Color Vision Mechanisms in the Monkey

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The monkey, *Macaca mulatta*, was chosen as the experimental animal for the investigation of the physiological mechanisms of color vision for two reasons: there is excellent behavioral evidence that the rhesus monkey has color vision (this is not true for some of the animals which have been used in similar investigations); furthermore, its color vision system is undoubtedly very similar to, if not identical with, that of man. There is good evidence (Walls, 1942) that color vision systems have evolved several separate times, once in the insects, again in fish, reptiles, and birds, and still again within the primate order. If this is correct, it would be little more than a coincidence if the way in which information about the wavelength of light is encoded in the visual system of monkey and man were the same as the manner in which it is accomplished in fish or birds. In any case, if one is interested in relating the ways in which various neural elements respond to different wavelengths of light under various conditions to the manner in which these lights are perceived, one cannot go wrong in studying an animal as similar as possible to man, for virtually all of the behavioral results from color discrimination have been obtained on the human observer.

The macaque lateral geniculate nucleus (LGN), from which most of the recordings have been obtained, consists of six layers of cells separated by fiber layers. These cells receive connections from the axons of the ganglion cells of the retina and are thus the fourth-order neurons in the visual pathway. Anatomical studies (Glees and Le Gros Clark, 1941) have given little evidence for interconnections at this level; the types of responses recorded here may well be essentially the same as one would obtain from ganglion cells in the retina. However, the highly laminated structure of the LGN, in which the optic projection from each eye splits three ways, presents the possibility of some clues being present as to the nature of the organization of the visual system in the differential responses of cells in the various laminae. For this, as well as for certain technical reasons, the LGN rather than the retina was chosen as the recording site.

METHOD

The experimental procedures have been more fully described elsewhere (De Valois et al., 1958b). The monkey, maintained under barbiturate anesthesia, is held in a stereotaxic instrument within a light-tight box. A double-beam optical system allows the presentation of light pulses to either or both eyes in a Maxwellian view. Monochromatic light is obtained with interference filters, which are combined with neutral-density filters to equate them in physical energy. The 1 to 2 μ tip diameter microelectrodes are inserted down through the intact brain until a single LGN cell is isolated. The responses of this cell to various monochromatic lights, presented in a random order with long pauses in between to minimize adaptation changes, are then recorded.

RESULTS

Patterns of Responses from Different LGN Layers

Hartline (1938), recording from single fibers in the frog optic nerve, found that some units respond during light stimulation, others at both the onset and offset of the light, and still others only at the offset of the light. These types of cells have been found since by numerous observers working with a variety of vertebrates. We have found essentially the same types of cells in the monkey LGN (De Valois et al., 1958a), where the different types are located in different layers of the nucleus. Most of the cells in the most dorsal pair of LGN layers give on-responses; in the intermediate layers one records both on- and off-responses; the cells in the ventral pair of layers are inhibited by light and fire off-responses.

Anatomical studies of the retina show several different types of ganglion cells of varying size and type of connection to bipolar and receptor cells. One may presume that one effect of the varying types of connections is to produce on, or off, or on-off responses from stimulation of the same receptors. Since each small portion of the central retina projects to each of the three LGN layers connected with that eye, it is probable that the different types of ganglion cells are sorted out for type in their projection to the various LGN laminae.

The function served by the separation of the cells of different response types into different LGN laminae is something of a mystery, for we have found no evidence for a maintanence of this segregation in the projection to the visual cortex (Smith et al., 1958).

Each LGN cell has been found to respond to stimulation of only one eye or the other, but not both; the projections from each eye are kept quite dis-

crete at this level. Light put into the "wrong" eye for a particular cell not only does not fire it, but also does not modify the response of this cell to light to the "right" eye when both eyes are stimulated together. (In the cat LGN and cortex it is often found that stimulation of one eye will not fire a particular cell but will modify its response to concomitant stimulation of the other eye.) Many cells in the monkey pregeniculate nucleus, on the other hand, respond to stimulation of either eye (see Fig. 1). This nucleus is in the pathway concerned with reflex pupillary movements, rather than in the retino-geniculate-striate system, but presumably the same retinal receptor cells feed into both systems. It is therefore of interest to note that these cells give prolonged on-responses with very little diminution of response for long periods of time (see bottom record, Fig. 1). This is in contrast to the fairly rapid slowing of response rate in time in the classical visual system, and would tend to indicate that the primary source of adaptation changes is somewhere in the neural network rather than in the receptor pigments as has been generally supposed. The fact that the steady potential responses recorded by Svaetichin from the retina also tend to be maintained with little change in time would tend to support this view.

