

TEMPORAL STRUCTURE IN ZEBRA FINCH SONG: IMPLICATIONS FOR MOTOR CODING

(Supplementary Materials)

Christopher M. Glaze and Todd W. Troyer^{1,2}
Program in Neuroscience and Cognitive Science, Dept. of Psychology,
University of Maryland, College Park, MD, USA

Summary

These supplementary materials address details related to three basic issues presented in our main manuscript. First, in the main paper we show that syllables and gaps have different elasticity in relation to changes in sequence length. Here we present investigations into factors in addition to interval type that might explain these differences. Second, we present data on the magnitude of deviation from the proportional scaling hypothesis. Finally, we present estimates of measurement error for our behavioral techniques. These latter two results may be of interest to others who use our behavioral techniques or who wish to investigate the issue of proportional scaling using electrophysiological techniques.

Factors related to elasticity differences

We have shown that syllables and gaps display different degrees of elasticity. However, syllables and gaps also differ in their mean length and overall variability. Thus it is possible that these or other factors are the true determinants of elasticity and the correlations with interval type simply follow as a consequence. In this section we explore relationships between length, variability, and elasticity. To start, we decompose an interval's elasticity coefficient, expressing it as a ratio of two separate terms. For the first term, we write the linear regression of interval length x_i vs. sequence length z as $x_i - \bar{x}_i = b_i(z - \bar{z}) + \epsilon_i$ where the regression coefficient $b_i = cov(x_i, z)/var(z)$ and ϵ_i is the residual. Factoring out \bar{x}_i and \bar{z} from the left and right sides and then dividing by \bar{x}_i we obtain

$$\left(\frac{x_i}{\bar{x}_i} - 1\right) = \frac{\bar{z}}{\bar{x}_i} b_i \left(\frac{z}{\bar{z}} - 1\right) + \frac{\epsilon_i}{\bar{x}_i}$$

Since $\left(\frac{x_i}{\bar{x}_i} - 1\right)$ and $\left(\frac{z}{\bar{z}} - 1\right)$ represent the fractional change in interval and sequence length respectively, the quantity $\frac{\bar{z}}{\bar{x}_i} b_i$ is equal to the interval's elasticity coefficient β_i . We will refer to b_i as an interval's "covariance ratio" and the ratio $\frac{\bar{x}_i}{\bar{z}}$ as the "length ratio". Therefore, elasticity is equal to the covariance ratio divided by the length ratio.

Figure 12 shows a scatter plot of the length ratio against the covariance ratio. The β coefficient for any interval is equal to the slope of the line joining the origin and that point. The dashed line represents $\beta = 1$. Points above the line have elasticity greater than 1 and points below have elasticity less than 1. For any given length ratio gaps tend to have greater covariance ratios, and for any given covariance ratio gaps have smaller length ratios. Thus, the difference in elasticity between syllables and gaps is not due to simple differences in length or covariance between types. Figure 12 also demonstrates that longer intervals experience greater changes in length than shorter intervals, a relationship that would not hold if, for example, increases in song tempo were accomplished by adding or subtracting a fixed amount from syllable and gap lengths.

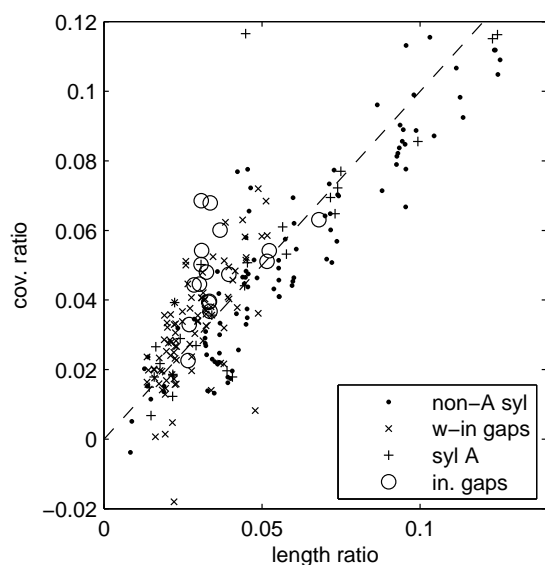


Figure 12. Relationship between length ratio (interval length divided by total sequence length) and covariance ratio (covariance divided by sequence variance). Elasticity is the ratio of these two quantities (equal to the slope of the line connecting each point to the origin). Dashed line: elasticity=1. The difference in elasticity between syllables and gaps is not a simple consequence of differences in length or covariance.

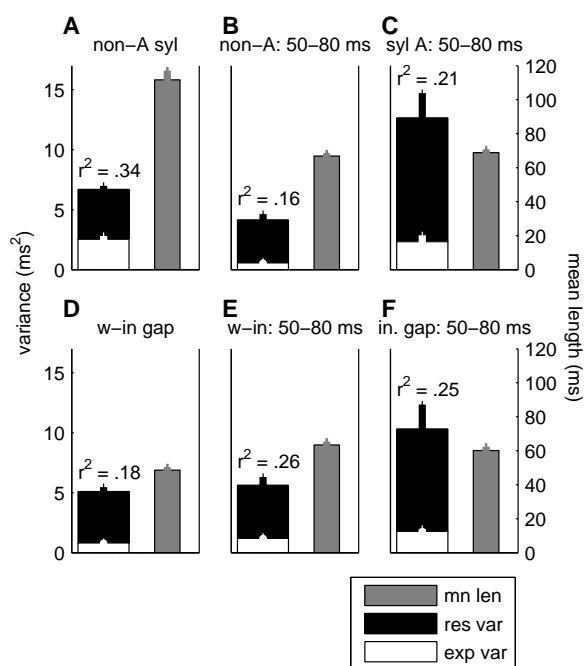


Figure 13. Components of variance. White: amount of variance explained by regression with sequence length. Black: residual variance remaining after regression. r^2 : explained variance/total variance. Gray: mean length of intervals considered. (A) Syllables other than syllable A. (B) Non-A syllables from 50-80 msec long. (C) Syllable A, 50-80 msec. (D) Gaps within motifs. (E) Gaps within motifs, 50-80 msec. (F) Inter-motif gaps, 50-80 msec.

