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Primate Color Vision

The macaque and squirrel monkey differ in their color vision and in the physiology of their visual systems.

Russell L. De Valois and Gerald H. Jacobs

Visual perception depends upon certain basic information: the intensity and wavelength of light coming from each point in a scene. Every animal with vision makes use of intensity information, and various animals appear to do so in much the same way. The situation is different, however, for wavelength information. Some animals have no color vision at all, others apparently discriminate wavelengths to some extent, and still others have excellent color vision. A number of years ago, Walls (*1*) argued that color vision has evolved independently in different classes of animals, human color vision having probably developed within the primate order. One basis for this view is the fact that many other mammals seem to have no more than rudimentary color vision, and that, in those lower animals which do have excellent color vision, the physiological means by which it is achieved may differ. Man, for example, has receptors containing different photopigments which provide the essential first step in differentiating wavelengths; some reptiles and birds, on the other hand, appear to have just a single photopigment in combination with oil droplets of various colors which serve to differentially filter the light reaching the pigment in different receptors.

Although evidence that the color vision of mammals developed independently from that of reptiles and birds is fairly strong, the course of that evolution within the mammals, or the extent to which color vision developed within the primates, is by no means so clear. Although no mammal other than the higher primates has been found with color vision approximating that of normal man, ground squirrels (*2*) appear to have some color vision, and, as Polson (*3*) has recently shown, the tree shrew (*Tupaia*) has color vision. This latter animal, which is intermediate between the insectivores and the primates, is highly diurnal, has an all-cone retina, and color vision of the deuteranopic variety.

Many tests have been made of color vision in primates, mostly in various Old World species. Many of the early studies were essentially anecdotal, but, in carefully controlled experiments, Grether (*4*) and Trendelenberg and Schmidt (*5*) showed that macaques and several other Old World primates have excellent color vision similar to that of normal human trichromats. These experiments included neutral-point tests, hue discrimination, and anomaloscope measurements.

The results of tests of New World monkeys have been quite different. Grether (*4*) found that *Cebus* monkeys had deviant color vision on all of his tests, and concluded that they were protanopic dichromats. The squirrel monkey (*6*) was also found to be deviant in hue discrimination, but the hue-discrimination test alone does not allow diagnosis of the type of defect. On the other hand, one spider monkey studied by Grether was found to have normal color vision and hue discrimination (the fact that this animal was a female whereas all of Grether's *Cebus* were males may be significant).

Unfortunately, in regard to the question of the evolution of primate color vision, no recent studies have been

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made of the vision of more primitive diurnal primates, unless the *Tupaia* referred to above is to be considered a primate. There are several diurnal prosimians whose color vision should be investigated.

These earlier experiments thus indicated striking differences between the color vision of Old World and New World monkeys, and for that reason it appeared to us worth while to extend these investigations and make a more extensive and systematic study of the macaque (*Macaca irus* and *M. nemestrina*) and the squirrel monkey (*Saimiri sciureus*), as well as other species. In addition, we are interested in the physiology of color vision. Comparative physiological studies of two species which differ in systematic ways in their visual behavior would, we thought, be valuable; determining what physiological differences are associated with behavioral ones should allow one to draw more firm conclusions about the relation between physiology and behavior. Insofar as macaque monkeys resemble normal human trichromats in their vision and squirrel monkeys resemble certain classes of humans with defective color vision, such physiological studies might also, we believed, provide useful information about normal and defective color vision in man.

One of us (R.DeV.) has been engaged for some time in studying the visual behavior and physiological responses of macaque monkeys; the other (G.H.J.) has been making similar studies of the squirrel monkey. We thought it might be of interest to bring together the behavioral and physiological studies of these two species in a detailed set of comparisons. Some of the behavioral and physiological data have been reported elsewhere (*7*).

Behavioral Tests

The same general type of test apparatus (see *8*) is used in all our behavioral tests of brightness perception and color vision. The basic situation is an oddity problem in which the monkey is required to discriminate that stimulus which differs from three others: a four-alternative, forced-choice test. Specific adaptations of the problem are described below. Human subjects, some with normal and some with defective color vision, were tested with the same apparatus.

Brightness-sensitivity tests. In the brightness-sensitivity tests the animals are presented with one flickering light and three steady lights, all of the same wavelength; they have to choose the flickering light to receive the reward. In successive blocks of trials, all four lights are dimmed until an intensity level is reached at which the animal can no longer discriminate the flickering light. In this way it is possible to determine an animal's sensitivity to a particular spectral region: in regions of low sensitivity, discrimination falls off rapidly as intensity is decreased; in regions of high sensitivity, intensity can be decreased considerably before chance performance appears. At low flicker rates, scotopic vision is tested, since low light intensities are involved, whereas at high flicker rates, high light intensities are required and photopic vision is measured. Thus the fusion intensities for each of several spectral points, found at low and high flicker rates, yield the scotopic and photopic spectral sensitivity curves, respectively.

Macaques have the same photopic and scotopic sensitivities as human beings with normal vision (*9*). This finding is the first of several indications that macaques and normal human trichromats have virtually identical vision. However, relative to macaques and normal human trichromats, respectively, squirrel monkeys and humans with defective color vision (see Fig. 1, A and B) have the same scotopic sensitivity but quite different photopic sensitivity. The squirrel monkey is very much less sensitive than the macaque to the long-wavelength portion of the spectrum, in this respect resembling protanopic and protanomalous humans.

