Stochastic resonance in visual cortical neurons: Does the eye-tremor actually improve visual acuity?

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Abstract

We demonstrate with electrophysiological recordings that visual cortical cell responses to moving stimuli with very small amplitudes can be enhanced by adding a small amount of noise to the motion pattern of the stimulus. This situation mimics the micro-movements of the eye during fixation and shows that these movements could enhance the performance of the cells. In a biophysically realistic model we show in addition, that micro-movements can be used to enhance the visual resolution of the cortical cells by means of spatiotemporal integration. This mechanism could partly underlie the hyperacuity properties of the visual system.

Key words: Stochastic Resonance; Hyperacuity; Cat; Retina; Visual Cortex

1 Introduction

Micro-movements of the eyes are a strong source of noise in the visual system. Even present while fixation, different types of involuntary eye movements exist that differ with respect to amplitude and frequency. Amplitudes range from a few seconds of arc for the microtremor up to 20 minutes of arc for microsaccades. The frequency spectrum ranges from less than 0.5Hz for the low drift to up to 100Hz for the microtremor (5). Here we show a possible role of eye micro-movements as a noise source that could lead to the effects of stochastic resonance and spatial acuity improvement.

Stochastic resonance is known as the effect that the signal detection of a normally nondetectable signal facilitated by noise and thereby reaches a detectable level. This phenomenon can only occur in non-linear systems like neuronal networks (for a review see (2)). We were able to show this effect in recordings in visual cortex cells. Spatial acuity improvement is not directly related to stochastic resonance but we show that it can also relate on motion noise. We demonstrate in a model how motion noise could affect the processing of vernier stimuli.

