Goldfish Retina: Organization for Simultaneous Color Contrast

Abstract. *The majority of ganglion cells in the retina of goldfish have receptive fields organized so that the cells respond particularly to simultaneous contrasts of color. The receptive fields are concentrically arranged. If the cell is excited by red light in the center, then it will also be excited by green light in the periphery, and inhibited by green light in the center or red light in the periphery. The occurrence of this arrangement and the reverse is about equal. The receptive field is much larger than had previously been thought.*

Simultaneous color contrast is a fundamental process in the perception of color. It is perhaps the most important process underlying color constancy of an object, which helps an animal recognize its friends and foes regardless of their surroundings and illumination (*1*). Most of the psychological findings on simultaneous color contrast come from experiments with humans, but behavioral experiments done on other animals, such as fish and birds, show that they also see color contrasts (*2*).

When physiological recordings are made, the results indicate that some cells do not respond to simultaneous color contrasts; for example, the typical opponent-color cell found in the goldfish retina (*3*), the primate lateral geniculate (*4*), and the ground squirrel optic nerve (*5*). Such a cell will give an "on" response to red light in the center of its receptive field and an "off" response to green light in the periphery of its receptive field, or some variation of this in which the colors red, green, and blue and the responses "on" and "off" are permuted. Since the excitatory and inhibitory processes underlying the "on" and "off" responses oppose or cancel each other, this cell will give little response to a red spot in a green surround. However, it will give a large response when its whole field is illuminated by green, which is followed by red. One can say, therefore, that such a cell responds to successive green-red color contrasts, but not to simultaneous green-red color contrasts.

Consider next a cell which gives an "on" response to red light in the center of its receptive field and an "on" response to green light in the periphery of its receptive field. If the excitatory processes from center and periphery reinforce each other, this cell will give its maximal "on" response to a red spot in a green surround. If the cell also gives an "off" response to green light in the center of its receptive field and to red light in the periphery, the response will be substantial when a green spot in a red surround is turned off. This type of cell can be said to respond optimally to simultaneous red-green color contrasts. The following results show that the majority of the ganglion cells recorded by metal microelectrodes in the goldfish retina are, in fact, of this type. However, the appropriate type of stimulus must be used to reveal the responses.

Results were obtained from over 200 units in the isolated retina (*6*) with the use of platinum-iridium microelectrodes (*7*) and a computer to display the results (*8*). All these were single units recorded extracellularly, as judged by the constancy of the spike shape, and had a sufficiently high signal-to-noise ratio to operate a trigger. Figure 1 shows records from one of these units, in response to various spots and surrounds centered on the receptive field of the unit. The records are in the form of single-stimulus histograms, with time bins of 20 msec. A dot indicates that no spikes occurred during that interval, and if spikes did occur, a numeral gives the number of discharges. The light was on for 1 second, and the records give the spike train for that second and the subsequent one.

A green spot of wavelength 500 nm gave an "on" response (Fig. 1, top line), and a red surround of wavelength 650 nm gave an "on-off" response with the "on" stronger than the "off" (third line). When the green spot and red surround were presented together, the "on" response to the combination was more vigorous than either of the "on" responses of the com-

