Impairment and Recovery of Song Syntax in Bengalese Finches: Implications for Learning and Vocal Motor Production

DuBois, J.G., Favoloro, C., Spradley, E.A., Urbano, C. M., & Cooper, B. G.
Psychology Department, Texas Christian University, Fort Worth, TX 76129

Introduction

Speech production is a complex, learned behavior that is controlled by the left hemisphere of the brain. When one side of the brain or body preferentially executes and controls a behavior, this is termed a "lateralized" behavior. The exact explanation of why lateralization exists is unknown, but it may increase efficiency by allowing for a neural specialization. Bengalese finches (*Lonchura striata domestica*) produce and discriminate song in a manner that is similar to the left-dominant control of human speech production and comprehension. That feature makes them a suitable animal model for studying lateralized, learned vocal behaviors.

The syrinx, the avian vocal organ, is responsible for producing the Bengalese finch song. The syrinx is bifurcated and each side possesses two sets of vocal folds, or labia. The neural innervation of the syrinx arises from the ipsilateral side of the brain. Sound production is lateralized in most species of birds. In Bengalese finches, the left side of the syrinx produces frequencies that are greater than 2.2 kHz and are tonal in quality. The right side produces frequencies that are lower that 2.2 kHz and are characteristically noisy. The dominant acoustic energy in the Bengalese finch song is greater than 2 kHz and is produced by the left side of the syrinx.

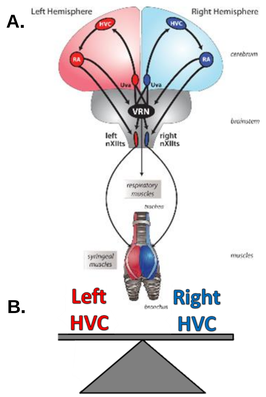

Figure 1. Bilateral organization of the song motor control system. In the posterior motor pathway (A), HVC projects to RA, which then projects to either the left or right nXIIts, which controls the parallel side of the syrinx. During normal functioning (B), input from left and right HVC balance each other out.

The avian brain is organized into discrete, interconnected nuclei involved in different components of song learning and memory, and song production, all directly influenced by premotor nucleus HVC. HVC controls many temporal and structural aspects of song, including song syntax, through the "direct" or posterior motor pathway (Figure 1). We can study lateralized control of song syntax in Bengalese finches by manipulating the balance between left and right HVC input into the posterior motor pathway; this can be done by administering small, targeted (micro) electrolytic lesions into either left or right HVC.

Methods

- Unilateral HVC microlesions were made in the left (n=4) or right (n=4) hemisphere in adult male Bengalese finches.
- Song was recorded continuously before and for 7 days after surgery.
- Data analysis
  - Motor control:
    - Syllables were separated into higher frequency (f_0 > 2.2 kHz) and lower frequency (f_0 < 2.2 kHz)
    - Calculated a post:pre ratio for the total number of unique syllables in PSD4 and PSD7. Did the of the number of unique syllables change after HVC damage?
  - Syntactic organization:
    - Syllables were assigned unique alphabet labels
    - Linearity – assesses the rigidity of syntax across renditions
    - Song sequence was coded into a java applet, the Songinator
  - Calculated a post:pre ratio for the average number of branch points (Figure 2) in PSD4 and PSD7. Did the number of branch points change after HVC damage?

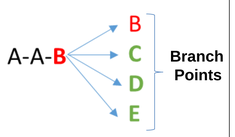

Figure 2. An example of branch points. The syllable denoted as B has 4 possible branch points: C, D, or E, or it can repeat itself.

