EFFECTS OF THE SYNAPTIC TRANSMISSION’S DYNAMICS ON POSSIBLE NEURAL CODES

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Abstract: The dynamics of the synaptic transmission can ultimately determine the
communication between neurons. We have deeper and deeper insight into the physiological
mechanisms of paired pulse facilitation and depression and their effects on synaptic plasticity,
as well as the spike frequency adaptation. Considering the fact that LTP and LTD is not
symmetric to the presynaptic activity we have to calculate the interactions of pre- and
postsynaptic spike sequences. To understand the genuine role of these processes in the neural
signal transmission, we formulate simple models to simulate their actions. This way we could
make qualitative estimations on the model neuron's input-output properties. We examined the
transmission of two parameters: the mean and standard deviation of synaptic currents. Our
results indicate that the measured effects of long-term potentiation on the dynamics of
synaptic transmission can not be considered as synaptic weight change at the biological
relevant activity level, regarding the transfer of membrane currents mean, and so the transfer
of firing rate. Other known facts, as the relatively low firing rate, spike frequency adaptation,
big spike frequency variability, make the simple firing rate code less appropriate for longer
period simulation of real neurons, as it is assumed in the majority of artificial neural network
models (ANN). Nonetheless, the other examined parameter, the standard deviation of synaptic
currents, which is closely related to the inter-spike-interval variation, behaves like the firing
rate in typical ANN models. Considering the fact that LTP and LTD is not symmetric to the
presynaptic activity we have to calculate the interactions of pre- and postsynaptic spike
sequences. The formation and possible operation of this type of "code" is discussed.

1 Introduction

It is exciting and so far unsolved question in neuroscience, how do the neurons communicate with
each another (Perkel, 1968; Mitchison., 1990). There are different theories, which emphasize
particular kind of neural response properties. The vast majority of ANN models imply that firing
rate transmits information between neurons [Gerstner & van Hemmen, 1992. Other models and
experiments claim that the fine temporal structure of neural responses integrate information in the
CNS [Singer, 1993]. This type of code could be much more efficient, than the ‘robust’ rate code
[Softky, 1994]. The timing precision of the neurons' action potential generation, its role in the signal
processing [König, 1996] and even the biological relevance of these models are disputed [Shadlen,
1994]. There are problems, nonetheless, with the firing rate code as well. In the CNS, the neurons’
background activity is low. In the same time the coefficient of variation of neuronal firing is high
[Softky & Koch, 1993]. Besides, the cortical pyramidal cells show considerable spike-frequency
adaptation. Some experimental results show that in cortical neurons the average value of the evoked
average EPSPs can be equal to the third decimal digits for 10 Hz and for 40 Hz poissonian spike
trains [Tsodyks, 1997]. There can be seen, however, remarkable decrease of postsynaptic potential
alteration as the stimulus frequency increases.
Here we used simple models, applying the recent experimental results concerning the dynamic changes of synaptic transmission and synaptic modification rules (Markram & Tsodyks, 1996), to investigate the neural transfer properties.

2 Dynamic redistribution of synaptic efficacy

The synaptic release of neurotransmitters is a probabilistic process. Experience dependent long-term synaptic modifications, do not alter the amplitude of excitatory postsynaptic potentials (EPSP) or the number of active synaptic contacts, but changes the reliability, the probability of synaptic transmission (Stevens, 1994). These synaptic modifications like long-term potentiation (LTP) or long-term depression (LTD) is claimed to be the fundamental mechanisms of learning in neural networks. Another striking property of synaptic transmission is that if we apply a higher rate of stimulation on the presynaptic neuron, which still evokes a ‘relatively’ low firing rate, the consecutive EPSPs’ mean amplitude decrease, until it reaches some static level. For LTP (or LTD) only the evoked EPSP’s initial value and the speed of decay changes. This is the so-called dynamic redistribution of synaptic efficacy (Makram, 1996). There are relatively good models for it (Tsodyks, 1997), but they use only the mean value of this efficacy. As we wanted to compute the deviation of evoked postsynaptic currents as well, we applied a binomial model of synaptic release (Burnod, 1989). For the simulation of the neurons’ firing patterns we introduced an ‘integrate and fire’ type neuron model with spike frequency adaptation. The input was taken to be a normally distributed random variable, supported by the Central Limit Theorem, since the number of converging synapses is large. We used the widely accepted alpha function for the synaptic currents’ simulation.

