Effect of target position and size on adaptive sensitivity of the surround mechanism of cat retinal ganglion cells[1]

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Summary. The spatial distribution of the surround's adaptive sensitivity was assessed in the receptive fields of cat retinal ganglion cells. The results provide evidence that the surrounds adaptive sensitivity is higher in the center of the receptive field of Y-cells than X-cells.

Information about the visual environment is processed by photoreceptors and retinal interneurons and transmitted to the brain via the axons of retinal ganglion cells. The receptive fields of most ganglion cells in the cat retina are concentrically organized with central and peripheral regions that are mutually antagonistic[3]. The photoreceptors and the interneurons that are involved in the generation of ganglion cell responses from these two regions are referred to as the center mechanism and surround mechanism[4-6]. The ganglion cells discharge to the photic stimulus is, therefore, a measure of the relative strength of the signals from the center and surround mechanisms. The magnitude of the signal from each response mechanism is dependent upon the spatial contribution of sensitivity within the mechanism, the luminance, duration, and spatial arrangements of the photic stimulus, and the adaptation state of the mechanism. It is the latter variable that the present study was designed to assess. More specifically, the experiments to be described sought to determine the spatial distribution of the surround's adaptation mechanism.

Single cell recordings were made from 47 optic tract fibers in lightly anesthetized adult cats. The animals initially were anesthetized with an i.p. injection of sodium pentobarbital (nembutal, 35 mg/kg). The animals remained anesthetized by continuously infusing urethane (40 mg/kg/h). The surgical procedures and recording methods were standard and have been described elsewhere.

The spatial properties of the surround's adaptation mechanism were assessed with 2 types of adapting stimuli: 1. concentric annuli with variable inside and outside diameters but of equal area; 2. concentric annuli with variable inside diameter and constant outside diameter.

The adapting annuli always were unmodulated in time. They were presented with an unmodulated spot in the center of the receptive field. The purpose of this stumulus was to desensitize the center response mechanism. A 3rd stimulus was presented with the steady adapting annulus and the steady adapting spot. This stimulus was an annulus that was modulated in time.

Figure 1 shows the effect of variations in the diameter of equal-area annuli upon adaptive sensitivity. In this experiment a spot, whose total area was the same as that of the adapting annuli, was used as an adapting stimulus when the middle of the receptive field was studied. Adaptive sensitivity was measured in the following manner. After mapping the receptive field, the cell was classified as type X or type Y by a contrast reversal stimulus[7,8]. Next, the surround mechanism was isolated using the method described by Bishop and Rodieck[9]. With this method, the luminance and/or size of a steady spot in the center of the receptive field is varied until a 'pure' surround response is produced by a modulated annulus in the receptive field periphery. A pure response is defined here as one whose time course remained invariant over a 0.9 log unit range, beginning at threshold luminance. The purpose of this procedure is to minimize the contribution of signals from the center mechanism. Once the surround was isolated, the luminance of the modulated annulus was varied until the

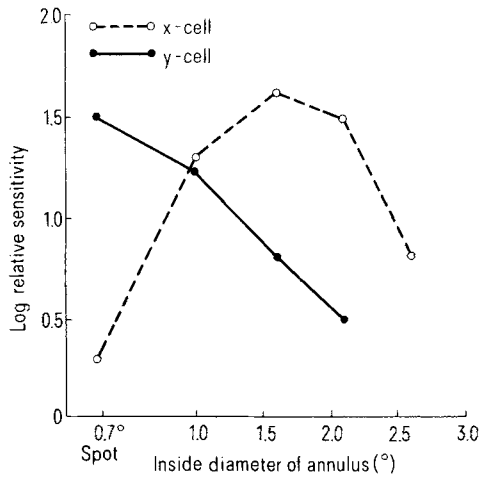

Figure 1. Adaptive sensitivity profiles determined with equal area annuli (and 0.7° spot for the center of the receptive field). Stimuli: (1) X-cell, luminance of 0.2° central adapting spot 20 candles/m^2; luminance of 2.0°×3.0° modulated annulus 2.1×10^{-3} candles/m^2; background luminance 3.6×10^{-4} candles/m^2 (2) Y-cell, 0.8° central adapting spot luminance 14 candles/m^2; luminance of 3.0°×4.0° modulated annulus; 2.7×10^{-2} candles/m^2; background luminance 3.6×10^{-4} candles/m^2. The modulated annulus had a duration of 500 msec at 0.3 Hz.

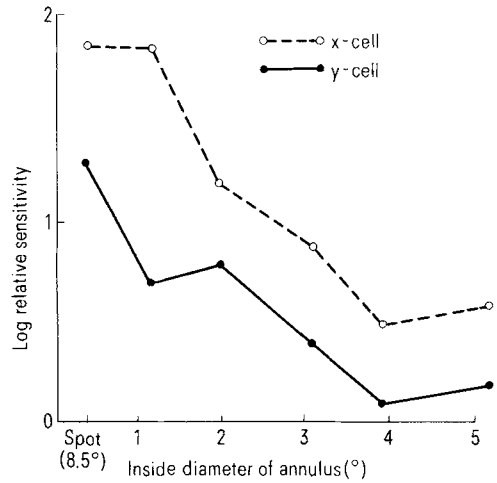

Figure 2. Area-adaptation curves for X-cell and Y-cell. Outside diameter of all adapting annuli was 8.5° with variable inside diameter. Stimuli: (1) X-cell, luminance of 0.4° central adapting spot, 22 candles/m^2; luminance of 3.5°×4.5° modulated annulus, 3.8×10^{-3} candles/m^2; (2) Y-cell, luminance of 1.0° central adapting spot, 2.0 candles/m^2; lumance of 2.0°×3.5° modulated annulus, 1.8×10^{-2} candles/m^2; background luminance, 3.6×10^{-4} candles/m^2. The modulated annulus had a duration of 500 msec, at 0.3 Hz.