2 Results

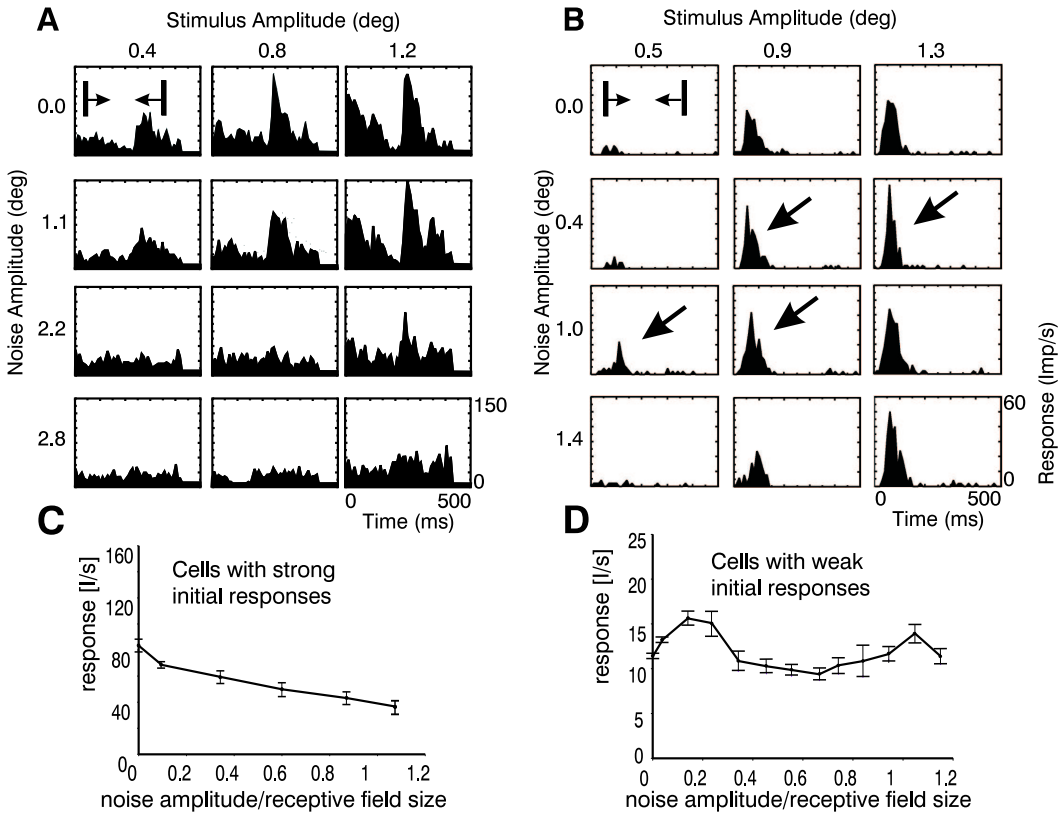

Fig. 1. Effect of stochastic resonance on visual cortical cells. (A, B) PSTHs of cell responses to a sinusoidally moving stimulus with different amplitudes of motion noise added. (C, D) Response amplitudes of the recorded cells as function of the noise level.

We recorded 74 cells in area 17 and 18 of anesthetized and immobilized cats and mimicked eye micro-movements by jittering the stimulus. A bar of optimal orientation, length, and width was first placed in the center of the RF and then moved back and forth with a small sinusoidal amplitude (0.2-4 deg). We determined which amplitude of the sinusoidal modulation elicits a small but clearly visible response and used this, a smaller and a slightly bigger amplitude

for three sets of tests. For each test, broad band motion noise with up to five different amplitudes (0.1-4.0 deg) was added.

Fig. 1A,B shows PSTH diagrams of two direction selective cells. The first cell responded best in the absence of noise (A). When noise was increased, responses weakened. The second cell shows better modulation for all three stimulus amplitudes when a small amount of noise is present (B, indicated by arrows). When the noise is further increased the response modulation deteriorates. A quantification of these results is shown in Fig. 1C,D. Part (C) shows the results where noise had a weakening effect on the cells response, which was observed preferably in cells with a strong initial response. Cells with a weak initial response show increased responses at certain noise levels (D).

2.1 Simulation results

To gain a better theoretical understanding how motion noise acts on the visual system, we designed a model of the retina with explicitly modeled photoreceptors, horizontal, bipolar, amacrine and ganglion cells. The model retina consists of a patch of hexagonally arranged cell units with a distance of 30 sec of arc, which corresponds to the cell density in the human fovea (for a description see (3)). The output of the retina is passed to a further layer with a ten-fold higher cell density compared to the retina. It is used as a read-out layer of the retinal output with a higher spatial resolution that allows us to see the neural representation of the stimulus after retinal processing. Similar to the experimental observations, we also found that simulated micro-movements will lead to increased responses in the read-out layer (data not shown). In addition to this, we discovered another effect, namely that noise in the range of the ocular microtremor improves spatial resolution. Due to the brevity of this article we only show the latter results. Microtremor consists of a small high frequency jitter of the eyes with a frequency in the range of 60-100Hz (1; 4). The mean frequency is about 84 Hz (1). There exists less consistent data about the amplitude of the microtremor, but it seems likely in the range of 6 sec of arc (1). Its functional role is so far unresolved.

Consider now the following (unrealistic) situation: a dot stimulus which is so small that its image falls between two adjacent photoreceptors. Could this dot become visible by means of eye micro-movements, which have an average amplitude of about the distance between 2 photoreceptors and, thus, lead to a random excitation pattern at neighboring receptors surrounding the dot (Fig. 2A)? The idea is that temporal low-pass filtering at all levels in the network would integrate the signal and spatial filtering together with the high cortical (read-out layer) magnification would then allow to locate the dot accurately by spatial averaging.

