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. The neurons show dynamically emerging and decaying activity. A change in the spatial layout of the stimuli yields dramatic differences in the strength and duration of transient neural activity.

Key words: Population dynamics, Visual masking, Transient activity, Contextual modulation

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 Hopfield associative memory and models of the Wilson-Cowan type [8,9].

In this contribution we show that the Wilson-Cowan model is equally well suited to describe transient phenomena emerging from a dynamical stimulus

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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.

2 The shine-through effect

To investigate transient dynamics psychophysically, a paradigm is needed that brings the visual system on the brink of its temporal limits. The recently discovered shine-through effect serves this need very well since performance can change dramatically even with a temporal parameter change of only about 5ms [2,3].

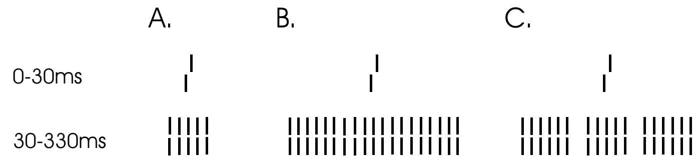

Fig. 1. A vernier precedes for a short time a grating of a variable spatial configuration. **A.** For gratings with less seven elements the vernier is invisible. **B.** For gratings with more seven elements shine-through occurs. The vernier appears superimposed on the grating looking wider and brighter. **C.** Shine-through diminishes strongly if an extended grating contains gaps. For a description of the methods, please refer to [2,3]. **Performance:** If the vernier is presented for the same duration in all three conditions, the performance of the observers is on average 91 ± 5, 57 ± 3, and 61 ± 3 percent correct responses for **A.**, **B.**, and **C.**, respectively.

In the psychophysical experiments a vernier, i.e. two abutting lines, precedes a grating of a spatial layout (see Fig. 1A). If the grating comprises less than seven elements the vernier is completely masked by the grating.
If the grating comprises 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 with the 25 element shine-through grating is better than with a 5 element grating (Fig. 1). 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, leaving out two elements and adding them at the ends of the grating degrades performance strongly while the overall energy of the grating remains constant (Figs. 1C). Therefore, explanations of these effects cannot be attributed to low level stimulus cues such as mask energy. High order explanations are needed. Surprisingly, the underlying neural mechanisms can, in spite of the complexity, be described by very simple models— as the following sections show.

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 in order to simplify an analysis of the mechanisms underlying its dynamics.

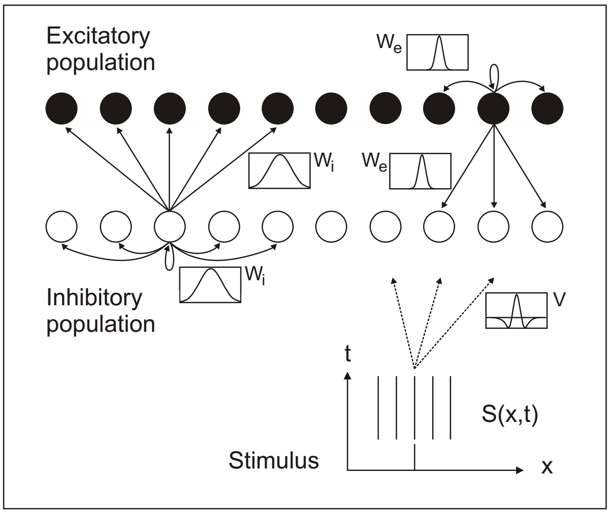

Fig. 2. Structure of model employed in the simulations. A spatio-temporal stimulus $S(x,t)$ is filtered by a difference of Gaussians and projected onto two populations in a one-dimensional neuronal layer. The two populations, an excitatory and an inhibitory one, are mutually coupled with synaptic weight functions described by the Gaussian kernels W_e and W_i, respectively.

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 [9],

$$\tau_e \frac{\partial A_e(x,t)}{\partial t} = -A_e(x,t) + h_e\left(w_{ee}[A_e * W_{ee}] - w_{ie}[A_i * W_{ie}] + I(x,t)\right) \quad (1)$$

$$\tau_i \frac{\partial A_i(x,t)}{\partial t} = -A_i(x,t) + h_i\left(w_{ei}[A_e * W_{ei}] - w_{ii}[A_i * W_{ii}] + I(x,t)\right) . \quad (2)$$

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 symbol $*$ denotes a convolution, i.e. $[A_i * W_{ii}] := \int A_i(x',t) W_{ii}(x - x')\, dx'$. 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,

$$V(|x - x'|) = \frac{1}{\sqrt{2\pi\sigma_E^2}} e^{-\frac{(x-x')^2}{2\sigma_E^2}} - \frac{1}{\sqrt{2\pi\sigma_I^2}} e^{-\frac{(x-x')^2}{2\sigma_I^2}} . \tag{3}$$

The width of the excitatory part of $V(t)$, σ_E, is chosen to be smaller than the width of the inhibitory part, σ_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.

