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THE PHYSIOLOGY AND MORPHOLOGY OF VISUAL COMMISSURES IN THE HONEYBEE BRAIN

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SUMMARY

Visual commissures of the honeybee brain were investigated by electrophysiological and histological methods.

1. A newly described serpentine optic commissure (SOC) consists of four neurones each of which has widely extending arborizations in both medullae and lobulae. The cells are monocularly sensitive, the best stimulus being a moving target.

2. Neurones of the posterior optic commissure (POC) connect the two medullae and show spatial opponency; the sign of the tonic response depends on the position of the stimulus in the receptive field of the cell.

3. The inferior optic commissure (IOC) assembles neurones that have ramifications in both lobulae. They show directional selectivity to a moving stimulus and this is often combined with an opponent tonic response.

4. The anterior optic commissure (AOC) contains neurones which are similar to those of the IOC and which connect the two lobulae. These show a preferential sensitivity to one direction of movement.

5. A single pair of cells close to the interoptic tubercle commissure is identified as being movement-sensitive without directional selectivity.

INTRODUCTION

Neuroanatomical investigations of the bee brain have revealed a variety of commissures which clearly transfer sensory information from one brain hemisphere to the other (Kenyon, 1896; Jawlowski, 1957; Mobbs, 1984). In this study, we have determined histologically the exact position of the most prominent commissures in the bee brain. This information has enabled us to make repeated intracellular recordings from preselected neurones, rather than making an arbitrary collection of responses, as was done in a previous study (Hertel, 1980). The aim of the experiments was the electrophysiological characterization of sensitivity to visual stimuli as well as their anatomical description. Our results indicate that each of these commissures has its specific response pattern to different kinds of visual stimuli. Therefore, it is suggested that the visual commissures are specialized pathways for the processing of different qualities of visual information.

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Key words: insect brain, visual system, interneurones.

MATERIALS AND METHODS

Electrophysiology

Worker bees (*Apis mellifera*) were placed in a metal tube and fixed at the neck with a tape strengthened with a small metal plate. The bees were kept like this for at least half a day before being used for electrophysiological investigation. To restrict movements the head was glued at its dorsal edge to the supporting tape with a small droplet of a wax–collophonium mixture.

Glass electrodes (Hilgenberg, o.d. 1 mm, i.d. 0·58 mm) were inserted into the brain, through a hole that had just been cut in the head capsule. Some electrodes were inserted in the anterior–posterior direction, through a hole either frontal to the lobula or midway between the median ocellus and the antennae. Other electrodes were inserted in the dorsoventral direction, through a hole between the dorsal rim of the compound eye and the lateral ocellus. The depth of the electrode tip in the brain tissue was monitored simultaneously *via* a digital display.

Conventional electrophysiological techniques were used for signal amplification, monitoring and storage. Electrodes were pulled on a Campden horizontal puller. The tips were filled with a 3% aqueous solution of the dye Lucifer yellow, and the shanks with 0·1 mol l^{-1} LiCl. The resistance of the electrode in the brain tissue was 150–250 MΩ. After recording, the cell was filled with dye by application of a negative d.c. current (25–60 nA for 1 min).

Optical stimulation was provided by a xenon lamp (XBO 900) projected *via* quartz neutral density filters, neutral density wedges, interference filters and light guides onto the bee, which was positioned in the centre of a perimeter apparatus. The light guide was at a distance of 3·5 cm from the bee eye, so that the emitted light was seen as an illuminated field of approximately 8° in diameter. To measure the spectral efficiency of the neurones, monochromatic light of equal quantal content was used. In some experiments, a second light guide from a different source was used to reveal possible substructures of the receptive field of the neurones. Movement sensitivity was tested by using a motor-driven endless loop of parallel black and white stripes (black 5°, white 8° visual angle). This pattern had 45°×40° of visual angle, and was illuminated from behind, *via* an opalescent screen, by six 3-W tungsten lamps. It was rotated at a constant velocity of 45° s^{-1}.

Histology

After intracellular labelling, the brain was processed for Lucifer yellow histology as described by Stewart (1978); the staining was first viewed and photographed in a wholemount preparation. The specimen was then embedded in epoxy resin (Spurr, 1969), and 25 μm frontal or horizontal sections were cut.

In addition, the profiles of visual commissures were investigated by cobalt injections into selected areas of the brain using the diffusion technique of Bacon & Strausfeld (1980); the brains were intensified according to the method of Tyrer & Bell (1974). After embedding in Durcupan (Fluca), 40 μm sections were cut in the frontal, horizontal or saggital plane.

The commissures were identified and the number of neurones they contained was estimated using a variety of different methods: Bodian stains (Gregory, 1980), cobalt backfills and methylene blue stains in frontal, horizontal and saggital sections. The anterior optic commissure was also investigated by electron microscopy.

Graphic reconstructions of stained cells were carried out directly *via* the drawing tube of the microscope and from colour slide (Ektachrome 400) photographs.

RESULTS

The results presented here were taken from stable recordings lasting longer than 5 min. As the neurones described below had at least one arborization in each hemisphere of the brain, and the electrode was inserted into the axon of the cell, these branchings were incompletely labelled in some cases. This is particularly true of the cell soma which, because it is connected *via* a tiny neurite, was sometimes missing. In addition, the fluorescence of very fine ramifications faded during the time of investigation. However, identification of most of these neurones was possible, since their axons ran in commissures that were well known from other single-cell markings of the same neurone type and from cobalt backfills.

No data exist which suggest that the commissural neurones investigated here have a mirror-symmetrical arrangement. For the serpentine optic commissure, however, our data clearly show that the cells are arranged in pairs (see below).

The paths of some of the neurones (see below) through the midbrain are shown in Fig. 1. The plane of a sagittal section through the bee brain is indicated in Fig. 1A. Such a section is seen in Fig. 1B as a line drawing, part of which is shown as a micrograph in Fig. 1C. The commissures were identified by cobalt injection (see Materials and Methods). In this section, the inferior optic commissure, some neurones in the dorsal bundle of the anterior optic commissure, the anterior interlobula pair, a few axons running in the interoptic tubercle commissure and the serpentine optic commissure are stained.

