DYNAMICS OF SECOND-ORDER NEURONS OF COCKROACH OCELLI

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ABSTRACT

The incremental responses from second-order ocellar neurons of the cockroach, Periplaneta americana, were measured. The responses consisted of two components, graded potentials and spikes.

Dynamics of the graded potential responses were studied using white-noise-modulated light with various mean illuminances. I found that (a) white-noise-evoked responses were linear, (b) the responses were an exact Weber function, that is the contrast sensitivity remained unchanged over a mean illuminance range of 4 log units, and (c) the dynamics of the responses remained unchanged over the same range of the mean illuminance. I conclude that (a) the graded potentials linearly encode contrast of fluctuation inputs and (b) the signal processing in the cockroach ocellus is different from that in other visual systems, including vertebrate retinas and insect compound eyes, in which the system's dynamics depend on the mean illuminance.

The dynamic relationship between graded potentials and spikes of second-order neurons was studied using sinusoidally-modulated light with various mean illuminances. A solitary spike was generated at the depolarizing phase of the modulation response. Analysis of the relationship between the amplitude/frequency of voltage modulation and the rate of spike generation showed that (a) the spike initiation process was bandpass at about 0.5-5 Hz, (b) the process contained a dynamic linearity and a static non-linearity, (c) the spike threshold at optimal frequencies (0.5-5 Hz) remained unchanged over a mean illuminance range of 3.6 log units. I conclude that (a) the spikes of second-order neurons encode decremental inputs whose contrast exceeded a fixed level, (b) the spike initiation process may be modeled by an integrate-and-fire generator and (c) the role of ocellar second-order neurons is to produce two kinds of signals, linear (graded) signals and nonlinear (spike) signals.
INTRODUCTION

Much knowledge has been accumulated about signal processing in visual systems, but we are still far from the full understanding of it. An approach to elucidate the visual processing is to analyze the relationship between the light input and the resulting responses of visual neurons. White-noise and sine-wave analysis, the most powerful means to analyze such input/output relationship, have been applied to neurons of vertebrate retinas (e.g., Victor and Shapley, 1979; Naka et al., 1979, 1987) and of insect compound eyes (e.g., Pinter, 1972; French and Jarvilehto, 1978). These analyses provided fruitful results but also showed a difficulty in understanding these complex visual systems.

One of the practical ways to overcome this difficulty is to examine simple visual systems, like cockroach ocellus, in which information processing is limited. Consider that the photic inputs which animals receive consist of three parameters, i.e., spatial, spectral and temporal parameters, and thus, the visual systems analyze these parameters to subtract some features of the external world. In cockroach ocellus, the photoreceptors consist of a single spectral type (green receptors; Goldsmith and Ruck, 1958), and all of the second-order neurons have identical receptive field (Mizunami et al., 1982). Therefore, the ocellus analyzes neither color nor spatial information, or more strictly, changes of color or spatial distribution of the light stimulus are translated into temporal changes of the stimulus intensity. The simplicity of the cockroach ocellus allows us to concentrate on the problem: how does the system process temporal changes of stimulus intensity?

This report summarizes my works on the dynamics of incremental responses of cockroach ocellar second-order neurons. White-noise-modulated or sinusoidally-modulated light was used to analyze the responses. The responses consisted of two components, slow potential and spikes. I first describe dynamics of the slow potential response, and then discuss the dynamic relationship between the slow potential and spikes.

MATERIALS AND METHODS

Preparation, stimulus and recording

Adult males of the cockroach, Periplaneta americana, were studied. The whole animal was mounted, dorsal side up, on a Lucite stage and fixed with bee's wax. The compound eyes and one of two ocelli were shielded from light by bee's wax mixed with carbon black. The dorsal part of the head capsule was removed and the dorsal surface of the brain was exposed.

Intracellular recordings were made from large ocellar second-order neurons, L-neurons, using glass microelectrodes filled with 2 M potassium acetate. The recordings were made in the ocellar nerve, to measure the dynamics of the slow potential response. Since the spikes of the L-neurons initiate in the ocellar tract of the brain (Mizunami et al., 1987), the recordings were made in the ocellar tract to measure the relationship between the slow potential and spikes. Stable recordings of over 60 minutes were feasible. These neurons were identified to be L-neurons, following criteria described previously (Mizunami et al., 1987).

A light emitting diode, LED, was used as a light source. The LED had a spectral peak at 560 nm. The LED was driven by a sinusoidal or white-