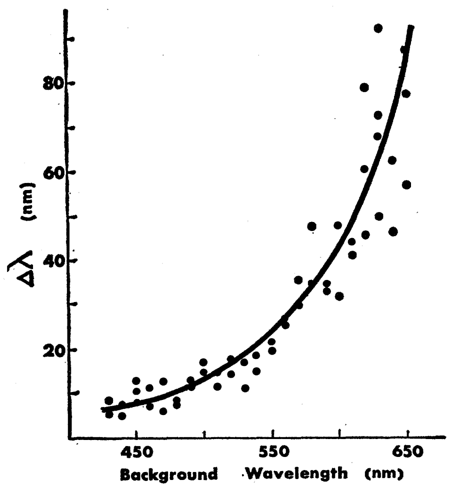

Fig. 2. Wavelength interval ($\Delta\lambda$) between those test-object wavelengths (above and below the background wavelength) which give a visual acuity of 1.0 min^{-1}. Line: least squares fit to log $\Delta\lambda$ plotted against background wavelength. Data points: session means for observer CC. Data from AS were similar, but showed a slightly narrower $\Delta\lambda$ interval at all wavelengths.

termined for a few wavelength pairs by the method of constant stimuli, in which the gratings were exposed for 0.5 second. The resulting acuity plotted against wavelength of the test object was almost identical to the same function determined by the method of adjustment. However, visual acuity was uniformly 0.2 min^{-1} higher when measured with the method of constant stimuli, which we attribute to the fact that a conventional 50 percent frequency-of-seeing threshold was used with the constant stimuli, whereas when the method of adjustment was used the grating had to be seen on each trial.

The effect of wavelength separation on acuity is not constant across the visible spectrum. Good acuity is attained with a small wavelength separation when both test object and background are illuminated with short wavelengths (Fig. 1*a*) while a wide wavelength separation is required to obtain the same acuity when adjacent bars are illuminated with long wavelengths (Fig. 1*c*). In order to describe the dependence of acuity on wavelength separation in a different part of the spectrum, the following measure was taken: functions similar to those in Fig. 1 were obtained by using backgrounds at 10-nm steps between 430 nm and 650 nm. The widths of these functions were measured at the point at which they cross an arbitrary criterion of 1.0 min^{-1} ($\Delta\lambda$ in Fig. 1*b*) and were plotted as a function of the background wavelength (Fig. 2). Contrary to our prior expectation this function does not closely resemble the normal wavelength discrimination function (*4*), particularly in that it does not rise in the short wavelength region. Log $\Delta\lambda$ increases linearly with background wavelength (mean product-moment correlation of 0.96) but we do not assign any physical meaning to this fact at present.

Even if the brightness of the test object and background are matched in the external stimulus, brightness gradients will exist on the retina as a result of diffraction caused by the system exit pupil. We do not believe that these retinal brightness gradients are the effective cues for discrimination in this situation, however. The $\Delta\lambda$ function (Fig. 2) rises more sharply than one would predict from a diffraction explanation. Also, retinal brightness contrast produced by diffraction will generally be less when the test object and background are equally bright than when either is black. If acuity were mediated by brightness contrast alone, it should be improved by increasing contrast. However, occluding one set of bars completely does not improve acuity once good acuity has been obtained by means of wavelength separation between test object and background. We therefore believe that good acuity is possible without significant brightness contrast on the retina.

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Specialized Receptive Fields of the Cat's Retina

Abstract. *Three new types of receptive field have been found in the cat's retina. The responses of these fields to flashing lights and moving objects suggest that the manner in which they code visual information may be quite different from that of the center-surround fields described in previous studies. These "specialized" fields were all found in the area centralis. A definite functional difference, corresponding to the known anatomical difference, between this region and the rest of the retina, is suggested.*

