Electrophysiology of the locust medulla

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Declaration

All of the work here is my own.

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Abstract

A general introduction to the electrophysiology of the locust (Locusta migratoria) optic medulla is given here. This is the most extensive study yet of this ganglion, an attractive site at which to study low level visual processing. We look at the role of neurons both as substrates for general visual processing, whose outputs may be used for many tasks, and as more specialised units contributing to a particular behaviour.

Attention is drawn to qualitative differences between two main types of cells. The first providing a generalised intensity map of a scene (chapter 3), whilst the second has a severly impoverished neural image (chapter 4). These latter code the timing of intensity changes (perhaps equivalent to the position of edges) with accuracy, but do not signal any further detail. The cells in chapter 5 can be placed under the rubric of those in chapter 3, but they are described in the context of a particular behavioural role, flight course control. A small study of behaviour is included, in which the spectral sensitivity of flight course control is examined in the light of recordings made here. Finally we mention some directionally sensitive cells (chapter 6). They do not resemble the other units described here, or the familiar directionally selective cells of insect lobula complex (Hausen 1981). These directional cells may also be best understood by looking at their role in one particular behaviour.

Most of the cells mentioned here have receptive fields of below 20^{o} in diameter, and are probably elements in regular arrays repeated at various frequencies relative to the visual sampling array provided by the compound eye. Thus they are engaged in retinotopic processing analagous to that in the vertebrate retinal ganglion and visual cortex. The medulla provides a promising preparation for comparitive studies between vertebrates and invertebrates. In this spirit a more general look at spatial vision from the perspective of the findings here is included (appendix).

Contents

Chapter 1 : Introduction

In studying vision we are looking at several steps in which patterns of radiant energy are collected by an animal, and cues abstracted to guide movement and recognition. The elements of the visual system, optical, chemical and electrical, can be approached in two principal ways. Either as parts of a transmission system, providing a reliable image to a homunculus in the centre of the brain. Or as devices for processing information to guide behaviour. The value of these approaches depends upon the level of processing under investigation. It appears reasonable to assume that lenses and photoreceptors are adapted to glean as much data as possible from the environment (Snyder 1977). Higher order processing requires abstraction of particular features such as hands (Gross et al 1972), we cannot describe cells here as elements in a generalised information transmission system. The difficulty in deciding how far the visual system can be seen as a simple transmission device is highlighted by Barlow (1981), who has been a major advocate of the use of the powerful analytical tools developed by communication and coding theory (Shannon & Weaver 1949; Barlow 1961; Jain 1981). These methods are limited to the interpretation of simple recoding for transmission, and do not help us understand how data should be analysed.

This work is an exploration of the insect medulla, a little studied optic ganglion. An attempt is made find a suitable way of describing the cells there. This may give some insight into the strategies used in early vision, where simple coding theory cannot provide an adequate framework for the interpreation of neural properties. The introduction looks briefly at other work in early vision which

highlights the differences between those who interpret cells as transmitters, and those who see them as interpreters of data.

The insect medulla may be compared with vertebrate ganglia which have been studied in more detail. Of particular interest are the retinal ganglion and the striate cortex. These resemble the medulla in having a columnar structure, with a fairly simple mapping of the retinal image onto the neurons (Hubel & Weisel 1962; Wassle et al 1981; Strausfeld 1984). This 'retinotopic' arrangement can be contrasted with higher order structures where cells have wide receptive fields which are not locked onto the retinal array. For example the 'space constant' cells whose receptive fields are fixed to a non-retinal reference frame, these occur in arthropods and vertebrates (Wiersma & Yanagisawa; 1971, Andersen et al 1985). The main focus of this work is to find how different aspects of a scene are encoded when the retinal image is mapped fairly simply onto neural space, but many units represent each point in the sampling array.

We now look at examples of how early visual processing has been studied, first by comparing feature oriented descriptions with those using coding theory to describe similar physiological properties. Secondly, a brief summary of the approach of Marr (1982) is given, as an example of how we might gain insight into the principles of design required beyond those set by communication theory. The best studied neural process in vision, lateral inhibition in the retina, can be seen from two perspectives. This inhibition means that a response in an element of an array will cause an opposite response in its neighbours. Ratliff (1961) suggested that the function of

lateral inhibition in the retina of Limulus was to enhance the contrast of edges, which he believed to be important in vision. In contrast Srinivasan et al (1982) show that a similar inhibiton in the fly lamina ganglion is suited to removal of redundancy in the retinal image. A process which allows optimal use to made of limited channel capacity, and can be seen as adaptation to coding all aspects of the retinal image with equal fidelity. In practice it is difficult to distinguish between these two models. We can calculate the efficency with which the strategy removes statistical redundancy, but 'edges' and their potential significance are less easy to define.

A further example of how the visual system can be seen either as a feature detector or a more generalised image coding system is exemplified by in interpretations of the striate visual cortex (area 17) in cat and monkey. The cells in area 17 of the cat show spatial antagonism. As in Limulus retina, cortical cells were originally seen as detectors of edge and line elements (Hubel & Weisel 1962). These authors saw that the edges of objects and orientations of lines are particularly important in scenes (see also appendix). An alternative view is that the same cells are adapted to provide a local spatial frequency analysis (DeValois et al 1978; Marčelja 1980). Although these authors, and others, do not always explain the advantages of spatial frequency analysis its general appeal may be that it is an efficent way of coding all aspects of any scene. In any likely scene correlation between spatial frequency channels will be (statistically) zero and hence optimal use is made of the available neural channel capacity (Bossomaier & Snyder 1986). The

differences between the coding and interpretive explanations of cortical function are highlighted by studies of development. Blakemore (1973), an originator of the idea that spatial frequency analysis is important, asserts that the development of the cortex is modified by experience so that "the system is optimally matched to its particular visual world". This would be unecessary if the cortex were performing a general local spatial frequency analysis. This would work equally well for all likely worlds.

The problem of how to analyse, rather than transmit, natural visual data efficiently was addressed by Marr (1982) and his colleagues. Recognising the complexity of the computations required in vision he emphasised the importance of simplifying the computational task for artifical vision. By analogy it was suggested that the brain would also use strategies which are computationally efficient. Three main stages of visual processing were suggested. The first produced a simplifed but essentially complete representation of the world, called the primal sketch. The second stage abstracted important 'tokens' from the primal sketch which signified the presence of structures such as edges and corners. These tokens could then be manipulated to allow, for example, recognition of objects, and reconstruction of the three dimensional world from the two dimensional retinal image. An important point exploited by Marr is that the world is constrained in a number of ways which may not be expected in an abstract mathematical scene. For example it is made of discrete opaque objects with continuous surfaces and sharp boundaries. These properties allow the visual system to solve problems, such as reconstruction of the three dimensional world,

which are otherwise insoluble (Poggio et al 1985). The point that the brain makes assumptions about the world was familiar to Gestalt psychology (Kofka 1935). Marr's work is the best attempt to delineate principles for efficient visual processing using these assumptions.

Whilst Marr approached the visual system as a mathematician and computer scientist the object here is to find the 'tokens' used in early visual processing by electrophysiological recording. The properties of cells are examined to see what aspects of a stimulus they encode. In this way we hope to build up a picture of the way in which an image is broken down in the medulla for further processing at higher levels. The medulla contains over thirty different cell types (Strausfeld & Campos-Ortega 1972; Strausfeld 1976; W.Ribi pers comm). These are repeated across the ganglion with one column of cells for each facet in the compound eye (There is not necessarily a different cell for each column in every anatomical class, some may be repeated at lower frequencies). Thus there is ample capacity to divide the input into sets of quantitatively different channels, coding different ranges of a stimulus feature like spatial and temporal frequencies. It may also have qualitatively different classes of output, with separate channels devoted to, say, hue and movement.

The arthropod optic medulla

The general organisation of the nervous system and even the identity of particular neurons is highly conserved in insects and crustaceans (Bullock & Horridge 1965; Thomas et al 1984) allowing comparisons to be drawn across these groups. Unfortunately there are few other electrophysiological studies of the arthropod medulla. This reflects technical difficulties in recording, and perhaps the complexity of the ganglion compared with other invertebrate neuropils. The most thorough work so far has been by Weirsma and his collaborators in decapods (reviewed by Wiersma et al 1982). Some cells called 'seeing fibres' have complex properties and wide receptive fields. Seeing fibres were described in terms of their behavioural correlates (Wiersma & York 1972). Weirsma saw that this type of description is not suitable for the simpler cells, associated with earlier processing. These fell into two main classes (Wiersma et al 1982). The sustaining fibres are insensitive to movments within their receptive fields, and give opposite responses to dimming and brightening. The movement fibres respond to movement within their receptive fields and give similar responses to dimming and brightening. The term sustaining fibre is used here, although it should be remebered that these units are sometimes quite phasic. We do not describe cells as movement fibres, because the conjectured function, analysis of movement, may be misleading. Previous work in the insect medulla has tended to concentrate on larger field cells (Horridge et al 1965; Honneger 1980; Hertel 1980) and is mentioned in the separate chapters but will not be described here.

Properties of inputs to the medulla

The medulla receives its primary inputs from the photoreceptors of the compound eye. These arrive either as direct projections from the long visual fibres, or from the lamina ganglion (Cajal & Sanchez 1915; Nowel & Shelton 1981). The properties of locust photoreceptors have been thoroughly studied, and the image projected by these cells is described below. The locust lamina has not been studied thoroughly, however it is probably similar to that of the fly. A brief description of the large monopolar cells recorded in the fly lamina may allow some understanding of the properties of the principal inputs to the locust medulla.

The retina

The locust retina has been the subject of several relevant electrophysiological studies. These give a good understanding of the properties of the sampling array, and hence the limitations on the information available to the brain.

The locust compound eye contains about 5000 facets (Horridge 1978), giving an almost global visual field, with little binocular overlap. The facets vary little across the eye, apart from a specialised dorsal rim region (Labhart et al 1984). Photoreceptive microvilli are interlocked making a fused rhabdom, so the eight cells in each facet have a common receptive field (Snyder & Laughlin 1973). The angular separation between facets in the eye, and hence points in the sampling array, varies from about 1^{o} to 1.25^{o} with increasing distance from the frontal-equatorial region (Horridge 1978). Thus the eye can sample frequencies up to 0.5 cycles.deg^{-1}.

All the experiments on the medulla were performed during the day, and most were on light adapted animals. Under these conditions the acceptance angle (width of the sensitivity function at half of the maximum) is 1.4^{o} (Wilson 1975). This angle increases on dark adaptation due to pigment migration, and further at night as the rhabdom increases in diameter (Williams 1983). The temporal properties of locust photoreceptors have been described by Howard (1981), and like the spatial properties these alter according to the light adaptation state. Unlike angular sensitivity temporal properties show no evidence of changes between day and night (Shi J personal communication). The locust light-adapted photoreceptor is somewhat 'slower' than that of other insects; the sensitivity drops to 50% of the maximum at about 40Hz in the light adapted state (Howard 1981; personal observations - fig 3.3). There is a small decline in sensitivity to low temporal frequencies, perhaps due to the movement of the pupil pigment (Howard 1981). No comparable attenuation of low spatial frequencies is observed in the fly retina (Dubs 1982).

A full description of the spatial and temporal properties of any system is greatly simplified if it is linear. The intensity response function of the photoreceptors is log-linear over large ranges (Matic & Laughlin 1981), but this approximates a linear response up to (Michelson) contrasts of about 0.3 (Pinter 1972; Howard 1981; and checked in the conditions used here). The locust photoreceptors described above are probably the short visual fibres which project to the lamina (Nowel & Shelton 1981). Short fibres are easily penetrated and their peak sensitivity ranges from 450nm and 480nm in

a dorsoventral gradient (Lillywhite 1978); these are probably the main 'green' sensitive input to the medulla. The long visual fibres have been less well studied, but they provide the UV inputs to the optic lobe, and have a peak sensitivity at 365nm (L.Marčelja personal communication, & see chapters 3,5).

The lamina

Most inputs to the medulla are relayed via first and second order interneurons in the lamina ganglion (Cajal & Sanchez 1915). The anatomy of the lamina is well studied, and is similar in different orders of insects (Cajal & Sanchez 1915; Strausfeld 1976; Nowel & Shelton 1981; Ribi 1981; Meinertzhagen & Armett-Kibel 1982), although the locust seems to have an additional monopolar cell (L6) (Nowel & Shelton 1981). The ganglion has a columnar structure with one cartridge for each facet in the eye. Each cartridge contains three cell classes which receive inputs from the photoreceptors (L1-3) and three which do not (L4,5,(6 in locust)). In addition there are four types of centrifugal cell, which originate in the medulla.

The electrophysiology of the large monopolar cells (L1,2) has been studied in the fly. The properties of these cells have been modelled on the basis that they are adapted to optimise transmission of information gleaned by the photoreceptors (Laughlin 1981; Srinivasan et al 1982) (see above), and do not process the inputs to extract any particular features. The first strategy which this model espouses is that the correlation of activity between channels, and hence redundancy in information transmission, should be minimised.

Secondly the dynamic range of the cells is used optimally by ensuring that each response state (membrane potential) of the cell is occupied equally often. In practice this means that the properties of the lamina cells differ from those of the receptors in two ways. Firstly the large monopolar cells show spatial and temporal antagonism which reduces redundancy (Dubs 1982; Srinivasan et al 1982). This is achieved by inhibition from neighbouring cells, and self-inhibition. Secondly, optimal use of dynamic range requires that the contrast response function of the cell is matched to the range of contrasts encountered in natural scenes (Laughlin 1981). This matching is achieved by means of a high gain synapse from the photoreceptors onto the non-spiking monopolar cells. Both large monopolar cells are hyperpolarised by brightening. The third monopolar cell of the fly lamina L3 has also been recorded and marked (Jarvilehto & Zettler 1973), it is fairly similar to L1 and L2 although the data given do not permit detailed comparison. Parenthetically, we note that the large flies like Calliphora from which these recordings of lamina cells were made are exceptional anatomically in having very similar L1 and L2 cells. In most insects, including the locust Schistocerca L2 has a wider dendritic field (Nowel & Shelton 1981),

Two further types of cell, both spiking, have been described by recording from the tract between the fly medulla and lamina (Arnett 1972). Sustaining fibres were excited by illumination in the receptive field centre, but had antagonistic flanks in the horizontal axis. The on-off cells gave a burst of spikes at light on and off, they did not show spatial antagonism. These cells may be L4,5 respectively (Laughlin 1984).

The medulla

The locust optic lobe resembles that of other insects and crustaceans (Bullock & Horridge 1965), and comprises the lamina, the medulla and the lobula complex. The medulla is the largest of the three ganglia, and contains over half the neurons in the insect brain (Strausfeld 1976). The optic lobe structure is columnar with many tangential layers. 15 layers are visible in the locust medulla (fig 1.1), but the principal divisions are the proximal and distal medullas and the intramedullary tract. These structures were visible in the preparation used here, and with tracheae provided useful landmarks during recording and after marking the cells. At present we have little idea about the functional significance of the layers of neuropil in the medulla, although 2-Deoxyglucose studies imply that there are differences in activity between the strata (Buchner et al 1984). This finding parallels observations made in the cat cortex, which shows a similar columnar structure with different layers in each column containing distinctive cell types (Hubel & Weisel 1962).

Unfortunately, the locust medulla is relatively intractable to Golgi staining (AD Blest, WR Ribi personal communication) however comparisons can be drawn with the fly which has been extensively studied (Strausfeld 1976). The fly medulla has a regular columnar structure, with one column for each facet in the compound eye. Columns are not clearly delineated as in the lamina (see also fig 1.1), but can be seen by mapping the projection from the retina onto the medulla (Campos-Ortega & Strausfeld 1972a). Each column in the fly medulla contains about 46 axon profiles, including inputs from the lamina (Strausfeld & Campos-Ortega 1972b). There are

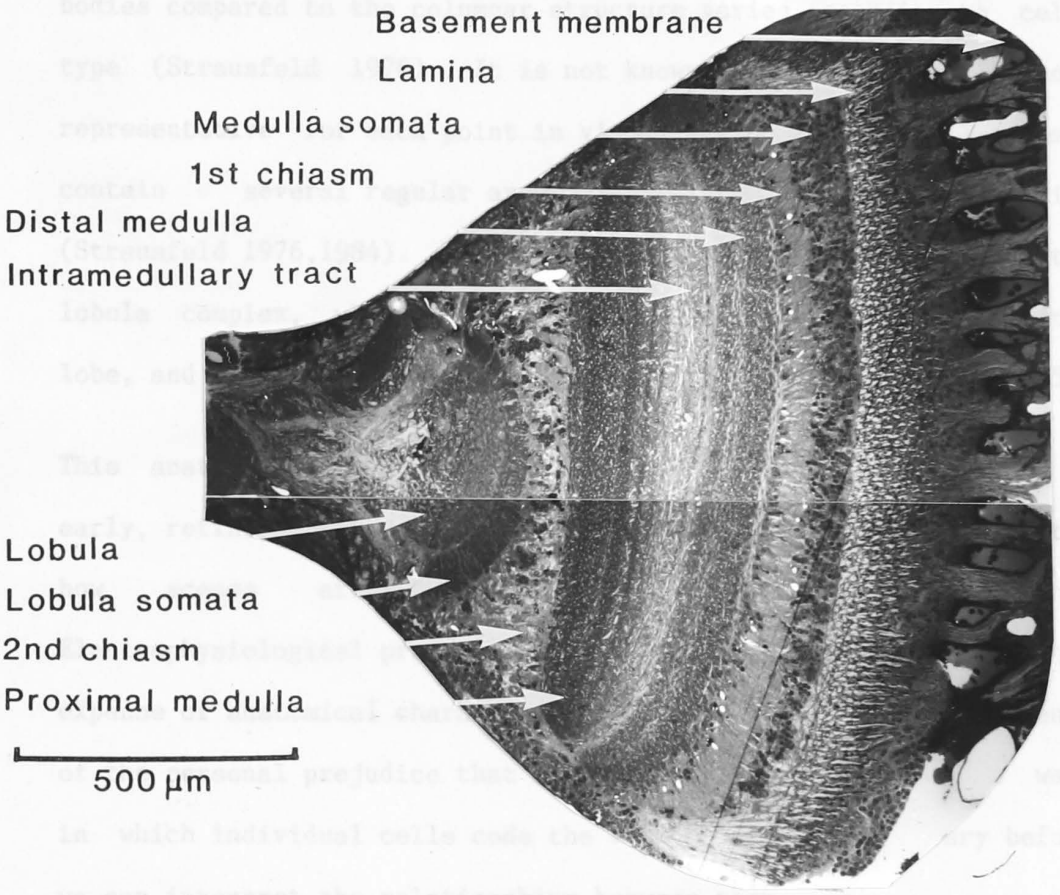


Fig 1.1

Radial vertical section through the locust optic lobe showing the main ganglia and tracts. The columnar structure visible in the lamina, due to the presence of the large monopolar cells, cannot be seen in the medulla. The layered structure of the medulla can be seen clearly . Fifteen layers were counted at high magnification. The large axon profiles visible in some layers are probably tangential cells. The section was prepared by fixation in 2.5% glutaraldehyde with 4% paraformaldehyde at pH7.5 (phosphate buffer). After post fixation in 1% osmium tetroxide the block was dehydrated in ethanol and propylene oxide, and embedded in araldite. Semithin sections were stained with toludine blue.

a further 74 classes of tangential cell. The frequency of the cell bodies compared to the columnar structure varies according to cell-type (Strausfeld 1976). It is not known how many cells have one representative for each point in visual space, and the medulla may contain several regular arrays repeated at various frequencies (Strausfeld 1976,1984). Many of the medulla cells terminate in the lobula complex, whilst others project to the contralateral optic lobe, and protocerebrum (Strausfeld 1976; Honneger & Schurmann 1975).

This anatomy implies that the medulla is suited to the study of early, retinotopic, visual processing and we may be able to find the how scenes are divided in early vision an insect. Electrophysiological properties are described in some detail, at the expense of anatomical characterisation. This is partly a consequence of the personal prejudice that a thorough understanding of the ways in which individual cells code the visual world is necessary before we can interpret the relationships between them.

Chapter 2 : Methods

The object of this study was to record from the small columnar neurons of the Arthropod optic medulla (Strausfeld 1976). Previously it has not been possible to obtain good recordings from these cells (DeVoe & Ockleford 1976; Hertel 1980). They have small neurites, and as in most arthropods the cell body is electrically isolated from active parts of the neuron. Trials were made in both cricket (Telogryllus), based on the success of Honneger (1980), and fly (Calliphora). No recordings were obtained from either preparation, but the locust (Locusta migratoria) was satisfactory. There are three reasons why the locust is a good preparation: It is easy to obtain animals of a constant age and sex from a laboratory culture. The large size and open structure of the optic lobe means that a good dissection can be made, and the preparation stabilised against body movement. Finally, the connective tissue within the optic lobe is easier to penetrate.

All recordings were made during the afternoon in female locusts five to ten days after their imaginal moult. At this age the body and tissues are in good condition for recording. The wheat fed animals were kept on a 12:12 L:D cycle, under mixed incandescant and Osram Daylight fluorescent illumination.

Electrophysiology

Intracellular recordings were made from the medulla of the right optic lobe, with animals maintained in a light-adapted state at 27°C. The animal was first immobilised and a collar set between the head and thorax with wax. Portions of the cranium were removed to expose the optic lobe. Much of the muscle at the back of the head,

and the ocelli, were then excised. A metal spoon was placed under the proximal part of the optic lobe and secured to a pillar, against which the front of the head was wedged and waxed. The preparation was perfused with Ringer's solution (Usherwood & Grundfest 1965) to prevent dessication, and with a gentle stream of oxygen blown from directly behind the head it remained viable for many hours.

Microelectrodes were pulled on a horizontal puller (Brown-Flaming P-77) from 1mm diameter borosilicate capillary glass (Hilgenberg). These had an initial tip resistance of 200 - 250MΩ when filled with 3M potassium acetate. The resistance often dropped to about 150MΩ after entering the tissue, even though the outer sheath was usually torn beforehand. After penetrating a cell a negative current of about 0.2nA, for a short period, often helped to improve the quality of recording. Using this preparation cells giving large graded depolarisations and/or action potentials could be held for over an hour. Recordings were amplified and displayed using standard equipment.

Cell Marking

Cells were marked by iontophoresis and pressure injection (Picospritzer) of Lucifer Yellow CH. About forty cells were marked, of which a few are described here. These are chosen to illustrate the position and general morphology of the units studied. It was not possible to make a thorough study of anatomy, and, in addition, it was difficult to obtain good electrophysiological recordings at the same time as marking cells. The electrodes blocked rapidly and became

unacceptably noisy. The best results were obtained by mixing the Lucifer Yellow with 2% (w/v) of lithium chloride, and spinning the solution in a microcentrifuge before each experiment. Once filled the specimens were fixed with 4% paraformaldehyde in Millonig buffer (pH 7.4), dehydrated in alcohol, cleared with methyl salicylate and viewed in whole mount using standard fluorescence microscopy.

Stimulation

The equipment here was designed for exploratory studies, and did not focus on any particular subject. Stimuli could be moved, flashed, and altered in contrast, area and hue. The most quantitative results were obtained using stationary spots. Stimuli were presented at fairly high luminance and low contrast to simulate natural conditions.

The ipsilateral eye faced a UV transparent, diffusing tangent screen, which was illuminated from behind with a xenon arc (XBO 75W) (chapter 5 only) or a 150W quartz iodide filament filtered to 5,500K (80A colour correcting filter). The illuminated region subtended 60^{o} at the locust's eye, and had a luminance of $200cd.m^{-2}$ under xenon illumination and 200 to $1000cd.m^{-2}$ with the filament (usually $500cd.m^{-2}$). Some stimuli (chapter 5) were provided by a focussed dissecting lamp, the absolute intensity of this source was not measured, and relative intensities only are given. Wholefield stimuli were provided by placing filters directly in front of the eye. In studies of spectral sensitivity (chapters 3,5) spectral filters were used. Two broad-band filters which had 70% tranmission at their peaks (365nm and 500nm), and half widths of 50nm were used

most often. With quartz optics these broad band filters gave approximately isoquantal illumination. Narrow band (10nm) interference (Schott, and Balzers), and gelatin neutral density filters (Kodak Wratten series) were also used. The neutral density filters were unsuitable as they are not spectrally flat below 450nm, individual calibration showed that the transmittance at 370nm is approximately half that at 500nm. The positions of stimuli are described relative to the animal in a level orientation, so the line viewed by the equator of the eye is called the horizon.

In most experiments stationary spots were used. These were projected from the tip of a plastic light-guide and had a similar spectral composition to the screen (quartz was used to look at UV sensitivity). The spots could be varied in intensity with quartz neutral-density filters or by modulation of the arc. A mechanical shutter (Uniblitz) allowed presentation or removal of the spots for periods down to 2ms (calibrated with a fast photodiode), with rectangular pulses. The spots could be varied in diameter from 2^{o} to 30^{o} with little effect on their quantal content. Pairs of spots (chapter 6) were obtained by splitting the arc beam, these could be presented and moved independently.

