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Efferent Control in the Anterior Lateral Eyes of Orb Weaving Spiders

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ABSTRACT—The anterior lateral (AL) eyes of the orb weaving spiders, *Argiope amoena* and *A. bruennichii*, have a single type of receptor cell with a maximum sensitivity at about 520–540 nm. Efferent optic nerve signals control the photoreceptor response in the AL eyes. Specifically, efferent signals decrease the threshold for light responses and change the waveform of responses. Similar changes in the threshold and waveform could be produced by exogenous application of octopamine, suggesting that it is an efferent neurotransmitter.

INTRODUCTION

The presence of efferent optic nerve fibers which control circadian sensitivity changes in the eye has been reported for *Limulus*, scorpions and spiders, and are reviewed by Fleissner and Fleissner [5] and by Barlow *et al.* [1]. In these eyes, efferent input to the retina is generated by an endogenous circadian clock located in the brain and enhances the retinal sensitivity. In *Limulus* and scorpion eyes, there is substantial evidence that octopamine is a neurotransmitter in the efferent fibers [1, 3, 5, 8, 9, 12]. Yamashita and Tateda [19] showed that efferent fibers in the optic nerve modulate the properties of photoreceptor cells in the anterior median (AM) eyes of orb weaving spiders, *Argiope amoena* and *A. bruennichii*. Efferent neurotransmitter in spider eyes has yet to be examined.

The anterior lateral (AL) eye of *Argiope* is the smallest among the four pairs of the eyes [14]. In preliminary experiments, we observed that circadian sensitivity changes of the AL eye occur synchronously with that of the AM eye. In the present study, we examined the effects of efferent optic nerve signals and the exogenous application of octopamine on the photoreceptor response of AL eyes.

MATERIALS AND METHODS

Female orb weaving spiders, *Argiope amoena* and *A. bruennichii*, were collected in open fields. Spiders were maintained on a photoperiod of 12 hr light (4:00–16:00 hr or 6:00–18:00 hr) and 12 hr darkness for a few days. Preparation and recording methods were similar to those described previously [18]. For electrical recordings from the AL eye *in situ*, the part of the chamber, that containing the cephalothorax, was filled with physiological saline. A small portion of the dorsal cuticle of the cephalothorax was removed with a sharp razor blade, exposing the optic nerve and retinal area. The physiological saline contained: NaCl, 217 mM; KCl, 5 mM; $MgCl_2$, 1.1 mM; $CaCl_2$, 4 mM and $NaHCO_3$, 3 mM [11]. To apply octopamine, the physiological saline in the chamber was replaced with saline containing 100 μM octopamine. The octopamine saline was made by adding DL-octopamine HCl to the physiological saline on the day of experiments. Intracellular photoreceptor potentials were recorded using glass pipette microelectrodes, and extracellular receptor potentials, electroretinograms (ERGs), were recorded by glass pipette microelectrodes or suction electrodes. A tungsten electrode was inserted into the eye to record ERGs from intact animals. The light emitted by a Xenon arc lamp was delivered to the eye *via* a quartz light guide 0.2 mm in diameter positioned in front of the corneal lens. The duration of illumination was controlled by an electromagnetic shutter and the intensity was adjusted by calibrated neutral density filters and wedges. Monochromatic light beams were produced with interference filters. The energy of the selected monochromatic lights was measured by a radiometer. The unit intensity (log I=0) of monochromatic lights at the output of the light guide corresponds to about 10^{14} quanta/cm^2/sec. For electrical stimulation, the distal cut end of the optic nerve was sucked into a suction electrode.

