Decrease in K⁺ conductance underlying a depolarizing photoresponse of a molluscan extraocular photoreceptor

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Summary. An identified neurone in the Onchidium abdominal ganglion responds to light with a depolarizing generator potential, so that this neurone functions as an extraocular photoreceptor. The light-evoked depolarizing response is produced by a selective decrease in K⁺ conductance.

Key words. Molluscan extraocular photoreceptor; depolarizing photoresponse; decrease in K⁺ permeability.

The hyperpolarizing photoresponse of most vertebrate ocular photoreceptors is produced by a decrease in membrane conductance to Na⁺ ions. This contrasts with the invertebrates studied to date, in which the hyperpolarizing or depolarizing response to light is associated with an increase in conductance to Na⁺ and K⁺ ions. Thus, a photoreceptor potential produced by a de-
crease in membrane conductance was not thought to occur in any invertebrate photoreceptor system. However, I have found that an identified photosensitive neurone (extraocular photoreceptor) in the ganglion of the marine gastropod mollusc Onchidium responds to light with a graded depolarizing receptor potential which is due to a light-evoked decrease in K⁺ conductance.

Materials and methods. The experiments were carried out on an identified neurone of the circumesophageal ganglion of Onchidium verruculatum. The photosensitive neurone identified as an extraocular photoreceptor in this study lies dorsally on the right upper quadrant of the abdominal ganglion, and has a relatively small spherical soma which is 80 μm or less in diameter. Thus, this neurone, designated as A-P-1, is distinct from the other giant photosensitive neurones (200-300 μm in diameter) which have been previously demonstrated in the same Onchidium ganglia.

The ganglia were placed in a 1 ml bath, and perfused with saline containing 450 mM NaCl, 10 mM KCl, 10 mM CaCl₂, 50 mM MgCl₂, 10 mM tris-hydroxymethylaminomethane (THAM)-HCl adjusted to pH 7.8. Variations in external K⁺ were made by adding or omitting KCl. Low Na⁺ or Ca²⁺ solutions were made by replacing Na⁺ or Ca²⁺ with THAM or Mg²⁺, respectively. Isethionate salts were used as Cl⁻ substitutes. All solutions were kept at the same temperature of 21-23°C. For intracellular recording, one or two single microelectrodes filled with 2.5 M KCl were inserted into the A-P-1. Current was applied to the cell through the second electrode, and a bridge circuit was used when a single electrode served both for applying current and for recording. White or monochromatic light from a tungsten quartz-tube source was used for photostimulation. The intensity of light stimulus was controlled by neutral density filters and the radiant energy flux was measured at the level of the preparation with a radiometer.

Results and discussion. The resting potential of A-P-1 was -45 to -55 mV, and the input resistance at these potentials was 15-20 MΩ. Some properties of the photoreceptor in an A-P-1 are shown in figure 1. White light stimulation, 30 s in duration, evoked a depolarizing generator (receptor) potential (fig. 1A). The amplitude of the depolarization was graded with the intensity of the light, and with brighter lights, spikes were superimposed on the graded depolarization (fig. 1B). The latency of onset of the light response was in the range of 300–500 ms, and usually it decreased with increasing light intensity. Membrane conductance changes during the photoresponse were studied by measuring the voltage drop produced by short (1s) hyperpolarizing constant current pulses. As shown in figure 1C, membrane conductance decreased during the depolarizing response to the same light stimulation as in figure 1A. In the dark, a slow depolarization of the membrane was seen nearly the peak value obtained during the photoresponse produced no significant changes in membrane input resistance (fig. 1D).

The possibility that these photoresponses are due to light-evoked synaptic transmission through a presynaptic neurone was ruled out in the following ways. Exposure to the high Mg²⁺ saline containing 4 times the normal level of Mg²⁺, which blocks synaptic transmission, had no significant effect on the response to light. Furthermore, the depolarization in response to light was maintained in the A-P-1 soma completely isolated from the ganglion by microdissection.

Monochromatic light also produced a slow depolarizing response in A-P-1 similar to that evoked by white light, and the waveforms of responses to any two monochromatic lights were identical when the light intensities were adjusted to give responses of equal amplitude. The spectral sensitivity (the reciprocal of the number of quanta at each wavelength which elicits a constant response), obtained from three experiments, had a peak at light of 490 nm in the range of 350 to 800 nm. These results suggest that a single intracellular photopigment is involved in the depolarizing photoresponse of A-P-1.

A series of experiments (figs 2 and 3) were performed to investigate the ionic species involved in the light-evoked membrane conductance decrease. When a constant light stimulus of 490 nm was presented at 5-min intervals to the dark-adapted A-P-1, a response of appropriate amplitude was reproducibly obtained under equal conditions of the resting potential and the external ionic composition. However, the light-evoked response was markedly altered by changing membrane potential levels by...