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A model of expectation effects in inferior temporal cortex

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Abstract

Preliminary experimental data suggests that primate inferior temporal cortex implements an automatic mechanism of expectation: inter-stimulus delay activity often increases or decreases monotonically. The slope of the activity is such that the maximum/minimum is always reached at the time of the onset of the second stimulus, adapting to the length of the interval. This mechanism could play an important role for a variety of neural computations that act on a time scale of a few seconds. We developed a model that reproduces such monotonically increasing activity by making use of short-term synaptic facilitation and network effects.

Keywords: Rising activity; Working memory; Short-term synaptic plasticity

1. Introduction

Experimental data from infero-temporal cortex (IT), obtained from behaving monkeys performing a delayed-match-to-sample task, suggests that delay activity is not constant: during the interval between the presentation of two stimuli (inter-stimulus interval, ISI), the firing frequency of single neurons has a tendency to either increase or decrease monotonically ([8], see also [3–5] for other cortical areas). There is preliminary evidence that increasing activity occurs predominantly in neurons that respond unselectively, i.e. the activity during the ISI is not correlated with the specific sample stimulus. Furthermore, the increase in firing rate is such that a plateau activity is reached at the time of the onset of a generic relevant event, which in our case is the

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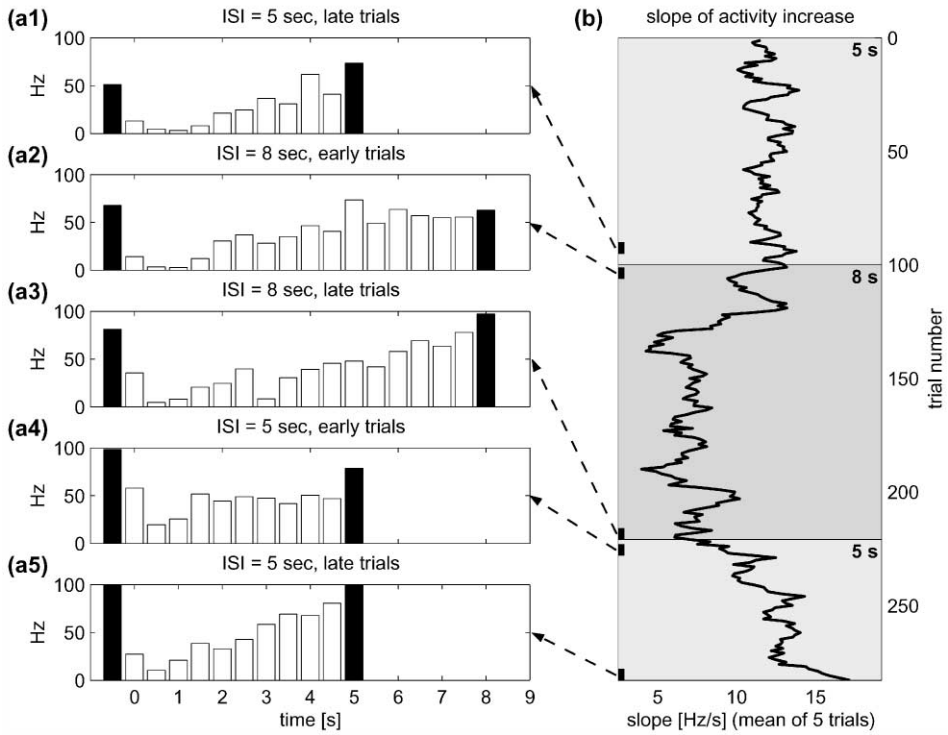

Fig. 1. Expectation effect in a paradigmatic IT cell of a behaving monkey. Firing rates during inter-stimulus interval, mean of five consecutive trials. Black bars represent the visual response. After many trials with an ISI of 5 s, we observe the rising activity of (a1). When changing to 8 s, the plateau activity is at first still reached after 5 s (a2). Several trials later we find rising activity throughout the ISI (a3). A further change back to 5 s initially produces no effect (a4), but steadily rising activity is again found after a few trials (a5). (b) Estimation of the slope of activity increase in 300 consecutive trials.

second stimulus. If the length of the ISI is changed, the slope of the activity increase is adapted accordingly, so that after only few trials of the experiment, the activity again reaches a plateau at the onset of the second stimulus. In order to illustrate this phenomenon we demonstrate the preliminary results from a paradigmatic IT neuron in Fig. 1. An extensive analysis of the experimental results will be published in [8]. This rising activity and the adaptation of the timing suggest that the activity of these neurons has a predictive function. We thus argue that some cells in IT cortex might encode an expectation for events in the immediate future. Unlike Rainer et al. [5], who found that a similar effect in prefrontal cortex seems to be *prospective coding*, (that is, selective to the following stimulus), the expectation effect in IT cortex does not appear to be prospective, since it occurs mainly in unselective cells.