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RESULTS

Circadian change in photoreceptor response

For recording ERGs from intact animals (Figs. 1–4), animals were prepared in the morning of the first day of the experiment and maintained under background illumination. After ending the background illumination at 16:00 hr on the first day, ERGs were recorded under constant darkness between 8:00 hr and 12:00 hr (daytime) and between 18:00 hr and 22:00 hr (nighttime) on the second, or the second and third days. Figure 1 shows daytime and nighttime ERGs to 540 nm light of 50 msec duration at various intensities recorded from the dark-adapted AL eye of an intact animal. Both for the daytime and nighttime ERGs, the latency, which is the time from the onset of light stimulus until the ERG response departs from the baseline, decreased with increasing stimulus intensity. The daytime and nighttime ERGs differ remarkably in both amplitude and waveform. In this experiment, the response amplitude was defined as the potential difference between the baseline and the maximum of each response. At low levels of illumination, nighttime ERGs were always larger than daytime ERGs (e.g. at log I=−4 in

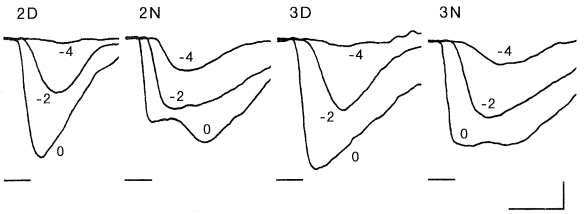

FIG. 1. Daytime and nighttime ERGs to 540 nm light stimuli of 50 msec duration at various intensities obtained from the dark-adapted AL eye of an intact animal during the day (8:00–12:00 hr) and at night (18:00–22:00 hr) for two days. The intensity is indicated for each ERG in log units. Horizontal bars indicate 50 msec light stimuli. 2D, second day; 2N, second night; 3D, third day; 3N, third night. Calibrations: 0.1 mV, 0.1 sec.

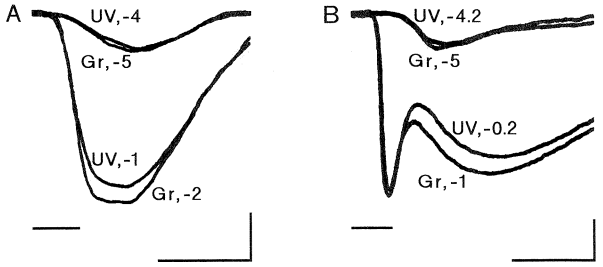

FIG. 3. Nighttime ERGs to 540 nm (Gr) of log I = −2 and −5, and to 360 nm (UV) of log I = −1 and −4 for A, and those to 540 nm of log I = −1 and −5, and to 360 nm of log I = −0.2 and −4.2 for B. A and B were obtained from different preparations. Calibrations: (A) 100 μV, 0.1 sec; (B) 50 μV, 0.1 sec.

Fig. 1), indicating that the ERG threshold decreased at night. On the other hand, at high levels of illumination, nighttime ERGs showed two peaks or trapezoidal waveforms, and were often smaller than daytime ERGs (e.g. at log I=0 in Fig. 1). Prominent two peaks or trapezoidal waveforms (cf. Figs. 1 and 3) were recorded from the dark-adapted eye. In contrast, ERGs recorded from light-adapted eyes often showed a single peak. After a bright light stimulation (e.g. Log I=0 of 50 msec duration), more than 10–15 min was required for the ERG waveform to recover to the dark-adapted level. The intensity-response relations for nighttime and daytime ERGs are shown in Figure 2. In this figure, for convenience, the ERG amplitude at maximum intensity (log I=0.67) for each curve was referred to as 1.0. The threshold intensity for nighttime ERG was about 1–2 log units lower than that for daytime ERG.

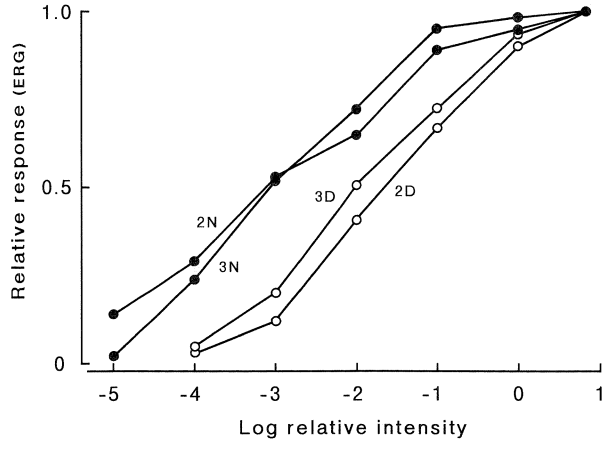

FIG. 2. Intensity-response relations for nighttime (closed circles) and daytime (open circles) ERGs. The same preparation as Fig. 1. The maximum value for each intensity-response curve is set at 1.0. 2D, second day; 2N; second night; 3D, third day; 3N, third night.