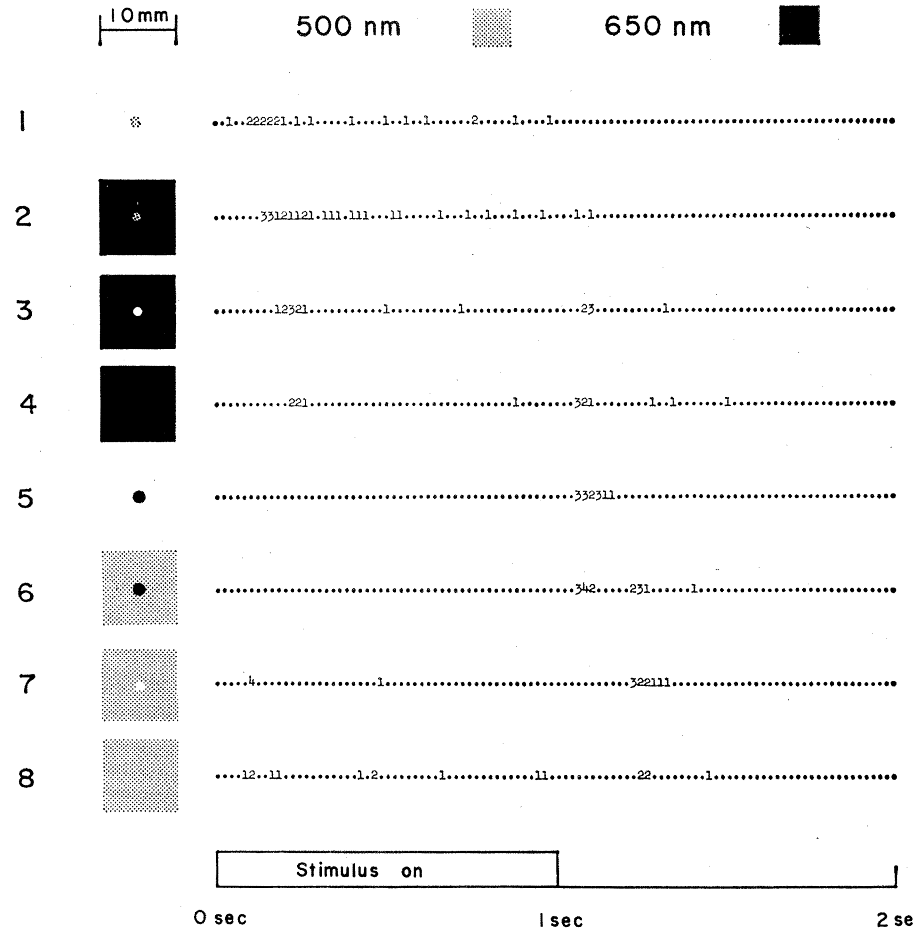

Fig. 1. Response of a ganglion cell to various spots in various surroundings. All spots and surrounds were centered on the receptive field. Solid areas were lighted by a wavelength of 650 nm of illuminance 9×10^{11} quanta cm^{-2} sec^{-1}; dotted areas, a wavelength of 500 nm of 1.5×10^{12} quanta cm^{-2} sec^{-1}; white areas not illuminated.

ponents (second line compared with first and third lines). Similarly the reverse stimuli (red spot, green surround, and their combination) all gave clear "off" responses (lines 5, 6, and 7). When the whole field was illuminated by red or green, the response was a fairly weak "on-off" (lines 4 and 8). Thus the strongest "on" response was obtained from a green spot in a red surround, and the strongest "off" response from a red spot in a green surround.

Two main subtypes of these color-coded cells were found in the goldfish. Figure 1 demonstrates the first; the second was the reverse, with "on" response to a red spot or green surround and "off" response to a green spot or red surround. The two subtypes are about equally common.

Behavior of another cell of the same type as the one shown in Fig. 1, but with an unusually high rate of spontaneous activity (10 spikes per second), is given in Fig. 2. The retina was illuminated by a 10-mm square divided into two parts by a straight boundary, with red on the left of the boundary and green on the right (the red was tungsten light filtered by a Kodak Wratten No. 29 filter; the green, tungsten light filtered by Wratten No. 61). Records were taken with the boundary placed in various positions parallel to each other, the distance of the boundary from the midpoint of the receptive field of the unit being marked beside each record. The 10-mm square was 3 to 4 mm wider than the whole receptive field of the unit (*8*), and the masking was arranged so that the edges of the square did not move when the boundary was moved. Thus all parts of the receptive field were illuminated by either red or green in all positions of the boundary. When nearly all of the receptive field of the unit was illuminated by green, there was no response (top line), the record appearing to be the same as a record of spontaneous activity; when nearly all of the receptive field was illuminated by red, there was also little response (bottom line). Intermediate lines show that when part of the field was illuminated by red, and part by green, either an "on" or an "off" response was obtained, depending on the position of the boundary.

The curve at the bottom of Fig. 2 gives a graphic representation of the results. It is a plot of the number of spikes during the 1-second illumination, minus the number of spikes occurring during the 1 second after the light was turned off, against the position of the boundary. (One can do this without distortion in this particular case, because no "on-off" responses were obtained.) The curve is reminiscent of the plot of a Mach band, which is the result of a contrast process (*9*); recent work has shown that Mach bands are seen in gradients of hue as well as gradients of brightness (*10*). Further experiments showed that the general shape of the curve was the same for red-green, red-black, and black-green boundaries and reversed for green-red, black-red, and green-black boundaries, so that it depended on the positions of the red and the green, but not on their relative intensity (*8*).

