Visual Neuroscience (1994), 11, 1019–1025. Printed in the USA.

SHORT COMMUNICATION

Directional hyperacuity in ganglion cells of the rabbit retina

NORBERTO M. GRZYWACZ,[1] FRANKLIN R. AMTHOR,[2] AND DAVID K. MERWINE[3]

[1]The Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco
[2]Department of Psychology and Neurobiology Research Center, University of Alabama at Birmingham, Birmingham
[3]Department of Physiological Optics, School of Optometry, University of Alabama at Birmingham, Birmingham

(RECEIVED September 13, 1993; ACCEPTED February 7, 1994)

Abstract

Biological visual systems can detect positional changes that are finer than these systems' acuity to sine-wave gratings, a property known as hyperacuity. Some systems can even detect changes finer that the photoreceptor spacing. We report here that rabbit's directionally selective ganglion cells not only detect positional changes in the hyperacuity range, but also discriminate the direction of their motion. Our experiments show that directional selectivity occurs for edges of light moving as little as 1.1 μm (26″ of visual angle) across the retina. This distance corresponds to a hyperacuity, since the acuity to sine-wave gratings of rabbit's On–Off DS ganglion cells is about 125 μm (50′). In addition, this distance is smaller than the minimal spacing between rabbit photoreceptors (1.9 μm or 46″), as estimated from cell-density studies (Young & Vaney, 1991). Such a hyperacuity suggests low-noise high-gain signal transmission from photoreceptors to ganglion cells and that directional selectivity can arise in small portions of retinal dendritic processes.

Keywords: Hyperacuity, Directional selectivity, Ganglion cell, Retina, Rabbit

Introduction

The first demonstration of the remarkable sensitivity of visual systems to positional changes was for human psychophysical displacement thresholds (5″ – Westheimer & McKee, 1977). They are lower than human grating acuity (and thus the term hyperacuity) and the spacing between foveal cones (27″). Studies of the neural substrate of hyperacuity demonstrated that retinal (Shapley & Victor, 1986; Lee et al., 1993) and cortical neurons (Swindale & Cynader, 1986) can detect displacements in the hyperacuity range. However, these studies did not explain how visual systems not only detect these displacements, but also discriminate their direction. In this paper, we investigate this discrimination, which we call directional hyperacuity.

Barlow and Levick (1965) demonstrated directional selectivity for slits of light moving about 40 μm (17′) across the rabbit's retina. But it has been argued that extended edges, rather than narrow slits of light, are a better stimulus for rabbit's directionally selective (DS) ganglion cells (Amthor & Grzywacz, 1993; Grzywacz & Amthor, 1993). Hence, it became of interest to measure their response to edges of light moving short distances. Demonstration of directional hyperacuity with moving edges would make the rabbit retina a good model for understanding the biophysics of this fine visual discrimination. This is because much is known about the physiology (Oyster, 1968; Wyatt & Daw, 1975; Amthor & Grzywacz, 1993; Grzywacz & Amthor, 1993), anatomy (Masland et al., 1984; Amthor et al., 1989; Famiglietti, 1991), and pharmacology (Caldwell et al., 1978; Ariel & Daw, 1982) of rabbit directional selectivity.

Reprint requests to: Norberto M. Grzywacz, The Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco, CA 94115, USA.

Methods

Eighteen On–Off DS ganglion cells of the rabbit were recorded extracellularly in an everted eyecup preparation (Amthor et al., 1984; Amthor et al., 1989; Amthor & Grzywacz, 1991, 1993). The eyes were from adult Dutch belt-pigmented rabbits weighing at least 1.3 kg. Animals were anesthetized with an initial dose of urethane (2 g/kg), followed by Pentobarbital given to effect. The amount of Pentobarbital brought the animal to a level of anesthesia in which no reflexive movement or change in heart rate resulted from a pinch to the paw. After anesthesia, the right eye was enucleated as the animal was killed with an overdose of Pentobarbital. The eyecup was then prepared as described elsewhere (Amthor et al., 1984; Amthor et al., 1989; Amthor & Grzywacz, 1991, 1993). It was superfused with a transparent medium similar to that in Ames and Nesbett (1981).

