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AN ASSOCIATIONAL HYPOTHESIS FOR SENSORIMOTOR LEARNING OF BIRDSONG

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Abstract

Songbirds learn to sing in a two stage process. First, the bird forms a sensory template by listening to and memorizing its father's song. Second, the bird practices singing and learns to match its song to the memorized template. Two experimentally well-supported hypotheses locate song sequence generation in nucleus HVc, and the sensory template in the anterior forebrain pathway (AFP). However, there is no known connection from the AFP to HVc. Furthermore, due to auditory feedback delay, reinforcement signals from vocalization are likely to reach the motor pathway after the burst of motor activity responsible for the vocalization. Thus, it is unclear how template information and auditory feedback could be used to guide learning of song.

A model of sensorimotor learning of syllables and song sequences is outlined that resolves these problems, using only simple associational and reinforcement learning. First, HVc uses auditory feedback to learn an efference copy, i.e. a prediction of the auditory vocalization that will result from premotor activity. Second, the AFP uses this efference copy, rather than auditory feedback, to compare to the template, and uses the result to reinforce appropriate sylla-

ble representations within RA. Sequence production results from an interplay of premotor activity and an auditory feedback-induced efference copy within HVc. Finally, by influencing the statistics of the RA patternsı resulting from HVc premotor activity, the AFP ensures that sequences generated in HVc are mapped onto the appropriate sequence of states within RA.

Introduction

Birdsong is a complex, learned motor act subserved by an anatomically well-defined set of brain nuclei. In the sensory phase of song learning, young birds hear and memorize a tutor song. Later, in the sensorimotor phase, birds match their vocalizations to the memorized song, using their own auditory feedback. Our model assumes sensory learning is complete and proposes a novel mechanism for the sensorimotor phase of learning.

Adult song in the zebra finch usually consists of a few short notes followed by a single sequence of syllables repeated from one to four times. We focus on learning this stereotyped sequence, or motif, and assume intrasyllable temporal structure is encoded in spatial patterns of neural activity. Thus our model's task is to learn a given set of spatial patterns of activity, and to produce these patterns in a given sequence.

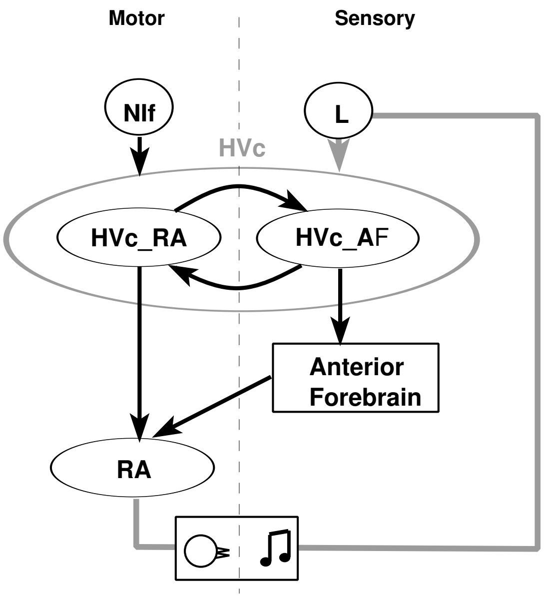

Figure 1.

The song system consists of two main anatomical pathways, both of which contain the nucleus HVc [2,8]. The motor pathway contains NIf, HVc and

RA. RA projects to the vocal motor nucleus and respiratory brain stem nuclei. The Anterior Forebrain Pathway (AFP) creates an indirect connection from HVc to RA (see fig. 1) and contains auditory neurons. HVc receives premotor inputs from NIf and auditory inputs from field L. HVc neurons that project to RA and those that project to the AFP form distinct populations [7]. These populations, which we name HVc_RA and HVc_AF, are highly intermingled and interconnected.

Lesion experiments demonstrate that song production depends on HVc and RA but is independent of the AFP in adults [8]. However, both the AFP and auditory feedback are critical for song learning [2,4,9]. One suggestion has been that the AFP stores the tutor template and provides a teaching signal via its connections to RA [3,6]. Experiments in singing birds also suggest that HVc generates motifs whereas RA activity relates to individual syllables [10].

Taking these as working hypotheses, two major problems are posed for any birdsong model. First, there is no known pathway from the AFP back to HVc. Thus it does not appear that teaching signals from the AFP guide learning within HVc. Second, the delay for auditory feedback to RA via the AFP approximately equals the time from the onset of one syllable to the next [5,11]. Thus an AFP teaching signal most likely returns to RA after RA is already producing the next syllable.

