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THE PROPERTIES OF SURROUND ANTAGONISM ELICITED BY SPINNING WINDMILL PATTERNS IN THE MUDPUPPY RETINA

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SUMMARY

1. A truncated spinning windmill pattern, illuminating only the receptive field surround, shown previously to activate amacrine cells, was used to elicit activity at the inner plexiform layer and to reduce the response of ganglion cells to test flashes at the receptive field centre.

2. The spinning windmill pattern reduced the ganglion cell response over its entire graded range by a fixed amount, and reduced the domain of test intensities required for graded activity.

3. The windmill effect was graded for windmill intensities over a domain of about 1000 to 1. The effect was constant for windmill velocities from about 0·05 to 0·5 rev/sec, and diminished beyond these velocities.

4. The windmill effect varied with windmill area as though each retinal point contributed to the reduction of ganglion cell response with a weighting which fell exponentially from the receptive field centre. The space constant was 0·35 mm.

5. The graded reduction in ganglion cell response was closely correlated with the graded increase in amacrine cell activity when the windmill intensity, area, and velocity were varied. It is inferred that amacrine cells, activated by the windmill, act to reduce the response range of the ganglion cells, primarily through a feed-forward pathway.

INTRODUCTION

Transient or moving background illumination of several different types has been shown to affect the response properties of vertebrate retinal ganglion cells. An annulus or spot flashed on the receptive field surround can antagonize responses to centre test flashes in cat (Winters & Hamasaki, 1976), goldfish (Afanador & Adams, 1974), turtle (Schwartz, 1973) and mudpuppy (Werblin, 1972; Werblin & Copenhagen, 1974; Copenhagen, 1975). This is probably only partly due to an increase in surround flux because similar antagonism of centre response can be produced by a spinning windmill pattern where total surround flux is constant (Werblin, 1972; Schwartz, 1973; Werblin & Copenhagen, 1974; Cleland & Levick, 1974*a*, *b*). For this reason it has been suggested that a second antagonistic mechanism sensitive to changing patterns of surround illumination acts on ganglion cells in

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addition to the steady surround mechanism described in the previous paper (Thibos & Werblin, 1978). It is unlikely that this second antagonistic mechanism is located at the outer plexiform layer because bipolar cells show no evidence of antagonism by changing surround stimuli (Werblin, 1972; Werblin & Copenhagen, 1974; Copenhagen, 1975). Instead, the available evidence implicates interactions at the inner plexiform layer because of the similarity in the time course of amacrine cell response, ganglion cell hyperpolarization, and ganglion cell antagonism by flashed surrounds (Werblin & Copenhagen, 1974; Copenhagen, 1975).

The effect of a spinning windmill surround upon the graded responses of *Necturus* ganglion cells has been described in a previous study (Werblin & Copenhagen, 1974). The purpose of the present study is to characterize more fully the effect by studying its dependence upon the intensity, area, and rotation velocity of the windmill pattern. Amacrine cell responses were measured for the same surround stimuli used to antagonize the ganglion cells. The results suggest that inhibition of ganglion cells by the amacrine cells described here is sufficient to account for the antagonistic effect of spinning windmill surrounds upon ganglion cell activity.

METHODS

Experimental methods were the same as described by Thibos & Werblin (1978) with the following addition. Windmill surround patterns described by Werblin (1972) and Werblin & Copenhagen (1974) were imaged on the retina using the optical stimulator in two ways. The first method employed an opaque mask located at the plane of the stimulator conjugate to the retina. In the second method, pie-shaped sections of orthogonally orientated polaroid material were placed in the conjugate plane and in series with a solid piece of polaroid. Modulation of the windmill pattern in these two methods was by rotating the opaque mask and the solid polaroid, respectively. In the opaque mask method the windmill pattern rotated about the centre of the receptive field but in the polaroid method the pattern was stationary on the retina while undergoing sinusoidal reversals of contrast. With both methods total light flux applied to the retina was constant. The convention used for specifying windmill intensity was to use the intensity of an annulus with the same inner and outer diameters and with the same total light flux. Unless stated otherwise, the opaque mask method was used exclusively in all experiments.

RESULTS

Graded antagonism in ganglion cells

The following experiments characterize the effect of spinning windmills on ganglion cell activity. The intensity–response function for small test flashes at the centre of the ganglion cell receptive field was measured both when the windmill pattern was stationary and when it was spinning. The difference in these two response functions was taken as a measure of movement-elicited surround antagonism.

Effect of spinning windmill surround on centre intensity–response function

The procedure used to determine a ganglion cell's intensity–response function for centre test flashes was the same as described in the previous paper (Thibos & Werblin, 1978). The windmill surround was annular with 1·0 mm i.d. and 2·0 mm o.d. and was placed concentrically to a 0·4 mm centre test flash. The windmill had four white and four dark blades of equal size. Its intensity was -4 log units (see Methods) and when spinning it rotated at a constant velocity of 0·3 rev/sec. The windmill surround was presented for 7 sec and the 1 sec test flash was presented 3 sec after the surround

