

## Decorrelation of spike trains by synaptic depression

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### Abstract

Synaptic depression modeled after that seen in cortical slices removes correlations from realistic spike sequences. If not removed, such correlations can lead to inefficient and redundant neural codes. We suggest that this redundancy reduction at individual synapses enables a neuron to better process information from multiple inputs. © 1999 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

Many hippocampal and neocortical synapses appear to be surprisingly unreliable, with only a small fraction of presynaptic action potentials successfully triggering vesicle release [8]. Despite this high failure rate, a neuron's ability to process information about its inputs may not be severely compromised. We suggest that the activity dependence of synaptic transmission enhances a neuron's information-processing capability by increasing the amount of information carried per vesicle release and by allowing the neuron to temporally filter individual inputs before integrating them.

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Previous studies have emphasized the benefits of removing correlations from natural visual images (see, for example [2]) and have suggested that such redundancy reduction may be one of the functional characteristics of the early visual system. Here we focus on reduction of the temporal autocorrelations observed in spike trains modeled after those recorded in area IT of awake monkeys freely viewing natural scenes (videos) [3]. We show that synaptic depression similar to that measured in cortical slices [1,6,9,10] removes correlations from these spike trains and demonstrate how integration of multiple inputs nevertheless produces correlated spike trains.

## 2. Model description and methods

Our work is based on a model that generates spike sequences with statistical structure similar to that of spike trains recorded in area IT of awake monkeys watching videos [3]. Model spike trains are constructed to simulate the spike sequences generated by a typical visually responsive neuron when an animal is making saccades and viewing a natural visual environment. At each saccade, a maximum Poisson firing rate  $r_{\max}$  is chosen from an exponential firing-rate distribution [3,4], and this value is held until the next saccade. Between saccades, spike sequences are generated at a rate  $r(t)$  which is set to 0 following a spike and recovers exponentially to  $r_{\max}$  with time constant 8 ms. Intersaccade intervals of mean duration  $\langle t_{\text{sacc}} \rangle = 365$  ms are chosen from a fit to an observed distribution of intersaccade intervals [11]. The probability density for an intersaccade interval of duration  $t_{\text{sacc}}$  is proportional to  $(e^{4.55t_{\text{sacc}}} + e^{8.82-54.28t_{\text{sacc}}})^{-1}$ . The mean of the exponential firing-rate distribution is chosen such that the long-time average firing rate of the cell is 15 Hz.

Synaptic transmission is modeled as in references [1,9,10]. In our model, however, synaptic amplitudes are interpreted as being proportional to the probability of synaptic transmission. After each successful transmission, transmitter release probability is reduced by an amount  $\Delta p$ , with a floor set at 0. Between transmissions,

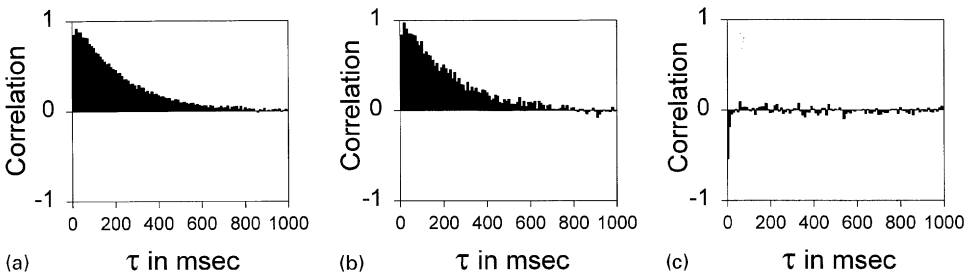


Fig. 1. Decorrelation achieved by synaptic depression. (a) Autocorrelation of a presynaptic spike train of average rate 15 Hz. Note that short-time negative correlations characteristic of post-spike refractory effects cannot be seen at this scale. (b) Autocorrelation of the successful transmissions through a randomly transmitting synapse. (c) Autocorrelation of the successful transmissions through a depressing synapse ( $\Delta p = 0.25$ ,  $\tau_d = 380$  ms) with the same average percentage of successful transmissions as in (b).

release probability recovers exponentially toward a fixed maximal value  $p_{\max}$  with time constant  $\tau_d$ . For the simulations shown,  $p_{\max}$  is set at 1.

