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Receptive Field Properties of Cat Retinal Ganglion Cells During Short-Term IOP Elevation

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Purpose. To examine and compare receptive field properties of cat retinal ganglion cells before and during intraocular pressure (IOP) elevation.

Methods. Responses of cat retinal ganglion cells to two sets of specially designed light or dark spots and annuli were recorded extracellularly. Receptive field properties were studied comparatively before and during short-term constant IOP elevation induced by keeping the retinal perfusion pressure at a critical level of about 30 mm Hg.

Results. All the responses, including properties of different types of receptive fields and different components of the cells' receptive fields, decreased during short-term IOP elevation. The responses of off-center cells were more tolerant of IOP elevation than those of on-center cells, whereas the responses of Y cells were less sensitive to IOP elevation than those of X cells. The responses of the centers of the receptive fields exhibited more pronounced resistance to IOP elevation than those of the surround. The peak responses of the post-stimulus time histogram of all cells declined less than the mean responses during IOP elevation.

Conclusions. The varied effects of short-term IOP elevation on different types (X and Y, on-center and off-center) of retinal ganglion cells and their receptive field properties may reflect the different degrees of ischemic effects on the retinal pathways that project to the different types of ganglion cells. Invest Ophthalmol Vis Sci. 1994;35:2758–2764.

Because of the role of elevated IOP in human glaucoma, many studies have examined the anatomic and physiological changes of the retina during intraocular pressure (IOP) elevation, either in acute elevation or in chronic elevation. However, there have been few investigations of the changes of the visual receptive field properties during IOP elevation.[1–4] Previous studies in our laboratory showed that Y cells in the cat retina and lateral geniculate nucleus are more tolerant than X cells during brief (<2 minutes) IOP elevation.[3–4] The purpose of this study was to compare further the receptive field properties of different types of cat ganglion cells during short-term (15 to 20 minutes) IOP elevation at a critical perfusion pressure level (about 30 mm Hg).

During experimentally induced short-term IOP elevation, the functional impairment was mainly caused by ischemia.[1–7] The function of retinal ganglion cells depends upon the retinal perfusion pressure but not upon the absolute IOP.[2–5] Thus, it is important to maintain a stable perfusion pressure because of the variation in the blood pressure among animals. We recently designed and developed an apparatus that readily allows the retinal perfusion pressure to be maintained at a given level. Using this apparatus, we studied various response properties of receptive fields (RF) of different retinal ganglion cells of cats during short-term IOP elevation to gain our understanding of the retinal mechanisms.

MATERIALS AND METHODS

Physiological Recording Procedures

The experiments were performed in 21 eyes of 13 adult cats. All investigations involving animals conformed to the ARVO Statement on the Use of Animals

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in Ophthalmic and Vision Research. The preparation for electrophysiological single-unit recordings was similar to that described previously.[2,3] Animals were anesthetized with urethane (200 mg/kg per hour) and paralyzed with gallamine triethiodide (10 mg/kg per hour) intravenously for the duration of each experiment. Body temperature was maintained at 38°C. The ECG, heart rate, and EEG were carefully monitored throughout each experiment, and care was taken that the animal remain conscious. Expired pCO_2 was maintained at approximately 4%.

The animals' eyes were protected from desiccation with proper contact lenses. The cat optic disk was projected upon a white screen positioned 114 cm from the eye and was used to determine the position of the area centralis. The clarity of the optics of the eyes was checked repeatedly during all experiments.

Animals were placed in a stereotaxic apparatus, and all pressure points and incisions were infiltrated with a long-acting anesthetic (1% lidocaine HCl) to prevent pain. Action potentials of single retinal ganglion cells were recorded extracellularly from the optic nerves with a tungsten-in-glass microelectrode. The impedances of microelectrodes were from 2 to 15 MΩ. The electrical signals were amplified with an extracellular or intracellular pre-amplifier (Nihon Kohden, Tokyo, Japan) and an AC/DC amplifier (FZG-IA, Liuhe, Nanjing, China) through the microelectrode, and then fed to a Compaq (Houston, TX) 386/20e computer via a window discriminator and a 1401 interface (Cambridge Electronic Design, Cambridge, UK).

