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# CONTROL OF IMPULSE DISCHARGE OF VISUAL INTERNEURONES BY THE RECEPTIVE FIELD SURROUND IN BUTTERFLY LARVAE

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## Summary

The influence of interactions between the antagonistic centre and surround areas of receptive fields on the electrical activities of medulla neurones was examined in the larval swallowtail butterfly *Papilio xuthus*. Weak signals from the surround had a significant depressive effect on the maintained discharge, which increased for on-centre cells or decreased for off-centre cells in response to illumination of the centre. Moderation of the maintained discharge suppressed saturation of the response and extended the graded response range of the neurones. Surround illumination also reduced irregular fluctuations in the membrane potentials and variability in the discharge rate of impulses. The results indicate that the spatial inhibitory mechanism is important for the larval visual system in order to increase the efficiency of signal processing.

## Introduction

Visual interneurones in both vertebrates and invertebrates have antagonistic areas within the receptive field; such areas in vertebrates usually have a concentric centre–surround structure. Antagonistic or inhibitory signals from the receptive field surround are important for the enhancement of contrast and flicker (Hartline *et al.* 1956; Ratliff *et al.* 1967) and for the adjustment of sensitivity or threshold (Barlow and Levick, 1976; Werblin, 1974; Werblin and Copenhagen, 1974; Thibos and Werblin, 1978). Lateral antagonism is also a fundamental neural mechanism for movement detection and is involved in colour coding (Barlow and Levick, 1965; Zrenner, 1983). In addition, a steady signal from the surround controls the maintained activities of spiking neurones; the level and variability of the spiking activities determine the response range and the signal-to-noise ratio of the neurones (Barlow and Levick, 1969*a*,*b*; Enroth-Cugell and Lennie, 1975). Insect visual systems contain interneurones with antagonistic receptive fields in the lamina (Arnett, 1971; Dubs, 1982; Laughlin, 1974; Menzel, 1974; Mimura, 1976; Zettler and Järvilehto, 1972) and in the medulla and lobula (Hertel, 1980;

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Honegger, 1980; Ichikawa, 1986; Kien and Menzel, 1977; Osorio, 1986, 1987), although in no case do the antagonistic receptive fields have a concentric form. Antagonistic signals from the surround area of the receptive field appear to be weak (e.g. Arnett, 1972; Ichikawa, 1986). A detailed analysis of the effects of such a weak signal on visual processing can be difficult because stray light from the test light shed on the surround affects the neighbouring central area of the receptive field, which dominates the response profiles of the neurones.

Butterfly larvae have an eye consisting of a small number of receptive units (six stemmata) with a large diameter, so we can stimulate individual units independently (Ichikawa, 1986). Although the number of optical units is greatly reduced, the larval visual system appears to be constructed according to the same architectural principles as the adult visual system with compound eyes (Ichikawa and Tateda, 1984; Toh and Iwasaki, 1982). These features make the larval visual system an interesting model for insect vision. The spatial and chromatic properties of the majority of neurones in the medulla of larval swallowtail butterflies have been characterized (Ichikawa, 1986, 1990, 1991). Many medulla neurones produced a strong, dominant response to stimulation of one particular stemma (centre) and a weak, antagonistic response to stimulation of other stemmata (surround). Because the receptive field of the stemmata as a whole almost covers a hemisphere of the visual space (Ichikawa and Tateda, 1982), a large area of the space forms the receptive field surround of these neurones. Stemmata located in close proximity to the centre stemma usually make a larger contribution to the surround response (Ichikawa, 1986). The receptive field centre is most important for colour coding, but the surround appears to play little or no role in colour coding (Ichikawa, 1986, 1990). In this paper, I report that illumination of the antagonistic surround affects the spiking activities of medulla neurones and increases the efficiency of signal coding in neurones. The present study demonstrates that the principles of lateral inhibition extend to the simple eye of the larval visual system.

