# Exploring Parallels Between Lateralized Control of Human Language and the Neural Control of Bengalese Finch Song Syntax


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## Introduction

Speech is a complex, learned behavior. In humans, speech production is controlled by Broca's area, a specific part of the brain in the left lateral frontal lobe. Because speech production is primarily controlled by one side of the brain, it is considered to be a "lateralized" behavior.

Songbirds are frequently used as an animal model for human language because they share similar patterns in the development of vocal learning. A bird's song consists of unique patterns of notes and syllables strung into phrases and motifs; this is known as syntax, and it is comparable to the grammatical rules of word ordering in human speech. In this experiment, the Bengalese finch (*Lonchura striata domestica*) was chosen as the model to explore whether they have lateralized song syntax, similar to language syntax control by Broca's area.

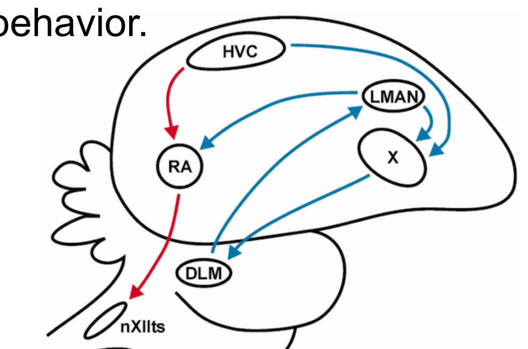


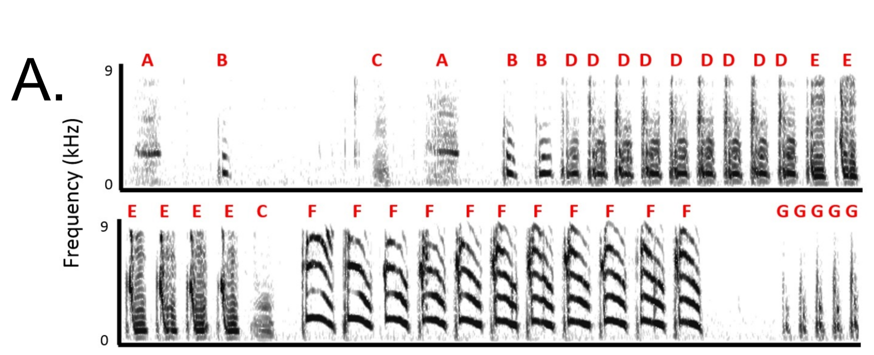

**Figure 1. The Pathways of Song Production.** In the Song Production Pathway (red), HVC directly projects onto RA. In the Anterior Forebrain Pathway (blue), HVC sends a signal to Area X, which then goes to the DLM, LMAN, and eventually RA. In both pathways, RA will ipsilaterally innervate the syrinx.

HVC is a premotor area in the songbird brain (Fig. 1) that regulates timing and sequencing of song syllables. HVC sends afferents to the posterior motor pathway necessary for song production, and the Anterior Forebrain Pathway, which controls song learning (Fig. 1). RA is the avian motor cortex, and controls oscine vocal organ motor production via the ipsilateral projections to the syrinx; the motor control of birdsong a lateralized behavior. This study seeks to determine if the syntactic construction of birdsong in the Bengalese finch is also a lateralized neural behavior, just as it is in humans.

## Methods

- Unilateral electrolytic HVC macrolesions were made in the left (n=4) or right (n=4) hemisphere in adult male Bengalese finches.
- Song was recorded at five different timepoints: before surgery (pre-song), four days after surgery (PSM4), seven days after surgery (PSM7), one month after surgery (PSM1), and five months after surgery (PSM5).
- Song Analysis (Figure 2):
  - Ten songs from each timepoint were selected for each bird
  - Syllables on spectrograms were given unique alphabet letters
  - Coded songs were entered into a java applet, the Songinator
- The Songinator calculates the following data from the coded songs:
  - Transitional probabilities for each syllable, meaning the likelihood that a certain syllable will follow another
  - Song linearity (SL), the way that notes are ordered in a song
  - Song consistency (SC), how often a particular path (motif) is followed
  - Song stereotypy (SS), a combination of linearity and consistency

A.

