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Neuronal Processing under naturally correlated input conditions

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Introduction

Correlations in the activity of neurons are an ubiquitous phenomenon [4] in mammalian cortex, whose function is not yet understood. The effect of correlated activity on single neurons has only been studied using fairly general correlational patterns for the input statistics.

In this study EFP-data from the visual cortex of cats [1] was used to generate more realistic correlational input patterns, whose most prominent feature is given by the correlated, yet phase-shifted activity of neurons belonging to populations of different preferred orientation. We studied their effect on single neuron processing and learning behavior using a detailed reconstruction of a L5 pyramidal cell from a cat's striate cortex.

Fig. 1: Model Cell used in the simulations (a) and enlarged view of the topographical ordering (b) of synapses from presynaptic cells of diff. preferred orientation on the dendritic section, which received input in this simulation.

Methods

In order to recreate the synaptic input a pyramidal cell receives in-vivo, we used multiple sources of information. Presynaptic neurons were divided into classes of preferred orientation (5 angular sectors, 36 classes). These orientation classes (OCs) were attributed a stimulus dependent mean firing rate, according to the tuning-curve of V1 pyramidal cells. The number of connections made with the model cell was determined based on the inter-connectivity histogram for V1 cells of varying preferred orientation.

The correlation pattern over different OCs was modeled according to findings [4], which indicate that cells in the same OC fire correlated with each other at no mean phase-lag. Further, cells in different OCs also fire correlated at the same correlation strength, but for a given stimulus their mean phase lag in respect to the optimally activated OC follows a quadratic relationship in angular separation of preferred orientation to the optimally activated OC (Fig.2). This can best be thought of as a wave of activation which is started by the optimally activated cells, followed sequentially by cells of increasing angular deviation in preferred orientation. The effects of introducing phase-lags were studied by using zero-phase-lagged stimuli as a control condition.

These stimuli were used as spike-trains arriving at 190 synapses located on a dendritic section in Layer 3 (Fig.1a) of our model cell in the NEURON simulator. Passive dynamics were used in the dendrites, Hodgkin-Huxley-style active dynamics in the soma and both the effect of excitatory input alone and in combination with inhibitory input were simulated using typical cellular and current parameter values from the literature. Parameters were tuned using the tuning-curve and the coefficient of variation of the interspike intervals as optimizing criteria.

To assess the effects of dendritic clustering of synapses from same or similar OCs all simulations were performed with different spatial distributions of connections made with cells from different presynaptic OCs. As described above, input only goes to the section in L3 (fig.1a). Their sequential structure and label are given in fig.3a-c.

Retrograde action-potentials (rAPs) [2] were simulated based on the model cell data from the NEURON simulations. Using somatic spiking times and the rAP's velocity arrival-times at individual synapses were obtained in MATLAB (Natick, Massachusetts). Based on the well established rAP-EPSP-timing-dependent, LTP-LTD-data for synapses of pyramidal cells [3] and others) a typical asymmetrical learning function was reconstructed and used to calculate synaptic weight changes at individual synapses.

To allow comparison with other modeling studies using reduced models of neuronal geometry, synaptic weight changes were recalculated subtracting the backward and both the backward and the forward dendritic propagation times.

This study therefore goes beyond preceding studies in the same or related fields by introducing naturally correlated input into the investigation of correlation effects and extended neuronal geometry into the area of rAP triggered synaptic learning.

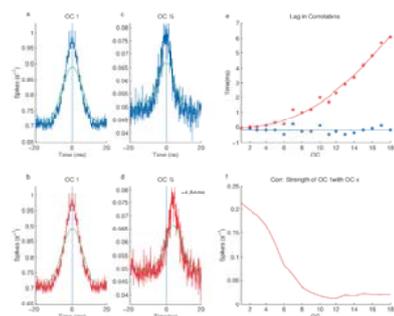


Fig.2: Raw cross-correlations of the input stimuli from different orientation-classes (OC) with the optimally activated OC (1a-d), lags in cross-correlation peak to the optimally activated OC (e) and raw peak-to-noise correlation strengths with the optimally activated OC.

