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Spatio-temporal firing patterns in the frontal cortex of behaving monkeys

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Summary — Recording the activity of several neurons in parallel in the frontal cortex of behaving monkeys reveals that firing times of neurons can maintain ± 1 ms accuracy even after delays of over 400 ms. The accurate firing structures were associated with behavior. Neural networks that can sustain such accuracy can learn 'learn' to bind with each other and thus may serve as building blocks for cognitive processes.

graph theory / synfire chains / cell assembly / synchrony / spatio-temporal firing patterns / frontal cortex / synaptic reverbation

The activities of single units are usually evaluated by estimating firing rates and correlation functions. By doing so, it is implicitly assumed that the spike trains represent stochastic point processes, for which the main parameters are the (possibly variable) firing rates and correlation functions. However, when evaluating the relations among the firing times of several neurons, it is common to find very precise timing.

Activity of 8–15 single units was recorded in parallel from the frontal cortex of monkeys performing a variety of localization and problem solving tasks. Patterns of firing in which three spikes appear repeatedly with the same intervals are called here spatio-temporal firing patterns (or patterns for short). The present study refers to patterns lasting for up to 450 ms, and in which the firing time is accurate to within ± 1 ms. Systematic searches for spatio-temporal firing patterns, using two independent algorithms, revealed thousands of cases, in which the same pattern repeated many times, way beyond the level that can be expected by chance. In many cases the patterns were associated with the monkey's behavior. In some cases, the entire response of a single unit was composed of such accurate firing patterns. The internal time-locking among spikes of any given pattern were tighter then the time-locking of the pattern to the external stimulus (± 1 ms *versus* 50 ms) (Abeles *et al*, 1993a). Often, the spikes which were involved in a patterns conveyed more specific information about the stimulus or the response as compared to all the spikes of a single unit. Some patterns may appear when a stimulus is delivered in one behavioral context, while others may appear when the same stimulus is delivered in another context.

The cross-correlation between each pair of cells was decomposed into the correlation in which the trigger spikes were limited to the spikes that took part in patterns and to correlations in which all the other spikes were used as trigger. In most cases the spikes that took part in patterns had stronger correlations with the other cells. In many cases the shape of this correlation was qualitatively different from the cross-correlations in which the spikes that did not take part in the patterns were used as trigger.

A simple neural network that can generate such patterns, and is consistent with the known anatomy of the cerebral cortex, is the syn-fire chain (Abeles, 1991). Insight of the properties of syn-fire chains was gained by simulating networks of neurons in which chains of feed-forward, diverging converging connections were laid. The simulations revealed that such chains convert diffuse (asynchronous) excitation into synchronized volleys of spikes that can propagate over many links with very little jitters in time. Thus, if one manages to record the activity of three neurons along a syn-fire chain, then whenever the chain is activated the same spatio-temporal firing pattern would appear. According to this view the relevant physiological parameter is the sequence of synchronously firing pools of neurons. The recorded spatio-temporal pattern merely indicates to the experimenter that a certain syn-fire chain became active.

In the experimentally-recorded spatio-temporal firing patterns, we found many cases in which two or more spikes from the same single unit participated in one pattern. This suggested that a given neuron may take part in more then one link of the syn-fire chain. When many neurons participate in several links along the same chain, the chain ceases to be a simple feed-forward structure. This type of syn-fire chain is an intermediate case between a multi-layer feed-forward network and an attractor network (*à la* Hopfield). Syn-fire chains with many such repetitions can exhibit reverberations, while still maintaining certain preferred sequences of firing constellations.

The simulations revealed that the same group of neurons may support more then one syn-fire chain. In such cases, the sequence of firing constellations contains information beyond that contained in the global activity level of the neurons in the network. One syn-fire chains can 'learn' the sequence of firing constellations that another syn-fire chain produces. By such a process, two syn-fire chains can bind to create a larger and more stable structure (Abeles *et al*, 1993b). The compound syn-fire structure produces new sequences of firing constellations which may recruit more syn-fire chains into more global coherently firing network.

The experimental data and the simulations support the idea that cortical activity is generated and maintained by reverberations in syn-fire chains, and that binding between such syn-fire activities in different brain regions is the mechanism for generating a hierarchy of representations (Bienenstock, 1995).

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