Since Kuffler (*1*) first described the concentric center-surround organization of the receptive fields of ganglion cells of the cat's retina, subsequent studies of these fields (*2–4*) have revealed only this form of organization, with one exception noted by Rodieck and Stone (*5*). However, Stone (*6*) has shown that the cells in the area centralis are much smaller than those in the peripheral retina, which raises the question whether the receptive fields of cells in this area also have the concentric center-surround arrangement. We have now made special effort to examine the receptive fields of units in the area centralis, recorded using varnished tungsten microelectrodes. The receptive fields were plotted on tangent screens placed at distances up to 5 m from the cat's eye. The location of these units in the area centralis (defined as the area of retina in which ganglion cell density exceeds 3000 cells per square millimeter) was checked histologically on whole mounts of the retina (*4*). The other techniques used were identical with those described by Rodieck and Stone (*4, 5*) except that, for some animals, decerebration was replaced by nitrous oxide anesthesia (70 percent N_2O_2 and 30 percent O_2) (*7*) and paralysis of the extraocular muscles and immobilization of the eyes were maintained by a continuous infusion of Flaxedil and Curare (*7*) (12.5 and 2.5 mg/hr, respectively).

It proved very difficult to isolate

single units in the area centralis, despite the high density of ganglion cells in this region. In the course of 35 experiments hundreds of electrode tracks were made in the area centralis, but we were able to examine the receptive fields of only 50 units. Among these 50 fields we noted 16 whose organization was quite different from the center-surround type, and which we have therefore termed "specialized." These specialized fields were classifiable into three types: C-type ("C" for center), diffuse, and On-Off receptive fields. One common feature of these types was the low rate of their maintained activity, which in most cases was less than five spikes per second for the range of ambient illumination used. Maximum illumination, provided by a tungsten filament lamp, produced screen luminance of 5 candela/m^2 on a screen

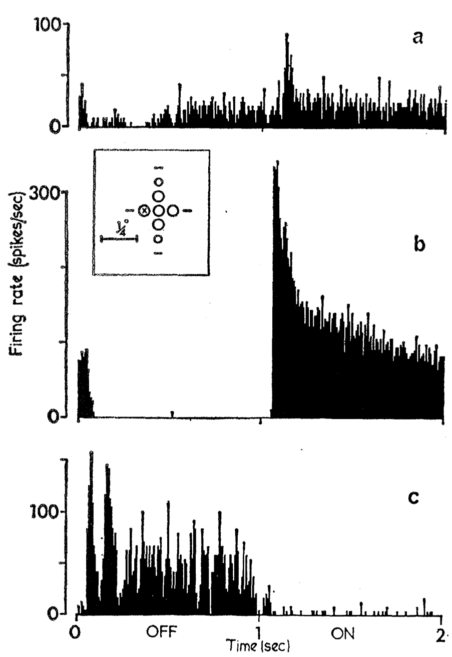

Fig. 1. (*a*) Averaged response histogram of the firing of a unit with an On-center, C-type receptive field in response to an ambient light flashing on and off. (*b*) Response of the same unit to a 15-min diameter spot of light flashing on and off in its receptive field. The inset at the top is a plot of the field, obtained using a spot 4 min in diameter. The circles indicate positions at which On responses were obtained, the size of the circles indicating the approximate strength of the response. The dashes indicate positions at which the stimulus spot elicited no response. The X marks the spot at which the histogram was obtained. The scale represents 15 min. (*c*) Averaged response histogram of the firing of a unit with a diffuse receptive field to a 2½-deg spot of light flashing off for 1 second and on for 1 second within the center of its field.

0.5 m from the eye. Minimum illumination was darkness. The possibility that these fields were actually center-surround fields distorted by poor optics seems excluded by two factors. First, care was always taken to bring the eye into focus on the tangent screen used. Second, in all cases center-surround receptive fields were observed in retinal areas immediately adjacent to the specialized fields, and in a number of cases on the same electrode track. Moreover, these specialized fields were examined at the same levels of illumination as the center-surround fields, so that the level of light adaptation could not be a cause of the differences between specialized and center-surround fields.

The most numerous type of specialized field recorded, the C-type receptive field, was distinguished from center-surround fields by two principal criteria. First, although the ten fields in this category resembled center-surround fields in that either strong On or strong Off responses could be obtained over an approximately circular central region (seven were On-center, three were Off-center), in no case could the opposite response be detected when the stimulus was located in the surround region, even when an annulus of light was flashed around the center of the receptive field and a number of responses were averaged. Second, the area of the center region which did respond to flashing spots was very small (mean diameter, 25 min; range, 22 to 30 min), much smaller than the center of the center-surround fields recorded in the area centralis (mean diameter, 1 deg; range, ½ to 1½ deg).