The objective of the present work was to develop a minimal model that reproduces this effect of monotonically increasing activity and its adaptation to the inter-stimulus

interval. We believe that this mechanism could prove to play an important role for a variety of neural computations that act on a time scale of a few seconds.

2. Model

It has been proposed that sub-populations of neurons in IT form attractors representing the different stimuli. These sub-populations can be in either of two stable states: in a resting state of only spontaneous activity or in an active state of high, persistent activity [1,7]. As a response to a brief, excitatory stimulus, the sub-population will jump to the active state and persistently fire at a high rate, sustained by reverberating synaptic excitation. For simplicity, we only consider one population that is selective to the visual stimulus (P^{SS}). Following a transient external input, elicited by the visual stimulus, the average firing rate in P^{SS} jumps from a low, spontaneous level to a higher level (Fig. 2a). This activity is persistent throughout the delay interval.

A second population, P^{EXP}, of randomly interconnected excitatory (P^{EXP}_{ex}) and inhibitory (P^{EXP}_{inh}) neurons, receives feed-forward excitation from all selective popula-

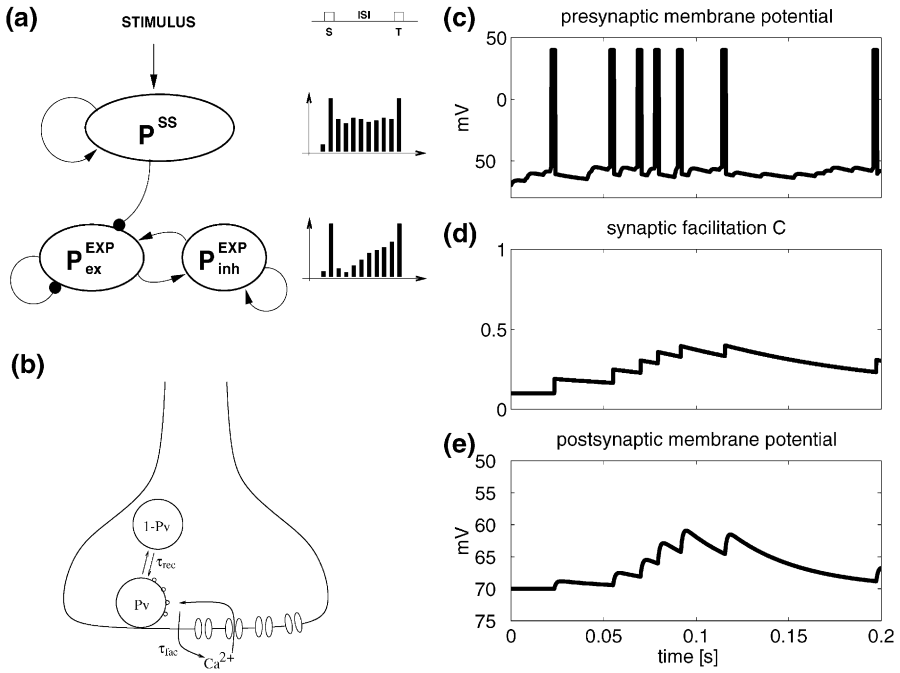

Fig. 2. Network and synapse models (a) Three populations: P^{SS}, receiving stimulus-triggered input, and P^{EXP}_{ex} and P^{EXP}_{inh}, the expectation cells. (b) Model synapse illustrating the two vesicle pools and calcium entry into the presynaptic bouton. (c) example voltage of a presynaptic cell, the time course of residual calcium C in the synapse (d) and the postsynaptic response (e).

tions, thus becoming unselective itself. As we show, by carefully choosing the synaptic dynamics of the network, P_{ex}^{EXP} may have an increasing activity during the delay interval, similar to the expectation effect described above. In an earlier model, we hypothesized that the pool of unselective expectation cells could be modeled by inhibitory neurons only (P_{inh}^{EXP}), which produced monotonically increasing activity. However, the time course of the activity, although slowed down by the network, was governed by the time course of the synaptic facilitation, which was not in good agreement with our observations. To obtain a less prominent negative convexity in the curve of the increasing activity, we had to add recurrent excitation; so P^{EXP} contains both excitatory and inhibitory sub-populations.