Color-vision tests. In our behavioral tests of color vision, three of the four stimuli are of one color (or are white); the fourth is of a different color. It is obviously important that the two colors seem of equal brightness to the monkey, so that he will not be able to use brightness as a cue for discrimination. The information gained from the brightness-sensitivity experiments allows us to assure this for each subject.

It has been suggested that New World monkeys are dichromats. One important difference between trichromats and dichromats is the fact that dichromats are unable to discriminate monochromatic from white light over a small portion of the spectrum—the neutral point. The initial color-vision test for the monkey subjects involved a search for a possible spectral neutral point. In that test the animal was required to discriminate various spectral stimuli from white light. The results, for both the macaque and the squirrel monkey, were negative; all the monkeys were able to discriminate all spectral wavelengths from white light (although the squirrel monkeys had some degree of difficulty initially at a certain point in the spectrum). The conclusion from this test is that neither of these species has dichromatic color vision, contrary to earlier suggestions.

Other imporant classes of color-defective vision include the trichromatic anomalies. To determine whether either of the two monkey species has anomalous vision, a modification of the anomaloscope, a standard device for testing human color vision, was used. In this test, three stimulus windows are illuminated with monochromatic yellow light and a fourth is illuminated with a variable mixture of red and green lights. The animal is first given a choice between a pure red and the yellows; then, in successive blocks of trials, green is added and red is subtracted until the mixture is pure green.

Macaques and normal human trichromats respond in the same way: they discriminate perfectly at either end of the red-green series, but they confuse certain red-green mixtures, in a narrow range, with yellow. Deuteranopic and protanopic human dichromats were also tested on this problem; they cannot discriminate red from yellow, or green from yellow. Squirrel monkeys fall between these extremes: they discriminate pure green or pure red from yellow but make errors over a broad range of mixtures. Furthermore, their "match point" (the range of red-green mixtures which they cannot discriminate from yellow) is noticeably displaced toward the red end of the spectrum with respect to that of the macaque or the normal human trichromat. This is the same result which one obtains from a human with protanomalous color vsion—a common type of defect which is in some ways intermediate between normal color vision and protanopia.

In another color-vision test, hue discrimination (the ability of subjects to detect differences in wavelength in different spectral regions) was examined. In this test, three windows are illuminated with light of a given wavelength—for example, orange light of 590-nanometer wavelength—and a fourth is illuminated by light of a different wavelength (the test light)—for ex-

ample, 620 nanometers. In successive blocks of trials the wavelength of the test light is shifted, in small steps, closer and closer to 590 nanometers until the animal can no longer discriminate the test light from the other lights. The test light is then set to some short wavelength—say, 560 nanometers—and gradually shifted in steps toward 590 nanometers to test the subject's ability to discriminate wavelengths on the short-wavelength side of 590 nanometers. Similar tests of wavelength discrimination were carried out on either side of 14 test wavelengths spaced across the spectrum.

The results, shown in Fig. 1C, indicate that macaque monkeys have hue discrimination similar to that of normal trichromats; for both species the function has two minima, at about 490 and 590 nanometers. The results for squirrel monkeys, on the other hand, differ drastically in two respects. First, the hue discrimination of squirrel monkeys is in general far poorer than that of the macaques. A problem involving a choice between an orange light and a slightly yellowish orange light, for instance, is elementary for a macaque but quite insoluble for a squirrel monkey. Second, the shape of the hue-discrimination curve is quite different for the macaque and for the squirrel monkey: the curve for the macaque shows two spectral regions of optimum discrimination (in

