APPENDIX VIII

Self-organization of neural networks into winnerless competition

The evolution of neural responses to odors in the antennal lobe of the locust follows temporal dynamics that do not lead to a static attractor or a closed limit cycle. Nevertheless, sufficiently similar inputs to the olfactory system lead to equal behavioral responses, and thus presumably to equal neural responses. This means that the time-varying responses to odors must act as dynamic attractors in neural dynamics space. To model these and other such attractors, Rabinovich et al. (2001) introduced a class of dynamical systems they termed competitive networks, or Winnerless Competition (WLC). These produce deterministic trajectories moving along heteroclinic orbits that connect saddle fixed points or saddle limit cycles in the system's state space. These saddle states correspond to the activity of specific groups of neurons, and the separatrices connecting these states correspond to sequential switching from one state to another.

In its original formulation, WLC was assumed to require closed loops in the network, i.e. closed loops of strong unidirectional connections with weak or no connections in the opposite direction (Laurent et al., 2001). This requirement led to cyclical behavior of the network (Fig. VIII.1), a property that is not shared by the biological networks in the olfactory system. Here, I show that closed loops are not required, and that relaxing that requirement eliminates the cyclical behavior, leading to activity more similar to that observed in biological networks (Fig. VIII.2).

More importantly, how a network can self-organize to produce the connectivity required for WLC remains unknown. In particular, the requirement for asymmetric connectivity suggests an interaction between each synapse and its corresponding synapse with the opposite connectivity, but these two synapses are typically far-removed from each other, making a specific direct interaction between the synapses difficult. I show here that a simple biologically-observed local learning rule suffices to create WLC in initially random networks.

WLC requires that for every pair of neurons (A,B) for which A projects strongly to B, B project weakly (if at all) to A. At a first glance, it seems impossible for a local learning rule to achieve this antisymmetric connectivity pattern, for the strength of a connection A to B depends on that of another synapse, potentially a long distance away. And yet closer examination reveals that a local rule can indeed do the job. Furthermore, the trick is accomplished by a rule that has actually been observed in biology, albeit in slightly different circumstances.

The rule in question was discovered in what have rapidly become classic studies by Markram et al. (1997) and Bi and Poo (1998). It is called spike-time dependent plasticity (STDP), and says that the synapse between neuron A and neuron B is strengthened if a spike in A immediately precedes one in B, but is weakened if a spike in A follows one in B (Fig. VIII.3). I propose that the antisymmetric character of this rule --which induces in the A-B and B-A synapses opposite changes upon a suc-