## Materials and methods

The preparation and the methods of recording and stimulation have been described in previous papers (Ichikawa, 1990, 1991). Fifth-instar larvae of the swallowtail butterfly *Papilio xuthus* L. were reared in our laboratory. After the mouthparts had been plugged with a quick-drying glue, the head of the larva was fixed with beeswax to an experimental chamber. The chamber was then filled with a physiological saline (in mmol $l^{-1}$ NaCl, 4; KCl, 40; $MgCl_2$, 18; $CaCl_2$, 3; glucose, 150; pH 6.5 with 2.5 mmol $l^{-1}$ $KH_2PO_4$–$KHCO_3$) and all of the head except for the right lateral part bearing the stemmata was placed in this saline bath. The brain was exposed by removing the frontal part of the cuticle of the head capsule. Circumoesophageal connectives were cut to reduce the transmission of movement of the oesophagus to the brain. A pair of stainless-steel insect pins was placed under the brain to serve as a platform. The tip of a glass pipette containing 1 %

Pronase was placed on the brain for 20–30 s to facilitate penetration by a glass pipette microelectrode. The microelectrode, filled with 1 mol $l^{-1}$ potassium acetate (30–50 MΩ), was inserted into the somata region of the medulla neurones between two imaginal discs (Ichikawa and Tateda, 1984). An indifferent electrode was placed in the saline bath. Intracellular responses were amplified in the conventional manner and recorded simultaneously on magnetic tape and a chart recorder.

Each stemma was illuminated independently *via* a quartz optical fibre (150 μm in diameter), the tip of which was placed within 50 μm of the surface of the corneal lens of the stemma. White light from a 500 W xenon arc lamp and monochromatic test light from a grating monochromator (Bausch & Lomb) equipped with a 150 W xenon arc lamp were introduced into each optical fibre with the aid of a small quartz half-mirror. Monochromatic light for the second test stimuli was obtained by interposing an interference filter with a transmission peak at 370, 450 or 580 nm into the pathway from the former light source. A rotary metal disc with various patterns of holes was placed in each light path to select the stemmata to be illuminated. The duration of illumination was controlled by a mechanical shutter. The intensity of the light was regulated with quartz neutral density filters and a quartz neutral density wedge. The light intensities were measured by a radiometer or a thermopile. The reference intensity of white light ($\log I_w=0.0$) corresponded to 3.2 W $m^{-2}$, and that of monochromatic light ($\log I_m=0.0$) to $2.4\times10^{13}$ quanta $cm^{-2}s^{-1}$. Contamination of adjacent stemmata by stray light scattered from a light path was determined in preliminary experiments by measuring photoreceptor responses and was less than −3 log units.

After successful penetration of a medulla neurone in the dark, six stemmata were separately illuminated with monochromatic test lights of a constant intensity ($2.4\times10^{11}$ quanta $cm^{-2}s^{-1}$) in order to identify the neurone (Ichikawa, 1990). The maintained discharge of the cell was analyzed after waiting for the activity of the units to become practically constant for 10 min in the dark or for 1 min with background illumination. Intervals between successive impulses for off-centre cells were analyzed using an interspike-interval analyzer (Nihon Kohden, DAB-1100) with a time resolution of 0.1 ms. For on-centre cells with relatively small spikes, a train of impulses was recorded on a chart recorder and the intervals were measured by eye.

## Results

Medulla neurones with an antagonistic receptive field have been classed into 16 spectral types (Ichikawa, 1990). Spectral types of neurones used for the present analyses were $UV^+b^-g^+$ ('on-centre' unit) and $G^-b^+$ ('off-centre' unit). Excitatory responses of the former were dominated by ultraviolet-sensitive photoreceptors, while inhibitory responses of the latter were dominated by green-sensitive photoreceptors (Ichikawa, 1986). These neurones were frequently encountered and showed a consistent antagonistic response. Fig. 1A shows typical responses

