Dynamics of neuronal populations modeled by a Wilson-Cowan system account for the transient visibility of masked stimuli *

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Abstract

We study the transient dynamics occurring in a Wilson-Cowan type model of neuronal populations to explain psychophysical masking effects. Our model network consists of a layer of excitatory and inhibitory neurons to which spatio-temporal stimuli are presented. The neurons show dynamically emerging and decaying activity. A change in the timing or the spatial context of the stimuli yields dramatic differences in the strength and duration of these transients. The observed phenomena allow for an explanation of masking experiments in which a briefly presented vernier is folllowed by a grating of a variable geometrical configuration (shine-through and feature inheritance). We find a good agreement between the persistence of the transient activity and the visibility of the vernier as reported by the observers.

1 Introduction

To survive in a complex and ever changing environment, an organism has to cope with sensory stimuli often varying on a short time scale. Information processing must therefore be dynamical and fast. In numerous situations it is not feasible to wait until the neural activation pattern of the brain settles into a steady state before an appropriate reaction occurs.
Nevertheless, most modeling studies neglect this requirement. Instead, static stimuli are presented, and the fixed points or limit cycles emerging in the models are studied. Two examples of such models are the classical Hopfield type of associative memory, and models of neuronal populations of the Wilson-Cowan type [1, 2].
This may lead to the conclusion that these models are inappropriate to describe the real dynamics in the brain. However, in this contribution we show that the Wilson-Cowan model is equally well suited to describe transient phenomena emerging from a dynamical stimulus pattern that in reality pushes the visual system to its spatio-temporal limits. The magnitude of the transient activity of model neuronal populations predicts the visibility of target elements reported by observers during psychophysical masking experiments. Due to the structural simplicity of the underlying model, one can analyze and identify possible mechanisms leading to the observed behaviour.
In the next sections, we will first explain the stimulus paradigms, then describe the model and its dynamics, and subsequently show the modeling results and compare them to the experimental

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*Oral presentation preferred.

findings. Finally, we will discuss the computational limits of the model and give an outlook on possible extensions.

2 Feature inheritance and shine-through

To investigate transient dynamics psychophysically, a paradigm is needed that brings the visual system on the brink of its temporal limits. The just recently discovered complementary effects of feature inheritance and shine-through serve this need very well since performance can change dramatically even with a temporal parameter change of only about 5ms [3, 4]. In both psychophysical
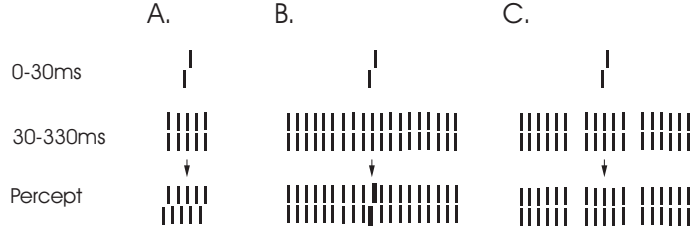

Figure 1: *A vernier precedes for a short time a grating of a variable spatial configuration.* **A.** *For gratings with less seven elements the vernier is invisible but may bequeath its offset to the grating (feature inheritance). Subjects indicate the direction of offset of the grating. If the vernier is presented for only 30ms inheritance occurs only for well trained observers.* **B.** *For gratings with more seven elements shine-through occurs. The vernier appears superimposed on the grating looking wider and brighter. Subjects indicate the direction of offset of the shine-through element.* **C.** *Shine-through diminishes strongly if the grating contains gaps. For short display times the vernier is invisible.* **Methods.** *Stimuli appeared on an analog monitor (Tektronix 608, Tektronix 606 or HP 1333 A), controlled by a Macintosh computer via fast 16 bit D/A converters (1 MHz pixel rate). Verniers and grating elements were 21' (arc min) long. Spacing between grating elements was 200-250" (arc sec). Subjects observed the stimuli from a distance of 1.2 or 2 meters in a room illuminated dimly by a background light. The luminance of the stimuli was around 80 cd/m^2.*

paradigms a vernier, i.e. two abutting lines, precedes a grating comprising a variable number of elements (see Fig. 1A). If the grating comprises less than seven elements the vernier is completely masked by the grating. Surprisingly, the vernier offset can be perceived at the grating that appears offset in the direction of the vernier (feature inheritance; Fig. 1A). However, this inheritance occurs only if presentation times of the vernier are sufficiently long.

