Pharmacological suppression of oscillatory synchronized discharges in retinal ganglion cells inhibits escape behavior of the frog

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In the frog retina OFF-sustained type ganglion cells (dimming detectors) generate oscillatory synchronized discharges with a light which is dimming. To elucidate the function of the oscillatory synchronization (OS) in the retina we performed behavioral experiments and multi-electrode recordings from dimming detectors. Frogs exhibited an escape behavior when an expanding dark spot was presented on a computer monitor. The probability of the escape behavior was higher as the final size of the expanding dark spot was increased. Multi-electrode recordings from the isolated retina revealed that the OS was enhanced as the final size of the expanding dark spot was increased. The OS could be blocked when the isolated retina was superfused with bicuculline, a GABA\textsubscript{A} receptor blocker. Injection of bicuculline into the eyes of the frog significantly suppressed the escape behavior but did not affect the optokinetic responses to a drifting grating. We conclude that the OS of dimming detectors in the retina is essential for triggering the escape behavior.

**Key words:** oscillatory synchronization, escape behavior, retinal ganglion cell

**Introduction**

The stimulus-evoked oscillatory synchronization (OS) of neural assemblies has been described in the visual systems, but the functional roles of this phenomenon remain to be elucidated. In the frog retina OFF-sustained type ganglion cells (dimming detectors) generate the OS. The OS depends on the size and spatial continuity of the dimming stimuli, and is suppressed by bicuculline, a GABA\textsubscript{A} receptor blocker (Ishikane et al., 1999). Frogs exhibit visually evoked escape behavior when a looming object is presented (Waldeck & Gruberg, 1995) and dimming detectors are assumed to be related to this escape behavior (King et al., 1999). To elucidate the functional role of the OS in the retina we examined how the escape behavior was modulated when the OS was suppressed by bicuculline.

**Methods**

**Behavioral experiments**

A bullfrog was placed in a transparent acrylic dome and its escape behavior was examined by manipulating the final size (visual angle, 10–55°) of an expanding dark spot which was displayed on an LCD. The optokinetic response was measured as the maximum angle of head rotation when a vertical square grating (spatial frequency, 0.1 cycles per degree) drifted horizontally (temporal frequency, 0–0.16 Hz). An ocular injection of bicuculline was given under anaesthesia, and the behavioral experiments were performed after recovery from the anaesthesia (2 hours after administration).

**Electrophysiological experiments**

Spike discharges were recorded from dimming detectors of the isolated frog retina with a planar multi-electrode array. Expanding dark spots were presented on a CRT and projected onto the retina through an optical system. The properties of the stimuli were the same as those used for the behavioral experiments. Sliding window cross-correlograms
were computed from the spike discharges to evaluate the temporally correlated activities.

**Results**

**Size dependence of the escape behavior and the OS of dimming detectors.**

*Behavioral experiments*

An expanding dark spot presented on the LCD could evoke the escape behavior. The probability of the escape behavior was higher as the final size of the expanding dark spot was increased, and when the spot diameter was larger than 50° the probability was saturated.

*Electrophysiological experiments*

Spike discharges to the expanding dark spot were recorded from dimming detectors and cross-correlograms were computed. The OS was detected when the final size of the spot was approximately 30°, and the strength of the OS increased as the final size of the spot was larger. These results suggested a strong correlation between the strength of the OS and the probability of the escape behavior.

**Effect of a GABA\(_A\) receptor blocker on the OS and the escape behavior.**

*Electrophysiological experiments*

We examined the effects of bicuculline on the responses of dimming detectors. Bicuculline increased the number of spike discharges but suppressed the OS completely even when the largest spot was presented.

*Behavioral experiments*

We examined the effects of bicuculline on the escape behavior to the largest expanding dark spot. Just after the ocular injection of bicuculline the probability of the escape behavior was significantly reduced (Figure 1). One day after the injection the escape behavior recovered to the control level. Suppression of the behavior was not observed after an injection of standard saline. We observed that bicuculline did not affect the optokinetic responses to drifting gratings. These results indicate that the reduction of the escape behavior could be attributed to suppression of the OS of dimming detectors in the retina.

![Figure 1. Reduction of the probability of the escape behavior after the injection of bicuculline (Bic). Control, before the injection. Washout, 24 hours after the injection. Error bars, S.E.M.](image)

**Discussion**

The present results demonstrate that the OS of dimming detectors in the retina is essential to triggering escape behavior. Because the strength of the OS depends on the stimulus size, the OS may encode the stimulus size. When a predator is approaching, frogs must escape. On the other hand, when small insects are flying nearby, frogs might attack them. It therefore seems to be a feasible assumption that the information coded by the OS of dimming detectors in the retina may be used to regulate the behavior of frogs.

**References**