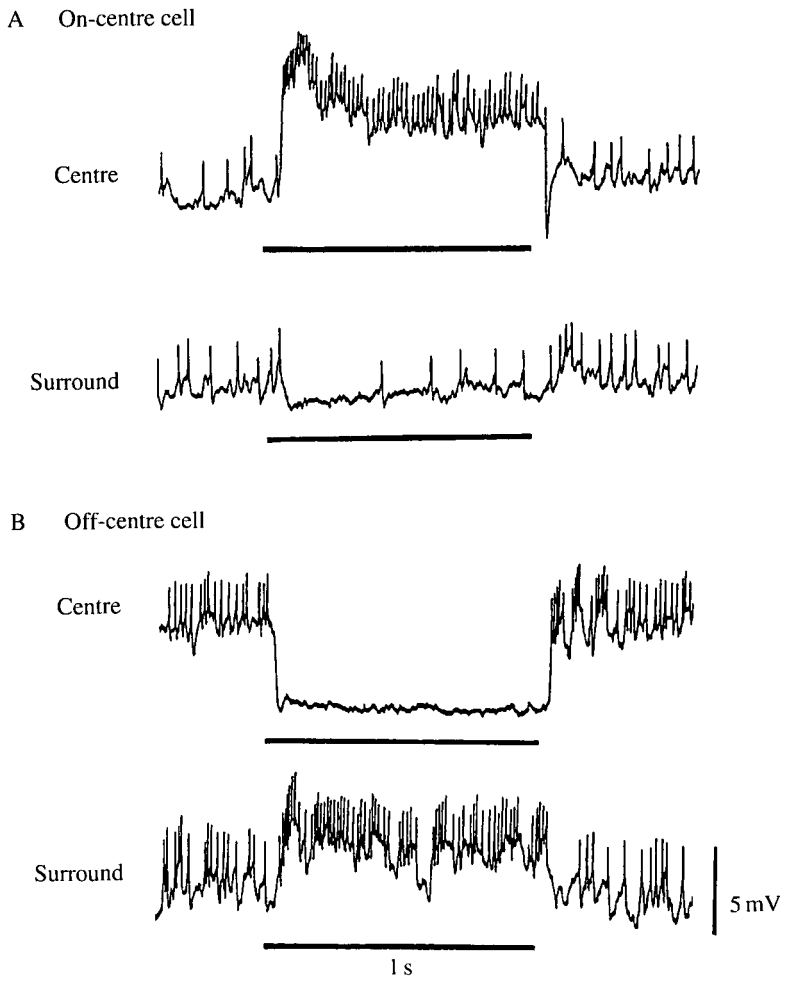


Fig. 1. Intracellular responses of two types of medulla neurones with an antagonistic receptive field to 1 s stimulation with white light (horizontal bars). (A) The on-centre cell shows strong excitation in response to illumination of stemma V (centre) and weak inhibition in response to illumination of the other five stemmata (surround). (B) The off-centre cell shows an inhibitory response to stimulation of stemma I (centre) and an excitatory one to stimulation of all the other stemmata (surround). $\log I_w = -4.5$.

from an on-centre cell exhibiting excitation in response to illumination of stemma V (centre) and inhibition in response to illumination of the other stemmata (surround). Fig. 1B shows an off-centre cell that exhibits an inhibitory response to stimulation of stemma I (centre) and an excitatory response to stimulation of the other stemmata (surround). Fig. 2 shows the response of the on-centre unit to a 1 s stimulus presented to the surround in the presence of a 3 s centre illumination. In order to demonstrate clearly the effect of illumination of the receptive field surround on the activity of the unit, the intensity of light at the centre was decreased to evoke an approximately half-maximal response and the intensity of

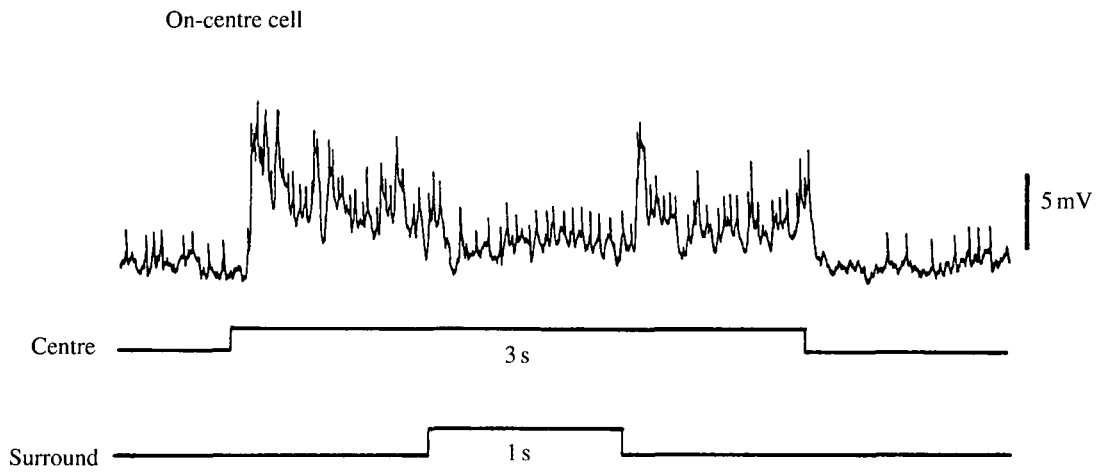


Fig. 2. An antagonistic interaction between the centre and the surround obtained from the same unit as that illustrated in Fig. 1A. Upward deflections of the trace beneath the record indicate a 3 s stimulation of the centre and a 1 s stimulation of the surround. Note that the intensity ($\log I_m$) of monochromatic light ($\lambda$=370 nm) for the surround (−2.0) is 2 log units higher than that for the centre (−4.0).