The responses of single units to visual stimulation were studied quantitatively with an image synthesizer (Innisfree, Cambridge, MA), an oscilloscope-based optical display (Tektronix 608, Tektronix, Beaverton, OR), and a computer controlled visual stimulus system (VS System, Cambridge Electronic Design). We recently developed an apparatus that allows the oscilloscope display to be moved to any point in the animal's visual field while keeping a fixed distance of 57 cm from the eye.

The responses of single retinal ganglion cells to drifting sinusoidal and contrast alternating sinusoidal gratings with low and high spatial frequencies were used to determine the cells' linearity and frequency doubling. The spatial resolution, receptive field size, tonicity of response, and sluggishness of response were also studied. Cells were classified as X- and Y-types,[8–11] as well as on-center and off-center types.

Visual Stimulation

Two sets of visual stimulus patterns were employed in this study for on-center and off-center ganglion cells. The first set, for on-center cells, was composed of two patterns: (1) a central-light spot having a diameter slightly less than the diameter of the center of the cell's receptive field, with a dark background; (2) a surround-dark annulus whose width was slightly less than the width of the surround of the cell's RF having a light background. These two stimulus patterns will elicit central and surround responses of the cell's receptive field, respectively. The second set of visual stimulus patterns for off-center cells was exactly the same as the first set, but it had opposite contrast. The luminance of the light spot or annulus was 10 cd/m^2, the darkness was 0.53 cd/m^2. Each of the two visual stimulus patterns of the same set was routinely represented in turn to be positioned at the center or surround of the cell's visual receptive field for 500 msec.

Twenty representations of each pattern were used to initiate the cell's average post-stimulus time histogram and to compile the time course of the cell's responses to different stimulus patterns. Two definitions of response amplitude, both in spikes per second, the peak amplitude of the post-stimulus time histogram, and the mean firing rate were used. Decay ratio was defined as the response amplitude during IOP elevation divided by that before IOP elevation, that is, the relative decay during IOP elevation.

Intraocular Pressure Elevation

Figure 1 shows the overall arrangement for keeping the perfusion pressure constant and for measuring the arterial blood pressure of the cat studied. To raise the IOP artificially, a cannula was inserted at the limbus into the anterior chamber of the eye studied. The cannula was connected to a U-type tube B containing bromoform (concentration = 2.89 g/ml) with heparinized (20 U/ml) physiological saline in both sides. The mercury manometer (M) was used to measure the arterial blood pressure (BP) through a femoral arterial catheter that also connected to the other end of the U-type tube B. By adjusting the difference in height between the two columns of bromoform to a certain value through syringes SY1 and SY2, the perfusion pressure (PP = BP − IOP) was kept stable (about 30 mm Hg, which was suggested by Grehn et al as being within the critical range for keeping minimal functioning of retinal ganglion cells).[2] The perfusion pressure value was calculated from the difference in height between the two columns of bromoform and from the difference in density between bromoform and saline. The duration of IOP elevation was always kept to about 20 minutes.

RESULTS

Time Course of Responses During IOP Elevation

Figure 2 shows the time course of the response of an on-center X cell to a set of stimuli at a perfusion pres-

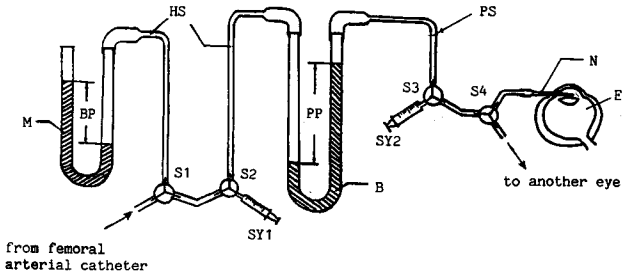

FIGURE 1. Diagram showing a system for elevating intraocular pressure and keeping constant perfusion pressure. B, bromoform; BP, arterial blood pressure; E, eye; HS, heparinized saline; M, mercury; N, syringe needle; PP, perfusion pressure; PS, physiological saline; S, three-way switch; SY, syringe.