Filters attached to a chart plotter (HP 7004B) with narrow perspex rods provided moving negative contrast stimuli. For many experiments (especially in chapters 4 & 6) a perspex rod (contrast -0.12, width 1.5^{o}) was used alone. The plotter could be moved at up to $250^{o}.sec^{-1}$. The plotter, Uniblitz shutter and arc lamp modulation were all driven by standard function generators.

The contrast of a stimulus is defined as : (I1-I2)/I2 where I1 and I2 are the intensities of the stimulus and background respectively. For sinusoidal flicker Michelson contrast is used:

$$I_{max}-I_{min}/I_{max}+I_{min}$$

Stimuli were calibrated with a radiometer using a vacuum photodiode (IL700), and camera exposure meter (Pentax spotmeter). All calibration is expressed as luminance or radiance. Stimulus contrast was measured with a radiometer (IL700) by focussing an image of the screen on a 0.5^{o} aperture at the position of the locust's eye. Intensity modulation of the spot was measured directly with a photodiode during experiments. Contrast measurements were made at the position of each cell's receptive field, so they were unaffected by the uneven illumination of the screen.

The receptive field area of cells is usually defined as region over which a stimulus could elicit a response. In some cases sensitivity profiles are given, but this was often impractical.

Behavioural studies (Chapter 5)

The spectral properties of the optomotor and dorsal light responses were tested using the equipment described by Horridge, Marčelja & Jahnke (1984). The stimulator oscillated through 20^{o} at 0.1 Hz , and head roll was recorded using a capacitative detector (Sandeman 1968), whilst the thorax was fixed to a support. The spectral efficency of the dorsal light response (or horizon displacement response) was tested at contrast 0.5 with the visual field divided in two, usually with a bright dorsal region. A similar arrangement

was used by Taylor (1981) in his study of the dorsal light response. The spectral sensitivity of the optomotor response was measured at high contrast and threshold radiance, with 20^{o} stripes. Stimuli were calibrated with the equipment described above.

Analysis

The medulla cells produced a combination of graded and action potentials in varying relative amplitudes (probably depending in part on the position of the electrode in the cell). The responses were analysed either by counting the number of action potentials, or signal averaging the continuous potential. The latter procedure was convenient and allowed accurate analysis of response timing, but the signal-averaged data included both spiking and graded components.

Records were amplified using a standard (laboratory built) current amplifier, and displayed on an oscilloscope. They were then recorded directly with a chart recorder or stored using an FM tape recorder (HP 3964A). The tape recorder gave a high frequency cut-off at about 1KHz. The tape was replayed for offline analysis with a computer (PDP 11 running DAOS), digitised at 600 to 1000 samples.sec^{-1} and analysed by averaging 10 to 100 stimulus cycles. Responses to sinusoidal flicker were studied by extracting the amplitude and phase of response components at integral multiples of the stimulus frequency, using the coefficents of a Fourier series representation (program written by A.C.James).

To estimate the variance of response latency to brief flashes (chapter 4) the following convenient method was used: The signal

averaged response waveform was modelled as a convolution of the individual response waveform with the latency distribution of the response peak. All three functions were assumed to be Gaussian. Since the convolution of Gaussians involves addition of variances, the variance of the response latency can be estimated from the widths of the individual and averaged waveforms. The accuracy of the assumption that the responses could be modelled as Gaussian was confirmed by measuring the widths of the responses at different heights, giving several estimates of the variance. The accuracy of these estimates was limited by the digitisation frequencies used (600-1000 samples.sec^{-1})

Chapter 3 :

Temporal and spectral properties of linear, sustaining cells

Summary

1. Intracellular recordings were made from of cells in the optic medulla of the locust which give opposite responses to dimming and brightening, and are insensitive to movement within their receptive field. These resemble the sustaining cells described in decapod optic lobe (Wiersma et al 1982).

2. The cells' receptive field areas vary from 2^{o} to 30^{o} in diameter. They receive inputs from both green and ultraviolet sensitive photoreceptors.

3. The responses to stationary flicker are approximately linear, although the cells are more responsive to depolarising than to hyperpolarising stimuli.

4. Cells are tuned to a range of temporal frequencies between 5Hz and 30Hz, and bandwidths vary from 1.5 - 3.5 octaves. Thus there may be range-fractionation of temporal frequencies.

5. One set of cells which have similar temporal properties but a variety of spectral properties and receptive fied areas are examined in more detail. They have a phasotonic response, and their response amplitude and phase can be modelled as an addition of two linear filters. These two inputs may differ in spectral sensitivity, facilitating dissection of a complex response into its components.

Introduction

Early visual processing involves division of the retinal input into qualitatively different channels coding separate aspects of the scene. In the vertebrate visual cortex different cells code motion, colour and form (Desimone et al 1985). Similarly, different cell types are found in the optic lobe of decapod crustaceans (Weirsma et al 1982). The firing rate of decapod sustaining fibres is a function of the overall light intensity, whereas jittery movement fibres respond to motion within the receptive field. Orthopteran insects also have a range of visual cells (Horridge et al 1965, Honneger 1980). This paper looks at a number of cells in the medulla of the locust optic lobe which can be placed in the general class called sustaining fibres by the earlier authors. These cells give opposite respones to dimming and brightening over the entire receptive field area, but are insensitive to movements within it. In the absence of anatomical and behavioural data the classification of the neurons here as one group is somewhat arbitary, and we cannot say whether they form a single functional class. Nonetheless they differ markedly from the other main group of cells in the locust medulla, which give similar responses to dimming and brightening, and are usually sensitive to movment within their receptive fields (chapter 4). A general summary of the temporal tuning properties of the sustaining cells is given, with a more detailed discussion of the temporal and spectral aspects of some responses. The object is to examine the function of sustaining cells, and describe the neural image conveyed by them.

Data analysis

Phase relations

The calculation of phase-shifts in responses to sinusiodal flicker, important in analysis of these cells, was complicated by the presence of a delay attributable to phototransduction (Kuster & French 1985) and signal transmission. When response phase was calculated (figs 6,7) the delay was measured by finding the time of onset of the impulse response (to a 2ms stimulus), which varied from 16ms to 40ms. Unfortunately this method is fairly inaccurate; a change of only a few millisecods in the calculated delay will have a marked effect on the estimated phase-relation between stimulus and response at high frequencies. A further potential source of error in calculation of phase relations is non-linearity of the response. However, this was probably not important as there was little or no effect of changing stimulus amplitude on the response phase up to the maximum stimulus amplitude used (fig 6b).

Sensitivity measurement

As far as possible the results here refer to measurements of true sensitivity profiles, in both spatial and temporal domains. Receptive-field width is defined as the region over which the sensitivity to a flash or flicker is over half that at the point of maximum sensitivity. Bandwidth is measured using a similar criterion: That is, the range of frequencies over which (linearised) response amplitude is over half of the maximum.

Results

The results describe the responses of about 30 units recorded intracellularly in the locust optic medulla. These fit loosely into the class called sustaining fibres by Weirsma (1982) and Honneger (1980). Two cells are illustrated in figure 1. The records included both graded and action potentials in varying relative amplitudes. Here we refer mainly to graded potential recordings, from which spikes were largely absent. This allows analysis with high temporal resolution. Records were analysed after digitisation at over 600 samples.sec^{-1}. The majority of cells did not spike in response to stimuli of moderate contrast.

The results give a general picture of the range of properties observed in locust sustaining cells. The temporal properties are of particular interest; we look at the linearity of responses and the ways in which the photoreceptor inputs are filtered. Some cells are studied in more detail to gain a better idea of the neural image they convey.

Contrast response functions

All cells were studied in a light-adapted state using stimuli of modest contrast. The relationship between stimulus and graded potential response amplitude was approximately linear over a smaller range of contrasts than the photoreceptors (Howard 1981; Personal observation). There was a marked departure from linearity above a contrast of at most 0.2 to sinusoidal flicker at the optimum frequency (figs. 2d,6b). Although results are not directly

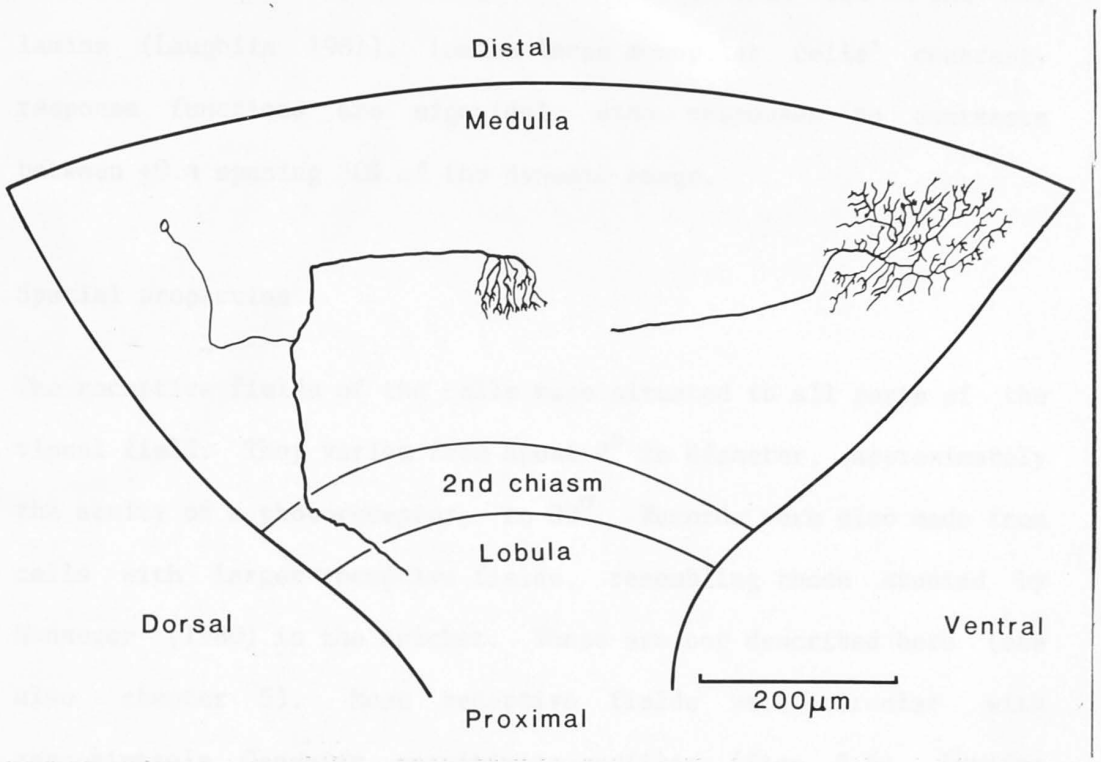


Figure 3.1

Diagram of the medulla showing two cells filled with Lucifer yellow CH. Both were sensitive to green light alone, and both were depolarised by dimming. The receptive field diameter of the smaller unit was below 10^{o} in diameter, and the larger unit had a field about 20^{o} across. The position of the cell body in the larger cell was unknown.

comparable, the response range is similar to that seen in the fly lamina (Laughlin 1981). Lamina large monopolar cells' contrast-response functions are sigmoidal, with responses to contrasts between ± 0.4 spaning 50% of the dynamic range.

Spatial properties

The receptive fields of the cells were situated in all parts of the visual field. They varied from about 2^{o} in diameter, approximately the acuity of a photoreceptor, to 30^{o}. Records were also made from cells with larger receptive fields, resembling those studied by Honneger (1980) in the cricket. These are not described here (see also chapter 5). Most receptive fields were circular with approximately Gaussian sensitivity profiles (figs 5,6). Lucifer Yellow fills of the two cells illustrated (fig 1), and others, showed that the area of dendritic fields corresponded to the physiologically recorded receptive field. This implies that receptive field areas were not underestimated because of response decrements during electrotonic conduction from distant dendrites. Approximately equal numbers of records were obtained from cells with receptive field diameters of 2^{o}-5^{o}, 6^{o}-15^{o} and 15^{o}-30^{o}. One unusual green sensitive cell had an antero-posteriorly elongated receptive field with dimensions at 50% sensitivity of 7^{o} by 25^{o}.

Evidence for antagonistic surrounds was obtained in some records, but in others there was no clear spatial antagonism. It was difficult to quantify the area or power of surrounds in the medulla cells, as inhibitory components in the response usually occurred after the initial depolarisation. The property was most apparent in

two cells which also exhibited spectral opponency. These units appeared to be 'double opponent' with UV-,G+ centres and UV+,G- surrounds (see also chapter 5). Parenthetically, we note that the large monopolar lamina cell (Lucifer yellow filled) whose response is illustrated in figure 3 had a marked antagonistic surround.

Temporal properties

Temporal aspects of the medulla cells' responses were studied in more detail than spatial. These included the tuning of the response, stimulus-response phase relations at different frequencies, and the linearity of the responses. Stationary sinusoidal flicker and brief (2ms) increments and decrements, which approximate impulses, were used.

Linearity

The graded-potential waveforms of the responses to flashes and sinusoidal flicker superficially resembled those of retinula or lamina cells. Photoreceptors give linear responses up to contrasts of about 0.3 (Howard 1981). Some medulla cells depolarised and others hyperpolarised in response to increasing light intensity; thus they may be designated as on and off cells respectively. However, unlike their inputs the medulla units often showed larger amplitude depolarisation than hyperpolarisation to pulses of low contrast (below 0.3 presented for 2ms), and clipping (half-wave rectification) of the responses to sinusoidal flicker (fig 2). This phenomenon, which implied that the cells were resting at the bottom

Figure 3.2

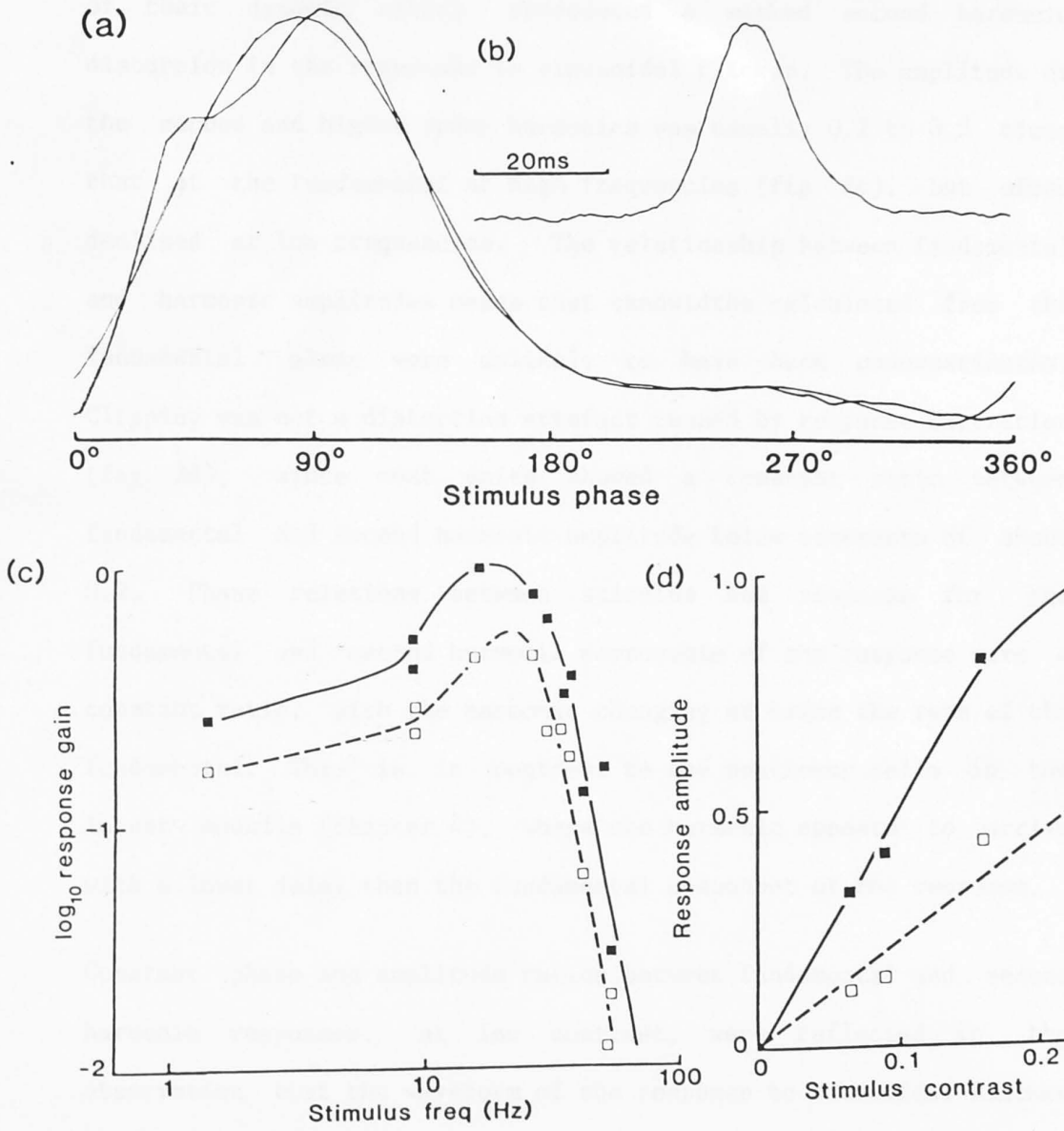
Responses of a cell showing half-wave rectification.

a. Response to 11Hz sinusoidal flicker, contrast 0.1, fitted with the curve obtained by measuring the components of the response at the fundamental and second harmonic frequencies. The amplitude of the fundamental component was twice that of the harmonic.

b. Signal averaged impluse response to a brief increment, the response to a decrement was negligible.

c. Frequency response curve for both fundamental and second harmonics, obtained with a contrast of 0.1 at a luminance of $500cd.m^{-2}$. In many units the relative amplitude of the harmonic declined at low frequencies.

d. Linear plot of response at fundamental and second harmonic frequencies against stimulus amplitude at 9Hz. Note that the harmonic component is not a saturation artefact


(a)
(b)
20ms
0°
90°
180°
270°
360°
Stimulus phase
(c)
0
-1
-2
log10 response gain
1
10
100
Stimulus freq (Hz)
(d)
1.0
0.5
0
Response amplitude
0
0.1
0.2
Stimulus contrast

of their dynamic range, introduced a marked second harmonic distortion in the responses to sinusoidal flicker. The amplitude of the second and higher order harmonics was usually 0.2 to 0.5 times that of the fundamental at high frequencies (fig 2c), but often declined at low frequencies. The relationship between fundamental and harmonic amplitudes means that bandwidths calculated from the fundamental alone were unlikely to have been underestimates. Clipping was not a distortion artefact caused by response saturation (fig 2d), since most units showed a constant ratio between fundamental and second harmonic amplitude below contrasts of about 0.2. Phase relations between stimulus and response for the fundamental and second harmonic components of the response gave a constant ratio, with the harmonic changing at twice the rate of the fundamental. This is in contrast to the nonlinear cells in the locust medulla (chapter 4), where the harmonic appears to arrive with a lower delay than the fundamental component of the response.

Constant phase and amplitude ratios between fundamental and second harmonic responses, at low contrast, were reflected in the observation that the waveform of the response to sinusoidal flicker was independent of frequency. Bearing in mind the constant distortion of the waveform we will look at the responses of the cells to sinusoidal flicker by describing responses at the stimulus frequency (fundamental) alone.

Tuning and phase relations

Temporal frequency tuning was examined to compare the properties of

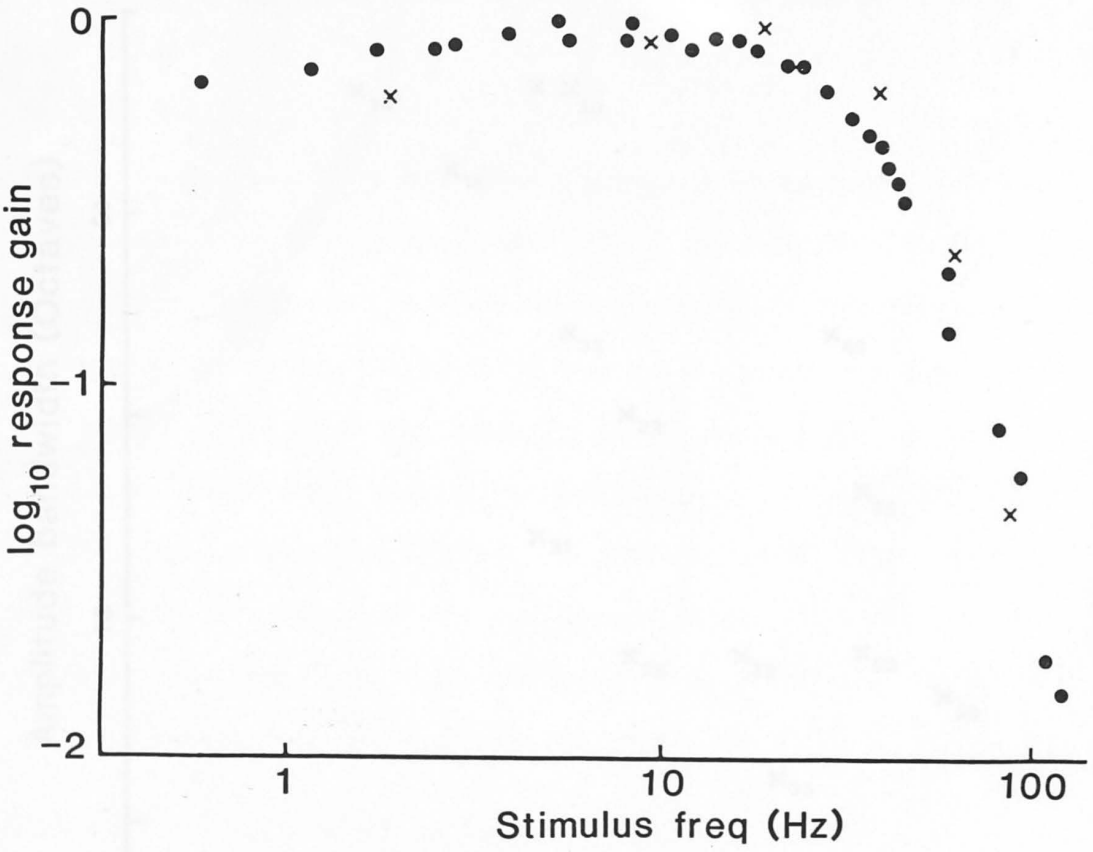


Figure 3.3

Frequency response curve for two light-adapted (500 $cd.m^{-2}$) retinula cells (●), and a lamina cell terminal (+). Phase relations in locust retinula cells are described by Howard (1981).

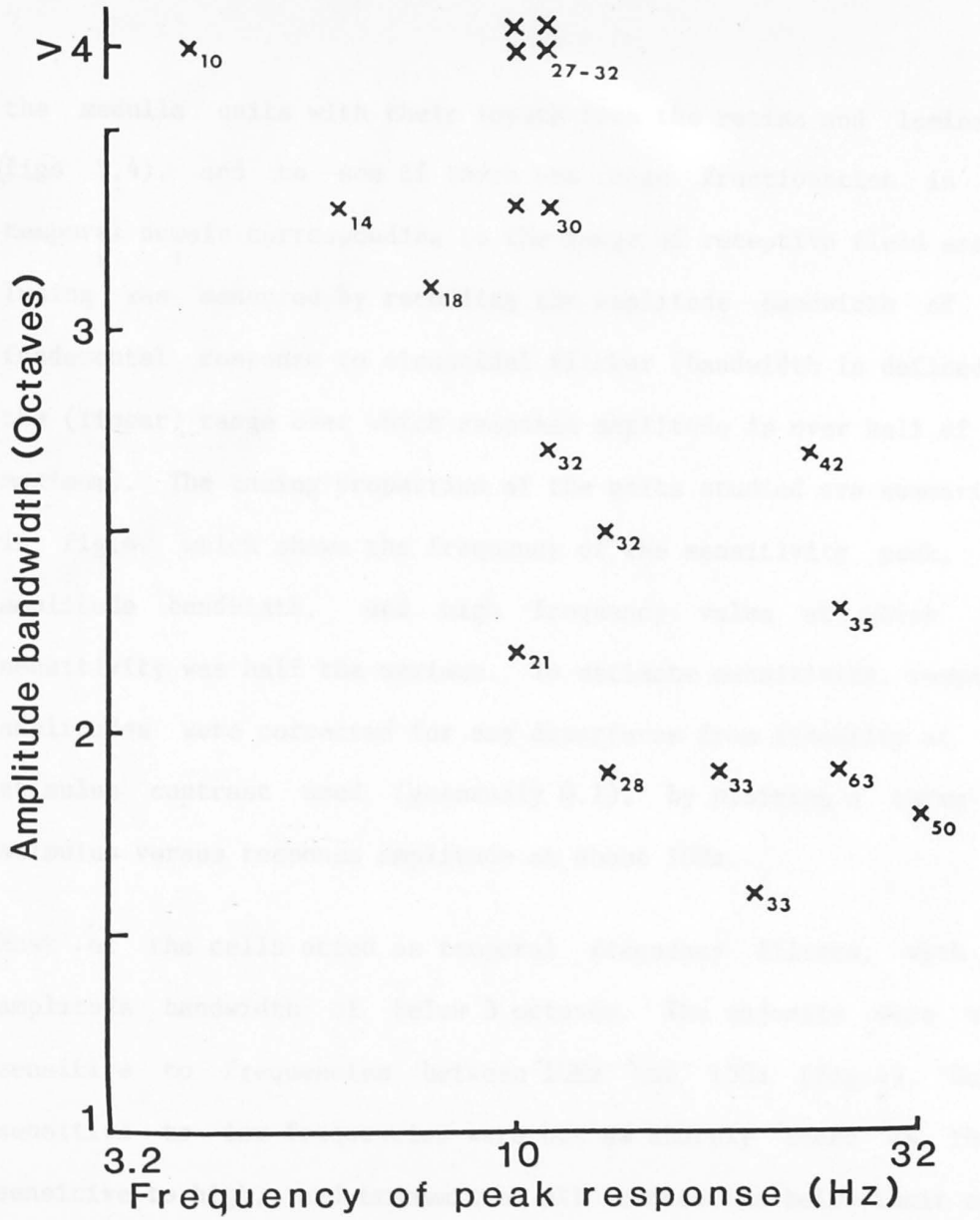


Figure 3.4

Amplitude bandwidths of cells plotted against frequency of peak response. Subscripts indicate the high-frequency value at which sensitivity was half of the maximum. There was no obvious correlation between receptive field area and tuning, and none of the records shown are thought to be from receptor or lamina cell terminals.

the medulla units with their inputs from the retina and lamina (figs 3,4), and to see if there was range fractionation in the temporal domain corresponding to the range of receptive field areas. Tuning was measured by recording the amplitude bandwidth of the fundamental response to sinusoidal flicker (bandwidth is defined as the (linear) range over which response amplitude is over half of the maximum). The tuning properties of the units studied are summarised in fig.4, which shows the frequency of the sensitivity peak, the amplitude bandwidth, and high frequency value at which the sensitivity was half the maximum. To estimate sensitivity, response amplitudes were corrected for any departures from linearity at the stimulus contrast used (generally 0.1), by plotting a curve of stimulus versus response amplitude at about 10Hz.

