THE PHYSIOLOGY AND MORPHOLOGY OF CENTRALLY PROJECTING VISUAL INTERNEURONES IN THE HONEYBEE BRAIN

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SUMMARY

Visual interneurones with projections into the median protocerebrum of the honeybee brain were characterized by electrophysiological and neuroanatomical methods. Extrinsic medulla neurones with wide ramifications in the medulla and terminations in the median posterior protocerebrum show spatial opponency in their tonic responses to stationary light.

Wide-field lobula neurones projecting into the dorsal lobe code the direction of movement of visual stimuli by changing the sign of their tonic response. Lobula neurones, with two branches ipsi- and contralateral to the oesophagus, are binocularly sensitive. A moving stimulus in either direction causes excitation or inhibition of these neurones, the sign of the response being dependent on the side of stimulation.

The presumed dendrites of an extrinsic lobula neurone, showing combined spectral and spatial opponency, differ markedly in shape from those of lobula movement-detecting neurones.

Neurones that connect the optic tubercle with the contralateral dorsal lobe are characterized. They show a non-directionally selective movement sensitivity within a binocular receptive field.

INTRODUCTION

The results of the preceding paper (Hertel, Schäfer & Maronde, 1987) suggested that the prominent visual commissures in the honeybee brain are all specialized for coding specific qualities of a light stimulus. Neurones of the posterior optic commissure, which connect both medullae, code the position of a visual stimulus; neurones of the serpentine optic commissure, each of which invade both medullae and lobulae, are highly movement-sensitive irrespective of the direction of motion. Neurones of the anterior and the inferior commissure connect both lobulae and show directional selectivity.

In this study we examine neurones within the commissures that connect the optic lobes to different sites in the protocerebrum. Some aspects of coding mechanisms

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in such cells have been reported by Homberg (1982) and Gronenberg (1984), particularly with respect to their multimodal sensitivities. Here we concentrate on neuronal elements that had been preselected by a neuroanatomical survey. The structure and location of the arborizations of these neurones in the optic lobe resemble those of the visual commissures (Hertel *et al.* 1987); they also show similar stimulus sensitivity. Our results favour the suggestion that neurones within specific bundles are also functionally related.

MATERIALS AND METHODS

All experiments were performed with worker honeybees (*Apis mellifera*). They were carried out under the same conditions as described in detail in the preceding paper (Hertel *et al.* 1987). A neuroanatomical survey was carried out using serial sections of visualized neurone populations stained by the cobalt backfill technique (Bacon & Strausfeld, 1980). In addition, dye was injected ionophoretically (Pitman, Tweedle & Cohen, 1972) to control the cobalt efflux from the electrode and to limit the number of neurones stained. Intracellular recordings were made using conventional electrophysiological techniques. After a successful recording the cells were stained with Lucifer yellow; this was followed by conventional histological treatment. Optical stimulation was provided by a xenon lamp (XBO 900); the light was projected *via* interference filters, a neutral density wedge and a light guide onto the bee eye. Movement sensitivity of neurones was tested with a motor-driven endless loop of a striped pattern (Hertel *et al.* 1987). Spatial opponency was tested by presenting a visual stimulus to the median eye region of both eyes consecutively; stimulation of the binocular visual field thus had no effect.

Our results derive from intracellular recordings that were stable for at least 5 min. Light of equal quantal content at various wavelengths was used to analyse the wavelength-dependent response of the neurones, and this enabled the spectral efficiency of different light stimuli to be measured.

In all figures the graphic reconstruction was from the same cell as the spike trace.

RESULTS

All neurones described below responded exclusively to visual stimuli. Other modalities tested, such as air puffs or scent, elicited no effect. Neurones are presented according to the position of their dendritic fields in a hierarchy of processing, and working from the periphery to the centre of the brain.

Extrinsic medulla neurones

Morphology

The identified extrinsic medulla neurones had wide arborizations covering almost the whole serpentine layer (stratum 4 of Ribi & Scheel, 1981) of the medulla (Figs 1, 2), and their small ramifications axially invaded neighbouring layers of this neuropile. Their axons left the medulla dorsoproximally and accompanied the