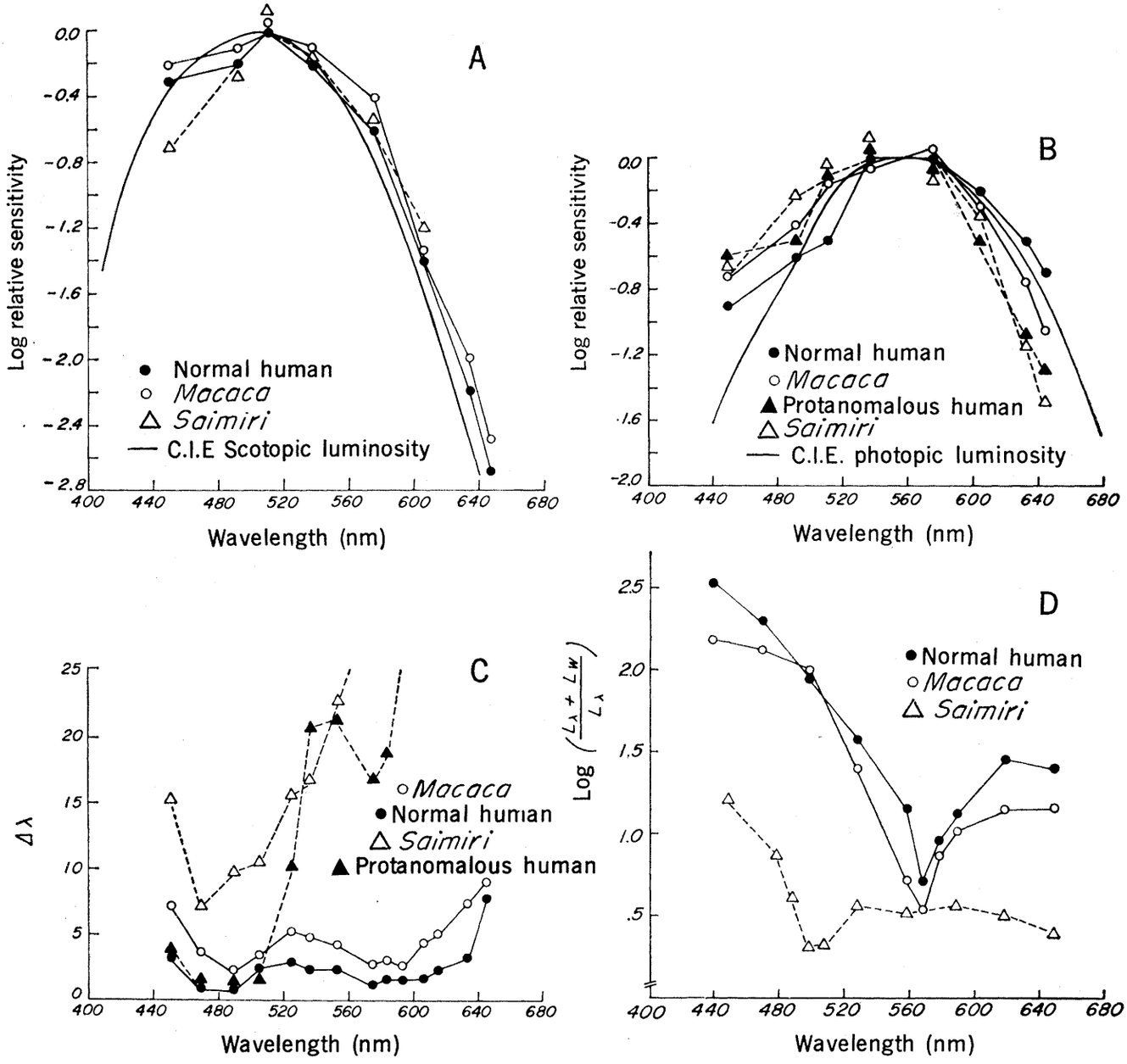

Fig. 1. Psychophysical tests of the visual capabilities of various primate species. (A) Scotopic spectral sensitivity, showing the essential similarity among species. (B) Photopic spectral sensitivity. The notable feature is the lower sensitivity at long wavelengths shown by the squirrel monkeys (*Saimiri*) and protanomalous humans. (C) Hue discrimination. The minimum discriminable difference in wavelength ($\Delta\lambda$) at each of 14 wavelengths was determined. Note that macaques and normal human trichromats have two regions of good hue discrimination, whereas squirrel monkeys and protanomalous humans have good hue discrimination only in the short-wavelength region. (D) Relative saturation of different spectral regions. On the ordinate is plotted the log of the reciprocal of the colorometric purity (percentage of monochromatic light in the mixture). ($L\lambda$) The amount of monochromatic light; (Lw) the amount of white light.

the orange and the blue-green), but that for the squirrel monkey shows only one, in the blue-green. In both these respects the squirrel monkey resembles the severely protanomalous human.

The final test is a test of spectral saturation (*10*). In this, the animal is trained to select some particular monochromatic light from three white lights. Once the animal can successfully do this, white light is added to the monochromatic stimulus, in succeeding trials, and the amount of monochromatic light is correspondingly decreased. This procedure is continued until the animal can no longer discriminate the colored light (now highly desaturated) from the three white lights. These tests are run at several different wavelengths.

The same pattern of results is obtained here as in the other experiments: macaques and normal human trichromats give one sort of result and squirrel monkeys and humans with color-vision defects give another (see Fig. 1D). For the macaque, all spectral regions except a small zone in the yellow are found to be quite highly saturated. For example, the addition of only a very small amount of monochromatic red light to white enables the macaque to distinguish the mixture from pure white. Much more yellow, however, has to be added to white in order for the macaque to distinguish the mixture from white. The whole spectrum is much less saturated for the squirrel monkey and the protanomalous human than it is for the macaque and the normal human trichromat. Furthermore, for the squirrel monkey, the least saturated part of the spectrum is not in the yellows but in the blue-greens.