On-Cells

The on-cells, which are found in the dorsal LGN layers, give only on-responses at all intensities of light, at least with the diffuse light stimuli employed in these experiments. As can be seen in Fig. 2, increasing intensities of light result in increasing sized response, the curve very closely approximating the psychophysical relation between the luminance of a light and its brightness.

A great number of the on-cells respond to only a relatively narrow portion of the visible spectrum. In fact, in the portions of the LGN which receive projections from the foveal parts of the retina, virtually all of the on-cells are of this single-peaked color-selective sort. In Figs. 3 and 4 are presented two examples of these narrow-band cells, a "red" cell and a "yellow" cell. In each figure the responses of the cell to various equal-energy monochromatic lights are superimposed. The signal marker at the top of each figure refers to each of the individual records. The average responses of all of the cells of each type which we have studied are presented in Fig. 5.

In the more peripherally-related parts of the nucleus, many of the cells have more than one peak, and the peak sensitivity changes from the dark to the light-adapted state, but in the foveally-related portions the narrow-band responses are found even in the completely dark-adapted state. It would thus appear that in the primate, in contradistinction to the situation in most lower vertebrates (Granit, 1947), there are numerous pathways for color which are not also connected with the scotopic system. This does not mean that these narrow-band elements are necessarily connected with receptors in a straight-
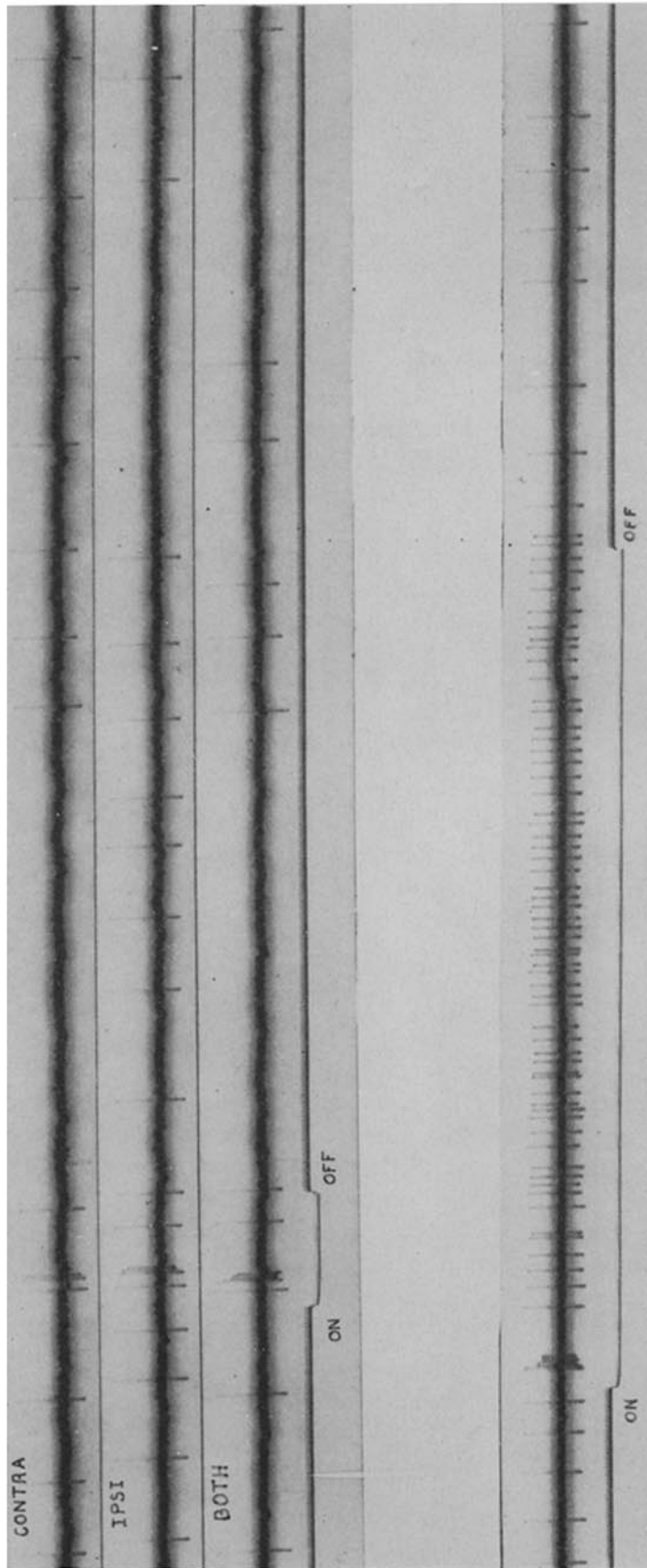
FIGURE 1. At top: superimposed records from a single macaque pregeniculate cell to light stimuli to the contralateral eye, insilateral eye, and to both eyes together. The signal marker refers to all three records. At bottom: recording of response of the same cell to a long light pulse (*ca.* 2 seconds).