The serpentine optic commissure (SOC)

The serpentine neurones were very striking compared to other nerve cells in the bee brain, because of their conspicuous structure. They have been described by Homberg (1982), Gronenberg (1984) and Schäfer (1984) with differing results. The discrepancies between their results made a detailed analysis necessary.

Morphology

The SOC consisted of two pairs of symmetrically arranged neurones that connected the two optic lobes; each serpentine neurone was also arranged symmetrically (Fig. 2A,B). Each had four extended arborizations, one in each medulla and lobula. The neurites coming from the medulla and the lobula of one side of the brain met in the lateral protocerebrum to form a serpentine axon which ran posterior to the pedunculus of the mushroom body, and then bent anteriorly to pass

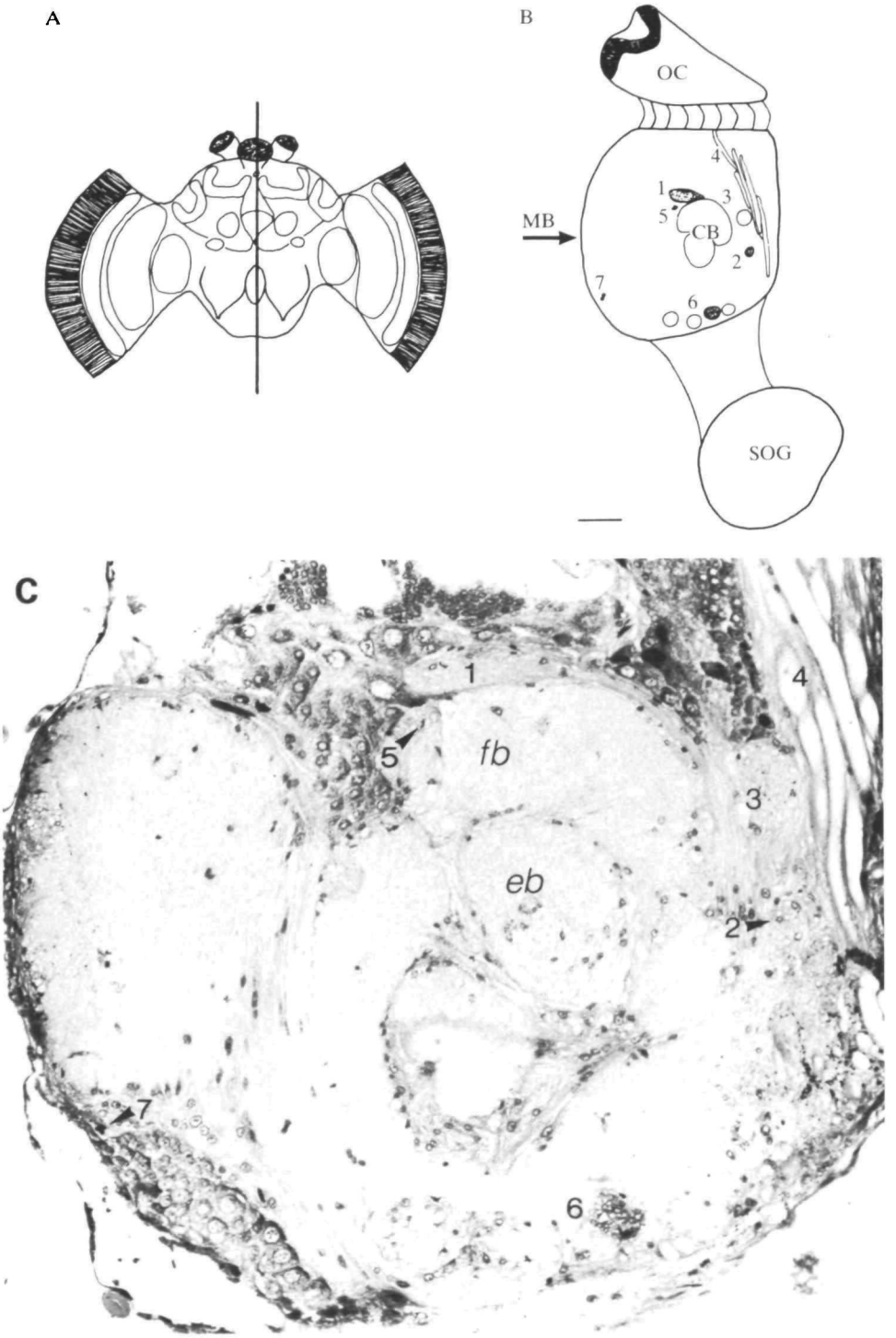


Fig. 1

the central complex at its anterodorsal part. There the axon dipped down and crossed the opposite pedunculus posteriorly; as it reached the lateral protocerebrum it divided into several neurites, one or two extending to the lobula (see below) and one to the medulla.

The ramifications in the medullae were almost identical: on both sides the main branches originated from the process which derived from the axon close to the pedunculus. Approaching the optic lobe the axon bent anteriorly and crossed the lobula dorsally. Then it separated into ventrally extending arborizations which entered the medulla neuropile anteriorly over its entire length. They gave rise to numerous branchings which projected to a layer that separated the proximal from the distal medulla (serpentine layer, Strausfeld, 1976), where they split into fine subdivisions.

Despite the symmetrical gross structure of this cell type, there were distinct differences with respect to the neuronal branchings in the lobula. One lobula was invaded by only a single process which branched into many small ramifications that extended throughout the entire posterior part of this neuropile, whereas the other lobula was innervated by two branches which left the axon. The anterior branch projected into the lobula from the dorsoposterior side and gave rise to a wide field consisting of rather thick branches at the most posterior rim of this neuropile, whereas the posterior branch entered the lobula ventrally and formed only small ramifications. In contrast to the arborizations in the medullae and the other lobula, which all showed a more finely branched substructure, the neuronal trees in this lobula had a strikingly smooth appearance.

The somata of these cells were located anteriorly in a triangle formed by the lateral calyx and the dorsal rims of the medulla and the lobula. As shown in single-cell labellings, the soma was found on the side with the smooth lobula branchings.