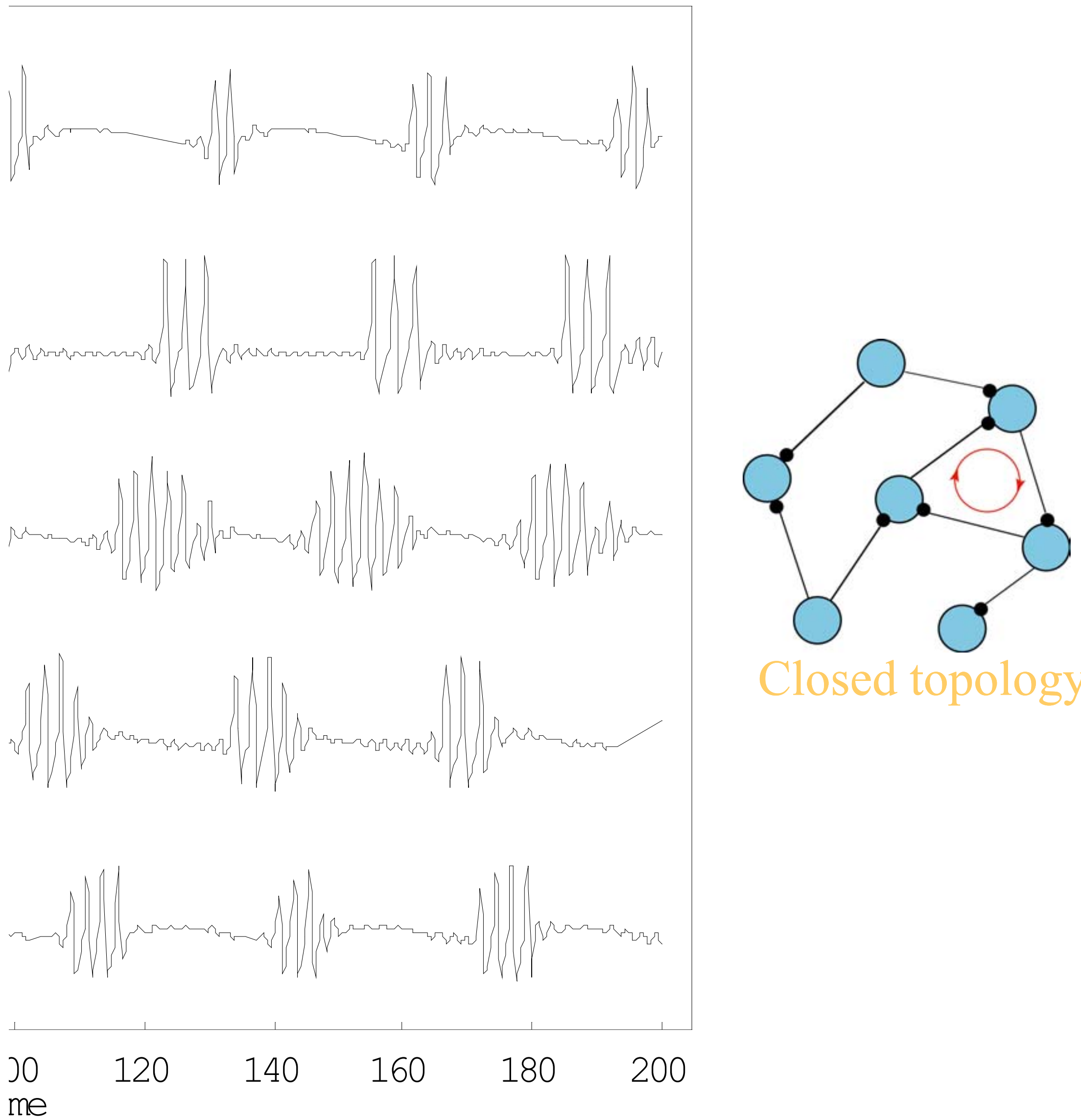

Figure VIII.1. The original formulation of WLC involves a closed topology, i.e. a ring of strong connections, leading to cyclic behavior. But networks in the antennal lobe of the locust to do not exhibit cyclic behavior, even with prolonged stimulus pulses (Wehr, 1999).

cession of quasi-coincident spikes across the neurons-- suffices to create WLC out of an network initially configured with random synaptic weights. Computer experiments by Valentin Zhigulin have confirmed this prediction (Fig. VIII.4).

The stability of the attractors produced by this learning rule remains to be determined. It is likely that