through pathway from one cone to one bipolar to one ganglion cell. We have no evidence one way or the other about possible interactions in the retina to produce these spectral sensitivities except that rods do not seem to be involved, except in the cases of the "blue" and the "510" cells. These two latter have been included with the single-peaked narrow-band cells because all of the "blue" cells we have found have a secondary peak to a varying degree at *ca.* 510 mμ, and most of the "510" cells have a secondary peak at 440 mμ (others with secondary peaks at 550, 590, or 620 have not been included in this analysis). If the "510" cell is taken to indicate a connection with some sort of rod receptor, this would leave us with four cone-related systems, one of which (the "blue") is very intimately related to a rod system.
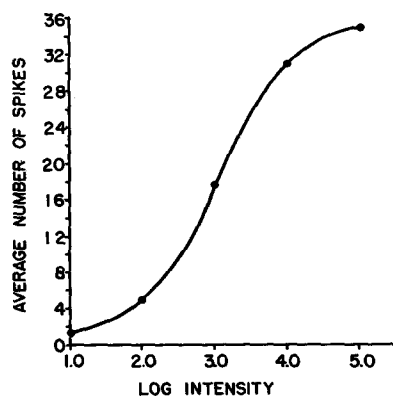

Figure 2. Plot of responses of on-cells to different intensities of light.

On-or-off Cells

A second variety of cell which we have recorded from, in the LGN, fires both on- and off-responses to light. These two phases of the response are, in general, mutually exclusive, *i.e.* the cell fires either an on-response or an off-response, depending on the wavelength of the light, but not both. In addition to the excitation at either on or off, there is an accompanying inhibition at off or on, respectively. For example, one variety of on-or-off cell fires an on-response to "red" and an off-response to "green." If the eye is stimulated with light of 650 mμ, this cell fires during the light, and is inhibited at the offset of illumination. A light of 480 mμ, on the other hand, will inhibit this cell, which then fires at the offset of the light pulse. In Fig. 6 the responses of such a "red-on, green-off cell" have been plotted. It can be seen that a light of 650 mμ leads to an increase from the spontaneous firing rate during the light, followed by a decrease in firing after the light. Light of 570 to 590 mμ has essentially no effect on the activity of the cell, and light of 500 mμ inhibits the cell, which then fires at the offset of stimulation.

