The Peripheral Antecedents of the Decision to Act

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Summary

How does one decide to act? In humans, the "decision" to initiate a behavior can occur several seconds before an action is undertaken and can even occur without conscious awareness. Here we explore whether we can predict when a nonhuman animal is going to engage in a self-initiated behavior.

Singing in songbirds is a learned behavior that is passed down from one generation to the next via imitative learning. Birds initiate song in response to the presentation of a female bird (directed) or spontaneously when in isolation from other birds (undirected). The production of song requires the control of respiratory, vocal organ, and upper vocal tract motor systems; these diverse motor systems are controlled by the activation of precise neural networks within specific areas of the songbird brain. Although much is known about the neuromuscular control of song, the neural and peripheral mechanisms underlying song initiation and termination have received less attention. Here we explore in two songbird species whether song initiation and termination can be predicted by measuring changes in respiratory patterns prior to, during, and after song. We quantified changes in respiratory rate and amplitude, as well as changes in time spent in the inspiratory versus expiratory cycle to determine whether specific features of respiration were tied to onset or offset of song. Measurements of respiratory patterns were undertaken in zebra finches (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata* var. *domestica*). Preliminary data suggest that respiratory patterns change predictably within the last second prior to when a bird initiates song. Following song, there is clear evidence of respiratory changes due to singing-related exertion. Our findings illustrate that the occurrence of self-initiated behaviors can be predicted by exploring peripheral song motor control up to one second prior to the onset of the behavior. These results illustrate that the decision to act can be predicted by changes in peripheral motor systems which likely serve as preparatory activity for the upcoming motor action.

Method

Subsyringeal air pressure was recorded from four Bengalese and six Zebra Finches in directed singing conditions. Each bird was accustomed to holding a pressure transducer on it's back held in place by an elastic band. The weight of the transducer was off-set by a counter balance arm to facilitate free movement of the bird around the cage. A cannula was then inserted surgically into the bird, allowing for measurement of subsyringeal air pressure changes inside the thoracic air sac before, during, and after spontaneously generated song events.

A.

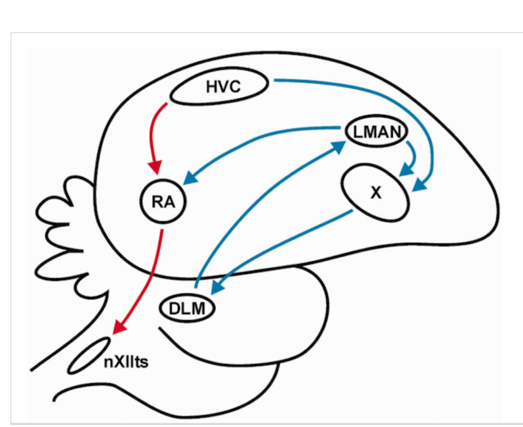


Figure 1. (A) Neural Control of Song. The HVC region of the brain is the main initiation site of song. In decision to sing, HVC Region projects to RA and X, which help aid the bird in controlling respiratory patterns necessary for song initiation, production and termination.

B.

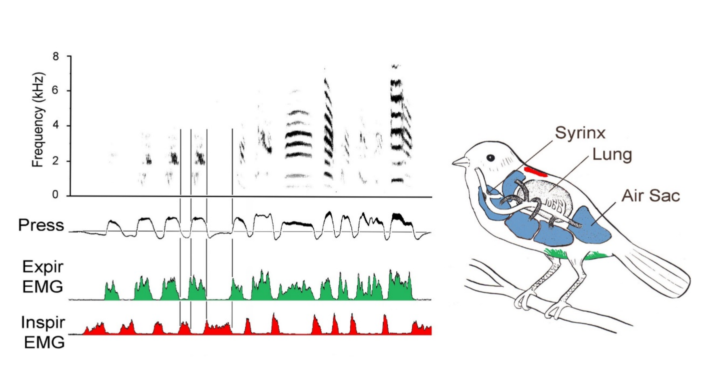


Figure 2. (B) Respiratory Control of Song. In finches, both expiration and inspiration are active processes. The syrinx (avian vocal organ) contains two sets of vibratory tissues that regulate airflow for expiration, inspiration, and vocalization occurs almost exclusively during expiration. Song breathing patterns are faster and higher amplitude than during quiet respiration.

C.