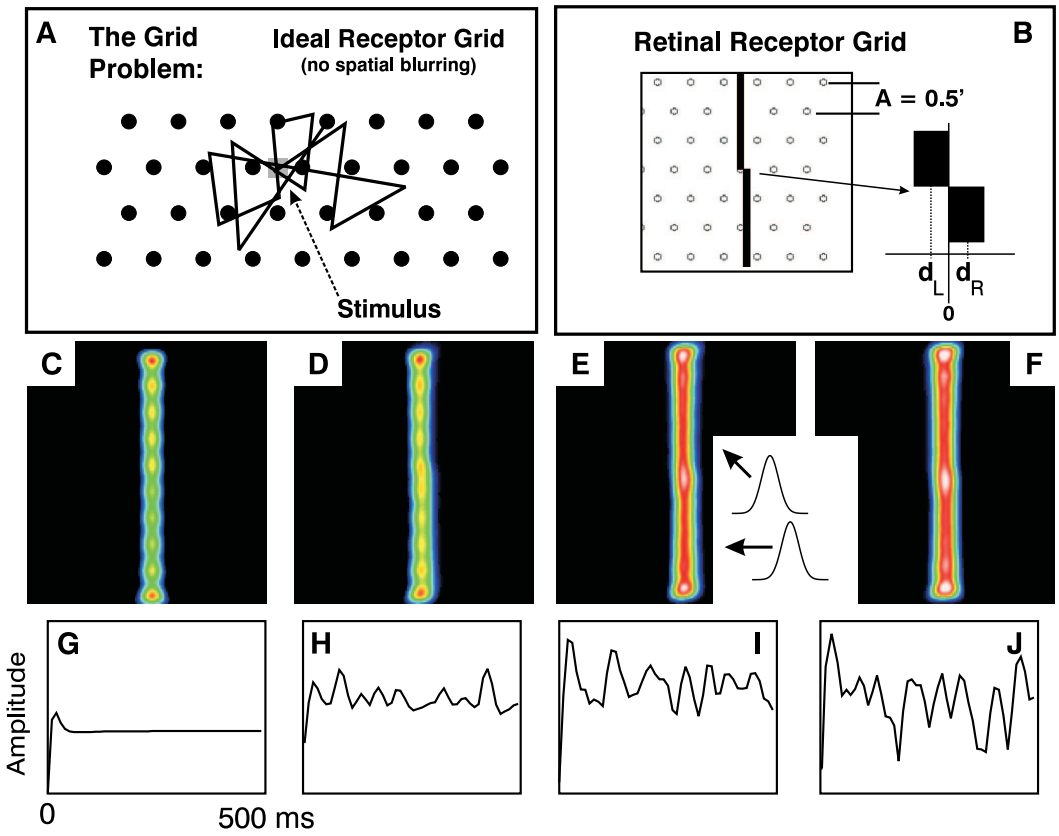

Fig. 2. Simulation results. (A) Schematic of a small stimulus on a ideal receptor grid. (B) The stimulus relative to the receptor grid in the retina model. (C-F) Responses of the read-out cell layer at different noise levels (0", 23", 56" and 78", respectively), averaged over 500ms. (G-J) Time course of the response of a cell in the read-out layer that is centered under the stimulus.

The stimulus used in the simulations is a typical vernier stimulus, which consists of two adjoining bars with a small relative displacement of $d = 7.5''$ (Fig. 2B). The displacement is smaller than the distance between two photoreceptors ($30''$) and, thus, cannot be resolved. Hyperacuity though allows the detection of displacements in the order of 4" to 10", which so far has been attributed to the spatial sampling of the ganglion cells and their overlapping receptive fields (6). In addition to these mechanisms, we investigated the role of the micro-movements on the resolution of vernier stimuli. To this end, the surface of the model retina is shifted both in the horizontal and vertical direction relative to the static stimulus to simulate the movements of the eye. It proved to be noise in the amplitude and frequency range of the ocular microtremor that shows a strong effect on acuity. Therefore the mean frequency used was 85Hz while the mean amplitude of the tremor has been varied (0"-90"). Another parameter that has been investigated was the width of the photoreceptor sensitivity profile (12"-48").

