

## CLASSIFICATION OF OCELLAR INTERNEURONES IN THE COCKROACH BRAIN

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### SUMMARY

Nine types of ocellar interneurons with arborizations in the ocellar tract have been identified in the cockroach, *Periplaneta americana*. These neurones are classified into (1) five types of 'PS-neurone', which project into the posterior slope, (2) two types of 'OL-neurone', which project into the lobula and medulla of the optic lobe, and (3) two types of 'D-neurone', which descend to the thoracic ganglia. When recordings were made in the ocellar tract, all types of neurones exhibited similar responses: a tonic hyperpolarization during illumination and one or a few transient depolarizations at the end of illumination. However, these neurones are classified into several physiological types from the responses recorded in their axons or terminal regions.

### INTRODUCTION

The cockroach has two ocelli and each ocellus contains about 10 000 photoreceptor cells, which converge on four large, second-order neurones (L-neurones) (Weber & Renner, 1976). There are apparently no differences among the four L-neurones, with regard to anatomy and response properties: all L-neurones have an ocellar arborization covering the entire region of the ocellar neuropile and project into the ipsilateral ocellar tract of the protocerebrum; and all of them exhibit light on-hyperpolarization and a few off-spikes (Mizunami, Yamashita & Tateda, 1982). Ocellar L-neurones have been well studied in various insects (Wilson, 1978*a,b*; review by Goodman, 1981; Milde, 1981, 1984; Milde & Homberg, 1984).

In locusts, a few third-order neurones have been found, and the mechanism of synaptic transmission between L-neurones and third-order neurones has been studied (Simmons, 1980, 1981, 1982). To further understand how ocellar signals are processed in the brain of insects, we recorded from and stained a number of neurones in the ocellar tracts, areas in which L-neurones terminate, in cockroaches. We now report the anatomy and response of nine ocellar interneurons of the cockroach brain.

Key words: ocelli, interneurons, cockroaches.

## MATERIALS AND METHODS

All experiments were performed on adult male cockroaches, *Periplaneta americana*, reared in the laboratory.

The insect was mounted, dorsal side up, on a Lucite stage. The dorsal surface of the head capsule was removed, and the brain was exposed by removing the jaw muscles. The oesophagus was excised and the brain was stabilized by inserting a glass rod into the oesophageal foramen. Care was taken not to disturb the tracheal system. In most experiments, a 1% solution of pronase type IV in cockroach saline (Yamasaki & Narahashi, 1959) was applied to the brain for 2 min, to facilitate insertion of the electrodes.

Glass capillary microelectrodes, filled with a solution containing  $2.5 \text{ mol l}^{-1}$  KCl and  $0.5 \text{ mol l}^{-1}$   $\text{CoCl}_2$ , were used for all intracellular recordings. The electrodes had a d.c. resistance of 50–100 M $\Omega$  and were inserted into the ocellar tracts or the posterior slopes of the protocerebrum.

After cessation of recordings, the neurones were filled with  $\text{Co}^{2+}$  by iontophoresis, *via* the recording electrodes. The injected brains were dissected out, fixed in Carnoy's solution, and intensified as whole mounts (Bacon & Altman, 1977). After the whole mount observations, some preparations were embedded in Epon 812, sectioned at 12  $\mu\text{m}$ , and stained with toluidine blue for light microscopy.

Each ocellus was illuminated separately by a green light-emitting diode positioned near the ocellus. Light was restricted to the ocellus with a short light guide, and the light intensity was adjusted by calibrated neutral density filters. Light flashes of 0.2–0.3 s were delivered at intervals of about 10 s.

## RESULTS

Recordings and cobalt injections were made for 95 ocellar interneurons which have branches in the ocellar tracts of the cockroach brain. We classified 79 of these neurones into: (1) five types of 'PS-neurone' (PS-I–PS-V), which project into the posterior slope neuropiles of the protocerebrum, (2) two types of 'OL-neurone' (OL-I–OL-II), which project into the optic lobes, and (3) two types of 'D neurone' (D-I–D-II), which descend to the thoracic ganglia. We could not classify the other 16 neurones, because the stainings were incomplete.