Fig. 1. Location of the visual commissures in the midbrain. (A) Frontal schematic representation of a bee brain. The bar in the middle indicates the plane for the 5 μm thick saggital section in B and C. (B) A schematic drawing showing the three main compartments: the median ocellus, the midbrain, and the suboesophageal ganglion. In the midbrain some prominent elements are inserted, which are given in detail and higher magnification (×125) in the light micrograph of C. Some fibres in the dorsal bundle of the anterior optic commissure (1) contain cobalt; the ellipsoid body and the fan-shaped body as parts of the central body, and the protocerebral bridge are indicated. The posterior optic commissure (2) is located below the protocerebral bridge (3). Oblique longitudinal sections through the big ocellar interneurones (4) are at the posterior side of the brain. Close to the border of the anterior optic commissure and the fan-shaped body run the axons of the serpentine optic commissure (5). Dorsal to the passage of the oesophagus is the inferior optic commissure (6). At the frontal surface of the brain the interlobula pair (7) is stained. Scale bar in B, 100 μm. Abbreviations for all figures: α, alpha lobe of the mushroom body; CA, calyx; CB, central body; *eb*, ellipsoid body; *fb*, fan-shaped body; LO, lobula; MB, midbrain; ME, medulla; OC, ocelli; OT, optic tubercle; SOG, suboesophageal ganglion; a, anterior; d, dorsal; p, posterior; v, ventral; r, right; l, left. All numbers inserted in Figs 3–6 indicate the depth of the neurone relative to the frontal brain surface. → indicates the side of signal input.

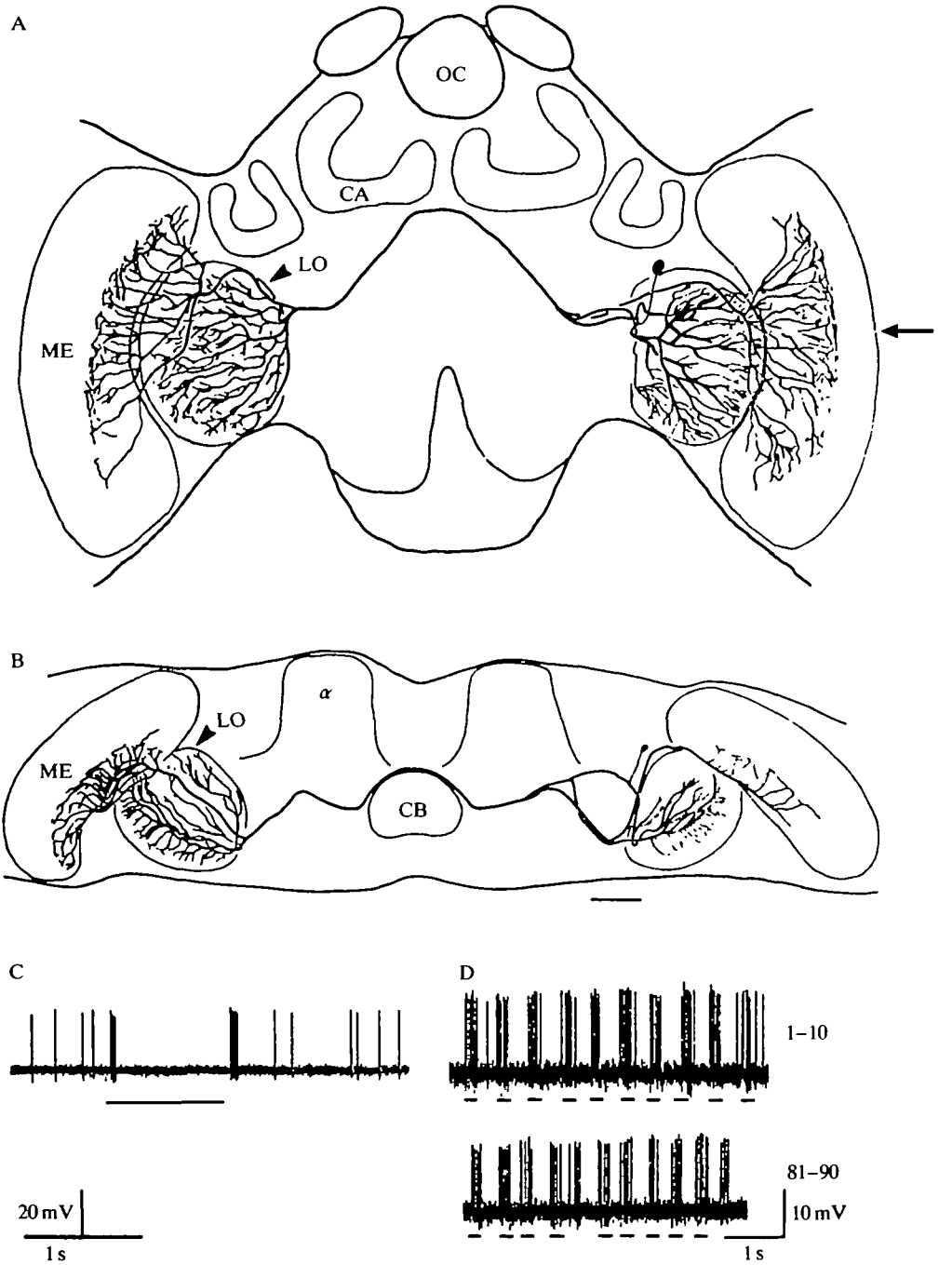


Fig. 2

Physiology

The serpentine cells from which recordings were made ($N = 25$) had a zero or very low spontaneous action potential frequency (0–5 Hz) under constant illumination. The receptive field was uniform and covered the entire visual field of only one eye. The input side always correlated with that side of the brain having the two lobula branches (see above).

A stationary flash of light elicited a brief phasic on- and off-response and a tonic inhibition during light-on (Fig. 2C). The best stimulus seemed to be movement, the neurone responding strongly to small objects moving in dim room light. There was no preference for direction of movement and repeated presentation of a moving stimulus caused no adaptation or habituation to the response (Fig. 2D).

On varying the size of a moving bar, it became evident that the magnitude of the response was correlated with the extent of the stimulus perpendicular to the movement; the direction of movement, however, had only a minor influence on spike frequency.