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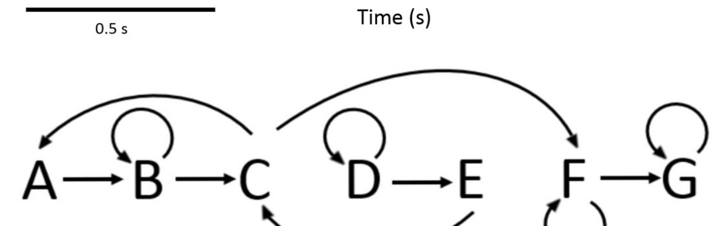
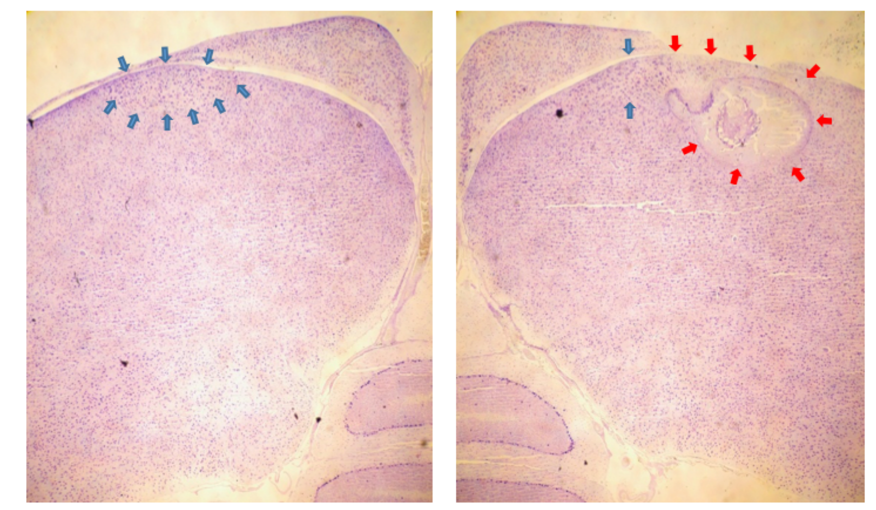



**Figure 2. Spectogram Analysis.** A) Song can be visually represented as a spectogram, which shows the frequencies and loudness the syllables. A syllable is defined as a unit of sound that is separated by silent intervals on either side. Each syllable is been assigned a unique letter. B) This is a graphical illustration of song syntax. Each letter represents a syllable, and the arrows illustrate all the potential variations in sequencing.

## Results: Lesion Verification

A.



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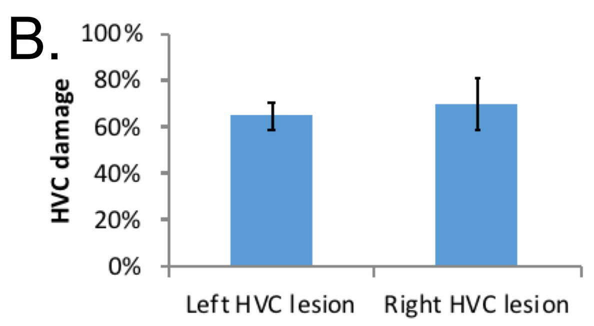


**Figure 3. Histological verification of lesion damage.** A) 50 µm thick, cresyl-violet stained coronal sections. The left photo depicts an intact right HVC nucleus with blue arrows showing the edge of the nucleus. The right photo shows the extent of lesioning performed on the left HVC. The blue arrows on this picture denote the edges of intact HVC, while the red arrows outline the amount of damage done to the tissue. B) The damage was assessed in an anterior-to-posterior direction in µm. On average, the left group showed 64.58% damage to the HVC, and the right group demonstrated 69.44% damage.