When recordings were made in the ocellar tract, all these neurones exhibited similar responses to illumination of the ocellus: a small tonic hyperpolarization during illumination of one or both ocelli, and one or a few large transient depolarizations at the end of illumination (Fig. 1A; Table 1). As shown in Table 1, some neurones (PS-I, II, V) exhibited tonic on-hyperpolarizing and transient off-depolarizing responses to illumination on one ocellus, some (PS-III, OL-II) exhibited tonic on- and transient off-responses to illumination of both ocelli, and the others (PS-IV, D-I, II) exhibited tonic on- and transient off-responses to illumination of one ocellus and exhibited small transient off-responses to illumination of the other ocellus. The amplitude of on-hyperpolarization increased with increasing stimulus light intensity, and then saturated (Fig. 1A). The amplitudes

of off-depolarizations varied little with the stimulus intensity. The on-hyperpolarizations and off-depolarizations of these interneurons correspond to tonic on-hyperpolarizations and off-spikes of the L-neurone (Fig. 1B, cf. Mizunami *et al.* 1982). The on-response of PS-neurons saturated at a slightly lower intensity than that of L-neurons. The off-depolarizations looked like transient PSPs, because the waveforms of off-depolarizations varied from response to response (Fig. 1C). However, they may include spike components.

Although these neurons exhibited similar responses in the ocellar tract, they were classified into several types from the responses recorded in their axons or terminal regions as described later (cf. Figs 2–6). We could not observe any responses from these neurons to sensory stimuli other than ocellar illumination: they did not respond to light stimuli applied to the compound eyes by a moving or stationary light spot or to wind stimuli applied to the head or antennae.

#### PS-I neurone

The PS-I neurone has arborizations in the ocellar tract and the proximal area of the ocellar nerve (Fig. 2A,B). The axon-like fibre runs through the ocellar tract posteriorly and enters the posterior slope. In the distal area of the ocellar tract, the

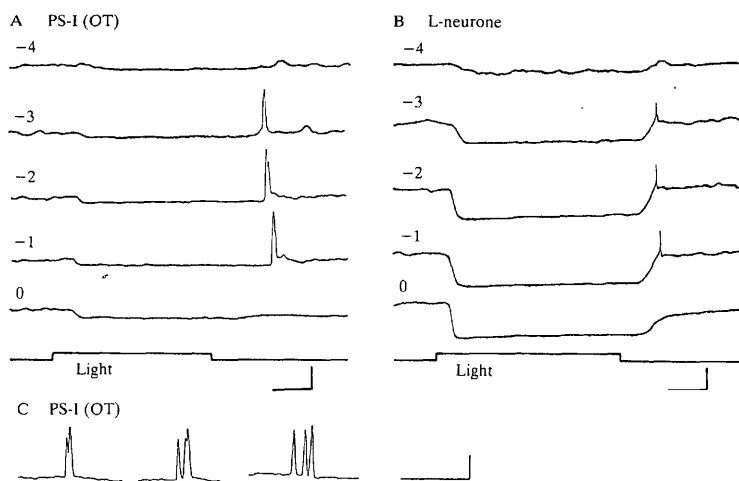


Fig. 1. Responses of ocellar interneurons recorded in the ocellar tract (OT). (A),(B) Responses of a PS-I neurone (A) and an L-neurone (B) to light stimuli of various intensities. Light was applied to the ocellus ipsilateral to its cell body location. (C) Examples of recordings from a PS-I neurone, showing the variation of waveforms of off-responses. In A and B, the light intensities are indicated to the left of each trace as  $\log_{10}$  attenuation (0 = 20 lx). In C, the light intensity is 2 lx. Calibrations: 10 mV, 50 ms.