Although no surround response could be detected in a C-type field, the unit's response to a flashing ambient light was always much weaker than it was to a spot flashing in the center region of the field, indicating a generally inhibitory influence of the surround (Fig. 1, *a*, *b*). However the form of the response to a flashing ambient light varied from unit to unit. A qualitative difference between C-type fields and center-surround fields was shown by their responses to cardboard figures moving across their receptive fields (Fig. 2). For example, the response of one On-center, C-type field to white cardboard bars moving before a grey background was a unimodal activation for a 1-deg-wide bar, and a bimodal activation for a 5-deg-wide bar (Fig. 2, *a* and *c*). Except for the low rate of maintained ac-

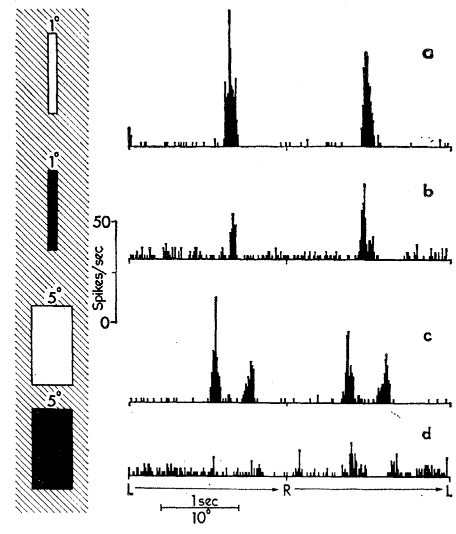

Fig. 2. Averaged response histograms of the firing of an On-center, C-type receptive field to cardboard bars moving back and forth across its receptive field. Each bar was 10 deg tall and moved horizontally before a grey background. In the first half of the histograms the bar was moving at 10 deg/sec from a point 10 deg to the left of the receptive field to a point 10 deg to its right. In the second half the spot moved in the opposite direction with the same speed. Thus the stimulus sequence took 4 seconds. In histograms *a* and *c*, white bars, 1 and 5 deg wide, respectively, were used; for histograms *b* and *d*, black bars were used.

tivity, these responses were virtually identical with those obtained from an On-center field of the center-surround type (*5*). However, the unit's response to a 1-deg-wide black bar was also a unimodal activation, while it gave almost no response to a 5-deg-wide black bar (Fig. 2, *b* and *d*). These latter responses were quite different from those given by an On-center, center-surround field (*5*). The responses of the C-type fields to both white and black objects cannot be explained without admitting some surround influence on the unit; however, the contribution of the surround was clearly different from that in a center-surround field.

Receptive fields with surrounds whose influence is purely inhibitory have been observed in the retinas of other species. The On-Off fields in the frog, pigeon, and rabbit retinas all have inhibitory surrounds (*8–11*). Barlow, Hill, and Levick (*9*) described fields with inhibitory surrounds in the rabbit retina which particularly resembled the C-type receptive fields, for they had On- or Off-centers, and were found mainly in the area where the density of cells was high. These fields differed from C-type fields, however, in possessing much larger center regions, and in responding selectively to slow rates of movement. Wiesel (*3*) noted that the antagonistic effect of the surround on the center response was much greater for receptive fields in the area centralis of the cat retina than for those in the peripheral retina. He did not describe fields with inhibitory surrounds in the area centralis, perhaps because the "area-threshold" measurements he made on the responses of area centralis units did not provide a distinction between center-surround and C-type receptive fields.

The two diffuse receptive fields examined were remarkable for their large size and their weak, oscillatory responses to flashing spot stimuli. The latter property made their fields difficult to plot, but the fields nevertheless appeared to have an irregular center-surround organization. One diffuse field consisted of an On-center, ½-deg in diameter, and a much larger (diameter, 15 deg) Off-surround. The unit responded maximally to a ½-deg spot flashing in the center region; this response had a low peak firing rate (78 spikes per second) and was slightly oscillatory. The second unit fired spontaneously in irregular bursts; it had an Off-center, On-surround field at least 15 deg in total diameter. Figure 1*c* shows the strongly oscillatory response of this unit to a 2½-deg spot flashing in the center region of its field. The period of the initial oscillation was 90 msec.

