

**The spatial and temporal effects of lateral inhibitory networks
and their relevance to the visibility of spatiotemporal edges**

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Abstract

The response dynamics of neurons in the visual pathway are driven, in part, by the dynamics of lateral inhibitory networks. Illusions of invisibility, such as the visual masking illusions, in addition to the dynamics of visibility itself, can be explained by the actions of such networks. Here we provide a descriptive model of a lateral inhibitory network in space and time. We provide physiological evidence that neurons in the early visual system of primates respond in a fashion predicted by these temporal dynamics. Furthermore, we discuss how the network predicts the existence of novel visual illusions and their physiological correlates.

Introduction

Illusions of invisibility are effects in which normally salient stimuli (called targets) are rendered invisible by other stimuli (called masks). We have previously investigated the spatial and temporal parameters of forward and backward masking illusions (a specific subset of invisibility illusions), as well as their physiological basis, with psychophysical, physiological, and optical imaging methods (Macknik and Haglund, 1999; Macknik and Livingstone, 1998; Macknik, Martinez-Conde and Haglund, 2000a). Because the spatial and temporal parameters that achieve visual masking of the target by the mask are highly precise, we could determine:

- ❖ The spatial and temporal parts of the target that are most responsible for the target's visibility
- ❖ The spatial and temporal parts of the mask that produce the greatest masking effect on the visibility of the target

We found that the parts of the target most important to conveying its visibility were its *spatial edges*. We also found that, temporally, the parts of the target's lifetime most important to its visibility were its onset and termination rather than its mid-life; that is, the target's *temporal edges* seemed to convey the strongest signal concerning the target's visibility. Similarly, the parts of the mask that were most important to its ability to suppress the perception of the target were the mask's *spatiotemporal edges*.

We moreover found that the neural correlates of the spatiotemporal edges of stimuli (both targets and masks) were transient bursts of spikes that occurred after the stimulus turned on and off, within neurons with receptive fields positioned at the spatial edges of the stimulus on the retinotopic map. In an independent set of studies, we also showed independently the importance of bursts of spikes to conveying the visibility of stimuli (Martinez-Conde, Macknik and Hubel, 2000, 2002).

Thus transient bursts of spikes conveyed the strongest neuronal signals from both targets and masks. Here we propose that the peculiar timing conditions associated with visual masking illusions, such as the fact that the mask can be presented either before or after the target while still rendering the target invisible, may be explained through a simple lateral inhibitory network, in which the transient responses to the mask's spatiotemporal edges inhibit the transient responses to the target's spatiotemporal edges. Because the target and mask do not overlap each other spatially, the circuit underlying masking must be called "lateral inhibition", as defined by (Hartline, 1949). Several previous groups have suggested that masking might be explained by lateral inhibition (Anbar and Anbar, 1982; Bridgeman, 1971; Francis, 1997, 1998; Lawwill, 1973). However, various aspects of these models do not match the timing parameters of visual masking discovered more recently, such as the importance of the target's after-discharge to its visibility (Macknik and Livingstone, 1998; Macknik et al., 2000a).

Here we propose a descriptive model to explain how a basic lateral inhibitory circuit (Ratliff, Knight, Dodge and Hartline, 1974) might account for the spatiotemporal properties found in illusions of invisibility. We also discuss this circuit's role in helping to form the transient nature of the responses to stimulus onset and termination. We moreover tested experimentally, by recording electrophysiologically from area V1 in the macaque monkey, if the neuronal patterns of activity behave in a manner predicted by such a network.

Results

Lateral Inhibition

Hartline, Ratliff and colleagues (Ratliff, 1961; Ratliff et al., 1974) proposed that a lateral inhibitory circuit has three components:

- 1) Excitatory input and output
 - a) Monosynaptic connections between the retina and the lateral geniculate nucleus (LGN), and between the LGN and cortex, are thought to be excitatory (Cleland, Dubin and Levick, 1971; Levick, Cleland and Dubin, 1972; Reid and Alonso, 1995).
- 2) Self-inhibition
- 3) Lateral inhibition as a function of excitation (thus inhibition follows excitation in time)
 - a) Spatiotemporal responses of neurons in the LGN and cortex show that excitation precedes inhibition (Ferster, 1986; Golomb, Kleinfeld, Reid, Shapley and Shraiman, 1994).