Table 1. Responses of the ocellar interneurons recorded in the ocellar tract

Types	No. of stainings	Illumination of ocellus	Responses recorded in the ocellar tract	
			On-hyperpolarization (mV)	Off-depolarization (mV)
PS-neurones				
PS-I	19	Ipsi	3.6 ± 3.1 (7)	25 ± 7 (7)
		Cont	0 (8)	0 (8)
PS-II	7	Ipsi	0.8 ± 0.8 (4)	25 ± 6 (4)
		Cont	0 (3)	0 (3)
PS-III	14	Ipsi	1.0 ± 0.8 (3)	20 ± 10 (3)
		Cont	0.5 ± 0.9 (4)	21 ± 12 (4)
PS-IV	3	Ipsi	5 ± 1 (2)	28 ± 2 (2)
		Cont	0 (2)	1.5 ± 0.3 (2)
PS-V	6	Ipsi	3 ± 3 (2)	29 ± 1 (2)
		Cont	0 (2)	0 (2)
OL-neurones				
OL-I	5	Ipsi	?	?
		Cont	6 (1)	14 (1)
OL-II	3	Ipsi	9 ± 4 (2)	23 ± 2 (2)
		Cont	9 (1)	25 (1)
D-neurones				
D-I	7	Ipsi	1 ± 1 (3)	14 ± 2 (3)
		Cont	0 (2)	1.8 ± 1.1 (2)
D-II	15	Ipsi	1 ± 1 (5)	16 ± 2 (5)
		Cont	0 (3)	1.6 ± 0.4 (3)

The responses of the ocellar interneurons recorded in the ocellar tract consist of two components, i.e. tonic on-hyperpolarizations and transient off-depolarizations. The amplitudes of on-responses at saturated intensities (1–3 lx at the ocellus), and those of off-responses at the same intensities are presented as the mean ± s.e. of the mean with the number of recorded neurones given in parentheses. Ipsi or Cont means that the ocellus ipsilateral or contralateral to the cell body position was illuminated. The number of neurones stained either in the ocellar tract or in the posterior slope is also shown.

fibre is about 7–8 μm in diameter and becomes thicker in the proximal area of the ocellar tract and in the posterior slope (up to 10–15 μm in diameter). From this fibre, arborizations extend into the posterior slope. The cell body is located in the pars intercerebralis at the lateral side of the ocellar tract. The PS-I and L-neurones run side by side in the ocellar tract and proximal part of the ocellar nerve (Fig. 2B).

The response of the PS-I neurone recorded in the posterior slope (Fig. 2C) was similar to that recorded in the ocellar tract (cf. Fig. 1A): it exhibited a small tonic hyperpolarization during illumination of the ipsilateral ocellus and a large transient depolarization at the end of illumination. The waveforms of the off-depolarizations varied from response to response (Fig. 2D). The off-responses looked like transient PSPs, but they may include spike components.

*PS-II neurone*

The PS-II neurone has a thin (5–7  $\mu\text{m}$  diameter) axon-like fibre running posteriorly from the ocellar tract to the posterior slope (Fig. 3A). There are arborizations in the ocellar tract and in the posterior slope. The cell body is located in the anterior part of the pars intercerebralis. In the posterior slope, the PS-II neurone exhibited transient depolarizations when the light directed to the ipsilateral ocellus was turned off (Fig. 3B). The neurone exhibited an on-hyperpolarization in the ocellar tract (Fig. 1A), but not in the posterior slope.

*PS-III neurone*

The PS-III neurone has four branches which diverge in an X-shape from a point on the midline of the brain. Each branch enters the ocellar tract or the posterior slope of either side, and extensive arborizations were evident in these regions (Fig. 3C). The branches are thick, especially near the midline of the brain (15–20  $\mu\text{m}$  diameter). The cell body is located in the anterior part of the pars intercerebralis, near the midline of the brain. In five out of 14 PS-III neurones stained, the branches entered the ocellar nerves. In the posterior slope, the PS-III neurone responded to illumination of either of two ocelli with a small tonic on-hyperpolarization and a large transient off-depolarization (Fig. 3D). When both ocelli were illuminated simultaneously, the amplitude of both on- and off-responses increased slightly.

*PS-IV neurone*

The PS-IV neurone has arborizations in the ocellar tract and projects into a wide area of the ipsilateral posterior slope (Fig. 3E). The cell body is located in the posterior slope. In the posterior slope, the PS-IV neurone exhibited a very small on-hyperpolarization during illumination of the ipsilateral ocellus and one or a few off-spikes (Fig. 3F). A small off-depolarization was observed at the end of illumination of the contralateral ocellus.

*PS-V neurone*

The PS-V neurone has arborizations in the ocellar tract and projects into a wide area of the posterior slope and anterior area of the tritocerebrum (Fig. 3G). The cell body is located in the ventral fork of the tritocerebrum. In the posterior slope, the PS-V neurone exhibited an off-spike (Fig. 3H).

