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# Spatial summation in simple cells: computational and experimental results

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**Abstract**

We study the influence of the input connection structure of a visual simple cell on the linearity of spatial summation within its receptive field. For moving sinusoidal grating stimuli the similarity of a cell's response to the given input can be measured in a single number, called relative modulation. Using relative modulation as cell measure we examine increasingly complex cell and connection models. However, we find that relative modulation is of limited use for assessing the details of the input connection structure. Comparing the results of a large scale simulation with experimental data allows conclusions about the ratio of excitation to inhibition in simple cells, and leads us to propose a refined version of an intracortical inhibitory connection structure, called cascaded inhibition.

## 1 Introduction

A key characteristic of visual simple cells is their receptive field structure, that is shaped by the processing of the simple cell and the properties of the input connections. In order to test the linearity of spatial summation within the receptive field of a simple cell, we adopt two types of cell models, basic and more realistic ones, and we introduce different connection structures. To characterize the linearity of spatial summation we use the *relative modulation measure*, that expresses the resemblance of a cell's output to a given, periodic sinusoidal input. An ideal half-wave rectifying cell leads to a relative modulation of $\pi/2$. Deviations from this ideal value can be used in the different models to assess the influence of the input connection structure on the non-linearity of spatial summation of the inputs. This theoretical study is supplemented by a series of experiments, that help us to evaluate the size of relative modulation in biologically realistic situations. To this end we have performed a series of experiments and measured the relative modulation for 84 simple cells in the primary visual cortex of cat.

## 2 Relative Modulation

Consider a single periodic sinusoidal grating stimulus of a specific temporal frequency leading to a response containing various output frequencies. We can characterize the input/output-transformation by a family of relative modulations $r_1 \ldots$ where the relative modulation of order $n$ is defined as $r_n = \frac{A_n}{A_0}$,

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where $A_n$ is the $n^{th}$ harmonic component and $A_0$ the DC component of the amplitude spectrum, with the fundamental frequency given by the input frequency. Hence, it is a measure how strong the output is modulated with the same frequency, or a higher harmonic, as the input when compared to the overall response. For ideal half-wave rectification of a sinusoidal input the first few relative modulations are $r_1 \approx 1.57$, $r_2 \approx 0.67$, $r_3 \approx 0.00$, $r_4 \approx 0.13$.

# 3 Basic Models

We start with a very crude cell model: a unit that adds constant spiking activity of rate $s = \sigma A$ to a sinusoidal input of amplitude $A$ and suppresses all output below a firing threshold $T = \tau A$ (see eqn. 1).

$$O(t) \quad = \quad \begin{cases} A\ sin(t) + \sigma A - \tau A & , \quad A\ sin(t) + \sigma A \ \geq \tau A \\ 0 & , \quad A\ sin(t) + \sigma A \ < \tau A \end{cases} \qquad (1)$$

We introduce two parameters, $\sigma$ and $\tau$, even though they are mathematically redundant, because of their direct physiological interpretation as spontaneous activity and output threshold. In order to mimic a simple cell with two receptive subfields we need at least two input cells (On and Off) that form the respective subfields of the simple cell. Depending on the spatial frequency of the grating stimulus and the receptive field size(s), the input cells are generally optimally stimulated at different times during a stimulus period, corresponding to a temporal phase difference between the inputs to the simple cell. Only an optimal spatial frequency of the grating results in a synchronous optimal stimulation of the adjacent On- and Off-subfield. Because of symmetry we restrict possible phase differences to $[0°; 180°)$. We call this very simplified model of a simple cell the 'basic push model', because the simple cell is only driven excitatorily. We find that the relative modulation in the basic push model strongly depends on the phase difference of the inputs as determined by the spatial frequency of the stimulus, and drops to zero for large phase differences.

A step to salvage the problems of the basic push model has been the introduction of additional, antagonistic inhibitory inputs (e.g.[2] [6]), resulting in the 'basic push-pull model' (see fig. 1A). In addition to the pure push model, the push-pull model contains as further parameters the ratios of excitatory to inhibitory inputs. It turns out that the relative modulation measure is independent of the spatial frequency of the stimulus only when the amplitude of excitatory and inhibitory inputs are equal. In general, the relative modulation remains sensitive to the spatial frequency of the grating stimulus. This is shown in fig. 1B for different ratios of excitation to inhibition within a simple cell subfield.
We find that modifications in the push-pull model, as proposed by Tolhurst and Dean [6], where the order in which summation and submission to threshold of the inputs take place are changed, do not lead to marked, unambiguous differences in the behavior of relative modulation. Hence, the relative modulation measure is rather insensitive to the considered subtle variations in spatial summation (data not shown).