3 Modeled pyramidal neurons input-output relation

Having a simple model of spiking activity and that of the dynamic changes of synaptic transmission, a composition of them can be constructed. We examined the transmission of two parameters of the model neurons’ activity: the mean and standard deviation of membrane current. If the different neuron’s activity is not correlated, then these two parameters can fully describe statistical properties of the neurons’ input.

To be able to compare input and output properties of modeled neuron, we computed the postsynaptic currents evoked by a simulated train of action potentials. Parameters of these currents were identical to those of the presynaptic ones.

Only the input and output synaptic currents were compared, because the membrane potential includes, for example, afterhyperpolarization and other currents as well. In this way the transfer properties of the simulated neuron has been characterized. We found the mean output current is nearly proportional to the input current's mean. Its dependence on the input current’s deviation is insignificant. Oppositely, the standard deviation of the output current depends on both the mean and deviation of the input currents.

The simulated neural activities are displayed on Figure 1. We can encounter spike-frequency adaptation besides the different consequences of random transmitter release. Both the gradual decrease of synaptic efficacy and integration of consecutive EPSCs can be observed.
Figure 1. - Effects of adaptation and redistribution of synaptic efficacy on postsynaptic currents. The lower line indicates presynaptic neuronal membrane potential. The upper inset shows postsynaptic currents elicited by presynaptic activity (lower inset).

A striking behavior of the modeled transfer of the currents’ mean is that there is no enhancement in its slope (Fig. 2.). Only a shift of the average value can be observed. It means that changes of synaptic transmission probability not manifested in an increase of the synaptic weights, but only in some kind of threshold shift!

Figure 2. - The Average evoked postsynaptic current as a function of average input current and transmission probability.

Small observable changes points to a direction against our prior expectation. The initial value of input current generates about 3 Hz activity, which is approaching cortical background activity. The other measured parameter behaves quite a different way. Figure 3 demonstrates the transfer properties of the 'currents deviation' at various levels of transmission probability on a fixed average input current value. It can be seen that the dynamic range of deviation transfer function is enlarging as transmission probability is increasing (corresponding to LTP). This finding indicates that transmission of this variable behaves like synaptic weights in usual ANN models. Change in transmission probability leads to simultaneous change in the slope of deviation input-output relation. Metaphorically speaking, the slope of this function can be regarded as a “synaptic weight”.

4 Conclusions and Discussion

There are considerable limits of firing rate code (see above). Our result indicates further doubts, that is long-term synaptic modifications do not obviously lead to the appropriate changes of synaptic weights. The standard deviation of synaptic currents can also convey information within CNS. This variable is as straightforwardly determined as the mean synaptic currents. The slope of the deviation input-output relation works like a 'pseudo' synaptic weight and appropriately reacts to LTP and LTD. For the use of this type of code it is necessary to solve the transformation of frequency code to this code, the formulation of neural transmission using this type of code, and at last some type of decoding from this code to the rate code (Orzo, 1993). Our results show that the model neuron transfer properties make this transformation possible:

- There is almost a linear dependence of the output deviation on input average at any level of LTP (corresponding to transmission probability). Namely, the higher the presynaptic current’s averaged amplitude is the lower will be the evoked postsynaptic current deviation. Certain experimental result (Tsodyks, 1997; Softky and Koch, 1993) can indicate the possibility of such a conversion.
• Further computation based on this code may occur like in the case of firing rate code - as in usual ANN models - because the corresponding variable transfers follow similar rules.
• Transformation from deviation to firing rate code can be achieved using paired pulse facilitation. The neurons with high variation in their membrane currents and so in their firing rate can generate higher than average EPSCs than neurons with low variation of firing rate, if they are capable of paired pulse facilitation. Astonishingly, this is the case of deep layer cortical pyramidal neurons (Thomson, 1993).

Additionally the accurate measurement of the standard deviation can be easier than that of the mean, depending on their distribution. The sensitivity of this code for different types of noise and propagation uncertainties is modest due to its peculiar determination. Neuromodulators, like acetylcholine (Tsodyks, 1997), can decrease the probability of transmitter release (LTD) and thus they are able to change the state and dynamics of the whole underlying network.

For adequate simulation of the brain functions, it is necessary to build models that can associate even temporally distant events. It is obvious that some type of activity has to remain after any recall process. However, this activity can not be coded in the neurons’ firing rate because of the spike frequency adaptation and the apparent absence of long-term elevated firing of the cortical neurons.

The interaction of the neurons’ action potential sequences has considerable effect on the long-term synaptic events. So it is important to find the appropriate neural firing parameters, which can be involved in these modifications.

References