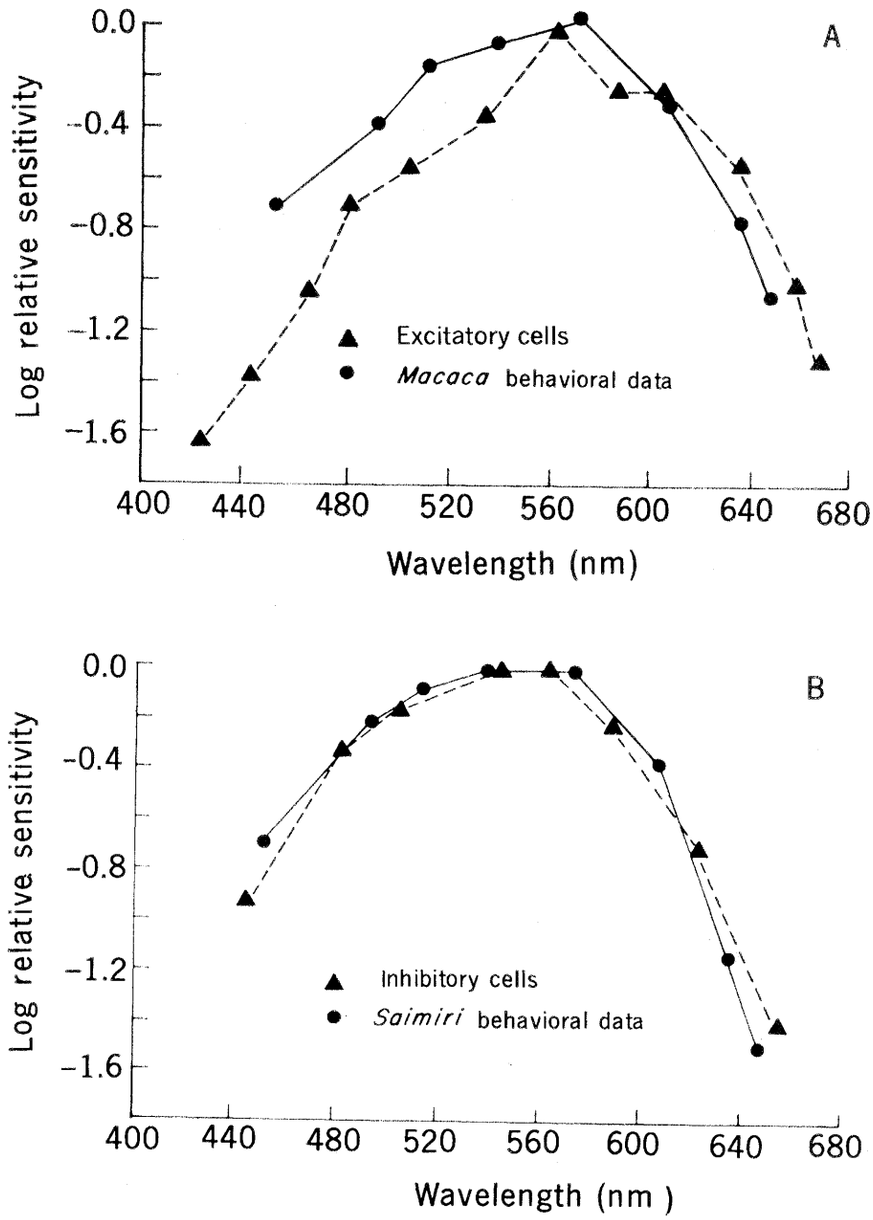

Fig. 2. Comparison of psychophysical measures of photopic spectral sensitivity with the spectral sensitivity of nonopponent cells in the visual system. This comparison is shown in (A) for the macaque and in (B) for the squirrel monkey (*Saimiri*). In the *Saimiri*, the lower sensitivity at long wavelengths is reflected in the lowered responsiveness of the inhibitory nonopponent cells. The sensitivity of the inhibitory cells of the macaque (not shown) agrees with that of the excitatory cells; the sensitivity of the excitatory cells of the *Saimiri* (not shown) agrees with that of the inhibitory cells.

These tests of brightness sensitivity and color vision lead in each instance to the conclusion that macaque monkeys and normal humans have essentially identical trichromatic vision. Squirrel monkeys, on the other hand, have much poorer color vision, and their color vision is qualitatively different from that of normal human trichromats, being similar to that of protanomalous humans. Similar but less complete studies of the *Cebus* monkey (*8*) give results which are much the same as those for the squirrel monkey. Grether's data (*4*) on the *Cebus*, from which he concluded that they were protanopes, are not really very different from ours. The protanomaly of both *Cebus* and *Saimiri* is quite severe, and it would be hard to distinguish this degree of protanomaly from protanopia without tests more complete than those Grether made.

The fact that these two most prevalent New World genera have poor color vision which, in both cases, is of the protanomalous type, whereas the most prevalent Old World primates, the macaques and man, have well-developed trichromatic vision, suggests a fundamental difference between these two branches of primates. Furthermore, a comparative study of the physiology of color vision in macaques and squirrel monkeys should provide a basis for extending our knowledge of the mechanisms of normal and defective color vision.

Physiological Tests

The data which provide information relevant to an understanding of the physiological mechanisms of normal and defective color vision come from experiments in which the electrical outputs of single cells in the lateral geniculate nucleus have been recorded when

the eye of the animal was diffusely illuminated with pulsed light of various wavelengths and intensities. Cells in the lateral geniculate nucleus are fourth-order neurons in the visual system which are conveniently located for intercepting visual information that has been processed by the retina and is being transmitted to the visual cortex. The details of the experimental situation and the major results have been presented elsewhere (*7*); here we summarize only the principal features relevant to the behavioral tests described above.

A general picture of the functional organization of the lateral geniculate nucleus has emerged from these experiments. Cells in this nucleus discharge "spontaneously" and respond to retinal stimulation with a modulation of the background-discharge rate in the direction either of increase ("excitatory" response) or decrease ("inhibitory" response). Two types of lateral-geniculate-nucleus cells can be distinguished, according to their response to monochromatic stimulation. Cells of one type show an increase in firing rate in response to all wavelengths, or a decrease in response to all wavelengths; cells of the second type show an increase in firing rate in response to some wavelengths and a decrease in response to others. Cells of the second type we call "spectrally opponent cells," because of the opposing responses produced by light from opposite ends of the spectrum; those of the first type we call "spectrally nonopponent cells" (*11*). Two types of nonopponent cells and four types of opponent cells have been identified.