We investigated the discrimination of direction of motion by On–Off directionally selective ganglion cells of rabbit by

using an extended edge undergoing the apparent motion explained in Fig. 1. Extracellular-spike responses were recorded for both preferred- and null-direction motions. We also recorded responses to the edge appearing and disappearing without moving. Poststimulus histograms for the no-motion conditions were subtracted from those obtained from the motions bin by bin in a base-subtraction procedure. This procedure allowed visualizing responses to motion in the absence of spikes elicited by the edge's appearance before motion (Amthor & Grzywacz, 1993; Grzywacz & Amthor, 1993)

In different experiments, several apparent-motion displacement magnitudes were used, ranging from 1.1 μm (26″) to 47 μm (19′). All conditions (combinatorial arrangements of displacement magnitudes, contrast polarity, and preferred and null motions) were presented in random order within an experimental set. The number of such sets in different experiments ranged from 30 to 100 and the random order was different for each set. The delay between the beginning of two consecutive stimuli within a set was 2250 ms.

The apparent-motion stimuli were generated on a Tektronix 608 monitor controlled by computer and a waveform generator (Innisfree, Cambridge, MA) projected to the eyecup from 85 cm through an achromatic plano-convex lens with 17-mm focal length and 12-mm diameter. The contrast of the stimuli was 99.2% (determined with a Spectra Pritchard photometer model 1980A-WB) and the mean illumination (and that of the homogeneous background) was 60 lx. We measured the sharpness of the moving edge on the monitor with the photometer from 1.5 m away and a 0.75′ slit. The edge moved in increments of 50 μm on the monitor, and for each position the luminance was read. It fell from 90% to 10% of maximum in 380 ± 30 μm (standard error). By taking into account the thickness of the slit, the 90%-to-10% edge's spread was 180 ± 50 μm on the monitor. (Under the assumption that the monitor's line-spread function is Gaussian, its spatial standard deviation is around 70 μm.) This spread made the task of responding with directional hyperacuity more difficult, since the shortest motions spanned only 1.1 μm in the retina or equivalently, 55 μm on the monitor. We did not expect the fluid covering the retina to affect this spread or the image's quality. The fluid's height was between 1–2 mm over the recorded cells. The diameter of its surface was about 3 cm, too large to produce much spherical aberration (due to