The spectral efficiency of the neurone was measured by using different monochromatic lights of equal quanta. The neurone responded to all three types of photoreceptors (u.v., blue and green), with a slight preference for green light, and therefore can be considered as being broad-band. However, no wavelength-selective differences were observed other than quantitative changes, which were balanced by changing the intensity of the spectral stimulus.

The posterior optic commissure (POC)

Morphology

The POC consisted of about 200 almost bilaterally symmetrical elements that connected the medullae of both optic lobes. A single POC cell is shown in Fig. 3A. Its axon invaded both medullae from the dorsoproximal side and branched into wide arborizations throughout the whole serpentine layer. From the medulla, the axon turned posterioventrally to cross the brain close to the posterior surface, slightly ventral to the protocerebral bridge. The somata of the POC neurones were located frontally to the lobula.

Physiology

All the POC neurones from which we recorded ($N = 15$) showed a constant spontaneous spike discharge between 10 and 25 Hz. The best stimulus was a

Fig. 2. Structure and responses of the serpentine neurone. *Camera lucida* reconstructions; (A) a frontal and (B) a horizontal view after intracellular marking. The axon runs anteriorly to the dorsal part of the central body and posteriorly to the pedunculi of the mushroom bodies. It connects wide branchings in the medullae and lobulae of both brain hemispheres. Scale bar, 100 μm. (C) Response to a stationary flash of green light (540 nm, 1 s), giving a phasic on and off excitation and a tonic inhibition during light-on. (D) A moving object elicits a phasic response whenever it passes through the receptive field. A repetition of the movement stimulus leads to the same phasic excitation at the beginning of a series (upper line: stimuli 1–10) as is observed at the end of a series (lower line: stimuli 81–90). For abbreviations see Fig. 1.

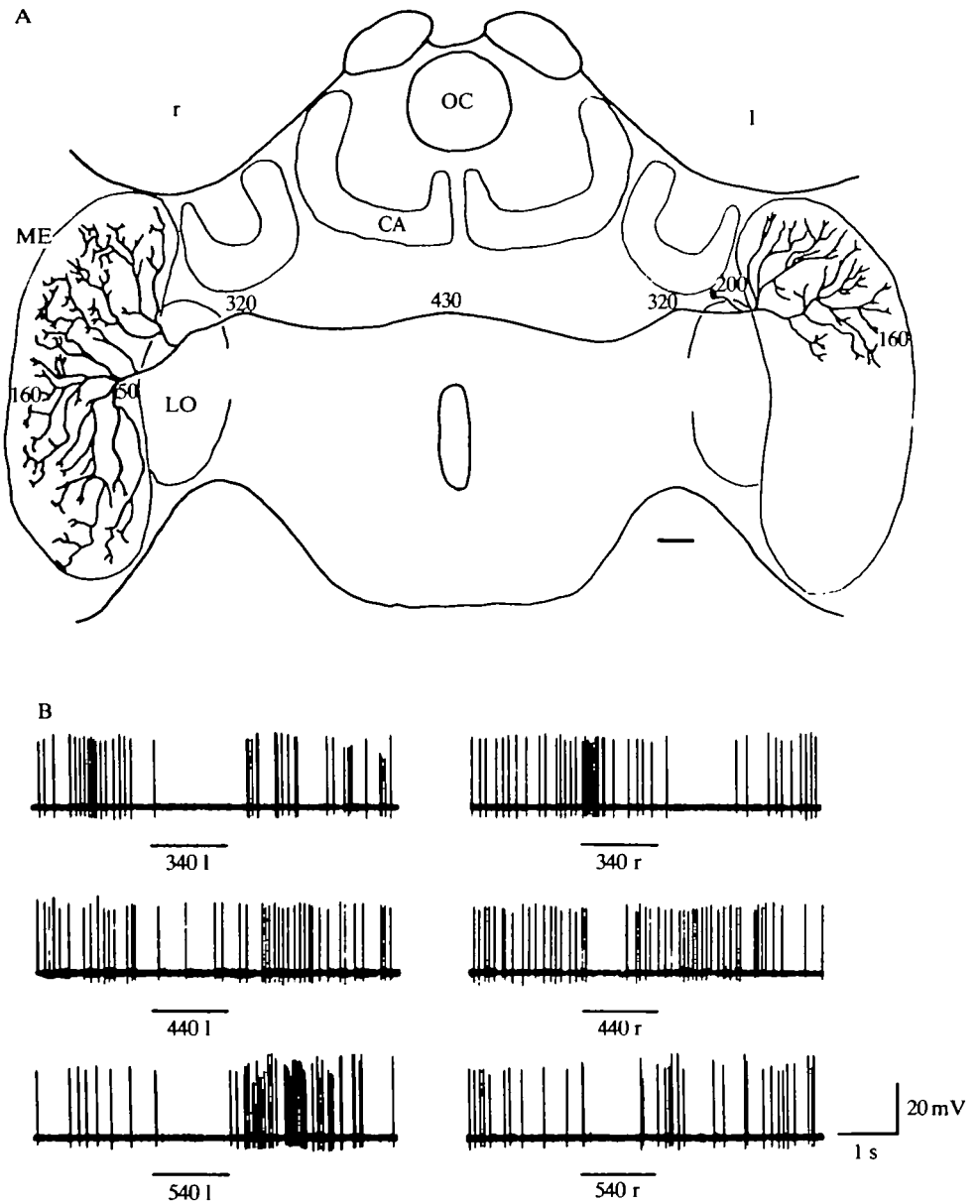


Fig. 3. Structure and response of a neurone in the posterior optic commissure. (A) Reconstruction of a cell in a frontal view from an intracellular marking. The axon connecting the two medullae runs along the posterior side of the brain, and gives rise to arborizations throughout the dorsal part of the serpentine layer of that medulla which is ipsilateral to the cell soma. In the contralateral medulla wide ramifications spread out through the whole serpentine layer. Scale bar, 100 μm. (B) Stimulation with blue (440 nm) and green (540 nm) light of equal quanta inhibits the cell both under right (r) and left (l) eye illumination. u.v. light (340 nm, equal quanta) causes an inhibition when presented to the left eye, but gives an excitation, followed by a long off inhibition, when shone onto the right eye. For abbreviations see Fig. 1.

stationary light, which elicited a tonic change in the spike frequency. The response showed spatial antagonism: either tonic excitation or inhibition depending on the location of the stimulus in the receptive field. For the cell shown in Fig. 3B, the wavelength of the stimulus was also varied. Green and blue light always inhibited this neurone, regardless of which eye was stimulated. Stimulation of the left eye with u.v. light resulted in inhibition, whilst stimulation of the right eye resulted in excitation. Therefore, this cell is able to detect the location of a combined spatial and spectral contrast, because it will increase the discharge frequency if a u.v.-reflecting object is in the right visual field, and decrease the discharge frequency when light of any spectral content illuminates the left visual field.