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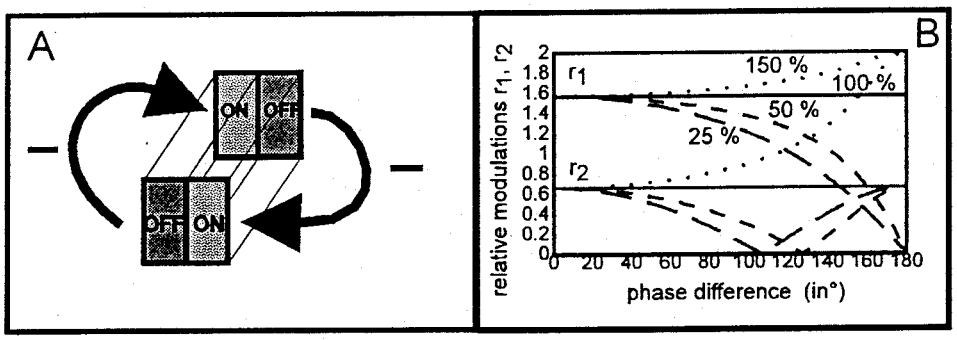


Figure 1: **A**) Setup of the receptive subfields in the push-pull model: receptive subfield size and position are identical but On- and Off-subfields are reversed in the antagonistic partners. **B**) Dependence of the first two relative modulations on temporal phase difference and ratio of inhibition to excitation in the basic push-pull models. Inhibition fixed at 150%, 100%, 50% and 25% of the excitation. Relative modulations $r_1$ and $r_2$ vary with temporal phase difference, except for the 100% case.

# 4 Experimental Results

Before we continue with simulation results from a more realistic model, we briefly describe some experimental findings: Since the spatial frequency of the grating stimulus is the easiest parameter to control, we investigate the relative modulation $r_1$ of simple cells in area 17 of anesthesized cat for different spatial frequencies of a sinusoidal grating stimulus (leading to a temporal phase difference of On- and Off-response between 0° and $\pm$ 135°). Cell responses are determined by extracellular, single cell recordings. For a total of 84 simple cells the relative modulation has been determined for these parameter values.

The studied simple cells fall roughly into two groups: In the first group the relative modulation remains nearly constant over the range of spatial stimulus frequencies studied (fig. 2A), while the relative modulation $r_1$ for members of the second group drops off significantly with increasing temporal phase difference (fig. 2B).

This result can be understood on the basis of the previously described effect: We have seen that relative modulation is independent of the stimulus spatial frequency for balanced excitatory and inhibitory inputs. However, this seems a special assumption, for which there is no obvious a priori reason. Hence, the grouping could reflect different strengths of excitatory and inhibitory inputs. This prediction could be tested with intracellular recordings from simple cells.

# 5 Models With More Realistic Connections

We proceed to present three different, biologically much more realistic models of intracortical inhibition, all of which are implemented in a modular computer model of about 16000 cells in the lateral geniculate nucleus and primary vi-

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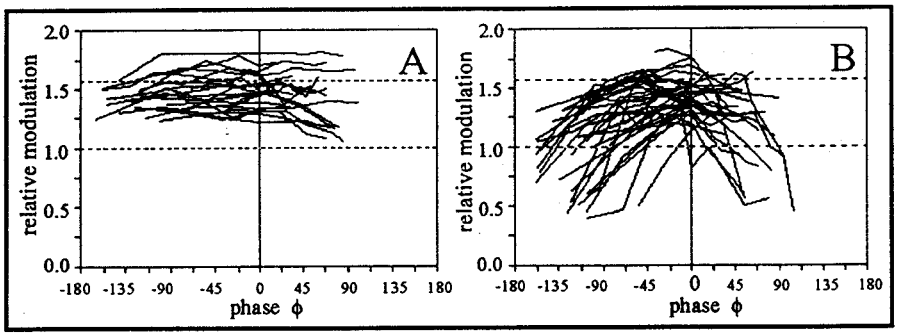


Figure 2: Relative modulation $r_1$ versus temporal phase for simple cells that are not phase-sensitive (excitation $\approx$ inhibition) (A), and cells that show a marked dependence on phase (B) (excitation $\neq$ inhibition).

sual cortex. The single cell model is based on a refined leaky integrate and fire mechanism. Details are described in [1] and [7]. The input of simple cells in the simulator consists of excitation from the lateral geniculate nucleus, in the fashion proposed by Hubel and Wiesel [3], and of inhibition from other cortical simple cells. We implement three different models of antagonistic intracortical inhibition in V1, corresponding to different types of spatial summation, all falling in the class of push-pull models: Firstly, the *strict sparse inhibitory model*: at most two simple cells of rather precisely matching but antagonistic receptive field properties are connected inhibitorily to any target simple cell. The target cell again inhibits these cortical source cells, resulting in an overall mutual inhibition. We have allowed two cortical cells to project to a simple cell to give room for some variability in order to make the model more robust. Secondly, a more permissive model, termed *weak sparse inhibition model*: the requirement of alignment of the preferred orientations and relative positions of the receptive fields are relaxed. But we still connect at most two simple cells to a given target cell. Thirdly, a newly introduced *cascaded intracortical inhibition scheme*: about 20–25 simple cells with loosely matching but antagonistic receptive fields are connected to a given target cell (figure 4A). Models corresponding to the sparse mutual intracortical connection setup have already been proposed earlier, e.g. [2] [6]. For all three models we present the same optimal sinusoidal grating stimulus and calculate the relative modulation $r_1$ for all cells. For those simple cells whose preferred orientation match that of the stimulus (up to $\pm 4°$) we obtain the distributions of relative modulations shown in figure 3.
Most notably is the difference between distributions corresponding to the sparse inhibitory and the cascaded inhibitory connection schemes. Whereas the former shows a bimodal distribution of relative modulations, in the later we observe only a single, somewhat more pronounced peak around a relative modulation of 1.5. This means that the cascaded model allows more simple cells to respond efficiently, i.e. with a substantial stimulus induced modulation, to the input stimulus. The peak at low relative modulations $r_1$ corresponds to simple cells which have not found an antagonistic partner which closely enough matches their