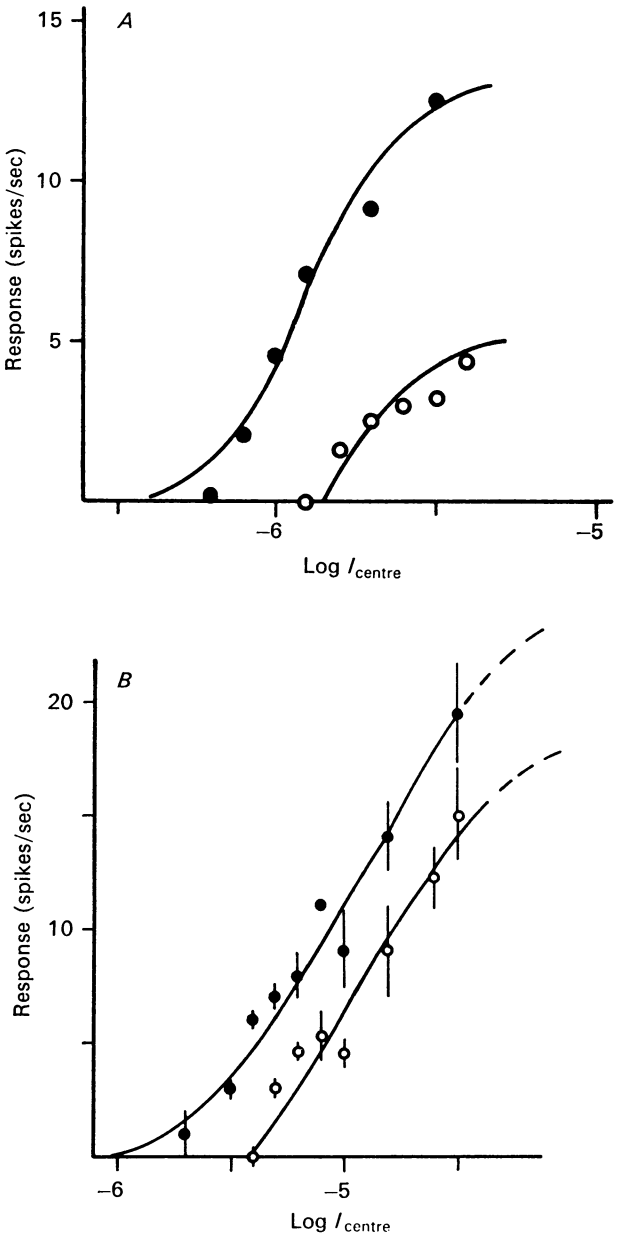

Fig. 1. The effect of a spinning windmill surround on a transient (*A*) and sustained (*B*) ganglion cell. Filled circles show responses to a centre test flash obtained when the windmill surround was stationary and open circles indicate responses when the surround was spinning. Template curves through the filled circles are from equation (1) ($N = 3{\cdot}4$ in *A*; $N = 1{\cdot}4$ in *B*). The template curves were shifted downward parallel with the ordinate to fit the open circles. Error bars show ± 1 S.E. for three or more response determinations.

appeared. This sequence was repeated every 15 sec. Stationary and spinning windmill trials were randomly intermixed.

Responses to the centre test flash obtained in the presence of a stationary windmill surround pattern are shown by the filled circles in Fig. 1*A* for a transient ganglion cell and in Fig. 1*B* for a sustained cell. In agreement with the previous paper, the centre intensity response function obtained in the presence of a steady windmill surround may be described by the formula

$$R = R_{\max} I^N/(I^N+\sigma^N). \quad (1)$$

For these data, $N = 3{\cdot}4$ for the transient cell and $N = 1{\cdot}4$ for the sustained cell. Control expts. indicated that a steady windmill surround had the same antagonistic effect as an annulus of the same dimensions and total light flux.

The response of these cells to centre illumination when the windmill surround was spinning is shown by the open circles in Fig. 1. The spinning windmill itself elicited no response but when it was spinning the centre response at each test intensity was reduced by an average of 7·5 spikes in the transient cell and 5·0 spikes in the sustained cell. The effect of the spinning windmill was generally less dramatic in the sustained cells and in four of the seventeen sustained cells tested there was no measurable effect. This may account for earlier failure to measure an effect of spinning surrounds on sustained ganglion cells (Werblin, 1972). All of the thirty-four transient cells tested were antagonized by the spinning windmill but usually the on responses were more strongly reduced than the off responses. Windmill antagonism could be demonstrated by both the opaque mask method and the polaroid method of generating the windmill pattern (see Methods), indicating that temporal modulation, rather than rotation, is the significant feature of the windmill stimulus.

Because the response at each intensity was reduced by the same amount when the windmill surround was spinning, the effect could be described by a downward shift of the template curve as shown in Fig. 1. This result was confirmed in the other transient cells studied in detail (both on and off responses in eight cells) as well as the sustained cells (three cells). In two of the transient cells the response curve also shifted laterally along the abscissa, although by less than 0·3 log units. It is suggested that the reduction of centre response by the windmill is due to neurally mediated lateral interactions rather than scattered light from the surround because (1) surround flux was constant and equal for both spinning and stationary surrounds, (2) in control experiments, centre illumination used to simulate scatter never reduced centre responses unless it also elicited a response and (3) it was possible to demonstrate spinning windmill antagonism when the centre was filled with steady illumination 1 log unit greater than the windmill intensity, thus making any scatter from the surround a small proportion of the total centre illumination.

Separate effects of steady and spinning windmills

The previous experiment shows that the spinning windmill causes the intensity–response curve to shift downwards. It has been shown (Thibos & Werblin, 1978) that a stationary surround causes the intensity–response curve to shift laterally, but under certain conditions can cause some downward shift as well. Therefore, it is important

to show here that the stationary and spinning windmills act in different ways, and that the effect of one cannot be duplicated by the other under any conditions.