## Left and Right HVC Lesion Groups and Song Linearity, Consistency, and Stereotypy

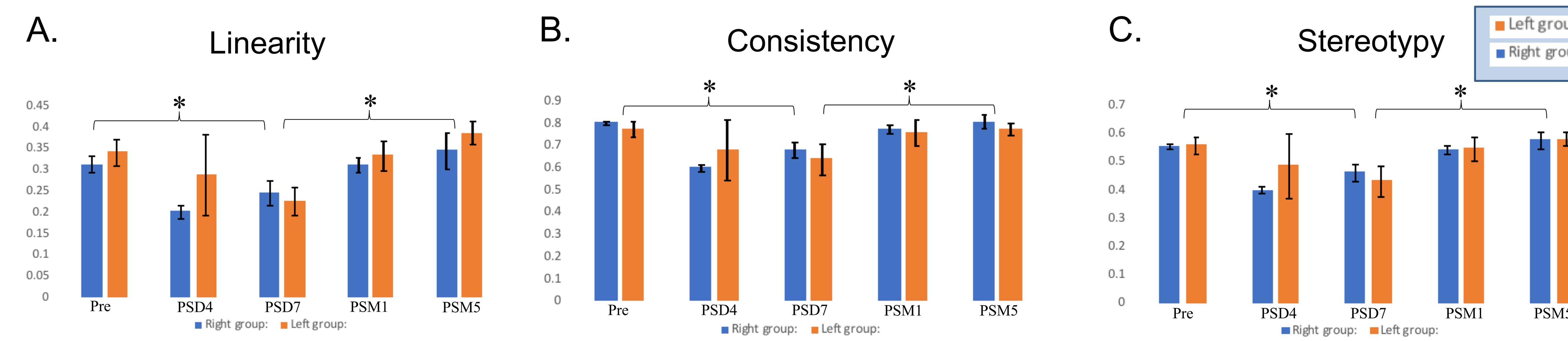


**Figure 4. Comparing song linearity, consistency, and stereotypy between the right and left lesion groups for each time point.** A-C) Bird BFS683 produced song that was so unpredictable that it couldn't be coded for timepoints PSD4 and PSD7. Because of this, data imputation was performed; the lowest data values from the left HVC lesion group were substituted in for the missing values at those time points. A repeated measures ANOVA test was run. A) For song linearity, there was no significant interaction between left or right HVC lesion and recording timepoint ($F(4,24)=0.437$, n.s.). There were no differences found between the left and right lesion groups ($F(1,6)=1.867$, n.s.). When comparing timepoints for each individual bird, however, linearity of syntax was disrupted ($F(1,4)=3.65$, $p<0.02$). B) For song consistency, no significant interaction effects between left or right HVC lesion and recording timepoint were observed ($F(4,24)=0.422$, n.s.). There were also no significant differences in song consistency when comparing the right and left HVC lesion groups ($F(1,6)=0.023$, n.s.). On the other hand, a significant difference between timepoints for each bird was found ($F(1,4)=3.494$, $p<0.022$). C) For song stereotypy, which is an average of song linearity and song consistency, there were no significant interaction effects between left or right HVC lesion and recording timepoint ($F(4,24)=0.42$, n.s.), and there were no significant differences between left or right HVC lesion on song stereotypy ($F(1,6)=0.023$, n.s.). However, left and right HVC lesion transiently disrupted song syntax; a significant change in song stereotypy was observed across recording timepoints ($F(1,4)=3.494$, $P<0.022$).

*The asterisked brackets above each graph signify significant differences between timepoints. For song linearity, consistency, and stereotypy, there were significant differences found between pre-song and song from PSD7 ($p<0.05$). In addition the differences for each data measure between PSD7 and PSM5 were significant, as well ($p<0.05$). These significant differences demonstrate the initial loss of syntactic structure at the beginning of the experiment, but then a recovery of that syntax by PSM5 at the end of the experiment.