We have also found other cells of this same variety which fire on to "blue" and off to "yellow" light, with here again a region in between, in this case
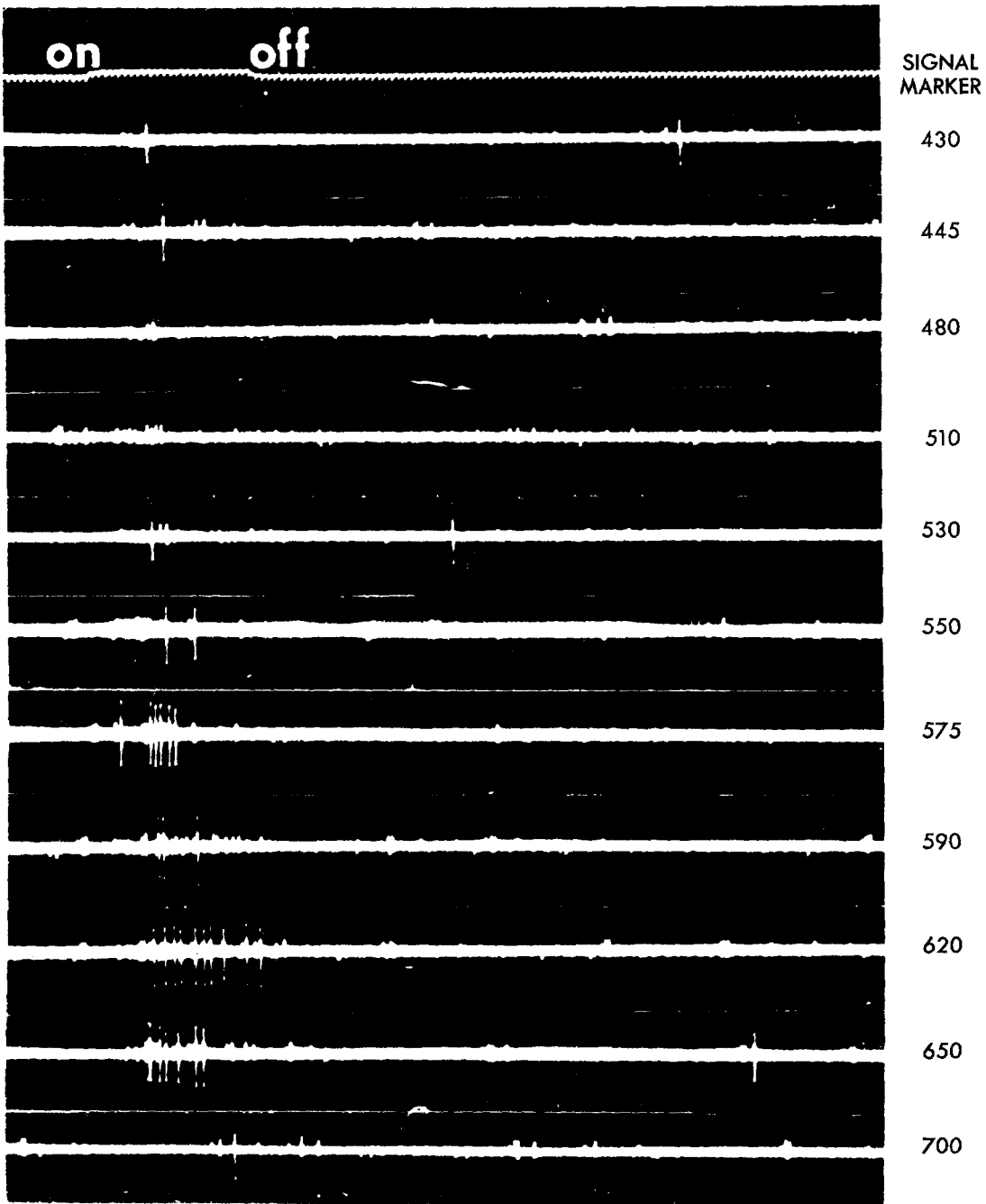
FIGURE 3. Superimposed records from a single "red" on-cell to variety of equal-energy monochromatic stimuli.
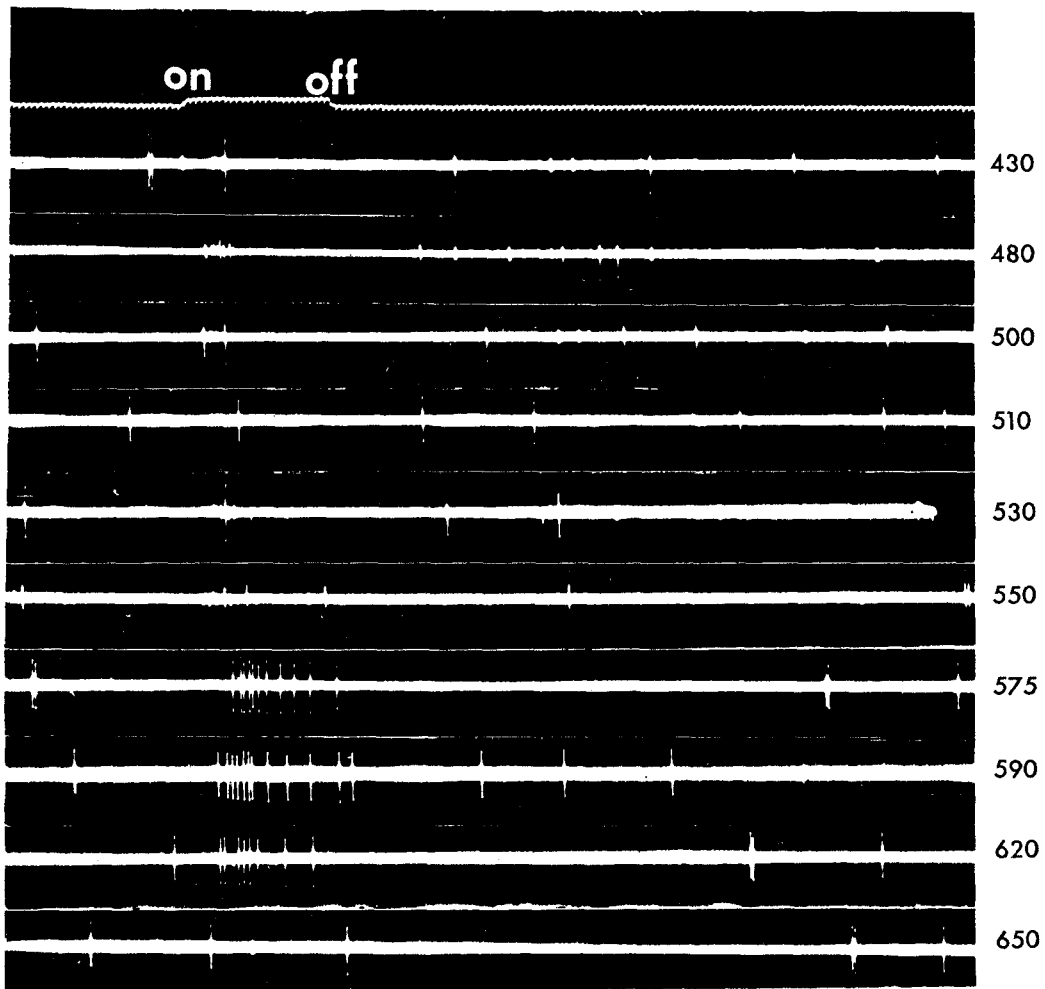
FIGURE 4. Superimposed records from a single "yellow" on-cell to a variety of equal-energy monochromatic stimuli.