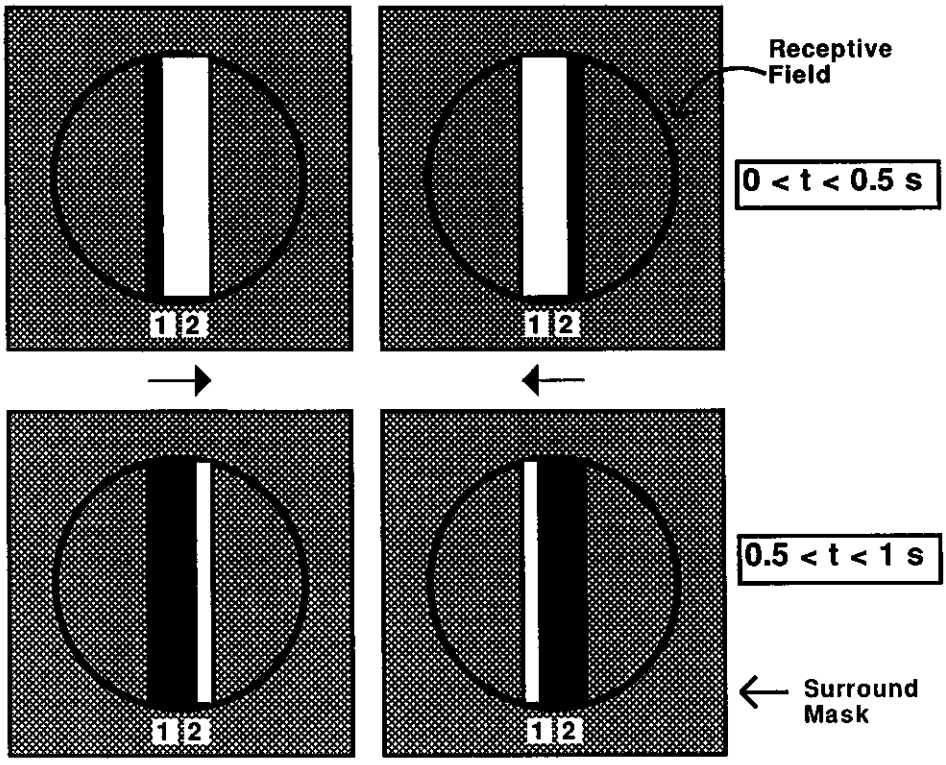

Fig. 1. Schematics of visual display used in experiments. The receptive field (circle) was masked (hatched area) to prevent surround interactions. The visible area always corresponded to 100 × 400 μm^2 in the retina, such that the long axis was perpendicular to the preferred direction. A dark (or light) edge (oriented parallel to the long axis of the visible area) appeared from a homogeneous background in a position of the receptive field, labeled 1, remained there for 500 ms, and then jumped a predetermined distance in the preferred direction to the position labeled 2. The edge remained at "2" for another 500 ms before the stimulus returned to the homogeneous background. Null-direction motion jumps from "2" to "1" were also delivered to the cell. The positions "1" and "2" were symmetrical about the center of the aperture. Furthermore, they were typically symmetrical about the center of the receptive field. The only exceptions occurred in experiments like the one labeled "position = 70 μm" in Fig. 3. For them, the midpoint between positions "1" and "2" was 70 μm away from the center of the receptive field. Because these displacements were back and forth from "1" to "2," they stimulated the exact same area of the retina each time for a given displacement magnitude.

a meniscus) at the center of the fluid's surface. The electrode was also not expected to cause aberrations, because its point of entry in the fluid was typically 3 mm away from the center and the diameter of the electrode's shank was 0.8 mm. To confirm these expectations, we looked at the image through the microscope used to aid electrode placement with a scaled piece of paper placed in lieu of the retina. This microscopic procedure was performed with and without fluid, and with and without the electrode. Presence of fluid or electrode did not cause detectable distortions, rotations, or abnormal magnifications of the image.

The statistical significance of the data obtained with the apparent-motion stimuli was analyzed in two ways: First, we compared the means of the integral of the based subtracted preferred- and null-direction responses with a t-test. Second, we performed an individual trial analysis on these integrals. This analysis compared preferred and null responses trial by trial, and computed the percentage of trials in which the preferred response was larger than the null one. (When the responses were equal, the analysis assigned a "winner"—preferred or null—randomly.) A trial-by-trial analysis, that is, comparing responses separately for trial 1, then for trial 2, and so on, reduced effects that large temporal separation might have on the comparisons. This analysis assumed that a comparison between two cells with opposite preferred directions and with properties identical to the recorded cell underlies the decisions on direction of motion. The analysis was equivalent to a two-alternative forced-choice paradigm (chance performance at 50%). In such a paradigm, a hit rate of P% (for example, 81%) corresponds to a false-alarm rate of $(100 - P)$% (only 19% in the example). In a system whose performance is limited by a Gaussian additive noise, the hit rate is a monotonic function of a single parameter called d' (Elliot, 1964; Green & Swets, 1966). Therefore, psychophysicists use d' to quantify performance (with threshold typically set at $d' = 1$). For comparison with psychophysical performances, we report d's of Gaussian-noise systems with hit rates as in rabbit DS cells.

The hyperacute behavior reported here was compared to minimal photoreceptor spacing and to square- and sine-wave grating acuity data. To obtain these data, the gratings moved in the preferred direction at various temporal frequencies, with the same contrast and mean luminance as described above, and the surround masked. At the optimal temporal frequency (≈4 Hz), we delivered 128 cycles of the stimulus, an amount comparable (actually, slightly larger) to that delivered in the hyperacuity task. Typically, the response became indistinguishable from the background activity at 8 cycles/mm, although occasionally, cells had small responses at this frequency. [The acuity—$\frac{1}{8}$ mm = 125 μm—was consistent with that of the starburst cell, an important excitatory drive to On-Off DS cells (O'Malley & Masland, 1993).] A manuscript describing the DS ganglion-cell acuity data in detail is currently in preparation.