*OL-I neurone*

The cell body of the OL-I neurone is located in the pars intercerebralis (Fig. 4A,B). A neurite extends posterolaterally from the cell body to the proximal end of an ocellar tract, where it sends branches into the proximal area of the ocellar tract, and then runs across the midline of the brain to the proximal end of the other ocellar tract. From here, some branches extend anteriorly into the ocellar tract and ocellar nerve, some branches extend posteriorly into the posterior slope, and an axon extends laterally. The axon arborizes in the lateral protocerebral lobe, and in the

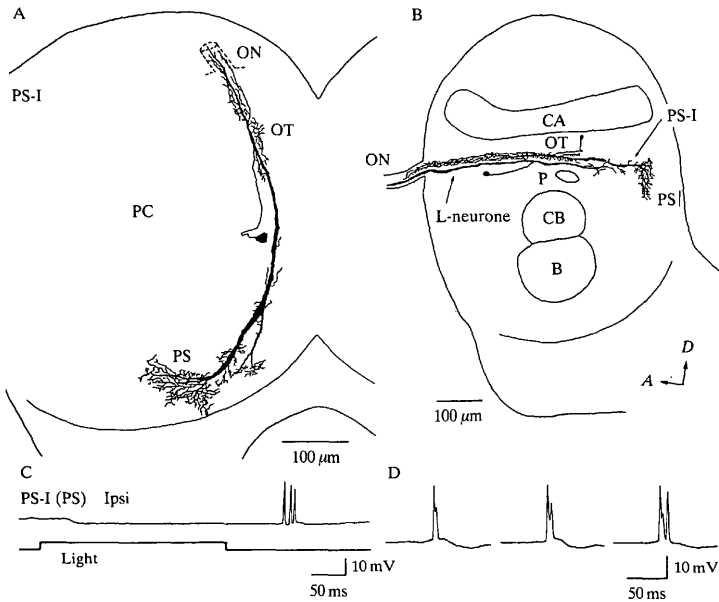


Fig. 2. Anatomy and responses of a PS-I neurone. (A) A drawing of a PS-I neurone viewed dorsally. (B) Lateral view of the anatomy of an L-neurone and a PS-I neurone in the brain. Each neurone stained was from a different cockroach. PC, protocerebrum; ON, ocellar nerve; OT, ocellar tract; PS, posterior slope; CA, calyx of the mushroom body; P, protocerebral bridge; CB, central body; B, beta-lobe of the mushroom body. D, dorsal; A, anterior. (C), (D) Potentials of a PS-I neurone recorded in the posterior slope. Ipsi means that light was applied to the ocellus ipsilateral to the cell body. A tonic on-hyperpolarization and transient off-depolarizations are observed (C). The waveforms of off-responses vary from response to response (D). The light intensity is 2 lx.

proximal area of the lobula neuropile and proximal area of the medulla neuropile of the optic lobe. In two OL-I neurones, the branches entered the proximal area of the ocellus. Recordings from OL-I neurones were made in the lateral area of the posterior slope contralateral to the cell body location. There was a discharge in the dark which decreased during illumination of the ocellus contralateral to the cell body location (Fig. 4C). At the end of illumination, the spike frequency increased slightly. There was also a slight decrease in spike frequency during illumination of the ipsilateral ocellus.

Fig. 3. Anatomy and responses of four types of PS neurones (PS-II–PS-V). The anatomy of PS-II (A), PS-III (C), PS-IV (E) and PS-V (G) neurones was drawn dorsally. Arrows indicate the cell bodies. OT, ocellar tract; PS, posterior slope; TC, tritocerebrum; PI, pars intercerebralis. Scale bars, 100  $\mu$ m. Responses of PS-II (B), PS-III (D), PS-IV (F) and PS-V (H) neurones were recorded in the posterior slopes. Ipsi or Cont means the light was directed to the ocellus ipsilateral or contralateral to the cell body location. In all recordings, the light intensity is 2 lx. Calibrations: 20 mV, 50 ms.