Figures 1 and 2 represent results obtained from over 50 percent of the cells that were sampled. In some cases the center and periphery were sufficiently antagonistic that very little response was obtained when the field was illuminated uniformly with either red or green light (Fig. 2); in other cases uniform illumination of the field did give a response (Fig. 1). Less frequently, other types of cells were also found; these have been described in more detail elsewhere (*8*).

The results shown in Figs. 1 and 2 are not predicted by the earlier work of Wagner, MacNichol, and Wolbarsht (*11*). Their sensitivity plots represent what turns out to be only the inner part of these receptive fields. The diameter of the inner part is generally 0.5 to 1 mm, but may extend to 2 mm. The outer part of the receptive field, hitherto unknown, is stimulated by the surrounds shown in Fig. 1 and extends

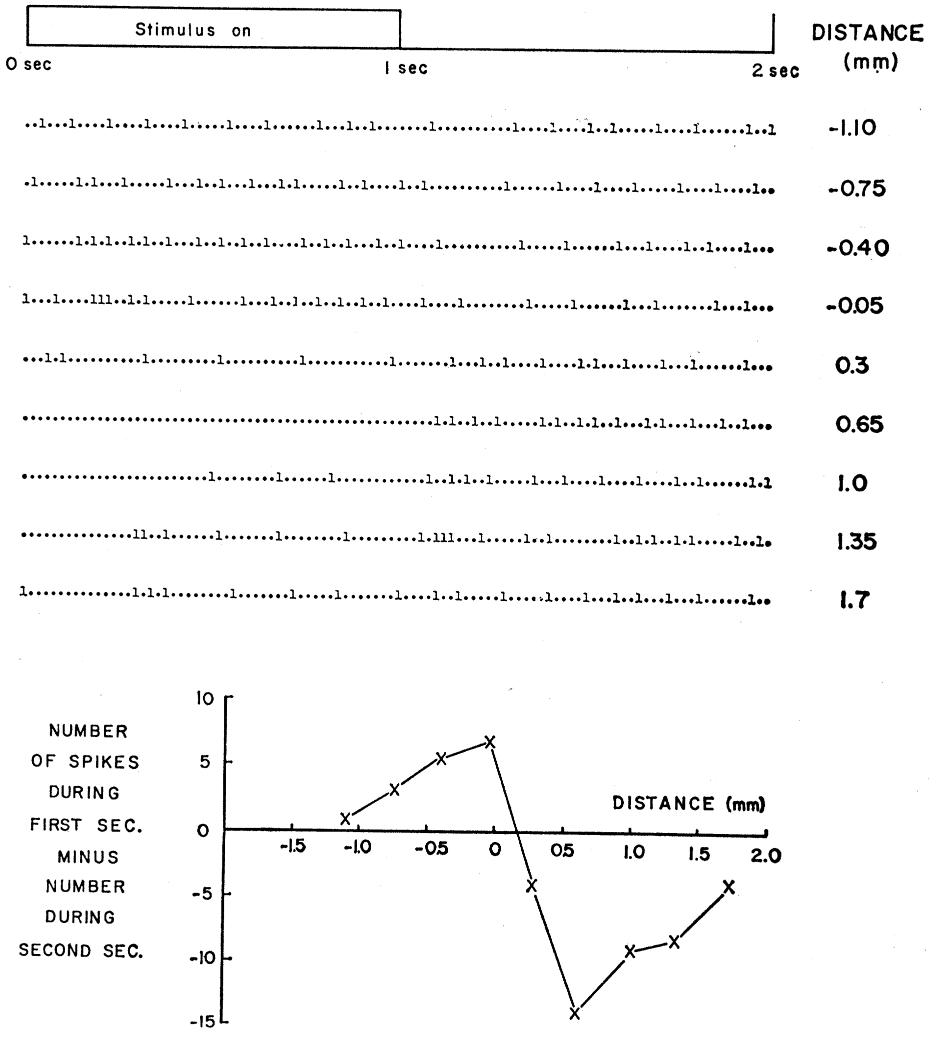

Fig. 2. Response of another cell to a red-green boundary placed in various positions parallel to each other. The distance is that of the boundary from the midpoint of the receptive field. The graph below the responses plots the number of spikes occurring while the stimulus was on, minus the number occurring during the 1 second after the stimulus was turned off.

out to a diameter of 5 mm or more. A stimulus of large area and low intensity, such as an annulus, was found to be much more effective in eliciting a response from the outer part than a stimulus of small area and high intensity, such as a spot. These investigators generally used spots as stimuli; hence it is not surprising that they did not discover the outer part of the receptive field.