If the grating comprises of more than seven elements, the vernier becomes visible as a shine-through element, that appears to be superimposed on the grating looking wider and brighter than the vernier really is (shine-through; Fig. 1B). Performance in the psychophysical experiments is better than in the feature inheritance condition (Fig. 2). Shine-through depends crucially on the spatio-temporal homogeneity of the grating. Even subtle deviations from this homogeneity diminish or even abolish the shine-through effect. For example, for a vernier presentation time of 20 ms a vivid percept of shine-through occurs that can be completely erased if the vernier is presented for 10 ms corresponding to two or three spikes of cortical neurons. Also spatial manipulations render the vernier invisible. Leaving out two elements and adding them at the ends of the grating degrades performance strongly while the overall luminance energy of the grating remains constant (Figs. 1C and 2). Therefore, explanations of these effects cannot be attributed to low level stimulus cues such as luminance. High order explanations are needed if based on a stimulus description level. Surprisingly, the underlying neural mechanisms can, in spite of the complexity, be described by very simple models— as the following sections show.
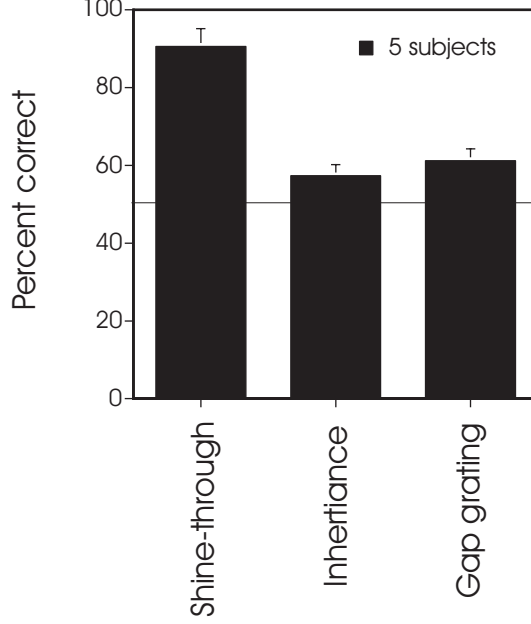
Figure 2: *The vernier was presented in all three conditions for the same duration. Only the spatial layout of the grating varies. Performance in the shine-through condition is clearly superior to that in the inheritance and in the gap condition. Inheritance is weak since vernier durations are short. Data adopted from Herzog & Koch, 2001).*

3   Model

In the model, we focus on the visibility of the vernier as a testbed for spatio-temporal interactions of neural populations. Since in the shine-through conditions the vernier appears as a bright flash superimposed on the grating, the processing of the vernier signal is expected to occur as a *transient* in the neural dynamics and not as a steady state. Our model employs the azimuthal axis only and neglects the second spatial direction and the orientation tuning of cortical visual cells, to simplify an analysis of the mechanisms responsible for the various psychophysical effects described in the previous section.

The network model consists of excitatory and inhibitory populations of cortical neurons (described by subscripts e and i, respectively) arranged along a one-dimensional axis parametrised by the variable $x \in \mathbb{R}$. The dynamics of the system are given by a set of Wilson-Cowan type equations [2],

$$\tau_e \frac{\partial A_e(x,t)}{\partial t} = -A_e(x,t) + h_e \left(w_{ee} \int_{\mathbb{R}} A_e(x',t) W_{ee}(x-x') \, dx' - \right. \tag{1}$$

$$\left. w_{ie} \int_{\mathbb{R}} A_i(x',t) W_{ie}(x-x') \, dx' + I(x,t) \right)$$

$$\tau_i \frac{\partial A_i(x,t)}{\partial t} = -A_i(x,t) + h_i \left(w_{ei} \int_{\mathbb{R}} A_e(x',t) W_{ei}(x-x') \, dx' - \right. \tag{2}$$

