

# Spike-Time-Dependent Plasticity and Heterosynaptic Competition Organize Networks to Produce Long Scale-Free Sequences of Neural Activity

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## SUMMARY

Sequential neural activity patterns are as ubiquitous as the outputs they drive, which include motor gestures and sequential cognitive processes. Neural sequences are long, compared to the activation durations of participating neurons, and sequence coding is sparse. Numerous studies demonstrate that spike-time-dependent plasticity (STDP), the primary known mechanism for temporal order learning in neurons, cannot organize networks to generate long sequences, raising the question of how such networks are formed. We show that heterosynaptic competition within single neurons, when combined with STDP, organizes networks to generate long unary activity sequences even without sequential training inputs. The network produces a diversity of sequences with a power law length distribution and exponent  $-1$ , independent of cellular time constants. We show evidence for a similar distribution of sequence lengths in the recorded premotor song activity of songbirds. These results suggest that neural sequences may be shaped by synaptic constraints and network circuitry rather than cellular time constants.

## INTRODUCTION

Reaching for or throwing objects, walking, and vocalizing are a few of the ways vertebrates interact with the world. Vertebrates also plan, visualize, or review action and event sequences. Underlying the time-varying patterns of muscle activation or sequential cognitive processing are sequences of neural activity. Such sequences are found in various parts of the brain, including the cortex (Schwartz and Moran, 1999; Andersen et al., 2004; Pulvermüller and Shtyrov, 2009; Luczak et al., 2007; Buonomano, 2003; Ikegaya et al., 2004; Tang et al., 2008), hippocampus (Nádasdy et al., 1999; Louie and Wilson, 2001; Pastalkova et al., 2008; Davidson et al., 2009), basal ganglia (Barnes et al., 2005), and the songbird HVC (Hahnloser et al., 2002; Kozhevni-

kov and Fee, 2007), under various behavioral states. The ubiquity of repeating sequential neural patterns across species, task and nontask conditions, and even in vitro suggests that the mechanisms for creating sequence-producing circuits may be quite general and robust. Yet little is known, from experiment or theory, about what these mechanisms might be. In this work, we investigate plasticity rules that could sculpt sequence-producing neural circuits out of initially disordered networks.

What are some of the properties of sequential neural activity patterns? Sequences are frequently much longer than the membrane and synaptic time-constants of individual neurons. The coding of sequences is sparse. For instance, individual premotor neurons in motor cortex are active in only small portions of a figure-eight arm tracing trajectory in monkeys (Schwartz and Moran, 1999). Similarly, hippocampal place cells fire at one or a few locations of a long track while the animal runs or as it rehearses its possible forward trajectories at a decision point (Pastalkova et al., 2008) or as it replays in sleep its place cell activation sequence (Louie and Wilson, 2001). Zebra finches produce song motifs lasting up to 1 s, while individual neurons in the high-level premotor center are each active for only single bursts of about 6 ms duration (Hahnloser et al., 2002) over the full song sequence. In other words, the high-level coding of sequential activity in the brain is sparse, with single neurons firing for small portions of the entire sequence.

Many sequential behaviors are also “modular,” composed of gestures or shorter sequences that can be flexibly arranged and combined. The underlying neural codes are also found to be modular, sometimes even when the behavior itself is not obviously so. For example, although the song of a zebra finch consists of a largely stereotyped single sequence of syllables, the neural drive underlying the song appears to consist of a concatenation of a disjoint set of separate subsequences of neural activity (Tanji, 2001; Glaze and Troyer, 2006; Wang et al., 2008; Davidson et al., 2009).

Several network-level models seek to explain the propagation of sequential neural activity. A number of such models can be grouped into the category of “synaptic chain” networks (Amari, 1972; Kleinfeld and Sompolinsky, 1988; Abeles, 1991; Drew and Abbott, 2003; Li and Greenside, 2006; Jin et al., 2007). In synaptic chain networks, the connectivity matrix is asymmetric or directional, with one group of neurons connecting to the next, and so on. Activity in the network flows in the direction of

the underlying connections. Such an architecture is consistent with the dynamics of sequence generation in the premotor nucleus HVC of songbirds (discussed in Fiete and Seung, 2008; Weber and Hahnloser, 2007). Synaptic chain models represent a first step toward understanding neural sequence generation, but the requisite network connectivity is hand designed and hard wired. There is relatively little experimental or theoretical understanding of how initially unstructured networks may organize into synaptic chain configurations. Similarly, it remains unknown how multiple neural subsequences of varying length (Tanji, 2001; Wang et al., 2008; Davidson et al., 2009) are formed.

Spike-time-dependent plasticity (STDP) rules demonstrably allow networks to perform next-step recall of sequentially presented inputs: STDP rules translate repeated sequential activations of pairs of neurons into a permanent increase in the synaptic strength from the first onto the second neuron (ordered by time of activation), while weakening the reverse connection (Bi and Poo, 1998, 2001; Abbott and Nelson, 2000), making STDP a natural candidate for explaining synaptic chain formation.