A

B

340 nm
ip

340 nm
co

440 nm
ip

440 nm
co

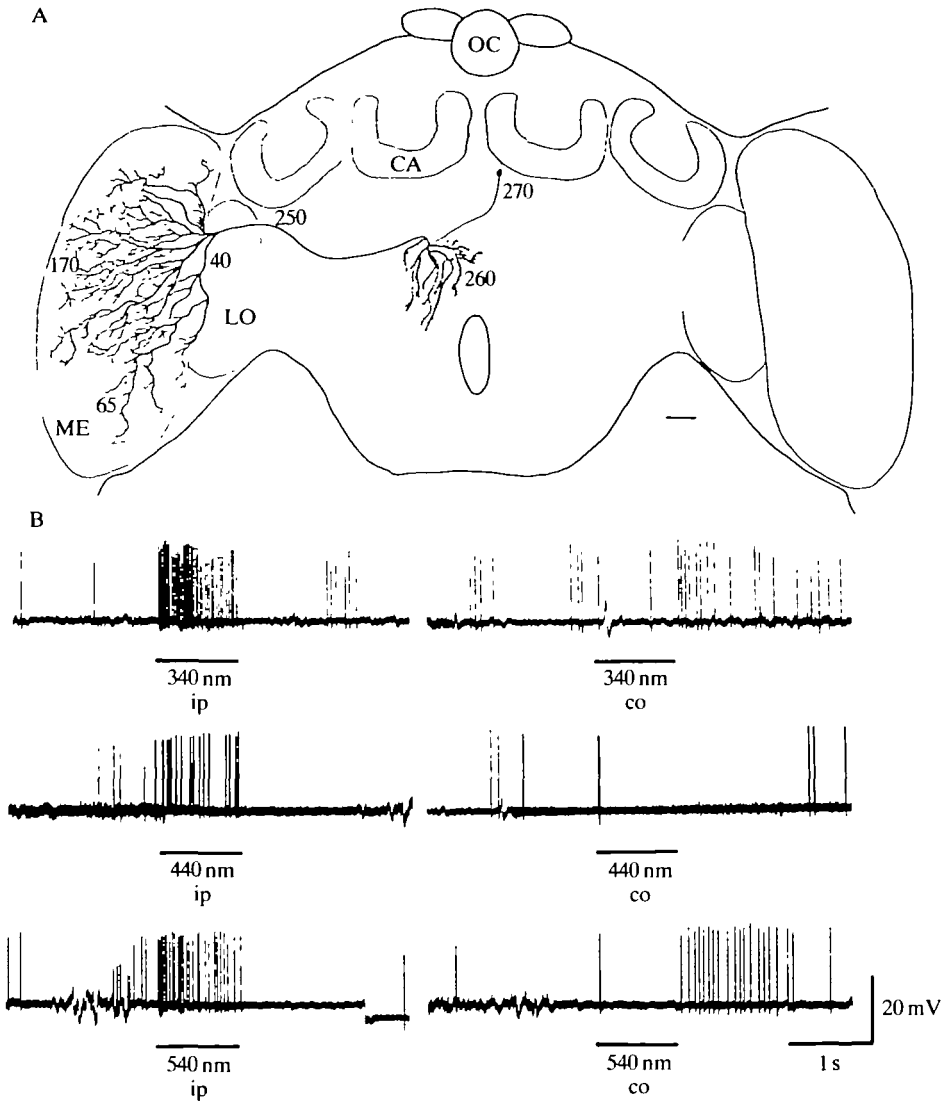540 nm
ip

540 nm
co

20 mV

1 s

Fig. 1. (A) Tangential medulla fibre with wide dendritic arborizations throughout the whole serpentine layer. The axon leaves the medulla at its proximoanterior side, bends posteriorly and projects to the ipsilateral side of the median protocerebrum, where it gives rise to fine terminal ramifications of blebby substructure. The soma is located in the medium protocerebrum close to the median calyx of the contralateral mushroom body. Scale bar, 100 μm. (B) The neurone exhibits spatial opponency in its binocular receptive field and is broad-band sensitive. Monochromatic stimulation (340, 440, 540 nm, equal quanta) of the eye ipsilateral to the medulla branchings elicits a tonic excitation, followed by an inhibition. Contralateral light inhibits the cell; the inhibition period is followed by a short excitatory rebound for u.v. and green light. Abbreviations for all figures: α, alpha lobe of the mushroom body; AL, antennal lobe; CA, calyx; LD, dorsal lobe; LO, lobula; ME, medulla; OC, ocelli; OT, optic tubercle; a, anterior; co, contralateral; d, dorsal; ip, ipsilateral; p, posterior; v, ventral. The numbers inserted indicate the depth of the neurone relative to the frontal brain surface.

posterior optic commissure (POC) to the median posterior protocerebrum. There the axons connected with their primary neurites which bent dorsally; the somata were located ventral to the median calyces of the mushroom bodies. Strong blebby branchings extended ventrally and contralaterally (Fig. 1A) or ipsilaterally (Fig. 2A) to the side of the soma.