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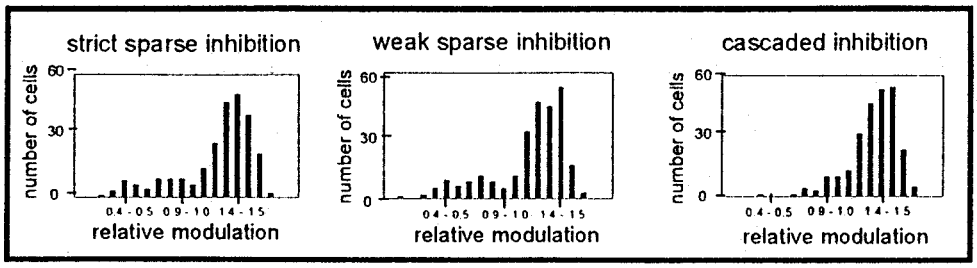


Figure 3: Distribution of relative modulation $r_1$ in the detailed models. Using a bin size of 0.1 the distribution of relative modulation is shown for the strict sparse inhibitory model, the weak sparse inhibitory model, and the cascaded intra-cortical inhibition scheme for stimulation with a grating of optimal spatial period (0° phase difference).

own receptive field properties. Hence, they correspond to the pure push model discussed earlier. The sharpening of the distribution in the cascaded case is more than a mere scaling effect of inhibition. The strength of the inhibitory input in the sparse inhibition model can be given the same strength as the overall input in the cascaded model, which still does not lead to the same distribution.

In order to determine the phase dependence in the detailed models we have calculated the behavior of the sparse and cascaded models for a temporal phase difference of 0°, 45°, 90° and 135° in the maximal response from the On and Off subfields.

When we select all cells with optimal orientation and use grating stimuli of different spatial period, we obtain the phase dependence of the relative modulation shown in figure 4B. In this diagram we have averaged all relative modulations $r_1$ above 1.0 and plotted the mean against phase difference.

Both of the sparse models show a greater phase dependence of relative modulation than the cascaded model. This might be an indication that the phase-insensitive cells found in the experiment are connected according to the cascaded connection scheme, whereas a sparse connection scheme more readily results in a phase dependence of the relative modulation.

# 6 Discussion

For the basic models relative modulation is of limited use for evaluating the (non)-linearity of spatial summation within simple cells. Even though in the basic models the number of parameters is relatively low, the precise role and size of each parameter cannot be determined, using relative modulation alone. Nevertheless, it may serve as one characteristic among others to describe the properties of simple cells, whether in models or experiments. When applied phenomenologically to a large number of cells, relative modulation may aid in

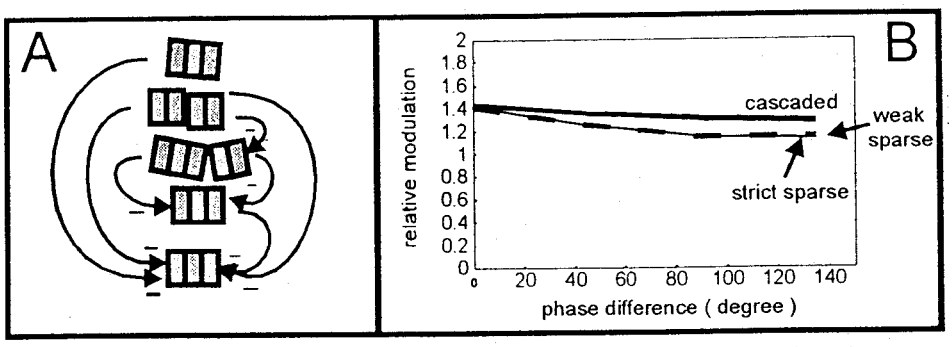


Figure 4: **A**) Cascaded intracortical connection scheme (schematic). **B**) Phase dependence of relative modulation in the three detailed models, based on the relative modulations at 0°, 45°, 90°, and 135° phase difference. The mean out of all cells with $r_1 \geq 1.0$ has been taken. Because of the skewness of the relative modulation distribution, the mean relative modulation is lower than the ideal value of 1.57.

the evaluation of biologically plausible connection models. On this basis we find a possible correspondence between the newly introduced cascaded intracortical connection scheme and the behavior of a large group of simple cells in cat, when the spatial properties of the stimulus are altered.

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