## Song Data Correlations Between Pre-Song and PSM1 or PSM5

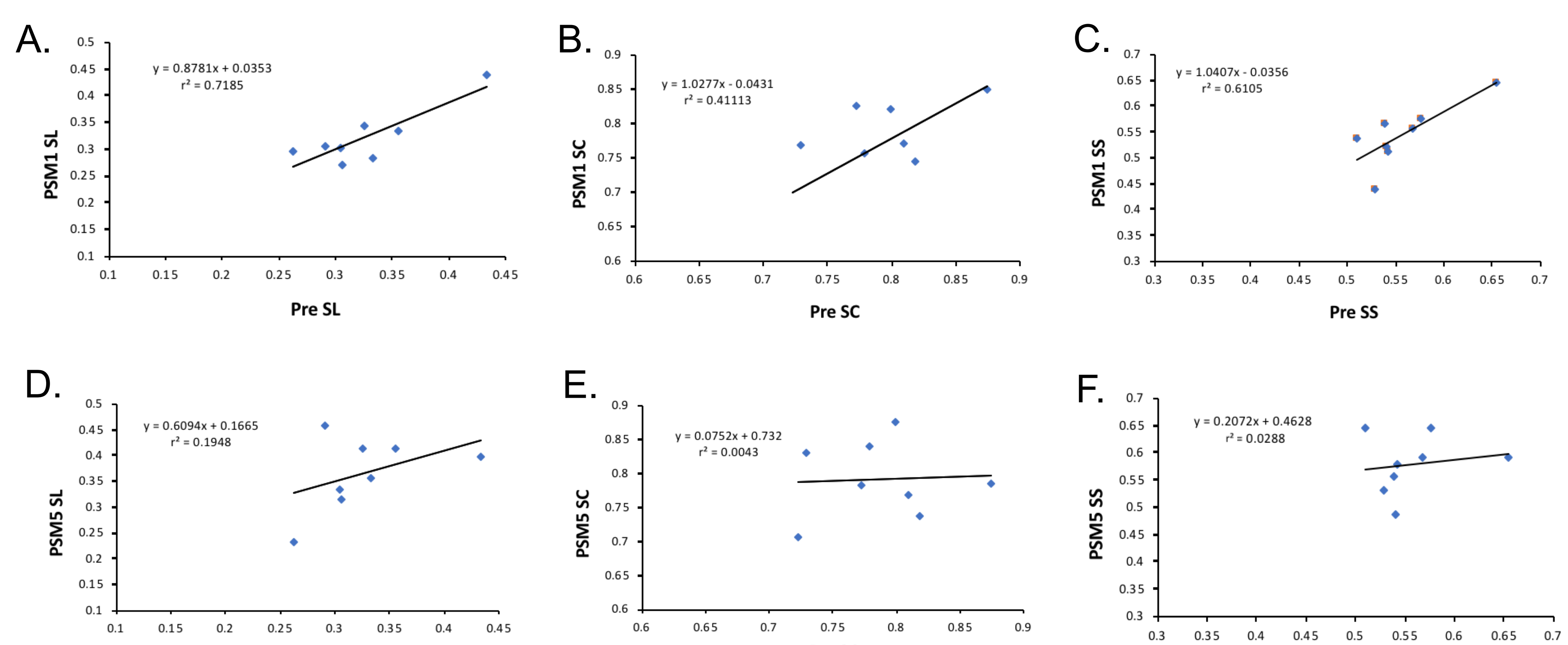


**Figure 5. Correlations between pre-song and PSM1 or PSM5.** To assess whether individual birds returned to their preles correlation between prelesion and PSM1, as well as PSM5, was calculated. A correlation of 1.0 would indicate that the Bengalese finches recovered to their baseline song. Correlations between pre-song and PSM1 (A-C) and between pre-song and PSM5 (D-F) for song linearity, consistency, and stereotypy are shown above. For PSM1, the correlations between each of the song data measures were decently strong. A) For song linearity, the correlation between pre-song and PSM1 had an $r^2$ of 0.7185 ($r(6)=.85$ $p<0.008$). This was a very significant correlation. B) The correlation between pre-song and PSM1 for song consistency exhibited an $r^2$ value of 0.41113 ($r(6)=.64$, $p<0.09$). This was marginally significant, especially when taking the sample size into account. C) For song stereotypy, the average between song linearity and consistency, the $r^2$ value came to 0.6105, which was shown to be significant ($r(6) = 0.78$, $p < 0.022$). However, the recovery did not persist beyond thirty days, as pre-song and PSM5 song data measure scores were no longer correlated. D) The correlation between pre-song song linearity and PSM5 song linearity only had an $r^2$ value of 0.1948 ($r(6)=44$, n.s). E) For song consistency, the $r^2$ value for the correlation between pre-song and PSM5 was only 0.0043 ($r(6)=0.06$, n.s). F) The song stereotypy correlation between pre-song and PSM5 had an $r^2$ value of 0.0288, which shows that the two time point stereotypies were no longer correlated ($r(6) = 0.17$, n.s.). The correlation results can be compared to the results from a previous study in which lateralized damage was performed on the motor neuron innervating each half of the bird syrinx, NXIIts. (Urbano et al., 2013. The left portion of the syrinx is specialized to produce louder, higher frequency sounds above 2.2 kHz, while the right syrinx produces sounds lower than 2.2 kHz. Following damage to the left NXIIts, songs mainly composed of lower frequency note syllables. Three of the birds in the study did eventually recover high frequency sounds; this has two possible explanations. First, it's possible that other respiratory muscles compensated for the loss of NXIIts function. Another possibility is that the task of innervating the left syrinx was taken over by the