Receptive fields resembling these diffuse fields have not been found in the retinas of other species, although oscillatory firing has been observed in the cat's retina by Doty and Kimura (*12*) and by Ogawa, Bishop, and Levick (*13*).

Four units with On-Off receptive fields were recorded in the central area, the diameters of their fields ranging from ½ to 1½ deg. Each unit responded with a burst of firing both when a spot of light in its receptive field flashed on and when it flashed off. An averaged response histogram of a typical response is shown in Fig. 3*a*; it was quite different from the On-Off responses obtainable from center-surround receptive fields (*4*). In particular, there was no maintained activity of the unit between the two bursts of firing. This form of response was elicited wherever the spot was flashed in the receptive field, except in one field from which pure On-responses were obtained at one or two peripheral points.

On-Off receptive fields constitute approximately 50 percent of the receptive fields recorded in the frog retina (*14*), and 30 percent in both the pigeon (*8*) and the rabbit (*9*) retina, but clearly they form a much smaller proportion of the receptive fields of the cat retina. Since the On-Off units of the pigeon and rabbit retinas were directionally sensitive—that is, they responded selectively to a certain direction of movement of a stimulus pattern across their receptive fields (*8*), the responses to movement of the cat's On-Off units were of particular interest. Figure 3*c* also shows the response of the one On-Off unit which was directionally sensitive to a bar of light moving across its field from left to right and back again. The unit was activated by movement from left to right but not by movement from right to left. Vertical movement produced equal activation for either direction, but whenever the movement had a left-to-right component the response was stronger than it was for the opposite direction. Similar results were obtained for movement of a black figure before a white screen—that is, for a stimulus of the opposite contrast.

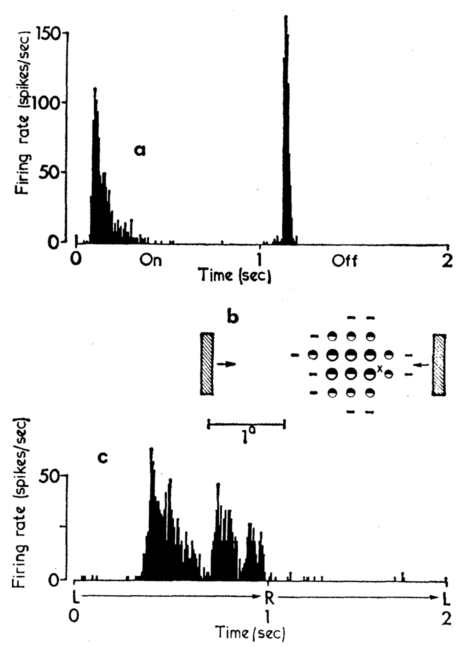

Fig. 3. (*a*) Averaged response histogram of the firing of an On-Off unit to a 15-min diameter spot flashing on for 1 second and off for 1 second in its receptive field. The position of the spot in the field is shown in *b*. (*b*) A plot of an On-Off receptive field: The positions at which On-Off responses were elicited by a 4-min diameter spot are shown by half-filled circles. The size of the circles indicates approximately the strength of the response. The dashes indicate positions at which the stimulus spot elicited no response. The X marks the spot at which the histogram in *a* was obtained. The cross-hatched bars indicate the end positions of a bar of light moved back and forth across the field. (*c*) Response of the On-Off unit to movement of the bar of light between the positions indicated in *b*. The unit fired only as the bar moved from left to right—that is, it was directionally sensitive.

The three other On-Off units were not directionally sensitive. One unit was excited by centripetal movement of a small spot in its receptive field and inhibited by centrifugal movement; it resembled an On-center field (*4, 9*). The other two units were equally excited by centripetal and centrifugal movements of the spot in their fields; they resembled the On-Off fields of the frog retina (*10*).

The difficulty we encountered in resolving units in the area centralis makes it probable that our electrodes recorded more successfully from the larger cells. Most of the cells of the central area are small, only 18 percent of them being larger than 15 microns in diameter (*6*). It is possible that the specialized fields, and in particular the C-type fields, belong to these small cells and hence may form a higher proportion of receptive fields in the central area than the present study suggests.

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