We speculated some time ago that the opponent cells were analyzing and signaling color information, since they give different responses to different wavelengths; the nonopponent cells, which respond similarly to all wavelengths, were thought to be concerned with the transmission of achromatic information. That same conclusion was reached by Svaetichin and MacNichol (*12*), on the basis of similar results from experiments on fish retinas. It is possible, we believe, by comparing quantitative measures of the responses of these cells with behavioral measures discussed above, to go beyond speculation and draw some firm conclusions about the roles of these cell types and thus about the physiological organization of the primate visual system.

The relative brightness of different

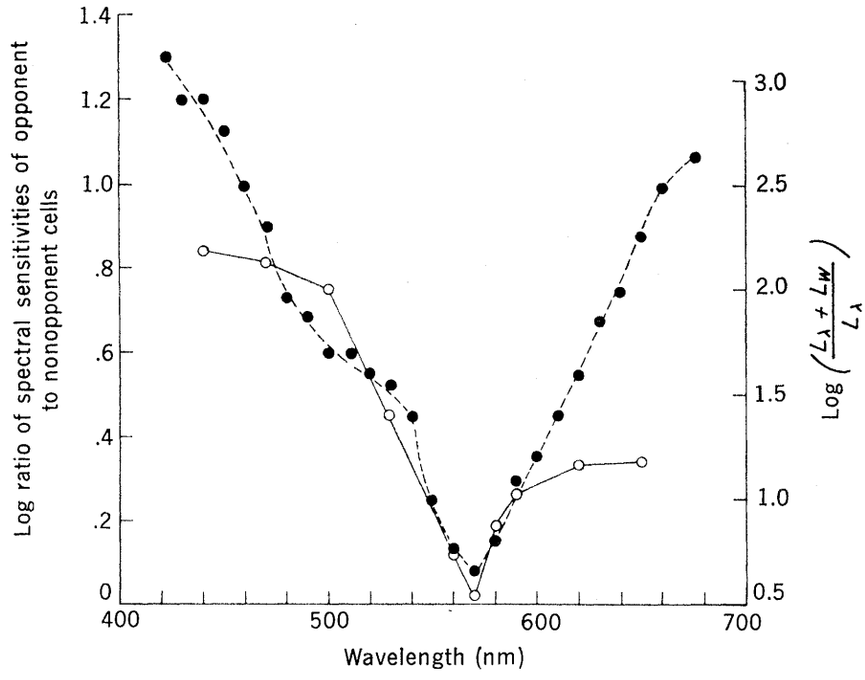

Fig. 3. Comparison of the relative saturation of various spectral lights, as determined in psychophysical tests of the macaque, with the relative sensitivities of macaque opponent and nonopponent cells at various wavelengths. (Solid circles) *Macaca* cells; (open circles) *Macaca* behavioral data. The ordinate at left, for the behavioral data, and the ordinate at right, for cell responses, have been adjusted for best fit. $L\lambda$ and Lw as in Fig. 1D.

spectral regions—the luminosity function—is really not as simple a matter as our discussion of the behavioral brightness tests, or the existence of a standard photopic luminosity curve, would suggest. The luminosity function depends considerably on the experimental methods used to determine it. In the general case, it appears likely that both chromatic and achromatic channels contribute to brightness. The nonadditivity of different spectral lights (that is, the failure of Abney's law) could be most easily explained if this were the case (*13*). The fact that multimodal luminosity curves are obtained under certain circumstances (*14*) is also consonant with this idea. However, in a flicker situation, such as we have used in the behavioral tests [the International Commission of Illumination (C.I.E.) standard photopic luminosity curve is also partially based on flicker data], the chromatic channels probably contribute little or nothing because they cannot follow rapidly flickering light. The relative brightness of various wavelengths as measured in a flicker situation, therefore, should depend on the extent to which they activate the achromatic channel. It is thus justifiable to quantitatively compare nonopponent-cell activity with behavioral measures of brightness determined in the flicker experiments. To make such a comparison, we recorded response of nonopponent cells to lights of different wavelengths at several different intensities in both macaques and squirrel monkeys. From these data, the intensity of light required to produce the same spike discharge rate at different wavelengths was determined. Although individual cells show considerable variability, averaging the responses of a number of macaque nonopponent cells (as the visual system does when the individual looks at anything other than a point source) produces a sensitivity curve which agrees very satisfactorily with the behavioral determinations.

The same comparison for the squirrel monkey data shows clearly that the spectral sensitivity of the nonopponent cells matches the deviant spectral sensitivity of this genus. This holds true for both the nonopponent excitatory and the nonopponent inhibitory cells. Both of these comparisons are shown in Fig. 2.

The saturation of a light is defined as the extent to which the light is chromatic as opposed to achromatic. If the opponent cells are signaling hue and the nonopponent cells are signaling the achromatic or white-black dimension, then one might suppose that the saturation of a stimulus light would be coded

by the difference between the amounts of opponent-cell and nonopponent-cell activity. That this holds in a rough way may be seen from the earlier discussion. White light strongly activates the nonopponent cells, but activates the opponent cells very little (since the opposing excitatory and inhibitory components are both activated by white light and thus tend to cancel each other out). Monochromatic light, on the other hand, strongly stimulates the appropriate opponent cells while at the same time affecting the nonopponent cells less than white light would.