A

B

340 nm
ip

340 nm
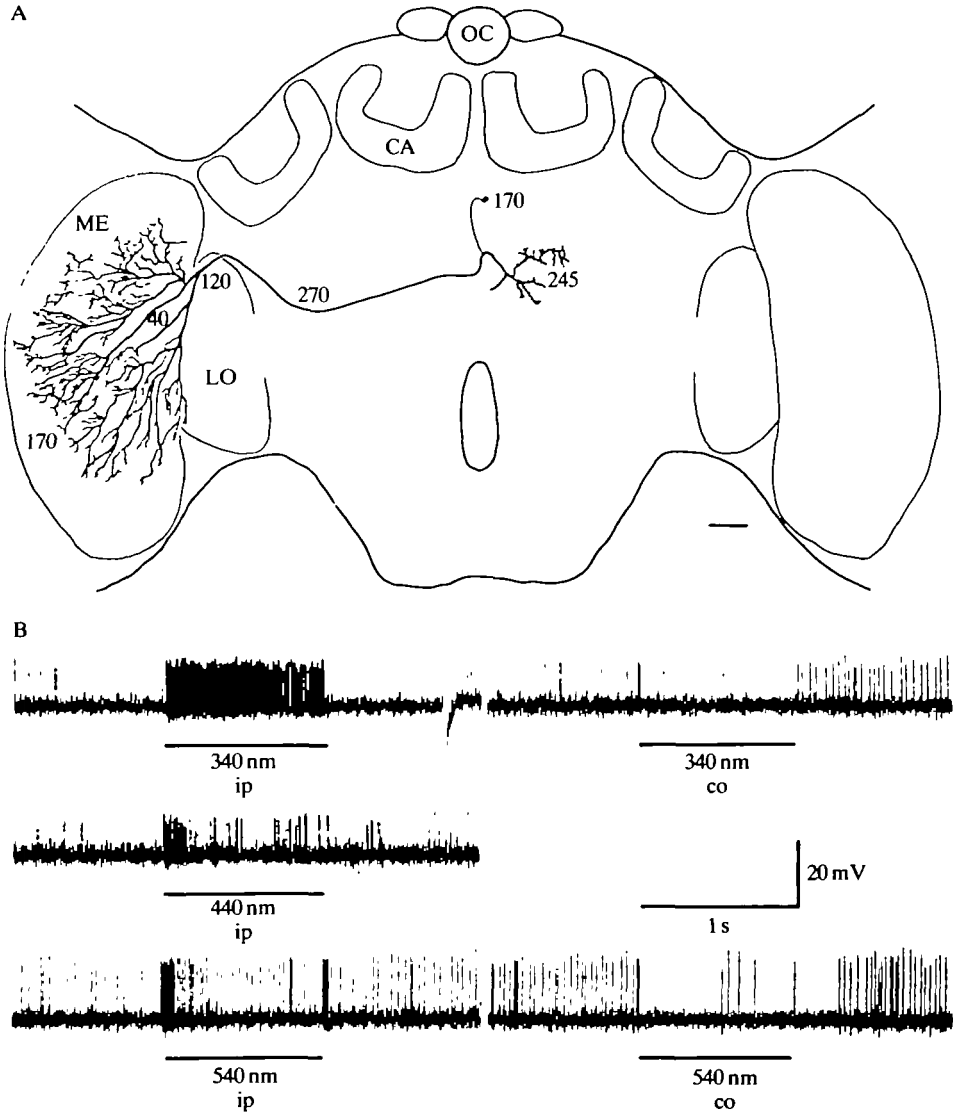co

440 nm
ip

20 mV

1 s

540 nm
ip

540 nm
co

Fig. 2. (A) Tangential medulla neurone with a branching pattern similar to that of the cell shown in Fig. 1A; this cell, however, terminates in the contralateral protocerebrum. Scale bar, 100 μm. (B) The neurone shows spatial contrast properties in its binocular receptive field. It also has an increased sensitivity to u.v. light, which, when applied ipsilateral to the side of the medulla arborizations, causes a strong tonic excitation. Blue and green light of equal quanta elicit only an on excitation, whilst contralateral green and u.v. light tonically inhibit the cell. Blue light was not tested. For abbreviations see Fig. 1.

Physiology

These unilateral wide-field medulla neurones from which we recorded ($N = 7$) were binocularly sensitive, and responded exclusively to stationary light stimuli. Light applied to the eye of the side with the medulla arborizations caused a tonic excitation of the spike discharge, and this was preceded by a short phasic component. The neurone in Fig. 1B had a low spontaneous activity, and the inhibitory effect caused by contralateral illumination was not particularly obvious. However, the neurone shown in Fig. 2 displayed its spatial opponency very clearly; whilst ipsilateral illumination caused strong excitation, contralateral illumination led to tonic inhibition (Fig. 2B). This spatial antagonism existed throughout the spectrum. The cell showed an enhanced tonic excitatory response to u.v. light; blue and green light elicited a more phasic on-response. On the contralateral side, u.v. and green light inhibited the cell almost equally.

Extrinsic lobula neurones

Motion-sensitive lobula neurones

The lobula in the bee is divided into two compartments: the distal layers, which are clearly stratified (layers 1–4; Ribi & Scheel, 1981), and a proximal layer which has a rather diffuse appearance. There are two major exit points from the lobula, where extrinsic fibres project to the protocerebrum or contralateral optic lobe. One is situated on the anterior side of the proximal part of the lobula and mainly gathers neurones that run to the optic tubercle. Most of the extrinsic lobula fibres, however, derive from the distal part, and leave it centrally at layer 5 (Ribi & Scheel, 1981), which separates the two main areas of this optic ganglion.

Each of the three neurones described below invaded only a single stratum of the distal lobula and connected it with the lateral protocerebrum, where it branched into the dorsal lobes (located posterior to the antennal lobes).

I. *Morphology*. The first of our three examples showed wide arborizations throughout a single stratum (layer 2; Ribi & Scheel, 1981) of the distal lobula. Fig. 3A gives a frontal view, Fig. 3B a horizontal one. This neurone projected *via* a short axon into the ipsilateral dorsal lobe, where it diverged, forming numerous varicose ramifications. The soma of the cell was located posteriorly to the lobula.

Physiology. This cell responded exclusively to monocularly applied stimuli. The response was a modulation of the spontaneous activity. A stationary flash of white light elicited a short on excitation, followed by an inhibitory rebound, and a strong off excitation. Stimulation by a moving grating demonstrated a strong directional preference (Fig. 3C): movement in a posterior to anterior direction caused a marked tonic increase of spike discharge, whilst movement in the opposite direction inhibited the cell.