Fig. 2 shows the effects of both stationary and spinning windmill patterns on the on response of an on-off ganglion cell. The curves show that the spin of a -4 log unit windmill causes a lateral shift of $\frac{1}{3}$ log unit and a decrease in maximum response from fourteen to ten spikes. This effect cannot be duplicated by a brighter stationary windmill because, as shown, a -3 log unit stationary windmill causes an even greater lateral shift of 1 log unit, but does not even begin to reduce the

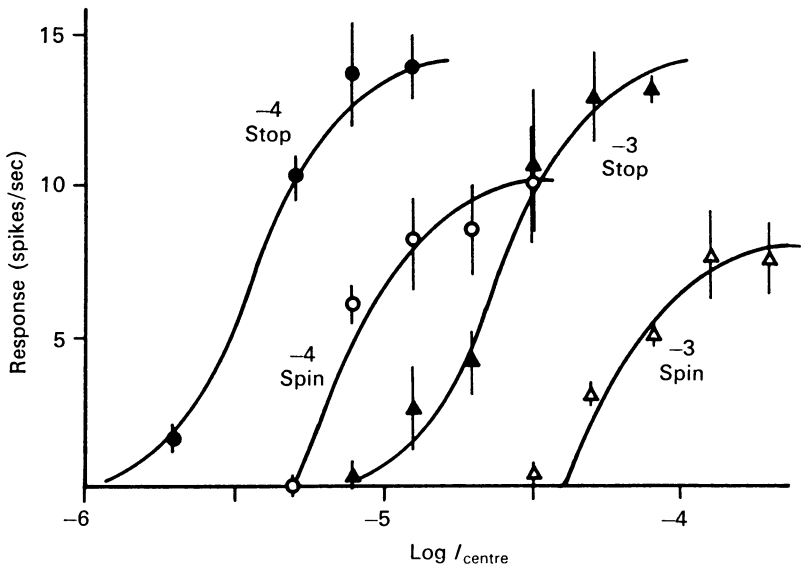

Fig. 2. Comparison of steady and spinning windmill antagonism. Filled and open circles show responses in the presence of stationary and spinning windmill surrounds of -4 log unit intensity, respectively. Filled and open triangles show responses in the presence of stationary and spinning surrounds of -3 log units, respectively. A template curve (eqn. (1), $N = 3{\cdot}4$) was fitted to the closed circles and translated laterally to fit the closed triangles, down and slightly laterally to fit the open circles, and down and laterally to fit the open triangles. Error bars are ± 1 S.E.

maximum response level. Brighter stationary windmills could be used to reduce the maximum response, but they would also cause lateral shifts greater than 1 log unit, so the effect of the spinning -4 log unit windmill cannot be duplicated with a stationary windmill of any intensity. These results support the notion that stationary and spinning windmill patterns affect different systems of lateral interactions in the retina, each with a distinct effect upon ganglion cell activity.

The data in Fig. 2 also demonstrate that the effect of spinning surrounds is dependent upon the surround intensity. An increase of 1 log unit in the spinning surround intensity reduced the maximum possible response from ten spikes (-4 log unit spinning windmill) to three spikes (-3 log unit spinning windmill). The next experiment examines this graded behaviour in more detail.

Graded windmill antagonism with intensity

The results of Fig. 2 indicate that increasing windmill surround intensity has two consequences. First, it shifts the intensity–response curve laterally along the abscissa, which is evident when the windmill is stationary, and secondly, it shifts the response curve down along the ordinate, which is evident when the windmill spins. It is this second antagonistic effect that is to be measured as a function of windmill intensity. A convenient measure of the spinning windmill effect is the normalized decrement in the maximum response that can be elicited, that is,

$$\text{Response decrement} = (R_{\text{stop}} - R_{\text{spin}})/R_{\text{stop}}. \quad (2)$$

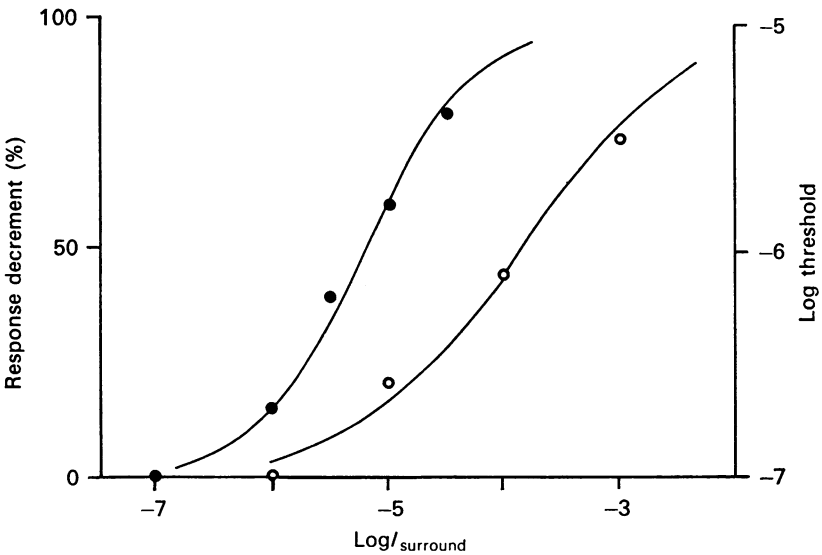

Fig. 3. Comparison of graded antagonism by steady and spinning windmill surrounds. Spinning windmill antagonism is defined by text eqn. (2) and is shown by the filled circles (left ordinate); the fitted curve is from equation (3) for $N = 0{\cdot}9$. Steady windmill antagonism in the same cell is measured by threshold for a centre test flash and is shown by the open circles (right ordinate); the fitted curve is for $N = 0{\cdot}6$.