Amount of variance explained by elasticity. We also examined the relationship between elasticity and overall variance by dividing the variance of each interval into the fraction that is explained by sequence length (“explained variance”) and the “residual variance” that is due to other factors. The proportion of explained variance as a fraction of the total variance is commonly denoted r^2 . Excluding syllables and gaps associated with motif boundaries, syllables tend to be more variable and have a greater proportion of explained variance than gaps (fig 12A,B; mean $r^2 = 0.343 \pm 0.022$ for syllables, 0.184 ± 0.014 for gaps, $p < 0.0001$). The residual variance is not significantly different (4.154 ± 0.306 for syllables, 4.300 ± 0.370 for gaps, $p = 0.715$). Therefore, the higher proportion is mostly due to the greater amount of explained variance for syllables (2.530 ± 0.253 ms² vs. 0.797 ± 0.069 ms² for gaps, $p < 0.0001$).

However, a closer examination reveals that the surplus of explained variance is confined to longer syllables. To control for length, we only considered intervals falling into the range where syllable and gap lengths have the greatest overlap (50-80 msec). For these intervals, we find that the situation is reversed (fig 13C,D). Gaps are more variable overall and have more variance explained by sequence length, both in an absolute sense and as a fraction of total variance. (total variance: 5.616 ± 0.720 ms² for gaps, 4.166 ± 0.529 ms² for syllables, $p < 0.05$; explained variance: 1.172 ± 0.126 ms² for gaps and 0.567 ± 0.080 ms² for syllables, $p < 0.0005$; r^2 : 0.261 ± 0.027 for gaps, 0.158 ± 0.020 for syllables, $p < .01$). As before, residual variances are comparable (4.445 ± 0.706 ms² for gaps and 3.600 ± 0.510 ms² for syllables, $p = 0.493$).

Turning to motif boundaries, variance and residual variance is greater among these intervals than other syllables or gaps of comparable length (fig. 13E,F; $p < 0.005$). The proportions of explained variability are greater for syllable A than for other syllables ($p < 0.025$) but not for inter-motif gaps relative to other gaps ($p = 0.525$).

Acoustic factors in elasticity. We also searched for acoustic factors that might predict elasticity for syllables. Four observers independently rated all 60 unique syllables using 3 broad classes based on our general experience with the varieties in zebra finch song: “short, noisy stack-like”, “medium or long stacks”, and “compound”. We also included an “undecided/other” category. Syllables were considered categorized if at least 3 observers agreed; all other syllables were classified as undecided/other. Across all syllables, 67% were unanimously classified and 76% had at least 3 in

4 classifying the same way. Seven were classified as short, noisy, stack-like, 33 as compound, 7 as medium-to-long stacks, and 13 remained as undecided; so the large majority of syllables were compound. We found no significant effect of syllable subtype on elasticity coefficients (respective means are $0.969 \pm .123$, $0.930 \pm .034$, $0.935 \pm .077$ and $0.873 \pm .069$, Kruskal-Wallis, $p = 0.23$). However, a larger sample size will be required to adequately resolve this question.

Deviance from proportional scaling

We have demonstrated that syllables and gaps do not scale proportionally with changes in sequence length. Physiological investigation into the neural mechanisms underlying this phenomenon will presumably rely on measuring deviance from a proportional scaling baseline. Because deviance from uniform scaling will only be detectable at the extremes of sequence length, we selected sequences in the outer 20th percentile of sequence lengths and calculated the fractional change from the mean sequence length. For each interval, we multiplied the mean interval length time the fractional change in sequence length. This represents the predicted length of the interval under the proportional scaling hypothesis. We compared this value to both the measured length of the interval and the best predicted length of the interval based on the linear regression with sequence length (see formula above). Across all intervals, the mean absolute deviation from proportional scaling was $1.565 \pm .014$ msec for the measured data and $0.454 \pm .004$ msec for the calculations based on the linear regression. If we select the interval with the maximum deviation per bird for each measurement, deviation from proportional scaling was 13.356 ± 1.273 for the measured data and $2.474 \pm .474$ msec for the regression calculations.

Estimate of measurement error

We gauged measurement error using an approach similar to the multiple regression used to assess effect sizes (see Results). For each gap in a sequence, we calculated the variance explained by a multiple regression with the sequence length, type sums and identity sums. We subtracted this value from the variance explained by the same factors plus the length of either the next syllable or previous syllable. The additional variance from the next syllable should capture onset jitter while that from the previous syllable should capture offset jitter. Since we are assuming that all additional variance explained by adjacent intervals is due to measurement error rather than physiological factors, this analysis is more likely to overestimate rather than underestimate measurement jitter. The variance

contributed by syllable onsets was $0.474 \pm .069 \text{ ms}^2$; offsets contributed $0.913 \pm .117 \text{ ms}^2$, from which we obtain rough estimates of .70 msec jitter in onsets and 1 msec jitter in offsets. These estimates are consistent with a variance “floor” seen in several different scatter plots during the early stages of data analysis (not shown). The difference between onsets and offsets is consistent with our observation that offset peaks tended to be noisier across sequences (see Methods).