A plausible mammalian descriptive model is shown in **Fig. 1a**, based on Hartline and Ratliff's original model. The model predicts that the strongest neural signals to a visual stimulus occur just inside the stimulus' spatial edges. Neural inhibition, moreover, is strongest just outside of the edge. Inherent to this model is the prediction that inhibition should be strongest at the spatial edges of stimuli, as we have shown perceptually (Macknik et al., 2000a). Aspects of this model may need to be revised for any given brain area. Other more complicated circuits could potentially generate the same behavior; the point here is to ask if the simplest possible inhibitory circuit could account for the various spatiotemporal properties found in visual masking.

The role of lateral inhibition through time

The primary question we address here is how the network would behave temporally. If we look at two of the neurons, one excitatory and one inhibitory, corresponding to the edge of the stimulus in **Fig. 1a** and follow their activity through time (**Fig. 1b**), we should expect a specific temporal pattern of response. As the network is activated initially, excitation is generated forming the onset-response, inhibition is then generated, which equilibrates the network (sustained firing), and after the stimulus is extinguished inhibition lags, followed by (what appears to be) a disinhibitory response (the after-discharge).

If lateral inhibition is the basis of visual masking, then we would expect subcortical and cortical cells to show these same response phases, because lateral inhibitory circuits generate inhibitory surrounds at both of these levels (Hubel and Wiesel, 1961, 1962). Adrian and Mathews (1927a, b, c), in the very first microelectrode recordings from the visual system (eel optic nerve), saw this temporal pattern of activity (**Fig. 1c**). We have replicated their experiment by recording from 28 neurons in area V1 of the anesthetized macaque while flashing a single oriented bar of optimal dimensions and contrast on each receptive field (**Fig. 1d**).

Fig. 2 shows the evolution of the response from a single neuron in area V1 to the presentation of a bar of optimal dimensions and varied durations. The sustained phase of the response was only apparent with long durations of target presentation, as one would expect if the cell was embedded within a lateral inhibitory network. Short-duration stimuli (less than 50ms) resulted only in transient phases of firing (an initial transient onset-response as well as a transient after-discharge).

The after-discharges, moreover, grew in size as the stimulus increased in duration, as first noticed by Adrian and Mathews (1927a, b, c). This is to be expected because stimuli should inhibit the network more intensely as their duration increases, resulting in larger disinhibitory after-discharge when the stimuli are extinguished. This is the same

process that generates firing in an off-center retinal ganglion cell when light is extinguished within the center (Kuffler, 1953).

We conclude that neurons in the visual system respond to stimuli in a temporal pattern that should be expected of any neuron within a Hartline-Ratliff lateral inhibitory network (Ratliff, 1961; Ratliff et al., 1974). The interplay of the temporal patterns of responses to targets and masks leads to visual masking illusions.

Discussion

Our previous experiments show that complicated delay-line circuits such as those in “dual-channel” models of visual masking (Breitmeyer and Ogmen, 2000) are not needed to explain the counterintuitive timing parameters found in visual backward masking. Moreover, our previous results also show that visual masking effects are extant subcortically and are not caused by feedback from the cortex (Macknik and Martinez-Conde, 2000; Macknik and Martinez-Conde, in press; Macknik et al., 2000a), so models of visual masking that require cortical circuits or feedback mechanisms can also be ruled out (Enns, 2002; Thompson and Schall, 1999). Here we propose that it is visibility itself that is complicated and that visibility is dependent on both onset and after-discharge responses together. One paradox that seems to arise from this conclusion is that it should be difficult to see long-duration stimuli while they are still on. However, the answer to this paradox is trivial: there is no such thing as a long-duration stimulus in the visual system (Coppola and Purves, 1996) due to retinal adaptation. Stimuli only seem long-duration because of the transient bursts of spikes that are generated by the continuous movement of the eyes and head, even during visual fixation (Martinez-Conde et al., 2000, 2002).