in the "greens," to which there is no response. The spectral response curves for these two types of on-or-off cells are plotted in Fig. 7. The curves are the averages of all of the cells of these types from which we have recorded. To simplify the figure, only the on-responses have been plotted; in each case, as has been noted above and illustrated in Fig. 6, the curve for the off-responses is the opposite of that for the on-responses.

The question arises of how these different cells respond to white light. The on-cells respond to white light just as they do to monochromatic light, although much greater energy is of course required for a given response to white light than to the appropriate monochromatic light in the case of the
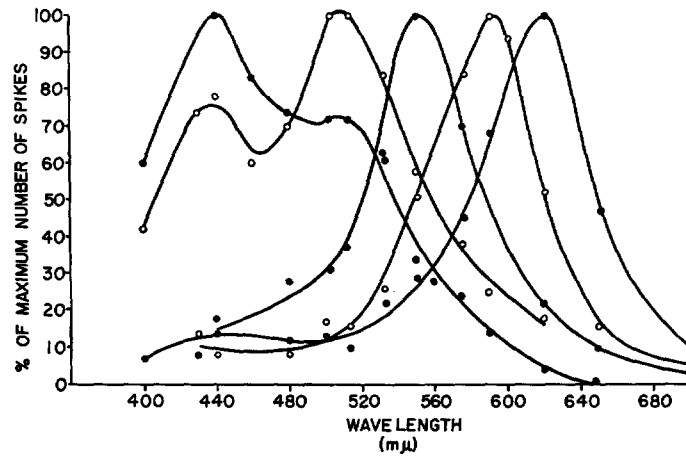
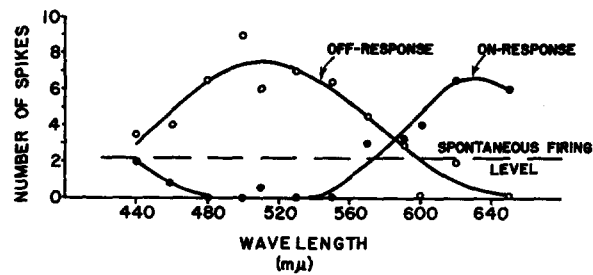FIGURE 5. Averaged results from the narrow-band on-cells.

FIGURE 6. Plot of the responses of a single red-on, green-off cell to various equal-energy monochromatic stimuli.
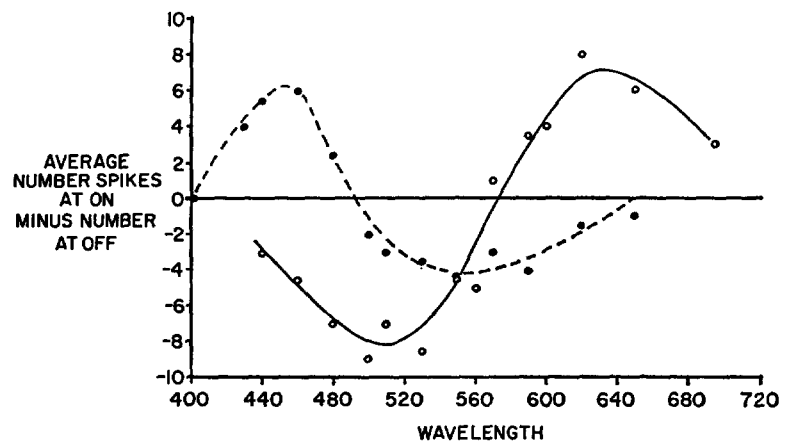

FIGURE 7. Averaged results of the on-responses of the on-or-off cells.

color-selective cells. The on-or-off cells, on the other hand, as might be expected from the balanced excitation and inhibition to complementary wavelengths, give virtually no response to white light. Their firing rate neither increases nor decreases from the spontaneous firing rate even in response to very intense white light.

The close parallel between the behavior of these on-or-off cells and the opponent-color system postulated by Hering and developed by Hurvich and Jameson (1957), is readily apparent. We also have little doubt that some retinal process similar to that found by Svaetichin (1958) in the region of the inner nuclear layer of the fish eye is a precursor to these LGN cell responses.