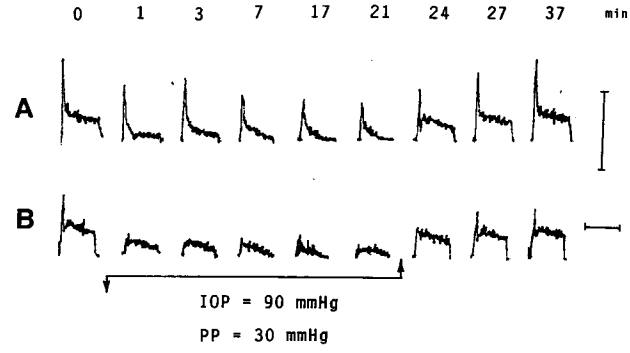

FIGURE 2. Response tracings of an on-center X ganglion cell before, during, and after IOP elevation (PP = 30 mm Hg). (A) On-center responses. (B) Off-surround responses. Scales: The vertical bar represents 75 impulses/sec; the horizontal bar represents 500 msec; the two arrows indicate the onset and offset of IOP elevation (IOP = 90 mm Hg, PP = 30 mm Hg).

sure of 30 mm Hg before, during, and after short-term IOP elevation (IOP = 90 mm Hg). The top row of traces (A) are the center responses to stimulus (1) and the bottom row of traces (B) are the surround responses to stimulus (2), respectively. For this cell, although all aspects of the responses to stimulus (1) and (2) decreased during IOP elevation, the peak of the surround responses (B) declined markedly, whereas the peak of the central responses (A) was less affected. After IOP elevation, the responses of both central and surround components gradually recovered. It is worth mentioning that the central responses were obviously more tolerant of IOP elevation than the surround responses. In a few cats tested, as soon as retinal perfusion pressure of 10 mm Hg was reached, the response of retinal ganglion cells ceased. This is consistent with previous reports.[2,5,12]

Difference Between X and Y Cells During IOP Elevation

The decay ratio of peak and mean firing rate responses of X cells and Y cells during short-term IOP elevation was compared for central response and for surround response. In general, Y cells were always more tolerant of IOP elevation than X cells. Figure 3 shows the histograms of decay ratios during IOP elevation in central peak responses of X and Y cells. The average decay ratio was 0.60 for 21 Y cells and 0.45 for 23 X cells. They were statistically different (Student's t-test, $P < 0.005$). The decay ratios of approximately 91% of X cells were below 0.60, whereas those of only 43% of Y cells were. The difference between X and Y cells was also significant when comparing the surround peak responses (t-test, $P < 0.025$). This difference in central responses between X and Y ganglion cells was also significant when mean firing rate was used as a response amplitude (t-test, $P < 0.005$).

Difference Between On-Center and Off-Center Cells During IOP Elevation

The decay ratio of peak and mean firing rate responses of on-center and off-center cells during short-term IOP elevation was compared either for the central response or for the surround response. In the overall population, off-center cells always exhibited higher tol-

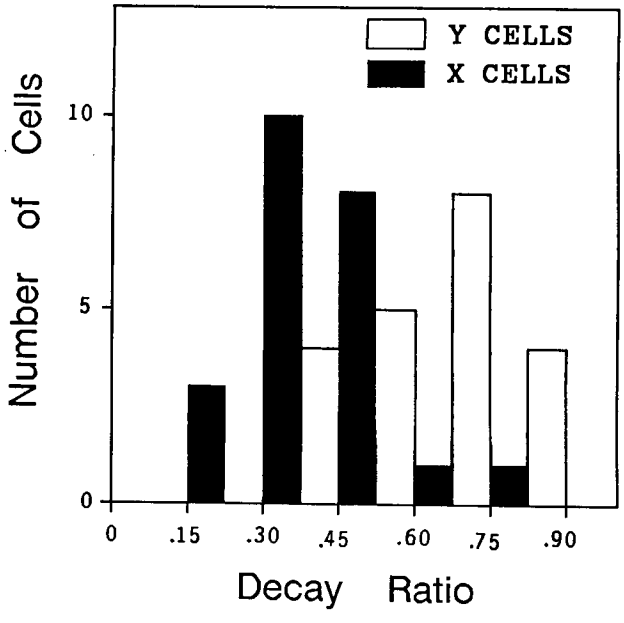

FIGURE 3. The distribution of decay ratios, defined as the response amplitude during IOP elevation divided by that before IOP elevation, of the X and Y retinal ganglion cells. The black columns represent data for X cells (N = 23) and the white columns represent Y cells (N = 21). Response amplitude was measured from the peak of post-stimulus time histograms collected from 50 bins with 10-msec bin width for 20 responses to the central stimuli.

