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Reading Neuronal Synchrony with Depressing Synapses

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A recent experiment showed that neurons in the primary auditory cortex of the monkey do not change their mean firing rate during an ongoing tone stimulus. The only change was an enhanced correlation among the individual spike trains during the tone. We show that there is an easy way to extract this coherence information in the cortical cell population by projecting the spike trains through depressing synapses onto a postsynaptic neuron.

Understanding how information about the world is represented and read out from large neuronal populations is one of the most challenging tasks of neuroscience. Recent experiments indicate that the timing of the individual spikes might be used to represent external or internal stimuli while the mean firing rate could even be constant (Vaadia et al., 1995; Mainen & Sejnowski, 1995; Meister, Lagnado, & Baylor, 1995; Alonso, Usrey, & Reid, 1996). At the same time, theoretical analysis of spike trains showed that individual spike times are much more reliable than those for random trains with the same mean and variance (de Ruyter van Steveninck, Lewen, Strong, Koberle, & Bialek, 1997). This raises the question of how the information encoded in a neural population is read out by a postsynaptic cell if this cell receives the same number of spikes during its integration time.

The list of experimental evidence that spike timings and correlation among spike trains may carry important information was recently enlarged by the study of deCharms and Merzenich (1996) on anesthetized monkeys. They recorded individual cells and local field potentials in the primary auditory cortex (AI) of the monkey while stimulating with a pure tone. Apart from transient activity increase at the tone onset and offset, the activity averaged over different presentations and different locations turned out to be the same during and before the tone. However, during the tone stimulus, the correlations among the individual spike times of two simultaneous recordings were significantly higher than before or after the stimulus. It was recently demonstrated that fast synaptic depression may facilitate transmitting synchronous activity of neuronal ensembles (Tsodyks & Markram, 1996, 1997; Abbott, Varela, Sen, & Nelson, 1997). We therefore propose that the information about the presence of the ongoing tone stimulus that is distributed over the AI neurons could be read out through frequency-dependent depressing synapses.

To test our hypothesis, we simulated the output of 500 AI cells by random spike trains (see Figure 1c) exhibiting the same statistical properties as reported in deCharms and Merzenich (1996). There is experimental evidence to assume that before and during the tone, the neurons fire in short bursts (R. C. deCharms, personal communication, 1997), say, with bursts of three to four spikes within 40–50 ms, repeated every 200–250 ms. During the tone, the burst onsets are assumed to be synchronized within groups of 100 neurons that are randomly assembled anew for each burst. Such a scenario is similar to the activity in the monkey frontal cortex during a reaching task, where synchronization among rapidly associated subgroups occurs in the presence of a constant mean firing rate (Vaadia et al., 1995). Since in our simulation the bursting times of the groups alternate during the ongoing tone, the overall firing rate of the population remains constant, apart from the short onset and offset of the tone when most cells burst together (see Figure 1d). Spike trains generated by this scheme produced cross-correlations (see Figure 1a), which match those calculated from the actual recordings (cf. deCharms & Merzenich, 1996).

The synaptic depression was modeled by assuming a limited amount of synaptic neurotransmitter, which recovers with a slow time constant of 800 ms (Tsodyks & Markram, 1997). Whenever a presynaptic spike arrives, a fixed fraction of 0.8 of the available transmitter is released. (More generally, this fraction could be transiently raised by each spike, introducing a fast facilitating component, although this would not change the main results.) The synaptic conductance rises instantaneously to an amplitude proportional to the released transmitter and decays with a time constant of 3 ms.[1] During a burst, the response of such a depressing synapse rapidly decreases for successive spikes due to the depletion of the transmitter and its slow recovery. But during a nonbursting period, the transmitter has time to recuperate, and this results in a strong postsynaptic response at the onset of the next burst. If we compare this dynamic response with that for a nondepressed synapse evoking on average the same postsynaptic potential, the depressed synapse will have a larger response at the burst onset and a smaller response toward the end of the about 50-ms-long bursts.

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[1] The maximal synaptic conductance was $\bar{g} = .15$ for the depressing synapses and $\bar{g} = .0073$ for the nondepressing synapses. The synaptic reversal potential was 0 mV in both cases.