The ERGs of similar waveforms were produced by every wavelength of monochromatic light if the stimulus intensity was adjusted properly, i.e. the ERG waveform was not dependent upon the stimulus wavelength. Two examples for nighttime ERGs are shown in Figure 3. The ERG waveforms for 540 nm of log I = −2 (Gr, −2) and 360 nm of log I = −1 (UV, −1), and (Gr, −5) and (UV, −4) in Figure 3A, and those for (Gr, −1) and (UV, −0.2), and (Gr, −5) and (UV, −4.2) in Figure 3B are very similar, respectively. These observations suggest that the AL eye has a single type of visual pigment.

Spectral sensitivity

The spectral sensitivity of dark-adapted AL eyes was examined by recording intracellular and extracellular receptor potentials. In fifteen cells, intracellular receptor potentials to 360, 480, 540 and 580 nm light stimuli of 50 msec duration at equal quanta were recorded between 10:00 hr and 14:00 hr. Light stimulation elicited a depolarizing receptor potential [17]. Waveforms of intracellular responses were similar to those of daytime ERGs shown in Figure 1. All fifteen cells showed a maximum response at 540 nm. In five of these cells, the intensity-response curves were determined at 540 nm. Spectral sensitivities were calculated assuming that the intensity-response curves for various wavelengths are all parallel to that for 540 nm. The average spectral sensitivities of these cells are shown in Figure 4 together with the mean spectral sensitivity curve determined

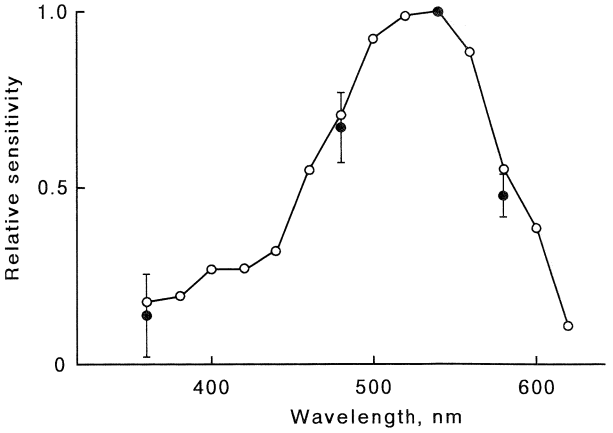

FIG. 4. Average spectral sensitivities at 360, 480, 540 and 580 nm for five receptor cells (closed circles) and the mean ERG spectral sensitivity curve obtained from three spiders (open circles). The sensitivities are referred to as 1.0 at 540 nm. Vertical lines indicate the standard deviation.

by the ERGs recorded from three intact spiders during the day and at night. We could not find any significant difference between the daytime and nighttime ERG spectral sensitivity curves. The sensitivities at four wavelengths for the intracellular potentials approximately fit the mean ERG spectral sensitivity curve, which had a single peak at 520–540 nm (Fig. 4). Chromatic light adaptation with 360, 480, 540 or 580 nm background light did not change the form of the ERG spectral sensitivity curve. Therefore, we conclude that the AL eye contains a single type of visual pigment.

Electrical stimulation of the optic nerve

To examine the effect of efferent signals on the ERG, current pulses at 2/sec were applied to the distal end of the cut ocellar nerve during the day for about thirty minutes. The ERG amplitude at a low intensity continued to increase gradually, at least, for thirty minutes. After the cessation of electrical stimulation, the ERG amplitude decreased gradually for about 60 min until a low value was reached again. The course of change in the ERG amplitude for the AL eye was similar to that for the AM eye reported by Yamashita and Tateda [19]. Figure 5 shows ERGs at various intensities recorded before and just after the cessation of current pulses for 30 min. After electrical stimulation, the ERG amplitude at a low intensity (log I=−4) increased, i.e. the ERG threshold decreased, and the response at a high intensity (log I=0) showed two peaks. The ERG threshold and waveform obtained before and after electrical stimulation are characteristic of those obtained from the intact eye during the day and at night, respectively (cf. Fig. 1), showing that the circadian change in the ERG of the AL eye is mediated by efferent signals in the optic nerve.

