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# Temporal variability in a synfire chain model of birdsong

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## Introduction

Zebra finch songs are highly stereotyped, making them especially well suited for in depth analysis of the neural mechanisms underlying sequential behaviors. The acoustic structure of song is arranged into vocal units, known as syllables, which are ordered into highly invariant sequences called motifs. However, recordings in high-level premotor nuclei during singing reveal spike bursts in individual neurons with two notable timing properties: first, burst times have millisecond precision, and second, the times have no obvious relationship to the timing of syllables or intersyllable gaps [1]. This has led to the hypothesis that the representation for song is clock-like, and is generated as neural activity propagates down a chain-like network of neurons known as a synfire chain [2,3].

Recent results from our lab supports both clock-like regulation and the syllable-based view of song organization. We used a dynamic time warping to make fine-grained measurements of song timing in several thousand songs from 10 adult birds [4]. We found song length variability that is driven by tempo changes shared across syllables, rather than an accumulation of independent variance; this yields positive correlations among the lengths of most syllables and intersyllable gaps. This global variability suggests that slow, modulatory effects have a strong influence on timing across song representations. However, we also found that syllables tended stretch and compress with tempo proportionally less than gaps (syllables were less "elastic"), contradicting the hypothesis of a uniform, clock-like representation. Finally, we found that, after subtracting the effects of song tempo, the residual lengths of the same syllable sung in different motifs ("same ID" syllables) were more strongly correlated than length deviations in different syllables. Further timing analysis based on spectral features revealed shared timing deviations between same ID elements on the sub-syllabic time scales [5]. In syllables with strong temporal cues, we could demonstrate that shared same ID timing deviations were specific to segments as short as 10 msec, i.e. a given 10 msec segment of song is correlated with the same 10 msec segment repeated over 1000 msec later, but is uncorrelated with the adjacent 10 msec segment of song.

In sum, our behavioral analysis has shown: (1) timing is dominated by tempo variations shared across syllables and gaps; (2) syllables are less elastic than gaps with respect to changes in song tempo; and (3) shared same ID deviations across motifs are specific to 5–10 msec segments of song. Here we demonstrate that a simple synfire chain model, subject to slow modulatory influences that vary from song-to-song, account for these three aspects of song timing. In the most simplified version of the model, we consider a single integrate-and-fire type neuron at each link in the chain. When threshold is reached, this triggers a stereotyped burst of spikes leading to a post-synaptic potential (PSP) in the next neuron. With this simplification, analytic results can be obtained on the speed of propagation over that link as a function of the shape of the PSP and the parameters of the model. We show that for most PSP shapes, the following conditions lead to results 1–3 above: (a) motif repetition by repeated propagation down a single chain of neurons; (b) modulation in neural excitability (modeled as distance to threshold) that changes from song-to-song and are spread nearly, but not exactly, uniformly across all neurons in the chain; (c) weaker synaptic connections between links in the chain that drive timing during inter-syllable gaps. Further timing results are explored by adding more realism to the model (realistic numbers of neurons and connections, background noise, feedback inhibition, etc.).

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