Results

Fig. 2 displays poststimulus histograms for 1.1 μm preferred- and null-direction motions of a bright edge for one cell. Comparison of the histogram's black bins with activity before the edge's appearance (arrow A) illustrates that the responses to preferred-direction motion were higher (average of 1.39 spikes per 0.5 s interval) than the background activity (average of 0.035 spikes per 0.5 s interval), indicating displacement detection. Furthermore, preferred-direction motion elicited more spikes than null-direction motion (average of 0.19 spikes per 0.5 s interval). Analysis of the histogram's time integral over 500 ms after the jump reveals that this difference is significant ($t = 5.02$, 198 degrees of freedom, $P < 0.001$). Individual-trial analysis (see Methods) shows that comparing responses of two such cells with opposite preferred directions would determine the motion's direction correctly 81% of the time ($d' = 1.24$). Hence, these results demonstrate a directional hyperacuity in DS ganglion cells of rabbit retina.

In experiments such as those reported in Fig. 2, responses were recorded as a function of motion displacement ranging from 1.1 μm (26″) to 47 μm (19′). Fig. 3 presents results of two such experiments, one for short-range motions using data from the cell in Fig. 2 (E514c1), and the other for a wide range of displacements from another cell (E516c1). For Fig. 3, we integrated the base-subtracted responses over 500 ms after the displacement.

Fig. 3 provides further illustration that DS ganglion cells respond with directional hyperacuity to motion. The figure reconfirms this finding for the On responses of E514c1 and presents the displacement behavior for E516c1. (There was no directional selectivity in the Off responses of E514c1 for distances smaller or equal than 2.2 μm. This is a first demonstration that, in general, the degree of directional hyperacuity depends on whether the stimulus is of an On or Off type.) Directional selectivity increases with distance, because of a rapid increase of preferred- but not null-direction responses. At short distances, it is apparent that for E516c1, preferred-direction responses were larger than null-direction responses even at 3.8 μm. This appearance is confirmed by statistics for the On ($t = 4.28$, 58 degrees of freedom, $P < 0.001$) and Off ($t = 6.24$, 58 degrees of freedom, $P < 0.001$) motions, and extended to the Off motion at 1.9 μm ($t = 2.21$, 58 degrees of freedom, $P < 0.025$). The motion responses were highly variable from trial to trial (see representative standard-deviation error bars in Fig. 3). However, as for cell E514c1, individual-trial analysis for cell E516c1 shows that comparing responses of two such cells with opposite preferred directions would determine the motion's direction correctly 82% of the time ($d' = 1.29$) for 3.8-μm motions. Consequently, the directional hyperacute performance is not just the product of extensive accumulation of multiple response trials, but is a robust feature of retinal processing.

It is also possible that the degree of directional hyperacuity depends on receptive-field position. [For 150 μm (1 deg) motions, directional selectivity can be elicited in multiple positions of the receptive field (Barlow & Levick, 1965).] To investigate this issue, we repeated the experiments in two or more positions separated by at least 70 μm (28′). Fig. 4, illustrates the co-dependence of directional hyperacuity on receptive-field position, and On or Off stimuli.

At position 0 μm, On, but not Off edges elicit DS responses for 4.4-μm displacements ($t = 2.42$, 198 degrees of freedom, $P < 0.01$, and 62% performance in individual-trial analysis or $d' = 0.43$). In contrast, at position 70 μm, Off edges now elicit strong DS responses ($t = 8.45$, 58 degrees of freedom, $P < 0.001$, and 84% performance in individual-trial analysis or $d' = 1.4$). [Variations in On and Off responses with position have been attributed to variations in the size of the On and Off strata of DS ganglion cells' dendritic trees (Amthor et al., 1984).] Directional selectivity for 4.4-μm displacements is a directional hyper-