Most of the cells acted as temporal frequency filters, with an amplitude bandwidth of below 3 octaves. The majority were most sensitive to frequencies between 10Hz and 15Hz (fig.4). Units sensitive to low frequencies were not as sharply tuned as those sensitive to high, and transmitted all frequencies below their cut-off point, but they cannot be seen as unfiltered outputs of photoreceptors (fig.3) since they responded less well to high frequencies. Indeed it is noteworthy that few cells responded as well as photoreceptors at high frequencies.

Some of the cells tuned to high temporal frequencies showed multiphasic impulse (2ms stimuli) response functions (fig.5). The tuning curves illustrated were obtained in response to sinusoidal flicker, and above 5Hz were these similar to the curves obtained by

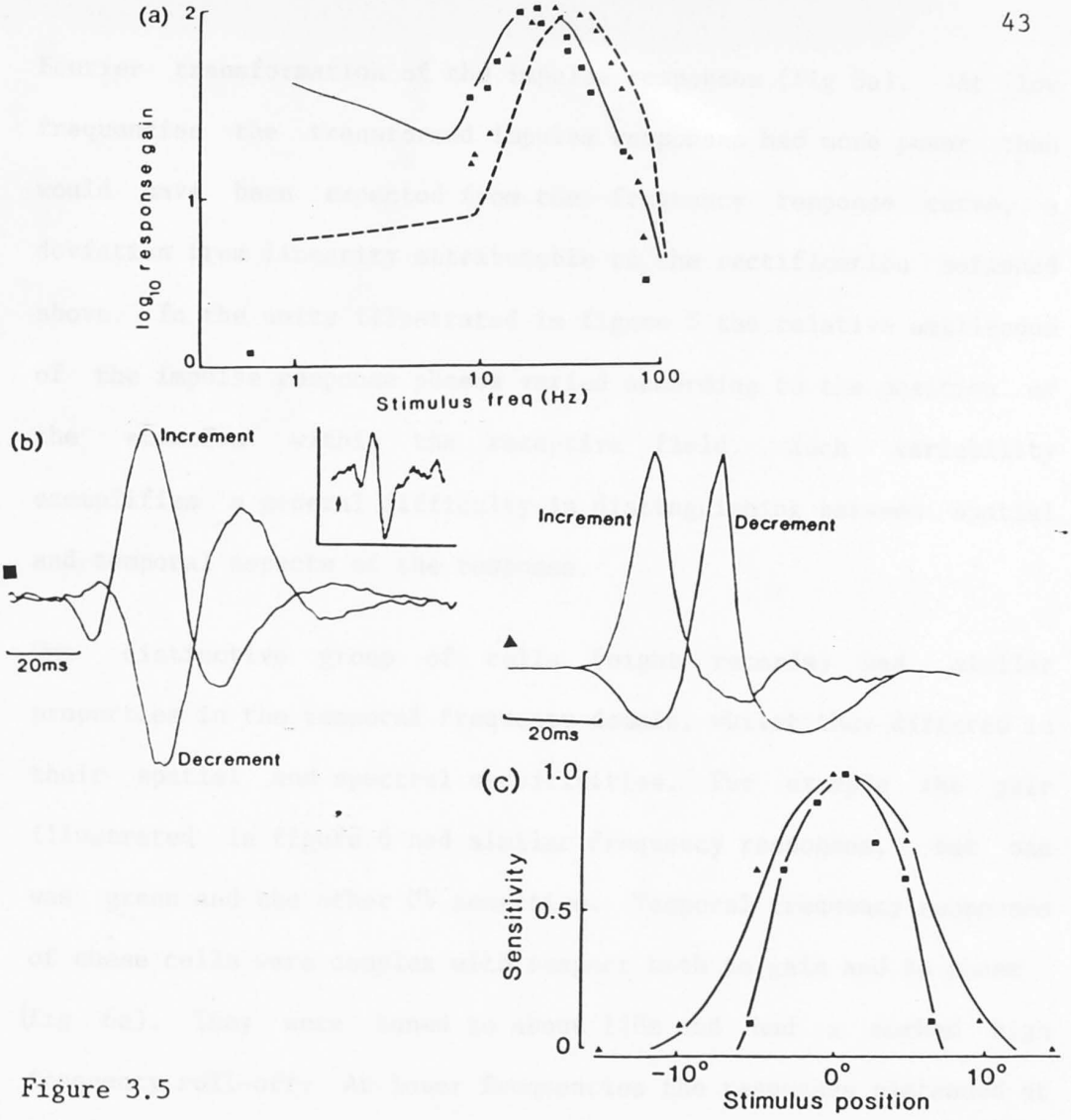


Figure 3.5

a: Logarithmic plot of gain against frequency for responses to sinusoidal flicker (contrast 0.15: symbols) and of the Fourier transformed impulse (2ms) responses (lines) for two green sensitive cells tuned to high temporal frequencies. One cell is represented by squares and the continuous line, the other by triangles and the broken line.

b: Signal-averaged (30 responses) and normalised responses of the cells to 2ms increments and decrements of contrast 0.25 over a 500 $cd.m^{-2}$ background. The relative amplitudes of the response components of these graded potential waveforms were affected by changing stimulus position.

c: Vertical angular sensitivity profiles of the same cells to 3^{o} diameter flashes.

Fourier transformation of the impulse responses (fig 5a). At low frequencies the transformed impulse responses had more power than would have been expected from the frequency response curve, a deviation from linearity attributable to the rectification metioned above. In the units illustrated in figure 5 the relative amplitudes of the impulse response phases varied according to the position of the stimulus within the receptive field. Such variability exemplifies a general difficulty in distinguishing between spatial and temporal aspects of the response.

One distinctive group of cells (eight records) had similar properties in the temporal frequency domain, whilst they differed in their spatial and spectral sensitivities. For example the pair illustrated in figure 6 had similar frequency responses, but one was green and the other UV sensitive. Temporal frequency responses of these cells were complex with respect both to gain and to phase (fig 6a). They were tuned to about 12Hz and had a marked high frequency roll-off. At lower frequencies the responses plateaued at about 30-50% of the maximum gain. These properties are expected in a 'phaso-tonic' response, where the tuned component is the phasic, and the plateau the tonic part of the response. These units also had similar stimulus-response phase relations. There was a phase lead to low frequency stimuli and lag to high, as might be expected from a tuned filter (Schwarzenbach & Gill 1984). In several of the cells the phase lag at high frequencies had an asymptote to 90^{o} (after correcting for the delay). This conclusion is tentative due to the poor signal to noise ratio, and the sensitivity to the estimate of response delay. The phase estimates at low frequencies were less

sensitive to these errors however, and the complexity of the low-frequency amplitude roll-off (fig 6a) seems to have been reflected in the phase relations. The phase lead observed is expected from a unit which is sensitive to the rate of change of the stimulus amplitude , rather than its value . If the units were acting as simple differentiators (single-pole high-pass filters) the lead would be expected to asymptote to a maximum of 90^{o} at low frequencies. In practice a marked decline in the lead was noted at stimulus frequencies below about 5Hz.

The responses of the medulla units described above (fig 6) could be produced by the addition of two types of input. One acting as a tuned filter, which behaved as a high-pass filter at low frequencies, and another which approximated a low-pass filter. If the latter dominated at low frequencies the response would show no phase shift. At intermediate frequencies the combined outputs of the low-pass filter and the tuned input would give a phase lead of less than the 90^{o} expected from a cell purely sensitive to the rate of change of stimulus amplitude. At high frequencies the roll-off of amplitude and phase would be determined solely by the tuned component, behaving as a low-pass filter. This rather elaborate suggestion was supported by two units in which tuned and low-pass components could be separated because they differed in spectral sensitivity (fig.7). In one cell the tonic component in the response was green and the phasic UV sensitive, whilst in the other the reverse applied. The former cell had a spectral opponent surround, and was tonically inhibited by widefield UV illumination, but excited by green.

Figure 3.6

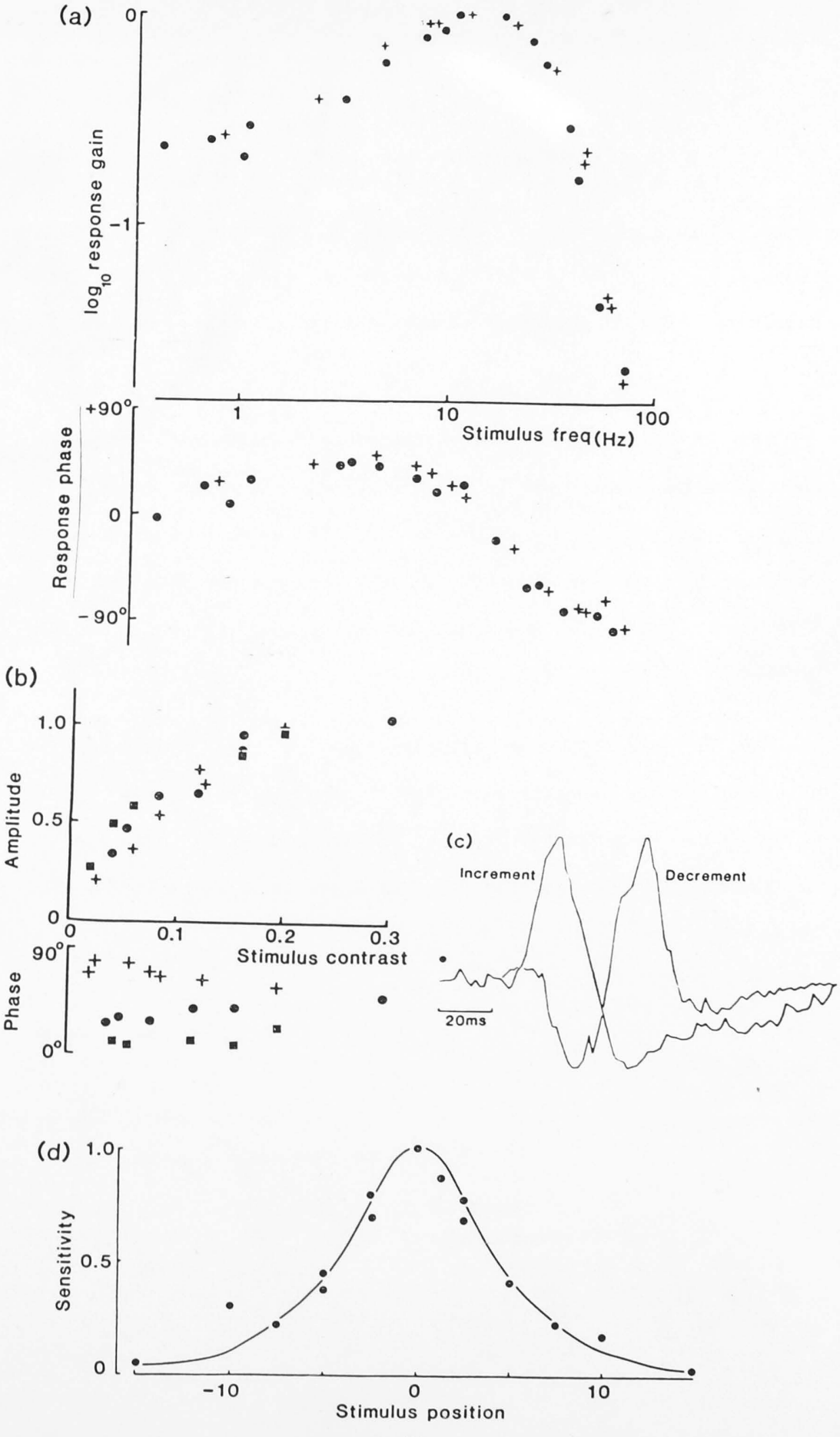
a: Bode plots of the responses of two similar units one UV (●) and the other green (+) sensitive. The stimulus contrast was 0.2 and diameter 10^{o}.

b,above: Contrast response curves for three units (illustrated in figs.5 & 6 and represented by their respective sympbols) to 10Hz modulation of a 10^{o} spot, normalised to the response at a contrast of 0.2.

below: Plot of fundamental response phase against stimulus amplitude for the three units. The plot shows only the relative phases of the responses, and does not indicate their relationship to the stimulus phase.

c: Signal averaged and normalised impulse responses of the UV sensitive unit to 2ms increments and decrements. Stimulus frequency 2Hz.

d: Angular sensitivity profile of the UV sensitive unit to 2ms increments of 5^{o} diameter spot. Data for vertical and horizontal axes are combined, and the curve is fitted by eye. Sensitivity measurements were calibrated from an intensity response curve to on-axis stimuli. Over twenty responses were averaged to obtain each data point.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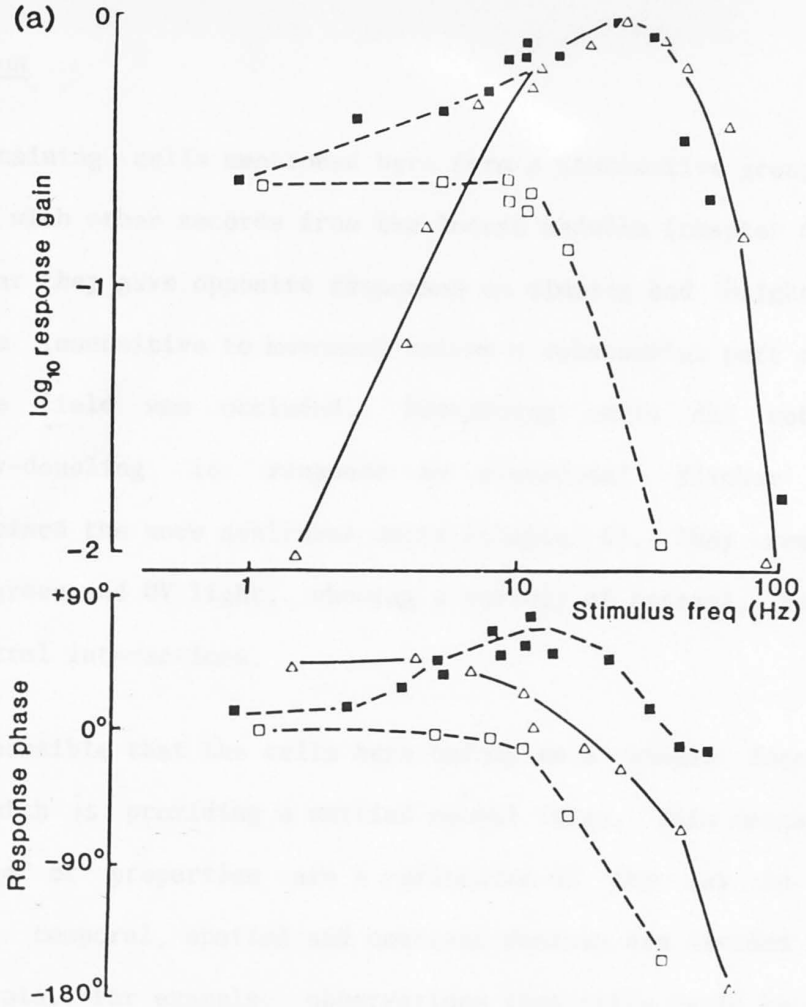
0
log10 response gain
-1
1
10
100
Stimulus freq (Hz)
+90°
Response phase
0
-90°
(b)
1.0
Amplitude
0.5
0
0
0.1
0.2
0.3
Stimulus contrast
90°
Phase
0°
(c)
Increment
Decrement
20ms
(d)
1.0
Sensitivity
0.5
0
-10
0
10
Stimulus position

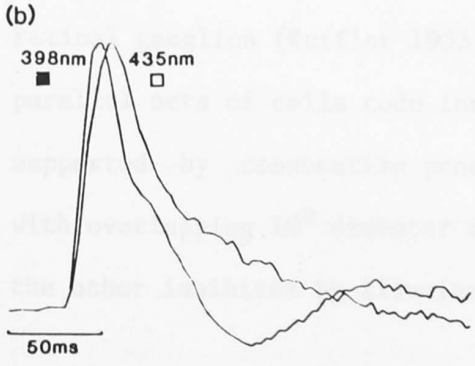
Figure 3.7

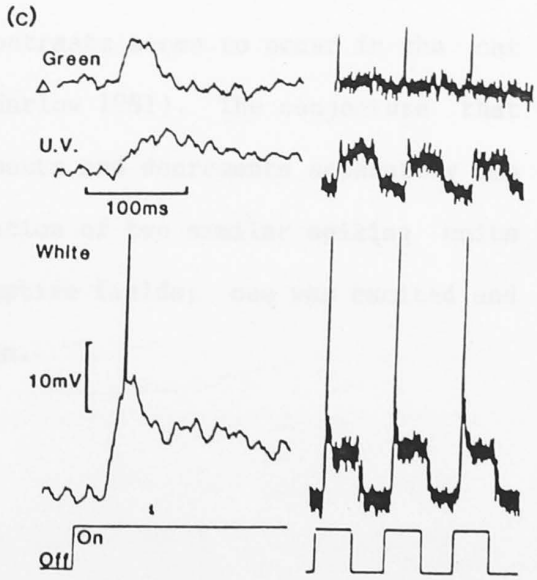
a: Bode plots of responses to green light (open symbols) and UV light (closed symbols) for two cells, designated by squares and triangles respectively. Both units had circular receptive fields with diameters of 10^{o} at half maximum sensitivity.

b: Normalised impluse responses of the unit designated by square symbols in 7a (sensitive to high frequency UV signals), to 435nm and 398nm 2ms pulses over a 50cd.m^{-2} screen. Note the negative-going component in the response to UV, this is consistent with the decline in sensitivity to low temporal frequencies seen at this wavelength. This cell was tonically inhibited by widefield UV and excited by widefield green illumination.

c: Raw data showing the responses of the unit designated by triangles above (sensitive to high frequency green signals) to a 0.5Hz square-wave flicker to green UV and white light. The phasic off-transient in the response to green light is obscured by baseline noise.


(a)
0
-1
-2
log10 response gain
1
10
100
Stimulus freq (Hz)
+90°
0°
-90°
-180°
Response phase


(b)
398nm
435nm
50ms


(c)
Green
U.V.
100ms
White
10mV
On
Off

Discussion

The sustaining cells mentioned here form a distinctive group when compared with other records from the locust medulla (chapter 4). In particular they gave opposite responses to dimming and brightening, and were insensitive to movement unless a substantial part of the receptive field was occluded. Sustaining cells did not show frequency-doubling in response to sinusoidal flicker which characterises the more nonlinear units (chapter 4). They responded to both green and UV light, showing a variety of spatial, temporal and spectral interactions.

It is possible that the cells here belong to a single functional class which is providing a unified neural image. This means that the range of properties are a reflection of the way in which spectral, temporal, spatial and contrast domians are divided in the insect brain. For example, observations that cells could be either depolarised or hyperpolarised by light, and that they gave larger responses to depolarising stimuli, imply that there may be separate sets of cells responsible for coding dimming and brightening. Similar range fractionation of contrasts seems to occur in the cat retinal ganglion (Kuffler 1953; Barlow 1981). The conjecture that parallel sets of cells code increments and decrements separately was supported by consecutive penetration of two similar spiking units with overlapping 10^{o} diameter receptive fields; one was excited and the other inhibited by illumination.

Temporal tuning

Cells were tuned to a range of different temporal frequencies, although we cannot say if the tuning observed (fig 4) is well suited to division of the temporal frequency domain into independent channels. As the cells were approximately linear it may be profitable to compare them to linear filters. (The half-wave rectification (fig 2) means that the cells might resemble Class-B electronic amplifiers, where the average output is near zero. These are operated in pairs to give an approximately linear output)

Temporal tuning requires a transformation of the retinal input. Most medulla units showed a decline in sensitivity at high and low temporal frequencies relative to photoreceptors (figs 3,4). This tuning resembles that observed psychophysically in man, where the attenuation of low frequency signals is expected to occur at early stages of neural processing (Kelly 1972). Most cells were tuned to frequencies between 10Hz and 15Hz (fig 4), whilst human peak sensitivity is to temporal frequencies of about 6Hz. The highest frequency which humans can detect (about 60Hz), is similar to the high frequency cut-off of light adapted locust photoreceptors (fig.3).

The tuning characteristics of the medulla cells ranged from those with amplitude bandwidths below two octaves to those which resembled low-pass filters (fig 4). There was a tendency for cells tuned to high frequencies to have relatively narrow bandwidths. The temporal bandwidths of the medulla cells can be compared to <u>spatial</u> tuning of vertebrate retinal ganglion cells and cortical cells (reviewed by

Shapely & Lennie 1985). In the cat these are about 3.5 octaves in the retinal ganglion and 1.5 octaves in the cortex.

The finding that several cells have distinctive gain curves and phase shifts, which could be attributed to addition of low-pass and bandpass filters allows us to quantify a phaso-tonic response (figs 6,7). The phaso-tonic property may be an adaptation to minimise phase distortions by a mechanism analagous to phase-lead compensation (Schwarzenbach & Gill 1984). This compensation is achieved by adding the outputs of low and high-pass filters, here the maximum phase-lead observed was 45^{o} at about 5Hz.

Spectral sensitivity

The cells were sensitive to both green (500nm) and UV (365nm) wavelengths. The similarity of cells responding to the two wavelengths (fig 6) suggests that the outputs of green and UV photoreceptors were being used to control similar behaviours, or perhaps combined to detect chromatic contrast.

The finding that in some cells phasic and tonic response components were sensitive to different wavelengths (fig 7) implies that they were not exploiting the spectral differences for hue discrimination. These findings parallel observations made in the bee and ground squirrel (Kien & Menzel 1977; Gur & Purple 1979), where different spectral inputs control different temporal components in the responses of visual interneurons. Whilst allowing us to analyse the phaso-tonic cells the likely function of these spectral properties is obscure. It is difficult to imagine a 'feature' which

would be effectively detected by the units illustrated (fig.7). Other cells from the locust medulla showing more familiar spectral opponency have been described elsewhere (chapter 5).

Conclusion

We cannot say whether the cells described here are elements of a single functional class, dividing the spatial, temporal and spectral dimensions between them to code various aspects of the scene. However it is clear that there could be range fractionation in these domains. Anatomical studies will be most important in resolving this question, if we can see where the cells project.

The sustaining cells may be best understood by looking at how they complement the other major group of cells recorded in the locust medulla (chapter 4). This latter group is purely green sensitive, and responds transiently to changes in intensity, without coding their amplitude or polarity. The two groups of cells are coding different aspects of the scene, with the sustaining cells described here signalling the relative luminance of different parts of the visual field, at a variety of scales. The other group signals the presence of abrupt changes in intensity, as are often found at object boundaries.

Chapter 4 :

Temporal properties of nonlinear, phasic cells

Summary

1. Intracellular recordings were made from the medulla of the locust optic lobe, a retinotopically arranged ganglion with one column of cells for each facet in the compound eye.