This relationship can be quantitatively tested by comparing the activity rates of opponent and nonopponent cells with measures of spectral saturation at various spectral points. As we have seen, for the macaque the spectral extremes are highly saturated, while the region around 570 nanometers is desaturated relative to other wavelengths. If the spectral-sensitivity curve for the macaque opponent cells is subtracted from that for the nonopponent cells, the resultant function is very similar to the behavioral curve (Fig. 3). We can, therefore, conclude that the long and short wavelength stimuli are highly saturated, because opponent cells are much more responsive to these wavelengths than nonopponent cells are. The saturation dip at 570 nanometers results from both the high sensitivity of the nonopponent cells to this spectral region and the relatively low activity of opponent cells at this point, where many of them are crossing from excitation to inhibition and are thus not responding at all.

Any monochromatic light, as we have seen, activates both the chromatic (opponent) and the achromatic (nonopponent) cells and should therefore appear desaturated, to some extent, relative to the theoretical situation in which only chromatic cells were activated. If we can assume that our recordings from the lateral geniculate nuclei of the macaque and the squirrel monkey have given us a reasonably unbiased sample of the total activity in the visual pathways, then we should be able to predict not only the relative saturation of different spectral regions, as we did in Fig. 3 for the macaque, but the overall saturation of the spectrum for both the macaque and the squirrel monkey. To do this, we have counted the total number of spikes evoked by each monochromatic light from all of the opponent and all of the nonopponent cells in our samples. The percentage of the total

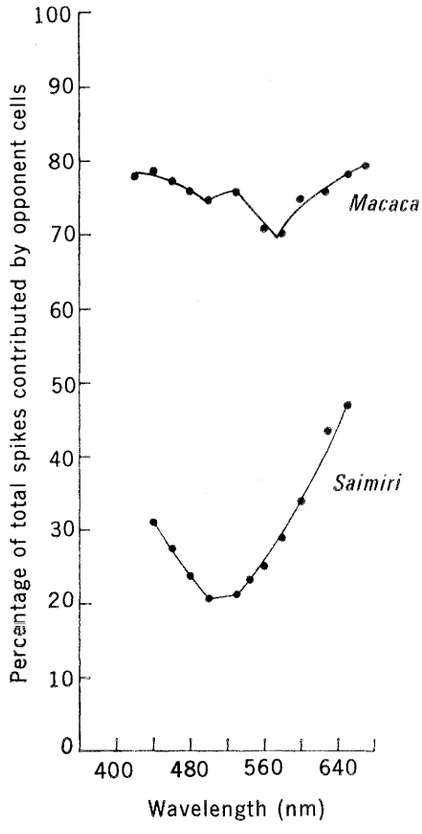

Fig. 4. Percentages of the total number of spikes contributed by spectrally opponent cells at each wavelength, as computed from the responses to monochromatic light of large random samples of macaque and squirrel-monkey lateral-geniculate-nucleus cells.

number of spikes contributed by the chromatic opponent cells gives an estimate of the overall saturation of the spectrum for each of these species.

Figure 4 shows these values for both the macaque and the squirrel monkey. Two things should be noted. (i) The proportion of the total spike count contributed by the opponent cells is much higher in the macaque than in the squirrel monkey. This is principally due to the relative paucity of opponent cells in the squirrel monkey—approximately 20 percent of the total cell population as compared with about 70 percent in the macaque, according to our samples (*15*). (ii) The minimum chromatic contribution occurs at wavelength of 570 nanometers for the macaque, whereas for the squirrel monkey it occurs at about 500 nanometers. This is perhaps attributable to the different photopigments in the long-wavelength receptors of the squirrel monkey, discussed below.

Both of these physiological features can be compared to the results of the behavioral tests of saturation (Fig. 1D). Although the differences shown by the physiological data between the opponent-cell contributions in macaques and in the squirrel monkeys are greater than would be expected from the behavioral data, they are certainly in the direction predicted by the finding from behavioral tests that the spectrum is more saturated for the macaque. The minimum saturation points at 570 and 500 nanometers for the macaque and squirrel monkey, respectively, are in agreement with the physiological data. This all supports the notion that the saturation of a light is encoded neurally by the proportion of the total response which is contributed by the spectrally opponent cells.

The hypothesis that the spectrally opponent cells are carrying information about hue can be tested by making several comparisons with behavioral data. First, it should be noted that opponent cells are not all the same. There is considerable variance among cells with respect to the spectral regions that excite or inhibit them. On a number of grounds we have concluded that cells may reasonably be divided into four classes: red excitatory, green inhibitory (+R−G); yellow excitatory, blue inhibitory (+Y−B); green excitatory, red inhibitory (+G−R); and blue excitatory, yellow inhibitory (+B−Y). The classes are named by color because, for example, the wavelengths which produce excitation in a +R−G cell (and inhibition in a +G−R cell) are just those wavelengths which appear red to an individual with normal color vision; those which produce excitation in a +Y−B cell are those which appear yellow to him; and so on. The colors of the different spectral regions correspond, not to the absorption peaks of the cone photopigments, but to the points of maximum response of the opponent cells (*7*).

Figure 5 shows schematically how the various types of cells in the lateral geniculate nucleus of the macaque respond to white light and to various spectral stimuli. The spike discharges depicted there are based on the averages of discharge rates recorded from a large population of lateral-geniculate-nucleus cells of the various types.