This measure describes the effect of spinning the windmill as long as the maximum response for a steady background, R_{stop}, does not decrease with surround intensity. We found this to be the case for surround intensities less than about -3 log units (Thibos & Werblin, 1978). To determine the magnitude of response decrement for a given windmill intensity, the test intensity was adjusted to elicit the maximum response when the windmill was stationary (R_{stop}) and then the response to this test was measured when the windmill was spinning (R_{spin}). Tests were made to ensure that the responses obtained were maximal.

The graded effect of a spinning windmill surround is shown by the filled circles in Fig. 3 for a transient cell and similar results were obtained for sustained cells. For comparison, the graded effect of the stationary windmill was also determined for this cell by measuring the increase in threshold to a centre test flash (see Thibos

& Werblin, 1978) and these results are shown by the open circles in Fig. 3. Both sets of data were fitted by the equation

$$f(I_s) = kI_s^N/(I_s^N + I_O^N) \quad (3)$$

where I_s is the surround intensity and k and I_O are constants. For this cell $N = 0{\cdot}9$ for the spinning windmill surround data, indicating the antagonistic effect was graded over about 2·8 log units. The average intensity span of surround antagonism for four cells was 2·5 log units ($N = 1{\cdot}0$). For the stationary surround data $N = 0{\cdot}6$, indicating graded antagonism over about 4·3 log units which is consistent with the value of $N = 0{\cdot}7$ determined from more complete data in the previous paper (Thibos & Werblin, 1978).

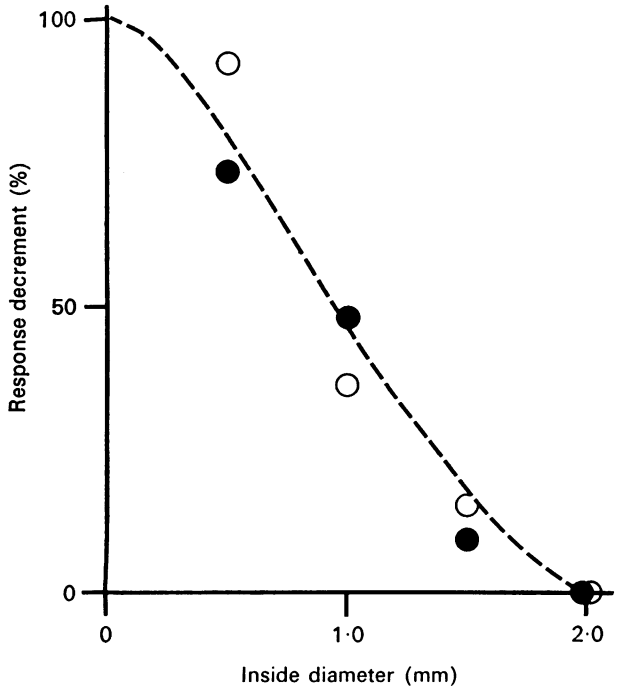

Fig. 4. Variation of ganglion cell antagonism with windmill size. Open and filled circles are results for two different cells. Windmill o.d. was fixed at 2·0 mm. The dotted curve is described by equation (4).

This comparison of the surround intensities which elicit measurable ganglion cell antagonism reveals two quantitative differences between the stationary and spinning surround effects. First, the span of surround intensities which elicits graded reduction of centre response is substantially less for spinning surrounds than for stationary surrounds. Secondly, the surround intensity which causes a just-measurable reduction of centre responses is less for the spinning windmill than for the stationary windmill. The implication of this latter result is that the two antagonistic effects can be elicited independently of each other. Stationary surround antagonism alone is elicited with a stationary windmill, spinning surround antagonism is elicited alone with a dim, spinning windmill, and both types of antagonism are elicited with a bright spinning windmill.

Graded antagonism with windmill size

The effect of windmill area was investigated by using windmills with the o.d. fixed at 2·0 mm and varying the i.d. from 1·5 to 0·5 mm. Its effect upon ganglion cell response was measured by the normalized response decrement to a 0·4 mm centre test flash. The windmill intensity was −4 log units. The results for two ganglion cells, shown in Fig. 4, indicate that antagonism due to the spinning windmill increased monotonically with windmill area.

We have found that the spatial characteristics of ganglion cell antagonism by steady surrounds can be described by integrating the surround weighting function over the region of the annular surround,

$$\text{Total antagonism} = \int_r^1 2\pi x W(x)\,\mathrm{d}x. \tag{4}$$

The weighting function $W(x)$ was chosen, because of the results of earlier experiments, to be exponential, $W(x) = \exp(-x/x_0)$, with a space constant $x_0 = 0{\cdot}25$ mm. There is no *a priori* reason to suppose that this model would also describe the data of Fig. 4. Yet, as shown by the dashed curve, these data are reasonably well described by eqn. (4) provided the space constant of the exponential function is increased to 0·35 mm which would indicate a narrower field of antagonism for the steady surround than for the spinning surround. This empirical relation gives a useful comparison between the extent of spatial summation of the two antagonistic systems. It is consistent with the linear spatial summation model of eqn. (4) but not intended as evidence for such linearity.