cell yielded a threshold surround response. This was determined by listening to an audio monitor and viewing an oscilloscope that displayed responses summed by the computer. Next the luminance of the modulated annulus was increased by 0.7 log units. Then an unmodulated adapting annulus was placed in the receptive field and its luminance was varied until a threshold response was obtained from the modulated annulus, i.e., the surround was adapted by 0.7 log units. This procedure was repeated for the other adapting stimuli. With this method adaptive sensitivity is defined as the reciprocal of the adapting luminance (expressed in log units) required to produce a threshold response.

The curves shown in figure 1 are representative of the 10 X-cells and 10 Y-cells tested in this experiment. X-cells usually had their highest adaptive sensitivity outside of the receptive field center, and Y-cells usually had peak sensitivity in the middle of the receptive field. This finding was confirmed in an experiment in which adapting target size was varied. All of the adapting stimuli in this experiment had an outside diameter of 8.5° and variable inside diameter. Adaptive sensitivity was measured in the same manner described for the 1st experiment. Data were obtained for 13 X-cells and 14 Y-cells in the experiment. Most of the area-adaptive sensitivity curves for these cells were similar to those shown in figure 2. The major finding to be gleaned from figure 2 is the difference between X- and Y-cell adaptive sensitivity changes when adapting flux is placed in the center of the receptive field. X-cells, in general, are affected minimally, whereas Y-cells show an abrupt change in sensitivity. In figure 2, compare sensitivities to a 8.5° adapting spot and a $0.7° \times 8.5°$ adapting annulus.

The results of the 2 experiments presented here provide evidence that the surround's adaptation mechanism has a stronger representation in the center of the receptive field of Y-cells than in X-cells. The spatial distribution of the surround's signal sensitivity profile has not been determined for cat retinal ganglion cells because of the difficulty in separating center and surround signals in the central portion of the receptive field. Based on indirect evidence, however, it was suggested by Hickey, Winters and Pollack[10] and Hammond[11] that signal sensitivity was greater in the receptive field center of Y-cells than X-cells. In the rhesus monkey, signals from the surround mechanism can be separated from signals from the center mechanism by using chromatic stimuli. De Monasterio[12] assessed the spatial distribution of surround signal sensitivity in the rhesus monkey and reports that the sensitivity profile of Y-cells is unimodally distributed with peak sensitivity in the center of the receptive field. The profile for X-cells was found to be distributed bimodally with low sensitivity in the receptive field center. The results of the present study are consistent with De Monasterio's signal sensitivity data.

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Mo-V interactions during N_2- and NO_3^--metabolism in a N_2-fixing blue-green alga *Nostoc muscorum*[1]

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Summary. Molybdenum (Mo), a group 6B element (applied in the form of sodium molybdate at a concentration of 0.0177 ppm), is required for N_2- and NO_3^--mediated growth of *Nostoc muscorum*. The amount of growth of such Mo-containing culutures is significantly enhanced by the addition of 0.0125 ppm vanadium (V), an element belonging to group 5 of the periodic table (applied in the form of sodium vanadate). At concentrations above 0.0125 ppm V proves growth-inhibitory to *N. muscorum* cultured with or without Mo. Mo and/or V exert(s) no apparent stimulatory/inhibitory effect on NO_3^--mediated growth of the organism.

Mo is known to be an integral part of the nitrogenase and nitrate reductase enzyme systems responsible for N_2 fixation and NO_3^- reduction in microorganisms, including blue-green algae[3-5]. Until recently, the concept of a Mo-containing polypeptide co-factor common to different molybdoenzymes including nitrogenase and nitrate reductase has had considerable support from genetic[4,6-8] and biochemical[9,10] studies. It has, however, recently been shown in a free-living N_2-fixing bacterium *Azotobacter vinelandii* that the Mo-containing co-factor is exclusively involved in nitrate reductase activity[11], and that an iron-molybdenum (Fe-Mo)-containing co-factor is responsible for nitrogenase function[12-14]. Genetic studies by my group on the simultaneous functional replacement of Mo by its structural analogues tungsten (W)[15] or chromium (Cr)[16] for both N_2 and NO_3^- metabolism in *Nostoc muscorum* strongly supported the suggestion that the Mo-containing co-factor is the precursor of a Fe-mo-containing co-factor in the N_2-fixing and NO_3^--reducing organisms[17]. During the present investigation I examined in the same organism *(N. muscorum)* whether vanadium (V) can function in place of Mo to any extent for N_2 fixation and/or NO_3^- reduction. The results show that while V fails to replace Mo functionally, like W or Cr[15,16], it stimulates the normal growth of the