Synchronous oscillations in frog retinal ganglion cells

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To investigate how visual information is coded by cell populations, we simultaneously recorded light-evoked spike discharges from multiple OFF-sustained type ganglion cells (the dimming detectors) of the frog retina using a planar multi-electrode array. Auto- and cross-correlation analyses were performed to evaluate temporal properties of the spike trains. With full-field, sinusoidally modulated diffuse illumination, cross-correlation analysis revealed the presence of long-range synchronous oscillations. The strength of the synchronous oscillations depended on the spatial properties of the light stimulus, which extended far beyond the "classical" receptive field that is defined by the spike discharge rate. These results suggest that synchronous oscillations may encode global features of visual stimuli and play a key role in perceptual integration.

Key words: frog, retina, ganglion cell, synchronous oscillation, stimulus dependence, temporal coding, population coding

Introduction

The Gestalt psychologists assumed that the visual system would automatically link the related parts together to form the objects in a visual scene. Recent studies have revealed that visual cortical neurons show synchronous oscillatory activities that depend on coherent features in the visual field (for a review, see Singer & Gray, 1995). These results support the hypothesis that synchronous oscillations may serve to bind the distributed neuronal activities into a unique representation. Frog retinal ganglion cells also show long-range synchronous oscillations (Ishikane et al., 1999). In the present study, we examined the stimulus dependence of synchronous oscillations so that we could understand information coding by cell populations.

Methods

Spike discharges were recorded from multiple OFF-sustained type ganglion cells (the dimming detectors) of the isolated frog retina with a planar multi-electrode array. We sometimes observed several spikes with different amplitudes and waveforms from a single channel. To isolate spikes originating from a given neuron, the template-matching technique was used. The stimulus images were generated on a CRT display which was driven by a PC and projected onto the retina through optics. Auto- and cross-correlograms were computed from the spike discharges to evaluate temporally correlated activities. In this study, the intensity of light stimuli was sinusoidally (0.25 Hz) modulated under all conditions.

Results

Oscillatory activities are generated by spot illumination which is larger than the receptive field of the dimming detectors. To examine the effects of spot size on the oscillatory activities, the center of the spot illumination was adjusted to the center of the classical receptive field of the cell. The spot intensity was sinusoidally modulated while the background intensity was maintained at the mean level of the modulation. As the spot size was increased up to the receptive field of the cell, the number of spike discharges

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increased almost linearly. But the auto-correlogram did not reveal the presence of oscillatory activities. However, spot illumination larger than the receptive field could evoke the oscillatory activities (∼30 Hz). A further increase in spot size strengthened the oscillatory activities but the number of spike discharges did not increase.

The generation of synchronous oscillations depends on the stimulus pattern. With a full-field modulated illumination, cross-correlation analysis revealed the presence of synchronous oscillations in the dimming detectors. The synchronous oscillations were not phase-locked to the stimulus onset indicating that these activities could originate from neural interactions. Synchronous oscillations were detected even in cell pairs more than 2 mm apart. However synchronous oscillations were not detected when two distant cells with non-overlapping receptive fields were stimulated with respective spots, the intensities of which were sinusoidally modulated in phase. When the continuity of the sinusoidally modulated full-field illumination was collapsed, by inserting a slit with the mean modulation intensity between two dimming detectors, the synchronous activities were weakened but not abolished.

Discussion

In this study, we examined how synchronous oscillations in the frog retina were affected by stimulus pattern. Synchronous oscillations were evoked only when the spot size was larger than the classical receptive field of the dimming detectors. This result suggests that synchronous oscillations among the dimming detectors may serve to discriminate the size of visual objects that are larger than each classical receptive field. The decrease of synchronous oscillations by spatial discontinuity supports the hypothesis that synchronous oscillations would encode global visual features covering many receptive fields. The frog retina transmits a highly selected and transformed representation to the brain (Lettvin et al., 1959; Maturana et al., 1960). It would not be surprising if the synchronous oscillations observed in the frog retina contribute to high-level processing.

Our results indicate that synchronous oscillations are induced by long-range neuronal interactions. The interactions might require phase-locking oscillatory modules extending horizontally across the retina. Amacrine cells make widely spread meshworks via reciprocal synapses, or gap junctions. Synchronous oscillations could be generated by these neural mechanisms.

Further studies are required to understand how synchronous oscillations in the retina contribute to the functions in the visual system.

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