Graded antagonism with windmill velocity

The above experiments were all conducted with windmill rotation velocity of 0·3 rev/sec. In the next experiment, velocity was varied while keeping the remaining surround parameters constant. The windmill had 1·0 mm i.d., 2·0 mm o.d., four white and four dark equal sized vanes, and −4 log unit intensity.

Response decrement to a constant test flash is shown for a transient cell in Fig. 5. The closed circles are for on responses and the open circles are for off responses. These data illustrate the finding mentioned earlier that on responses were generally more strongly reduced by the windmill than off responses in transient on-off cells. Responses were reduced by roughly a constant amount for rotation speeds between 0·05 and 0·5 rev/sec but reduced to a lesser extent outside these limits. Rotation speeds less than 0·025 rev/sec were not tested.

Amacrine cells

In the experiments which follow, the response properties of amacrine cells are determined under the same stimulus conditions used above to study ganglion cells. Amacrine cells were rarely recorded intracellularly and consequently the following results are based on a limited sample of five cells. They were identified by criteria used in previous studies (Werblin, 1972, 1977).

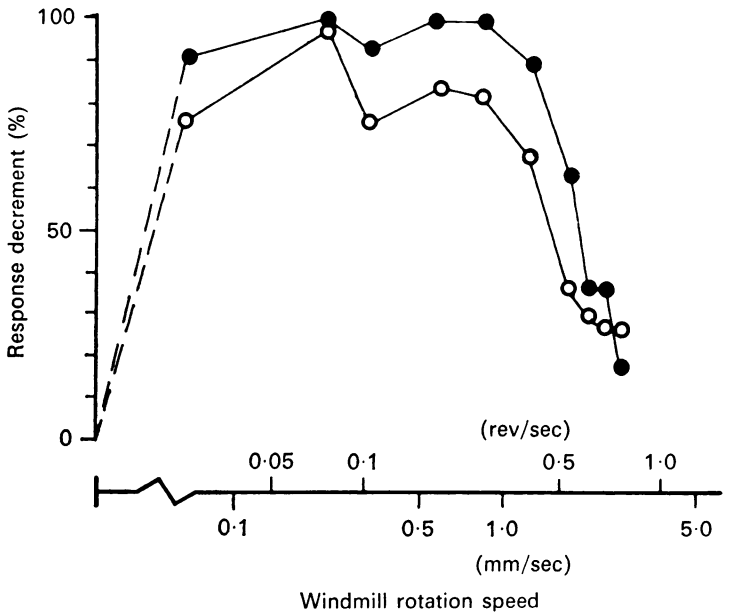

Fig. 5. Variation of ganglion cell antagonism with windmill rotation speed. Reduction of on and off responses in a transient cell are shown by the filled and open circles, respectively. Abscissa shows both angular velocity in rev/sec and linear (tangential) velocity of a point on the windmill midway between the inside and outside diameters.

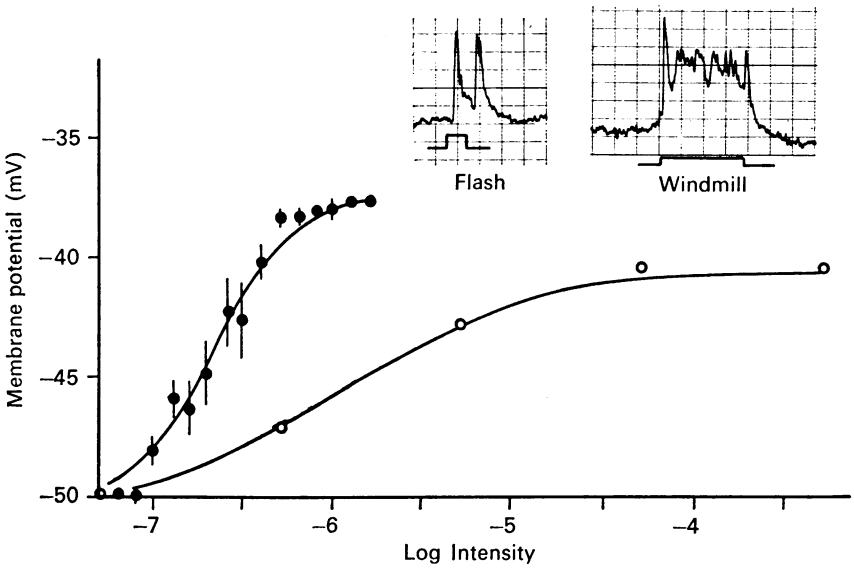

Fig. 6. Amacrine intensity–response functions. Filled circles show magnitude of peak response to a centre test flash. Open circles show magnitude of steady response to a spinning windmill surround pattern. The curves through the filled and open circles are for text eqn. (5) for $N = 2{\cdot}0$ and $N = 1{\cdot}1$, respectively. Inset shows typical intracellular records for a 1 sec centre flash and a 4 sec spinning windmill; calibration: 1 sec/division; 2 mV/division.

Intensity–response function

Intensity–response functions were obtained for a centre 0·4 mm, 1 sec flash and for a 4 sec presentation of an annular windmill with 1·0 mm i.d. and 2·0 mm o.d., rotating at a constant velocity of 0·3 rev/sec. The results are shown in Fig. 6. The filled circles show peak response to the centre test flash with no surround present and the open circles show average plateau response to the annular windmill placed concentric to the centre test flash. The inset in Fig. 6 shows a typical transient response to the flash and sustained response to the windmill. The windmill response was taken to be the mean potential during the plateau of the response.