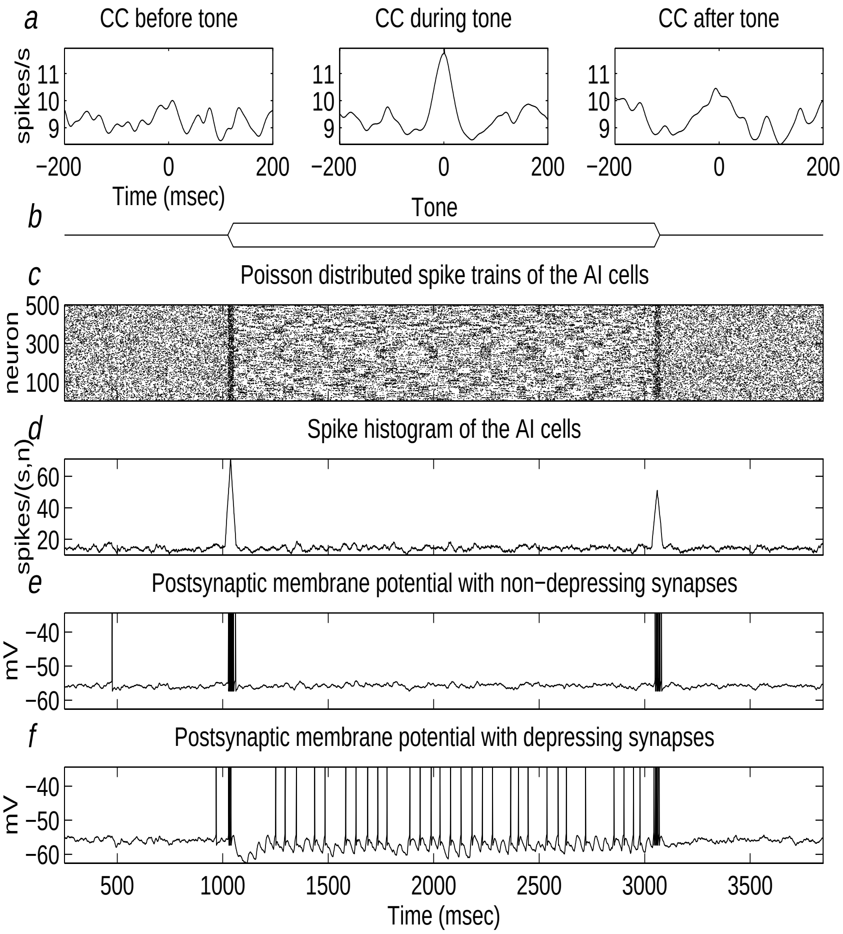

Figure 1: Applying a tone stimulus (b, amplitude envelope), the model auditory cells respond at the onset and offset, but during the stimulus they correlate their bursts only among randomly assembled subgroups (c, spike raster; a, cross-correlations (CC) among spike trains). Since the mean firing rate is on the background level during the tone (d, spikes per second per neuron), a postsynaptic neuron gathering the spike trains through synapses of constant weight would respond only at the stimulus onset and offset (e). With depressing synapses, however, the postsynaptic neuron detects the correlated bursts and fires during the tone as well (f).

Feeding the synthetically generated spike trains into a leaky integrate-and-fire neuron[2] showed that the synaptic depression is indeed able to detect the partial synchrony in the burst times. With nondepressing synapses, the postsynaptic membrane potential follows the presynaptic mean firing rate (see Figure 1d) and is continuously below threshold apart from the tone onset and offset (see Figure c). With depressing synapses, however, the partially synchronized bursts pushed the postsynaptic membrane potential across threshold repeatedly during the stimulus (see Figure 1f). The spikes are triggered at burst onsets when a group of recovered AI neurons starts to fire. During such a burst, the postsynaptic membrane potential decreases because of the synaptic depression and eventually falls below the potential average. Since the bursts are not synchronized in the absence of the stimulus, high responses at burst onsets are canceled by depressed responses at burst ends before and after the tone (see Figure 1f). One could ask whether it would be possible for a postsynaptic neuron with nondepressing synapses to detect the synchrony by selecting any particular subpopulation of AI cells. However, this is difficult since the composition of the synchronized subgroups changes randomly.

The example shows that rapidly depressing synapses enable the brain to extract coincidence information that otherwise would be hidden or would require additional circuits. Since speed and strength of the depression are known to be regulated by the timing between pre- and postsynaptic spikes (Markram & Tsodyks, 1996), such a timing also determines the capacity for extracting the coincidence information in the presynaptic population. The message and its decoding mechanism appear to be dynamically interwoven, and this generates the power of cortical information processing but also makes it difficult to break the neural code.

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[2] The membrane time constant was chosen to be 20 ms, the resting potential was −70 mV, and the threshold was set to −53.6 mV.

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