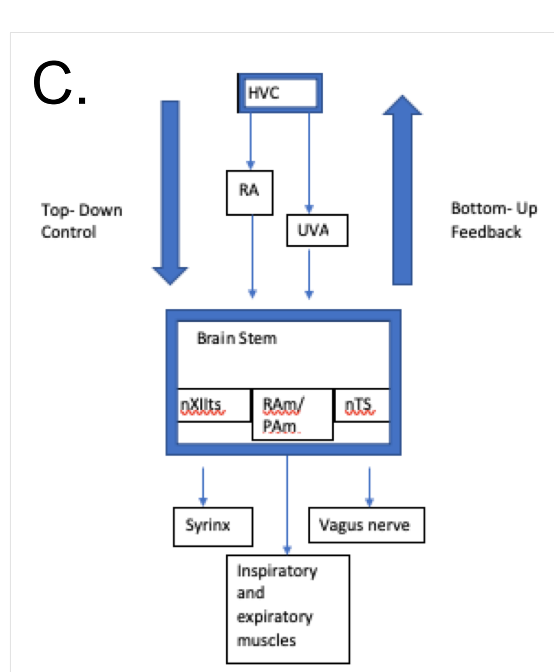
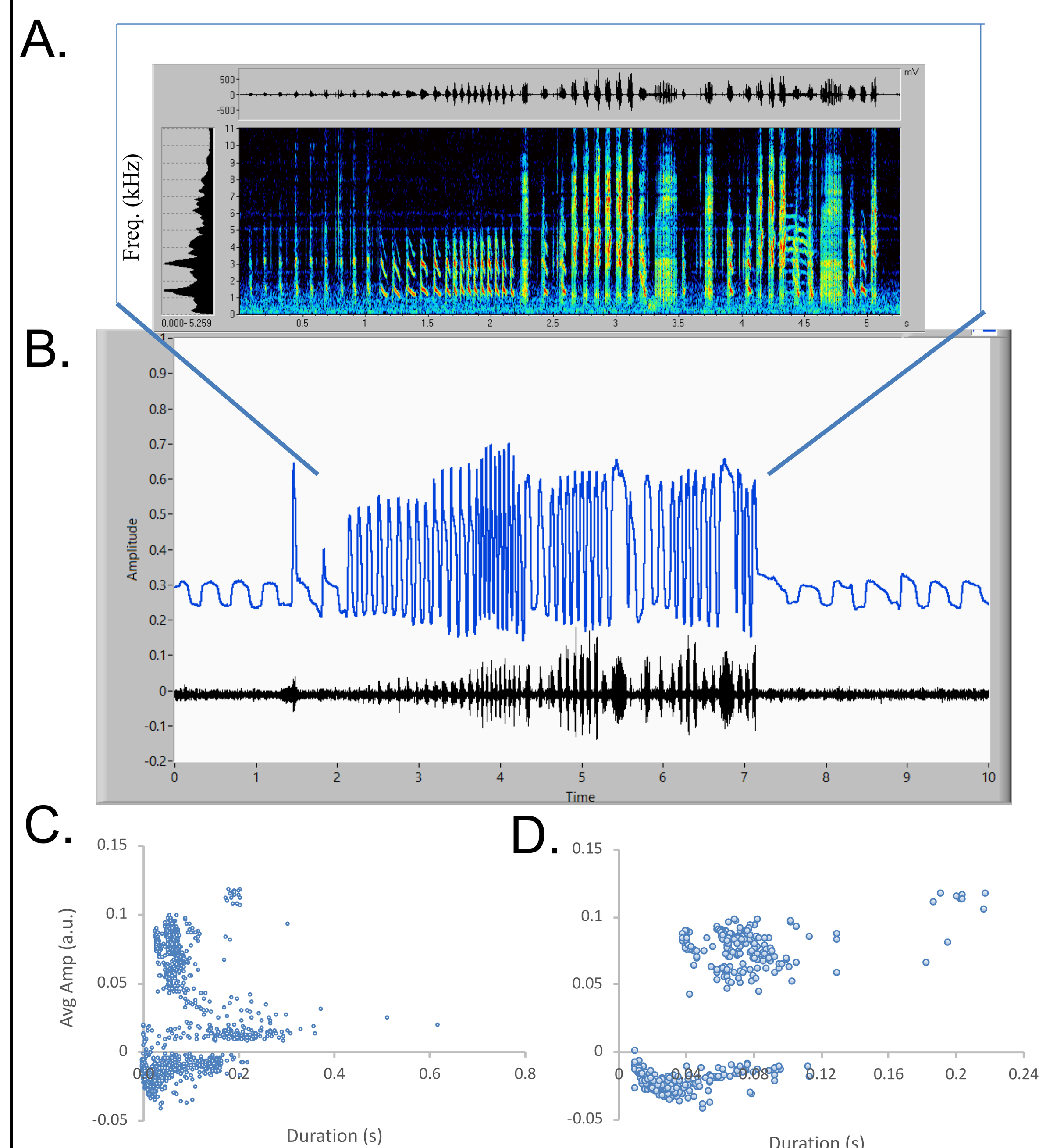