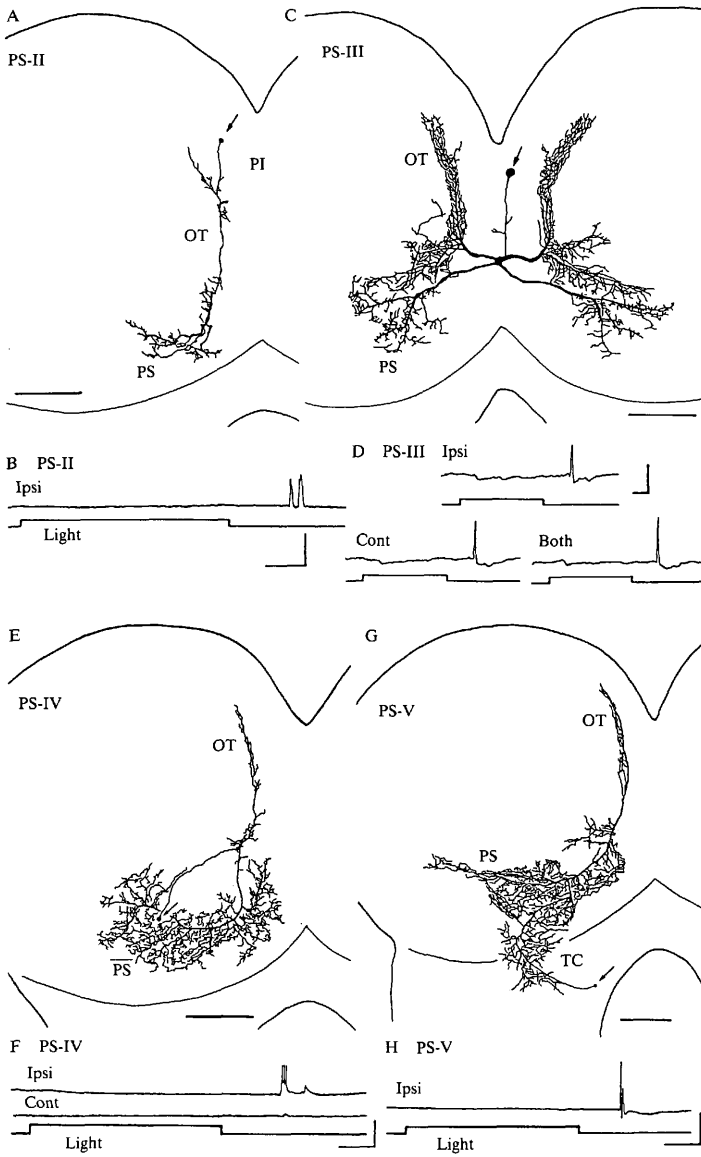


Fig. 3





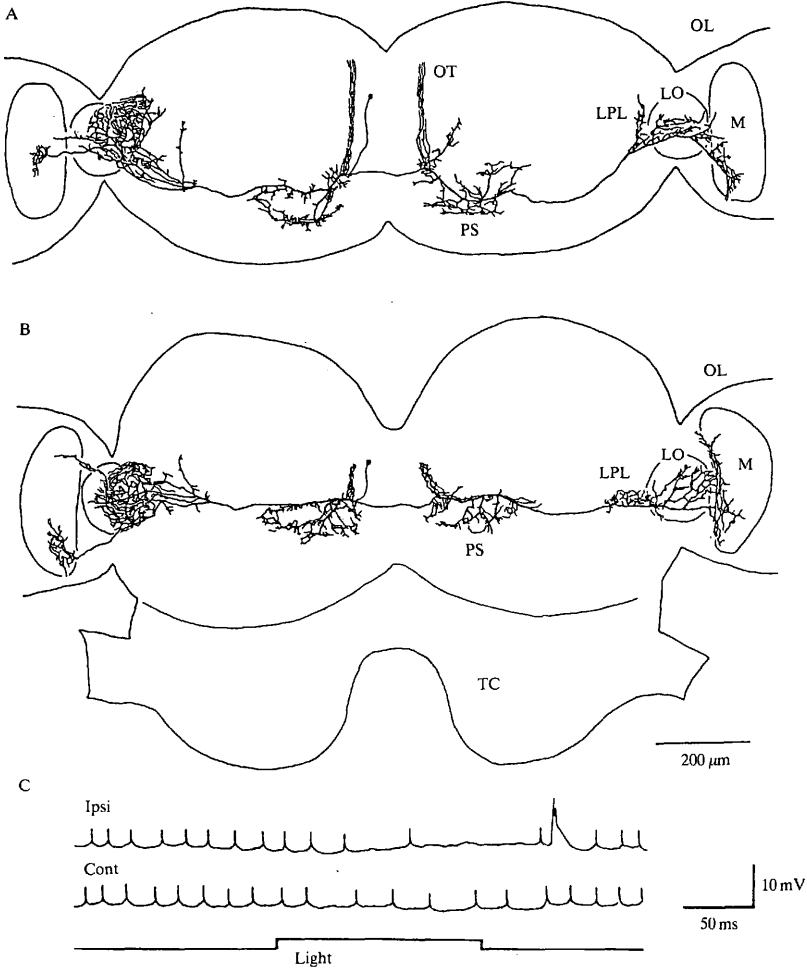


Fig. 5. Anatomy and response of an OL-II neurone. (A),(B) Drawings of an OL-II neurone viewed dorsally (A) and posteriorly (B). OT, ocellar tract; PS, posterior slope; TC, tritocerebrum; OL, optic lobe; LO, lobula; M, medulla; LPL, lateral protocerebral lobe. (C) Responses recorded in the medial area of the posterior slope. Ipsi or Cont means that light was applied to the ocellus ipsilateral or contralateral to the cell body location. Light intensity: 2 lx.

Fig. 4. Anatomy and response of an OL-I neurone. (A),(B) Drawings of an OL-I neurone viewed dorsally (A) and posteriorly (B). OC, ocellus; OT, ocellar tract; PS, posterior slope; LPL, lateral protocerebral lobe; OL, optic lobe; LO, lobula; M, medulla. (C) Responses recorded in the lateral area of the posterior slope, from the axon. Ipsi or Cont means the light was applied to the ocellus ipsilateral or contralateral to the cell body location. Light intensity: 2 lx.

