notes. **C)** The EP duration decreases significantly as birds repeatedly sing introductory notes ($F(3,12) = 3.923$, $p = .037$, $\eta_p^2 = .495$). The peak amplitude does not change as a function of order within the sequence.

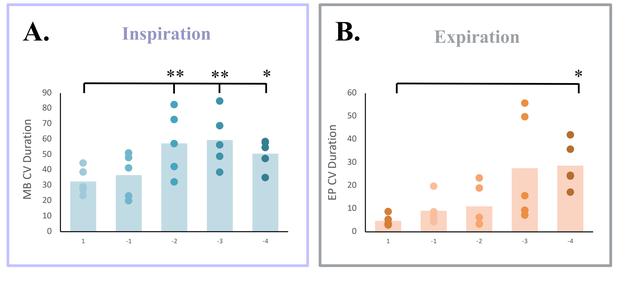

Fig. 5 – Motor Stereotypy emerges during the production of the introductory note sequence. **A)** Coefficient of variation (CV) for MBs during the introductory note sequence and the first song syllable illustrates a significant increase in motor stereotypy emerging by the last introductory note MB compared the earlier MBs in the sequence ($F(4,16) = 6.802$, $p = .002$, $\eta_p^2 = .630$). **B)** Motor stereotypy emerges early in the introductory note sequence for the EPs, as only the -4 introductory note is significantly different than the first song syllable EP ($F(4,16) = 3.909$, $p = .02$, $\eta_p^2 = .497$).

Are introductory notes a form of song motor preparation or motor practice?

2. Respiratory analyses of the zebra finch introductory notes compared to a target introductory note or song syllable

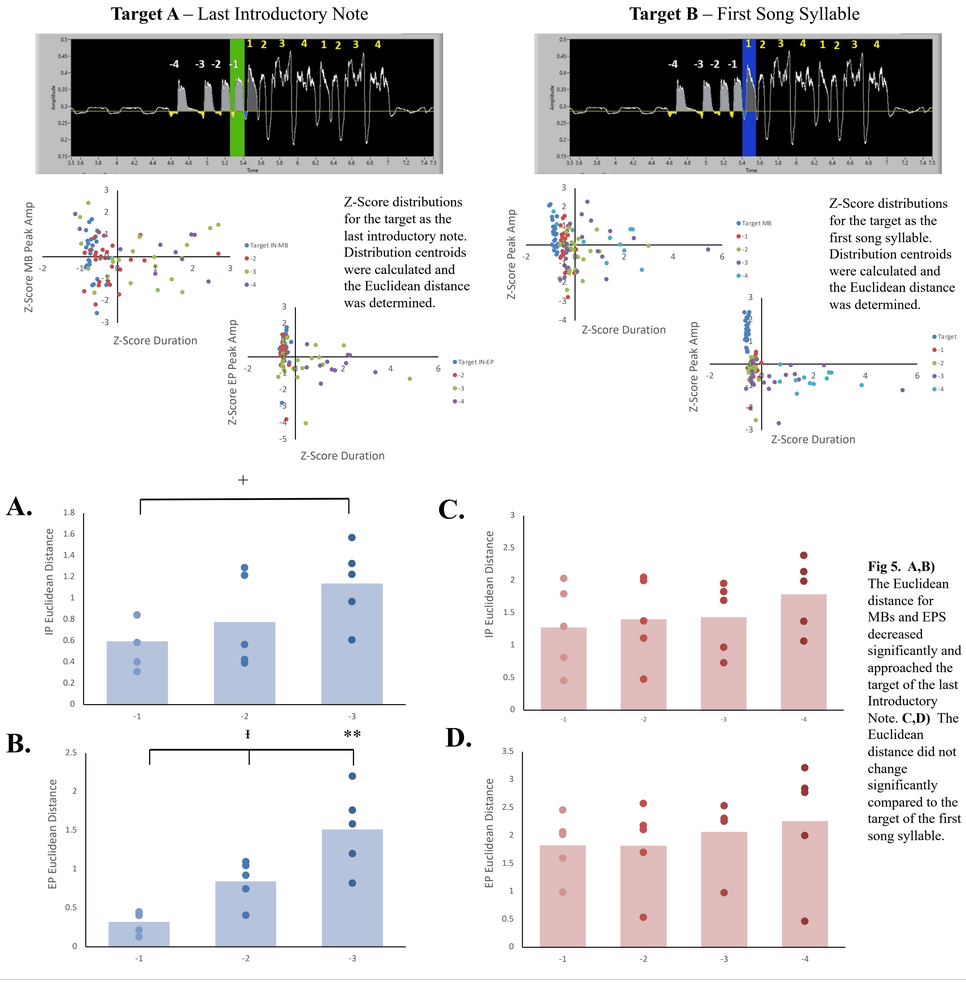

Fig 5. A,B) The Euclidean distance for MBs and EPS decreased significantly and approached the target of the last Introductory Note. **C,D)** The Euclidean distance did not change significantly compared to the target of the first song syllable.

CONCLUSIONS

1. The results illustrate that introductory notes show a closest approximation to the last introductory note in the sequence and not to the first song syllable; this finding was even true for the mini-breaths, where birds are preparing the air supply for the upcoming song syllable and are aphonic. We expected to see greater preparatory activity for the mini-breaths because they are unique respiratory feature of song, and they lack temporal modulation and variation characteristic of sound production. Given the more stereotyped and fast tempo required to produce these motor gestures, we expected to find the greatest preparatory activity.

2. This suggests that introductory notes may function as a form of motor practice for refining the production of the introductory notes themselves but not for song. Alternatively, introductory notes may allow for a biomechanical enhancement of song production by bringing the thoracic cavity into a rapid movement pattern that generates the fast respiratory tempo of song.

3. Our next experiment will attempt to disrupt song onset during introductory notes. If the introductory notes are a form of motor preparation for the stereotyped motor control of song, then one should be able to disrupt song onset by perturbing either behaviorally or physiologically motor control of song.

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