II. *Morphology*. The cell body was located dorsoanteriorly to the right medulla (Fig. 4A). It gave rise to a primary neurite which ran to the median protocerebrum; here this neurite divided, and formed a large axon which connected two different neuropiles. Ipsilaterally to the soma, it bent posteriorly and invaded the dorsal lobe
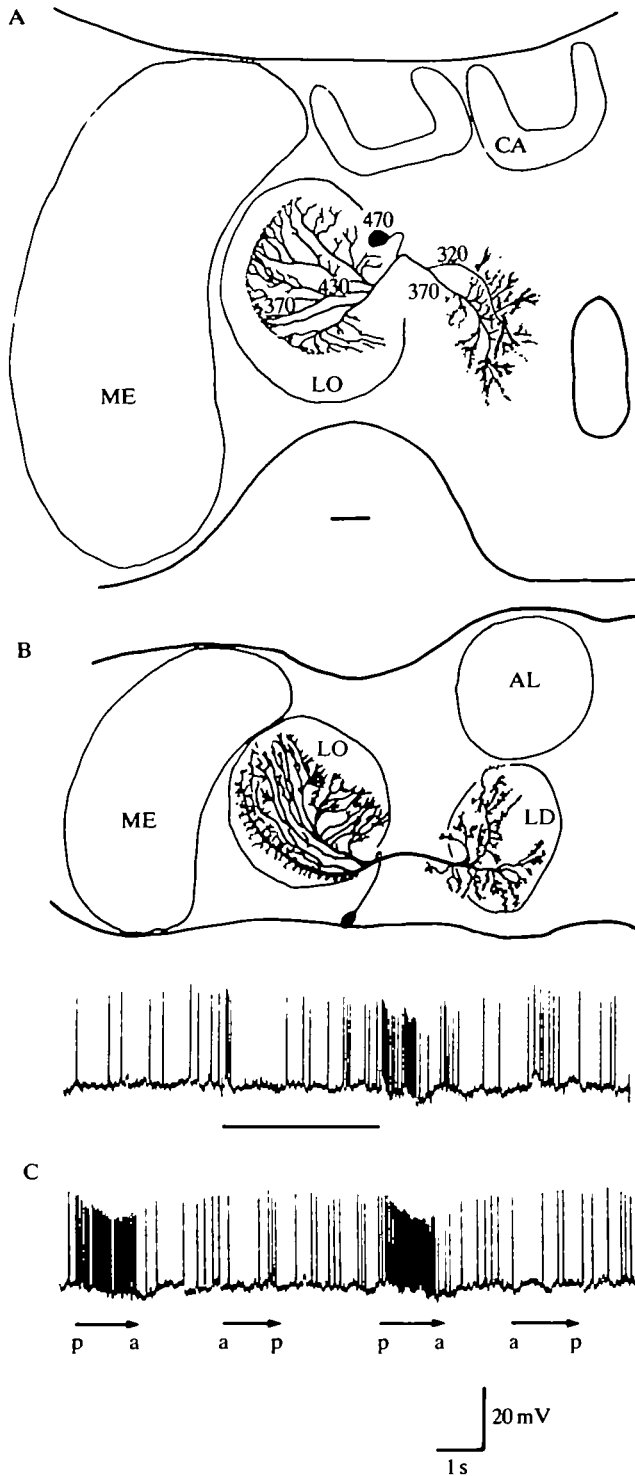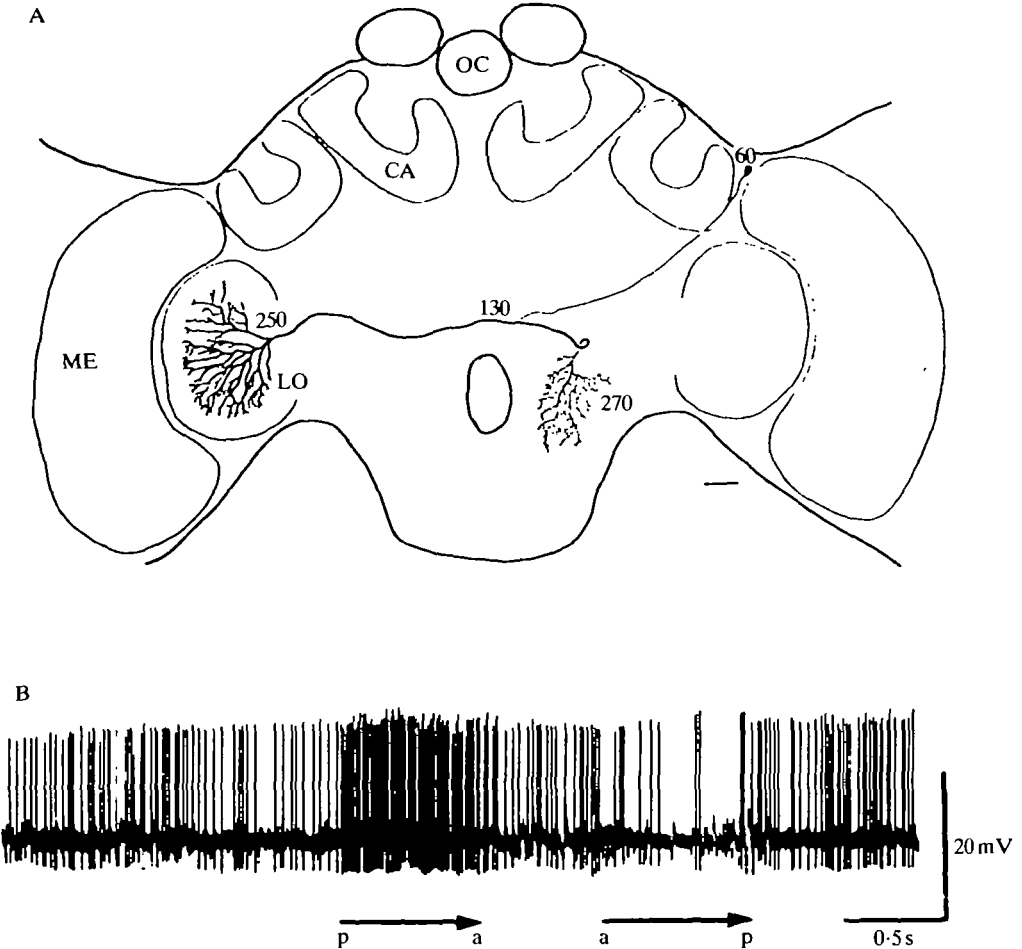
Fig. 3

A

B

Fig. 4. (A) Movement-sensitive neurone which connects layer 3 of the distal lobula with the contralateral dorsal lobe. Scale bar, 100 μm. (B) The neurone responds to a moving grating with directional selectivity within a wide receptive field, covering the whole eye ipsilateral to the lobula arborizations. It shows a tonic excitation to movement in a posterior to anterior direction; movement in the opposite direction causes inhibition. For abbreviations see Fig. 1.

