

## **Hebbian mechanisms underlying the learning of Markovian sequence probabilities**

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Most natural sensory and motor events do not occur in isolation, but are embedded in sequences with rich probabilistic structure. Despite the ubiquity of such learned probabilistic sequences, little is known about neural mechanisms that allow the statistical structure of sequential experience to be embedded within patterns of synaptic weights. Here, we investigate conditions under which Hebbian synaptic plasticity sculpts unstructured networks to quantitatively reflect the conditional probability of sequential events in their synapses. We show through analytics and simulations that Hebbian plasticity with pre-synaptic competition develops synaptic weights proportional to conditional forward transition probabilities  $[P(s(t+1)|s(t))]$  present in the input sequence, and are thus appropriate for sequence generation. In contrast, post-synaptic competition develops weights proportional to the conditional backward probabilities  $[P(s(t-1)|s(t))]$ , which interestingly are reflected in auditory responses of Bengalese finch (Bf) song circuitry. We demonstrate that to stably but flexibly reflect the conditional probability of a neuron's inputs and outputs, local Hebbian plasticity should approximately balance the magnitude of synaptic depression relative to potentiation (a competitive force that triggers weight differentiation) with the weight dependence of synaptic change (a homogenizing force that stabilizes weights). These forces control the rate at which structure is learned and the entropy of the final distribution of synaptic weights. Thus their relative balance induces a prior over learnable transition distributions. For a range of balances, we find robust sequence learning, including the learning of probabilistic syllable sequences generated by Bfs. Together, these results demonstrate remarkably simple correspondences between biophysics and probabilistic sequence learning: the site of synaptic competition dictates the temporal flow of learned probabilistic structures and the balance between competitive and homogenizing forces dictates a prior expectation of the randomness of the sequence to be learned. This yields a novel mechanism for priors over sequence distributions to be embedded within synaptic biophysics.