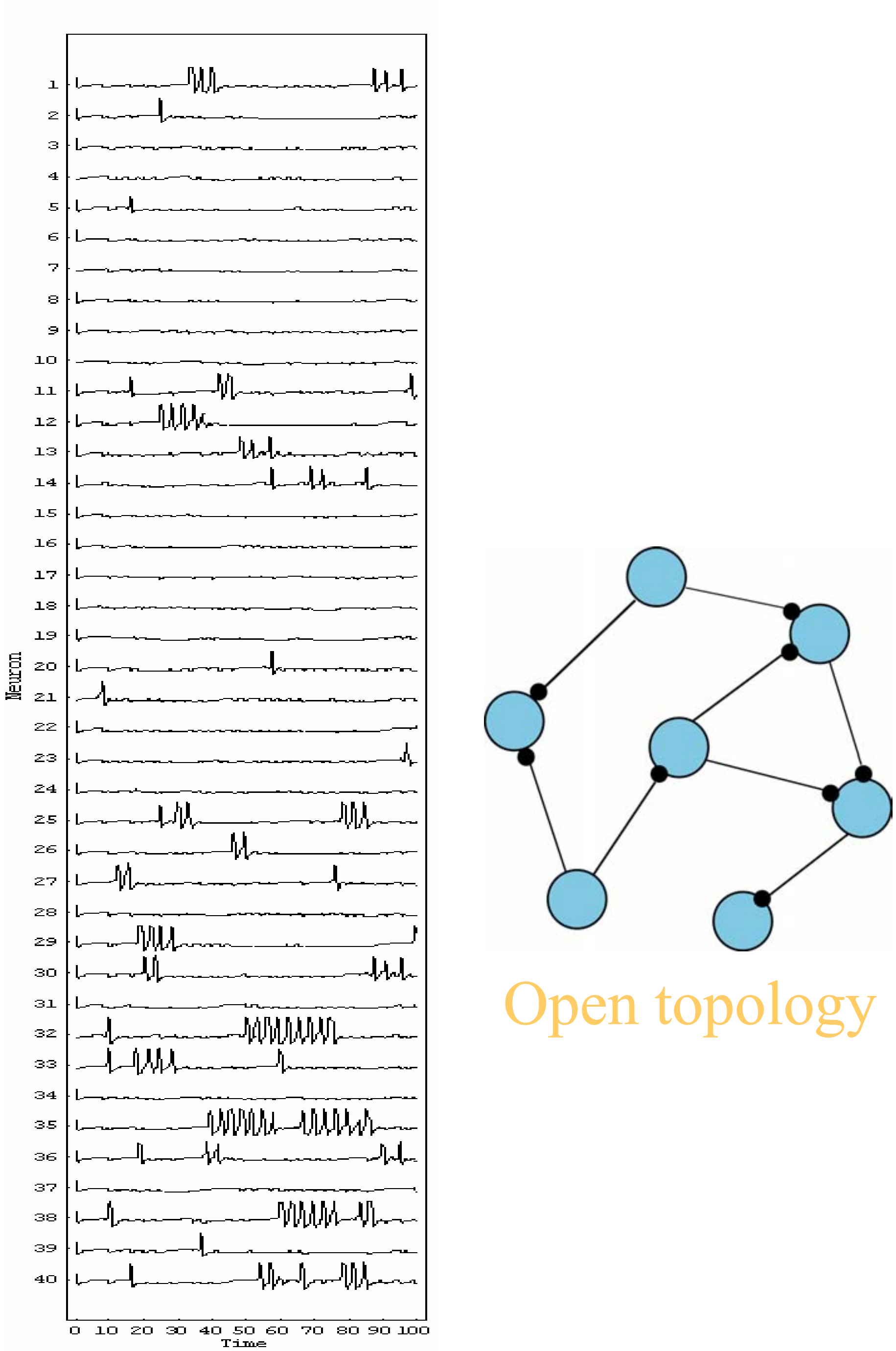

Figure VIII.2. Eliminating closed loops causes network activity to lose cyclic behavior, but preserves the dynamic nature of the network's response, emulating the behavior of biological networks more closely.

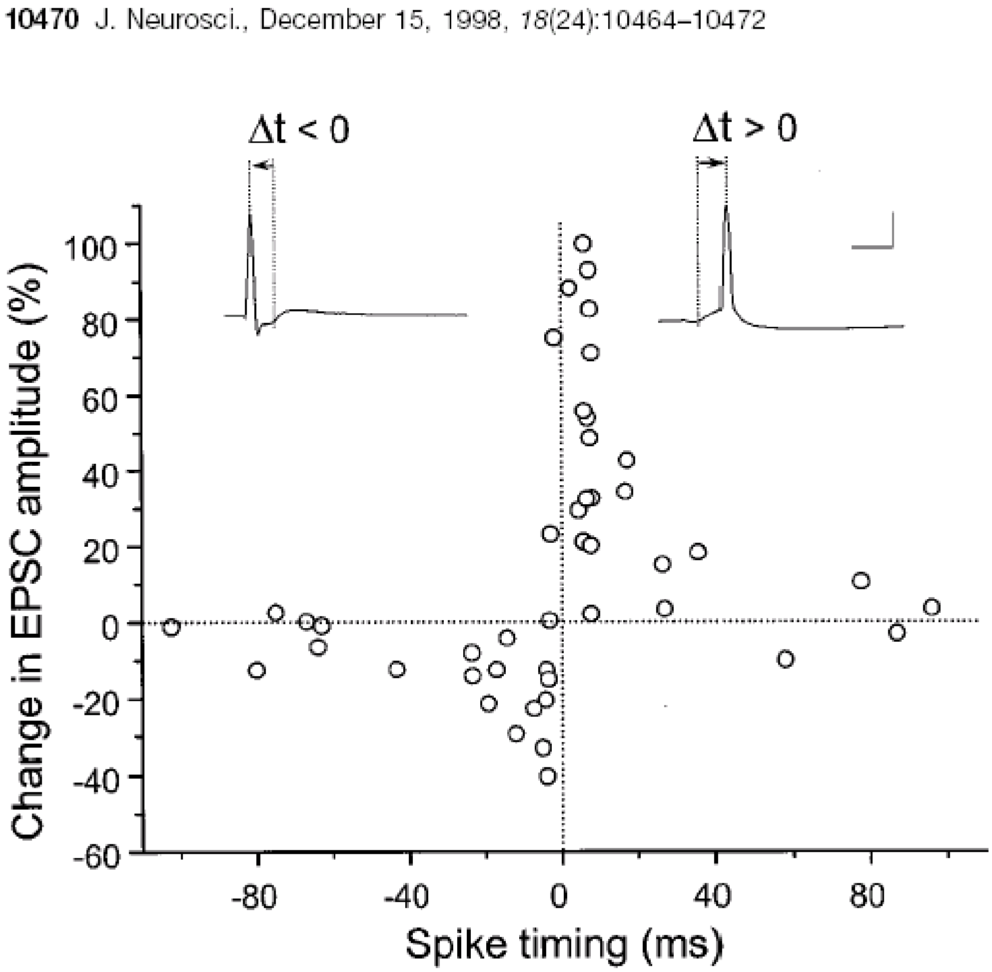

Figure VIII.3. Spike-time dependent plasticity (from Bi and Poo, 1998).

additional contraints, such as a multiplicative factor in the learning rule that makes synapses that are far from their initial values less prone to further modification, need to be introduced for this purpose.