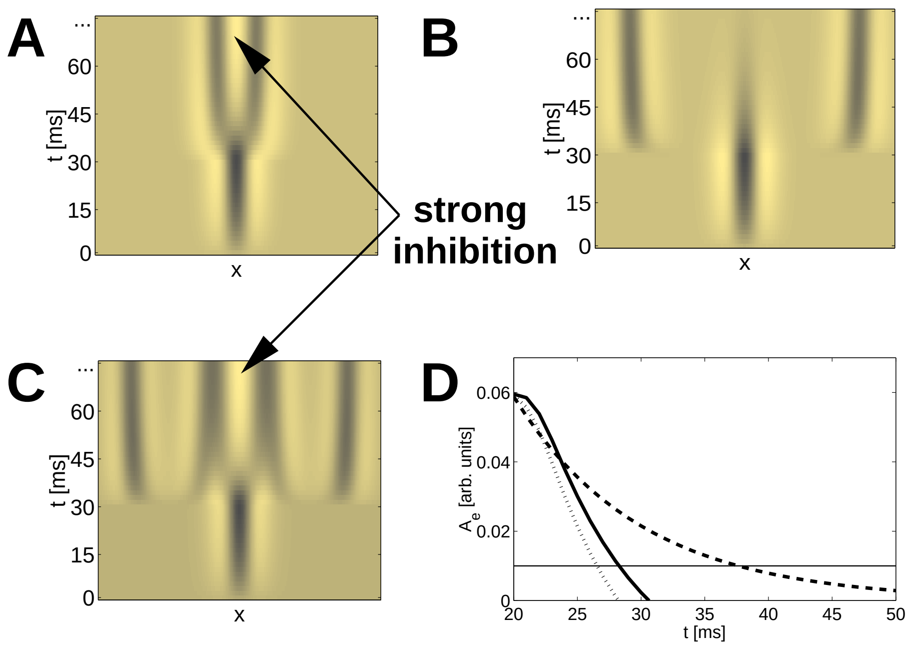

Fig. 3. Spatio-temporal activation pattern emerging from the Wilson-Cowan model in **A.** 5 element grating, **B.** the shine-through, and **C.** the gap condition. The activation levels $A_e(x, t)$ are coded in shades of grey (dark for high activation). The x-axis corresponds to the location of the neuronal population x, and time t in milliseconds is shown on the ordinates. 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 elements), 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 in **D.**, where the rapidly decaying solid and dotted curves correspond to the 5 element grating and the gap grating conditions, respectively. The dashed curve shows the slower decay in the shine-through condition.

Vernier visibility is assessed through the length of the time interval for which the neurons representing the vernier are above some threshold (i.e. determined by the background noise). 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 5 element, shine-through, and gap grating conditions are given in Fig. 3. 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. 3D) of the activity patterns in Figs. 3A, B and C taken at the center population reveals that the central peak in the 5 element condition decays faster 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. 3A).
However, if the extended grating comprises 25 elements, the edges are too remote to exert a substantial inhibitory influence on the center (Fig. 3B). Thus, the activity elicited by the vernier is sustained by feedback excitation, and decays much more slowly than in the 5 element condition. Removing elements from the grating of 25 elements (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. 3C).
Perceptually, the fast suppression of the vernier activity by the small central grating shown in Figs. 3A and C leads to a complete masking of the vernier element. On the other hand, conditions which allow a longer persistence of the vernier activity like the one in Fig. 3B result in a conscious perception of the vernier and its displacement. Thus, the occurrence of shine-through is 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 object visibility and emergence. In particular, transient activation of neuronal population instead of fixed points of the dynamics determines the visibility of the target element.
Using quantitative stimulus conditions, it is possible to calibrate our model,

and to make quantitative predictions [4]. Furthermore, our model explains also experiments with irregular stimuli [5].

References

[1] W. Gerstner, Population dynamics of spiking neurons: fast transients, asynchronous states, and locking. *Neural Computation* 12 (2000), 43–89.

[2] M.H. Herzog and C. Koch, Seeing properties of an invisible element: feature inheritance and shine-through. *Proceedings of the National Academy of Science, USA* 98 (2001), 4271–4275.

[3] M.H. Herzog, M. Fahle, and C. Koch, Spatial aspects of object formation revealed by a new illusion, shine-through. *Vision Research* 41, (2001), 2325–2335. Please read Erratum: *Vision Research* 42 (2001), 271.

[4] M.H. Herzog, U.A. Ernst, A. Etzold, and C. Eurich, Local interactions in neural networks explain global effects in the masking of visual stimuli, *submitted to Neural Computation.*

[5] M.H. Herzog, M. Harms, U.A. Ernst, C.W. Eurich, S.H. Mahmud, and M. Fahle, Extending the shine-through effect to classical masking paradigms, *in revision, Vision Research.*

[6] B.W. Knight, Dynamics of encoding in neural populations: some general mathematical features, *Neural Comp.* 12 (2000), 473–518.

[7] D.Q. Nykamp and D. Tranchina, A population density approach that facilitates large-scale modeling of neural networks: analysis and an application to orientation tuning. *Journal of Computational Neuroscience* 8 (2000), 19–50.

[8] H.R. Wilson and J.D. Cowan, Excitatory and inhibitory interactions in localized populations of model neurons, *Biophys. J.* 12 (1972) 1–24.

[9] H.R. Wilson and J.D. Cowan, A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue, *Kybernetik* 13 (1973) 55–80.

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