light to the surround was increased so that it was 2 log units greater than that for the centre. The light shed on the surround reduced both the discharge rate of impulses and the amplitude of slow depolarization. It also reduced the fluctuation (noise) of the membrane potentials that increased as a result of the illumination of the centre. The predominance of the centre was apparent from the incomplete suppression of the excitatory centre response by surround stimulation. Fig. 3 shows results of similar experiments obtained by varying the intensity of surround stimulation in the presence of centre illumination of a constant intensity. The numbers of impulses during a 1 s surround stimulation decreased linearly with increasing intensity of the surround stimuli. As the three curves are almost parallel, there is probably a subtractive interaction between the centre and surround mechanisms. When the intensity of illumination of the centre was −4.1 log units, at which point the cell showed about half-maximal response to excitation, the surround required stronger illumination, approximately 3 log units higher, to cancel the centre response. At higher intensities of centre illumination ($\log I$=−3.7, −3.1), the strongest stimulus applied to the surround did not extinguish responses from the centre.

The rate of spike discharge of medulla neurones during prolonged background illumination was usually maintained at a constant level and depended on the intensity of the background illumination. Fig. 4 shows the rates of the maintained discharge of the on- and off-centre cells, at various intensities of background illumination, on the centre alone or on the whole receptive field (centre plus surround). The maintained discharge when illumination was on the centre alone increased or decreased faster than when the whole receptive field was illuminated.

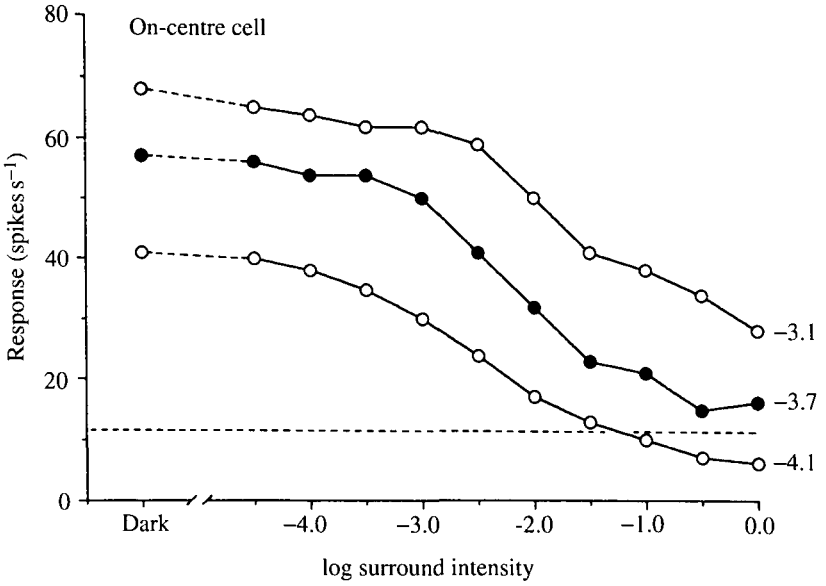


Fig. 3. Depressive effect of surround illumination on the centre response of the on-centre unit shown in Fig. 2. Connected points plot the number of spikes discharged in a 1 s period of surround illumination of various intensities in the presence of a 3 s centre illumination of a constant intensity indicated (as $\log I_m$) next to the curve. The interrupted line indicates the rate of discharge in the dark. Monochromatic light ($\lambda$=370 nm) was used for centre and surround illumination.

The difference between the curves represents the contribution of the surround. The antagonistic surround mechanism has an effect equivalent to that of shifting the maintained discharge curve along the abscissa by 1 or 2 log units to a higher intensity. The responsiveness of an on-centre unit at different background configurations is shown in Fig. 5. In this experiment 1 s monochromatic stimuli (370 nm) were presented to the receptive field centre to test the sensitivity of the cell. It was apparent that background illumination of the surround acted to release the cell from a compression of the graded response range that results from an elevation of the maintained discharge level caused by illumination of the centre. Similar results were obtained from off-centre cells (data not shown). Strong background illumination shed on the centre of on-centre cells often made the maintained discharge intermittent; the intensity–response functions were saturated at a lower level and declined with further increases in the stimulus intensity (Fig. 5). This abnormal behaviour of the cell suggests an important role for surround antagonism in the maintenance of the normal activity of medulla neurones. It is possible that surround illumination changes the response threshold, as was noted in mudpuppy retinal bipolar and ganglion cells (Thibos and Werblin, 1978). Brief flashes (50 ms in duration) at an intensity near threshold were repeatedly shone on the centre in the presence or absence of steady background