The solid curves in Fig. 6 are graphs of the equation

$$V = V_{\text{dark}} + V_{\max} I^N / (I^N + \sigma^N) \qquad (5)$$

where I is the intensity of either the spot or windmill stimulus. In agreement with earlier work (Werblin & Copenhagen, 1974), the span of spot intensities giving

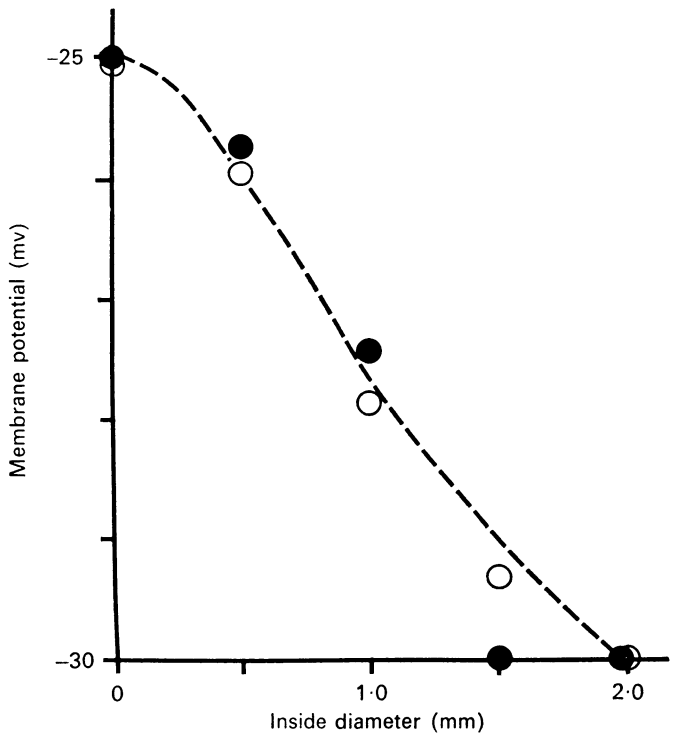

Fig. 7. Variation of amacrine response to a spinning windmill with windmill size. Open and filled circles show two determinations of response magnitude for this cell. The dotted curve is described by eqn. (4).

graded centre response is about 1·3 log units (N = 2·0). This is near the 0·9 log unit span of the average transient cell (see Table 1, Thibos & Werblin, 1978). For the windmill stimulus, the span of intensities giving graded responses was larger, about 2·3 log units (N = 1·1) which is comparable with the 2·5 log unit span of intensities giving graded antagonism in a typical ganglion cell.

The gradation of response with windmill area

The gradation of amacrine response with windmill area was determined by fixing the o.d. at 2·0 mm and varying the i.d. from 1·5 to 0·0 mm. The windmill intensity was −4 log units, the same as in the ganglion cell experiment of Fig. 4. The magnitude of the steady depolarization to a 4 sec presentation of the spinning windmill was determined twice for each value of i.d. and the results are plotted in Fig. 7.

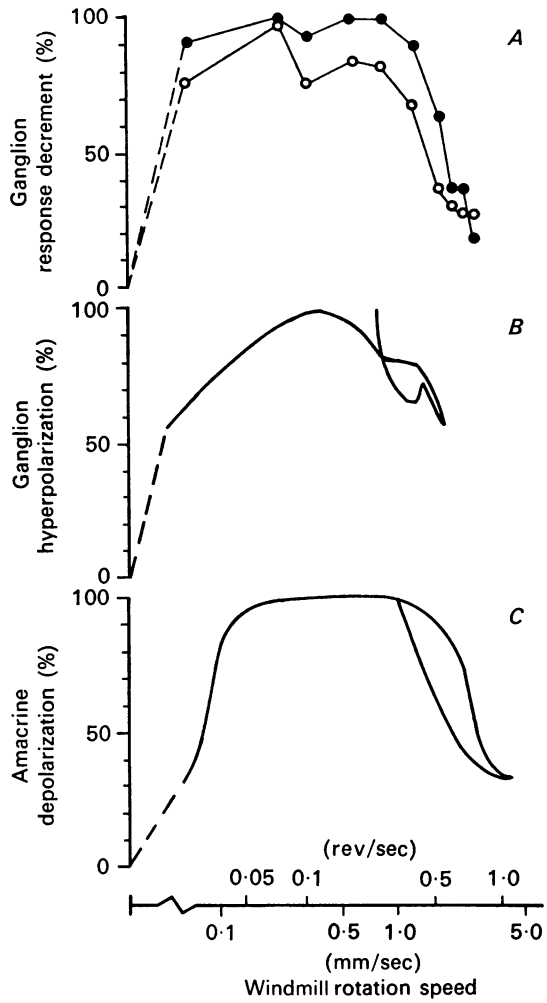

Fig. 8. Comparison of velocity results. Ganglion cell antagonism, ganglion cell hyperpolarization, and amacrine depolarization due to windmill surround are shown in *A*, *B*, and *C*, respectively. *A* is repeated from Fig. 5. *B* and *C* are smoothed tracings from intracellular records. Maximum (100 %) response in *B* is 6·5 mV hyperpolarization and in *C* is 3·0 mV depolarization. Abscissa as in Fig. 5.

To compare these data with ganglion cell antagonism by spinning windmill surrounds, the curve fitted to the ganglion cell data of Fig. 4 is also shown here in Fig. 7. This curve, derived using an exponential weighting function with a constant

of 0·35 mm, (eqn. (4)) indicates a similar extent of spatial summation in amacrine cell activity and antagonistic surround activity of ganglion cells elicited by the spinning windmill.