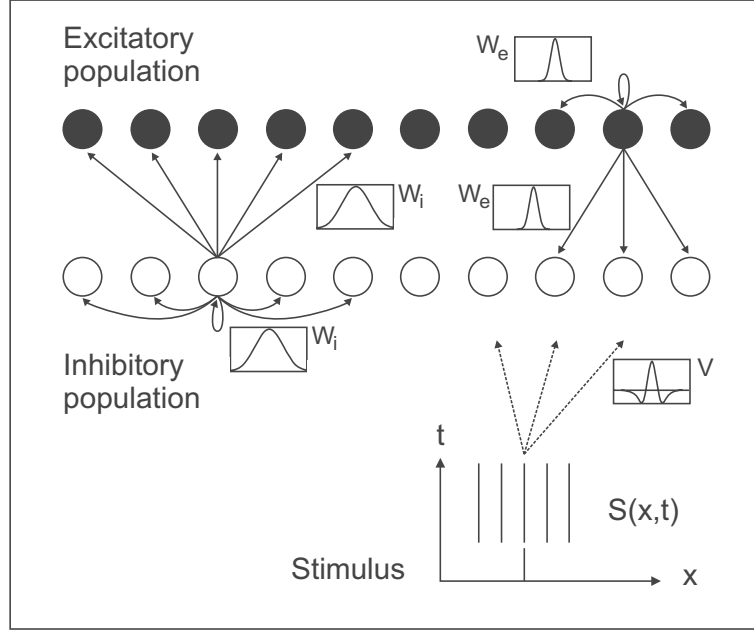$$\left. w_{ii} \int_{\mathbb{R}} A_i(x',t) W_{ii}(x-x') \, dx' + I(x,t) \right) .$$

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Figure 3: *Structure of model employed in the simulations. A spatio-temporal stimulus $S(x,t)$ is filtered by a difference of Gaussians and projected onto two populations in a one-dimensional neuronal layer. The two populations, an excitatory and an inhibitory one, are mutually coupled with synaptic weight functions described by the Gaussian kernels W_e and W_i, respectively.*

A_e and A_i denote the firing rates of the excitatory and inhibitory populations, respectively, τ_e and τ_i are the associated time constants, h_e and h_i are neural transfer functions, in this case choosen to be piecewise linear, w_{kl} indicate synaptic weights of population k acting on population l, $k,l \in \{e,i\}$, and W_{kl} are translation-invariant interaction kernels of population k targeting population j assumed to depend only on their distance $|x - x'|$. The interaction kernels are modelled as normalized Gaussians with standard deviations σ_e and σ_i. For simplicity, we assume the network to be highly symmetrical ($w_{ee} = w_{ei}$; $w_{ie} = w_{ii}$; $W_e := W_{ee} = W_{ei}$; $W_i := W_{ie} = W_{ii}$). Both neural populations receive the same spatio-temporal input $I(x,t)$ which is computed as the spatio-temporal stimulus $S(x,t)$ convolved with a Mexican-hat type of kernel function $V(x,t)$ whose integral vanishes,

$$V(|x - x'|) = \frac{1}{\sqrt{2\pi\sigma^{(e)2}}} \exp\left(-\frac{(x-x')^2}{2\sigma^{(e)2}}\right) - \frac{1}{\sqrt{2\pi\sigma^{(i)2}}} \exp\left(-\frac{(x-x')^2}{2\sigma^{(i)2}}\right). \qquad (3)$$

The width of the excitatory part of $V(t)$, $\sigma^{(e)}$, is chosen to be smaller than the width of the inhibitory part, $\sigma^{(i)}$ to take into account on-off receptive field properties of LGN neurons. $S(x,t)$ models the spatio-temporal stimulus intensity along the azimuthal component which is taken to be 1 whenever the vernier or a bar of the grating is presented, and 0 else.

Vernier visibility can be assessed through various measures including the length of the time interval for which the neurons representing the vernier are active and the overall network activity in the neighborhood of the vernier activity. Here we employ the simplest approach of considering only the former. This measure is motivated by the argument that the longer an activation associated with the vernier persists the more information our visual system collects about the vernier, and this in turn increases visibility. The number of model parameters was reduced by considering symmetries, and the range of parameter values restricted by qualitative neurophysiological consideration. Parameters were then adjusted using a specific subset of stimulus conditions.