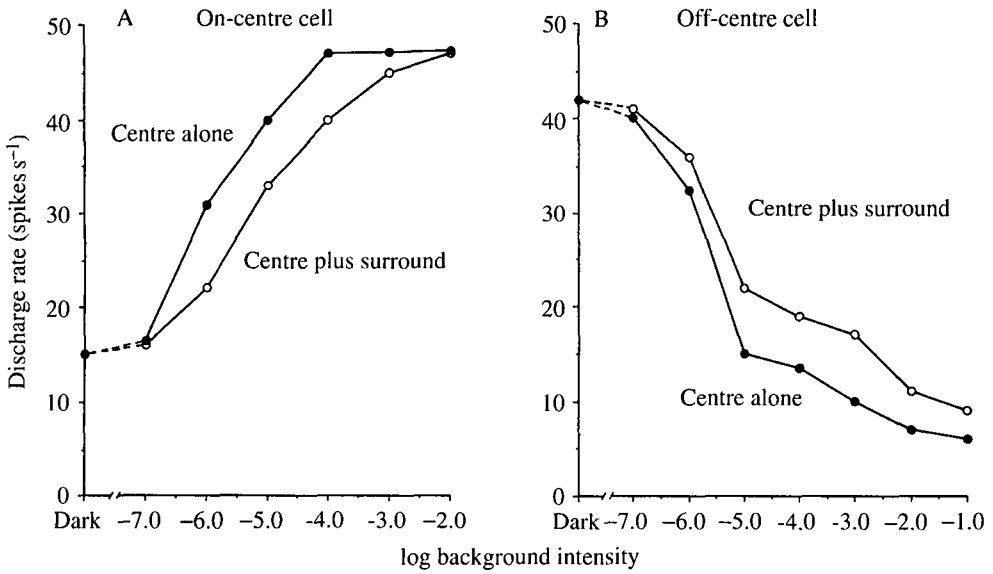


Fig. 4. Maintained discharge rates of two types of cells in the presence of a steady background of white light on the centre alone or on both the centre and the surround. Centre illumination increases the discharge rate for an on-centre unit (A) or decreases the rate for an off-centre unit (B). Surround illumination depresses these changes in the discharge rate.

illumination on the surround. Summed responses obtained at different background configurations showed no significant differences.

Surround illumination reduced irregular fluctuations in the membrane potential and caused the firing of the spikes to become fairly regular. Variability of the maintained discharge was examined by measuring intervals between successive spikes in the presence of a steady background illumination on the centre alone or on both the centre and the surround. Fig. 6 shows histograms of such interspike intervals in the two types of cells. The surround illumination increased the mean of the intervals for the on-centre unit and decreased that for the off-centre unit. The standard deviation of the distribution of interspike intervals (S.D.) for both cells decreased. The relative variability or coefficient of variation, which was defined as S.D./mean, was also decreased by surround illumination. Fig. 7 shows the coefficient of variation as a function of background illumination. As illumination of the centre increased, the coefficient of variation for both cells first increased, reaching a maximum at illumination levels of −5 or −4 log units, and then declined to the level seen in the dark-adapted state. The depressive effect of the surround on the coefficient of variation was insignificant or weak at lower levels of background illumination (<−4.0 log units), but was evident at higher background levels (>−3 log units). Similar results were obtained from three on- and four off-cells. Surround illumination at −2.0 log units decreased the coefficient of variation by 0.09±0.03 (on-centre cells) or 0.12±0.05 (off-centre cells).