Examples of the activity of the read-out cell layer for different tremor am-

plitudes are shown in Fig. 2C-J. Parts C and G show the case where no microtremor is present. In this case, the displacement of the lower bar of the vernier stimulus is not visible in the activity distribution. When weak tremor with amplitudes of 23" and 56" is added, the displacement becomes visible (D,E) and the membrane potential of the cells noisy (H,I). With a tremor of higher amplitude, the displacement is still visible, but in this case the activity distribution gets much broader compared to the weak tremor (F) and the fluctuations in the membrane potential more noisy (J).

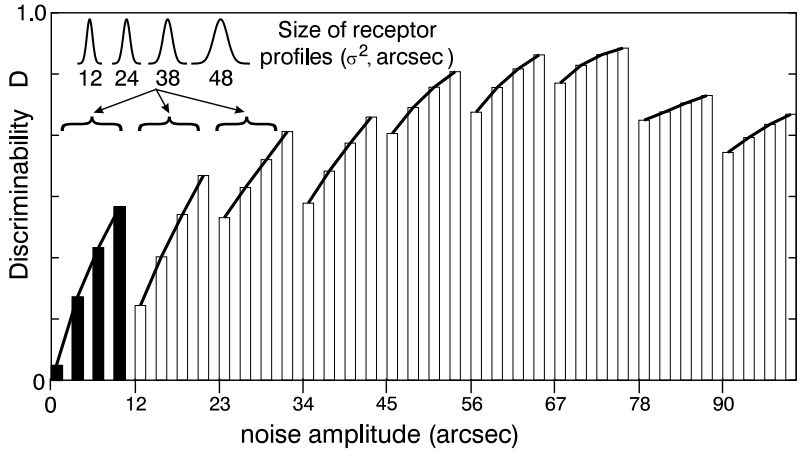

Fig. 3. Quantification of the simulation results. Shown is the discriminability of a vernier stimulus as function of the receptor profile width and noise level (see text).

To quantify these results, the activity distributions of the upper and lower bar have been averaged over 500ms and horizontal cross-sections have been fitted by a gaussian distribution (see Fig. 2E, inset). Then a correlation function between the fitted gaussians of the upper and lower bar distribution is computed, which is maximal if the two distributions are located at the same positions as the stimulus. If a_L^f and a_R^f are the amplitudes of the upper and lower fitted gaussians, respectively, σ_L^f and σ_R^f the variances, d_L^f and d_R^f the locations of the peaks of the two distributions and d_L and d_R the real positions of the bars in the stimulus (as in Fig. 2), a value for the discriminability of the bars is calculated by

$$D = \int_{-\infty}^{\infty} a_L^f \cdot a_R^f \cdot exp\frac{(x-(d_L^f - d_L))^2}{2(\sigma_L^f)^2} \cdot exp\frac{(x-(d_R^f - \mathrm{d}_R))^2}{2(\sigma_R^f)^2} dx. \qquad (1)$$

This measure increases as the peak positions of the representations of the two bars get closer to the real positions of the bars in the stimulus. Additionally, it increases with the amplitude of the responses. Values for D were computed for different noise amplitudes and photoreceptor sensitivity profile widths (Fig. 3C). As expected, a wider tuning of the photoreceptor sensitivity leads to a better discriminability. But microtremor has an even stronger impact. As its amplitude increases, the discriminability reaches much higher values for low

amplitudes. Beyond a certain level of noise, it decreases again. The reason for that is that now the distance between the two bars is overestimated, as the activity spreads over a wide area of the retina. Additionally, the mean response amplitude decreases because the cells receive only brief excitation by the now fast moving stimulus.

3 Conclusions

Ocular micro-movements act as a source of noise in the visual system. Normally noise is an unwanted aspect and engineers try to eliminate it in their systems as good as possible. In this study, on the other hand, we have focused on two apparently paradoxical effects (stochastic resonance based amplitude enhancement & noise induced spatial acuity improvement) and we were able to provide some evidence that the inevitably existing micro-movements of the eyes could actually lead an improved visual signal transmission.

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