Figure 3. (C) HVC exerts top-down control in stimulating the brainstem motor cortex to prepare for song production. Conversely, The brainstem provides bottom-up feedback to HVC to report the respiratory system's air supply for song.

Differences in Respiratory Patterns between Zebra Finches and Bengalese Finches



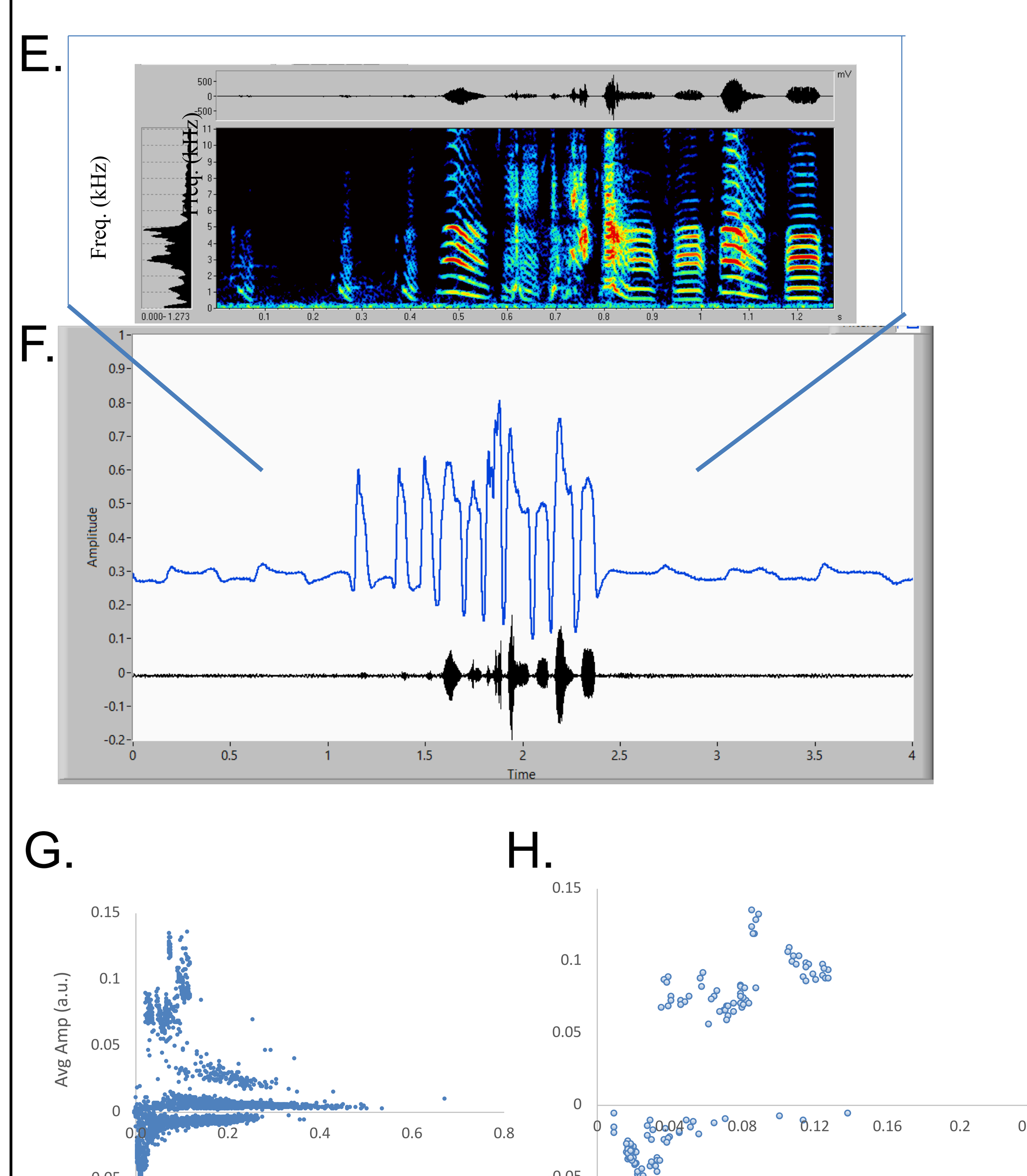


Figure 3. Respiratory patterns vary between songbird species. The Bengalese finch song (A-D) is composed of a semi-variable, repeated sequence of song syllables (A). The driving respiratory patterns illustrate rapid alternation between song syllables, and many syllables are repeated multiple times (B). Scatterplots (C) display the duration and amplitude of the respiratory patterns before, during, and after song (~50 song repetitions). Song respiratory patterns are produced by shorter duration, higher amplitude expiratory pulses, EPs (D). An example zebra finch song (E-H), is composed of a repeated sequence of 7 different syllables (E), each syllable is produced by a unique respiratory pattern (F). Scatterplots (G) display the duration and amplitude of the respiratory patterns before, after song, and during 50 song repetitions. Song respiratory patterns are produced by a mix of shorter and longer duration, higher amplitude EPs (H).