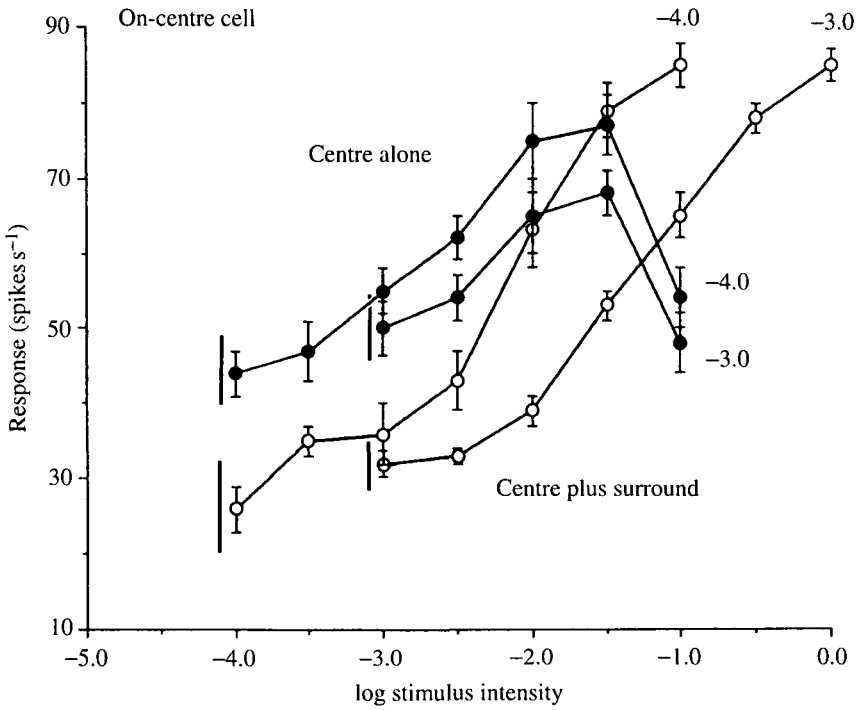


Fig. 5. Intensity–response functions of an on-centre unit in the presence of a steady background illumination on the centre alone or on both the centre and the surround. Monochromatic light (370 nm) was shed on the centre (stemma II) for 1 s and the number of spikes during stimulation was plotted. Each point is a mean of three responses. Vertical bars on the curves are the standard errors of the response. The logarithm of the relative intensity of white background illumination is shown above each curve. Thick bars beside the curves indicate the range of spike numbers for 1 s before stimulation.

## Discussion

A class of visual interneurones in the fly lamina has antagonistic areas in the receptive field, an on-region (centre) and an off-region (surround) (Arnett, 1971). The off-region of the lamina neurone needs 1 log unit brighter illumination than does the on-region in order to extinguish completely the on-discharge elicited by stimulation of the on-region (Arnett, 1972). The surround of the receptive field of butterfly larval medulla neurones needed much more intense illumination, that is 3 log units or more, to produce a similar result (Fig. 3). Although such a weak signal from the surround appeared to be trivial, it had a functionally significant influence on the rate and the variability of the maintained discharge (Figs 4, 6, 7). The rate of the maintained discharge limits the response range of the neurones (Fig. 5), while the variability affects the sensitivity or threshold of the cells (Barlow and Levick, 1969*a*).

Depression of the maintained discharge by the receptive field surround at various levels of background luminance has been examined in cat retinal ganglion