right hemisphere, which would indicate that birdsong production is a very plastic process. Similar reorganization of neural control has been observed in human aphasic and stroke patients. However, overall, there was a relatively low retention rate of the high frequency syllables. This is speculated to be due to the fact that producing these sounds by alternate methods is physiologically taxing. The results of this study can be compared to the results seen here; by PSM1, it is possible that other brain regions could have taken over for the damaged HVC. However, by PSM5, perhaps became too exhausting for the bird to keep up the same levels of linearity, consistency, and stereotypy observed at PSM1, so perhaps the level of effort to maintain these levels dropped off.

## Conclusions

- **The HVC macrolesion 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.**
- **There were no lateralization effects observed in the experiment. Both the interaction effects (between left or right HVC lesion and recording timepoint) and the between-subject effects (left HVC group vs right HVC group) proved to be insignificant for song linearity, consistency, and stereotypy.**
- **The within-subject effects (comparing different timepoints for each individual bird) did prove to be significant. Birdsong syntax was transiently disrupted following lesion through PSD4, but original syntax was eventually recovered by PSM1.**
- **A significant correlation for song linearity, consistency, and stereotypy between prelesion song and song at PSM1 is exhibited. This demonstrates that the Bengalese finches nearly return to their original syntactic structural levels by PSM1.**
- **Due to the neuroplasticity of the brain, it is possible that the lack of lateralization or the correlation between the two timepoints is due to neural remodeling following surgery. For example, the contralateral HVC could have taken over the responsibilities of the lesioned HVC when it was rendered nonfunctional. Another possibility is that the ipsilateral LMAN compensated for the damage by innervating the RA when the HVC stopped sending signals so that syntactic structure of the birdsong was at least partially maintained.**
- **The decrease in the correlation between pre-song and PSM5 compared to PSM1 for song linearity, consistency, and stereotypy could be due to the fact that it was too physiologically challenging for the bird to maintain the song syntax structure.**


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