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

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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 produces 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 than 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.

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 (fH > 2.2 kHz) and lower frequency (fL < 2.2 kHz).
    - Calculated a post/pre ratio for the total number of unique syllables in PSD4 and PSD7. Did the proportion 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 application.
  - 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?

Results: Lesion Verification

- A. Damage along the A-P axis
- B. Left HVC, Right HVC
- C. HVC microlesion

Left and Right HVC Microlesions Alter the Pattern of Syllable Production

- A. Pre-song
- B. Post-surgery Day 4
- C. Post-surgery Day 7

Lateralized Effects on Sequence Variability

- A. Presong
- B. Post-surgery Day 4
- C. Post-surgery Day 7

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

Figure 2. An example of branch points in a song. Different possible branch points are represented by letters A, A’, B, C, D, E, and F.

Figure 3. Histochemical verification of lesions. (A) Cresyl violet stained section shows a right HVC lesion and the intact, contralateral nucleus. Blue arrows denote edges of HVC while red arrows illustrate the extent of tissue damage. (B) Anesthetized bird in a coronal plane section of a left HVC lesion 50 µm. Less than 50% of HVC is damaged.

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 (f0) < 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 returns to baseline by PSD4. C) Measuring PSD4 and PSD7 increases the number of unique syllables in the song repertoire. Although both groups show a decline in unique syllables at PSD7, only the right HVC microlesion group returns to baseline level.

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 microlesions 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.