erance of IOP elevation than on-center cells, no matter which response index was used. Figure 4 shows the histograms of decay ratios during IOP elevation in central peak responses of on-center and off-center cells. The average decay ratio was 0.62 for 14 off-center cells and 0.48 for 30 on-center cells. This difference was statistically significant (t-test, $P < 0.005$). More directly, 73% of on-center cells had decay ratios lower than 0.60, but 43% of off-center cells had decay ratios below 0.60. Thus, the effects of short-term IOP elevation on retinal ganglion cells were cell-type dependent. It should be noted that between on- and off-center cells, the difference in tolerance of IOP elevation for the surround peak responses was also significant (t-test, $P < 0.025$).

Comparison of Central and Surround Mechanisms of RF During IOP Elevation

Although both the central response and the surround response declined synchronously during short-term IOP elevation, their decay rates were different. In Figure 2, the surround peak response disappeared during IOP elevation, whereas the central peak response decreased slightly. Figure 5a shows the time courses of peak responses of central (asterisks) and surround (squares) mechanisms for an on-center X ganglion cell. The two curves are parallel to each other and are constantly separated. The decrease of the surround response was greater than that of the central response.

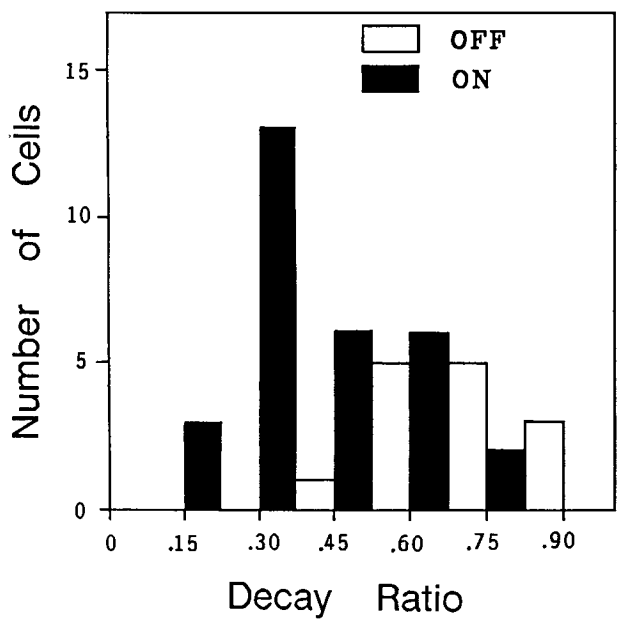

FIGURE 4. The distribution of decay ratios, which was defined as the response amplitude during IOP elevation divided by that before IOP elevation, of the on-center and off-center retinal ganglion cells. The black columns represent data from on-center cells (N = 30), and the white columns represent data from off-center cells (N = 14).

In many cases, the surround responses returned to normal levels earlier than did central responses, as shown in Figure 5a.

The average decay ratio for the central response (0.52) during IOP elevation was higher than that for the surround response (0.44) when using either the peak of the post-stimulus time histograms as response amplitude (t-test, $P < 0.05$) or the mean firing rate (t-test, $P < 0.005$). For clarification of this issue, we defined relative decay ratio as the ratio between the decay ratio of the surround response and the decay ratio of the central response. Figure 5b shows the histograms of relative decay ratio for peak responses of 44 cells. The mean relative decay ratio was 0.81 ± 0.32 (SD). Relative decay ratios of approximately 66% of the cells studied were <1 and only approximately 34% were >1, showing a clear difference (t-test, $P < 0.002$). This indicates that the central excitatory mechanism was more tolerant of IOP elevation than the surround excitatory mechanism, in contrast to the lower sensitivity of the RF periphery mechanisms to IOP elevation reported by Grehn et al.[2]