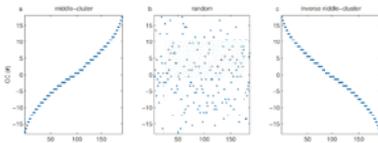


Fig.3: Different spatial distributions of synapses made with presynaptic cells of varying orientation classes. Cells of OC 1 belong to the same orientation class as the simulated cell.

Results

First we examined the change in the model cell's tuning curve for three different spatial distributions (fig.3) and the two excitatory input conditions described above. Since the spatial and thus electrotonic separation of a synapse and the soma for a given stimulus orientation depends on its position in the dendritic tree, we find for the distributions in fig.3a/c significant shifts (25) in preferred orientation (fig.4a/b), whereas the random distributions yield zero-centered tuning-curve, i.e. in accordance with the preferred orientation carried by the input-distributions.

We therefore conclude, that the model-cell's tuning-curve's angular position depends not only on the statistics of the input, but also on the spatial distribution of the presynaptic terminals on the dendrites. There does not seem to be a strong dependence on the lags between the OCs

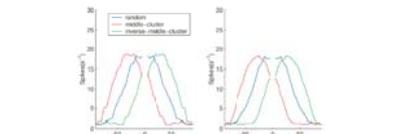


Fig.4: Tuning curves of the model cell for the different spatial distributions (compare to fig.3 and the inset) and for the zero-phase-lagged excitatory-only (a) and the phase-lagged excitatory-only (b) input conditions.

Next the time-dependence of the model cell's output and input was analyzed by cross-correlating input and output spike-trains for each OC and determining the peak shift. Under the zero-phase-lagged condition the model cell's activity followed the presynaptic classes at a constant lag of ~2ms (fig.5a). This behavior changed under the two phase-lagged conditions, where only the OCs, which differed in their own to the model-cell's preferred orientation by less than -50, preceded the model cell, whereas all others followed the model cell (fig.5b/c). This result was consistently observed for all three spatial distributions (fig.3). If the average lag over all OCs is considered, no conclusion can be drawn, since it is almost 0.

This peculiar phenomenon arises due to the presynaptic correlation-structure and the fast (~2ms) and reliable spike-elicitation. Since the cross-correlation will only pick up the relationship of certain sets of spikes in different spike-trains, it fails to serve as an analytical method for disentangling the connection between pre- and postsynaptic cells. In conclusion, caution has to be taken in certain types of experiments, e.g. in-vivo experiments, where the connection structure is unknown and two-cell recordings and the cross-correlation method are used to determine it.

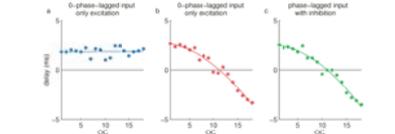


Fig.5: Output-Input-Relationship in time between the simulated postsynaptic cell and presynaptic cells of different orientation classes for the zero-phase-lagged excitatory-only (a), phase-lagged excitatory-only (b) and phase-lagged, excitation-inhibit (c) input conditions.

Investigating the learning behavior (see Methods) first synaptic weight changes were analyzed for each OC and each stimulus orientation for the three input conditions. All conditions show similar weight change patterns on a coarse scale (fig.6 top row). However, under the zero-phase-lagged condition all weight change is positive, which can only be seen on the higher resolution colormap in fig.6 (bottom, left). Comparing this to the results for the other two conditions (fig.6, bottom, middle and right) at the same resolution shows, that both positive and negative weight changes occur.

In summary phase-lagged, correlated stimulus statistics in combination with the spike-timing-dependent learning rule can account for OC-specific synaptic weight-change, whereas zero-phase lagged, correlated input leads to uniform synaptic strengthening.