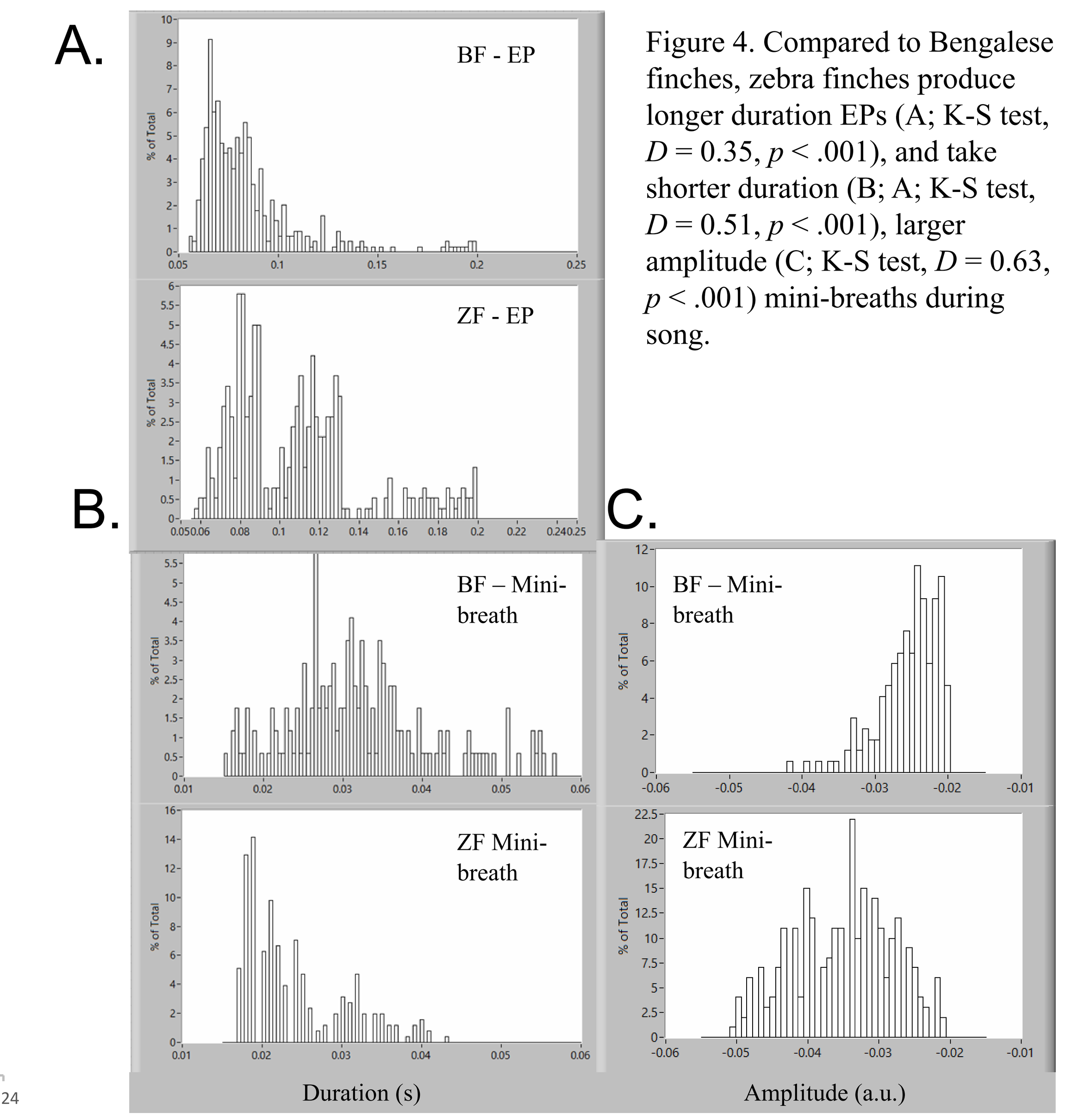


Figure 4. Compared to Bengalese finches, zebra finches produce longer duration EPs (A; K-S test, $D = 0.35$, $p < .001$), and take shorter duration (B; A; K-S test, $D = 0.51$, $p < .001$), larger amplitude (C; K-S test, $D = 0.63$, $p < .001$) mini-breaths during song.