2. The paper describes a novel class of visual interneuron, which gives highly phasic responses, typically a single spike, to any suprathreshold stimulus. Although forming a distinctive class these cells vary in receptive field area and other properties.

3. Response timing is quite precise. Typically the standard deviation of the spike latency is 2ms. The responses occur at the same time to increments and decrements, so the cells could not signal stimulus polarity. Spike timing is however affected by changing stimulus contrast, this may cause distortions in the neural image.

4. The cells do not spike in response to stimuli presented at over 10Hz, or to sinusoidal flicker. Graded potential responses to sinusoidal flicker elicit a powerful second harmonic response component.

5. A simple description of the way in which the responses of this group of cells could be obtained by linear and nonlinear operations on the photoreceptor input is given.

Introduction

Efficient coding and analysis in vision may depend upon decomposition of the retinal image into separate components. At a neural level such decomposition requires filters which respond in an invariant fashion to one aspect of a stimulus, whilst remaining insensitive to others (Craik: in Sherwood 1966). This paper describes a new group of cells from the medulla of the locust optic lobe which give a simple response, often a single spike, to all suprathreshold stimuli. The cells are insensitive to gradual changes in intensity but respond well to brief flashes or steps. Responses to dimming and brightening are often indistinguishable, and response timing is quite precise. The ability to code the presence and timing of a suprathreshold intensity change accurately, but to ignore other properties of the stimulus means these cells are acting as filters at an early stage in vision. This paper aims to characterise the stimulus properties eliciting a spiking response from these cells. In addition, the integrative processes required to give the non-linear outputs observed here are examined by looking at graded potential responses and features of the receptor potential abstracted by the cells.

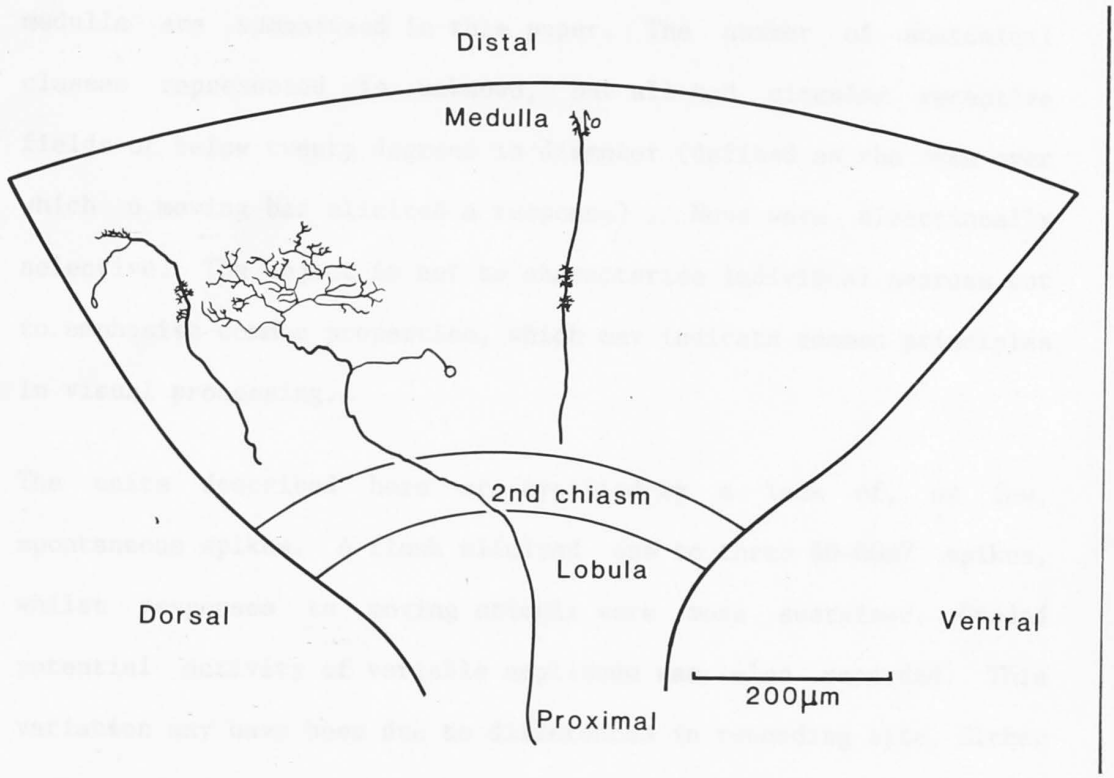


Figure 4.1

Diagram of the medulla showing three cells filled with Lucifer yellow CH. The neurite diameters are not drawn to scale. The two smallfield cells were probably confined to a single column, and had receptive field diameters similar to that of a single facet. Both were more sensitive to dimming than to brightening, but gave frequency doubled responses to flicker at about 10Hz (as fig 8). The larger field cell had a receptive field diameter of about 20^{o}, and gave a single spike to both dimming and brightening.

Results

The properties of thirty cells recorded intracellularly in the medulla are summarised in this paper. The number of anatomical classes represented is unknown, but all had circular receptive fields of below twenty degrees in diameter (defined as the area over which a moving bar elicited a response) . None were directionally selective. The object is not to characterise individual neurons but to emphasise common properties, which may indicate common principles in visual processing.

The units described here are typified by a lack of, or few, spontaneous spikes. A flash elicited one to three 40-60mV spikes, whilst responses to moving stimuli were more sustained. Graded potential activity of variable amplitude was also recorded. This variation may have been due to differences in recording site. Either axons or dendrites may have been penetrated (somata are electrically isolated and inactive). The spikes had somewhat irregular waveforms (figs 2, 7), but we cannot say whether this was due to the electrophysiological nature of these responses, or to the recording site. In several cells, perhaps when the axon was penetrated, spikes were the only form of electrical activity. The spikes are likely to have been the main outputs of these cells.

The spike responses were distinctive. The number of spikes was small and independent of stimulus amplitude, and in several smallfield cells the response comprised just one spike (fig.2). This thresholding (all-or-nothing) property means that the proportion of stimulus presentations giving a response, rather than mean response

amplitude, was the best measure of the efficacy of a stimulus. Graded responses alone were elicited by sinusoidal flicker.

Cells would not spike in response to stimuli presented at over 10Hz, leaving only a graded potential response (fig 2d), and sensitivity increased to a maximum at a stimulus frequency of about 2-4Hz. If a cell was adapted to a high rate of stimulus presentation an increase in contrast elicited a spike. Thus although the cells' activity was low each spike gave a reliable indication that an unusually high contrast had been encountered.

Spatial properties

Receptive fields were approximately circular and fell into two groups: Those of about 2^{o} to 5^{o} in diameter, and those of 7^{o} to 20^{o} in diameter (figs 2&3). These groups are designated as smallfield and widefield respectively. The receptive field areas measured electrophysiologically corresponded with the spread of dendritic fields in Lucifer fills (fig 1). Smallfield cells gave indistinguishable responses to brightening and dimmimg at all positions in the receptive field. Widefield cells had more complex properties, including inhibitory surrounds. When two spikes occurred at different intervals after a brief flash they often had different receptive fields (fig 3). Receptive field areas measured with low contrast flashes were similar to those recorded using moving stimuli.

Amongst several interesting spatial properties the cell class illustrated in figure 2 showed local adaptation (fig. 2d). Another

Figure 4.2

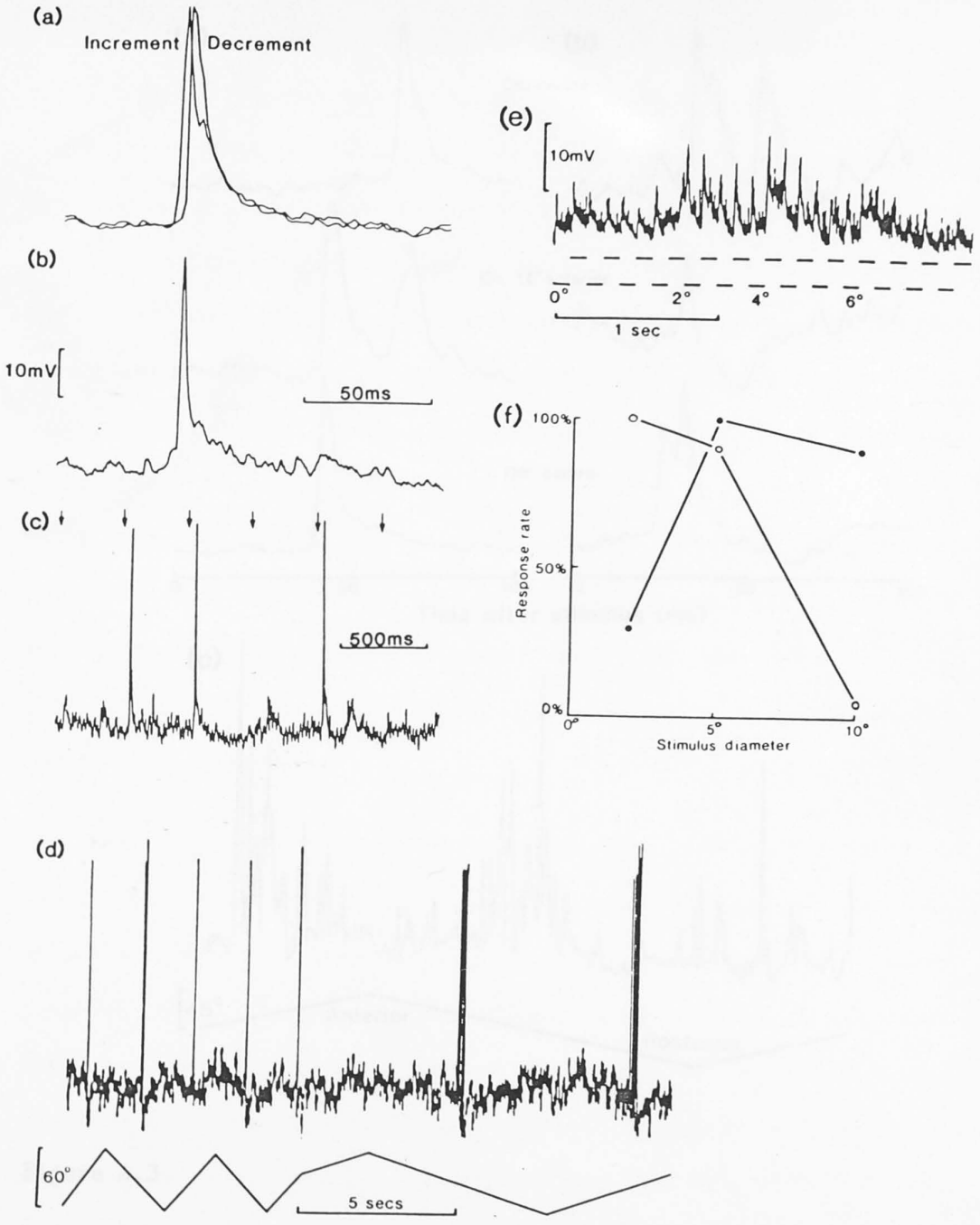
Several aspects of a smallfield cell class (2 records).

a: Normalised signal averaged responses to 3.5ms increments (left) and decrements (right), contrast 0.6. 20 responses were averaged in each curve. A single response is shown in b. In all illustrations of responses the origin is the time of stimulus onset.

c: Response to a 3Hz train of flashes (arrowed) close to threshold. Note the all-or-nothing nature of the response.

d: Receptive field measured with a 2^{o} spot flickering at 5Hz. The spot was moved in 2^{o} increments through the receptive field. Note the graded response due to high stimulation frequency, and local adaptation. More thorough measurements showed that the sensitivity to a 2^{o} spot dropped by 50% 2^{o}-3^{o} from the receptive field centre, and by 90% 5^{o} from the centre. The local adaptaton indicates subunits were present in the receptive field which may also explain why the response to a moving bar (contrast 0.1, width 1.5^{o}) in e included more than one spike.

f: Response frequency to isoquantal stimuli of different areas. Brightening (○) and dimming (●). Whole-field stimuli of high contrast did not elicit spikes to either dimming or brightening. The asymetry in the responses to increments and decrements was not recorded in other units, and may be indicative of an on-sensitive inhibitory surround. Other experiments showed that the regions of greatest sensitivity to brightening and dimming were coincident.


(a)
Increment
Decrement
(b)
10mV
50ms
(c)
500ms
(d)
60°
5 secs
(e)
10mV
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Response rate
0°
5°
10°
Stimulus diameter

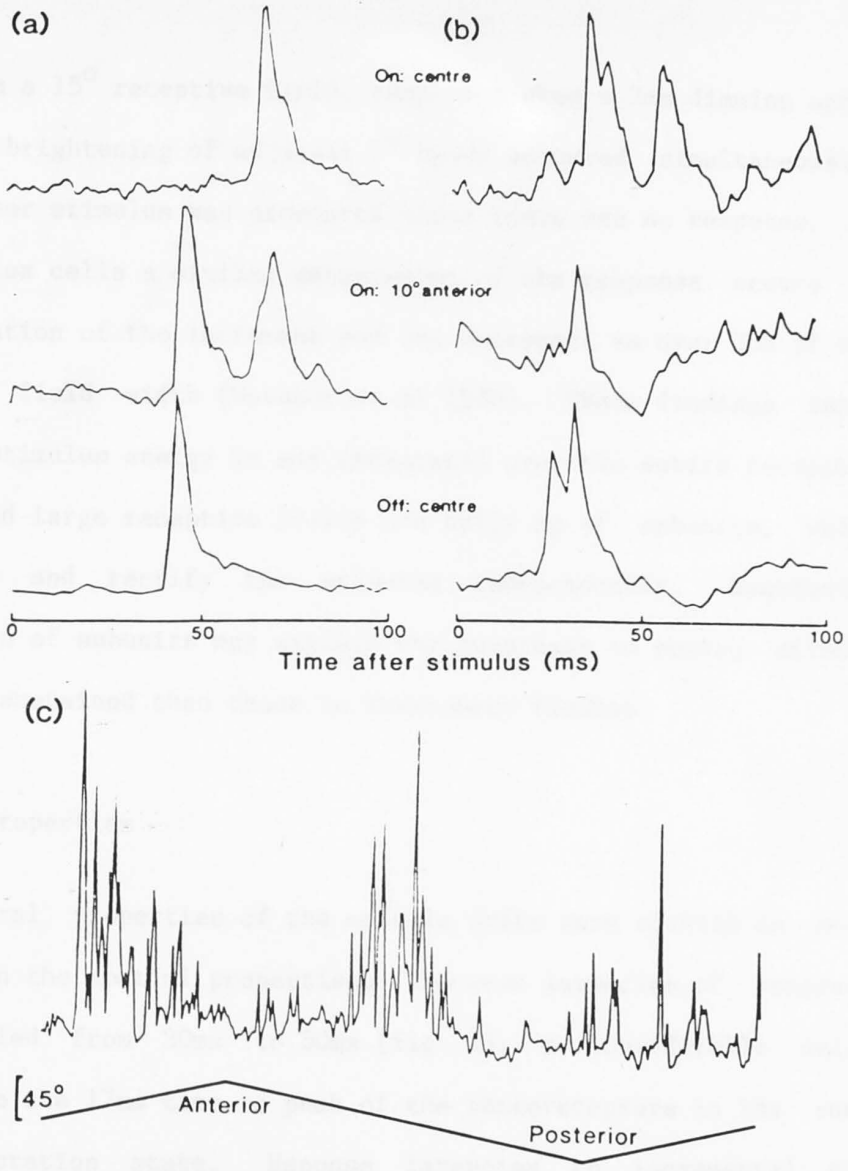


Figure 4.3

Responses of two cells a and & b with receptive field diameters of 15^{o}, measured with a moving bar, to 10ms flashes. Responses to 20 10ms bright flashes in the receptive field centre (top) and 10^{o} anterior (middle), and to dimmimg (bottom). The inhibitory component in the response of b (10^{o} anterior) formed an antagonistic surround.

c: The response of the cell illustrated in a a 45^{o} horizontal movement of a perspex bar (contrast 0.15, width 1.5^{o}) through the receptive field at 1 Hz. 10 stimulus cycles averaged.

cell, with a 15^{o} receptive field, responded when a 2ms dimming and a similiar brightening of adjacent 2^{o} spots occurred simultaneously. When either stimulus was presented alone there was no response. In cat complex cells a similar enhancement of the response occurs if the separation of the increment and the decrement is over 25% of the receptive field width (Movshon et al 1978). These findings imply that the stimulus energy is not integrated over the entire receptive field, and large receptive fields are built up of subunits, which adapt to and rectify the stimulus independently. Sequential stimulation of subunits may explain why responses to moving stimuli were more sustained than those to stationary flashes.

Temporal properties

The temporal properties of the medulla units were studied in more detail than the spatial properties. The mean latencies of response peaks varied from 30ms to 50ms (fig 4); a considerable delay compared to the 17ms time to peak of the photoreceptors in the same light adaptation state. Reponse latencies to incremental and decremental pulses were strikingly similar, especially in smallfield cells which gave only a single spike (fig 2). When more than one spike was elicited the timing of at least one of the responses coincided for dimming and brightening in all the records described here (eg. figs 3 & 7). Units giving more than one spike to pulses gave only a single response to the intensity change in square wave flicker (fig 7). A most important feature, which could be seen in all records, was the low variability in response latency. The standard deviation of the time to peak was estimated to be about 2ms

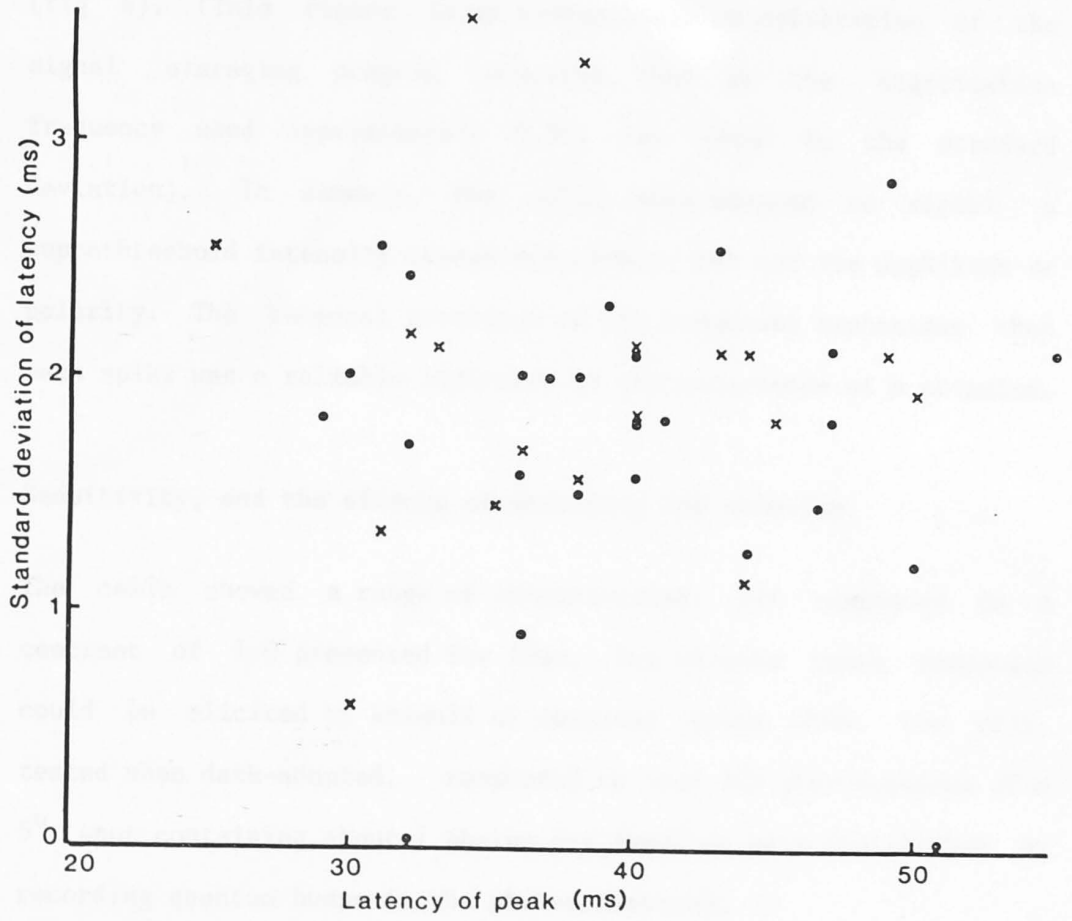


Figure 4.4

Latencies and standard deviations of the response peaks of 31 units to flashes of 10ms or less in light adapted eyes (brightening (●), dimming (×).

(fig 4). (This figure is an overestimate as calibration of the signal averaging program indicated that at the digitisation frequency used approximately 0.5ms was added to the standard deviation). In summary, the cells seem adapted to signal a suprathreshold intensity change accurately, but not its amplitude or polarity. The temporal precision of the responses emphasises that each spike was a reliable indicator of the occurrence of a stimulus.

Sensitivity, and the effects of modifying the stimulus

The cells showed a range of sensitivities; all responded to a contrast of 1.0 presented for 10ms, but in some cases responses could be elicited by stimuli of contrast below 0.01. One cell, tested when dark-adapted, responded to over 50% presentations of a 5^{o} spot containing about 1 photon per facet on axis (calibrated by recording quantum bumps in the photoreceptors).

In addition to finding absolute sensitivities, stimulus duration and contrast were varied. This was to see how the latency and variance of the response time changed, and to estimate the integration time of the cells. As cells gave no independent estimate of stimulus amplitude changes, latency would probably cause distortion of the neural image, reminiscent of the inverse contrast effect observed psychophysically (Coltheart 1980). The effect of changing contrast on response latency was studied at a constant stimulus duration (10ms). In addition the relationship between contrast and stimulus duration was examined by measuring the contrast threshold (that eliciting responses to about 75% of presentations) at various flash

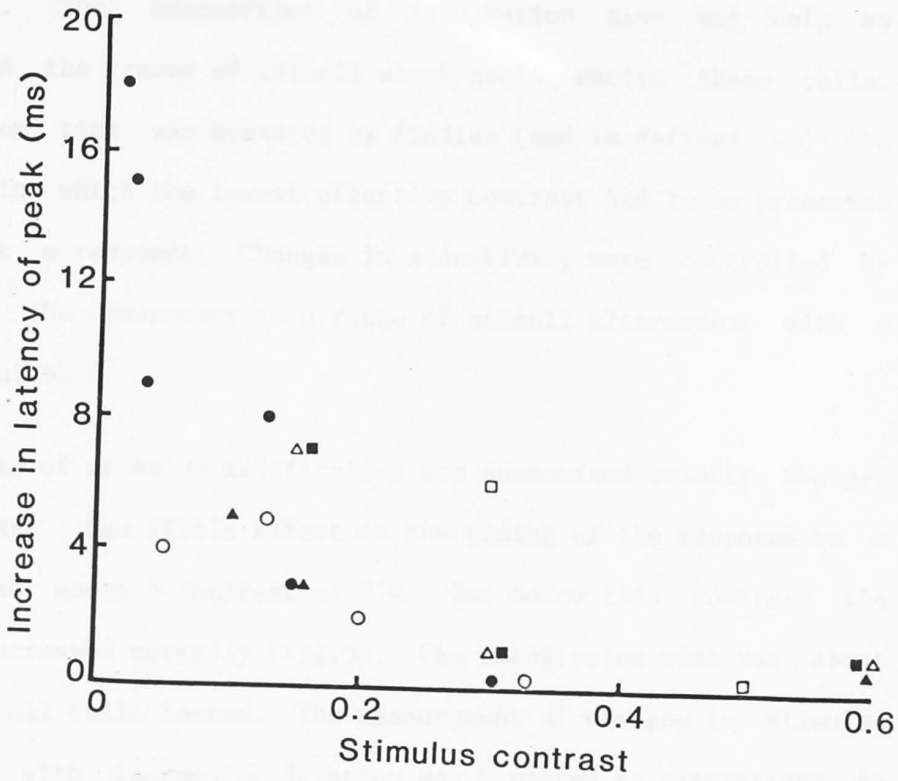


Figure 4.5

Contrast plotted against increase in latency of time to peak. Little change could be seen above a contrast of about 0.4 for 10ms flashes. Open symbols: Responses of 3 cells to 10ms flashes. Closed symbols : Responses of 3 different cells to flashes of threshold duration, ranging from 2ms to 23ms. The symbol (●) refers to the cell class illustrated in figure 2.

durations. The measurement of integration time may help us understand the range of stimuli which could excite these cells. Integration time was measured by finding (and is defined as) the duration for which the lowest effective contrast had to be presented to elicit a response. Changes in sensitivity were controlled by measuring the responses to a range of stimuli alternating with a test stimulus.

The effects of stimulus modification are summarised briefly. Changes in contrast had little effect on the timing of the response to a 10ms flash above a contrast of 0.4, but below this contrast the latency increased markedly (fig.5). The integration time was about 25ms in all cells tested. The measurement of changes in stimulus efficency with increasing duration was hampered by alterations in sensitivty. In the four cells tested, however, the product of stimulus contrast and duration was constant at threshold (Bunsen-Roscoe law) up to the integration time. These results show that the cells responded to a suprathreshold stimulus energy occurring in a period of less than 25ms, and that response timing was affected by stimulus amplitude.