Fig. 3. Unilateral lobula neurone with wide tangential ramifications into a single lobula layer and terminal branches in the dorsal lobe. (A) A frontal view of the cell; (B) a horizontal view. The lobula branches are restricted to the second distal layer. In the *camera lucida* drawing this is concealed because the layers of the lobula are curved, and the superposition of consecutive sections during reconstruction gives the impression of branches extending throughout the whole lobula. They are connected *via* a short axon with the terminals, which arborize throughout the dorsal lobe. This is a neuropile which is located posteriorly to the antennal lobe. Scale bar, 100 μm. (C) The monocular response of this neurone to white light. A stationary light is coded by a phasic on excitation, followed by a short inhibition, and a prolonged off excitation (upper trace). A grating moved in a posterior to anterior direction leads to a strong excitation, whereas movement in the opposite direction causes a slight inhibition (lower trace). For abbreviations see Fig. 1.

with wide varicose ramifications. It projected to the contralateral side in a small median tract close to the passage of the oesophagus, and entered the distal part of the lobula at its central exit point. From here it spread with wide arborizations through a median stratum (layer 3; Ribi & Scheel, 1981).

Physiology. The neurone was sensitive to a moving striped pattern given to the eye contralateral to the cell soma. The cell was directionally selective, and modulated its 25 Hz spontaneous action potential discharge according to the direction of stimulation. Movement from posterior to anterior caused a tonic excitation, whilst movement in the opposite direction caused an inhibition (Fig. 4B). Wavelength dependency was not tested.

III. *Morphology.* A third lobula neurone is illustrated in Fig. 5A. It arborized between layers 1 and 2 in the distal lobula. The axon was carried by the inferior optic commissure (IOC), and gave rise to fine blebby ramifications within the dorsal lobes ipsi- and contralateral to the oesophageal passage. The cell soma was situated between the medulla and the lateral calyx of the mushroom body close to the anterior brain surface.

Physiology. This binocular cell had a uniform, wide receptive field to stationary flicker (Fig. 5B). It responded exclusively to blue light and gave a weak on and off excitation. Strong responses were elicited by a moving stimulus. This cell was remarkable since, in contrast to the uniform response to stationary flicker, it also showed a spatial antagonism. Excitation or inhibition by movement depended only on which eye was stimulated, and not on the direction of movement. A moving stimulus presented to the eye ipsilateral to the cell soma always inhibited the cell. The same kind of stimulus given to the opposite eye, however, caused tonic excitation. Therefore, in contrast to the previously described lobula neurones, this cell was able to detect the side of the animal at which a movement took place; however, it could not discriminate the direction of movement.

Colour-coding lobula neurones

In addition to the many centrally projecting movement-sensitive lobula fibres we have analysed ($N = 35$), we found only a small number of neurones ($N = 3$) that were sensitive only to stationary light. From amongst these we have selected a neurone (Fig. 6) that exhibited both spectral and spatial coding properties.

Morphology. The cell was found close to the posterior surface of the brain (Fig. 6A). It had a small arborization within the dorsal part of the most distal lobula layer (stratum 1; Ribi & Scheel, 1981) that was connected *via* an axon to varicose ramifications which expanded from the lateral to the median protocerebrum. The cell soma was located on the proximoventral rim of the lobula near the posterior surface of the brain.

Physiology. This lobula neurone was binocularly sensitive to stationary light (Fig. 6B). The action potential discharge was differentially modulated by both the wavelength of the light flashes and their location. Short wavelength light (340 and 440 nm) presented to the eye ipsilateral to the cell soma caused a brief on inhibition. Green light (540 nm), however, produced a brief on excitation. The same spectral
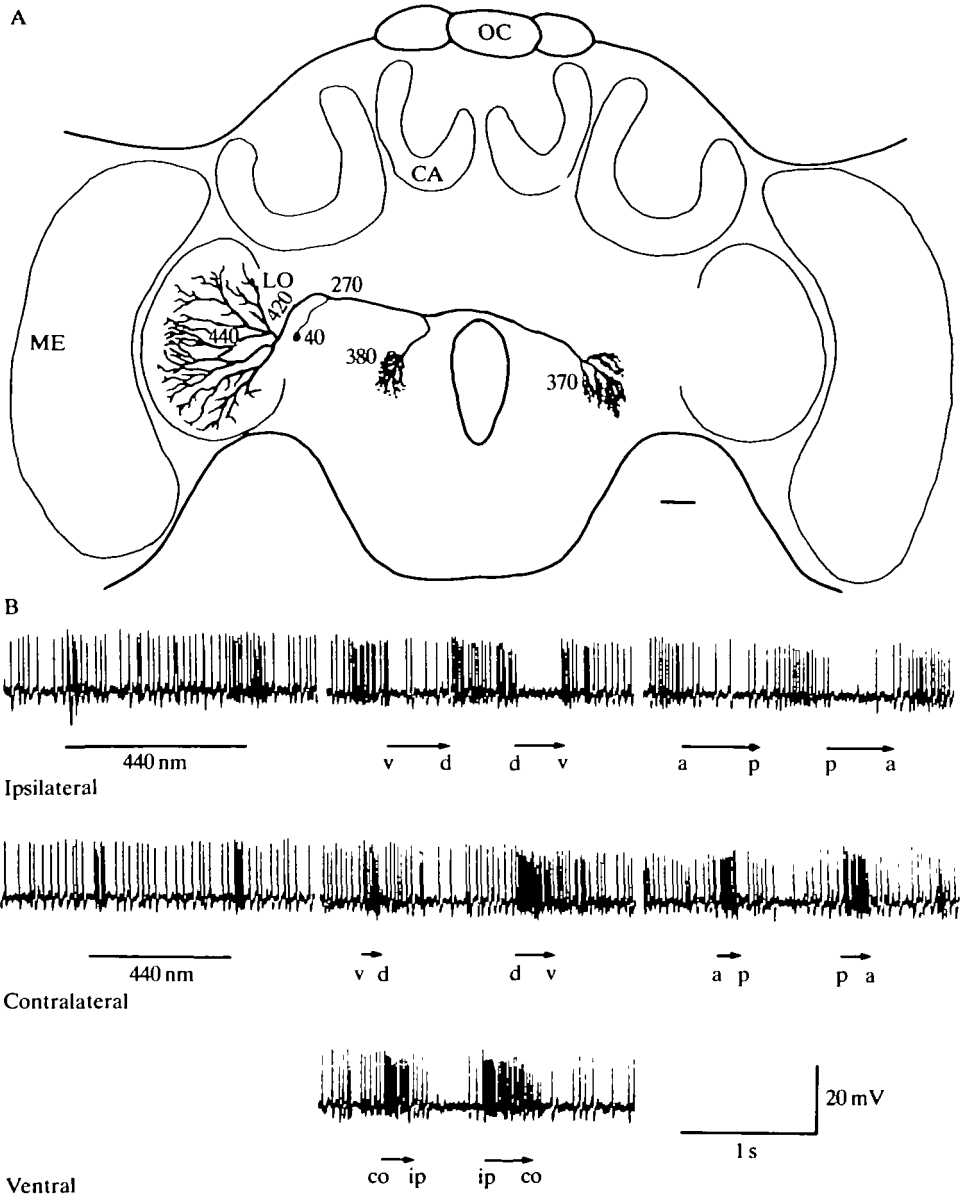
A