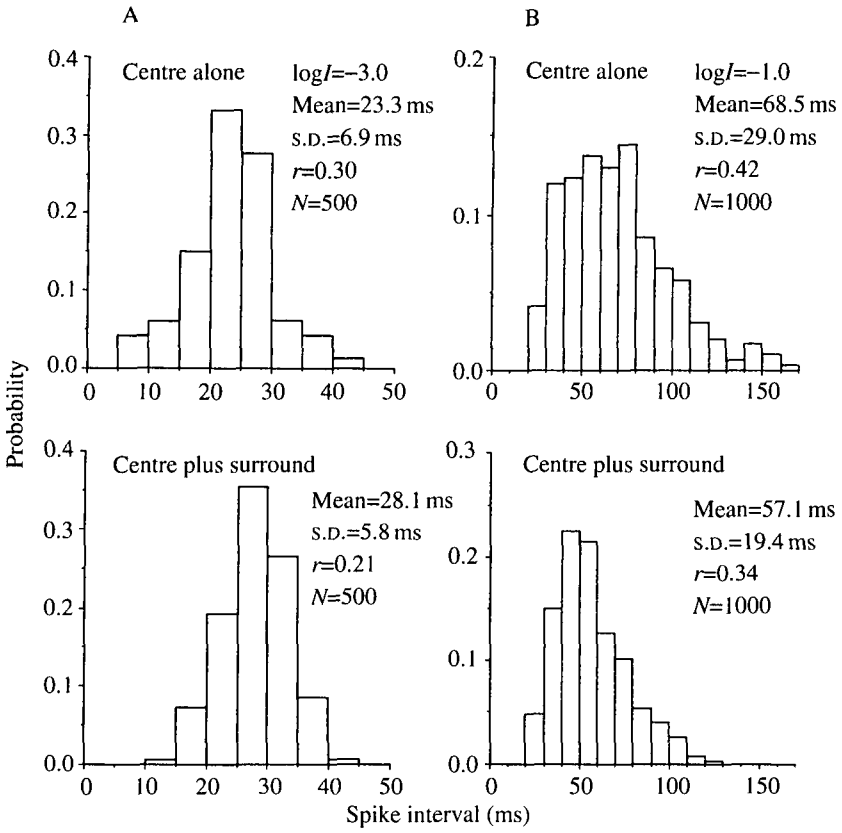


Fig. 6. Distributions of interspike intervals of an on-centre cell (A) and an off-centre cell (B) under two different background configurations. The intensity of background illumination ($I_w$) was −3.0 (A) or −1.0 log unit (B). Serving as the receptive field centre was stemma V (A) or I (B). S.D., standard deviation of the intervals; $r$, coefficient of variation; $N$, number of intervals.

cells (Enroth-Cugell and Lennie, 1975; Enroth-Cugell *et al.* 1975). The maintained discharge rate of the cells could not usually be related to the background luminance by a monotonic function and the contribution of the surround to the maintained discharge varied from one cell (type) to another. The surround for some cells (the X-cells) had a relatively consistent depressing influence on the maintained discharge, either at a wide or a limited range of background luminance; for some cells (the Y-cells) the surround effects were weak or inconsistent (Enroth-Cugell and Lennie, 1975). These complex centre–surround antagonisms may be due to lateral interactions that occur at multiple layers of the retina (Werblin, 1974; Werblin and Copenhagen, 1974). The maintained discharge of the larval medulla neurones changed monotonically with the background illumination and the surround had a consistent, subtractive effect on the maintained discharge of the neurones at intensities above −6.0 log units (Fig. 4). Thus, the centre–surround antagonism may be fairly constant over a wide range of

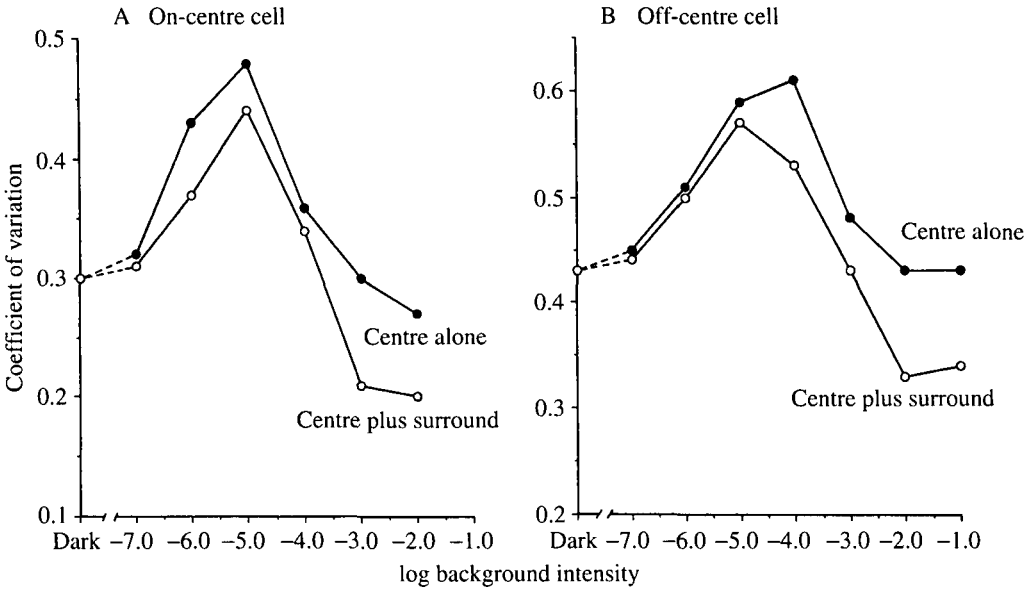


Fig. 7. Dependence of the coefficient of variation of interspike intervals on the level of background illumination. Data were obtained from the same units as for Fig. 6.

illumination and possibly occurs at a single stage of the visual pathway in the optic lobe.