Effects of octopamine

Octopamine application during the day produced effects on the ERG similar to endogenous efferent activity. After the application of octopamine (100 μM), the ERG amplitude at a low intensity increased over a period of thirty minutes to a maximum plateau value. Figure 6 shows ERGs at various intensities recorded before and about thirty minutes after octopamine application. After octopamine application, the ERG amplitude at a low intensity (log I=−4) increased, i.e. the ERG threshold decreased, and the response at a high intensity (log I=0) showed two peaks. The ERG intensity-response curves obtained before and 60–90 min after octopamine application are shown in Figure 7. After octopamine application, the ERG threshold decreased by about 2 log units. In contrast, when the ERG showed nighttime characteristics with endogenous efferent signals, exogenous application of octopamine had a little or no effect on either the ERG threshold or ERG waveform. These observations suggest that octopamine is an efferent neurotransmitter, as reported for *Limulus* and scorpion eyes.

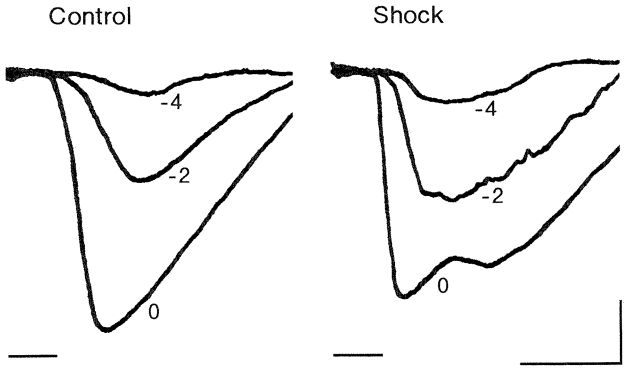

FIG. 5. ERGs to white light stimuli of 50 msec duration at various intensities recorded during the day before (Control) and just after the cessation of electrical stimulation (Shock) of the distal end of the cut optic nerve at 2 Hz for 30 min. The spider was kept in the dark for about two hours before the start of electrical stimulation. Calibrations: 50 μV, 0.1 sec.

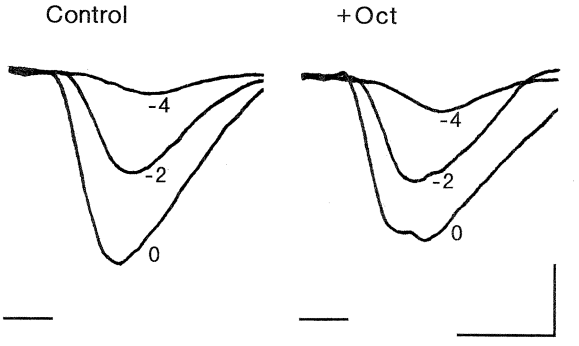

FIG. 6. ERGs to white light of 50 msec at various intensities recorded during the day before (Control) and about 30 min after (+Oct) the presence of exogenous octopamine (100 μM). The optic nerve was severed between the eye and the brain. The spider was kept in the dark for about two hours before the start of octopamine application. Calibrations: 100 μV, 0.1 sec.

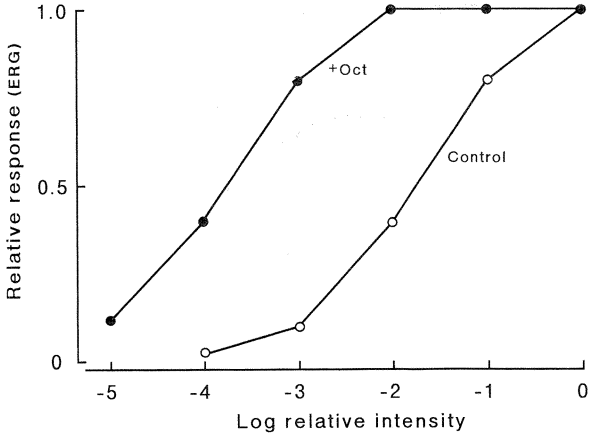

FIG. 7. Normalized ERG intensity-response curves obtained from the eye with cut optic nerve before (Control) and 60–90 min after (+Oct) the presence of exogenous octopamine (100 μM). The optic nerve was severed between the eye and the brain. The spider was kept in the dark for about two hours before the start of octopamine application. The maximum value for each curve is set at 1.0.