If the opponent cells are carrying information about hue, then the extent to which they give different responses to different wavelengths should correspond to the extent to which these wavelengths are discriminable in behavioral tests. In the macaque and in the nor-

mal human trichromat, small differences in wavelength are most easily discriminated in the orange and blue-green portions of the spectrum; these are also the spectral regions at which many cells shift from inhibitory to excitatory responses, or vice versa, and thus show large differences in firing rate relative to firing rate in response to neighboring wavelengths. The relationship has been tested quantitatively in the macaque (*16*) by recording the extent to which single cells can detect (that is, respond to, by a change in firing rate) a shift from one wavelength to another, nearby wavelength. This corresponds to a visual situation in which one looks back and forth between two colored surfaces, stimulating a region of the retina with first one and then another wavelength. Such tests show that the +R−G and +G−R opponent cells can detect very small shifts in wavelength in the orange region of the spectrum but that they do worse elsewhere; the +Y−B and +B−Y cells, on the other hand, detect wavelength shifts best in the blue-green region. The combined activity of all these cells accounts for the double-peaked hue-discrimination curve found in behavioral tests of macaque monkeys and shown in Fig. 1B. This result also provides very strong evidence for the view that opponent cells are transmitting information about the hue of the stimulus light.

Similar hue-discrimination studies have not been made with the squirrel monkey, but the fact that most of its opponent cells are of the +Y−B and +B−Y variety would lead one to predict the predominance of the 500-nanometer minimum in the squirrel monkey's hue-discrimination curve which was found in behavioral studies.

Finally, what can be said about the relationship between these lateral-geniculate-nucleus cells of various types and the photoreceptors in the retina? There is good spectrophotometric evidence for the presence of three different cone photopigments in the macaque retina, with maximum absorption at about 445, 540, and 570 nanometers, respectively (*17*). Lateral geniculate neurons reflect the combined activity of these different types of retinal receptors: there are no straight-through pathways to the brain from, say, cones with photopigment having an absorption peak at 540 nanometers ("540-nanometer pigment cones"). Nor should we expect any, for the multiple interconnections in the visual pathway are presumably there to provide for active data processing rather than simple transmission of information. It seems clear that the opponent cells reflect an organization in which the output of one type of cone is subtracted from that of another through the interplay of excitation and inhibition. Our evidence indicates that the +R−G and +G−R cells receive inputs from the 540- and 570-nanometer pigment cones, and that the +Y−B and +B−Y cells receive inputs from the 445- and 570-nanometer cones (*18*).

No spectrophotometric measurements have yet been made on the squirrel-monkey retina, but our recording studies suggest that in the squirrel monkey the short- and middle-wavelength pigments, with absorption maxima at 445 and 540 nanometers, respectively, are probably the same as in the macaque but the long-wavelength pigment is different from that in the macaque, having an absorption maximum at a shorter wavelength.

In the squirrel monkey, as in the macaque, the +R−G and +G−R cells respond to the difference between the outputs of the long- and middle-wavelength receptors. The +R−G cells, for instance, show excitation in response to a light to the extent that that light is absorbed more by the long-wavelength than by the middle-wavelength receptor, and inhibition to the extent that the converse is true. Inasmuch as the absorption curves of long-wavelength and middle-wavelength photopigments are more similar in the squirrel monkey than in the macaque, one should expect less net excitation and inhibition—that is, lower firing rates. This indeed appears to be the case: in particular, the +G−R cells in the squirrel monkey show considerably lower firing rates than the corresponding cells in the macaque. In addition, RG (+R−G and +G−R) cells are found proportion-

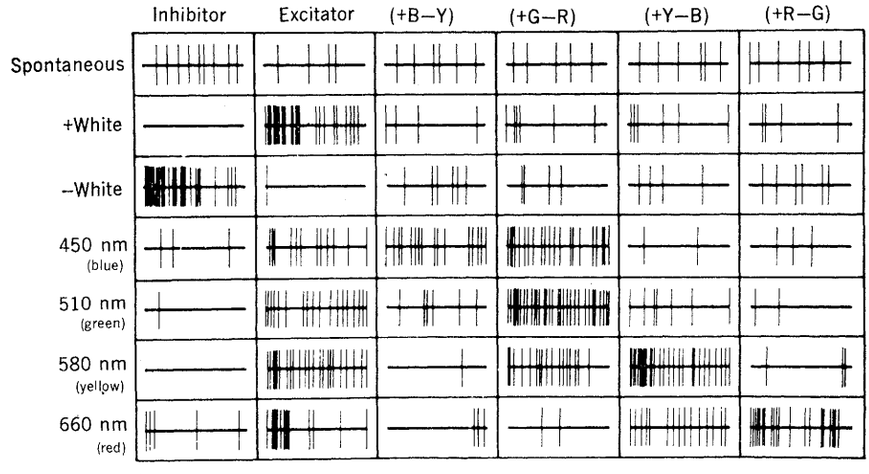

Fig. 5. Summary of discharge patterns of the six principal types of macaque lateral-geniculate-nucleus cells in response to various light flashes. The spike patterns were drawn to match the average firing rates of the large sample of cells from which recordings were made. (+White) Increment in white light; (−White) decrement in white light.