Results: Lesion Verification

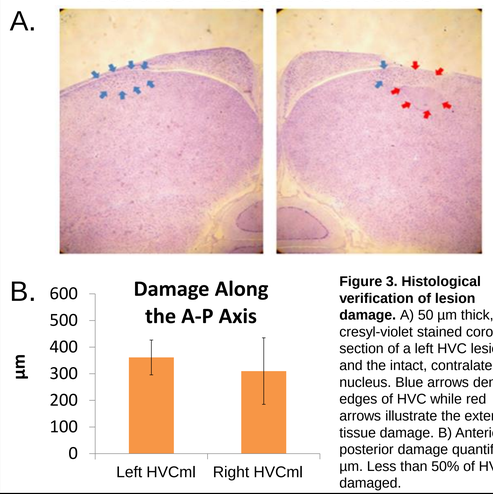

Figure 3. Histological verification of lesion damage. A) 50 µm thick, cresyl-violet stained coronal section of a left HVC lesion and the intact, contralateral nucleus. Blue arrows denote edges of HVC while red arrows illustrate the extent of tissue damage. B) Anterior to posterior damage quantified in µm. Less than 50% of HVC is damaged.

Left and Right HVC Microlesions Alter the Pattern of Syllable Production

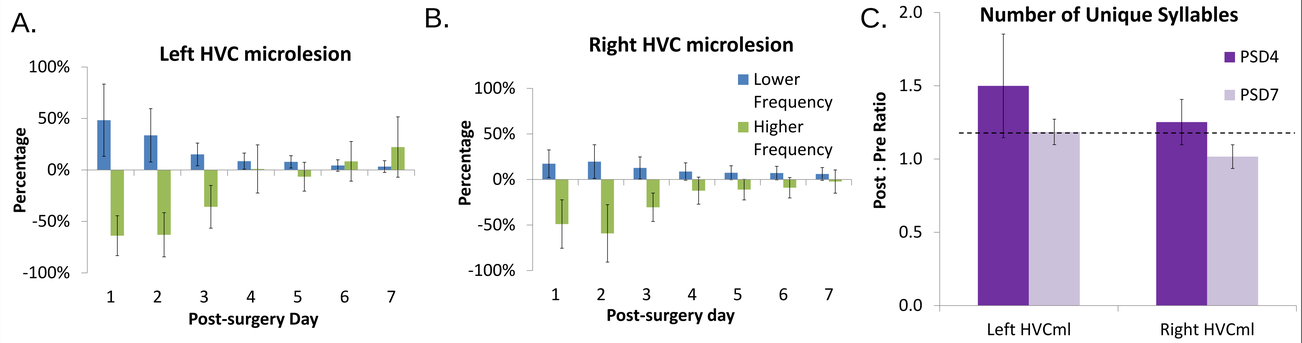

Figure 4. Types and number of syllables produced after HVC microlesion. A, B) in both left and right HVC microlesion groups, lower frequency (LF) syllables with a fundamental frequency (f_0) < 2.2 kHz is the dominant syllable type whereas there is a 50% decrease in the production of higher frequency (HF) syllables. This pattern is most evident in the first three days post-surgery and largely recovered by post-surgery day 4 (PSD4). C) Both left and right HVC microlesion groups exhibit an increase in unique syllables in the song repertoire at PSD4. Both groups also show a decline in unique syllables at PSD7, however, only the right HVC microlesion group returns to baseline level.