Our main contribution is to outline an hypothesis for sensorimotor learning in both HVc and RA in which the template is stored *exclusively* in the AFP, and teaching signals from the AFP reinforce associations with *current* patterns of activity in RA. The essential idea is that HVc uses auditory feedback to map the current motor command to a prediction of the auditory result. The AFP, based on a comparison of this prediction with the template, alters intrinsic connections within RA as well as the motor map from HVc to RA.

Methods

Our model uses Hebbian learning in simple networks of rate-coded, point neurons to implement associations between distributed patterns of activity. These same properties are retained by closely related, but more realistic network models [1]. Our hypothesis proposes an architecture and dynamics that lead, in stages, to appropriate learning of song. A combination of analysis and simple simulations indicates that each stage of the learning will occur as hypothesized for simple linear networks with saturation. More complete simulations are in progress to verify that all stages can be accomplished in a single network. A detailed presentation of the model and simulation results is beyond the scope of this article.

Results

NIf encodes timing in our model by producing a premotor burst to begin each syllable. Initially, NIf activity is propagated down the motor side of the system and the bird sings random, mumbling sounds. HVc_AF receives this auditory feedback. Premotor HVc_RA activity thus becomes associated with the resulting HVc_AF sensory activity. Note this feedback signal is not evaluated by the AFP and is assumed to return to HVc *before* the onset of the next NIf burst. As this association grows, premotor activity in HVc_RA elicits an efference copy in HVc_AF of the related sensory activity. This map is updated during the end of each syllable, so the proper motor-to-sensory map within HVc is continually maintained even as other parts of the system develop.

We assume the AFP evaluates the efference copy and gives two separate teaching signals to RA. The first, a scalar reinforcement signal, determines the magnitude of change for both the HVc_RA to RA and the intrinsic RA connections. This reinforcement is nonzero only for vocalizations that resemble the template syllables. Thus HVc_RA activity gets mapped to the subspace of RA activity containing the tutor syllables. Since this signal is greatest for actual tutor syllables, autoassociation creates attractors in RA corresponding to these patterns. At this point the bird sings syllables that closely match the tutor, sung in random order.

Random connections back from HVc_AF to HVc_RA cause each HVc sensory signal to bias the subsequent HVc premotor activity in a fixed but random direction. This leads to a fixed but random sequence of motor commands in HVc, resulting in a corresponding random sequence of syllables in RA. Generation of correct sequences is guided by the template stored in the AFP. However, the AFP projects to RA but not to HVc. Therefore, signals from the AFP are used to adjust connections "downstream" of HVc. In particular, the AFP uses its second, vector-valued teaching signal to guide associational learning of the HVc_RA to RA connections.

To accomplish this, the teaching signals from the AFP are used to bias RA activity toward the "correct" sequence. More specifically, a syllable sung out of sequence results in a mismatch between the HVc and AFP signals converging on RA. Sometimes this relatively small AFP signal causes RA to produce the correct syllable. By biasing the statistics of which RA syllables follow a given HVc_RA pattern, associational learning on the HVc_RA to RA connections remaps HVc motor commands to the proper RA sequence. When the HVc and AFP signals converging on RA match, the bird reproduces the complete memorized motif.

Summary and Conclusions

We have outlined an hypothesis for how simple associational and reinforcement learning rules can be used to address difficult issues in birdsong sensorimotor learning. A sensory template stored in the AFP combined with auditory feedback guides the learning process through three distinct phases:

- Hebbian learning within HVc is used to associate initially random premotor signals in HVc_RA with the raw auditory feedback signals arriving in HVc_AF. As this motor-to-sensory mapping within HVc develops, premotor activity in HVc_RA comes to elicit an efference copy signal in HVc_AF.
- The efference copy signal is compared with the template stored in the AFP and the resulting scalar signal is used to build syllable representations in RA. In particular, reinforcement guided autoassociational learning of intrinsic RA connections creates attracting states within RA corresponding to the tutor syllables. Auditory feedback guided autoassociational learning creates the corresponding attracting states within HVc_AF.
- Random associations in the HVc_AF to HVc_RA connections lead to a random but stereotyped sequence of premotor commands within HVc. Vector valued teaching signals from the AFP are used to bias RA activity in the direction of the correct sequence. Associational learning between HVc_RA and RA is used to remap the random premotor sequence in HVc onto the proper sequence in RA.

Our model proposes specific functional roles for the various connections both within and between the nuclei in the motor pathway of the song system. Sequence generation results from the reciprocal interaction between a random sensory-to-premotor map and a premotor-to-sensory efference copy developed while learning individual syllable representations. We believe that the model provides a useful framework to guide further theoretical and experimental investigations into song learning.

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