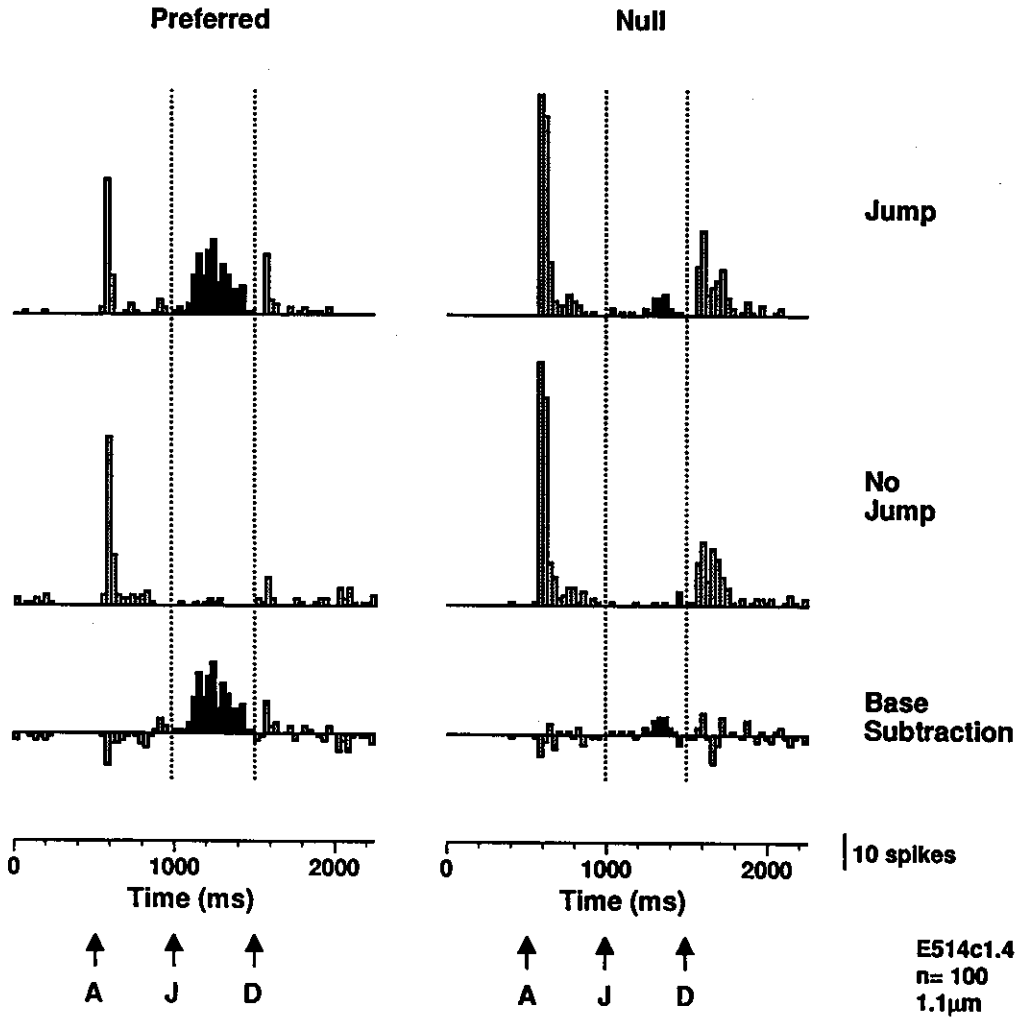

Fig. 2. Poststimulus histograms for a 1.1 μm (26″) motion of a bright edge. Histograms labeled "Jump" are responses of one cell to 100 trials of preferred- and null-direction displacements. Histograms labeled "No Jump" are responses to the edge appearing and disappearing without being displaced. Histograms labeled "Base Subtraction" are the result of subtracting bin by bin the "No Jump" histograms from the "Jump" histograms. This subtraction was shown to correspond to the response to the jump in the absence of spikes elicited by the appearance of the edge before the motion (Amthor & Grzywacz, 1993; Grzywacz & Amthor, 1993). The times of appearance, motion jump, and disappearance of the edges are marked with the arrows labeled A, J, and D, respectively. While the majority of the histogram is textured, we painted the histograms' portion between J and D in black to emphasize the response to the displacement itself. Moreover, the black bins are the data used in later figures. Base-subtracted responses to preferred-direction displacements are larger than those to null-direction displacements. This difference at such a short motion displacement (smaller than photoreceptor spacing) indicates that this cell exhibits directional hyperacuity.

