known representativeness, data are presented excluding them as well as including them. For the latter case see the table. For the case where they are excluded, the 2nd column of the table should be changed so that the proportion of contemporary South-Americans with 'neolithic' face representation is 40 out of 181 (22.1%) instead of 61 out of 219 (27.9%). The test for heterogeneity in the case excluding the 2 Indian tribes above yielded $\chi^2 = 418.8$, df = 3, $p \ll 0.01$, and the test for linear trend of proportions[29] yielded $\chi^2 = 385.2$, df = 1, $p \ll 0.01$. The proportion of heterogeneity explained by the linear trend is 385.2/418.8, or 92%. Thus, similar conclusions emerge from both sets of samples; most of the variability in 'neolithic' representation proportions is associated with a linear trend in relation to literacy rates.

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Spatial distribution of signal and adaptive sensitivity in the receptive field surrounds of cat retinal ganglion cells[1]

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Summary. A comparison was made between adaptive and signal sensitivity profiles of the surround response mechanism of cat retinal ganglion cells. The 2 profiles were found to be similar for X cells but the surrounds of Y cells appear to pool adaptation over a smaller retinal region than they pool signals.

Most receptive fields of cat retinal ganglion cells have a concentric organization with central and peripheral zones that are mutually antagonistic[3]. The response of the cell is thought to be controlled by two spatial overlapping response mechanisms; one that predominates in the middle of the receptive field, the center response mechanism, and one that predominates in the periphery of the receptive field, the surround response mechanism[4-6]. A response mechanism is an aggregate of photoreceptors and interneurons.

The magnitude of the signal that the ganglion cell receives from a response mechanism is dependent upon the mechanism's adaptation state. Rushton[7] posited that the effects from field adapting stimuli are physiologically pooled within the retina. The neural substrate, the adaptation pool, serves to reduce sensitivity in regions of the visual field that are not directly stimulated by adapting flux.

There is evidence that both the center[8-10] and surround[11] response mechanisms of cat retinal ganglion cells physiologically pool the desensitizing effects produced by steady illumination of their receptive fields. Moreover, for the center mechanism, the adaptive pooling area, i.e., the retinal region over which adaptation is pooled, is the same size as the region over which signals are pooled - the signal pooling area[8-10]. It has also been demonstrated that the spatial distribution of adaptive and signal sensitivity are similar for the center response mechanism[10].

The present study was undertaken to assess the spatial relation between the adaptive and signal summing areas of the surround response mechanism of cat retinal ganglion cells. Also, it was our intention to compare the spatial distribution of adaptive and signal sensitivity within these regions.

There are 2 major types of cat retinal ganglion cells: X cells and Y cells[12]. It was suggested by Cleland et al.[13] that X cells are concerned primarily with the processing of spatial information and Y cells may constitute an early stage in the

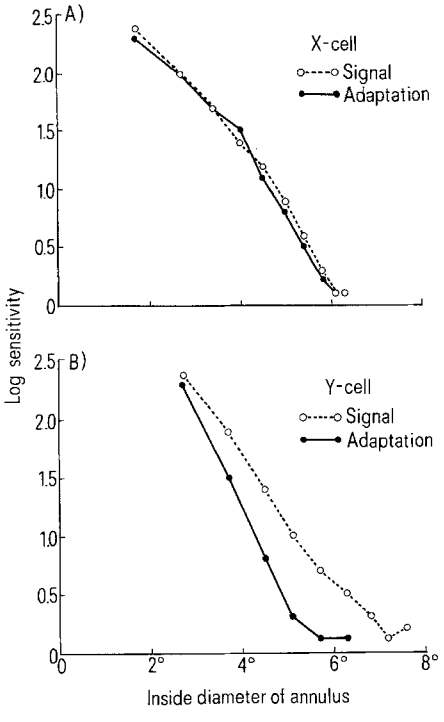

Figure 1. Signal and adaptive sensitivity profiles. Stimuli: *A* X cell, luminance of 0.2° central adapting spot, 22 candles/m^2; luminance of $3.0 \times 3.7°$ modulated annulus for adaptation study, 7.3×10^{-2} candles/m^2; background luminance, 9.7×10^{-3} candles/m^2; *B* Y cell, 0.8° central adapting spot luminance, 1.6 candles/m^2; luminance of $3.0° \times 3.7°$ modulated annulus for adaptation study, 1.7×10^{-3} candles/m^2; background luminance, 3.6×10^{-4} candles/m^2; all modulated stimuli had duration of 500 msec, at 0.3 Hz.

development of a cell sensitive to movement. Another purpose of the present study, therefore, was to assess differences in the manner in which X and Y cells process spatial and/or adaptive information.