In the majority of our recordings the receptive field of each cell covered both eyes. Stimulation of one eye led to excitation, but stimulation of the opposite eye led to inhibition, irrespective of the wavelength of the light. Spatial antagonism could also appear between the lateral and binocular frontal part of the two eyes, or was restricted to only one eye in the rarer monocularly sensitive neurones.

The inferior optic commissure (IOC)

Morphology

The IOC consisted of about 210 neurones which connected the lobulae of both brain hemispheres. The axon of each unit crossed the brain almost rectilinearly, ventrally to the β-lobes of the mushroom bodies and close to the passage of the oesophagus (Fig. 4A). The axon entered both lobulae posteriolaterally where it gave rise to multiple arborizations. These branches extended tangentially into the layer that separates the distal and proximal lobula neuropile (layer 4 of Ribi & Scheel, 1981), and invaded the columns of the distal lobula where they divide into numerous finer dendrites. The cell soma lay ventrally and close to the curvature between the optic lobe and the suboesophageal ganglion.

Physiology

All recordings from neurones in the IOC ($N = 10$) showed spontaneous discharges with a frequency between 15 and 35 Hz. Most of the cells did not respond to a stationary light flash. A moving visual stimulus, however, was very effective and elicited either excitation or inhibition, depending on the direction of movement (Fig. 4B). In the majority of our recordings, this directional selectivity was restricted to one eye, and the main axes of the antagonistic sensitivity were mostly found in the dorsoventral or anteroposterior plane. No striking correlation was found between the substructure of the presumed dendritic arborizations of the neurones and the optimal direction of movement of the stimulus. The cells show broad-band sensitivity with some preference for green light stimuli.

The anterior optic commissure (AOC)

Morphology

Electron microscopic investigations showed that the AOC was composed of about 3200 neurones which crossed the brain at the dorsal rim of the central body

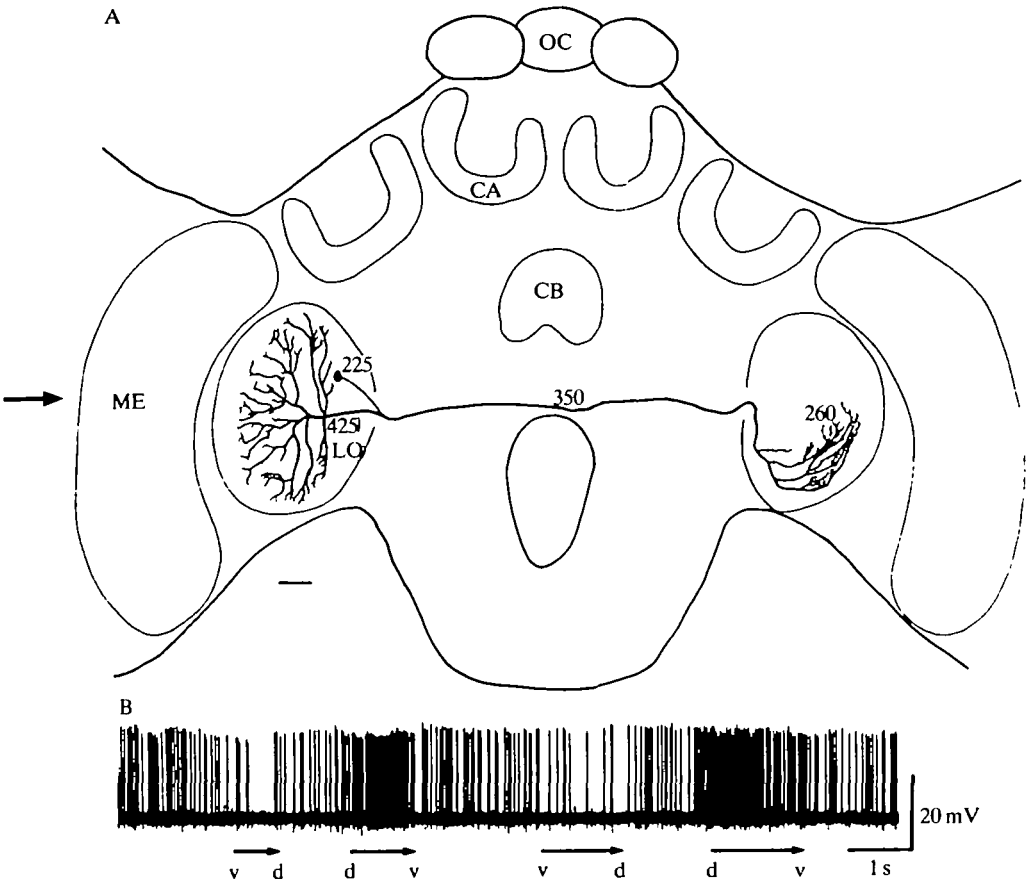


Fig. 4. Structure of a neurone from the inferior optic commissure. (A) The frontal view shows a reconstruction of an intracellular marking. The axon of the cell crosses the brain slightly dorsal to the oesophagus and projects tangentially into the distal lobula. The opposite lobula is invaded by varicose arborizations which branch in the ventral part of the lobula. Scale bar, 100 μm. (B) The neurone is sensitive to monocular motion and shows a directionally selective response. A movement at the right eye in a dorsoventral (d → v) direction causes excitation; movement in the opposite direction inhibits the cell. For abbreviations see Fig. 1.