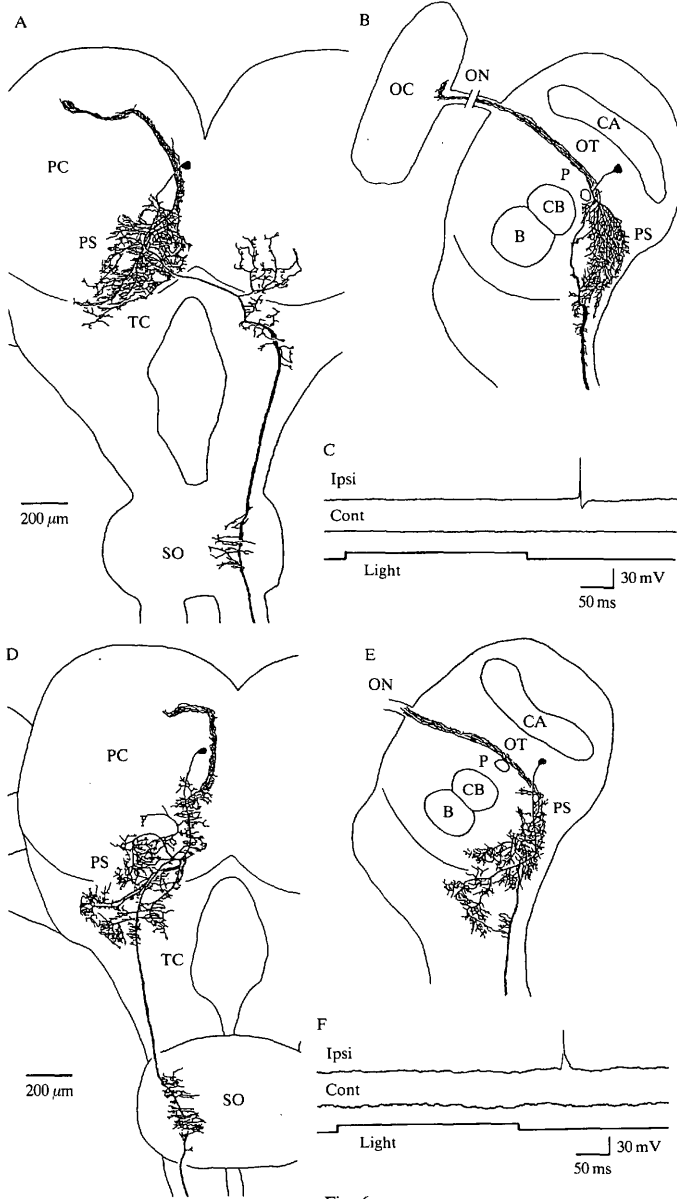


Fig. 6

*OL-II neurone*

The OL-II neurone has arborizations in the bilateral ocellar tracts and projects into the bilateral optic lobes and lateral protocerebral lobes (Fig. 5A,B). It also has arborizations in the bilateral posterior slope. The cell body is located in the pars intercerebralis near that of the OL-I neurone. In the optic lobe ipsilateral to the cell body, the arborizations cover almost the entire region of the lobula and the medial area of the medulla. In the contralateral optic lobe, the arborizations cover almost the entire region of the lobula and the proximal region of the medulla. The response of the OL-II neurone was similar to that of the OL-I neurone. When recordings were made in the posterior slope ipsilateral to the cell body position, near the proximal end of the ocellar tract, the neurone exhibited a discharge in the dark which decreased during illumination of the ipsilateral ocellus (Fig. 5C). The spike frequency also decreased slightly during illumination of the contralateral ocellus.

*D-I neurone*

The D-I neurone has a large cell body (25–35  $\mu\text{m}$  in diameter) in the posterior part of the protocerebrum (Fig. 6A,B). It has arborizations in the ocellar tract, ocellar nerve, posterior slope and tritocerebrum and has a thick axon descending ipsilaterally. The axon arborizes in the suboesophageal ganglion and further descends to the thoracic ganglion. When recordings were made in the posterior slope, the D-I neurone showed one or a few spikes when the light directed to the ipsilateral ocellus was turned off (Fig. 6C). In the ocellar tract, a small off-depolarization was observed when the light directed to the contralateral ocellus was turned off (see Table 1), but the small off-response did not elicit spikes in the posterior slope.

*D-II neurone*