To study the temporal integration properties of the cells further, and to look at the relationship between the photoreceptor response (fig.6d) and the medulla units' responses, two subthreshold flashes were presented at varying time intervals. Pairs of subthreshold pulses were made by dividing a 4ms flash a little above threshold contrast (giving spikes to all presentations) into two 2ms halves. Care was taken to ensure that these results were reliable by repeating measurements, and checking that there was no response to a

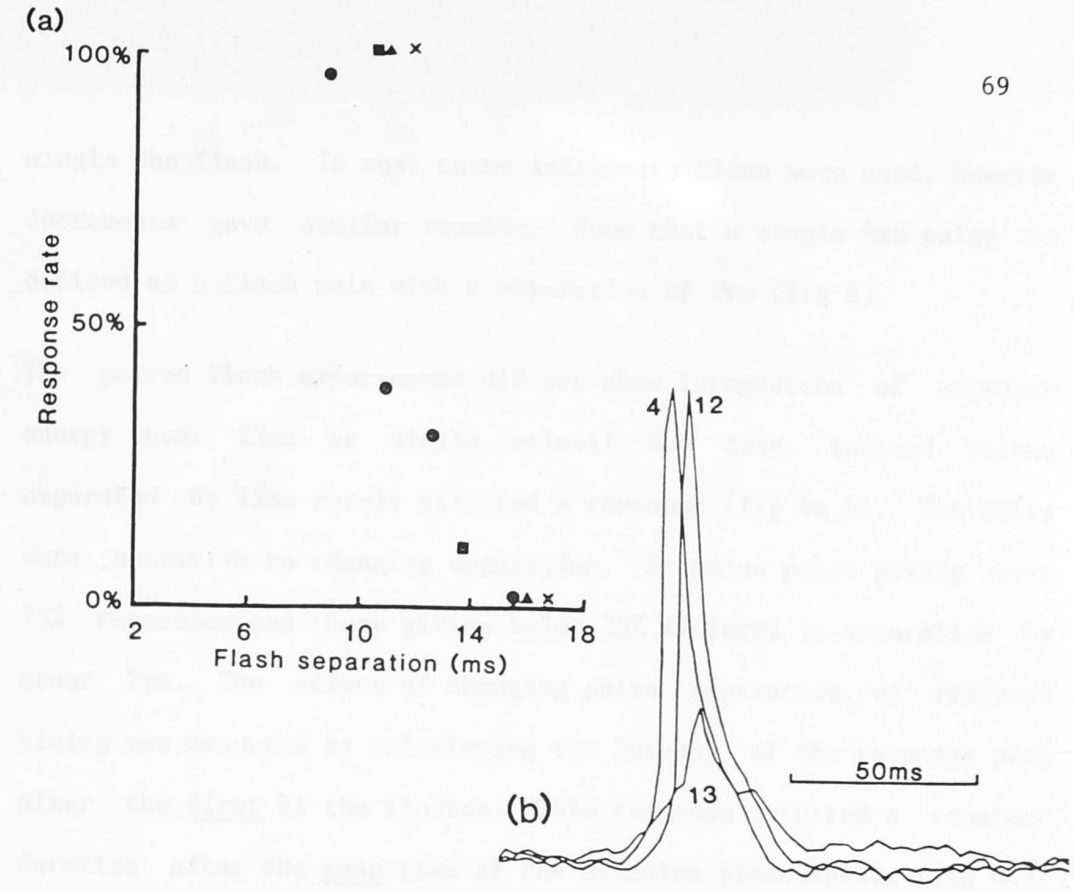
Figure 4.6

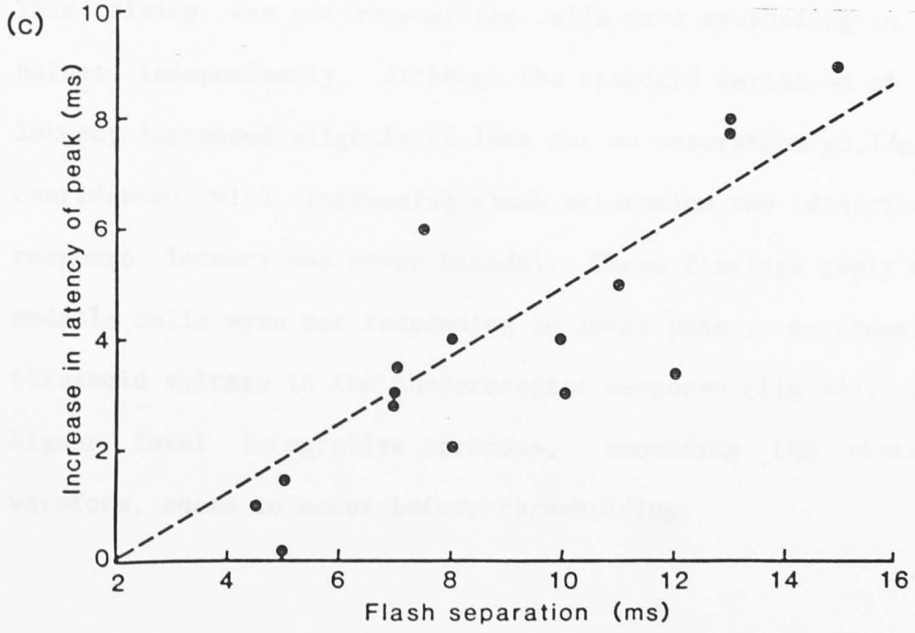
a: Proportion of stimulus pairs eliciting responses plotted against flash separation, for four cells (One symbol represents the responses of one unit). Note the rapid decline in response with increasing separation.

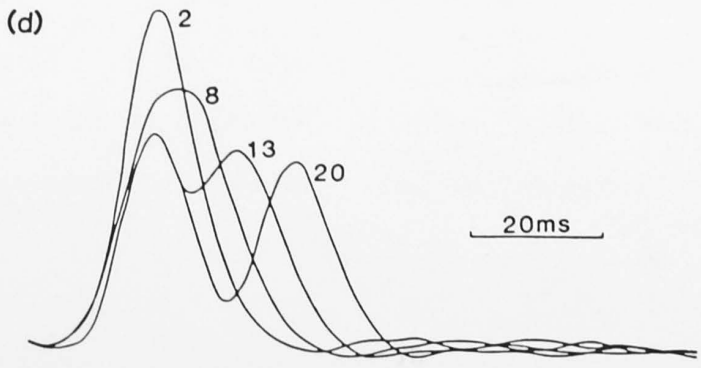
b: Effect of increasing separation of the stimulus pair in one unit. The averaged responses to 13 stimulus pairs are shown for flash separations of 4ms (left), 12ms (right) and 13ms (lower) on the same scale.

c: Increase in latency of the responses of eight cells plotted against onset separation time of two subthreshold 2ms flashes. The minimum possible separation of 2ms gave a continuous 4ms stimulus. Linear regression line plotted: slope 0.62 ± 0.29 (95% confidence).

d: Photoreceptor responses to flash pair stimuli at separations (from left to right) of 2,8,13 and 20ms. The trough was equal to 25% of the response amplitude at a separation of 13.5ms and 50% at 17ms.


(a)
100%
50%
0%
Response rate
2
6
10
14
18
Flash separation (ms)
4
12
13
50ms
(b)


(c)
Increase in latency of peak (ms)
0
2
4
6
8
10
2
4
6
8
10
12
14
16
Flash separation (ms)


(d)
2
8
13
20
20ms

single 2ms flash. In most cases increments alone were used, however decrements gave similar results. Note that a single 4ms pulse is defined as a flash pair with a separation of 2ms (fig 6).

The paired flash experiments did not show integration of stimulus energy over 25ms as single stimuli had done, instead pulses separated by 15ms rarely elicited a response (fig 6a,b). The cells were sensitive to changing separation. Stimulus pairs giving over 75% responses and those giving below 25% differed in separation by about 2ms. The effect of changing pulse separation on response timing was measured by calculating the latency of the response peak after the first of the flashes. This response occurred a constant duration after the mean time of the stimulus presentation (fig 6c). This timing was not because the cells were responding to the two pulses independently. Although the standard deviation of response latency increased slightly (0.16ms per ms separation $\pm$0.17ms at 95% confidence) with increasing flash separation the distribution of response latency was never bimodal. These findings imply that the medulla cells were not responding to local peaks, or crossings of a threshold voltage in the photoreceptor response (fig 6d). Instead a higher level integrative process, smoothing the photoreceptor waveform, seems to occur before thresholding.

Graded potential responses

The results so far have described the spiking components of the responses, whose large amplitude, high sensitivity and low variance imply that they were the principal outputs of the cells. The thresholding behaviour, and the similarity of responses to increments and decrements showed that the cells were non-linear. The bases for these nonlinearities were studied by examining the graded potential responses to sinusoidal flicker. This flicker provided a quantifiable stimulus with which to examine the spike-generating mechanism.

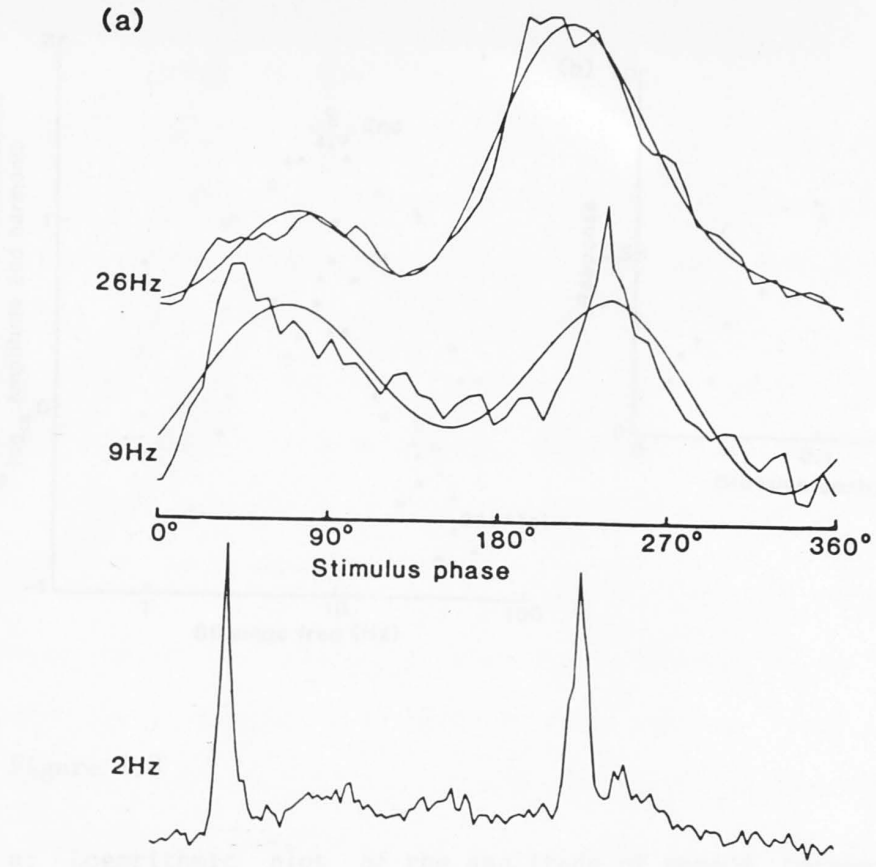
Studies were performed by sinusoidally modulating a stationary 10^{o} spot at between 0.5Hz and 100Hz. Contrasts used fell within the linear range of photoreceptor operation, and were usually below 0.15. These stimuli seldom elicited spikes; as expected from the observations that the cells would not fire at over 10Hz and the integration time was 25ms. The effects of changing stimulus area and position were largely ignored, although controls indicated that there were no qualitative changes when the stimulus was modified.

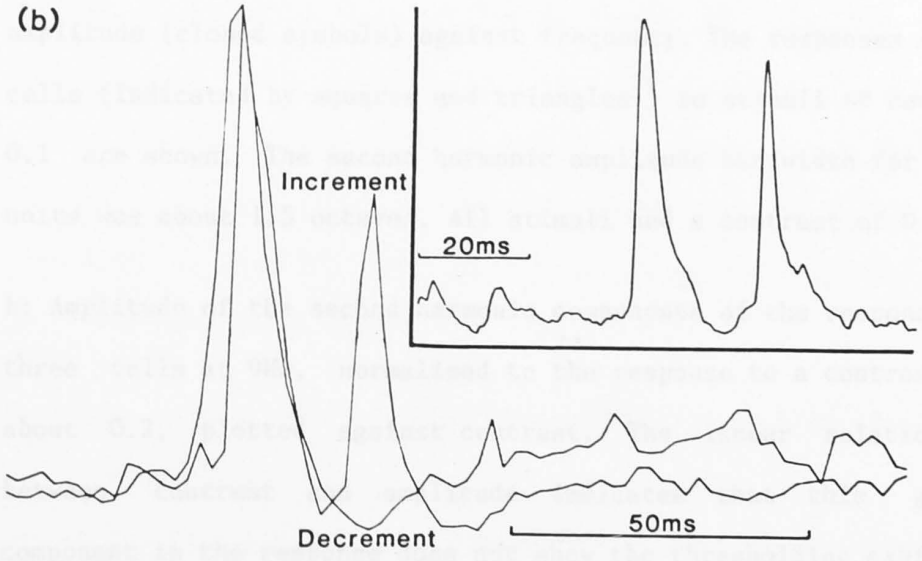
Although weak and noisy, the graded potential responses to sinusoidal flicker could be analysed after averaging the responses to 30 to 100 stimulus cycles. All showed a marked second harmonic component up to stimulus frequencies of 30Hz. The relative amplitudes of responses at the fundamental and second harmonic frequencies varied considerably, with the harmonic usually dominating between 5Hz and 20Hz (figs 7a,8a). In some cells the power was apparently 'drained' from the fundamental, giving a pure

Figure 4.7

a: Normalised responses to sinusoidal flicker at 26Hz (above) and 9Hz (centre), and to square wave flicker at 2Hz (below). All stimuli had a contrast of 0.1. The responses to sinusoids are phase shifted to compensate for the delay in the second harmonic component's response, which was less than that of the fundamental. The cell showed higher sensitivity to dimming than brightening, and at contrasts below 0.075 responded with spikes only to the dimming edge of a square wave. The responses are fitted with curves obtained by adding the first two harmonics in the response, as measured by Fourier analysis. The residual discrepancies represent the contribution of higher frequency components to the responses.

b: Responses of the cell to stationary flashes showing a pair of spikes to 10ms brightening and a single spike to dimming (20 responses averaged). Note that the response to a simple edge, in the square wave flicker response, elicited only a single spike to both phases. Inset: single response to a bright flash.


(a)
26Hz
9Hz
0°
90°
180°
270°
360°
Stimulus phase
2Hz


(b)
Increment
20ms
Decrement
50ms

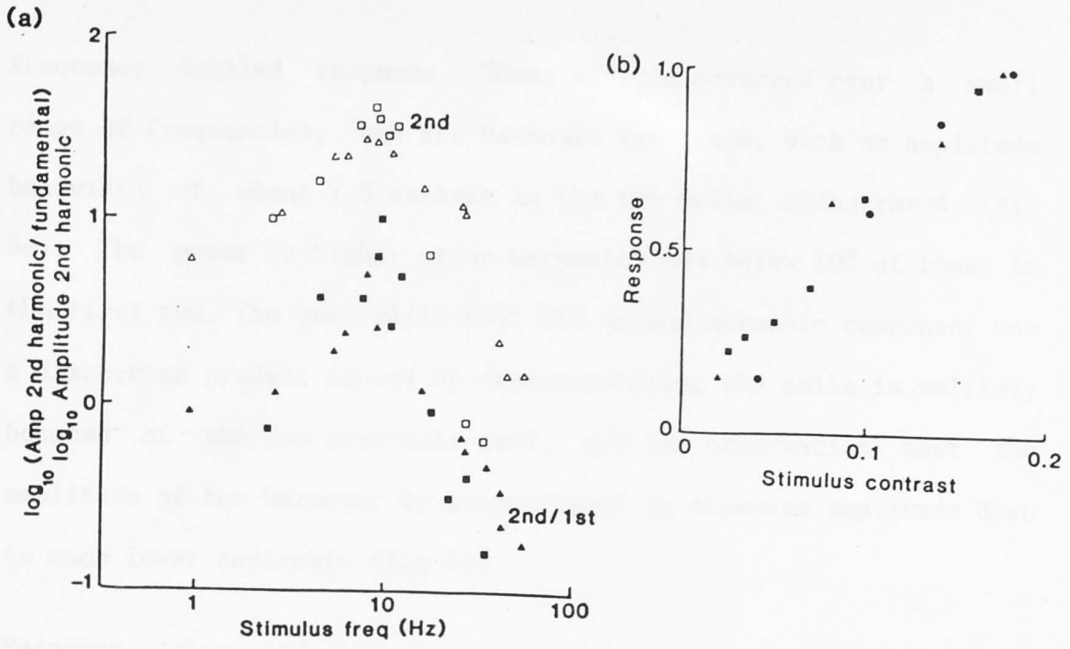


Figure 4.8

a: Logarithmic plot of the amplitude of second harmonic (open symbols), and of the ratio of second harmonic to fundamental amplitude (closed symbols) against frequency. The responses of two cells (Indicated by squares and triangles) to stimuli of contrast 0.1 are shown. The second harmonic amplitude bandwidth for both units was about 1.5 octaves. All stimuli had a contrast of 0.1.

b: Amplitude of the second harmonic components of the responses of three cells at 9Hz, normalised to the response to a contrast of about 0.2, plotted against contrast. The linear relationship between contrast and amplitude indicates that this graded component in the response does not show the thresholding exhibited by the spikes.

frequency doubled response. These effects occurred over a small range of frequencies, and the harmonic was tuned, with an amplitude bandwidth of about 1.5 octaves in the two cells illustrated (fig 8a). The power in higher order harmonics was below 10% of that in the first two. The possibility that the second harmonic component was a distortion product caused by overstimulating the cells is unlikely because of the low contrasts used, and the observation that the amplitude of the harmonic is proportional to stimulus amplitude down to much lower contrasts (fig 8b).

Response delay and the phase relationship between stimulus and response were calculated by plotting phase against frequency for fundamental and second harmonic components of the response (fig 9). The eight sets of responses analysed in this way showed a longer delay in the response of the fundamental frequency component (above 50ms) than of the second harmonic (below 50ms). This implies that different inputs were driving the separate components of the response. In all cells studied the plot of phase vs frequency (fig.9) gave a straight line with zero phase shift (or 0.5 cyles for the fundamental) at 0Hz. This means that the response behaved as though it was associated with a pure time delay.

The responses to sinusoidal flicker here are different from those of the other major class of cells in the locust medulla (Chapter 3). The latter had relatively small harmonic distortions, and there was no evidence for a difference in the delay of the responses at the fundamental and second harmonic frequencies. Furthermore, changes in the response phase with changing stimulus frequency in the other cells could not be attributed to a pure delay, as seems to be the case here.

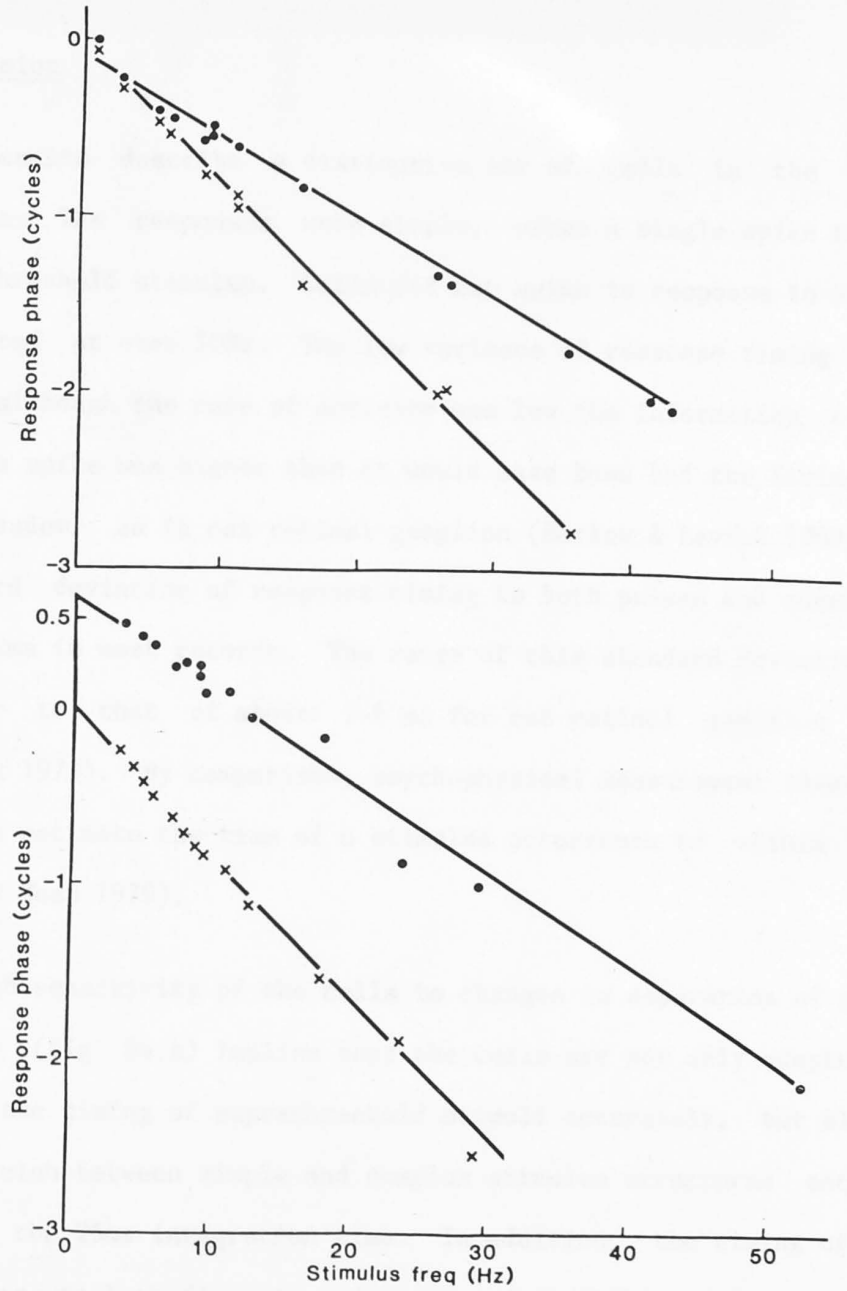


Figure 4.9

Plots of phase against frequency at the fundamental (●) and second harmonic (×) frequencies for two cells. The slope of the plot is approximately equal to the delay in the response for the fundamental and twice the delay for the harmonic frequency. Lines are fitted by linear regression. The slopes shown in the upper plot correspond to delays of 55ms for the fundamental and 44ms for the harmonic, those in the lower plot are 50 and 38ms. The lower plot shows the results for the cell illustrated in figure 7.

Discussion

The results describe a distinctive set of cells in the locust medulla. The responses were simple, often a single spike to any suprathreshold stimulus. Cells did not spike in response to stimuli presented at over 10Hz. The low variance of response timing meant that although the rate of activity was low the information content in each spike was higher than it would have been had the firing been more random, as in cat retinal ganglion (Barlow & Levick 1969). The standard deviation of response timing to both pulses and edges was about 2ms in most records. The range of this standard deviation is similar to that of about 1-6 ms for cat retinal ganglion cells (Levick 1973). By comparison, psychophysical measurement shows that we can estimate the time of a stimulus occurrence to within 200us (Burr & Ross 1979).

The high sensitivity of the cells to changes in separation of paired flashes (fig 6a,b) implies that the cells are not only adapted to signal the timing of suprathreshold stimuli accurately, but also to distinguish between simple and complex stimulus structures occuring within the 25ms integration time. In addition, the timing of the responses to both discrete and continuous stimuli was locked to the mean time of stimulus presentation (fig 6c). These results, at least superficially, bear comparison with human spatial vision (Watt & Morgan 1983). The ratio between the accuracy with which we can measure location, about 5", to the line separation of 25" required to recognise a bimodal intensity distribution, can be compared with the ratio between the standard deviation of response latency of 2ms, and the maximum separation of 13ms over which two subthreshold

flashes were treated as one suprathreshold stimulus by the medulla cells. 13ms is the shortest intrastimulus interval at which a trough is visible in the photoreceptor waveform (fig 6d). This is perhaps the theoretical limit at which simple and composite stimulus patterns can be distinguished. Similarly, psychophysical measurements show that spatial position is assigned to the centroid of a non-uniform intensity distribution, just as the medulla cells responded to the mean time of stimulus presentation of a paired pulse (fig 6a).

This discussion looks at the components of the photoreceptor signal abstracted by the medulla cells, and the processes converting this signal into the observed responses. A simple model is built to explain some properties of the cells, including linear and nonlinear response components. Finally, we look briefly at possible functions of such units in spatial vision.