Respiration is Faster and Higher Amplitude during Song

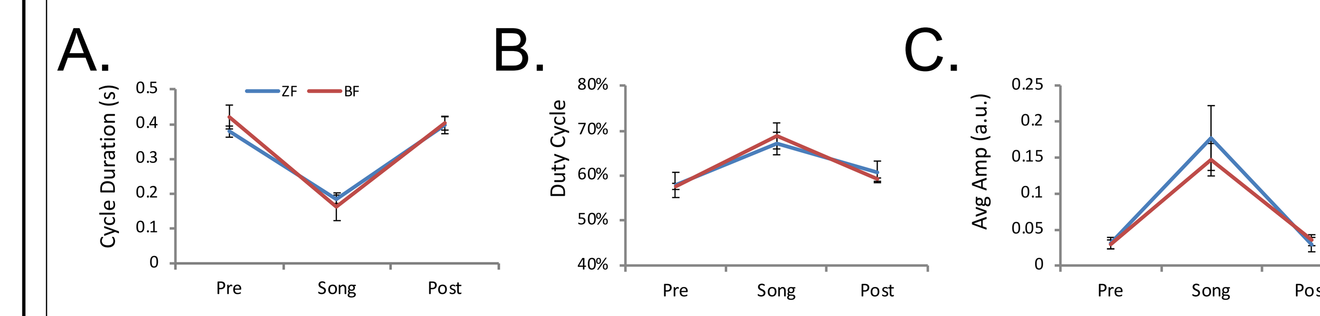


Figure 5. Song respiratory patterns are distinct from quiet respiration before (-5s) and after song (+5s). The respiratory patterns are shorter duration (A), and increased time exhaling (B), and higher amplitude (C).