Comparison Between Peak and Mean Firing Rate During IOP Elevation

The average response amplitude of peak responses during IOP elevation was always higher than that of mean firing rate whether the central response or the surround response was studied. A typical time courses of peak (asterisks) and mean firing rate (squares) of the surround responses for an off-center Y cell is shown in Figure 6a. Figure 6b shows the histograms of relative decay ratios (equal to the ratios of the mean firing rate of responses divided by those of peak responses) for central responses of 44 cells. The mean relative decay ratio was 0.89 ± 0.25 (SD). The histograms clearly show that relative decay ratio of 75% of cells studied were <1, and it was >1 in only 25% of the cells. This indicates that the peak response was more tolerant of IOP elevation than the mean firing rate response (t-test, $P < 0.05$). However, this difference was even more pronounced when the surround response was used as an index (the mean relative decay ratio was 0.70 ± 0.26, t-test, $P < 0.002$).

DISCUSSION

This is the first study to compare the properties of different types of cat retinal ganglion cells and different components of the cell's receptive field responses during IOP. The results provide evidence that IOP elevation affects the properties of the cell's receptive field differently for X and Y cells, on-center and off-center cells, central mechanisms and surround mechanisms, as well as the peak and mean firing rate of the cell. The findings also support the idea that the isch-

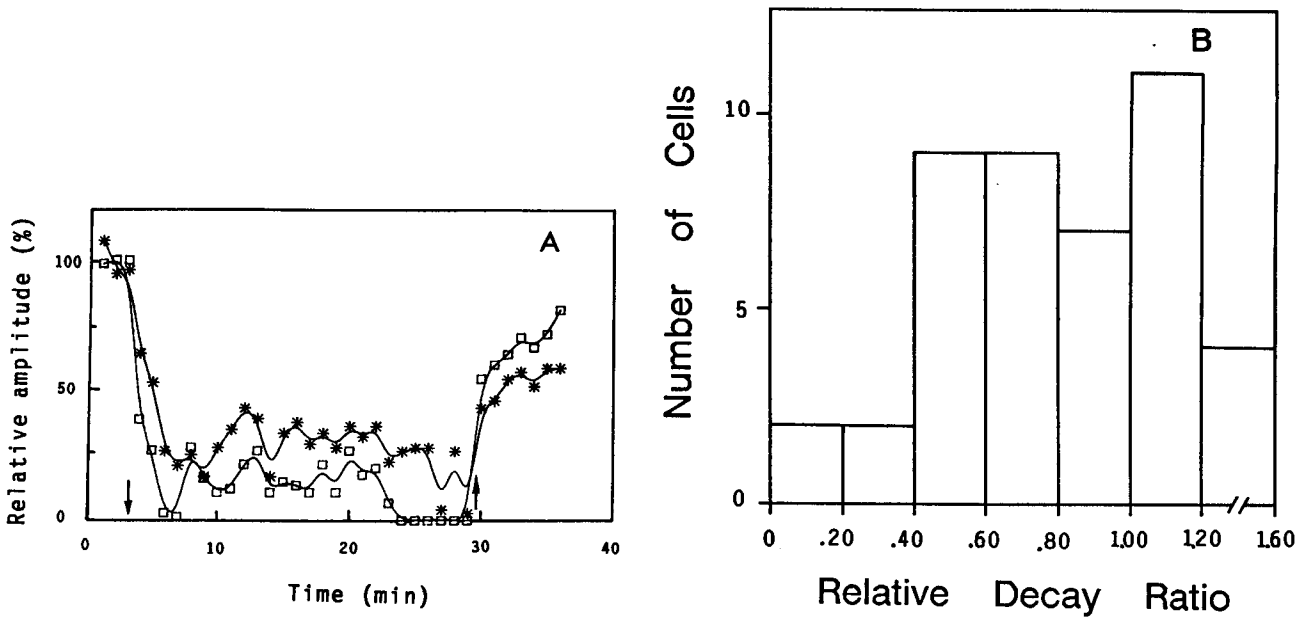

FIGURE 5. A comparison of the different tolerance of elevated IOP of central and surround responses of the receptive field of retinal ganglion cells. (**A**) The time course of central (asterisks) and surround (squares) peak responses of an on-center X cell before, during, and after IOP elevation (IOP = 90 mm Hg, PP = 30 mm Hg). The two arrows indicate the onset and offset of IOP elevation. (**B**) The distribution of relative decay ratios for the surround and central responses for 44 cells. A cell with a relative decay ratio <1 means that the decrease in its surround response is sharper than its central response during IOP elevation.