B

Ipsilateral

Contralateral

Ventral

Fig. 5. (A) Neurone with wide arborizations in lobula layers 1 and 2 and blebby ramifications which invade the dorsal lobes of both sides. Scale bar, 100 μm. (B) The cell is only sensitive to blue light (440 nm), and an on and off excitation is produced regardless of whether the illumination is ipsilateral or contralateral to the lobula branchings. The response to a moving grating is even stronger and shows spatial antagonism. The cell is inhibited by ipsilateral movement irrespective of its direction. Contralateral movement, as well as horizontal movement in the ventral binocular field, always causes excitation. For abbreviations see Fig. 1.

A

B

340 nm ——————
            ip   co

440 nm ——————
            ip   co

540 nm ——————
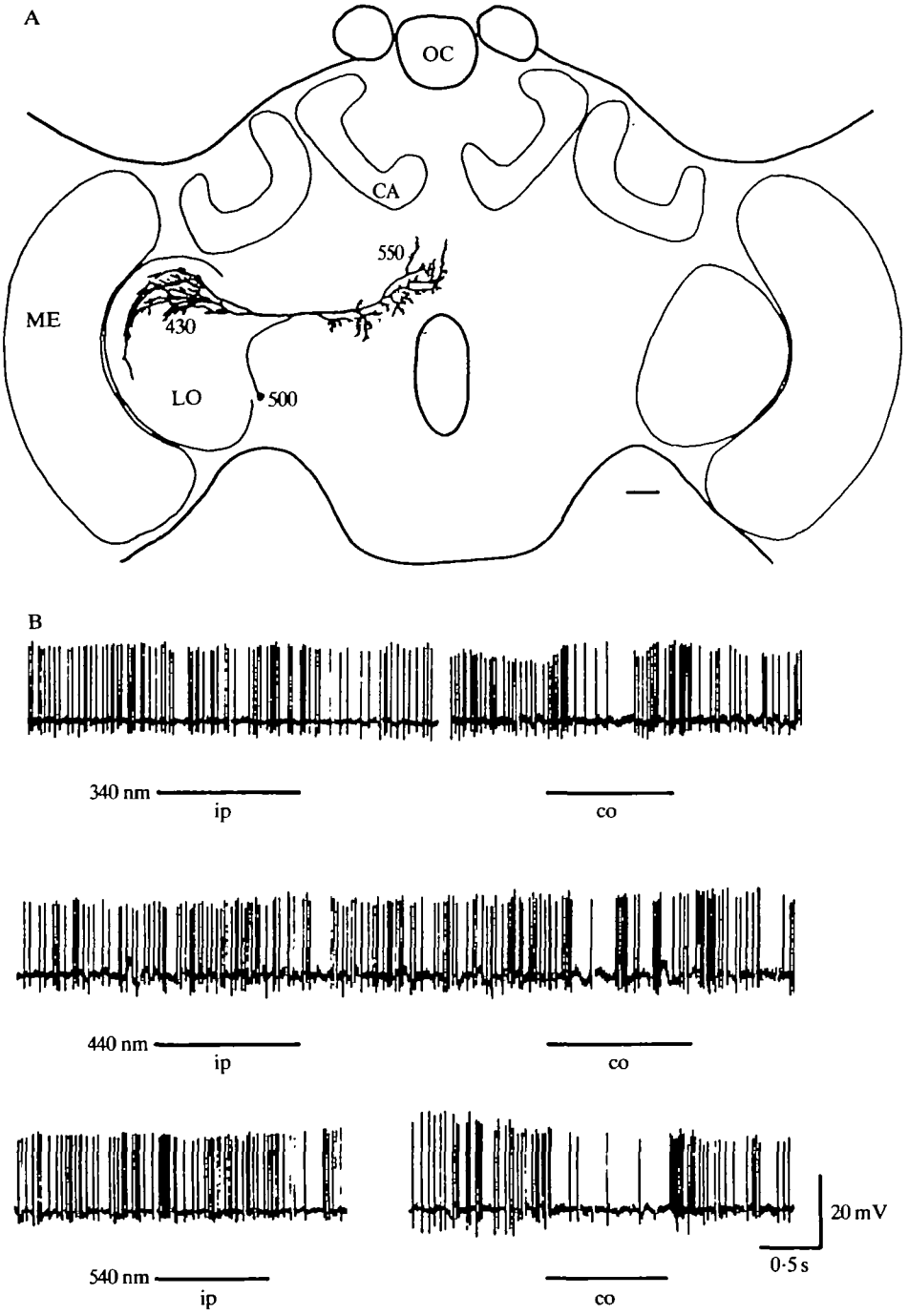   ip   co

20 mV

0·5 s

Fig. 6

stimuli shone onto the contralateral eye caused opposite responses, u.v. light producing an on excitation and green light eliciting a strong inhibition. These results indicate a double opponent receptive field with each eye giving opposite responses.