A. Fröhlich & H. Hertel, unpublished observations). From sagittal sections at the midline of the brain three different bundles, probably of different origin, could be identified. Each bundle was wrapped in a separate sheath of glial cells. The axon diameters of most cells were below 1 μm, and these cells could not be characterized using intracellular recording techniques. The dorsal bundle of this commissure consisted of about 180 neurones, and of these only 14 cells had axon diameters of about 3 μm and were thus recordable. Fig. 5A shows a diagrammatic reconstruction of such a cell. Neurones of this kind bypassed the mushroom bodies anteriorly, bent ventrally and invaded both lobulae with wide arborizations. The ramifications ipsilateral to the soma had a distinct bleb-like substructure. The cell bodies were located proximal and posterioventral to the lobula.

Physiology

The neurones from which recordings were made ($N = 4$) fired at a constant, high, spontaneous frequency of about 50 Hz. They responded to monocular visual stimulation contralateral to the cell soma. The receptive field covered the whole eye. In the example presented in Fig. 5B, stationary blue (440 nm) and green (540 nm) light of equal quantal content elicited only a slight on–off excitation; u.v. light did not result in excitation. In other cells of this sub-bundle the response to stationary light was a tonic inhibition. All neurones were motion-sensitive with a preference for unidirectional movement. The neurone in Fig. 5B showed its strongest response to movement of a striped pattern when the movement was in a dorsal to ventral direction. Other neurones showed a preference for movement in other directions.

The anterior interlobula pair

Finally, we present some additional data on neurones with characteristic anatomy which have already been described in great detail as 'HR' (horizontal regressive) movement detectors (DeVoe, Kaiser, Ohm & Stone, 1982).

Morphology

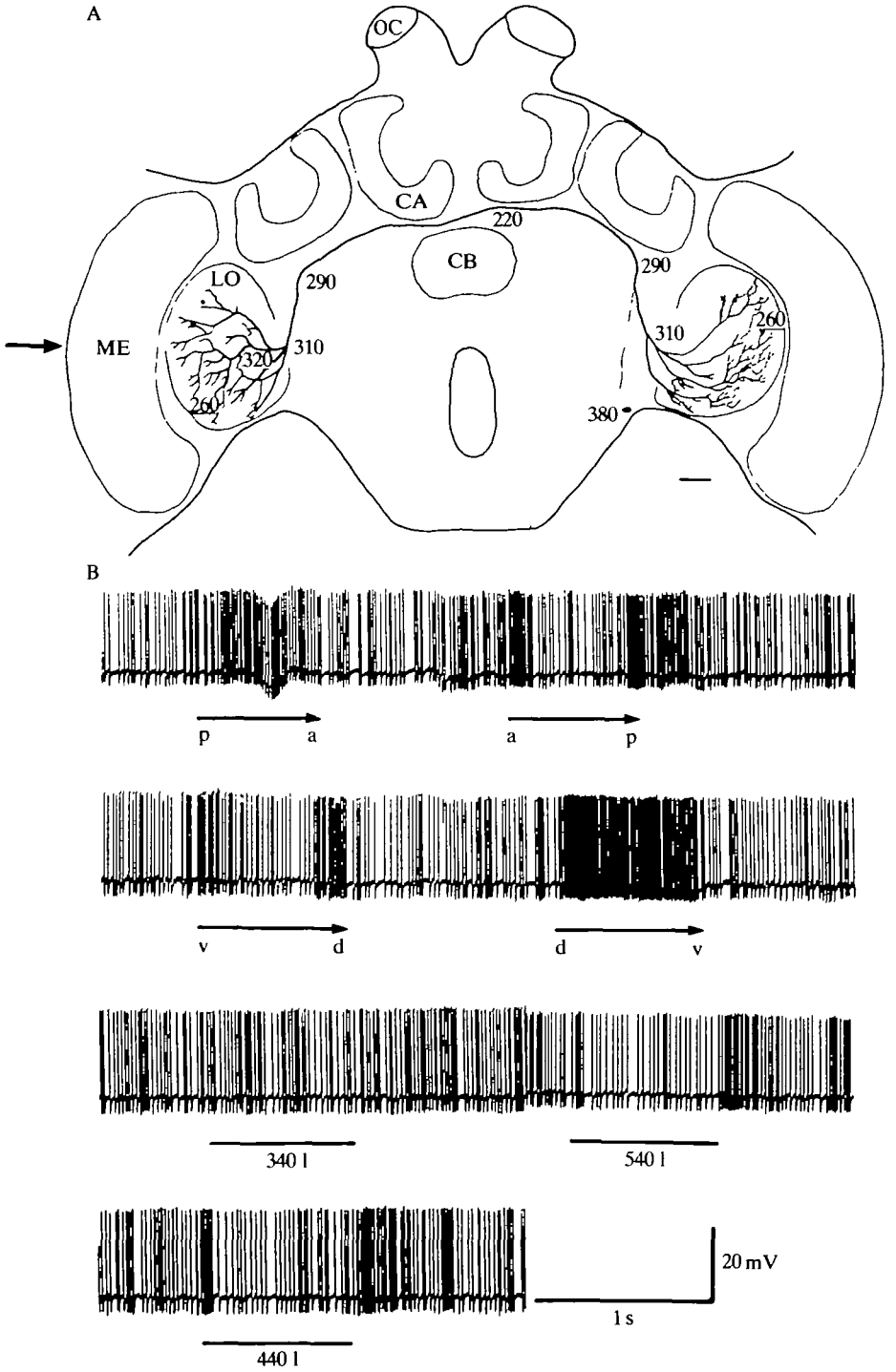
Cobalt backfill histology clearly showed that there was only one pair of these cells in the bee brain, and that this pair was arranged mirror-symmetrically. Both neurones had two wide tangential arborizations in each lobula (Fig. 6A,B) and were very conspicuous since they were connected by an axon that ran very close to the lobula-to-optic tubercle tract (the anterior optic tract of Kenyon, 1896, and Strausfeld, 1976). This axon passed the optic tubercles posteriorly, and then crossed the brain parallel to the interoptic tubercle commissure near the frontal surface of the brain. Furthermore, these two neurones were the only cells observed so far in which the primary neurites ran in parallel with the two axons for such a long distance.