emia induced by the short-term IOP elevation, which leads to a decrease of retinal perfusion pressure, causes the reduction of ganglion cell responses.

As previously reported,[3] we also observed that Y cells are more tolerant of short-term IOP elevation than X cells in the cat retina, although different criteria (half decay IOP and response amplitude at constant IOP or perfusion pressure) and different periods of IOP elevations (1 to 2 minutes and 15 to 25 minutes) were employed. Similar differences between X and Y relay cells in the cat lateral geniculate nucleus have been reported when IOP was briefly elevated.[4] This suggests that the effects of the brief and the short-term IOP elevation on X and Y cells may be based upon a similar mechanism. The difference in tolerance to brief IOP elevation between X and Y cells in the retina may reflect the metabolic and anatomic differences. X and Y cells differ in cell body size, receptive field size, maintained discharge rate, and response pattern.[13,14] There is some evidence that Y cells may have more intracellular reserves of adenosine triphosphate, oxygen, and potassium than X cells at least during early ischemia induced by IOP elevation.[12,15–17] This may explain why Y cells are more tolerant than X cells of short-term, but not to chronic, ischemia; large-diameter fibers of retinal ganglion cells are often first affected in glaucoma.[18,19] Further investigation is needed to compare the behavior of X and Y cells during chronic IOP elevation, which more closely resembles glaucoma.

It is interesting that the on-center retinal ganglion cells were more sensitive to IOP elevation than off-center cells in the cat because these two types of ganglion cells have their bipolar–ganglion cell connections in different sublaminae in the inner plexiform layer. Kolb and colleagues showed that the ganglion cells with dendrites branching in sublaminae b (proximal) are of the on-center type, and those with dendrites branching in sublaminae a (distal) are of the off-center type.[20,21] According to Bartl (1978) and Shou et al (1985), the electroretinogram is less susceptible to the effects of an acute increase in IOP than the visual evoked potential, which depends on the functioning of the retinal ganglion cells.[22,23] Thus, the retinal depth-dependent effects of IOP elevation on on- and off-center cells may imply that the synaptic site between bipolar–ganglion cells is the place most sensitive to ischemia induced by IOP elevation, and that the pressure gradient in the retina at the critical level of perfusion pressure causes different degrees of local ischemia.

The finding that central responses of the RF of ganglion cells were less sensitive to the elevated IOP than the surround responses can be explained in this way. The central responses of ganglion cells mainly reflect the input from bipolar cells, and the surround