Autocorrelations are calculated according to the formula

$$C(\tau) = \frac{\langle s(t)s(t + \tau) \rangle - \langle s(t) \rangle^2}{\langle s(t) \rangle^2}, \quad (1)$$

where  $s(t)$  is a sum of delta functions corresponding to either presynaptic spike arrivals or successful transmissions, and  $\langle \rangle$  indicates time averaging. The denominator normalizes for effects due solely to a change in average rate and sets the value for perfect negative correlations to  $-1$ .

### 3. Results

#### 3.1. Decorrelation at a single synapse

Fig. 1 illustrates the decorrelating effect of synaptic depression. The presynaptic spike trains generated by our saccade model are characterized by strong positive correlations (Fig. 1a). Figs. 1b and c show autocorrelations for the sequences of transmission events resulting from these presynaptic trains' arrival at a synapse that transmits with constant probability (Fig. 1b) and a synapse with the stochastic dynamics of depression outlined above (Fig. 1c). For realistic parameters of synaptic depression, the positive correlations in the presynaptic train are almost completely removed (Fig. 1c). Random failures of synaptic transmission alone do not produce decorrelation (Fig. 1b). Rather, it is the activity-dependent dynamics of synaptic depression that achieve decorrelation by transmitting spikes following a rate change more reliably than spikes occurring during the intersaccade periods of constant-rate firing.

Fig. 2 illustrates the effects of changing the magnitude of depression by adjusting  $\Delta p$  and the recovery time from depression by varying the time constant  $\tau_d$ . This can yield almost complete decorrelation (center), introduce strong negative correlations (bottom right), or decorrelate on short time scales while introducing negative correlations on longer time scales (bottom left). Not surprisingly, decorrelation is maximal when  $\tau_d$  is close to the time scale of the input correlations.

#### 3.2. Integration of many decorrelated synaptic inputs

If each synapse decorrelates its transmissions, why are correlated spike trains seen at all? To address this question, we examine the effect of integrating EPSPs from 30 stochastic, depressing synapses using an integrate-and-fire neuron with membrane time constant 30 ms. Each input to the neuron consists of a positively correlated spike train generated by the saccade model discussed above. Consistency requires that the statistics of input and output spike sequences in recurrent cortical circuits should be the same [7]. Fig. 3b shows the configuration of inputs which was found to produce