Windmill velocity

In all of the above experiments the windmill speed was constant during each presentation to the retina. This procedure was too time consuming for studying the intracellular responses of amacrine and ganglion cells because of the brevity of the recordings in amacrine cells. Therefore, in these experiments, the windmill rotation velocity was smoothly increased from 0·3 rev/sec to 1·0 rev/sec and then smoothly decreased to zero in a period of about 15 sec. The resulting change in membrane potential was normalized by the maximum potential change and plotted against log windmill velocity.

Fig. 8 shows the relationship of windmill velocity to ganglion cell hyperpolarization (Fig. 8*B*), and amacrine cell depolarization (Fig. 8*C*) determined by the variable speed method. The effect of windmill velocity on ganglion cell antagonism (Fig. 8*A*), described earlier in Fig. 5, is also included. Similar intracellular responses were obtained in another two ganglion and two amacrine cells. Each of the curves in Fig. 8 is maximum in the range of 0·05 to 0·5 rev/sec and falls off outside these limits. The similar shapes of the curves supports the view that amacrine depolarization by the windmill leads to ganglion cell hyperpolarization, which would account for the reduced response of a ganglion cell to illumination of its receptive field centre.

DISCUSSION

Comparison of amacrine and ganglion cell results

The effects of the spinning windmill on ganglion and amacrine cell activity are compared using a three dimensional format in Fig. 9. The data were obtained under conditions of either constant intensity or constant size and thus the curves shown here represent orthogonal cross-sections of a two-dimensional function. The ganglion cell data in Fig. 9*A* are replotted from Figs. 3 and 4 and the amacrine cell data of Fig. 9*B* are replotted from figs. 6 and 7. Some discrepancy in the two cross-sections is evident and probably due to variability among different cells. Nevertheless, these cross-sections of the two-dimensional surfaces describing ganglion cell antagonism and amacrine response are in general agreement. Together with the study of ganglion cell i.p.s.p.s (Werblin, 1977) these results suggest that ganglion cell antagonism by spinning windmill surrounds may be mediated by a direct inhibitory input to ganglion cells from an amacrine cell network with broad receptive field.

Derivation of the bipolar–ganglion cell transfer curve

Fig. 10 shows a graphical method for approximating the transfer curve relating bipolar to ganglion cell activity. The method involves plotting the bipolar and ganglion cell responses as a function of log test intensity in the presence of various surround conditions, and then correlating the responses for the two cell types for each common test intensity. The ganglion cell response data, in the presence of two different intensities of stopped and spinning windmills is shown in quadrant 1,

taken from Fig. 2. The bipolar response data in quadrant 3 is approximated from the results in the accompanying paper which show that the bipolar response is well described by eqn. (5) where $N = 1{\cdot}2$ (Thibos & Werblin, 1978). That study also showed that the steady surround acts to reposition the bipolar curves along the log intensity axis. Two bipolar response curves are included in quadrant 3, starting at -6 and -5 log units approximately. These positions correspond to the positions of the ganglion cell response curves in the presence of two fixed surround intensities labelled -4 stop and -3 stop respectively.

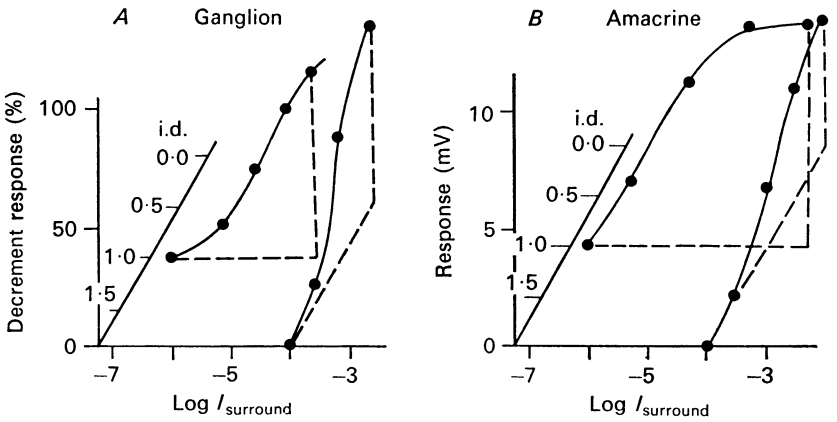

Fig. 9. Comparison of spatio-intensity results. Ganglion cell antagonism and amacrine response due to windmill surround is shown in *A* and *B*, respectively, using the same three-dimensional format. Abscissa is windmill intensity, ordinate is experimental measurement, and Z-axis is size of annulus as specified by the i.d. (mm).

The transfer relation shown by the solid curve in quadrant 2, is common for the pairs of ganglion and bipolar cell responses in the presence of the stopped windmill. It is rather steep suggesting that the ganglion cell response is graded only over a narrow region of the initial response range for the bipolars.

The transfer curves for bipolar–ganglion cell activity in the presence of the spinning windmill are shown by the dashed curves in quadrant 2. They are shifted vertically along the ganglion cell response axis primarily, although there is also some lateral shift. This suggests that the effect of the spinning windmill is to initiate lateral interactions which subtract a fixed quantity from the response of the ganglion cell at a point somewhere proximal to the formation of the transfer curve itself. If, for example, the lateral interactions subtracted from the bipolar cell signal directly, the transfer curves would be expected to shift laterally along the bipolar response axis rather than vertically.