acuity, since the acuity to square- and sine-wave gratings of rabbit's On–Off DS ganglion cells is about 125 μm (50′; Fig. 3; see Methods). (In this regard, the minimal distance for which Barlow and Levick observed DS responses with slits of light also constitutes directional hyperacuity. However, this distance is more than an order of magnitude larger than the minimal values reported here.) We conclude that the mechanism allowing for directional hyperacuity has multiple replicas in the receptive field, but depends on contrast polarity.

We completed the several-hours-long experiments on directional hyperacuity in 18 cells (13 with the protocol of Fig. 1 and five with a protocol using a central position for the motions' beginning). In all cells, the preferred-null bias was identical for displacements smaller than 15 μm (6′) and larger, continuous motions, indicating that all cells had correct directional hyperacuity. (That small displacements had always the same preferred direction as large motions indicates that directional hyperacuity is not due to edge-of-receptive-field effects. They could induce artifactual directionality, but not always in the correct direction.) Four out of the 13 cells (31%) tested with displacements smaller than the minimal photoreceptor spacing (1.9 μm) showed directional selectivity for these displacements. [The minimal photoreceptor spacing was estimated by assuming tight hexagonal packing, and maximal cone and rod densities of 16,000 and 308,000 cells/mm^2 respectively (Young & Vaney, 1991). However, the spacing relevant for directional selectivity might be much higher, since rod bipolar and amacrine cells do not appear to contact On starburst cells (Famiglietti, 1991), which