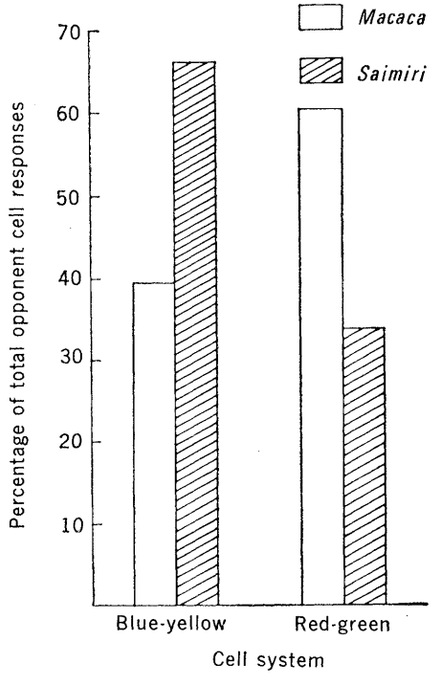

Fig. 6. Comparison, for opponent cells of the squirrel monkey and the macaque, of the percentages (relative to the total number of spikes) of spikes contributed by cells in the BY (+B−Y and +Y−B cells) and the RG (+R−G and +G−R cells) systems in response to various spectral lights.

ately less frequently in the opponent-cell population of the squirrel monkey than in that of the macaque. The net result of both these factors is that, in the macaque, the RG cells contribute a larger proportion of the total spike output of the opponent cells than the BY cells do, whereas in the squirrel monkey the reverse is true (see Fig. 6). Consequently, in the squirrel monkey, both the hue-discrimination and the saturation-discrimination functions are principally determined by the BY system, with its neutral point around a wavelength of 500 nanometers and its best hue discrimination in this region. The macaque, on the other hand, shows predominance of the RG system in both these behavioral tests.

The dichromatic protanope or deuteranope may be the limiting case of such a displacement in absorption curve of one of the long-wavelength pigments; here the long- and middle-wavelength receptors would have the same absorption characteristics, and the +R−G and +G−R cells would have zero activity, if they are present at all (*19*).

Summary

The evidence obtained from a comparison of the results of behavioral and physiological studies of the macaque and the squirrel monkey seems to reflect the considerable differences between the color vision of Old World and New World monkeys. These data also give us insight into the mechanisms of normal and defective color vision in man. The visual systems of macaque monkeys and normal humans are nearly identical. In both these systems the outputs from the various cones are added together in one set of information channels (nonopponent cells) to indicate the whiteness-blackness of a light. This channel is also the principal determinant of the brightness of a light. In other channels (opponent cells) the output from one of the three cone types is subtracted from the output of one of the others, in various combinations, to signal the hue of the light. The ratio of opponent to nonopponent cell activity in response to a flash of light signals the saturation of the light. The opponent cells are very sensitive to small differences in wavelength, particularly in certain spectral regions, and provide the organism with information about color differences in different parts of the visual field.

Squirrel monkeys and protanomalous humans, on the other hand, possess color vision which is both weak and deviant from the normal. The weak color vision can be attributed to a paucity of opponent cells, relative to the number in the macaque. The dominance of the 500-nanometer minimum in the relative saturation of the spectrum is attributable to the relatively few RG cells in the animal's (and presumably the protanomalous human being's) visual system, and to the low activity rate in the RG cells, due to the spectrally displaced photopigment present in the long-wavelength receptors.

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9. Similar results have also been obtained in several other recent studies: D. S. Blough and A. M. Schrier, *Science* **139**, 493 (1963); A. M. Schrier and D. S. Blough, *J. Comp. Physiol. Psychol.* **62**, 457 (1966); N. A. Sidley and H. G. Sperling, *J. Opt. Soc. Amer.* **57**, 816 (1967).
10. Brightness, hue, and saturation are three subjective dimensions of color. The degree of saturation of a light refers to the extent to which it has hue and thus differs from the achromatic white-gray-black colors. Monochromatic lights differ considerably in their relative saturation, short and long wavelengths being more saturated than the middle spectral region. The spectrum is in general much less saturated for color-blind observers than for normals; the neutral point in the spectrum of dichromats referred to above is of course a spectral region of zero saturation for them.
11. Both of these types of cells may be spatially opponent, in that they respond with excitation or inhibition depending on the location of the light in the receptive field. Some of these spatial features have recently been indicated for the macaque [T. N. Wiesel and D. H. Hubel, *J. Neurophysiol.* **29**, 1115 (1966); W. R. Mead, thesis, Indiana University (1967)]. Here we are considering only the responses of the cells to light flashes which cover the whole receptive field, a situation comparable to that commonly used in studies of visual psychophysics.
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15. It might be remarked that the cat would have a score of essentially zero on this scale, since no clear evidence has been found for any but the slightest opponent activity in the cat's visual system. This is consonant with behavioral tests which indicate that the cat has only rudimentary color vision.
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19. The reader may note that the sorts of relationships between the psychophysical and physiological data suggested here bear an obvious similarity to the conceptions of the color-vision process originally enunciated by Hering, and recently elaborated by Hurvich and Jameson in their opponent-colors theory [*Psychol. Rev.* **64**, 384 (1957)]. Our data, however, comprise only a general substantiation of such theoretical notions, since at a number of points the physiological data are in disagreement with their theories. A conclusive formulation of the physiological processes involved in color vision will require considerably more detail from electrophysiological studies.
20. This work was supported by U.S. Public Health Service grant NB-02274 and National Science Foundation grants G-24125 and GB-4150.