For our computer simulations, we use leaky integrate-and-fire neurons with absolute refractory period to model both pyramidal cells and interneurons. Synaptic input causes an instantaneous increase and subsequent exponential decay of an AMPA-, NMDA- or $GABA_A$-type current.

$$\dot{V} = \frac{V_{rest} - V}{\tau_{mem}} + G_{syn} I, \quad \dot{I} = -\frac{I}{\tau_{syn}} + \sum_k s_k \delta(t - t_k). \tag{1}$$

A background of spontaneous activity coming from other populations of neurons is emulated by adding random, high frequency and low amplitude synaptic input.

Synapses are modeled as stochastic units that underlie short-term plasticity; long term changes in synaptic efficacy are not considered. Depression is modeled according to the one-vesicle hypothesis and the two pool model of vesicle recovery (Fig. 2b, see also [6, Eq. (2)]). Synaptic release takes place with a probability of $P_{rel} = P_v C^n$, where P_v is the probability that a vesicle is ready to be released. C^n is the probability for calcium to be bound to all n binding sites of the vesicle ($n = 4$, [2]). After release, P_v is reset to zero and recovers exponentially. The presynaptic calcium concentration determines the facilitating behavior of the synapses. When the synaptic bouton is depolarized by a presynaptic action potential, channels open and calcium enters the bouton, changing the binding probability C by an amount proportional to C^0 (Eq. (3)). This C^0, and to a lesser extent also τ_{rec} and τ_{fac}, are the crucial parameters which, by controlling facilitation, determine the speed with which the activity of the P_{ex}^{EXP} population increases. C incorporates the effect of residual calcium in the presynaptic bouton: it is increased at each action potential, its summation causing facilitation by enhancing the release probability.

$$\dot{P}_v = \frac{1 - P_v}{\tau_{rec}} - \sum_k \delta(t - t_{rel}^k) P_v, \tag{2}$$

$$\dot{C} = -\frac{C}{\tau_{fac}} + \sum_k \delta(t - t_{sp}^{k-}) C^0 (1 - C). \tag{3}$$

All synapses used in our simulations implement the above described internal dynamics—by choosing different sets of parameters, synapses can be made to behave predominantly facilitating or depressing. In general, however, there is a phase of facilitation (due to accumulation of residual calcium) followed by depression (due to vesicle depletion), see Fig. 2c–e.

Note that the delay interval is on the order of seconds, whereas none of the time constants of our model synapses and neurons exceed 1 s (the longest time constant being $\tau_{\mathrm{fac}} = 1$ s).

3. Results

Our goal was to have a monotonically increasing activity over a period of several seconds in the $P_{\mathrm{ex}}^{\mathrm{EXP}}$ population as a response to a brief stimulation of the stimulus-selective population P^{SS} in the resting network. The driving force for this increase is provided by the recurrent excitatory connections that come into play as P^{SS} enters the high activity state. If synaptic transmission is constant or depressing, the reaction time of the network is very fast—too fast in fact for the time scale of the expectation effect (Fig. 3a). By making the self-excitation of $P_{\mathrm{ex}}^{\mathrm{EXP}}$ slowly facilitating, starting from a low release probability, the network can be slowed down such that the activity rises monotonically over several seconds (Fig. 3b). Furthermore, if we also introduce