But simulation studies make it clear that STDP rules with bounds on individual synaptic strengths are largely unsuccessful at producing networks that autonomously generate long or sparse neural activity sequences (Aviel et al., 2003; Levy et al., 2001; Suri and Sejnowski, 2002; Rao and Sejnowski, 2003; Nowotny et al., 2003). This is because STDP tends to enhance population synchrony (temporal bunching) and concentrate activity in a few winning neurons (spatial bunching): the forward synapse between a pair of neurons firing in close succession will be strengthened, thereby further decreasing the lag between their firing times and thus promoting their synchrony (Buonomano, 2005). A neuron that fires frequently early on will have its inputs strengthened and will also tend to successfully drive its outputs, quickly becoming a hub that drives simultaneous activity in a large fraction of the network. These results illustrate the difficulty encountered in explaining how various brain areas could organize to generate sequential patterns of neural activity.

One method for forming long sequences using STDP is to consider a network of intrinsically bursting neurons and sequentially grow a chain by restricting synaptic plasticity to just the few neurons at the end of the growing chain (Jun and Jin, 2007). However, this approach does not allow for the simultaneous formation of multiple chains and requires a separate scheme for producing a range of chain lengths.

A cellular property that has not been linked with sequence-producing networks or sequence learning is heterosynaptic competition. Heterosynaptic competition for synapse growth or total synaptic strength has been documented at both pre- and postsynaptic neurons. For example, postsynaptic neurons balance activity-dependent potentiation of an input synapse by inducing heterosynaptic depression among other input synapses, conserving the total synaptic weight onto the neuron (Royer and Paré, 2003). Similarly, the dependence of long-term potentiation on the synthesis of new proteins provides neurons with the ability to constrain the strengthening and weakening of outgoing synapses on the full-cell level (Huber et al., 2000; Fonseca et al., 2004, 2006).

We show that when STDP is combined with heterosynaptic competition for scarce synapse-building resources on the level

of individual neurons, initially random neural networks robustly self-organize to form multiple synaptic chains of different lengths. If inputs to the network are sequential and dense, the combined plasticity rules drive the network to rapidly learn unary versions of the input sequence. Surprisingly, a network with these plasticity rules self-organizes to produce long unary chains of activity even if the training inputs are temporally random, with no sequential structure.

For concreteness, we identify our model network with the songbird premotor area HVC. The reasons for this choice are that, first, HVC appears to originate sequential activity, rather than inheriting it as sequential input from an upstream area (Nottebohm et al., 1976, 1982; Bottjer et al., 1984; Hahnloser et al., 2002; Fee et al., 2004; Long and Fee, 2008); second, the constituent neuron types and their activity patterns during song are well-characterized (Mooney, 2000; Hahnloser et al., 2002; Mooney and Prather, 2005; Kozhevnikov and Fee, 2007); and third, HVC is thought to possess an underlying synaptic chain structure (arguments in Fiete and Seung, 2008; Seung, 2009). We demonstrate that the lengths of the chains formed by learning obey a power law that resembles the distribution of HVC chain lengths, as inferred from electrical stimulation experiments in songbirds. The model, because of its genericness, could be applied to other areas where sequences are known to originate and where the underlying network architecture is that of a synaptic chain. In these cases, it would lead to similar predictions on the distribution of chain lengths and on the elements required for chain formation.

## RESULTS

### The Model

The songbird HVC consists of three cell populations.  $HVC_{RA}$  neurons display unary activity sequences, send recurrent collaterals within HVC, and project downstream to the next nucleus (RA) in the motor pathway. Inhibitory interneurons fire tonically throughout the song motif and project within HVC.  $HVC_X$  cells send outputs to a distinct anterior forebrain pathway that is not necessary for song production in adults.

Our simple network model consists of excitatory neurons with modifiable recurrent synapses (Figure 1A). These represent the  $HVC_{RA}$  neurons. The model includes an inhibitory unit that sums the activity of all excitatory neurons and in turn provides equal global inhibition to all of them. This global inhibitory unit represents the pool of inhibitory interneurons in HVC. We do not include  $HVC_X$  neurons in our model.

The excitatory neurons receive external inputs with temporally random activations (no sequential structure or temporal correlations), except where specifically noted. Initially, the recurrent weights between excitatory neurons are all assumed to be small and random. All weights between the excitatory neurons undergo STDP with an antisymmetric learning window, schematized in Figure 1B. Crucially for the success of sequence formation, in addition to STDP we impose a nonlinear competition across synapses at each neuron, by imposing heterosynaptic long-term depression (hLTD) when the weights at a neuron hit a limit (Figure 1C). The rule is summarized by the summed-weight limit rule.

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