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SHORT COMMUNICATION

SYNAPTIC TRANSMISSION BETWEEN SECOND- AND THIRD-ORDER NEURONES OF COCKROACH OCELLI

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The insect ocellus contains a large number of photoreceptors which converge on a small number of large second-order neurones, called L neurones. The L neurones exit from the ocellus and project into the ocellar tract of the brain, where they make synapses with third-order neurones (reviewed by Goodman, 1981). Response characteristics of L neurones have been well documented (Goodman, 1981; Mizunami *et al.* 1986), but less is known about ocellar third-order neurones. In locusts, three types of ocellar third-order neurones, which descend to the thoracic ganglia, have been found (Simmons, 1980, 1981; Reichert *et al.* 1985), and the transmission characteristics between L neurones and some of these descending neurones have been documented (Simmons, 1981). In the present paper, we examine whether the transmission characteristics reported by Simmons (1981) are specific to descending ocellar third-order neurones or are generally applicable to a variety of ocellar third-order neurones, including those terminating within the brain. Experiments were made on cockroaches, *Periplaneta americana*.

The ocellar tract of the cockroach contains axons of four L neurones (Mizunami *et al.* 1982) and arborizations of nine types of ocellar-driven neurones. The ocellar-driven neurones, which we term third-order neurones, comprise five types which project into the posterior slope of the protocerebrum (PS-I, -II, -III, -IV and -V neurones), two types projecting into the optic lobe (OL-I and -II neurones) and two types descending to the thoracic ganglia (D-I and -II neurones; Mizunami & Tateda, 1986). We inserted two electrodes into the ocellar tract to record simultaneously the potentials of an L neurone and a third-order neurone, and then fill the neurones with Lucifer Yellow or cobalt ions.

Both L neurones and PS-I neurones hyperpolarized in response to an ocellar illumination (insets in Fig. 1A): synaptic transmission between them was non-inverting. At the off-set of illumination, the L neurone generated spikes, usually once, and the PS-I neurone generated a corresponding transient depolarization. The transient depolarization appeared to consist of postsynaptic potentials (PSPs), produced by the spikes of L neurones, but it may also have contained regenerative components produced by PSPs. Similar tonic on-hyperpolarizations and transient off-depolarizations were observed from all nine types of third-order neurones.

Key words: synaptic transmission, ocelli, cockroaches.

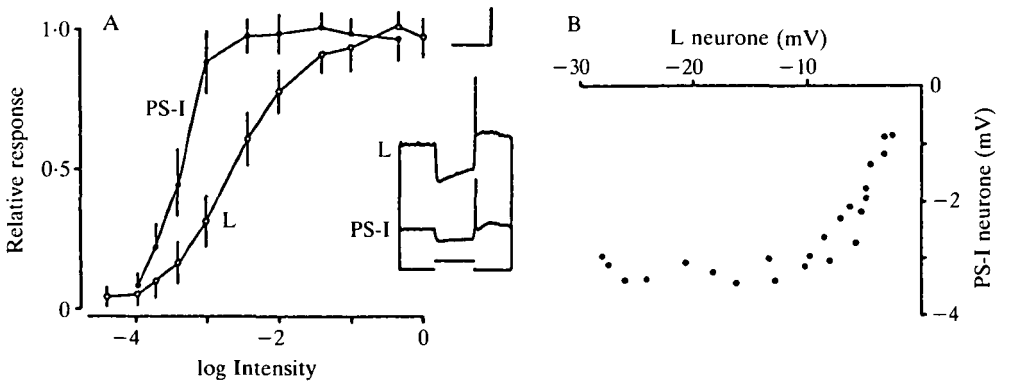

Fig. 1. (A) Peak amplitudes of hyperpolarizing responses of an L neurone and a PS-I neurone, recorded simultaneously, are plotted against the logarithm of stimulus light intensity. An ocellus was illuminated by a light-emitting diode. The other ocellus and compound eyes were light-sealed with beeswax mixed with carbon black. Amplitudes of responses are normalized to the maximal value. Averages of four or five measurements are shown with the standard deviations. The light intensity at 0 log unit is 3 lx. Insets: typical recordings from an L neurone and a PS-I neurone. The light intensity is −2 log units. Calibration: 20 mV for L neurone and 10 mV for PS-I neurone, 0·5 s. (B) Peak amplitude of responses of a PS-I neurone plotted against that of an L neurone.