Wagner, MacNichol, and Wolbarsht showed that the response to red light was obtained from a smaller area than the response to green light in what I have called the inner part of the receptive field, and my results confirmed this. Consequently, they referred to a center and a periphery. In this report I suggest a new terminology—namely, red center, red periphery and green center, green periphery, the green center always being as large, or larger, than the red center. In this new terminology, the periphery of Wagner, MacNichol, and Wolbarsht is an area that is in the center for green, but in the periphery for red.

The fact that the center for green is larger than the center for red explains in part why the response to a green surround contained a weak "on" component, as shown on line 7 of Fig. 1. Scattered light was also a factor here, as it was in the response to a red surround, shown on line 3 of Fig. 1 (*8*). Thus the cells are not quite the simultaneous color-contrast detectors that theory would suggest. Nevertheless, they are appropriately organized to mediate the behavioral response that fish have been shown to give when faced with a contrast of colors.

Recent work has shown that cells with a similar organization are found in the monkey cortex (*12*). Other comments suggest that such cells may also exist in the monkey lateral geniculate (*13*) and the carp retina (*14*). Hence, the type of organization of the receptive field described in this report for ganglion cells of the goldfish retina may be much more common than had previously been thought.

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Visual Form Discrimination after Removal of the Visual Cortex in Cats

Abstract. *Adult cats were trained to discriminate between erect and inverted triangles after simultaneous ablation of cortical areas 17, 18, and most of 19 of both hemispheres. Postoperative training proceeded through a graded series of similar triangle pairs in which the members of each pair were equated for luminous flux.*

Earlier studies investigating the function of the striate area of the cerebral cortex by Lashley (*1*), Klüver (*2*), and Smith (*3*) supported the general conclusion that this area of the brain is essential in mammals for performance of visual pattern or form discriminations. Recent work by Meyer (*4*) and by Wetzel *et al.* (*5*) has tended to confirm this conclusion with regard to the adult cat. However, evidence that some striate-decorticate animals can learn to discriminate form has appeared consistently within the studies reporting generally negative results. Data reported by Lashley (*1*, pp. 453–454), Smith (*3*, p. 262), Meyer (*4*), and Wetzel *et al.* (*5*) indicated that, from the group with lesions, one or more animals in each study had mastered the discrimination in the time allotted. Since the majority of lesioned animals did not reach the performance criterion in this period, the exceptional animals were merely described as such.

In 1961 Doty (*6*) presented evidence that adult striate-decorticate cats could discriminate triangles from circles as readily as normal controls. In his work, however, cortical ablation had been carried out on the animals as neonates. In addition, recent work on the primitive primate *Tupaia glis* indicates that removal of its striate cortex has no effect on its visually guided behavior in general or on its ability to discriminate between erect and inverted triangles (*7*).

With these indications that the striate area might not be essential for form discriminations, I reinvestigated this problem in the naive adult cat, giving special attention to three procedural variables: (i) the size of the brain lesion, (ii) the length of postoperative training, and (iii) the method of presentation of the stimuli.

The experimental handling of the first two of these variables by Smith (*3*), Meyer (*4*), and Wetzel *et al.* (*5*) imposes qualifications on specific conclusions which can be drawn from these investigations concerning the functional role of the striate cortex. First, all of these studies involved lesions of the neocortex which extended well beyond the striate area (area 17) and, in fact, well beyond the visual cortex [areas 17, 18, and 19 as defined histologically for the cat by Otsuka and Hassler (*8*)]. Second, arbitrary limits were set for the length of postoperative training. Therefore, the present study was designed to determine whether adult cats (i) with lesions limited to the anatomically defined visual cortex, and (ii) given extended postoperative training, could reach a high level of performance on a visual form discrimination.

The third and perhaps most important aspect of the procedure was the stimuli to be used. The choice of stimuli and method of their presentation during training were influenced by the desirability of working with