The vertical repositioning of the transfer curves, suggesting subtraction from the ganglion cell signal itself, is consistent with studies of the electrical response properties of the ganglion cells. The spinning windmill causes a hyperpolarization in the ganglion cells (Werblin, 1972) and the hyperpolarization is mediated by an i.p.s.p. with time course and receptive field properties similar to that for the amacrine cells (Werblin, 1977).

Comparison of the effects of steady and spinning windmill surrounds

Steady and spinning windmill surrounds have qualitatively different antagonistic effects on the response of the ganglion cell to test illumination presented at its receptive field centre. A stationary surround shifts the cell intensity–response curve laterally (Thibos & Werblin, 1978) while the spinning surround shifts the response curve predominantly downward (Fig. 2). Steady surrounds appear to reposition the intensity *domain*, but spinning windmills reduce the *range* of graded response

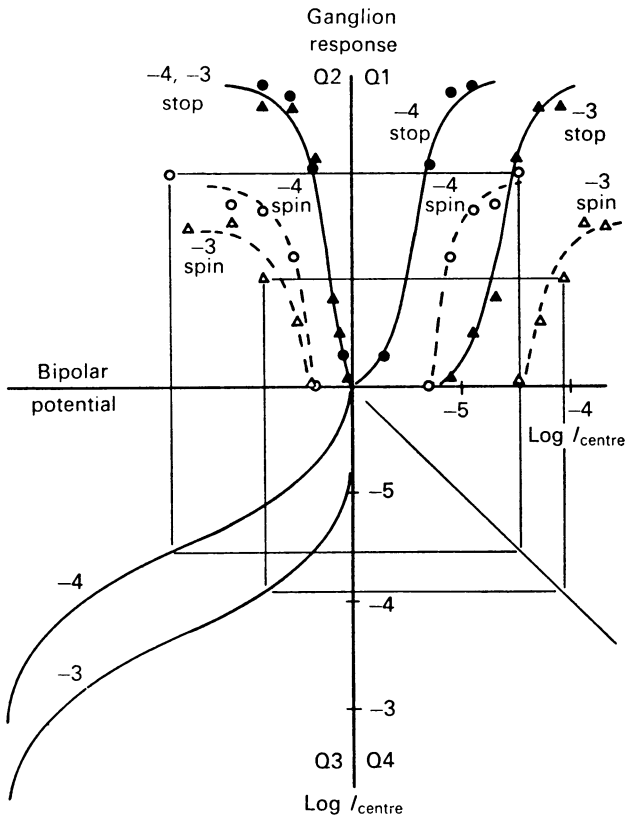

Fig. 10. Transfer curve for bipolar–ganglion cell response. Quadrant 1 (Q1) shows the response of a transient ganglion cell as a function of log intensity in the presence of two stationary windmills of −4 and −3 log unit intensity (solid curves). The response of the ganglion cell in the presence of the spinning windmills is given by the dashed curves. Q3 shows the approximate response of the bipolar cell, with $N = 1{\cdot}2$ in eqn. 5 for two different steady surrounds corresponding to those for the ganglion cell in quadrant 1. The vertical and horizontal lines indicate how the points on the transfer curve in Q2 were derived by correlating the responses for bipolar and ganglion cells at each log test intensity. The transfer curve for the stationary surround is given by the solid curve in Q2. The transfer curve for the bipolar–ganglion cell in the presence of the spinning windmill is given by the dashed curves in Q2. These curves have the form of the solid transfer curve, but are shifted primarily vertically along the ganglion cell response axis, suggesting that spinning windmills subtract from the ganglion cell response.

without greatly affecting the intensity domain. This difference between steady and spinning surrounds cannot be eliminated by manipulating the surround intensity (Fig. 2) which suggests the two effects are due to separate systems of lateral antagonism.

The two antagonistic surround systems differ in three important quantitative ways. First, the surround intensity which gives a just-measurable decrement in ganglion cell activity is about 1 log unit less for the spinning than for the stationary windmill. Secondly, the span of surround intensities giving graded antagonism is about 1·5 log units less for spinning surrounds than for steady surrounds. Thirdly, the extent of spatial summation of surround illumination, as measured by the space constant of an exponential weighting function, is 0·25 mm for steady surrounds but 0·35 mm for spinning surrounds. These differences are evident when comparing the surfaces in Fig. 9 with the corresponding curves describing steady surround antagonism (Fig. 10, Thibos & Werblin, 1978). Along an axis of constant intensity, the surfaces in Fig. 9 are steeper than was found for steady surrounds. But along an axis of constant size, the surfaces here are less steep than was found for steady surrounds.

Comparison with other retinas

A recent report, using methods similar to those in this study (Jakiela, 1978) has shown that the response of cat retinal ganglion cells, to centre illumination, is suppressed by a spinning windmill. Both on- and off-centre cells, of X and Y classification are affected (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; Cleland & Levick 1974*a*,*b*).

The response in all ganglion cell types in the tiger salamander retina are similarly affected (X. Wunk & F. S. Werblin, in preparation), and Schwartz (1973) has shown a similar effect in the turtle retina. Suppression of the response appears to be mediated by a direct inhibitory input to the ganglion cells of mudpuppy and tiger salamander from the amacrine cells (Werblin, 1977; X. Wunk & F. S. Werblin, in preparation).

The suppression of ganglion cell response by targets moving in the receptive field surround may be a general feature of retinal function. Its physiological significance remains obscure.

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