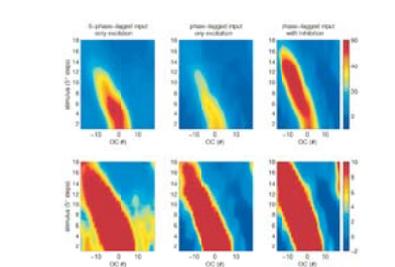


Fig.6: Colormap coding the average amount of weight change a synapse from an orientation class (abscissa) received for a stimulus of a certain orientation (ordinate). Data is shown on two different scales (colorbars on the right) to emphasize the importance of sign (bottom) versus amplitude (top) of weight change.

Since our results diverge in this respect from the ones obtained by Song et al. (2000), which were using zero-phase-lagged input and single compartment simulations, we tried removing delays introduced by neuronal geometry to allow for more reasonable comparison. Removing only the time required for back-propagation (~25% of total propagation time) resulted neither in a considerable quantitative nor in a qualitative change in weight change pattern (Fig.7 top row).

However, removing the peak-to-peak, passive forward propagation time lead to a remarkable, global change in the pattern (Fig.7 bottom row). Under all three conditions the pattern of synaptic weight changes almost reversed. The described results did not depend strongly on the relation between positive and negative peak-heights of the asymmetric learning rule, as had been indicated by Song et al. (results not shown).

We conjecture, that the inversion is a consequence of the fast and reliable spiking, probably triggered by the first few spikes, which then, however, drive synapses from their own and neighboring OCs into the LTD window of the asymmetric learning function. Together we conclude that propagation times have an important role in shaping the OC-specific pattern of weight changes.

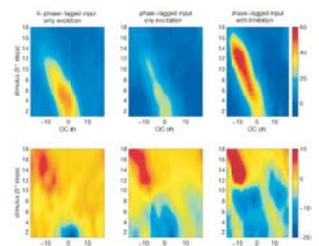


Fig.7: Shows the data from fig. 6 if only dendritic backward (top) or both the backward and forward (bottom) propagation times are removed in determining the synaptic weight change for the zero-phase-lagged excitatory-only (a), phase-lagged excitatory-only (b) and phase-lagged, excitation-inhibit (c) input conditions.

Conclusions

In this work we have examined a model of a visuo-cortical L5-pyramidal cell under very specific input conditions, which are likely to be present in the active visual cortex. Input statistics carrying the experimentally observed phase-lagged correlation-structure lead to several interesting changes in the processing and learning behavior of the model cell, when compared to input of zero-phase lagged, correlated statistics.

Looking at the output-input-relationship we found that the cross-correlation method becomes problematic, if the connectivity of two neurons should be established, based on in-vivo two-cell recordings. It can be seen, how, ever, that if the two measured cell have similar preferred orientation, this problem vanishes.

Further the learning behavior, characterized by the OC-Stimulus-pattern of synaptic weight changes takes qualitatively distinct shapes for zero-phase-lagged versus phase-lagged input, since only the latter yields differential changes in synaptic weight. We speculate, that this could be a function of phase-lagged input, since it would serve to stabilize tuning-curves. On the other hand, the results for zero-phase-lagged input yield an unrealistic, uniform strengthening.

Dendritic propagation times were a crucial aspects for the formation of intuitively meaningful patterns of synaptic weight changes. Since the results of this simulation excluding both forward and backward propagation times lead to changes in synaptic weights, which were incompatible with global longterm stability, conclusion reached by means of simulation studies using very reduced neuronal geometry should only cautiously be evaluated.

As an aside preliminary investigations into different spatial distributions of presynaptic OC on the dendritic section lead to an incompatibility hypothesis, which states that either are tuning-curves partly determined by this distribution or the distribution has to be random, as is generally assumed, but experimentally still pending.

Experimentally these results could most likely be verified (or falsified) by use of modern optical imaging techniques. This study should be followed by more precise modeling studies investigating the precise relationship between spatial synaptic clustering of OCs and the present input statistics.

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