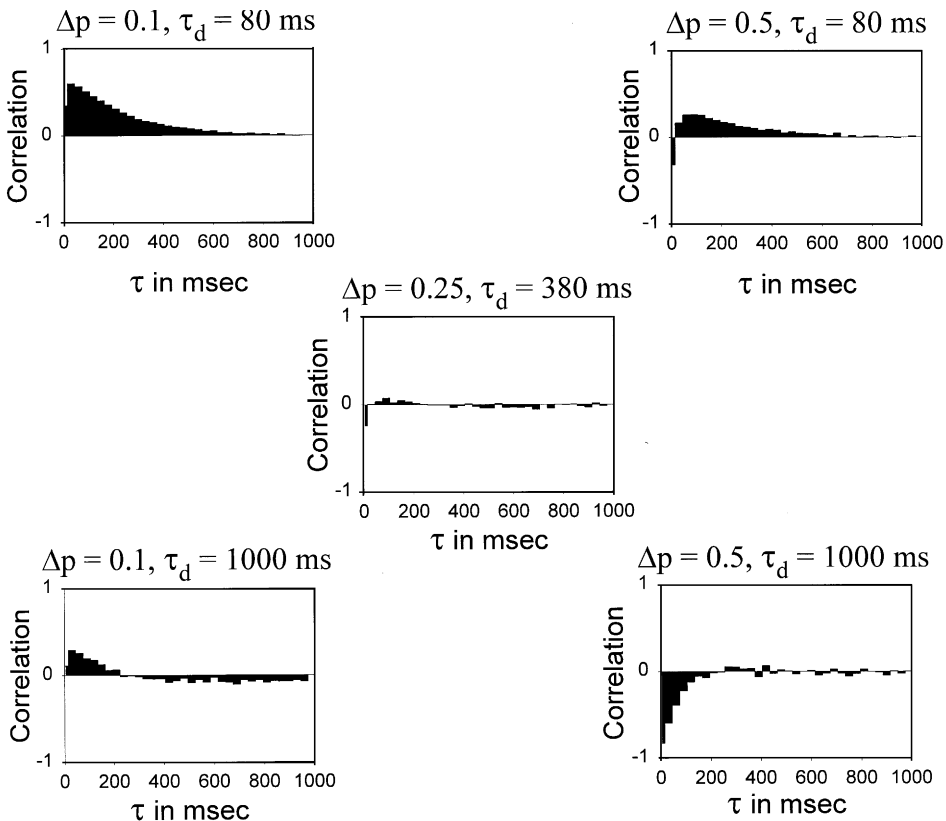


Fig. 2. Autocorrelation of the successful transmissions through a synapse with the specified values of  $\Delta p$  and  $\tau_d$ . Columns left to right show  $\Delta p = 0.1, 0.25, 0.5$ . Rows top to bottom show  $\tau_d = 80, 380$  and  $1000$  ms. Presynaptic trains are as in Fig. 1a.

output spike sequences with statistics consistent with the presynaptic input spike sequences. At each saccade, a subset of inputs (dotted lines) with identical maximum rates  $r_{\max}$  arrive synchronously at the neuron. These synchronous inputs are then followed by an asynchronous subset of inputs (solid lines) with the same rates as the first group but with rate changes that are delayed with the length of the delay chosen from an exponential distribution of mean  $\tau_{\text{arr}}$ . The synchronous subset consists of 43% of the total inputs. The mean delay in arrival time  $\tau_{\text{arr}}$  matched the depression time constant  $\tau_d = 380$  ms. Other simulations (not shown) indicate that the synchronous subset is required to match the short-time correlations, while the asynchronous subset fills out the longer-time correlations. We note that the arrival of a large synchronous group of inputs followed by an exponentially decaying group of inputs would be expected if a feedforward group of inputs were to excite a neuronal population and cause a reverberation of activity, with each loop back to the neuron multiplicatively decayed in amplitude.