A Hering type model is most successful in accounting for color-contrast effects in vision, in which a monochromatic light stimulus induces the complementary color in neighboring spacial regions (simultaneous color contrast) and in the same region at a later time (successive color contrast).

The optical arrangement we used in these experiments did not enable us to study simultaneous color contrast, but we did record the interactions of light stimuli occurring in succession in time (De Valois *et. al.* 1959). If one thinks of the red-on, green-off cell as signaling red by an increase in firing rate, and green by a decrease in firing rate the response of this cell to a single pulse of monochromatic light can be seen to exhibit the characteristics of successive color contrast. Thus in a psychophysical experiment a pulse of "red" light induces "green" as an after-effect, and this cell is inhibited ("green") at the termination of a "red" light. Correspondingly, it is excited ("red") at the termination of stimulation with "green" light. It is perhaps more convincing to observe its response when stimulation by one wavelength is followed by a light stimulus of the complementary wavelength. A "red" light seen after inspecting a "green" light for a time is redder than if it had not been preceded by the "green" light. It can be seen in Fig. 8 that there is a larger response when a "red" light follows a "green" than when it is presented alone. What is happening, of course, is that the on-response to "red" is summing with the off-response to "green." The corresponding process occurs with the inhibitory response, as can be seen in Fig. 9. Here, when care is taken to choose light levels which do not produce complete inhibition to either stimulus alone, it can be seen that there is more inhibition ("green") when the "red" light preceded the "green" light.

Off-Cells

We have not studied the off-cells as extensively as the other systems in the LGN. Most of these cells have a quite high level of spontaneous activity which
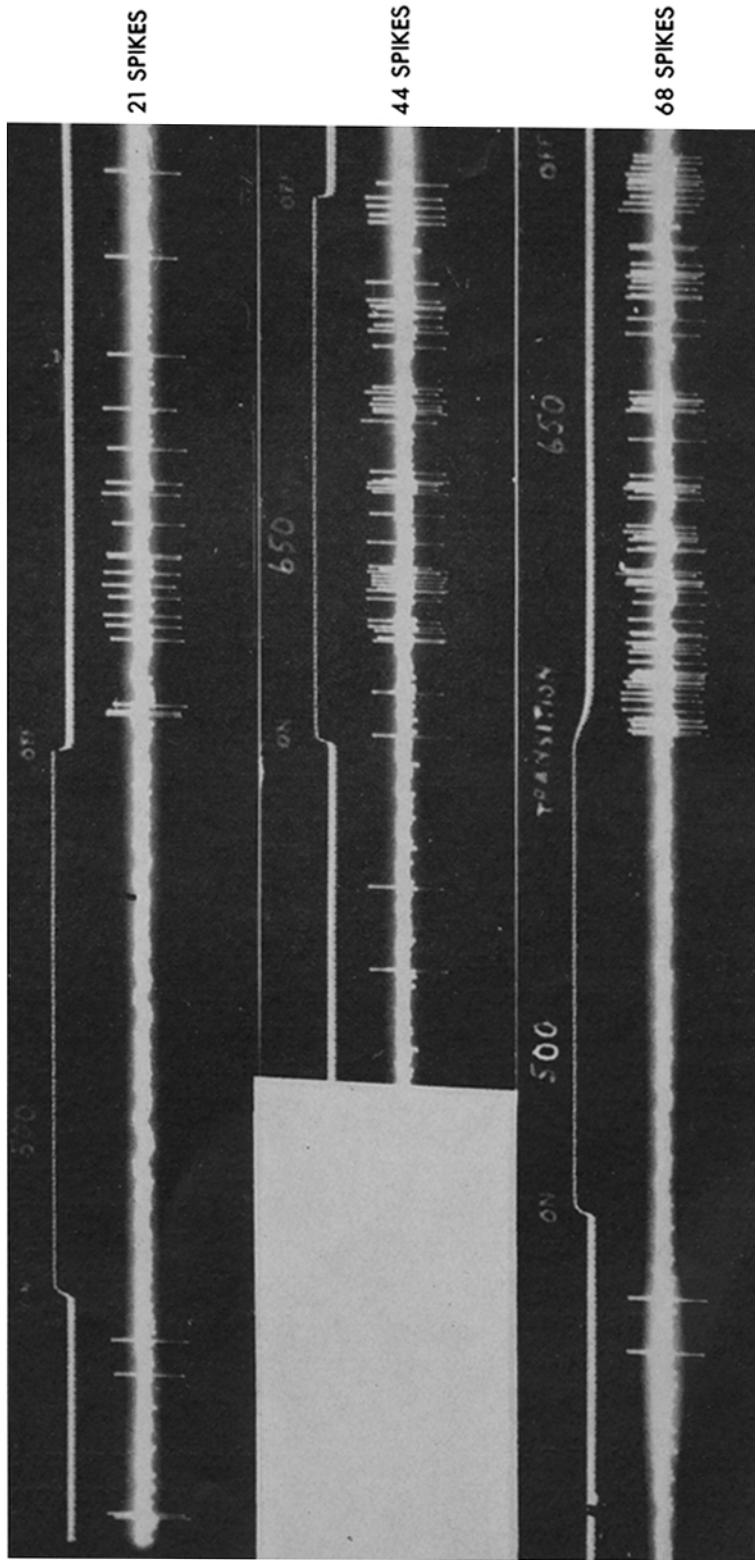
21 SPIKES