DISCUSSION

In *Limulus* and scorpion eyes, octopamine induced changes in photoreceptor responses that mimicked those generated by efferent optic nerve signals [1, 5, 7] . As shown in the present study, octopamine also mimicked the efferent actions on photoreceptor responses in the AL eye of *Argiope*. Octopamine may be a common neurotransmitter in the efferent optic nerve fibers in these various animals.

The AM eye of *Argiope*, which is referred to as the principal eye, contains 400 to 500 photoreceptor cells [13]. Yamashita and Tateda [18] reported that the AM eye has three types of receptor cells, with maximum sensitivities at about 360 nm (u.v. cell), 480–500 nm (blue cell) and 540 nm (green cell). In contrast, the AL eye contains only 40 to 60 receptor cells [14]. As shown in the present study, the AL eye has a single spectral type of receptor cell. Therefore, it seems unlikely that the AL eye is capable of color discrimination.

As shown in the present study, ERGs at high intensities recorded from the dark-adapted eye at night show two peaks or trapezoidal waveforms (cf. Figs. 1 and 3). In preliminary experiments, we observed that when ERGs showed two peaks or trapezoidal waveforms, intracellular responses also showed two peaks or trapezoidal waveforms. An example is shown in Figure 8. In this figure, intracellular and ERG responses to white light of 50 msec duration were recorded simultaneously at night. Both responses show similar trapezoidal shapes characteristic of nighttime response. In addition, the ERG latency decreased with increasing stimulus intensity (cf. Fig. 1). These observations suggest that photoreceptors in the AL eye have, at least, two factors which contribute to the two peaks or trapezoidal waveforms, and to the change in the latency. It has been reported that the ventral photoreceptors of *Limulus*, which are controlled by efferent fibers, have various factors. For examples, ventral photoreceptors contain both light-activated and voltage-sensitive conductances [4]. Payne and Fein [10] showed that the light response of the dark-adapted ventral photoreceptors is not linear with flash intensity, and proposed a model of transduction in which light activates two parallel cascade reactions. Johnson *et al.* [6] reported that two sizes of single-channel events (40 and 15-pS events) are seen during the illumination of ventral photoreceptors and concluded that these events are due to different conductance states of the same channel. Photoreceptors of the locust *Schistocerca* have voltage activated transient and sustained potassium currents which modify the frequency response of the membrane and suppress the amplitude of light-induced depolarizations [15, 16]. The transient and sustained currents are prominent in the day and at night, respectively [2]. 5-Hydroxytryptamine could drive the potassium conductance from the day to the night state [2]. In the AL eye of *Argiope*, some of these factors may be present, but we did not examine this point in the present study.

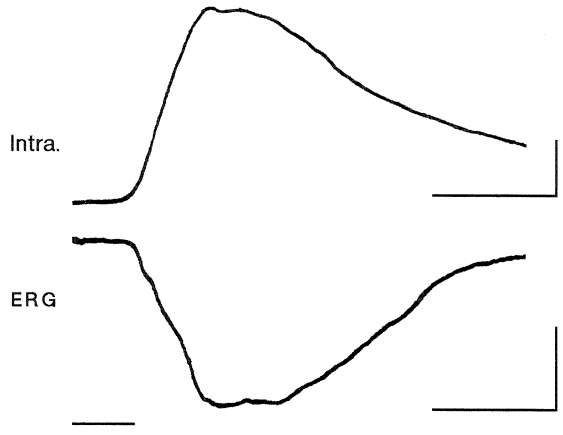

FIG. 8. Intracellular (Intra.) and ERG responses to white light of 50 msec duration at log I=0 recorded simultaneously at night. Calibrations: (Intra.) 5 mV, 0.1 sec; (ERG) 0.5 mV, 0.1 sec.

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