The D-II neurone has a large cell body (35–50  $\mu\text{m}$  in diameter) in the posterior protocerebrum near that of the D-I neurone (Fig. 6D,E). It has arborizations in the ocellar nerve and the ocellar tract on the ipsilateral side to the cell body and in bilateral posterior slopes and the tritocerebrum. The axon of this neurone descends contralaterally through the suboesophageal ganglion to the thoracic ganglion. In three of 15 D-II neurones stained, the branches entered the proximal part of the ocellus. The response of the D-II neurone was very similar to that of the D-I neurone (Fig. 6F). It generated one or a few spikes when the light directed to the ipsilateral ocellus was turned off.

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Fig. 6. Anatomy and responses of D-neurons (D-I, II). (A),(B) Drawings of a D-I neurone viewed dorsally (A) and laterally (B). (C) Responses of a D-I neurone recorded in the posterior slope. (D),(E) Drawings of a D-II neurone viewed dorsally (D) and laterally (E). PC, protocerebrum; TC, tritocerebrum; SO, suboesophageal ganglion; OC, ocellus; ON, ocellar nerve; OT, ocellar tract; PS, posterior slope; P, protocerebral bridge; CB, central body; B, beta-lobe; CA, calyx of the mushroom body. (F) Responses of a D-II neurone recorded in the posterior slope. Ipsi or Cont means that light was applied to the ocellus ipsilateral or contralateral to the cell body location. In C and F, the light intensities are 2 lx.

## DISCUSSION

We identified nine types of ocellar interneurons which have branches in the ocellar tract or in the ocellar tract and ocellar nerve. The responses of these neurones recorded in the ocellar tract are all similar to those of L-neurones, and also similar to those of third-order ocellar neurones of locusts reported by Simmons (1980, 1981). The ocellar tract is the neuropile area where the L-neurones make synapses onto the postsynaptic cells (locusts: Guy, Goodman & Mobbs, 1979; cockroaches: Toh & Hara, 1984). In addition, Toh & Sagara (1984) suggested that the ocellar nerve of cockroaches is also the synaptic region between L-neurones and the third-order neurones. Thus, the nine types of neurones reported here are probably third-order neurones. Simmons (1981, 1982) reported that L-neurones make excitatory synapses onto the third-order neurones in locusts. Probably all the neurones found in this study also receive excitatory synapses from L-neurones.