What aspect of the retinal input controls the response ?

The task of the cells seems to be reliable signalling of the timing of intensity changes. The main criterion required is that the stimulus should give a threshold intensity change within a period of about 25ms. This corresponds to the duration required for presentation of stimuli at the lowest effective contrast, and applies to both dimming and brightening.

The simplest explanation of the responses observed in the medulla is that the cells fire when a threshold photoreceptor voltage is

reached. However a glance at the receptor potentials elicited by pairs of flashes presented with varying separations (fig 6d) shows that the cells would fire at the same time in response to separations of 2ms and 13ms. In fact the response to the longer separation was correlated with the small trough in the photoreceptor waveform. Measurement of photoreceptor voltage would also be an unreliable way of distinguishing between separations of 13ms and 20ms. In practice cells responded well to the shorter but not the longer separation. A similar inspection of figure 6d shows that the cells were not responding to local peaks in the photoreceptor response.

The response to the mean time of stimulus presentation in the two pulse experiments could be attributed to an integration above the photoreceptor level. The medulla cells responding to a peak in the low-pass filtered photoreceptor signal. Futhermore, a system with an integration time of 25ms (and a symetrical impulse response), would allow integration of discrete flash pairs for periods of up to approximately half that time, just as was observed here. Integration will introduce a delay in the response, which partly explains the long latencies observed here (fig 4). A benefit of integration is that the signal would be smoothed, reducing noise and perhaps allowing accurate timing of the response.

Although we have stressed the accuracy of the response timing there was a clear increase in latency observed at low contrasts (fig.5). The cells failed to signal the timing of the stimulus independently of its amplitude below a contrast of 0.4 for a 10ms flash. Since the mean contrast in natural scenes, viewed by neighbouring facets in a

fly's eye or a centre-surround ganglion cell is about 0.4 (Laughlin 1981; MacKerras et al 1986) there may be distortions in the neural image due to the variation in response latency. The increase in latency here resembles the inverse contrast effect observed psychophysically (Coltheart 1980), in which the perceived duration of a stimulus is inversely proportional to its contrast. This effect of contrast on latency, occuring within the linear range of the photoreceptor response, appears inconsistent with the suggestion made above that the peak of a waveform is the primary cue used to estimate stimulus timing, perhaps the crossing of a threshold voltage is critical.

Responses to sinusoidal flicker

Responses were nonlinear, with the second harmonic dominating the response at the stimulus frequency over part of the frequency spectrum, usually around 10Hz (fig 8a). In some cases the amplitude of the harmonic response was over 50 times that of the fundamental. This frequency doubling is expected in a unit giving similar responses to dimming and brightening, and the delay of the harmonic response (fig 9) was similar to the latency of the spike responses. The shorter delay of the response at the harmonic than at the fundamental frequency implies that signals arrive in the medulla cells via separate pathways.

Whilst a second harmonic response would allow similar responses to dimming and brightening the stimulus-response phase relation may partly explain the precision of response timing. The linear

relationship between stimulus frequency and response phase (fig 9) means that the response can be modelled as a function of stimulus amplitude, after a pure delay proportional to the slope of the curves plotted. The absence of frequency dependent phase shifts would reduce distortions in the neural image, and give a response timing unaffected by temporal frequency components in the stimulus. The second harmonic response was rather narrowly tuned, with an amplitude bandwidth of about 1.5 octaves (fig 8a). Narrow frequency tuning may lead to ringing in the response, and it is possible that the response at the fundamental frequency, arriving with a delay, served to damp any ringing.

It was suggested above that the all-or-nothing spike response was produced by measuring the peak of a low-pass filtered photoreceptor response. The linear relationship between stimulus amplitude and second harmonic response amplitude (fig 8b) implies that this thresholding operation was an intrinsic property of the medulla cells described here.

In summary a simple model of the properties of the cells describing several of the observations may be as follows:

1. The photoreceptor response is filtered giving a smoothed output with an integration time of 25ms, and perhaps a tuning to about 10Hz. The impulse response of this filter should be symetrical to account for the stimulus-response phase relationship.
2. The output of this linear stage of processing is squared to give a frequency doubled response.
3. A thresholding operation, in the cells recorded here, gives spikes.

4. A futher output from stage 1 arrives without frequency doubling, but after a delay.

There are several inconsistencies between the model and observations. Most notably reciprocity between stimulus duration and contrast (Bunsen-Roscoe law) appeared to hold over the entire integration time. Stimulus efficency should decline with increasing duration in a linear filter where subthreshold pulses summed over only half the integration time.

Conclusion

This chapter describes a variety of interneurons from a retinotopic ganglion in the locust, which convey an impoverished image of the world to the brain. Several properties of these cells suggest they may act as neural filters of the kind envisaged by Craik (in Sherwood 1966). They code the timing of single suprathreshold intensity changes accurately, but are insensitive to other aspects of the input. Indeed it is possible that secondary aspects of the stimulus, such as its amplitude or whether it is an increment or a decrement, are potential sources of distortion in the image encoded by these cells.

Little can be said about the function of these cells at this stage. In particular we do not know whether their outputs are used alone to control certain behaviours, or if they are viewed in parallel with the outputs of other units to provide a more complete representation of the world. Luminance information is probably conveyed by other cells found in the medulla which give graded or

spiking responses at rates proportional to light intensity within the receptive field (Chapter 3). Although they may loosely be described as 'edge detectors', the medulla cells are unlikely to be acting as, or receiving outputs from, a set of spatial filters (Marr & Hildreth 1980). This is because widefield cells had subunits in their receptive fields and were probably sensitive to high spatial frequencies.

Chapter 5 :

Ultraviolet sensitivity and spectral opponency

Summary

Intracellular recordings in the medulla of the locust optic lobe reveal units showing UV sensitivity, and spectral opponency. Previously only a single population of photoreceptors had been recorded in the locust retina, with peak sensitivity from 450-480nm (Lillywhite, 1978). Behavioural measurements show that the dorsal light response is elicited only by UV light, unlike the optomotor response whose spectral sensitivity is probably attributable to inputs from the green sensitive cells. The possibilty that the cells described may be involved in maintainence of level flight is discussed.

Introduction

Insects use a variety of different visual behaviours to maintain level flight (reviewed by Wehner 1981). For convenience these may be divided into two functional groups : those which act as inertial systems correcting transient deviations, such as the optomotor response (Buchner 1984) and the ocellar response (Taylor 1981); and a number of sustained responses which provide a general course control, perhaps by orienting to the horizon or dorsal illumination (Goodman 1965).

The retinula cell inputs and higher order neurons controlling the optomotor reponse have been studied in the fly (Hausen 1981; Buchner 1984), and it has been shown that the short visual fibres drive directionally sensitive cells in the lobula plate. Similarly, Wilson (1978) has described the ocellar neural system of the locust showing how it is suited to rapid control of flight. In contrast, only two isolated studies have thrown light on the neural basis of horizon detection by the compound eye. Hertel (1980) suggested that a phasic neuron in the bee optic lobe possessed a combination of spectral and spatial opponencies which suited it to the task. Werhahn (1976) showed that the long visual fibres are used for height orientation by the fly Musca, whereas the short visual fibres subserve orientation to similar vertical stripes by Drosophila (Morton & Cosens, 1978).

This paper describes neurons recorded in a survey of the medulla of the locust optic lobe. These cells are distinctive in posessing UV sensitivity, spectral opponency and tonic responses. It is argued

that these properties suit the units to horizon detection, a suggestion corroborated by the finding that the dorsal light response driven by the compound eye is UV sensitive; although spectral opponency was not detected in the response.

Results

To demonstrate the presence of UV sensitivity and spectral opponency, six of the many cell types recorded in the medulla are mentioned here. The results are presented by describing the properties of individual cells, and no attempt has been made to draw quantitative comparisons between similar units. Apart from their chromatic properties all of these cells are distinctive in having substantial tonic components in their responses. Most cells in the medulla have more phasic responses.

The first two cells described showed a much higher sensitivity to UV than to green light, indicating that a previously unreported receptor type exists in the locust retina. The other four cells showed spectral opponency; since the ocelli were absent this also indicates that more than one receptor class occurs in the compound eye. Cell 3 had a fairly small circular receptive field, and was the simplest of the opponent units; like all the opponent cells described here it was inhibited by UV and excited by green light (units with the reverse opponency have also been penetrated). Cells 4 and 5 were inhibited by UV and stimulated by green light, with narrow receptive fields extending along the horizon. These properties might suit them to the signalling of roll or pitch, by measuring changes in the relative intensities of long and short wavelength illumination, the ratios of which differ markedly about the horizon. The possibility that such units could discriminate roll from pitch is exemplified by the observation that cell 4 had an ipsilateral, and cell 5 a contralateral receptive field. Finally, cell 6 had a receptive field covering the entire ipsilateral eye. The properties of these cells are now described in more detail.

Cell 1. Fig.5.1

This small field ($<3^{o}$) UV sensitive unit had the simplest properties of the cells mentioned. Such a cell may have provided inputs to any of the others described, as it was recorded distally, in the 1st chiasm. The latency was the shortest measured at 20ms , which is consistent with light-adapted photoreceptor latencies (Howard 1981). The response to UV and green light in comparison to the unfiltered white screen is shown in fig.5.1, together with the responses to white flashes (inset). The waveform is similar to that of a photoreceptor, which with the distal recording site suggests that the cell was a long visual fibre. (More recently UV receptors, with a single peak sensitivity at 370nm have been recorded in the proximal part of the retina (S.McFadden pers. comm)). This retinula cell class is present in the locust, projecting directly from the retina to the medulla (Nowel and Shelton 1981). The small spikes noted here have been recorded in locust retina (Shaw 1968), and in presumed long visual fibres in dragonfly (Laughlin 1974). The absence of spikes during some of the recording (fig.5.1 inset) indicates that they were due to injury.

Cell 2. Figs.5.2,3.

Like cell 1 this unit was depolarised by UV and insensitive to green light, but the receptive field was about 20^{o} in diameter (fig.5.2). The cell was marked with Lucifer yellow (fig.5.3).

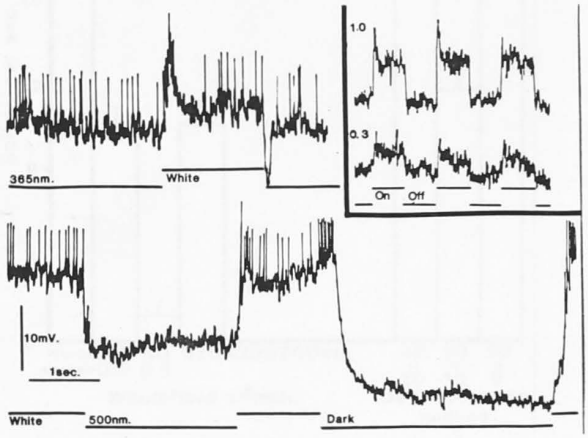


Figure 5.1

Responses of cell 1 to isoquantal ($5x10^{17}$photons/m^2sr.sec) widefield illumination at 365nm and 500nm, and a dark control, produced by placing wideband chromatic, and an opaque filter in front of the eye viewing a white screen. Inset: Responses to 3^o spots of contrast 1.0(Upper) and 0.3(Lower) presented at 0.5Hz.

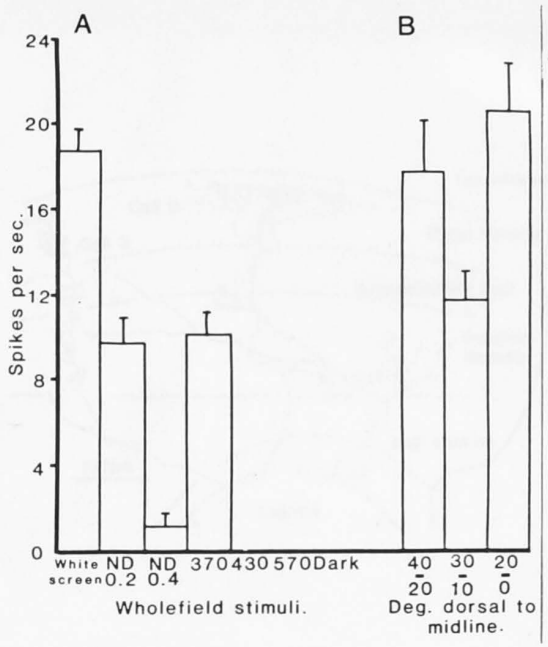


Figure 5.2

a: Mean spike rate of cell 2 after 20 seconds adaptation to whole field stimuli. The three chromatic sources were approximately isoquantal ($4x10^{16}$ photons/ m^2sr. sec). The Wratten neutral density filters have densities 0.3 units greater than their nominal value to 370nm light. All samples are based on 10 second sample of the response, with standard deviations shown calculated with the assumption that the occurrence of spikes follows Poisson statistics.
b: Spike rate of cell 2 in response to dimming 20^{o} square regions of a white screen with Wratten filter (Density 0.2). The stimulus was placed in 3 overlapping positions on a vertical axis between 0^{o} and 20^{o} caudal of the midline, with the response to each position tested 3 times for 5 seconds immediately after dimming. The cell was insensitive to dimming outside this region, and, in contrast to cell 1, a 5^{o} black spot had no effect on the firing rate.

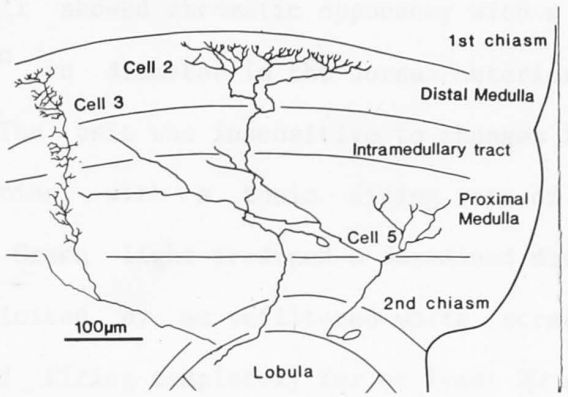


Figure 5.3.

Drawing of cells 2,3 and 5 filled with Lucifer yellow CH, reconstructed from anterior and posterior views. The boundaries of the structures shown are approximate, and the neurite diameters are not drawn to scale. The distal parts of cells 2 and 3 were well filled, whereas it is probable that parts of cell 5 were overlooked. The body of cell 3 was probably at the end of the secondary neurite in the medulla, and removed during the preparation for microscopy.

Cell 3. Fig.5.3

This cell showed chromatic opponency with a receptive field less than 20^{o} in diameter in the dorsal anterior part of the visual field. The unit was insensitive to changes in widefield achromatic illumination, with a tonic firing rate of about 10 spikes per second. Green light produced a sustained discharge at double the rate elicited by an unfiltered white screen, whereas UV light inhibited firing completely for at least 20 seconds. The cell was filled with Lucifer yellow (Fig.5.3), and was close to the dorsal margin of the medulla.

Cell 4. Figs.5.4,5,6,7

The best characterised of all the units described, cell 4 was excited by green and inhibited by UV light (fig.5.4) with a narrow receptive field disposed along the horizon; properties that may be useful for horizon detection. Other features of interest are the presence of an inhibitory surround, and adaptation of the response.

The responses to a variety of wavelengths, and to white light are shown in figs.5.4 and 5.5, relative to spontaneous activity in the dark. Opponency, combined with the localised receptive field, is compelling evidence for more than one receptor type in small regions of the retina. This is in contrast to Lillywhite's (1978) observation that all retinula cells have a spectral sensitivity which can be attributed to a mixture of rhodopsins with peaks at 450nm and 500nm, whose ratio changes gradually in a dorsoventral gradient with no local variation.

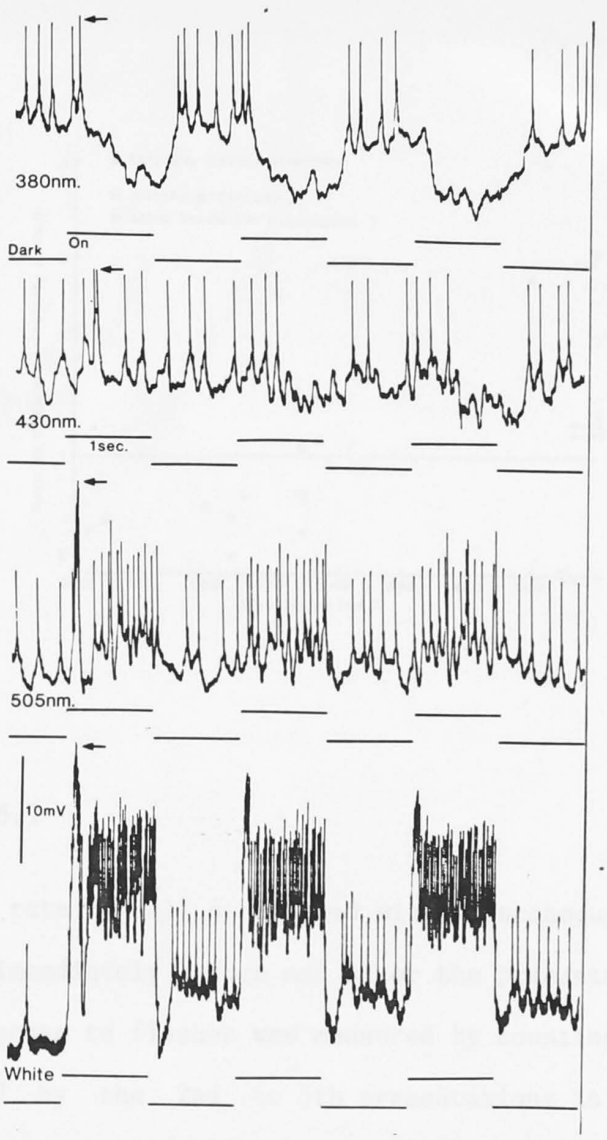


Figure 5.4

Response of cell 4 to chromatic, and white light presented as a 10^{o} spot over a dark background directly in front of the animal. Each trace shows the response to the first three flashes after 30 seconds dark adaptation. Note the transient depolarisation to the first flash in each case (arrowed), which is attenuated or absent in subsequent presentations. Effective intensities of the spots are given in the legend to Fig.5.

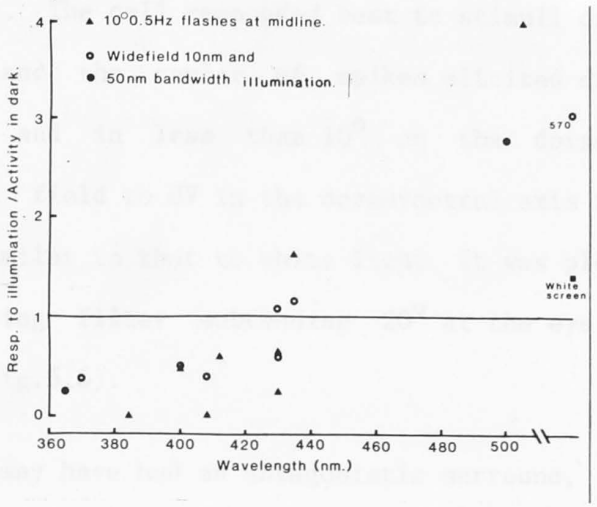


Figure 5.5

Firing rate of cell 4 compared with spontaneous activity during the period immediately before and after the presentation of test stimuli. The response to flashes was measured by counting the number of spikes elicited by the 2nd to 5th presentations in a series like that illustrated in Fig.4. The effective intensities of the flashes were : 370nm 8; 383nm 45; 401nm 52; 408nm 100; 412nm 40; 430nm 130; 435nm 180; 505nm 340 x 10^{13} photons/m^2sr.sec. The wide field stimuli were provided by placing filters in front of the eye illuminated with a focussed microscope lamp. This gave relative intensities as follows: Wide band filters, 365nm 8; 500nm 260; Narrow band filters. 370nm 1; 400nm 2; 408nm 4; 430nm 6; 435nm 10; 505nm 40; 570nm 110. The white screen had a luminance of 1000cd.m^{-2}. The responses to green and to white light were luminance dependent.

The receptive field was mapped with 5^{o} white flashes (contrast 9) (fig.5.7). The cell responded best to stimuli directly ahead of the animal, and the number of spikes elicited dropped by 50% 50^{o} caudally and in less than 10^{o} on the dorsoventral axis. The receptive field to UV in the dorsoventral axis is shown in fig.5.6 and is similar to that to white light. It was plotted by moving a UV transmitting filter subtending 20^{o} at the eye behind the white screen (fig.5.6).

The unit may have had an antagonistic surround, as isoquantal white flashes subtending 10^{o}, 30^{o} and 60^{o} elicited responses of 7,2 and 0.5 times the spontaneous rate respectively. The flashes were centred on the horizon 20^{o} caudally, and projected over an illuminated screen. The possibility that UV inputs had a lower sensitivity threshold than the green ones, which would also explain this observation, was precluded because dim 10^{o} flashes were always excitatory.

Finally we turn to the waveform of the response, illustrated in fig. 5.4. The main features are, an adapting phasic depolarisation to all wavelengths (arrowed), followed by the more tonic chromatic opponent reponse. The phasic response had a shorter latency (40 - 45ms) than the tonic (65 - 70ms for both depolarisation and hyperpolarisation), which was measured after the phasic component had adapted. The tonic depolarisation to long wavelengths also showed some signs of adaptation. This is most evident in the response to 430nm flashes, which in the course of the three presentations illustrated in fig.5.4 changed from excitation to inhibition. This effect was

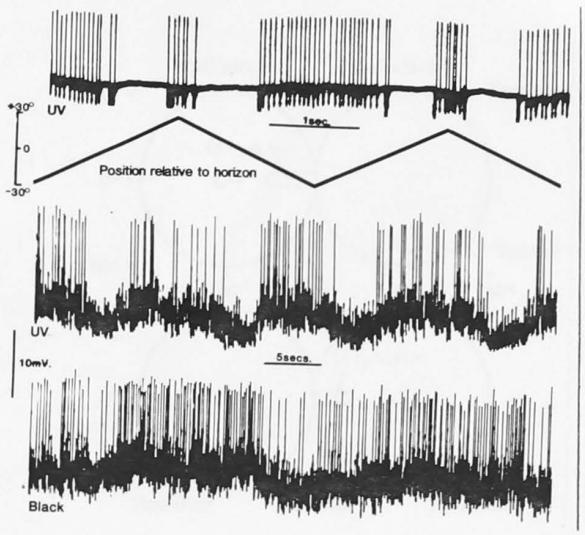


Figure 5.6.

The responses of cell 4 (middle), and cell 5 (above), to vertical movement of a 20^{o} diameter UV filter on an illuminated screen. In both cases inhibition occurred in receptive fields close to the midline, but appear to be in different places because the head is tilted, and the receptive field of cell 5 was in the contralateral eye. The lower trace is a control for cell 4 showing that there is no response to a black target (The irregular firing is uncorrelated with the target position) and indicates that the unit is more sensitive to chromatic than to luminance signals. No control is shown for cell 5, but the regular firing pattern was completely unaffected by similar green, and black filters.

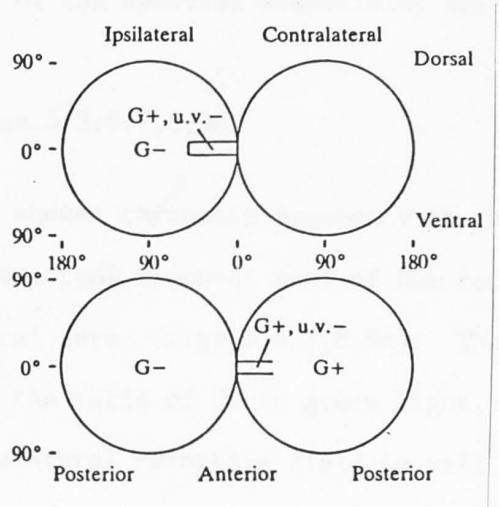


Figure 5.7

Diagram of the receptive fields of cell 4 (Above) and cell 5 (Below). No data are available for the extent of the inhibitory surround of cell 4, or the lateral extent of the spectral opponent receptive field of cell 5. In addition the contribution of UV sensitive inputs outside the regions designated G+,UV- is unknown, and UV as well as green receptors may contribute to the inhibitory surround.

repeatable after 30 seconds dark adaptation, and makes accurate measurment of the spectral sensitivity difficult.

Cell 5. Figs.5.3,6,7,8,9A.

This unit showed chromatic opponency at the horizon, like cell 4, but the spectral opponent part of the receptive field was in the contralateral eye (figs.5.6,7,8,9A). The sensitivity to a small change in the ratio of UV to green light, in a restricted part of the contralateral receptive field is well illustrated in fig.5.6, showing the response to vertical movement of a UV filter against a white background. Activity drops sharply from the normal spontaneous rate to nothing, despite the fact that the absolute amount of UV was reduced and the receptive field was not filled by the filter.