Lateralized Effects on Sequence Variability

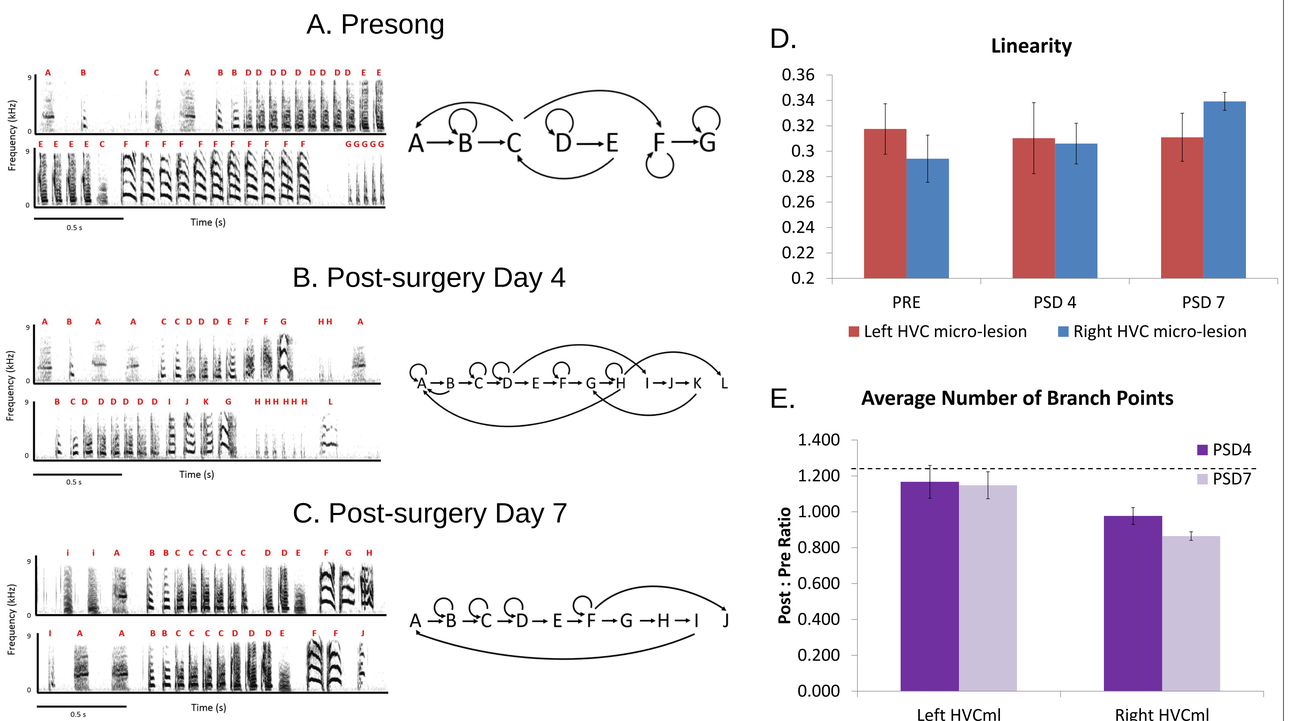

Figure 5. Left and right HVC microlesions have differential effects on syllable branch points. A-C) Sample spectograms (visual representation of sound) of pre-surgery song (A) and songs from PSD4 (B) and PSD7 (C) and a graphical illustration of song syntax. Each syllable is represented by a letter of the alphabet and arrows illustrate all the potential variations in sequencing. As we could not directly match syllable labels in all animals over the course of the week, labels are consistent only within each timepoint. D) Measures of song linearity as an indicator of syntax variability. Although a 2x3 repeated-measures ANOVA was nonsignificant, song syntax in the right HVC microlesion group becomes more linear between PSD4 and PSD7. E) Using average number of branch points as an indicator of syntax variability, results show that while left HVC microlesions result in an increase in branch points, songs in the right HVC microlesion group exhibit a gradual decline that is most prominent in PSD7. A decline in number of branch points is an indicator of an increasingly rigid song, thus explaining the increase in song linearity.

Conclusions

- **The HVC microlesion technique produced equivalent tissue damage to the left and right hemispheres. Therefore, we can rule out the possibility that differential effects are due to differences in the magnitude of HVC ablation.**
- **Left and right HVC microlesion songs mostly contained LF syllables during the first three days and returned to baseline by PSD4. HF syllables were most likely to be deleted after HVC damage.**
- **Songs contained more novel unique syllables at PSD4. Although both groups show a decline, only RHVC microlesion birds returned to baseline at PSD7.**
- **Interestingly, despite the increase in syllables in both groups, right HVC microlesions exhibit an increasingly rigid or stereotyped song. The average number of branch points per syllable does not increase at PSD4 and actually decreases at PSD7, offering an explanation for the increase in song linearity in the right HVC group**
- **Left HVC microlesion birds, on the other hand, exhibit an increase in the number of branch points in both post-surgery timepoints. This suggests that song syntax in left HVC lesion animals is more variable.**
- **Intact left and right HVC typically work in concert in a system with bilateral connections in the brainstem. We proposed to determine whether differential effects would occur should the "balance of power" shift between the left and right hemispheres.**
- **These results suggest that a "dominant" left HVC produces atypically stereotyped song whereas a "dominant" right HVC produces atypically variable song.**

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