We suggest that, whatever the circuit that causes masking may be, it is probably simple since recordings from area V1 and the lateral geniculate nucleus (combined with previous psychophysical results) indicate that masking occurs independently within very different tissues such as the cortex and thalamus (and perhaps retina). This, together with the finding that the spatiotemporal edges of masks convey the strongest perceptual masking, leads us to conclude that the mechanism of masking could be the simplest possible form of neural inhibitory circuit. Hartline and Ratliff’s local inhibition model, the basis of lateral inhibition, meets the theoretical requirements (Ratliff et al., 1974). This simple model’s behavior moreover predicts the complicated temporal dynamics of the responses to visible stimuli over time. These temporal dynamics are apparently conserved over disparate phylogenetic classes, as shown in the comparison of visual responses from the eel and the primate in **Fig. 1**.

The behavior of the model through time moreover predicts new percepts and illusions. From this model we have predicted previously the Standing Wave of Invisibility illusion (the first visual illusion to be predicted by primate physiology), the Static Masking illusion, the Unfilled Flicker illusion, and Temporal Fusion (Macknik and Livingstone, 1998; Macknik and Martinez-Conde, 1998; Macknik et al., 2000a; Macknik, Martinez-Conde and Haglund, 2000b). (Visit <http://neuralcorrelate.com> for demonstrations of these illusions, and other related effects.) Computational models based on lateral inhibition can explain similar types of illusions of invisibility, such as the entire family of Shine-Through effects (Herzog, Fahle and Koch, 2001; Herzog, Koch and Fahle, 2001).

Finally, even seemingly high-level masking effects could be explained by this model, such as object substitution (Enns and Di Lollo, 1997). Object substitution is an effect in which a target object can be suppressed by a masking object of similar shape, even though the mask does not abut the target spatially (as is necessary in other types of masking discussed here). This effect can also be explained with a lateral inhibitory model, if one considers that, in areas of the visual system that process objects, space is no longer retinotopic, and is instead mapped for objects. Lateral inhibitory networks in such areas would exhibit a similar behavior as in lower retinotopic areas, but with inhibitory effects spanning object space, rather than retinotopic space. This would then account for the fact that the mask must be a similar shape to the target (which would make them near each other in object space), and that the target and mask need not be near each other retinotopically.

Methods

Primate Neurophysiology

Stimuli were presented on a NEC 5FG monitor at a refresh rate of 100Hz. The monitor subtended 32° by 25° at a viewing distance of 58.5cm. All stimuli were black against a background of 18% contrast white (CIE $x=0.333$, $y=0.333$, 26.74 lumens) in a dimly lit room. The dimensions of the target, a single oriented bar, were optimized for each neuron. Standard electrophysiological techniques for recording from anesthetized paralyzed animals were used (Hubel and Livingstone, 1987).

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Figure Legends

Figure 1. (a) A representation of the lateral inhibition model originally proposed by Hartline and Ratliff (Ratliff, 1961; Ratliff et al., 1974). The four excitatory (highlighted in green) neurons in the center of the upper row receive excitatory input from a visual stimulus. This excitation is transmitted laterally in the form of inhibition, resulting in edge enhancement of the stimulus: the neuronal underpinnings of the Mach Band illusion (Mach, 1965). **(b)** One excitatory and one inhibitory neuron taken from the spatial model in **Fig. 1**, now followed through an arbitrary period of time. Several response phases are predicted, including the onset-response, and the transient after-discharge (Adrian and

Matthews, 1927a). **(c)** Reprinted from Adrian & Matthews (Adrian and Matthews, 1927a); figures 4 & 5). The *top* figure is the peri-stimulus time histogram of neuronal firing rate from the eel optic nerve when the retina was stimulated by a disk, 36 mm in diameter and 830 candles/m² in intensity. Duration of the stimulus is denoted with the black bar below the recording. The *bottom* figure is similar, except that the disk was 12.8 mm in diameter. Notice that the histograms retain their characteristic shape across different physical intensities, and that each response to the target is subsequently followed by a prominent after-discharge. **(d)** The average response, from 28 neurons in separate recording sites in area V1 of a cynomologous monkey when visually stimulated for 500 milliseconds with an optimally oriented bar (some recording sites may not have been orientation selective, in which case orientation was arbitrarily chosen). The white bar on the bottom of the histogram represents the time in which the target was on.

Figure 2. Recording from a typical single neuron from monkey area V1 that was stimulated with a target of various durations. The magnitude of the after-discharge grows in size as the target duration increases.