Optic tubercle

Of all the visual neuropiles the cells in the optic tubercles remain the least investigated since these neurones were difficult to record from. The results in Fig. 7 are given for a neurone that connected one optic tubercle with the contralateral dorsal lobe.

Morphology

The soma of this cell was situated lateral to the pedunculus of the mushroom body (Fig. 7A). It sent a primary neurite anteriorly to the proximal part of the ipsilateral optic tubercle. There the neurite divided into a fine arborization which entered the optic tubercle, and an axon that bent towards the posterior protocerebrum, and then projected with blebby divisions into the dorsal lobe. On its way to the dorsal lobe it gave rise to a second blebby branching dorsal to the oesophagus.

Physiology

The neurone was binocularly sensitive to stationary and moving stimuli (Fig. 7B). When stationary light was applied to either eye there was a tonic inhibition, followed by an off excitation. A moving grating always excited the cell tonically, an effect independent of the location and the direction of movement.

DISCUSSION

A basic problem in analysing visual information processing at the level of single neurones is the determination of the direction of signal flow. Our data suggest that smooth branchings are the input areas, whilst blebby ramifications are the terminals of a neurone. This is particularly obvious for the monocularly sensitive lobula cells (e.g. Figs 3, 4). They all have wide extending arborizations throughout the optic lobe ipsilateral to the side of signal input, and their axons project centrally and give rise to tiny processes with a striking blebby appearance. These cells are obviously orientated in the direction of signal flow, and it seems unlikely that they transport information centrifugally. Only a few centrifugal visual cells have been described up to now (Hausen, 1976). These are the V1, DCH and VCH neurones of the fly, and all have varicose ramifications at their output side in the lobula plate. An electron

Fig. 6. (A) This neurone is located close to the posterior surface of the brain and connects the distal lobula with the posterior median protocerebrum (posterior slope region). Scale bar, $100\,\mu\text{m}$. (B) The cell is binocularly sensitive and shows signs of double opponency. Short wavelength light presented ipsilaterally to the lobula ramifications elicits an on inhibition, whilst long wavelength light causes an on excitation. Stimulation of the contralateral side leads to the opposite response: short wavelength light elicits an on excitation, whilst long wavelength light inhibits the cell. For abbreviations see Fig. 1.
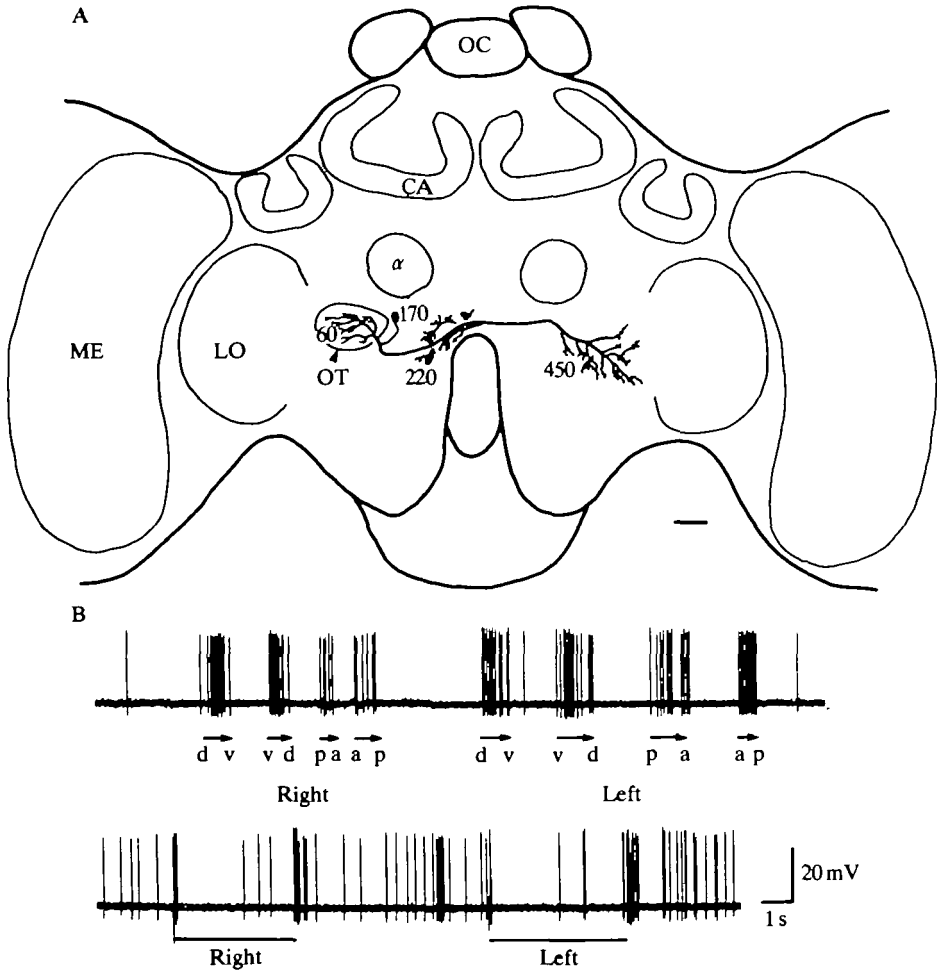
Fig. 7. (A) This neurone sends fine arborizations into one optic tubercle, this neuropile being located ventrolaterally to the α-lobe of the mushroom body. It invades the contralateral dorsal lobe with varicose branchings, and gives rise to additional blebby ramifications close to the passage of the oesophagus. Scale bar, 100 μm. (B) Stationary white light applied to the left or right eye causes inhibition, which is followed by an off excitation. A moving stimulus excites the cell, the response being independent of the direction of movement. For abbreviations see Fig. 1.