Acknowledgement

The validity of the ideas above was demonstrated experimentally by Valentin Zhigulin.

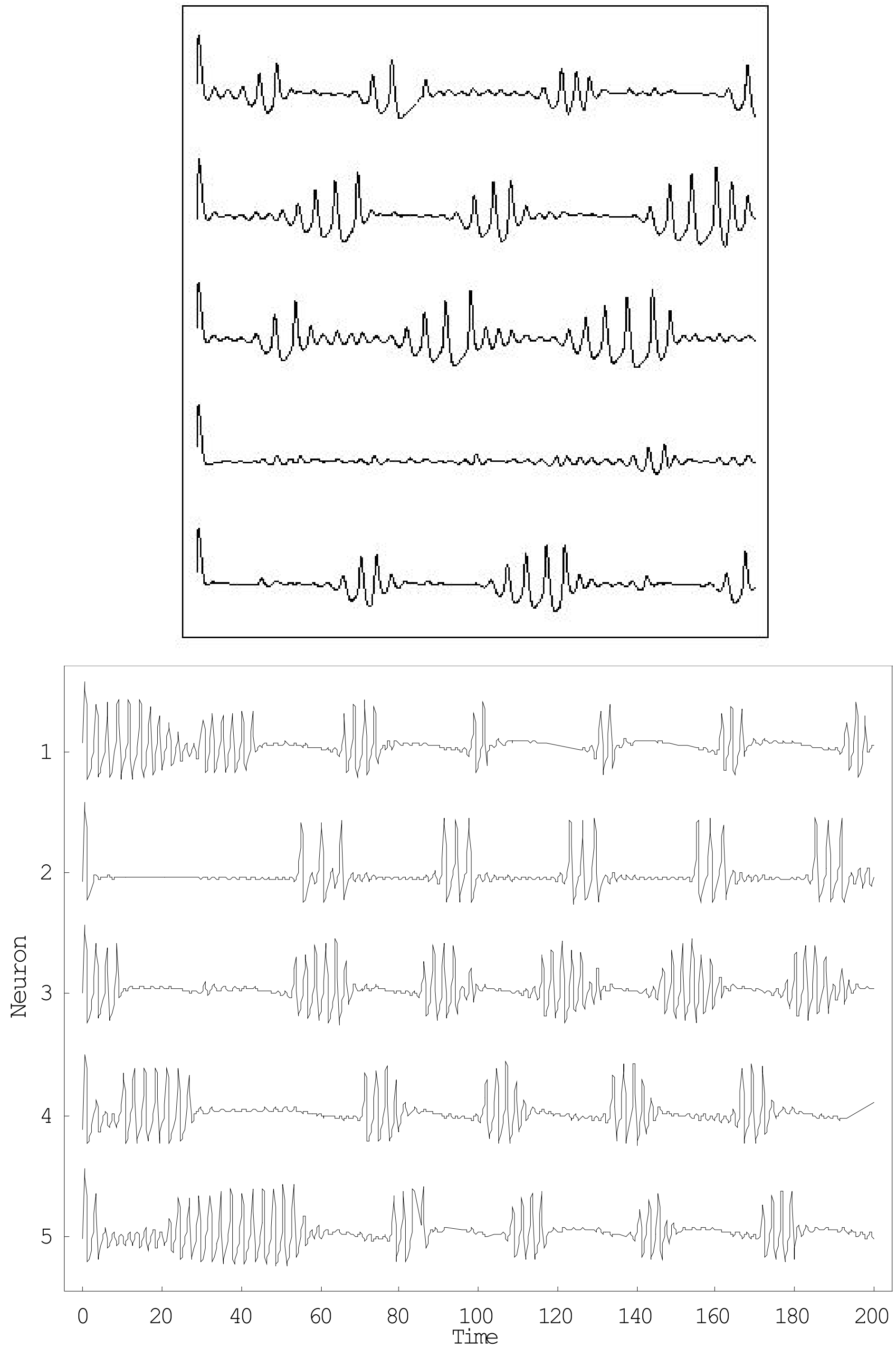

Figure VIII.4. STDP produces WLC in excitatory (top) and inhibitory (bottom) initially randomly connected neural networks.