An important difference between this unit and cell 4 is that excitatory inputs were received from the entire contralateral eye; the spectral opponent region of the receptive field being due to an area of UV inhibition embedded in the wide excitatory field. Stimulation of any part of the ipsilateral eye inhibited activity, irrespective of wavelength (fig.5.7). This spatial opponency emphasises the possible role in allowing the locust to compare inputs received by the two eyes with one another. The presence of contralateral inputs to the medulla is consistent with Honegger and Schurmann's (1975) observation that axons project directly between medullas of the cricket, Gryllus campestris.

As in cell 4 the response to repeated ipsilateral flashes adapted. When moved by a few degrees the spot elicited an unadapted response.

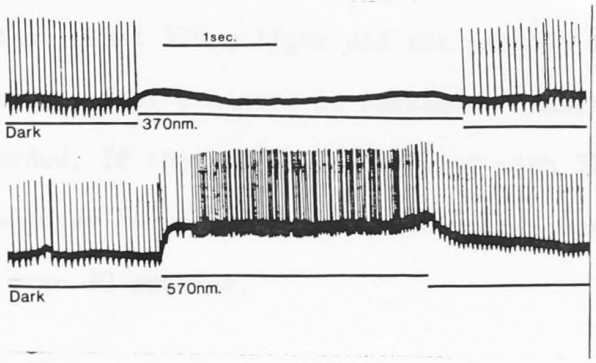


Figure 5.8.

The response of cell 5 to whole field, contralateral illumination. Intensities are given in the legend to Fig.5.

By comparison this localisation of adaptation was not seen in cell 4. A powerful long term adaptation effect was indicated by the observation that 370nm light did not inhibit firing if the eye was illuminated after a minute in darkness; instead a weak excitation was recorded. If the eye was stimulated with 570nm or 430nm light up to 30 seconds before UV illumination there was a total inhibition, lasting over 30 seconds.

Two similar units were penetrated, in one of which prior illumination was not necessary for UV to elicit inhibition. Another was incompletely filled with Lucifer yellow by pressure injection (fig 5.3). There was no evidence of any arborisation or axon outside the proximal region of the medulla, and it is unlikely that this unit projected directly to the contralateral eye.

Cell 6. Figs.5.9B,10.

This cell was excited by green and inhibited by UV light, throughout the ipsilateral eye's receptive field. Two sets of records were made after ocellar removal, and unlike ocellar units (Wilson 1978) there was a large tonic component in the response. For example the firing rate showed no adaptation after 30 seconds in response to a 0.1 log unit dimming (0.4 at 370nm).

Whilst previous units were excited by a white screen the firing rate of cell 6 was depressed by white light compared with the dark activity. This implies that the UV-sensitive inputs dominate the green in 'white' light. The chromaticity of Wratten filters to a UV sensitive system is shown by the observation that a filter of

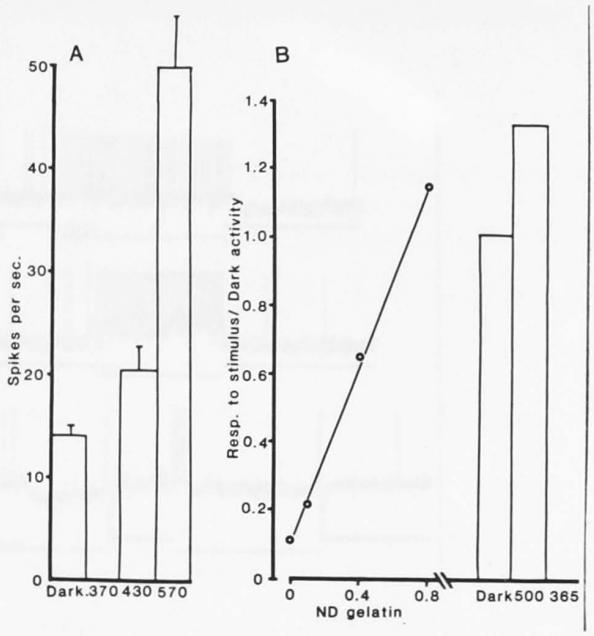


Figure 5.9

a: Response of cell 5 to widefield contralateral stimuli. Total inhibition by 370nm light was sustained for over 30 secs. Other data were obtained by measuring spike rate over a 5 - 10 second period. Stimulus intensities are given in the legend to Fig.5 (widefield).

b: Response of cell 6 to widefield stimuli, relative to activity during dark periods before and after each stimulus presentation. The screen luminance was $1000cd.m^{-2}$; the 365nm and 500nm chromatic filters gave radiances of 1 and $4x10^{15}$ photons/m^2sr.sec respectively. The Wratten neutral density filters of nominal densities 0.1, 0.4 and 0.8 had values of 0.36, 0.72, and 1.1 units at 365nm, and were close to their nominal densities at 500nm. The differences between the response to 500nm and the 0.8 density unit Wratten gelatin and the dark controls are highly significant (Prob. less than 0.001, and 0.004 respectively, assuming Poisson statistics.). The cell had a tonic response with no adaptation to a 0.1 log unit filter in 30 secs, and a maximum activity of 55 spikes per sec.

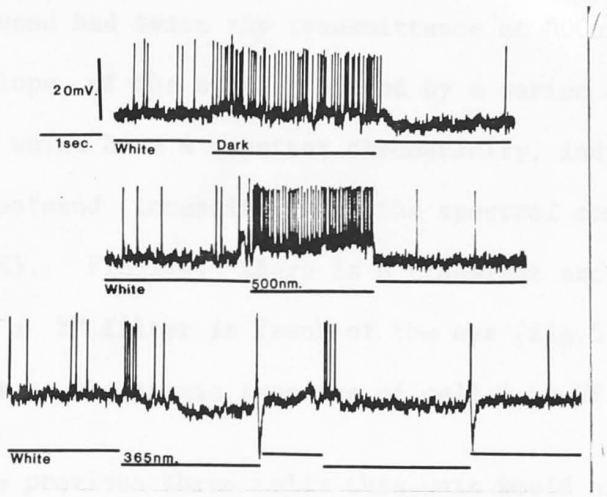


Figure 5.10.

Response of cell 6 to widefield stimuli, produced by placing filters in front of a white screen. Note the transient excitation to dimming with a UV filter (Hyperpolarisation recorded on the removal of the 365nm filter may be a stimulus artefact). Data on illumination are given in the legend to Fig.8A.

density 0.8 excites the cell more than darkness. All the gelatin filters used had twice the transmittance at 500nm as at 370nm. The steep slope of the curve produced by a series of neutral density filters, which have a constant chromaticity, indicates that the unit would confound intensity with the spectral composition of light (fig.5.9B). Finally, there is a transient excitation produced by placing a UV filter in front of the eye (fig.5.10), which may be analagous to the phasic response of cell 4 to UV light.

Like the previous three cells this unit would signal changes in the position of the horizon, increasing its firing rate as the eye viewed more of the dim green ground. The wide visual field means that the unit is less well adapted to accurate localisation of the horizon than cells 4 and 5. Nevertheless there are related functions to which it is suited. For example the small effect of spectral compared with luminance changes on activity mean that the cell might have a role in setting the adaptation state of the visual system; altering the relative sensitivity to green and UV light, or mediating a conversion from opponency to pooling of inputs on adaptation to dim conditions.

Behaviour. Fig.5.11.

The properties of the cells described above suggest that UV sensitivity and chromatic opponency have a role in behaviour, so the spectral responses of the animal were tested using stimuli found to elicit the optomotor (Thorson 1966), and dorsal light responses (Taylor 1981). The spectral sensitivities of the optomotor response

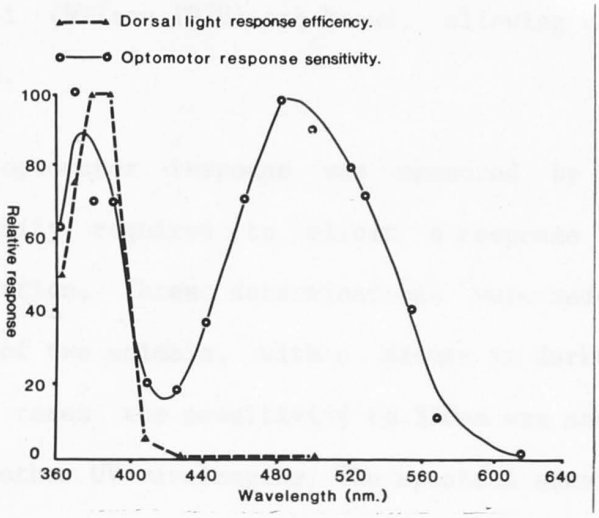


Figure 5.11.

Spectral sensitivity of the optomotor response and spectral efficency of the dorsal light response. The optomotor threshold after 60 minutes dark adaptation was approximately $5x10^{14}$photons/m^2sr.sec at 499nm. The dorsal light response was tested at UV intensities of 1 to $5x10^{17}$photons/m^2sr.sec, and with green light up to 10^{19}photons/m^2sr.sec.

in other insects (Kaiser & Liske 1974; Kaiser 1975), and locust ocelli (Wilson 1978) are known, allowing useful comparisons to be drawn.

The optomotor response was measured by finding the threshold intensity required to elicit a response after an hour's dark adaptation. Three determinations were made at each wavelength on each of two animals, with a minute in darkness between tests. In both cases the sensitivity to 370nm was anomalously high compared with other UV wavelengths. The spectral sensitivity of the optomotor response, tested in this way (fig.5.11), is similar to curve obtained for fly optomotor (Kaiser 1975) and landing responses (Tinbergen & Abeln 1983). UV sensitivity is rather high and variable; a point which needs clarification, but may in part be due to similar variability observed in locust short visual fibres (Lillywhite 1978, L.Marčelja pers. comm.).

The dorsal light response shows quite different spectral properties (measured as spectral efficency), with little or no response to wavelengths above 410nm. The wavelength dependence of the response amplitude is shown in fig.5.11, measured after ocellar ablation, at high radiance and contrast 0.5, with a bright dorsal hemisphere. Green light (500nm) of 20 times the maximum UV intensity was used without eliciting a response (In two of the five animals tested a small response occured, however the amplitude was less than 20% of that to UV, irrespective of intensity). Green light in reverse contrast, (i.e. with the ventral field brighter than the dorsal) neither elicited a response, nor affected the response to UV over a wide range of intensities.

Discussion

The results show that spectral opponency occurs amongst the outputs of the locust compound eye. This suggests that at least one spectral class of receptor exists in addition to the population of green cells described by Lillywhite (1978), and it is conjectured that these are UV sensitive long visual fibres. The tonic responses and spatial properties of some of the neurons described suggested that they have a role in controlling a sustained orientation to the horizon. Moreover, it is evident that the response to a bright dorsal hemisphere, and the optomotor response can be distinguished from one another by their spectral properties. There is no evidence that colour vision is used in the dorsal light response, but it probably receives an input from the UV receptors. The optomotor response probably uses inputs from green sensitive cells, resembling the fly, the bee and the butterfly (Kaiser & Liske 1974; Kaiser 1975; Horridge et al 1984), although high sensitivity to 370nm may reflect a contribution from UV receptors.

Flight control by the locust appears to use at least three separate visual mechanisms. The optomotor response, and the two responses to dorsal illumination and/or horizontal contrast; one driven by the ocelli, and the other by the compound eyes. It is interesting to see how these three behaviours compliment one another in their spatial, spectral and temporal properties. The optomotor response has high spatial and temporal acuity (Buchner 1984), with a spectral sensitivity resembling the short visual fibres in the fly (Hardie 1979), and perhaps in the locust. This high spatial resolution is in marked contrast to that of the unfocussed ocelli, which are UV

sensitive and, like the optomotor response, give a short latency phasic response (Wilson 1978; Taylor 1981). The ocellar and optomotor responses act as inertial systems allowing the animal to correct transient deviations from the flight path; using fine structures, and changes in overall illumination of the ocelli respectively. The UV sensitivity of the ocelli means that they will be particularly sensitive to changes in the amount of light received from beneath and above the horizon (Wilson 1978). The compound eye mediated dorsal light and horizon responses are relatively sluggish and sustained, allowing tonic orientation to the horizon, from which transient deviation could be corrected by the other responses (Goodman 1965; Taylor 1981).

Let us turn to the properties required by a neural system which is to give tonic orientation to the horizon. The animal must be able to obtain a large amplitude signal, free from local distortions, and discriminable from other objects in the environment. The most straightforward requirement is to have high acuity in the vertical but not the horizontal axis. Cells with horizontally elongated receptive fields like 4 and 5 described above would be sensitive to changes in illumination as the animal tilted about its horizontal axes, but less responsive to vertical structures.

The effect of poor horizontal acuity may be enhanced by temporal blurring, ensuring that the animal is able to locate the true horizon, without being distracted by local variations caused by vegetation and landscape. Such temporal blurring may be implemented by a neural system with a long integration time, explaining the long

latency of the compound eye mediated dorsal light response (Taylor 1981). The cells described here have more tonic responses than the majority of units recorded in the medulla (Personal observation).

We now consider the spectral properties required for detection of the horizon; which is distinguished by having a high UV and a low green contrast (Wilson 1978). However, since the sky is normally brighter than the ground at all wavelengths spectral opponency, as observed here, will attenuate the signal provided by the horizon. This indicates that opponent units would be unsuited to horizon detection, but perhaps adapted to another role; for example the navigational task described in the bee by Rossel and Wehner (1984). Alternatively there may be a more subtle explanation for the use of chromatic opponency in horizon detection; for example colour contrast may distinguish the horizon from other structures with high contrast at all wavelengths, such as silhouetted vegetation. Finally, the green input may serve as an adaptation mechanism, effectively backing-off the UV signal to maintain the units in a state of high sensitivity to changes in UV illumination. At present the function of spectral opponency in the locust, and its role in the dorsal light response awaits more stringent behavioural and electrophysiological studies, as well as measurements of the spectral properties of natural scenes.

Chapter 6 :

Directionally selective cells

Summary

Intracellular recordings of a distinctive class of directionally selective cell from the medulla of the locust optic lobe are described. Dye marking shows that these cells have their dendrites in the distal part of the medulla, and project through the lobula complex.

The cells are excited by upward movment, and have receptive fields of about 20^{o} in diameter. They are sensitive to a wide range of angular velocites from $0.02^{o}.sec^{-1}$ to over $200^{o}.sec^{-1}$. The cells are sensitive to stationary flicker and have different response latencies to dimming and brightening. Evidence is presented which suggests that directional computation depends, at least in part, on an inhibitory interaction between flicker sensitive channels.

Introduction

Directionally sensitive cells are found in both the lobula and medulla of the insect optic lobe. Those in the lobula complex have been best studied in the fly, (Hausen 1981, Egelhaaf 1985b) and have also been described in the locust and the bee (Kien 1974, DeVoe et al 1982). The main function of these widefield cells is thought to be analysis of visual flowfields, allowing flight stabilisation (Buchner 1984), and fixation of objects detectable by their relative motion against a background (Egelhaaf 1985a). Few records of directionally selective cells have been made in the insect medulla , but Collett and King (1975) described cells in Syrphid flies with smaller receptive fields than those recorded in the lobula. These units had antagonistic surrounds and would also have been suited to detecting small objects moving relative to the background.

The basis for directional sensitivity has been studied at both behavioural and electrophysiological levels. In the fly it is known that selectivity of the widefield cells in the lobula plate depends upon interactions between luminance channels which compute the phase shift of the stimulus between pairs of (approximately) adjacent facets of the compound eye (reviewed by Buchner 1984). Directional responses in widefield cells of both vertebrates and invertebrates may be the result of local interactions between non-directional inputs on the widefield cells themselves, or by the confluence of small field motion detectors (Barlow & Levick 1965; Torre & Poggio 1978; Buchner 1984; Strausfeld 1984). If they exist, the small field motion detectors in the fly are expected to be in the medulla, which is the ganglion distal to the lobula complex.

This paper describes a new type of directionally sensitive cell in the locust medulla, which is unlikely to be in the pathway to the cells of the lobula complex. The medulla cells, amongst the most easily recorded units in the ganglion, were excited by upward movement and had receptive fields 10^{o}-20^{o} in diameter. Like the cells of the lobula complex they were sensitive to motion within the homogenous receptive field. The cells were very sensitive to stationary flicker, and unlike the fly lobula plate neurons they had different response latencies to brief increments and decrements (Zaagman et al 1977). The axons projected directly to the protocerebrum, whilst the dendrites were in the distal part of the medulla. A unit with a receptive field diameter of about 2^{o} is also mentioned.

Results

The cells described here include all the directionally selective units recorded in the medulla. Most form a distinctive class, and were the most easily recorded units in the locust medulla. Five cells were filled with Lucifer yellow (fig.1). The medulla is a columnar neuropil, with one column of cells corresponding to each facet in the compound eye (rev. Strausfeld 1984). The disorganised, circular dendritic fields were in the distal part of the medulla, and extended over several such columns. The axons projected through the lobula complex, but their destination was not found. The cell bodies were in the medulla and attached to the axons by a short neurite. We now describe the responses in more detail, first to moving bars which may help us to understand the function of these cells, and then to stationary flashes to look at the basis for directional sensitivity.

Responses to moving bars

Responses to horizontal and vertical movement were studied with 1.5^{o} wide bars of contrast -0.12. The bars' length exceeded the receptive field diameter. The most distinctive feature of the responses was the very wide range of angular velocites over which the cells gave directional responses (fig. 3). The lowest angular velocities tested revealed a directionally selective response to a displacement corresponding to the width of a photoreceptor's receptive field (Wilson 1975) in about a minute. The highest angular velocity tested was $250^{o}.sec^{-1}$, and this also elicited a strong directional response.

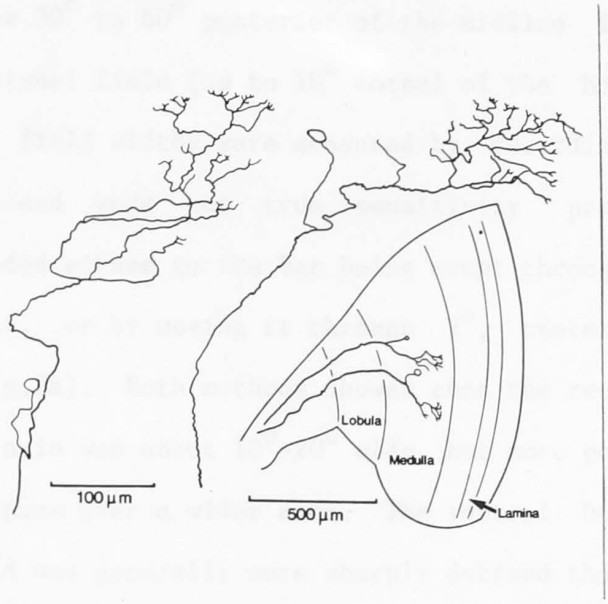


Figure 6.1

Drawing of two cells filled with Lucifer Yellow CH, showing the dendritic structure, and the approximate positions of the cells in the optic lobe. The lower neuron has been moved downward for clarity. The dendritic fields were approximately circular in the plane parallel to the eye surface. Three other cells were marked, and had dendritic fields intermediate between those of the two illustrated. All the cells' somata were above the centre of the medulla.

The cells faced from 30° to 60° posterior of the midline in the ventral part of the visual field (up to 10° dorsal of the horizon) (fig 2b). Receptive field widths were measured by recording the response amplitude, and were not true sensitivity profiles. Responses were recorded either to the bar being swept through the entire receptive field, or by moving it through 2°, centered in various positions (fig.2a). Both methods showed that the receptive field in the vertical axis was about 10°-20° wide, but more powerful stimuli elicited responses over a wider area. The ventral boundary of the receptive field was generally more sharply defined than the dorsal. The cells varied markedly in their sensitivity to horizontal motion, as they did to stationary stimuli, however the receptive fields were approximately circular. There was no evidence for spatial antagonism in the responses to moving bars, and stimuli of all sizes elicited a directional response. This contrasts with recordings from the Syrphid medulla, where smallfield directionally selective cells show spatial antagonism, and respond preferentially to small targets (Collet & King 1975).

Responses to stationary stimuli

Whereas the moving stimuli used were all darker than the background, stationary stimuli were produced with bright spots. These were presented singly, as brief (2ms-10ms) increments or decrements, or as sustained flashes. Alternatively, pairs of flashes were presented with varying angular separations to give apparent motion illusions (eg. Morgan 1980). These were either presented for long periods (up to 1 second) and switched to give a 'phi' illusion, or a pair of

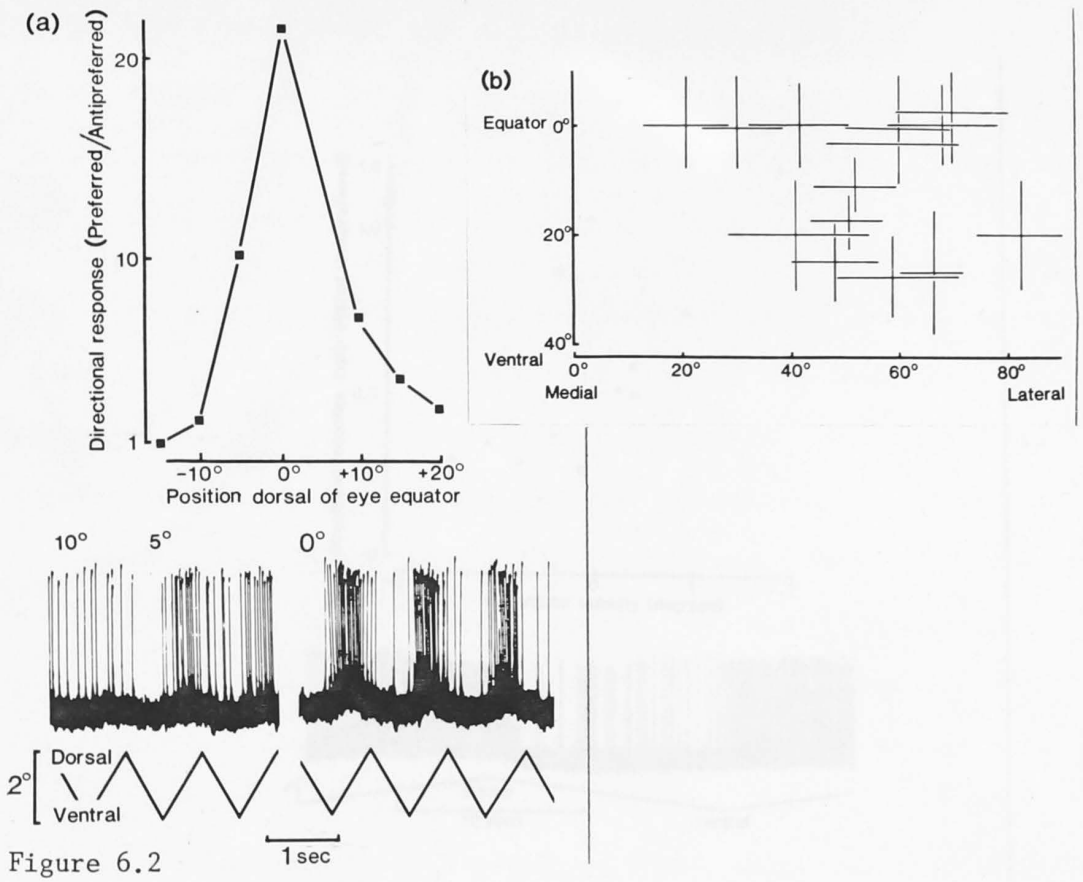


Figure 6.2

a,Above: Receptive field in the vertical axis of a cell, measured by moving a bar through 2^{o}. The number of spikes elicited in response to 10 stimulus cycles were averaged at each point. No responses were obtained outside the region shown. Below: Raw data illustrating the responses to the moving bar (contrast -0.12, width 1.5^{o}).

b: Plot of the receptive field areas and positions of several cells. Receptive fields were measured with moving bars and stationary flashes, and the lines show the extent of the regions for which the response was half maximum. The low sensitivity of some - units to horizontal movements means the results are unreliable, however the receptive fields were approximately circular. Powerful stimuli elicited responses up to 20^{o} from the receptive field centres. It was not possible to place stimuli more than 35^{o} ventral of the horizon.

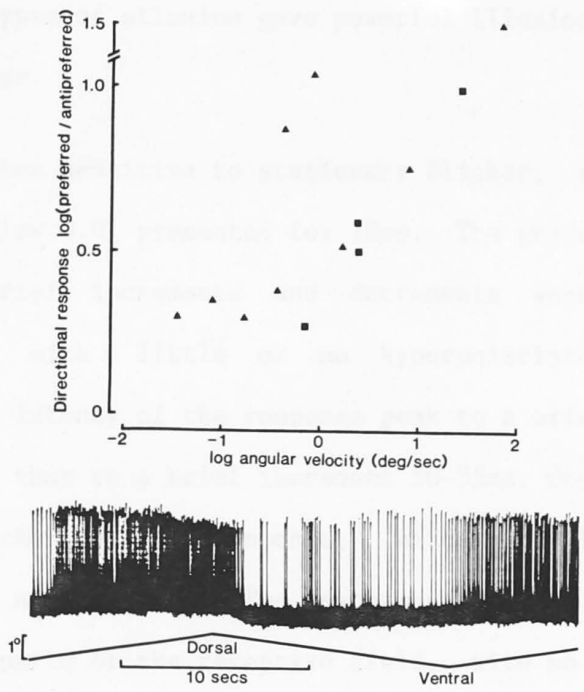


Figure 6.3

Above: Log plot of directional sensitivity against angular velocity for vertical movement of the bar through 1^{o}-10^{o} for two cells, indicated by squares and triangles respectively.