The principal source of variations in the interspike interval of medulla neurones may be the fluctuations in generator potential of photoreceptors, as suggested from work in an eccentric cell in the lateral eye of *Limulus polyphemus* (Ratliff *et al.* 1968; Shapley, 1971*a*). Fig. 8 shows voltage fluctuations of the generator potential in the soma of a photoreceptor cell in the butterfly larval eye under conditions of different background illumination. Small discrete potentials are seen in the dark (Ichikawa and Tateda, 1980). The amplitudes of the irregular fluctuation of membrane potentials caused by random absorption of photons increased with an increase in the intensity of illumination, became maximal at $-6$ or $-5$ log units and then declined. The change in the variability of photoreceptor membrane potential with background intensity appears to be similar to that for the coefficient of variation of interspike intervals of medulla neurones (Fig. 7). However, fluctuations of photoreceptor membrane potential differ at $-7$ log units and at $-2$ log units, where the medulla neurones show similar coefficients of variation. Thus, in addition to the fluctuation in membrane potential of photoreceptors, other factors, such as intrinsic noise generated during neural transmission and filtering properties of visual pathways to the medulla neurones, may affect variability in the discharge of neurones.

Lateral inhibition has been observed in a variety of visual systems and fulfils a number of roles in signal processing (see Introduction). The present study extends this generalization to the larval visual system with stemmata. The mechanisms of

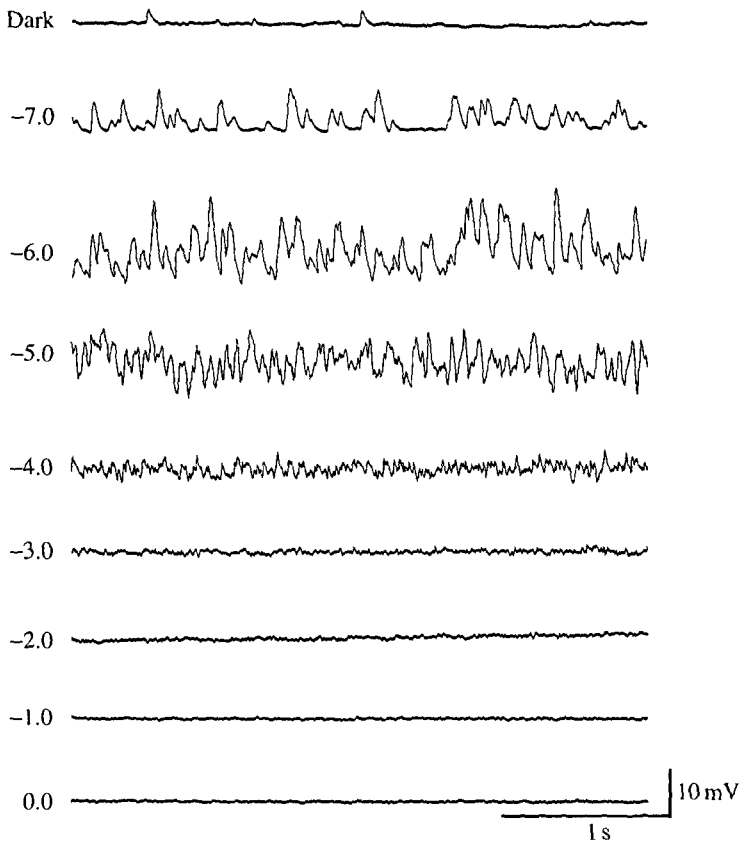


Fig. 8. Fluctuations of membrane potentials recorded from the soma of a photoreceptor cell in a stemma at various background illumination. Values of $\log I_w$ are given on the left. The photoreceptor is a distal green-sensitive cell (Ichikawa and Tateda, 1980).

the inhibition have been intensively studied in the eccentric cells of the lateral eye of *Limulus*. The inhibition of these cells is mediated by axon collaterals (Hartline *et al.* 1956). Although the inhibitory mechanism reduced the mean rate of maintained discharge of the cells, it usually increased the variability or the relative variability of the spike discharge rate (Shapley, 1971*b*). This occurs because the inhibitory signals, in the form of spikes, add low-frequency fluctuations to the membrane potentials of a postsynaptic cell. The surround of larval medulla neurones invariably reduced the relative variability of the maintained discharge rate (Fig. 7). Antagonistic signals from the surround may be produced by summing weak graded signals from many photoreceptors in the surround stemmata. The neural mechanisms responsible for the antagonistic interactions in the larval optic lobe remain to be examined (Toh and Iwasaki, 1982).

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