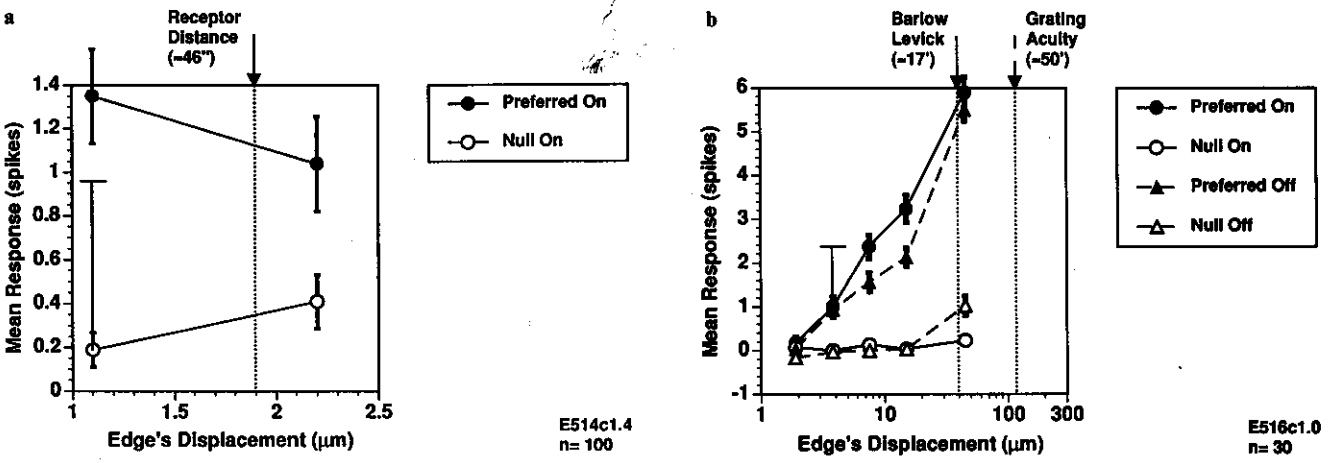

Fig. 3. Preferred and null responses as a function of displacement. The ordinates are the mean number of spikes during 500 ms after the displacement. This number corresponds to the mean integral of the black portion of base-subtracted histograms like those in Fig. 2. The bold error bars are standard errors of the ordinates, while the thin error bars are representative standard deviations. Solid and dashed lines correspond to responses to bright (On) or dark (Off) edges, respectively. For comparison's sake, we labeled with arrows and dotted lines the minimal photoreceptor distance, minimal distance for which Barlow and Levick observed DS responses with slits of light, and sine-wave grating acuity. a: Responses of the cell in Fig. 2 to one hundred short-range motion trials. This cell was particularly sensitive to On edges (responses to Off edges were not DS for these displacements—data not presented). Its directional selectivity threshold was at least 70% better than the photoreceptor spacing. b: Responses of another cell to a wide range of displacements over 30 trials. The preferred, but not null responses, rise fast with displacement for both On and Off stimuli. Already at displacements below photoreceptor spacing (and below Barlow and Levick limit, and grating acuity), one observes directional selectivity. These two cells provide further evidence that On–Off DS ganglion cells of the rabbit retina exhibit directional hyperacuity.

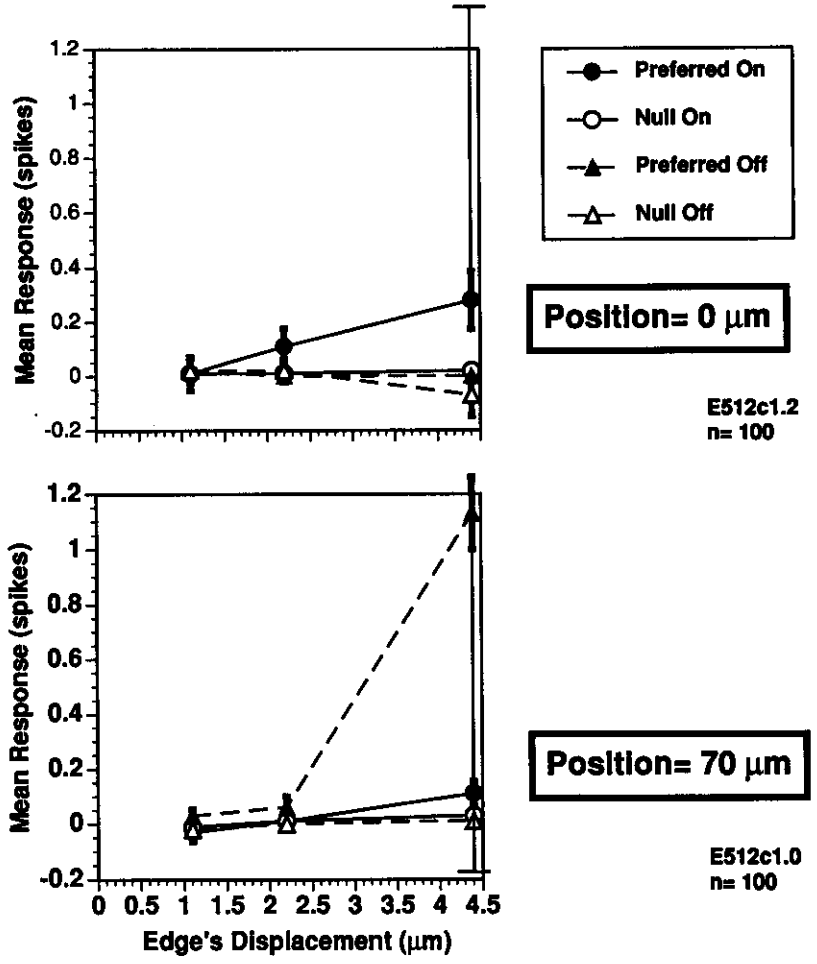

Fig. 4. Co-dependence of directional hyperacuity on receptive-field position, and On or Off stimuli. The meaning of ordinates, error bars, and solid and dashed lines are the same as in Fig. 3. This experiment was identical to those in Fig. 3, but the cell was stimulated over 100 trials with motions whose centers were separated by 70 μm. At the position labeled 0 μm, only On responses showed directional selectivity for 4.4-μm displacements. In contrast, at the position labeled 70 μm, the Off responses were the ones displaying strong directionality for the same displacements. Because these displacements were lower than the acuity to square- and sine-wave gratings (Fig. 3), this directional selectivity corresponds to a directional hyperacuity. Therefore, directional hyperacuity, but not preferred and null directions, depends on receptive-field position and contrast polarity.

might be the site where the computation of directional selectivity for On stimuli takes place. Consequently, the incidence of cells showing directional selectivity for displacements smaller than the photoreceptor spacing might be much higher than 31%.] In three cells, there was directional selectivity at 1.1 μm (Fig. 2). The directional hyperacuity of these highly sensitive cells was only at most a factor of 5.2 worse than human performance.