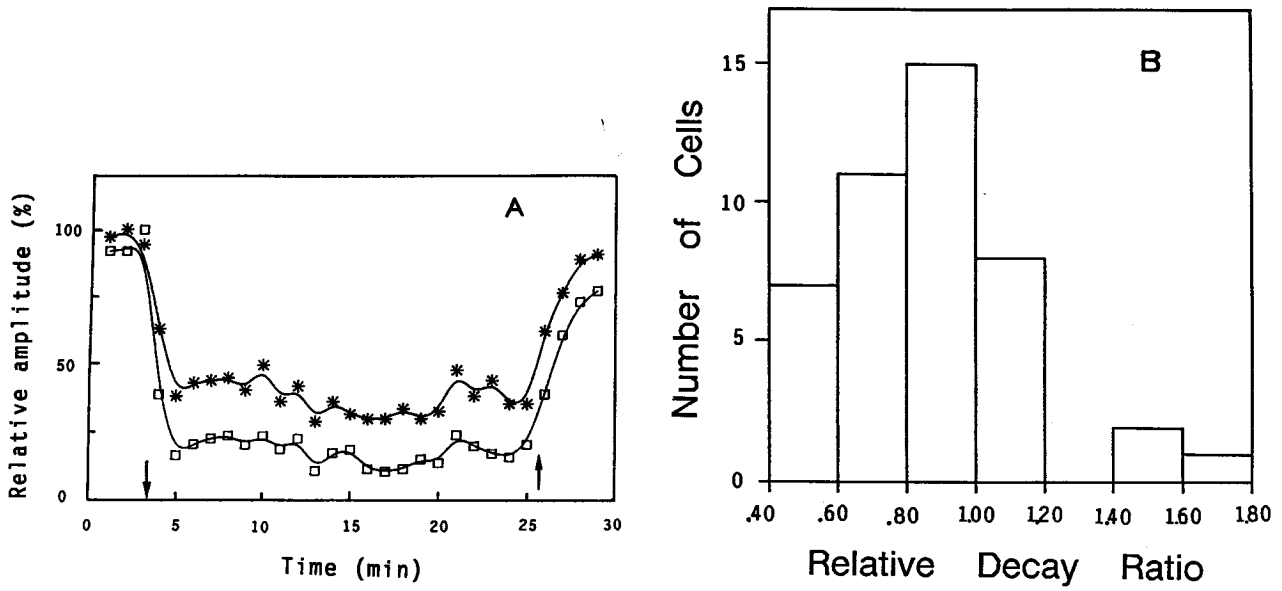

FIGURE 6. A comparison of the different tolerance to elevated IOP of the peak and mean firing rate of the retinal ganglion cells. (**A**) The time courses of the peak (asterisks) and mean firing rate (squares) surround responses of an off-central Y cell (IOP = 95 mm Hg, PP = 30 mm Hg). The two arrows indicate the onset and offset of IOP elevation. (**B**) The distribution of relative decay ratio histograms between the mean firing rate and peak responses of the receptive field center for 44 cells. A cell with a relative decay ratio <1 means that the decrease in its mean firing rate response is sharper than its peak response during IOP elevation.

responses reflect the laterally inhibitory input from horizontal cells through photoreceptor to bipolar cells and from amacrine cells.[24–27] Both pathways of the central and surround mechanisms of ganglion cells are affected by the elevated IOP, but the longer multiple synaptic pathway of the surround mechanisms should be more influenced.

Grehn et al reported that the RF-periphery mechanisms were less sensitive to center mechanisms.[2] They put a steady light annulus on the cell's surround of the receptive field and stimulated the center with a sinusoidally modulated light spot to test RF-periphery effects on the central responses. The stimuli they used were different from those we employed. Therefore, it is difficult to compare the results of the two studies. The difference in contrast sensitivity of the center and the surround responses of cat ganglion cells in the hypoxia experiments was not significant.[28] Perhaps lateral pathways, which have more synapses than center pathways, are more susceptible to ischemia, but not hypoxia, because real capillary perfusion and availability of oxygen cannot be linearly related to perfusion pressure.[29–31] In fact, in a recent study in which the phosphorescence image technique was used, both the optic nerve head and retinal oxygen tension were maintained as the IOP increased, and hypoxia developed only after the blood flow to the eye was stopped in the cat.[32]

The peak response reflects the fast component of the inputs to a retinal ganglion cell, whereas the response of the mean firing rate reflects the overall components of inputs, including both fast and slow components. Compared with the others, the fast component may employ shorter pathways with less synapses. This could cause the peak component to exhibit high tolerance of elevated IOP. Therefore, the early and short peak of a post-stimulus time histogram should reasonably be more tolerant than the late and long plateau, which is approximately proportional to the mean firing rate, in the duration of each response.

In conclusion, the results presented here suggest that the different effects of short-term IOP elevation on different types (X and Y, on-center and off-center) of retinal ganglion cells and different mechanisms or components of the receptive field properties may reflect the different degrees of ischemic effects on the retinal pathways that project to ganglion cells.

Key Words

receptive field, intraocular pressure elevation, perfusion pressure, retinal ganglion cell, cat

Acknowledgments

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