44 SPIKES

68 SPIKES

FIGURE 8. Responses of a single red-on, green-off cell. Top record: response to 500 mµ alone. Middle record: response to 651 mµ alone. Bottom record: response when 650 mµ follows 500 mµ.
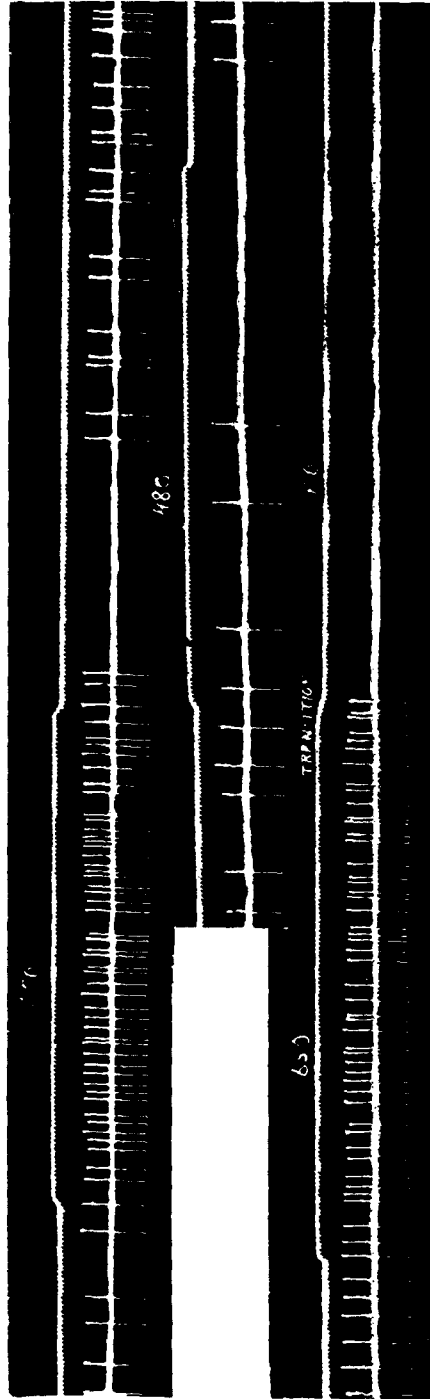
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FIGURE 9. Responses for single red-on, green-off cell. Top record: 650 mμ alone. Middle: 480 mμ alone. Bottom: 650 mμ followed by 480 mμ.
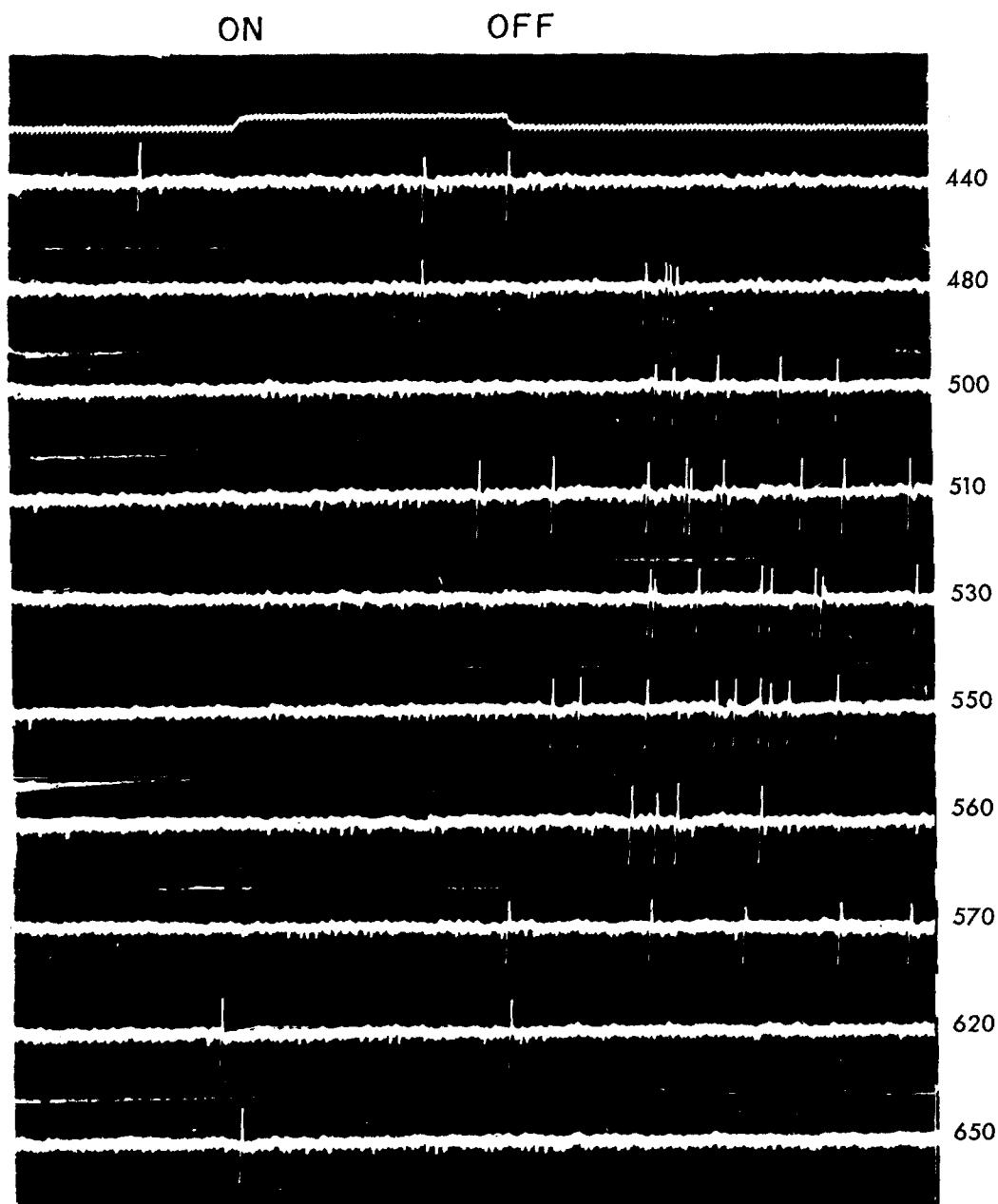
FIGURE 10. Response of single cell in LGN to various wavelengths of light.