Discussion

Directionally selective cells must overcome two problems to display directional hyperacuity: (1) they must respond to small displacements, and (2) they must do so in a DS manner. The first problem is raised by the wide receptive-field centers of bipolar cells. Their diameters are about 300 μm (Dacheux & Raviola, 1986) and arise from photoreceptor gap junctions (Smith & Sterling, 1990), and not dendritic processes (Dacheux & Raviola, 1986). If one assumes that the photoreceptors' receptive field has a Gaussian profile of 75 μm standard deviation (two standard deviations on each side of center $\Rightarrow$ 300 μm diameter), and that the monitor's line-spread function is Gaussian with a 70 μm standard deviation (see Methods), then a 1.1 μm displacement would cause at most 0.8% change in photoreceptors' response. (This is consistent with the 0.5% sine-wave grating's contrast necessary to elicit directional selectivity—Grzywacz et al., 1990.) This 0.8% change would correspond to at most 0.8 mV modulation. Thus, such a small photoreceptor voltage should generate reliably about one spike for the best ganglion cells (Fig. 2), implying low noise and high gain (Shapley & Victor, 1986). Spatial filtering of photoreceptors electrical coupling should help to reduce noise. High gain could arise from photoreceptors' resting transmitter release (Fain, 1977; Fain et al., 1977), high-pass filtering of bipolar-cell inputs to inner plexiform layer (Werblin et al., 1988), and recruitment of several DS subunits (Barlow & Levick, 1965) across the edge. We wish to emphasize the recruitment, since in our experiment, the edge spanned 400 μm over the photoreceptor array (Fig. 1). Therefore, even for the smallest displacements used (1.1 μm), the edge (including its spread) would cause a small increase in light stimulation (<0.8%) in up to 18,000 photoreceptors. Furthermore, analysis of null-direction inhibition (Amthor & Grzywacz, 1993) and preferred-direction facilitation (Grzywacz & Amthor, 1993) recently suggested that the best stimuli to elicit directional selectivity from the rabbit's retina are large edges, rather than small objects.

The second problem raised by directional hyperacuity arises because the ganglion- and amacrine-cell dendritic processes apparently involved in directional selectivity are several hundred micrometers long (Amthor et al., 1984, 1989; Masland et al., 1984; Vaney, 1990; Famiglietti, 1991; Yang & Masland, 1992). Hence, as postulated by some models (Torre & Poggio, 1978; Koch et al., 1982; Grzywacz & Amthor, 1989; Vaney, 1990; Borg-Graham & Grzywacz, 1992), directional selectivity probably requires a small portion of these processes. In these models, directional hyperacuity would involve shunting inhibition, for which there is evidence (Amthor & Grzywacz, 1991). Because displacements causing barely significant responses elicit directional selectivity (Figs. 3 and 4), we conclude that it occurs for all displacements eliciting any response. Such directionality might arise from temporally sustained inhibition (Amthor & Grzywacz, 1993), which for slowly moving edges would be asymmetric and always present.

Acknowledgments

We thank Suzanne McKee for reading the manuscript critically. Also, thanks are due to William Belzer and Mark Villa for computer programming, Lorraine DeAngelis for technical assistance, and Doug Taylor for help with the estimate of the edge's sharpness. This work was supported by National Eye Institute grant EY08921 and by an award from the Paul L. and Phyllis C. Wattis Foundation to N.M. Grzywacz, by National Eye Institute grant EY05070 and a Sloan Foundation grant to F.R. Amthor, by Office of Naval Research grant N0014-91-J-1280, and by National Eye Institute core grants to Smith-Kettlewell and University of Alabama at Birmingham.

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