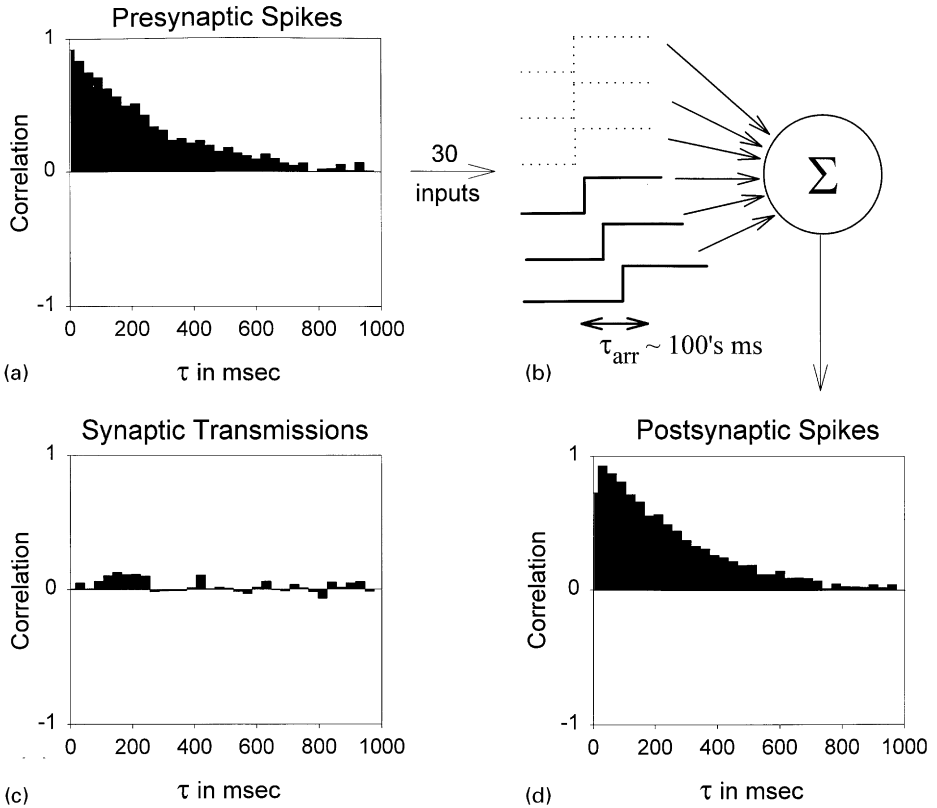


Fig. 3. Configuration of inputs required to match input and output correlations. (a) Autocorrelation of presynaptic spike trains. (b) Pattern of arrivals of an identical change in rate along 30 presynaptic inputs to an integrate-and-fire neuron. 43% of arrivals are synchronous (dotted lines) and the remainder arrive asynchronously (solid lines), with density of arrivals decaying exponentially over time with  $\tau_{arr} = 380$  ms. (c) Autocorrelation of successful transmissions through a synapse with  $\Delta p = 0.2$ ,  $\tau_d = 380$  ms. (d) Autocorrelation of the postsynaptic spike train.

## 4. Discussion

### 4.1. Implications of decorrelation at a single synapse

Our results show that depressing synapses with realistic dynamics decorrelate spike trains typical of those recorded in behaving animals. Decorrelation, while not completely equivalent to information maximization, is an effective way of compressing information while minimizing total synaptic transmission and thus utilization of synaptic resources. Such information compression could be important in allowing a neuron to respond to its changing inputs while filtering out constant inputs. In this sense, it is a manifestation of the cortical gain control mechanism discussed in Ref. [1].

However, decorrelation goes beyond the simple notion of cortical gain control by systematically eliminating temporal redundancy in inputs rather than just normalizing against different input rates.

While this paper has focused on the information-compression benefits of decorrelation, synapses might also be tuned to transmit or remove particular types of correlations. Facilitation, for example, has been argued to be effective in reliably transmitting bursts while filtering out intermittent spikes [5]. While synaptic depression removes positive correlations from spike trains, facilitation removes negative correlations characteristic, for example, of refractory effects. This suggests that the amount and type of short-term plasticity seen in different brain regions may be related to typical regional patterns of neuronal activity.

#### 4.2. Consistency of input and output statistics

We have demonstrated how correlated spiking can arise in a neuron which integrates decorrelated trains of EPSPs. The correlations emerge as a result of integrating cross-correlated inputs whose ‘spatial’ correlations cannot be removed by the synapse-specific mechanisms of synaptic depression. The conversion of spatial correlations to temporal correlations occurs because membrane potential fluctuations produced by a rate change at one input are extended over time by the arrival of the *same* rate change along correlated afferents.

Keeping spatial correlations while removing temporal ones could be advantageous in information processing. While the redundancy inherent in temporal correlations might be useful in averaging away noise, such temporal filtering would be inherently slow; spatial averaging, in contrast, is instantaneous.

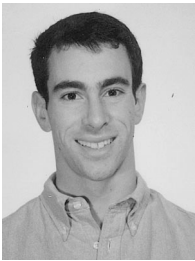
### 5. Conclusion

We have seen that depressing synapses may act as temporal filters that remove redundancy from realistic inputs. By eliminating autocorrelations at individual synapses, neurons become more sensitive to information-rich changes distributed across their inputs. Thus, synaptic unreliability combined with short-term plasticity may increase, rather than decrease, a neuron’s information-processing capability.

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