microscope study on spiking interneurones in the locust by Watson & Burrows (1985) verifies that smooth arborizations received predominantly input synapses while varicose neurites are areas of output.

We, therefore, consider the big arborizations in the optic lobe to be dendrites, and the varicose sites to be output areas. The same interpretation also holds for the big commissural neurones which pass from one side of the brain to the other (Hertel *et al.* 1987). Those cells with a monocular input also have rather smooth arborizations at the visual input site, and blebby swellings on the contralateral ramifications.

The wide-field medulla cells (Figs 1, 2) are arranged in parallel with the neurones of the posterior optic commissure (POC); they leave this axon bundle in the median protocerebrum, and terminate in the posterior slope region. Ocellar fibres and sensory projections from the antennae [the $B4_1$-tract of Pareto (1972), which is the $T6_1$-tract of Suzuki (1975)] also extend into this part of the brain. This neuropile is known to be a relay station between sensory and descending elements (Strausfeld, 1976). The response of the medulla cells we describe here is analogous to that of the POC neurones: one can hypothesize that the antagonistic binocular response may come about from an inhibitory interaction between corresponding but oppositely orientated POC fibres. Thus, ipsilateral light would cause an excitation of the cell, whilst contralateral stimuli would cause an inhibition. The non-commissural visual cells have their dendritic arborizations in the same medulla layer as the POC cells and, therefore, may receive the input for their opponent response to contralateral light *via* the POC fibres.

Spatial antagonism of medulla cells has been described for several other insect species. In the cricket, the receptive field organization of such neurones shows a centre–surround antagonism (Honegger, 1978, 1980), whilst in bees this antagonistic mechanism is expressed in adjacent parts of the cell's receptive field of one eye. Alternatively, in the case of binocular cells this spatial antagonistic response may be separated between both eyes. In this respect the bee medulla resembles that of the locust, in which Osorio (1986*b*) described a cell having a spatial opponency separated between both eyes. In addition he analysed medulla cells displaying a clear spectral opponent response, which were also found in the bee medulla (Kien & Menzel, 1977; Hertel & Maronde, 1987; Hertel *et al.* 1987).

In the fly (DeVoe & Ockleford, 1976), the cricket (Honegger, 1978, 1980) and the locust (Osorio, 1986*a*) there exist medulla neurones that are strongly sensitive to movement, and some of these are directionally selective. In the medulla and the lobula of the moth (*Sphinx ligustri*) there are neurones displaying different mechanisms of movement sensitivity (Collett, 1970, 1971). In bees, neurones which have their dendritic ramifications restricted to the medula have not been found to be sensitive to movement. Furthermore, no cells in the medulla have been found to show directionally selective responses; this is a major characteristic of the cells of the lobula.

All neurones from which we recorded and which terminated in the dorsal lobe were found to be movement-sensitive. Whilst the cell coming from the optic tubercle (Fig. 7B) responded to motion in all directions, most of the tangential elements from the distal lobula were directionally selective.

The dorsal lobes of the deutocerebrum in the bee brain are located posteriorly to the antennal lobes. These regions receive sensory input from the antennae, and contain dendrites of antennal motoneurones (Pareto, 1972; Suzuki, 1975). In addition, interneurones descending into the thorax exhibit branching in the region of this neuropile (Goodman *et al.* 1987; Hertel & Maronde, 1987). This suggests that the dorsal lobes are important structures with regard to the transfer of sensory information to the motor systems. In fact, the dorsal lobes are probably the relay

stations between some motion-sensitive neurones and the antennal motor neurones that are responsible for a well-known antennal tracking behaviour in insects: the animal responds to a moving stimulus with a corresponding movement of its antennae (Erber & Schildberger, 1980; Erber, 1984).

Of the lobula neurones from which recordings have been made only a small number were insensitive to moving stimuli but sensitive to spatial contrast, and they thus show properties more frequently associated with medulla cells in recordings made from the bee brain (Hertel, 1980; Hertel et al. 1987; Hertel & Maronde, 1987). The cell shown in Fig. 6 received its input from all three receptor types of both eyes, and showed an antagonistic response to u.v. blue and green light. It was excited by ipsilaterally presented green light as well as by contralaterally applied u.v. light, but was inhibited by contralateral green and ipsilateral u.v. light. This is the first time that a cell in the bee brain has been shown to have double opponency. However, the intensity was not as pronounced as that described for cortical cells in monkeys (Michael, 1978). For example, the receptive field of the cortical neurone is much smaller and exhibits centre-surround antagonism.

Compared with the number of recordings from bee neurones coding movement or space, only a few cells showing wavelength dependency have been found so far. This may be a consequence of neurone size, but it is more likely that these cells are located in substructures of the brain on which we did not focus. A promising locus in the brain for finding such cells might be the dorsoproximal exit of the medulla, since the only identified neurones with such properties were recorded from this region (Hertel & Maronde, 1987).

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