Single cell recordings were made from 50 optic tract fibers in adult cats. The femoral vein was used to infuse continuously a mixture of urethane (40 mg/kg/h), Flaxedil (40 mg/h), Ringers with lactate (3.0 m/h), and atropine sulfate (0.05 m/h). Corneal contact lenses with 3.8 mm artificial pupils were fitted and retinoscopy performed. The cats faced a tangent screen located 120 cm in front of the head. Body temperature was maintained at 38 °C and Pco_2 held at 4–5%. EEG, EKG and femoral arterial blood pressure were continuously monitored during the experiments. Cells were classified as type X or Y by an 8.0° bipartite contrast reversal stimulus[12,14].

After mapping a cell's receptive field and classifying it, the cell's surround mechanism was isolated using the method described by Bishop and Rodieck[15]. Next, the adaptive sensitivity profile was determined. The targets were annuli with variable inside and outside diameters but whose total area remained constant. Signal sensitivity profiles were determined by adjusting the luminance of each (temporally) modulated annulus so as to produce a weak suprathreshold surround response (peak firing rate between 20 and 70 spikes/sec) of constant time course and strength. Henceforth this response will be referred to as the criterion response. The signal sensitivity profile is thereby defined as the function relating the diameter of the annulus and the log of the reciprocal of the luminance required to produce the criterion response.

The adaptive sensitivity profile was measured in the following manner. First, the criterion response was produced by a modulated annulus in the receptive field surround; its luminance was then increased by 0.7 log units. Next, an unmodulated field adapting annulus was positioned in the receptive field surround and its luminance adjusted until the criterion response was produced. This procedure was repeated for other field adapting annuli to measure the adaptive sensitivity profile. The adapting annuli were the same targets used in the signal sensitivity study. The adaptive sensitivity profile, then, is defined by the relation between annulus position (diameter) and the log of the reciprocal of the luminance required to produce the criterion response.

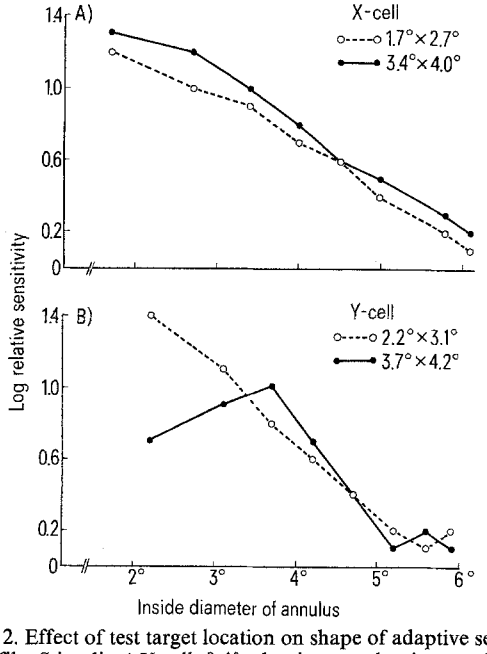

Figure 2. Effect of test target location on shape of adaptive sensitivity profile. Stimuli: *A* X cell, 0.4° adapting spot luminance, 94 candles/m^2; background luminance, 9.17×10^{-3} candles/m^2; both modulated test annuli had the same area. *B* Y cell, 1.0° adapting spot luminance, 65 candles/m^2; background luminance, 9.17×10^{-3} candles/m^2; both modulated annuli had the same area. Modulated annuli for X and Y cell had 500 msec duration, at 0.3 Hz.

Figure 1 shows typical X and Y cell sensitivity profiles. Two of the 17 X cells tested gave results that are similar to those of the X cells in figure 1A. Both the slope and spatial extent of the two profiles were found to be very similar. The Y-cell data were more variable. 7 of the 16 Y cells tested had signal and adaptive sensitivity profiles that were difficult to distinguish. 9 Y cells tested gave results that indicate that the surrounds of these cells pool adaptive information over a smaller retinal region than they pool signals. Data from a representative cell in this group are given in figure 1B. For cells like those in figure 1B the slope of the adaptive sensitivity profile was found to be steeper and the profile did not extend as far into the periphery of the receptive field as the signal profile.

A 2nd experiment was conducted to assess the spatial relation between the surround's adaptive and signal pooling areas. If the surround pools adaptive information over a smaller region than it pools signals, the shape of the adaptive sensitivity profile should be dependent upon the location of the test target. Figure 2 shows typical results from this experiment. 8 of the 9 X cells tested in this experiment gave results that were similar to those of the X cell in figure 2A: for these cells the location of the test target did not affect the shape of the adaptive sensitivity profile. 7 of the 12 Y cells tested, however, gave evidence that the signal pooling area is larger than the adaptive pooling area (fig. 2B).

It is important to point out that the signal and adaptive sensitivity profiles were very similar for many of the cells for which test target position had a significant effect. These results may be interpreted to indicate that there are adaption subunits within a more global physiological pool, an inference drawn by Harding[10] for the center mechanism. It is reasonable to speculate that there is more than 1 stage of adaptation within the retinal circuitry. For example, the photoreceptors themselves may have an adaptation mechanism and there may be an adaptation mechanism within one or more synaptic layers in the retina.

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