Below: Raw data showing the response to slow movement. Note that the excitatory discharge continued after the direction of motion had reversed. This effect, which was obtained consistently appeared to occur over a constant angle of about 0.1^{o}, and probably reflects the detection limit for directional selectivity.

brief flashes were presented in rapid succession followed by a long interval. Both types of stimulus gave powerful illusions of motion to the experimenter.

The cells were often sensitive to stationary flicker, responding to contrasts of below 0.01 presented for 10ms. The graded potential responses to brief increments and decrements were primarily depolarisations, with little or no hyperpolarising response components. The latency of the response peak to a brief decrement was 30-35ms, and that to a brief increment 50-55ms. One record (out of 15) gave the reverse response, with the low latency depolarisation to an increment. The responses to brief stimuli were similar in all parts of the receptive field, with no sign of an antagonistic surround. The receptive field areas measured with stationary stimuli were similar to those to moving bars.

Responses to phi-flashes differed from the sum of those to stationary flicker in having a sustained excitation (up to at least 1 second) after apparent motion in the preferred direction. Flicker elicited only a phasic depolarisation to dimming (fig 4b). In contrast to the excitation elicited by sustained phi-flashes, the response to consecutive brief flashes implied that the basis for directional sensitivity was mainly an inhibitory interaction between two excitatory flicker sensitive inputs (fig 5). The figure shows the response to a pair of 2ms increments separated by 3^{o} and presented at an interval of 60ms, followed by a break of 600ms. When the lower flash was presented first, simulating motion in the preferred direction, the response to both stimuli was equal, whereas

if the upper flash was first there was no response to the second. This inhibition occurred at all flash separation times tested between 10ms and 100ms. Successive presentation of two flashes in the same position gave a response similar to that elicited by apparent motion in the preferred direction.

The effect of changing the separation distance of 2^{o} diameter spots forming a phi pair is shown in figure 4a. The directional response was maximum at a separation of 2^{o}-3^{o}. This finding was replicated in two other units. The size of the spots used caused an overlap at lower separations, and the signal was correspondingly reduced. The results are thus consistent with the suggestion that directional computation is performed between adjacent facets (reviewed by Buchner 1984). (The interommatidial angle in the lateral part of the locust eye is about 1.25^{o} (Horridge 1978), and the angular sensitivity half width 1.5^{o} (Wilson 1975).) There was no evidence for an antagonistic surround, as the cells responded well to widefield motion, and never showed a reversal of directional preference with increasing flash separation. This is in contrast to observations in the fly lobula plate neuron H1, where an inhibtory surround to the elementary movmement detector causes a reversal of directional sensitivity occurs when pairs of bars are presented at separations of over 5^{o} (Srinivasan & Dvorak 1980; T. Maddess personal communication).

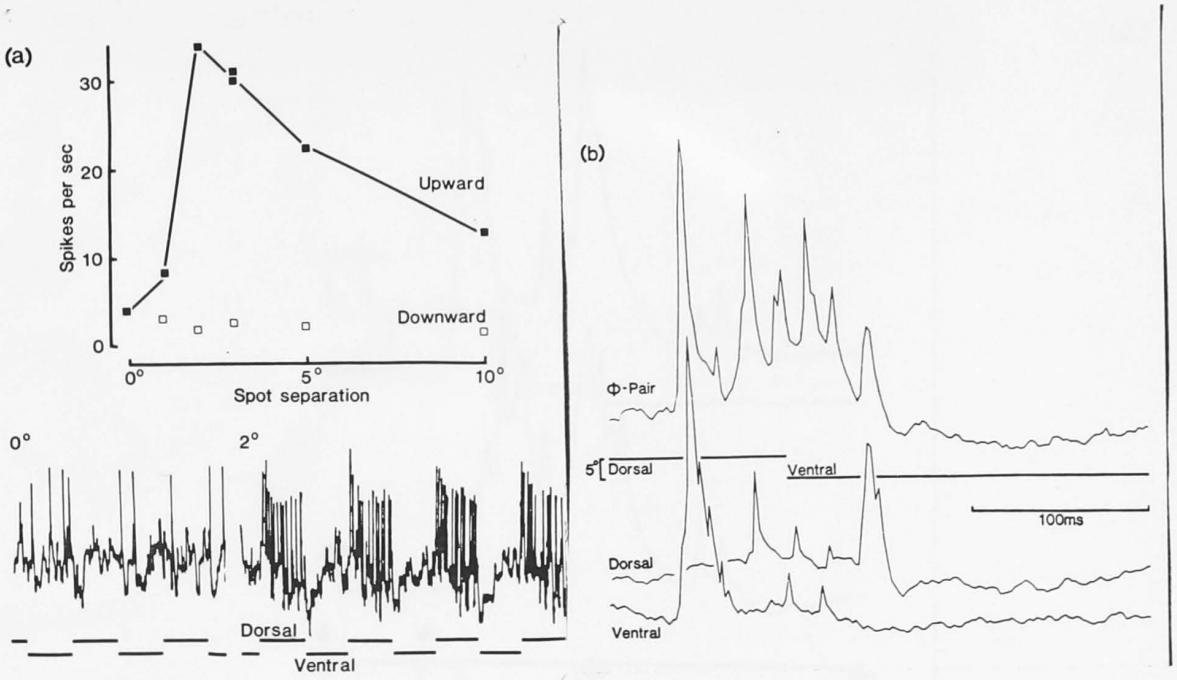


Figure 6.4

a,Above: Response of a cell to phi-flashes, (diameter 1.5^{o}, contrast 0.05) presented at 1Hz with a 50:50 duty cycle. The responses to ten stimulus cycles were averaged to obtain each data point.

Below: Raw data showing the spontaneous firing rate when the flashes were superimposed, and the response to the optimal stimulus separation.

b: Signal averaged (15 cycles) responses to phi-flashes with the spots separated by 5^{o} (above), and responses to each of the flashes presented independently (below). Where the flashes were presented separately the spot was on for the period when it was on as part of the phi-flash pair, for the rest of the cylce the screen was uniform. Note that the response to the paired flashes differed from the the responses to the stationary stimuli in showing a sustained excitation to the apparent upward movement, whereas the phasic components of the phi-flash response are attributable to the dimming of the separate spots.

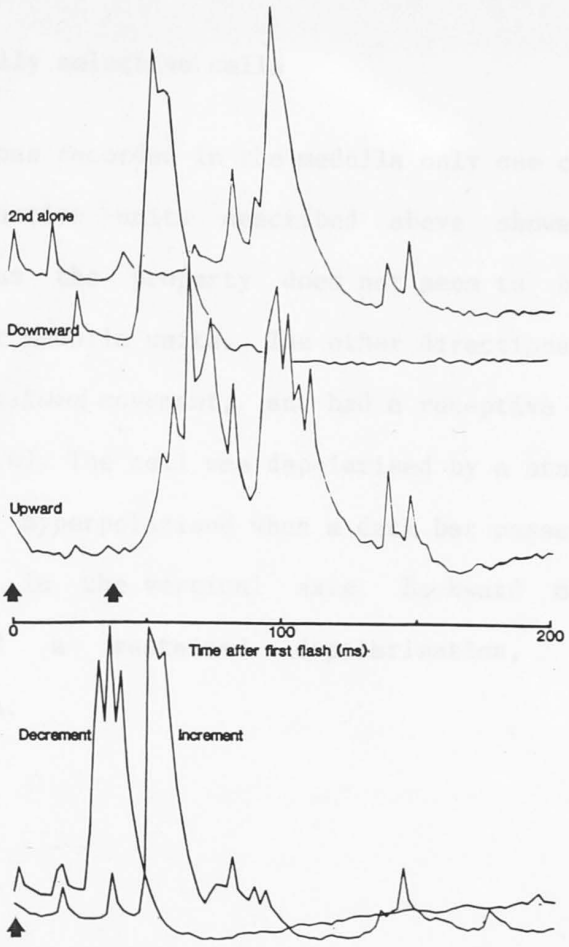


Figure 6.5

a: Normalised responses to brief (2ms) increments (contrast 0.4), simulating downward (middle) and upward (bottom) motion. The top trace shows the response to a single spot, (indicated by the second arrow) in the position and at the time of the second flash of the pair simulating downward motion, and empahises the inhibitory nature of the directional interaction. Sequential presentation of flashes in the same position gave a response similar to that elicited by apparent motion in the preferred direction. If both spots were presented simultaneously in different positions the response resembled that to a single spot. The responses shown are the average of 15 stimulus cycles presented at 1.7 Hz. Arrows indicate the timing of the flashes. The responses of the unit illustrated comprised both graded and action potentials.

b: Normalised responses of the same cell to brief increments and decrements.

Other directionally selective cells

Of the many neurons recorded in the medulla only one cell type apart from the distinctive units described above showed directional selectivity. Thus the property does not seem to be of general significance for medulla units. The other directionally selective cell preferred backward movement, and had a receptive field diameter of about 2^{o} (fig.6). The cell was depolarised by a stationary flash, and transiently hyperpolarised when a dark bar passed through the receptive field in the vertical axis. Backward motion of the stimulus caused a sustained depolarisation, and forward hyperpolarisation.

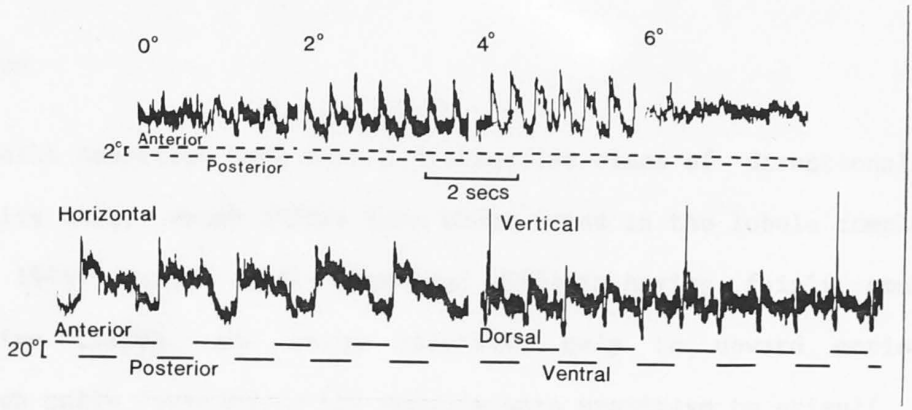


Figure 6.6

Responses of a smallfield cell sensitive to backward movement. Above : Responses to 2^{o} horizontal movements of a 2^{o} wide black bar centered in four different positions 2^{o} apart. The receptive field was in the lateral dorsal part of the visual field, and the assignation of 0^{o} for the initial position is arbitary.

Below: Reponses of the cell to longer movements of the bar. Note the sustained responses to horizontal motion, which persisted after the stimulus had left the visual field, and the movement stopped. The transient responses of the cell to vertical movement reflect the small receptive field area, and the fact that the unit was hyperpolarised by dimming.

Discussion

Function

The cells described here form a distinctive class of directionally sensitive unit, which differ from those found in the lobula complex (Kein 1974; Hausen 1981; Egelhaaf 1985) in having fairly small receptive fields, and being sensitive only to upward motion. Although cells recorded in the medulla were sensitive to stimuli in all parts of the visual field the receptive fields of the directionally selective cells were restricted to the lateral-ventral parts. These observations imply that they were contributing to a fairly specific visual behaviour.

One possible function for directionally sensitive cells with small visual fields is fixation and tracking, and units adapted to these functions have been described (Collett & King 1975; Egelhaaf 1985b). However an important property of the units mentioned by these authors was the presence of spatial antagonism, which rendered the cells insensitive to widefield motion and helped detection of small objects against the background. There was no evidence for spatial antagonism here, with either stationary or moving stimuli, and the cells were equally or more responsive to widefield compared to smallfield motion. Therefore it appears unlikely that the units were adapted to orientation toward small objects (Cooter 1979); a conclusion reinforced by the finding that receptive fields occupied a lateral position.

The high sensitivity observed to low angular velocites of a moving bar reflects a performance which could probably not be matched by a

human observer with the spatial resolution of a locust, and reinforces the conclusion that arthropods can detect movement direction at very low angular velocites (Horridge & Sandeman 1964). The time taken for the response to change after direction reversal at low velocites (fig 3) implied that the cells were sensitive to angular displacements of below 0.1^{o}, and had integration times of at least three seconds. The function of this sensitivity to low angular velocites is not known, although the downward facing receptive fields suggest it is unlikely to be for celestial orientation, as implied by Horridge and Sandeman (1964) in the crab. An interesting possibility is that the cells could signal the motion of the ground at 90^{o} to the direction of flight. Detection of lateral slip may allow the animals to fly parallel to the airflow, giving an active contribution to the tendency of migrating locusts to fly downwind (Rainey 1976). The receptive fields of the cells were disposed in a pattern which suited them to this task. There is no evidence that the cells could have distinguished slip over the land from simple body roll.

Mechanism of directional selectivity

The dendrites of the cells were situated in the distal part of the medulla, which implies that they are unlikely to have been postsynaptic to smaller field directionally sensitive elements. Thus it is likely that the directional sensitivity depended upon the properties of the marked cells, and their synaptic inputs. The mechanisms responsible for conferring directional selectivity have been widely discussed elsewhere (eg Barlow & Levick 1965; Torre &

Poggio 1978), and the properties of the medulla units conform, at least in part, to those predicted by these authors. In particular computation of motion is performed between inputs which respond to flicker, and the primary basis for directionality seems to be an inhibition. The responses to a pair of brief flashes simulating motion in the preferred direction were indistinguishable from the responses to two single flashes presented separately (fig.5). If the motion simulated was in the antipreferred direction the response to the second flash was abolished. The absence of a hyperpolarising component in response to motion in the antipreferred direction is consistent with the suggestion that the inhibitory input acts by shunting rather than hyperpolarising the membrane (Torre & Poggio 1978).

The reponses to phi-flashes, where illumination was sustained, suggested that there may also be an excitatory component in the directional response. The transient responses of the cell to the switching of the spot from one postion to another were similar to the phasic responses to flicker, whilst the directional component of the response was expressed as a sustained excitation after apparent motion in the preferred direction. The possibilty that excitatory interactions give directional selectivity was raised by Mimura (1972) in a study of the fly optic lobe.

Appendix:

Bipartitioning of natural scenes in early vision

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BI-PARTITIONING OF NATURAL SCENES IN EARLY VISION

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A conceptual framework for understanding spatial information processing in early vision is presented. It is consistent with various perceptual phenomena, recent intracellular recordings, and shown to be effective in digital simulation. The starting hypothesis is that visual pathways compartmentalize spatial information into channels that are individually highly active so comparatively few, reliable channels represent the spatial world. This demands that the visual system exploit those very special properties that are peculiar to natural scenes; as opposed to mathematically contrived scenes such as white noise or a scene composed of low frequencies only. One essential characteristic of natural scenes is that they are composed of discrete objects. Thus, the spatial channels of early vision are taken to be devoted to coding objects. There are two salient characteristics of objects: their global outline often manifested by borders of comparatively high local contrast (dominant borders), and their internal structure characterized by textured detail and low

spatial frequency variations. We hypothesize that bi-partitioning of visual information, with a separate channel devoted to each of these object manifestations will allow efficient coding. One channel is sensitive to borders of local high contrast only, while the job of the other is to "fill-in" regions within these borders, e.g. with textural information.

The bi-partioning hypothesis is consistent with various perceptual phenomena. For example, the suggestion that internal features of comparatively low contrast are processed differently from dominant borders (those which make up the global outline of objects) is consistent with the observation that a graded 'staircase' illumination induces a Chevreul illusion,[1] (ref. 2, page 276) while a single, isolated border does not. Additional evidence comes from illusions demonstrating that brightness is not merely a function of intensity. For example, a pale disc with low contrast nonuniformities appears uniform when viewed against a dark background (page 275, ref.2) suggesting again that dominant borders are handled differently from the internal 'filling in' process. Finally, we can clearly see the effect of dividing up an image into regions with borders by considering the famous "block portrait" of president Lincoln produced by Harmon and Julesz.[3] This portrait contains sufficient information for recognition, but the face is nonetheless unintelligible when viewed close up. In other words, it is the segmentation by perceptually dominant borders that prevents one from seeing the face.

Whereas perceptual phenomena can be open to alternative interpretation, striking evidence for bi-partitioning is seen in the medulla of the insect optic lobe. The insect medulla is a large

ganglion with a columnar retinotopic structure resembling regions of the vertebrate brain involved in early vision.[4] Intracellular recording from the medulla reveals two principal classes of cells, which show marked qualitative differences.[5,6] The first group are approximately linear and code the average light intensity within their receptive fields. We believe these cells are suited to signalling structural detail. The second group is nonlinear, and is suited to coding the presence of dominant borders.

The linear cells[5] give opposite responses to dimming and brightening, they are tuned to a range of stimulus temporal frequencies between 10Hz and 30Hz. These cells also vary in receptive field area and their spectral properties. Thus hue and other structural detail may be coded at this level. The nonlinear cells[6] are green sensitive, they give phasic responses, typically one spike, to both dimming and brightening (Fig 1). Moreover these cells show marked adaptation, (Fig 1 inset), quickly ceasing to respond to a repeated stimulus of constant amplitude presented at over 10Hz. If, after adaptation, a more powerful stimulus is presented they give the normal response. This property may allow the cells to ignore textural detail whilst responding to locally dominant object boundaries. Thus, it seems that the nonlinear cells are suited to signalling the occurrence of locally dominant intensity changes with precision, but not to coding the amplitude of the signal, or its polarity. Their outputs would provide a basis for construction of a 'cartoon' of objects in a scene. Cells equivalent to this non-linear group have not been described in the vertebrate eye. However the property of contrast adaptation, an important component for the dominant border

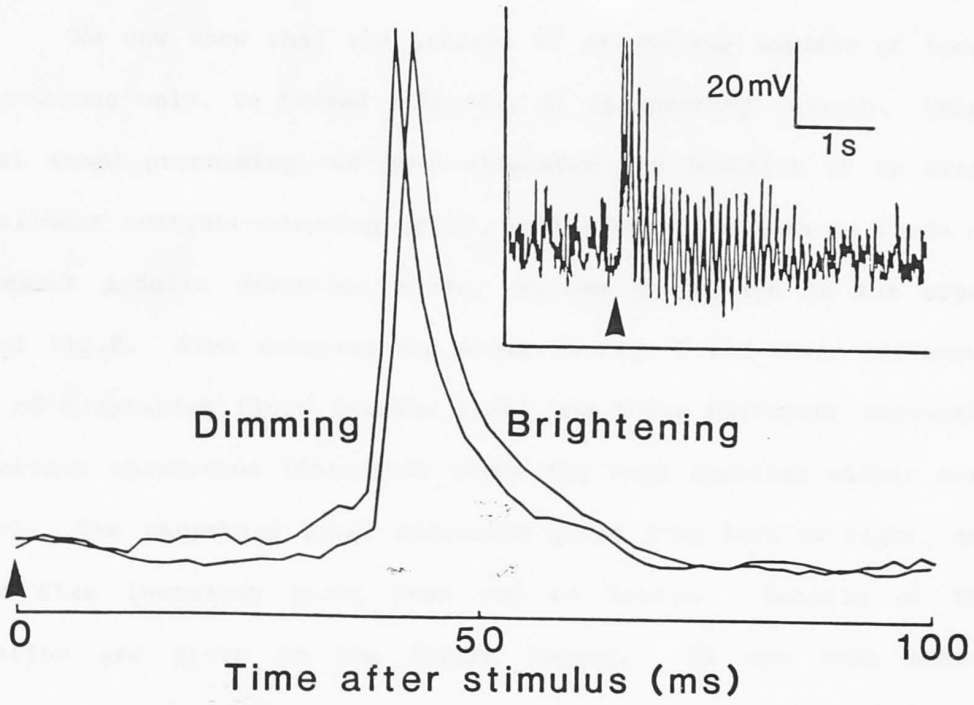


Figure 1. Responses of a thresholding cell in the locust medulla to brightening and dimming. The responses to 10 presentations of suprathreshold 2ms pulses (arrowed) are averaged. This unit had no spontaneous activity and produced a single spike to any suprathreshold stationary stimulus. Note the similar latencies of the responses to increments and decrements.

Inset: Response of the cell to a 10 Hz continuous train of pulses commencing at the arrowed point. No stimulus was present prior to this point.

channel, is displayed by cat retinal ganglion cells.[7]

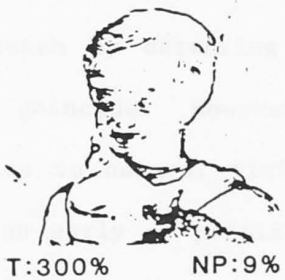
We now show that the process of extracting borders of local high contrast only, is indeed effective at delineating objects. Using digital image processing, we have simulated the function of an array of nonlinear contrast-adapting cells, with properties akin to those of the insect medulla described above, on the photograph in the upper left of Fig.2. Nine examples are shown in Fig. 2 for three different sizes of adaptation field (window size) and three different strengths of contrast adaptation (threshold above the mean contrast within each window). The threshold level increases going from left to right, and window size increases going from top to bottom. Details of the simulation are given in the figure legend. We see that border extraction is not accurate when each neuron's adaptation field is confined to a very small neighbourhood (top row). It improves considerably when the size of the adaptation field is increased (middle row). However, when the field size is made so large as to cover the entire picture, performance deteriorates (bottom row). This global adaptation is, in effect, equivalent to applying a fixed threshold to all picture locations. Such a process is not effective in selecting locally high-contrast features. When the threshold is set to a low level, virtually all intensity fluctuations in the image are signalled, including features not associated with borders. On the other hand, when the threshold is raised to eliminate the latter, several important segments of the border begin to drop out as well, such as the outline of the lady's right shoulder, right cheek and the folds in her dress. The results show that the intermediate-sized adaptation field performs best. Not only does it detect borders

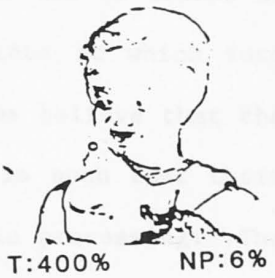
Figure 2. Simulation of responses of a two-dimensional array of nonlinear contrast-adapting units viewing the scene shown on upper left. The physiological properties of these neurons are modeled in three stages. First, the given image comprising 256x256 pixels (obtained from the JPL Digital Image Library, Caltech, Pasadena) is spatially differentiated (using a Sobel operator[12]) and the absolute magnitude of the first derivative at each pixel location is stored in another 256x256 array. Second, the effect of contrast adaptation is introduced by centering a square window on each pixel of the new image (in turn), and computing the mean value of the pixels within this window. In effect, a local mean value of the derivative is computed for each position in the array; the size of the window corresponds to the size of the visual field over which contrast adaptation takes place. Finally, in a third array in which all pixels have previously been initialized to zero (white), we set to 1 (black) those pixels from the derivative image whose value exceeds the local mean by a threshold percentage, T. The figure illustrates the results for various threshold levels and various window sizes. The influence of window size is perhaps best assessed by comparing pictures which contain similar numbers of black pixels (e.g. the rightmost picture in each row). These numbers, NP, are expressed as a percentage of the total (256X256).

Window size

5x5

40x40





256x256

accurately, but it also eliminates internal speckle. Furthermore, its performance is relatively insensitive to the choice of threshold level; in neurophysiological terms, this robustness is obviously an advantage.

Finally, we note that our suggestion that high contrast edges should be extracted at an early stage is fundamentally different from the theory of edge detection proposed by Marr and Hildreth.[8] Their primal sketch is a rich recoding of the retinal image, whereas the output of our nonlinear filters is severely impoverished, providing global outlines. Locally dominant borders can of course be extracted from the primal sketch by detecting points at which zero crossings in several channels coincide. However, we believe that the importance of object boundaries to natural vision is such that their 'tokens' should be extracted as early as possible in processing. The detection of edges may occur in parallel with the spatial filtering operations used to give the primal sketch, or with a spatial frequency representation.[9,10] These latter types of filtering disperse the information about borders across several channels; recombination of the outputs is potentially both inefficient and noisy compared to detection of borders by a single non-linear operation on the retinal image.

In summary, we propose that the strategy of early spatial vision is to 'tailor' the visual channels to the dominant characteristics of natural scenes. This leads to a channel for dominant borders and another for 'filling in' the region within these borders. It is tempting to explore this approach in other sensory modalities. For example, the dominant manifestations of human vowel

sounds are the so-called formant frequencies.[11] It will be interesting to learn if channels in the early auditory pathways are "tailored" to these salient speech characteristics.

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