On the contrary, the cyclic differences may be exactly related to the motility of the animals which have been previously described, as similar evolutions, in our laboratory with the same strain[12]. This observation may support the assumption of Evans[13] that octopamine may play a similar role as compared to its catechol analogue noradrenaline in the vertebrate nervous system. But, except at the ecdysis, a great difference appears between gregarious and both solitary groups where octopamine contents are always at the highest level. Since gregarious animals are much more active than solitaries[12] and show the smallest values of octopamine, it becomes contradictory to claim that motility is directly related to the contents of octopamine. It leads us to consider that the genuine situation must be related to the pool of amines, particularly dopamine[3] and thus gives rise to the problem of the differentiation of the specific receptors in both types of animals, gregarious and solitary. In fact, we recently showed that specific receptors exist for octopamine in the locust brain[14]. So the phase differentiation may correspond to a differential organization of receptors during the ontogenesis since octopamine is now well-recognized as a neurotransmitter[15-18].

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Effect of adapting target size on the gain of the surround response mechanism in X- and Y-cells in cat retina

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Summary. The adaptation field of the surround mechanism of X and Y retinal ganglion cells in the cat was assessed with variable size, unmodulated adapting spots. Both an on-inhibition measure and an off-discharge measure of surround gain was used. Results suggest that the surround mechanism in Y-cells is strongest in the receptive field middle but weak or nonexistent in the middle of X-cell receptive fields.

The activity of cat retinal ganglion cells is thought to be controlled by 2 processes which overlap spatially[2]. These processes are referred to as the center and surround response mechanisms and initially it was believed that each mechanism could be described by a Gaussian curve which peaked in the middle of the receptive field. Studies over the past 13 years indicate that retinal ganglion cells can be divided into at least 2 subgroups based on their responses to a number of different stimuli[3-11], and are most commonly reffered to as Y- and Y-cells[3]. Recent investigators[12,13] have suggested a difference in the spatial distribution of the surround mechanism in X- and Y-cells; they postulate that the surround mechanism is most sensitive in the middle of the receptive field of Y-cells but weak or nonexistent in the middle of X-cell receptive fields.

One way to assess the spatial distribution of the surround mechanism is to determine the mechanism's adaptation receptive field. This method assumes that the adaptation receptive field for the surround mechanism corresponds to its signal receptive field. Several studies have shown this to be the case for the center mechanism[7,14,15]. In the experiments to be described here we assessed the adaptation field of the surround of X- and Y-cells with variable size, unmodulated adapting spots.

Material and methods. Lacquer coated tungsten microelectrodes were used to record the action potentials of 41 on-center optic tract fibres from lightly anesthetized (Nembutal) adult cats. Details of the animal preparation, recording system and optical system are described elsewhere[16]. A contrast reversal stimulus[3,17] was used to classify the cells as X or Y: this stimulus consisted of a bipartite spot (3.0°) centered in the receptive field. The light and dark hemifield was reversed (0.5 Hz) by cross polarizing filters. At the null position the response of X-cells to the light and dark reversal of the target was unmodulated. Y-cells, however, responded with 'on transients' at each reversal of the hemifield. All flashing stimuli in the study were rectangular in time with a duration of 500 msec and frequency of 0.3 Hz and were superimposed upon a steady background of 3.1 candles/m^2. Receptive field centers were typically 0.7-1.2° for X-cells and 1.5-2.0° for Y-cells.

2 experiments were conducted. In the first experiment the effect of variable size adapting spots (the luminance of which was adjusted to keep the gain of the center mechanism constant) upon the gain (defined as the ratio of response magnitude to stimulus magnitude) of the surround mechanism was measured. The gain of the surround mechanism was assessed by measuring the ability of a flashing annulus (4.0° × 10.5°) in the periphery of the receptive field to suppress an excitatory response generated by a flashing center spot placed in the middle of the receptive field. In the second experiment variable size, equal flux (i.e. luminance x-area was held constant) spots were used as the adapting targets. The measure of surround gain was the off-discharge produced by a flashing annulus (4.0° × 10.5°) placed in the receptive field periphery.

Results and discussion. Results from a typical X- and Y-cell in the first experiment are shown in figure 1. On the abscissa is plotted adapting spot size and on the ordinate is percent inhibition. Percent inhibition is defined as the ratio of the reduction in response strength (peak firing rate) resulting from the simultaneous presentation of center flashing spot in the receptive field center plus flashing annulus in the receptive field periphery, to the response to the center spot alone, times 100. As the size of the adapting spot was increased its luminance was adjusted to maintain a constant response to the center flashing spot alone. This assured that the gain of the center mechanism remained unchanged and the effect of the flashing peripheral annulus was always measured against a constant excitatory signal coming from the center of the receptive field.