Physiology

In our recordings ($N = 2$) these neurones had a spontaneous activity of about 30 Hz, and responded only to monocular stimulation. A stationary light flash elicited a phasic on and off excitation (Fig. 6C). The cell was also movement-sensitive but, in contrast to the results of DeVoe *et al.* (1982), in our experiments did not show any directional selectivity. Instead it responded to a moving stimulus with a tonic excitation, independent of the direction of movement. If the cell was hyperpolarized to reduce the high level of spontaneous activity it did not change its characteristics but the non-directional movement sensitivity became even more evident.

DISCUSSION

Although there have been detailed investigations of the photoreceptors in the compound eye of the bee (Menzel & Blakers, 1976; Wehner & Bernard, 1980; Ribi, 1981; Meyer, 1984), only a few studies have been undertaken on neural processing.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d
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340 l
540 l
20 mV
1 s
440 l

Fig. 5

Some electrophysiological data on lamina monopolar cells have been presented by Menzel (1974); a limited number of higher-order interneurones in the medulla and lobula have been investigated and some of these were identified by dye injection (Kien & Menzel, 1977*a*,*b*; Hertel, 1980); Erber & Menzel (1977) classified central visual interneurones with respect to their movement sensitivity; DeVoe *et al.* (1982) identified similar cells by dye injection; whilst Homberg (1982) and Gronenberg (1984) looked for multimodal inputs to these neurones.

With the exception of the lobula plate neurones of the fly (Hausen, 1984) no systematic analysis of visual commissures has so far been undertaken in insects. The small size of high-order visual interneurones still prevents a systematic electrophysiological investigation, and thus only a few of these cells have been analysed in the bee brain. Nevertheless, our histological data indicate that there is an equal chance of making a recording for all neurones in the visual commissures. This does not apply to the anterior optic commissure, where most neurones resist recording since they have a relatively small diameter (below 1 μm).

These commissures connect both optic lobes and, therefore, provide direct information exchange between the different stages of the visual system. All neurones described here have wide arborizations at the side of the signal input, which is as one would expect since they have wide receptive fields which cover either one entire eye or both in the case of binocular-sensitive cells. Our observations suggest that different visual coding mechanisms can be attributed to specific commissures of the bee brain.

The high sensitivity of the serpentine neurones to a moving visual stimulus is a distinct feature that allows the neurone to be positively identified from recordings. To clarify the functional significance of this neurone, it is necessary to distinguish which of the ramifications in both medullae and lobulae are input areas and which are output areas. As mentioned above, the only striking difference in the fine structure amongst the four arborizations is the rather smooth appearance of one lobula field, the other three looking very blebby. In all recordings from monocular cells, blebby ramifications were never on the side of signal input (Hertel & Maronde, 1987). Assuming that very similar appearances under the light microscope suggest similar functions, it is most unlikely that the two medulla fields are the inputs of the cell, in view of the fact that this cell only has a monocular input. It is more than likely,

Fig. 5. (A) Reconstruction of a neurone that runs in the dorsal bundle within the anterior optic commissure. The cell connects the two lobulae. The lobula ipsilateral to the soma is invaded from the ventral side by branches with obvious bleb-like structures. In the opposite lobula branches divide widely in the third layer. Scale bar, 100 μm. (B) The neurone is monocularly sensitive to light coming from the side contralateral to the cell soma. The strongest response is to a moving grating. A horizontal movement (anterior to posterior, a$\rightarrow$p, and *vice versa*) gives only a very slight response. Vertical downward movement (dorsal to ventral), however, causes a strong excitation; the opposite direction leads to a very weak change in the activity of the cell. The neurone shows an enhanced sensitivity to long-wavelength light (440 nm, 540 nm), which gives an on and off excitation, and a slight tonic inhibition. u.v. light (340 nm) elicits no response. For abbreviations see Fig. 1.

therefore, that the smooth ipsilateral lobula arborization is the locus of signal input to the serpentine neurone.

The symmetrical arrangement of the serpentine neurone implies a possible function in comparing visual information arising from the two compound eyes. When the bee approaches an object during flight the moving visual world stimulates both compound eyes almost equally, which results in an equal stimulation of the serpentine cells. Any deviation from this situation would result in an asymmetrical input to the serpentine system and this, coupled with a compensating mechanism, could be used for symmetry detection during the asymmetrical approach of the bee towards an object, e.g. a flower.