Respiratory Changes Predict Song Onset

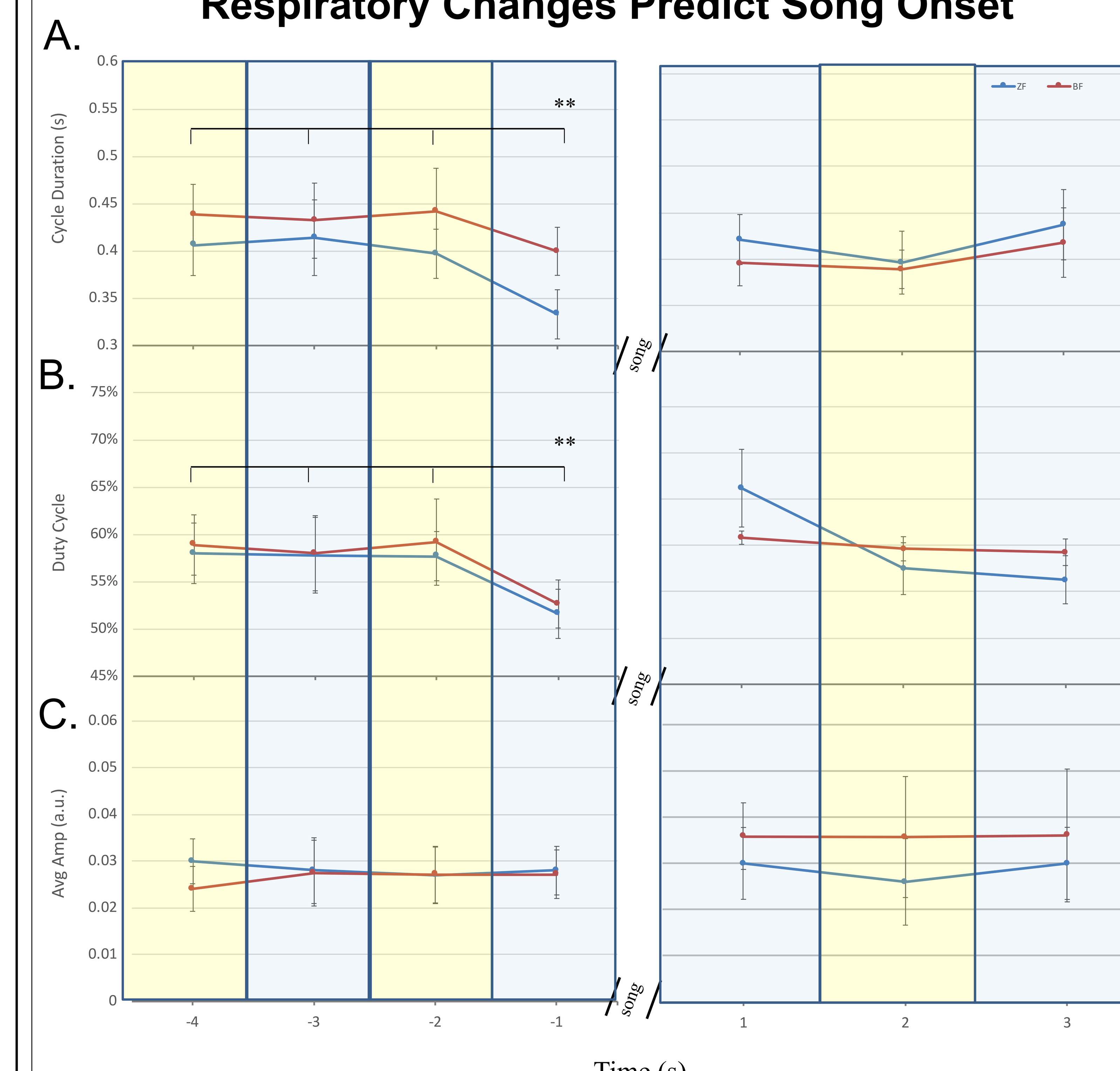


Figure 6. Changes in song respiratory patterns occur in the last second prior to singing. The decrease in the cycle duration (A-left panel; $F(3,24) = 7.71$, $p < .001$) and increase in the time spent in the inspiratory phase of respiration (B-left panel; $F(3,24) = 7.47$, $p < .001$) forecast the onset of song in zebra finches (blue) and Bengalese finches (red). Respiratory amplitude does not change before or after song. The changes in respiratory tempo are most evident in zebra finches. These respiratory changes likely reflect motor planning necessary to initiate song. After song, only zebra finches spend a greater time exhaling (B-right panel). This is likely due to hyperventilation that occurs during zebra finch song. ** indicates statistical significance.

Conclusions

1. The neural control of song requires a top-down control of song respiratory patterns to generate the changes necessary to drive airflow for sound production. Simultaneously, bottom-up feedback is necessary to ensure that sufficient air supply is available to produce the intended vocalizations.
2. Here we demonstrate that respiratory features of song vary depending on species and is likely due to differences in acoustic structure of the vocal patterns.
   a) zebra finches produce songs with shorter duration, higher amplitude inspirations and produce more longer duration expirations during song than Bengalese finches.
   b) Song onset can be predicted by respiratory changes that occur prior to song (~1 s), including a shortening of respiratory cycle duration and an increase in time spent inhaling during the cycle. Although both species show changes in respiratory patterns, the change in respiratory duration is most pronounced in zebra finches. This species difference is likely due to the differing respiratory features of song.
   c) After song, zebra finches show changes in song respiration that are not observed in Bengalese finches. It is likely that this species difference is due to hyperventilation that occurs during song.
   d) Therefore, the top-down control of song prepares the ventilator patterns necessary to prepare the bird to sing by increasing time spent inhaling to provide the air supply for song and post-song changes in respiration allow for recovery from singing-related exertion.
   e) This model system can be used to explore the interplay between central and peripheral motor systems necessary for initating and terminating complex, learned behaviors, like human speech.