The peak amplitudes of the hyperpolarizing responses of an L neurone and a PS-I neurone were plotted against the logarithm of the stimulus intensity (Fig. 1A). The dynamic range of the PS-I neurone was much narrower than that of the L neurone. Fig. 1B shows the peak amplitude of the hyperpolarizing response of a PS-I neurone plotted against that of an L neurone. The amplitude of the hyperpolarizing response of the PS-I neurone did not increase with an increase in the hyperpolarizing response of the L neurone above 10 mV. A similar saturation of responses was detected from all other third-order neurones, by simultaneous recordings with L neurones (PS-II, D-I and D-II neurones) or by comparing responses recorded in different preparations. Simmons (1981) observed a similar saturation of hyperpolarizing responses from descending third-order neurones of locust ocelli.

At the off-set of a hyperpolarizing current pulse applied to an L neurone, a spike was evoked in that cell, followed by a transient depolarization in a PS-I neurone (Fig. 2A). The time-course of the transient postsynaptic depolarization was slower than that of the presynaptic spike (Fig. 2B), possibly due to the time constant of the postsynaptic neurone. We measured the delay between the start of the presynaptic spike and the postsynaptic depolarization. The averaged delay of five repeated measurements from the preparation shown in Fig. 2 was $1{\cdot}7 \pm 0{\cdot}1$ ms. In other records of an L neurone and a PS-I neurone, there was a delay of $1{\cdot}4 \pm 0{\cdot}2$ ms ($N = 4$). Similar synaptic delays (1–2 ms) were measured between L neurones and some other third-order neurones: namely a PS-II neurone, an OL-I

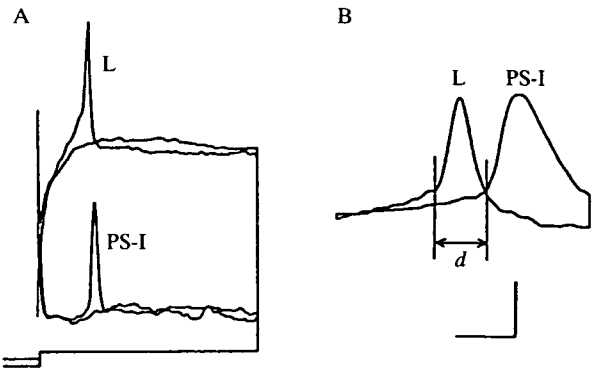

Fig. 2. (A) At the off-set of a hyperpolarizing current pulse of 2 nA applied to an L neurone, a spike is evoked in the L neurone, which is followed by a transient depolarization of a PS-I neurone. Hyperpolarizing constant-current pulses of 1 and 2 nA, 0·5 s, were applied through the recording electrode connected to bridge circuits. (B) Recordings in A are shown on a shorter time scale, for the measurement of synaptic delay (*d*). Calibration: 10 mV for L neurone and 6 mV for PS-I neurone, 10 ms (A) and 2 ms (B).

neurone, two D-I neurones and a D-II neurone. These results suggest that the synapses are chemical and monosynaptic. Care must be taken when considering whether the transmission is monosynaptic based on the synaptic delay, because there is the possibility that electrical connections are interposed. This possibility seems unlikely in the present study because electrical synapses, i.e. gap junctions, are not observed among neurones in the ocellar tract of the cockroach (Toh & Hara, 1984).