is inhibited by light. At the termination of the light the cell fires an off-response. Although a few narrow-band cells have been found, most show a quite broad spectral sensitivity with peak responses at ca. 510 or 550 mμ or both. The inhibitory phase in particular is extremely sensitive to light; the

cells often inhibit to a light of two or more log units below the usual level required for a response in an on-cell. The generally greater sensitivity of an off-cell with peak response at 510 mμ than an on-cell with a corresponding peak response suggests the presence of two different types of rods, a suggestion that has often been made from psychophysical considerations. The cell illustrated in Fig. 10 is unusual in its low spontaneous firing rate but exhibits a typical spectral response.

DISCUSSION

For almost a century now color vision has been subject to disputes—often violent—between the proponents of different theories of color vision. Although this has sometimes been advantageous in the arousal of interest in the area and the generation of new experiments, its negative aspects have become increasingly obvious. One of the reasons for these continuing disparate positions has been that virtually all color vision theories have been formulated in terms of physiological processes, and until recently there has been very little physiological evidence available to support or disprove any positions. Furthermore, the adherents of different color theories generally emphasize different aspects of the vastly complex problems of color vision: the Helmholtzians supporting their position from considerations of color mixing and certain types of color blindness, the Hering supporters pointing out the basic opponent nature of color vision in the phenomena of contrast and in certain aspects of color blindness. Although these two sides are often discussing different facts in supporting their respective positions and can handle only certain aspects of the problem each assumes that they have the whole truth.

We would like to suggest that no single simple theory of color vision is going to be adequate, for the system is not organized in a simple manner. Our evidence and that of Svaetichin indicate that there is an opponent hook-up of complimentaries as was postulated by Hering. On the other hand, there clearly are also pathways, in the on-cells, in which there is no such relationship between complementaries, just as Helmholtz insisted. Furthermore, although we have shown the presence of cells with peak sensitivities at four different spectral loci ("red", "yellow", "green", and "blue"), the basic trivariant nature of the color vision system and the evidence of Rushton (1958) and Weale (1960) from studies of pigment absorption indicate the presence of only three different photopigments (red, green, and presumably blue).

The evidence we have presented indicates that the information coming presumably from the same color receptors is encoded in a number of different manners in the retinal nervous system. The resulting different color systems undoubtedly play different roles in various aspects of color perception.

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