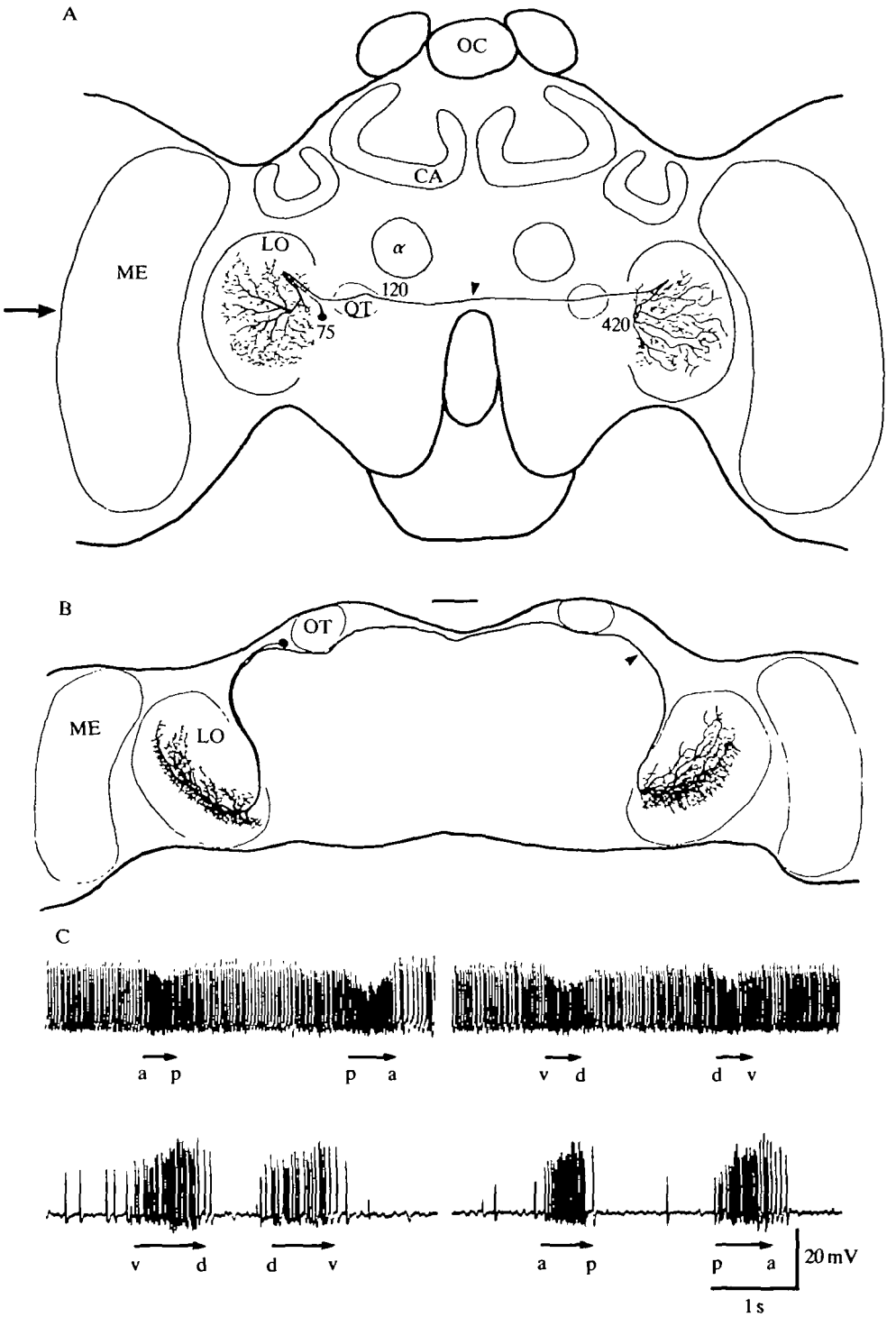
POC neurones have very similar response characteristics to those described by Honegger (1980) for the 'sustained medulla neurones' of the cricket. However, in contrast to his results, we never found a circular centre–surround antagonism of their receptive fields. All the POC cells were large-field neurones and this is not surprising considering the wide extent of their arborizations in the medulla. In other POC cells the antagonistically acting substructures in the receptive fields were also found to be much smaller, covering only about one-quarter of the eye.

An obvious antagonistic mechanism is seen in POC neurones which all have high spontaneous activity. The sign of the antagonistic response depends on the position of the stimulus in the receptive field and requires two different inputs, one excitatory and one inhibitory.

The neurone illustrated in Fig. 3 displays an additional spectral opponency. A similar combination of spatial and spectral opponency has been described for a medulla cell in the locust (Osorio, 1986*b*).

It is highly likely that the principal functions of POC cells is the analysis of intensity and/or spectral patterns, since they exhibit characteristic response patterns to spectral light flashes. As they show no movement sensitivity during 'fast forward' flight the POC cells may only play a minor role. However, the bee will often hover during approach to an object, enabling adjustments to be made in its position relative to the contrast field of the object (Wehner & Flatt, 1977). In such a situation the contrast pattern of the bee's visual field remains constant (as opposed to when the bee is in 'non-hovering' flight) and the POC cells will respond to any change in contrast.

Fig. 6. A neurone of the interlobula pair. (A) Reconstruction in a frontal view from two cobalt-injected cells. (B) Horizontal view. The left side is reconstructed from a Lucifer yellow-injected cell after intracellular recording, the right lobula branchings are the result of a separate cobalt marking. The arrowheads indicate the point of graphic connection. This unique neurone invades layer 5 of both lobulae, and extends distally with smaller branchings into layer 4. The interconnecting axon has a symmetrical shape. It bends anteriorly at the proximal side of the optic lobes, crosses the frontal surface just behind the optic tubercles, and follows the interoptic tubercle commissure through the midbrain. The soma is lateral to that optic tubercle which is at the side of the signal input. The primary neurite accompanies the commissural axon centrifugally up to its entrance into the lobula. Scale bar, 100 μm. (C) This cell has a visual field that covers the entire eye that is ipsilateral to the cell soma. It responds to a moving pattern with excitation, irrespective of the direction of the stimulus (upper trace). This becomes more evident after reducing the spontaneous activity by hyperpolarization of the membrane potential (lower trace). For abbreviations see Fig. 1.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a p
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20 mV
1 s

Fig. 6

Movement-sensitive cells in the IOC showed directional selectivity, different cells having differing optima for specific directions of movement. We found neurones with antagonistic responses to forward–backward or upward–downward movement of a striped pattern. Binocular-sensitive cells were found that are probably involved in the analysis of rotatory or translatory movement, and these cells showed antagonistic responses to opposing or equal directions of movement. Our data do not reveal obvious structural diversities that can be traced back to those functional differences. This is in contrast to the H1 and V2/V3 system of the fly, in which specific coding properties can be attributed to identified neurones which differ markedly in structure (Hausen, 1984).

Neurones with similar physiological properties, such as those belonging to the IOC, have often been reported in other insects (Collett, 1972; DeVoe & Ockleford, 1976; Dvorak, Bishop & Eckert, 1975; Hausen, 1984; Osorio, 1986*a*). One of the most investigated commissural cells in this context is the H1 neurone of the lobula plate of the fly (Hausen, 1984).

The most prominent commissure in the brain, the AOC, probably does not group neurones of similar function. There are indications that this fibre bundle functions as a bridge between the hemispheres, and contains elements of different origin, as described in *Drosophila* (Fischbach & Lyly-Hünerberg, 1983). The projection areas of the neurones in this dorsal part of the AOC, from which we recorded, are very similar to those of the IOC fibres. There are only minor differences concerning their function in coding the direction of movement.

The reason we presented our results from the anterior interlobula pair of neurones, described as HR movement detectors by DeVoe *et al.* (1982), is that we did not see the distinct directional selectivity they found. Instead, the same kind of tonic excitation was always measured, irrespective of the direction of movement. Directional selectivity in motion detection was found in many other lobula neurones (IOC, AOC and lobula extrinsic cells; Hertel & Maronde, 1987).

Our investigation of visual commissures demonstrates that these consist of neuronal elements which code for specific qualities of a visual stimulus. The data now provide the basis for a more quantitative analysis, which should describe functional subclasses that probably have substructures in common.

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