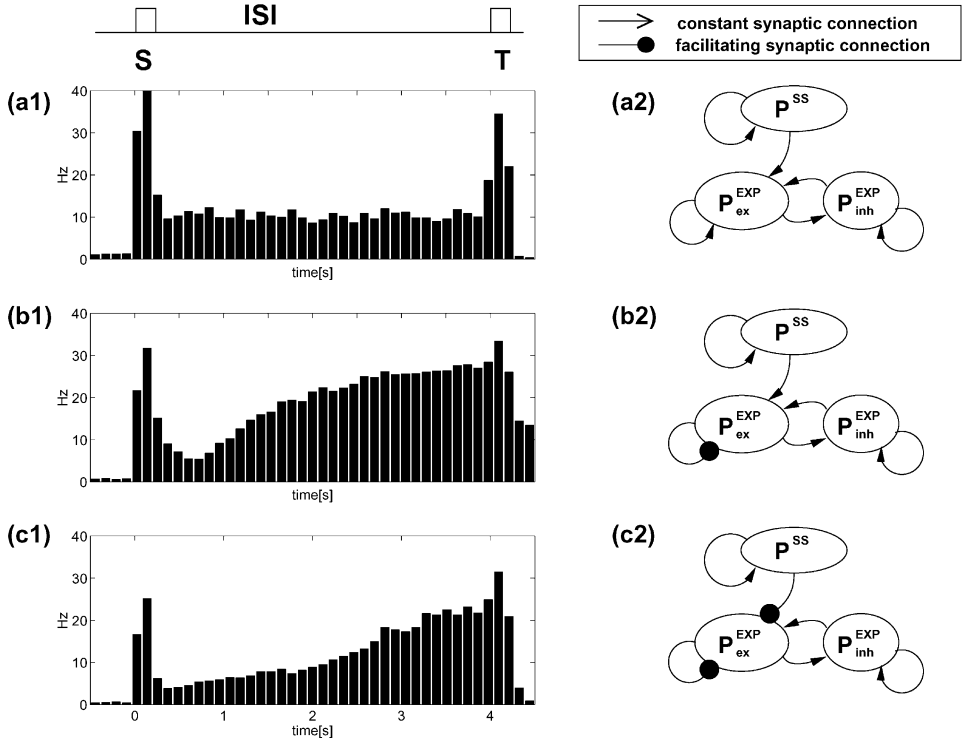

Fig. 3. Synaptic facilitation produces constant activity increase. (a1) Mean activity of $P_{\mathrm{ex}}^{\mathrm{EXP}}$ with no slow facilitation present (a2). Facilitating recurrent connections (b2) lead to increasing activity in $P_{\mathrm{ex}}^{\mathrm{EXP}}$. Constant increase over several seconds (c1) can be achieved when both recurrent and feed-forward connections are facilitating (c2). $P_{\mathrm{ex}}^{\mathrm{EXP}}$: 800 cells, $P_{\mathrm{inh}}^{\mathrm{EXP}}$: 200 cells, P^{SS} : 200 cells.

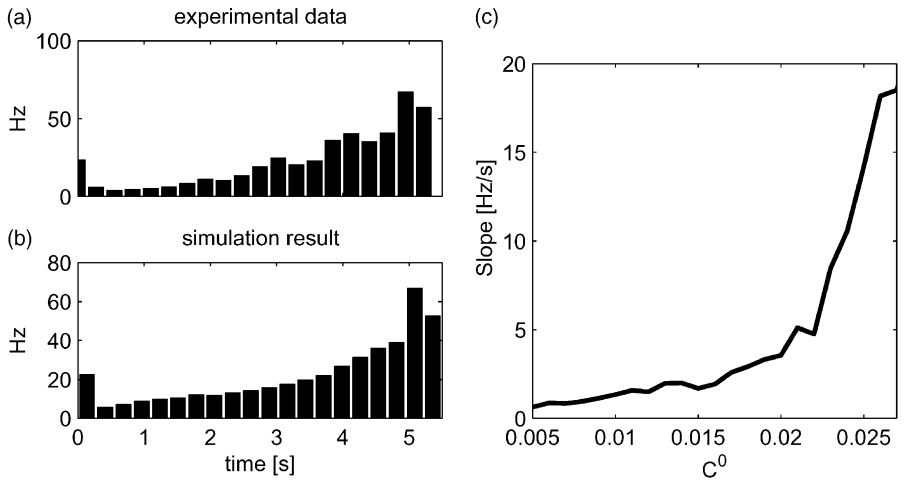

Fig. 4. Simulation results. (a): rising delay activity from behaving monkey (one cell, mean of many trials). (b) Mean firing rate in a simulated population P_{ex}^{EXP} (800 cells). (c) The slope of activity increase depends strongly on the parameter C^0, which controls the presynaptic calcium influx.

facilitation at the synapses of the feed-forward ($P^{SS} \Rightarrow P_{ex}^{EXP}$, Fig. 3c) connections, the resulting time course of the activity increase looks very similar to the experimental data (Fig. 4a,b). The reason for this additional slowdown is the initial lack of feed-forward drive for the self-excitation in P_{ex}^{EXP}.

The plateau point of the activity is reached after an interval of 2–8 s, depending mainly on the facilitation parameter C^0, which represents the calcium influx after presynaptic depolarization (Fig. 4c). Thus, by modulating the presynaptic calcium channels, the network adapts its timing for the prediction of the second stimulus onset.

4. Conclusions

The present study shows that synaptic facilitation can explain a slow (several seconds) increase in population activity, as observed in experiments with behaving monkeys. The rate of activity increase in a recurrent network can be slower than the synaptic time constants. The time course of the activity of IT cells can be nicely reproduced by making use of short-term synaptic plasticity in the appropriate network architecture.

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