We could not observe any responses from the nine types of neurones to sensory stimuli other than ocellar illumination. However, it is possible that more sophisticated stimuli, e.g. combinations of some sensory stimuli, may evoke responses in these neurones. For example, D-neurones have branches in the posterior slopes and in the tritocerebrum, in addition to the ocellar tract, and therefore D-neurones most probably receive inputs from some sensory organs other than ocelli.

When recordings were made in the axons or terminal regions, the nine types of neurones exhibited different responses. For example, the PS-I and III neurones exhibited tonic on-responses and transient off-responses, PS-II, V and D-I, II neurones exhibited only off-responses, and OL-I, II neurones exhibited a discharge in the dark which was inhibited during illumination. The differences in responses among these neurones reflect differences in membrane properties of the axons, since they exhibited similar responses in the ocellar tracts.

As a result, some of the ocellar interneurons may be specialized to transfer either sustained or transient signals. Behavioural studies of some insects suggest that the ocellus transmits signals related to the levels of light intensity (honeybees: Schricker, 1965; locusts and crickets: Jander & Barry, 1968; fly: Hu & Stark, 1980), as well as to rapid changes in intensity (dragonflies: Stange & Howard, 1979; Stange, 1981; locusts: Taylor, 1981*a, b*). In the cockroach ocellus, the former signals would be transferred *via* PS-I, III and OL-I, II neurones and the latter signals *via* PS-I-PS-V and D-I, II neurones. On the other hand, these neurones may also make output synapses in the ocellar tract. In this case, all these neurones would transfer both sustained and transient signals in the ocellar tract.

The off-responses of PS-I-PS-III neurones looked like transient PSPs, because the waveforms of off-responses varied from response to response. However, Simmons (1981) reported in locusts that the amplitudes of off-spikes of L-neurones changed depending on the amplitude and duration of preceding hyperpolarization. To clarify if the off-responses of PS-I-PS-III neurones are PSPs or spikes, or both, current injection experiments are necessary (M. Mizunami & H. Tateda, in preparation).

In most insects, some of the L-neurons have terminal branches in the posterior slope (see review by Goodman, 1981). In the cockroach, however, no L-neurons have branches in this region (Mizunami *et al.* 1982). Instead, the PS neurones relay ocellar signals to the posterior slopes. Strausfeld (1976) and Strausfeld, Bassemir, Singh & Bacon (1984) reported that the posterior slope has neural connections to the higher order centres of the brain. They also reported that descending neurones of the brain originate from the posterior slopes. We think that the PS-neurones relay ocellar signals to the neurones projecting into the higher order centres and/or regulate the activities of the descending neurones.

The anatomy of some neurones reported here is similar to that of the neurones stained using cobalt-fillings of ocellar nerves. The anatomy of the PS-V neurone is similar to that of LS(I) neurones of the cockroach reported by Koontz & Edwards (1984), and also similar to that of the NLS(I) neurones of the locust reported by Goodman & Williams (1976). An axon projecting from the ocellar tract to the optic lobe was identified in the cockroach (Bernard, 1976; Koontz & Edwards, 1984), and this axon may be that of the OL-I neurone. The neurones projecting from the ocellar tract into the optic lobe have been noted in other insects (see review by Goodman, 1981). An axon descending contralaterally from the ocellar tract was noted in the cockroach by Bernard (1976), and this axon is probably that of the D-II neurone. Edwards & Koontz (1984) stained a large cell body in the protocerebrum, and considered the cell body is that of one of the second-order neurones [LL(X) neurone]. However, the cell body has a size and location that is in good agreement with that of the cell bodies of D-neurones. Therefore, the cell body is possibly that of D-I or D-II neurone, not that of the second-order neurone. In locusts, several descending neurones were detected in the ocellar tract (Williams, 1975; Goodman, Patterson & Mobbs, 1975; Guy *et al.* 1977; Simmons, 1980; Reichart, Rowell & Griss, 1985), and some of these neurones were found to be third-order (Simmons, 1981, 1982). The D-neurones of cockroaches are probably homologous to some of these neurones.

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