The synaptic delay measured in this study was slightly shorter than that noted by Simmons (1981) between L neurones and third-order neurones of locust ocelli (2·5–3 ms). The difference may be because Simmons measured the delay between slowly rising pre- and postsynaptic potentials, whereas we measured the delay between rapidly rising pre- and postsynaptic potentials. Burrows & Siegler (1978) observed that the measured delay was shorter when the rate of rise of the pre- and postsynaptic potential change was larger, at synapses between non-spiking interneurones and motoneurones of locust thoracic ganglia. In addition, Simmons recorded synaptic potentials in the cell body, so the longer delay may have resulted from signal attenuation due to passive propagation.

The hyperpolarizing response of a PS-I neurone was accompanied by an increase in membrane resistance of about 0·3–0·5 MΩ (Fig. 3A). Similar resistance increases during hyperpolarizing responses were observed from a D-I neurone and a PS-II neurone. These resistance increases are comparable with an increase of 0·1 MΩ at the cell body of locust third-order neurones, which should be somewhat less than the change in the synaptic region (Simmons, 1981). When a PS-I neurone was hyperpolarized by steady extrinsic currents, the amplitudes of both on-hyperpolarizing and off-depolarizing responses increased (Fig. 3B).

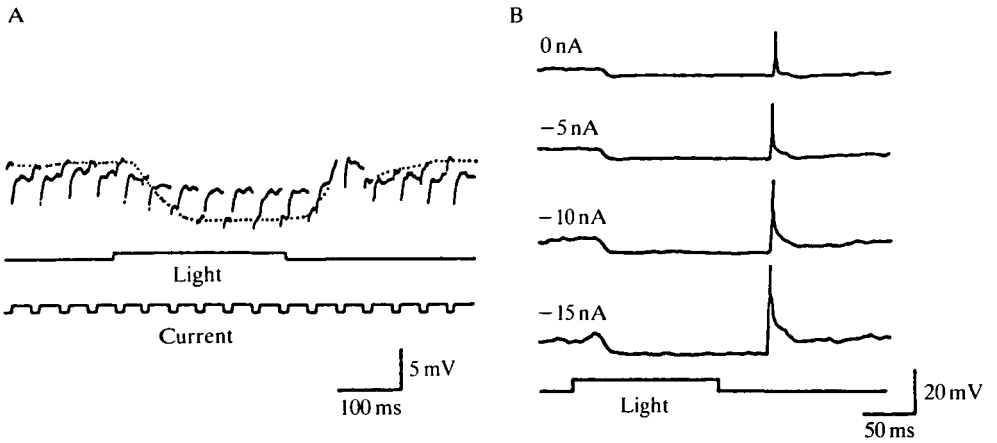

Fig. 3. (A) Changes in membrane resistance of a PS-I neurone during a hyperpolarizing response, measured by brief extrinsic hyperpolarizing currents. Potentials during current pulses were bridge-balanced. (B) Change of the response of a PS-I neurone caused by the injection of steady hyperpolarizing currents. Light intensities in A and B are 0·3 lx.

Similar effects of steady hyperpolarizing currents were observed in a PS-II neurone and in a D-I neurone. The results indicate that the equilibrium potential of the synaptic input is more positive than the normal resting potential, as in the case of locust descending third-order neurones (Simmons, 1981).

We conclude that L neurones make excitatory synapses with a variety of third-order neurones. The excitatory transmission is tonically maintained under normal resting potentials, so that hyperpolarizing responses of L neurones produce hyperpolarizations in third-order neurones. Because a fairly strong light stimulus brings the potential of L neurones negative to the threshold of transmission, the range of light intensities coded by a variety of third-order neurones is much compressed. These characteristics are similar to those of the synapse between L neurones and descending third-order neurones of locust ocelli (Simmons, 1981), suggesting that these are common characteristics of the synapse between second- and third-order neurones of insect ocelli. It would also be interesting to see if similar characteristics were in operation in third-order neurones of insect compound eyes, since photoreceptors and second-order neurones, at least, show similar properties in the two systems (Laughlin & Hardie, 1978; Laughlin, 1981).

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