As can be seen in figure 1 adapting spots restricted to the middle of the receptive field had little effect on the gain of the surround mechanism in both X- and Y-cells. The results were different for both cell types, however, for adapting spots larger than 1.0° in diameter. Larger spots resulted in a decrease in the gain of the surround mechanism in X-cells, as is evidenced by the decrease in percent inhibition, and an increase in the gain of the surround mechanism in Y-cells. Since the gain of the surround mechanism of X-cells showed no change for small spots but a substantial decrease to large spots its adaptation receptive field appears to have a weak representation in the receptive field center and strong representation in the receptive field periphery[12,13]. Y-cells generally have larger centers than X-cells[3,5,7] so the luminance of the adapting spot had to be decreased as spot size increased. Thus, there was a decrease in the adapting flux in the middle of the receptive field as spot size increased. If the surround mechanism of a Y-cell has a strong representation in the middle of the receptive field[12] then the larger adapting spots should have produced a relative increase in the gain of the surround mechanism. As shown in figure 1 this was found to be the case.

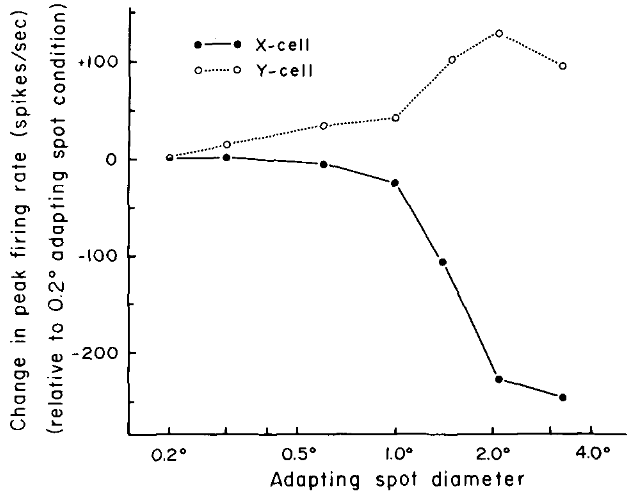

Fig. 1. Change in percent reduction of a constant response to a flashing spot in the receptive field middle by a simultaneously flashing annulus as the size of central steady adapting spots increased. (The luminance of the steady adapting spots was appropriately adjusted to keep the center response constant.) X-cell, center flashing spot: 0.71° diameter 5.07 cd/m^2; 0.3 Hz. Flashing annulus: 4.0°× 10.5°; 0.68 cd/m^2; 0.3 Hz. Central steady adapting spots: 0.68-51.92 cd/m^2. Y-cell, center flashing spot: 1.43° diameter; 2.79 cd/m^2; 0.3 Hz. Flashing annulus: 4.0°× 10.5°; 1.04 cd/m^2; 0.3 Hz. Central steady adapting spots: 5.56-98.92 cd/m^2. Background illumination: 0.19 cd/m^2.

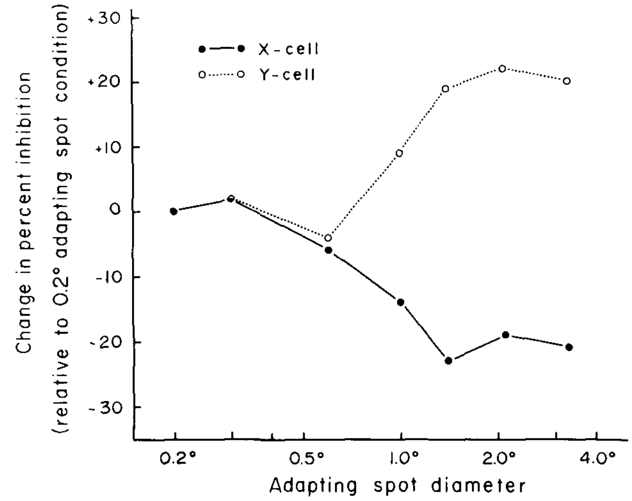

Fig. 2. Change in strength of the off-discharge to a flashing peripheral annulus as the size of central steady equal-flux adapting spots increased. X-cell, flashing annulus: 4.0°× 10.5°; 1.72 cd/m^2; 0.3 Hz. Central steady adapting spots: 0.84-98.92 cd/m^2. Y-cell, flashing annulus: 4.0°× 10.5°; 1.46 cd/m^2; 0.3 Hz. Central steady adapting spots: 0.84-98-92 cd/m^2. Background illumination: 0.19 cd/m^2.

In the second experiment a different measure of surround mechanism strength was used, the magnitude of the off-discharge produced by a flashing annulus placed in the receptive field periphery. The results for a typical X- and Y-cell in this experiment are shown in figure 2. Adapting spot size is plotted on the abscissa and the strength of the off-discharge (peak firing rate expressed in spikes/sec) is scaled on the ordinate. The results of this experiment in which off-discharge is used as the measure of surround gain are similar to the results from the first experiment, in which an on-inhibition measure was used. Adapting spots confined to the middle 1.0° of the receptive field had very little effect on the strength of the off-discharge in both X- and Y-cells. Adapting spots larger than 1.0° had opposite effects on the 2 cell types. The gain of the surround mechanism, as indicated by the strength of the off-discharge, showed a decrease for larger adapting spots for X-cells and an increase for Y-cells.

If the signal profile and the adaptation profile of the surround mechanism are similar then the results of these 2 experiments are consistent with the receptive field models for X- and Y-cells of Hickey, Winters and Pollack (1973) and Hammond (1975). They suggest that the surround mechanism in Y-cells is unimodal with peak sensitivity in the middle of the receptive field whereas in X-cells the surround mechanism is bimodally distributed and is weak or nonexistent in the receptive field middle.

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