Accepted to the *10th International Conference on Cognitive and Neural Systems (ICCNS)*, May 17-20, 2006, Boston University, Massachusetts

The self-organized growth of synfire patterns

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The connectivity of the neocortex displays striking regularities that account for its functional specialization. Synaptic contacts reorganize during pre- and post-natal development via epigenetic factors involving interactions between extrinsic and intrinsic sources of neural activity. We propose a neural network that models the development of such structures as a process of *spatiotemporal pattern formation*. We show the spontaneous and simultaneous emergence of ordered chains of synaptic connectivity and wave-like propagation of neural activity. These simple linear structures were first called "synfire chains" by Moshe Abeles. They consist of synchronous groups, feed-forward connections and waves of activity. In our model, starting from a disordered network with broad diffuse connectivity and low stochastic activity, some synaptic connections become selected and strengthened to the detriment of others. This "focusing of innervation" is accompanied by a gradual increase in sustained correlated firing. In a true self-organized fashion, connections and correlations reinforce each other through heterosynaptic *cooperation*, while the global stability of the network is maintained through a constraint of heterosynaptic *competition*. Hebbian plasticity is one of the major principles underlying the development and tuning of the nervous system. Cortical neurons are highly sensitive to nearly synchronous inputs amongst afferent connections, while synaptic contacts are rewarded by successful transmission events. This work describes how a neural network may become spontaneously structured as a result of these two principles, which are given a straightforward mathematical form. We propose a very simple model based on binary neurons, fixed weight increments and uniform graphs, and show that regularities already emerge under these conditions. In a fully-connected network of N $\{0, 1\}$-valued excitatory neurons, cell i fires at time t with probability $P[x_i(t) = 1] = 1 / (1 + \exp(-(V_i(t) - \theta) / T))$. The "temperature" T determines the amount of noise in the system. The membrane potential is given by $V_i(t) = \sum_j w_{ij}(t)\, x_j(t - \tau_{ij})$, where w_{ij} is the weight of $j \rightarrow i$ and τ_{ij} a fixed transmission delay (time is discrete, in steps of roughly 1 ms). Synaptic weight modification occurs in three simple stages. First, all weights are potentiated according to a Hebbian rule: for each $j \neq i$ such that $x_j(t - \tau_{ij}) = x_i(t) = 1$, a small positive increment α is added to w_{ij} (Fig. a). Second, competition pulls all converging and diverging weight sums, $\sum_j w_{ij}(t)$ and $\sum_i w_{ij}(t)$, towards a fixed target s_0. This is done by correcting w_{ij} with a term $-\gamma\, \partial H / \partial w_{ij}$, where H measures a global quadratic difference between the sums and s_0. Finally, weights are clipped, when necessary, to remain in the interval [0, 1]. The network also contains a few "seed" neurons, which send out stronger connections than average. Each seed neuron reliably triggers the same group of cells, thereby creating an initial synchronous pool P_0. Through its repeated (yet not necessarily periodic) activation, P_0 starts recruiting neurons "downstream" and eventually becomes the root of a developing synfire chain $P_0 \rightarrow P_1 \rightarrow P_2 \rightarrow \dots$ (Fig. b). The growth of the chain is recursive and akin to the growth by accretion of a crystal from an inhomogeneity. Under the dual activity-connectivity dynamics, the aggregation of P_{k+1} by P_k is a form of "Darwinian" evolution. In a first phase, noise acts as a *diversification* mechanism, proposing multiple candidates—neurons that happened to fire after P_k and whose contacts from P_k increased by α (Fig. a). In a second phase, competition driven by s_0 acts to *select* among these: the large pool of candidates shrinks and rounds up a final set of winners P_{k+1}. This accretion process is not strictly iterative, as successive pools in the chain develop over broadly overlapping periods of time. As soon as a new pool P_{k+1} reaches a critical mass, its activity is high enough to trigger the growth of the next pool P_{k+2}. Thus, the chain extends in length before widening and, in a spatially reorganized view of the network, typically presents a "beveled" head of immature pools at the end of a mature trunk (Fig. b). Fig. c reveals the growing profile of a chain in four snapshots of the network's total activity following the activation of a seed neuron at different times. At a larger, *mesoscopic* scale of organization, Fig. d illustrates the concurrent growth of multiple chains and hints at the possibility of wave synchronization and coalescence, via dynamical binding (arrows), in a "self-woven tapestry" of synfire patterns.