4   Results

Numerical results for the feature-inheritance, shine-through, and gap conditions as described above are given in Fig. 4. The grayscale-coded activities A_e of the excitatory populations show peaks at the position of the vernier and at the edges of the gratings, whereas almost no activity emerges for the inner grating elements. The cross-section (Fig. 4D) of the activity patterns in Figs. 4A, B and C taken at the center population reveals that the central peak in the feature-inheritance condition decays earlier than in the shine-through condition. This behavior is explained by the strong inhibition radiating from the active neurons representing the nearby edges of the grating (see arrows in Fig. 4A). However, if the extended grating comprises 25 elements, the edges are
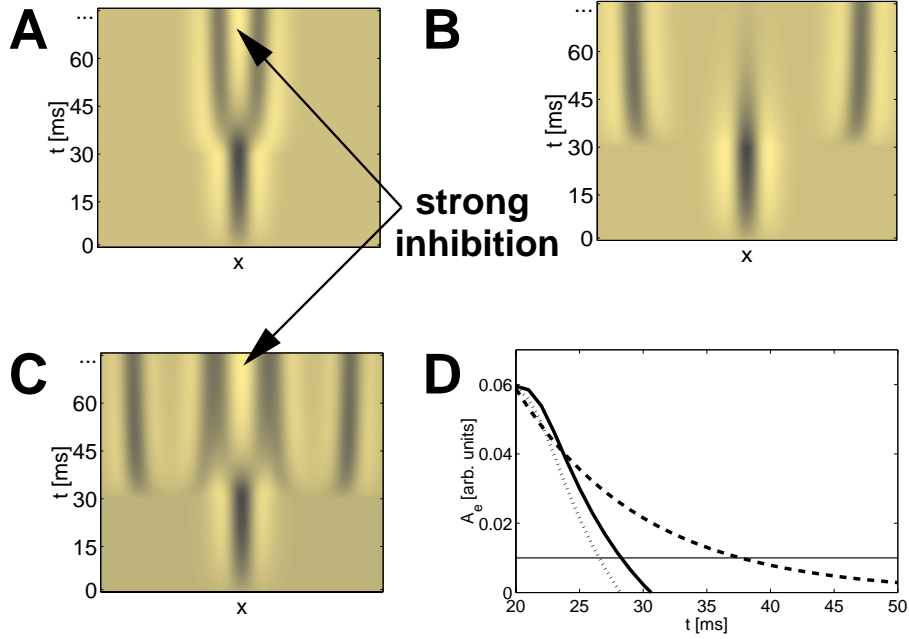

Figure 4: *Spatio-temporal activation pattern emerging from the Wilson-Cowan model in* **A.** *the feature inheritance,* **B.** *the shine-through, and* **C.** *the gap condition. The activation levels $A_e(x,t)$ are coded in shades of grey (dark for high activation). The ordinates correspond to the location of the neuronal population x, and time t in milliseconds is shown on the abszissae. While in* **A.** *and* **C.***, the central peaks are rapidly suppressed by the inhibition spreading from the two side peaks (located at the edges of the populations stimulated by the grating comprised of 5 double bars), in* **B.** *its activity persists while the two side peaks appear on the more distant edges of the large grating comprised of 25 double bars. The activation of the center population $A_e(0,t)$ is shown again in* **D.***, where the rapidly decaying solid and dotted curves correspond to the feature-inheritance and gap-conditions, respectively, while the dashed curve shows the slower decay in the shine-through condition.*

too remote to exert a substantial inhibitory influence on the center (Fig. 4B). Thus, the activity elicited by the vernier is sustained by feedback excitation, and decays much more slowly than in the feature-inheritance condition. Removing elements from the grating of 25 bars (see stimulus in Fig. 1C) re-introduces edges leading to an enhanced activation, whose inhibitory surround again suppresses the vernier activity as fast as in the feature inheritance condition (see arrows in Fig. 4C). Perceptually, the fast suppression of the vernier activity by the small central grating shown in Figs. 4A and C leads to a complete masking of the vernier element and, in the first case, to a subsequent erroneous binding of its feature, the displacement, to the grating. On the other hand,

conditions which allow a longer persistance of the vernier activity like the one in Fig. 4B result in a conscious perception of the vernier and its displacement. Thus, the occurrence of feature inheritance and shine-through are explained with the transient dynamics of a Wilson-and-Cowan type model.

5 Discussion

Our results demonstrate that even a structurally simple model based on only two partial differential equations is sufficient to explain psychophysical phenomena of feature binding and emergence. In particular, transient activation of neuronal population instead of fixed points of the dynamics determines the visibility of the target element.
The simplicity of the model equations allows for an analytical integration under certain conditions. The goal of this mathematical treatment is to identify the most important parameters, and to study their influence on the visibility. On success, this approach will allow for a calibration of the model using experimental data.
Currently, we are also investigating the extension of the model to study experiments where a) the two-dimensional structure of the stimuli will be important, and b), where not all elements will have the same orientation. Mathematically, the structure of the model will remain similar, as the dependent variable x can simply be extended from one to represent three or more dimensions in feature space.
Finally, we would like to note that the differential equations used here to describe spiking neuronal populations in terms of their mean firing rate are not always adequate. Fluctuations and oscillations on a fast time scale are averaged out as has been already described by Wilson and Cowan [1, 2]. Current research focuses on the questions under which conditions these additional temporal phenomena matter (especially if one describes stimuli changing on timescales of 30 ms and below), and which level of description is appropriate to cover the full dynamics [6, 5, 7].

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