The Feynman

LECTURES ON
PHYSICS

MAINLY MECHANICS, RADIATION, AND HEAT

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Color Vision

35–1 The human eye

The phenomenon of colors depends partly on the physical world. We discuss the colors of soap films and so on as being produced by interference. But also, of course, it depends on the eye, or what happens behind the eye, in the brain. Physics characterizes the light that enters the eye, but after that, our sensations are the result of photochemical-neural processes and psychological responses.

There are many interesting phenomena associated with vision which involve a mixture of physical phenomena and physiological processes, and the full appreciation of natural phenomena, as we *see* them, must go beyond physics in the usual sense. We make no apologies for making these excursions into other fields, because the separation of fields, as we have emphasized, is merely a human convenience, and an unnatural thing. Nature is not interested in our separations, and many of the interesting phenomena bridge the gaps between fields.

In Chapter 3 we have already discussed the relation of physics to the other sciences in general terms, but now we are going to look in some detail at a specific field in which physics and other sciences are very, very closely interrelated. That area is *vision*. In particular, we shall discuss *color vision*. In the present chapter we shall discuss mainly the observable phenomena of human vision, and in the next chapter we shall consider the physiological aspects of vision, both in man and in other animals.

It all begins with the eye; so, in order to understand what phenomena we see, some knowledge of the eye is required. In the next chapter we shall discuss in some detail how the various parts of the eye work, and how they are interconnected with the nervous system. For the present, we shall describe only briefly how the eye functions (Fig. 35–1).

Light enters the eye through the *cornea*; we have already discussed how it is bent and is imaged on a layer called the *retina* in the back of the eye, so that different parts of the retina receive light from different parts of the visual field outside. The retina is not absolutely uniform: there is a place, a spot, in the center of our field of view which we use when we are trying to see things very carefully, and at which we have the greatest acuity of vision; it is called the *fovea* or *macula*. The side parts of the eye, as we can immediately appreciate from our experience in looking at things, are not as effective for seeing detail as is the center of the eye. There is also a spot in the retina where the nerves carrying all the information run out; that is a blind spot. There is no sensitive part of the retina here, and it is possible to demonstrate that if we close, say, the left eye and look straight at something, and then move a finger or another small object slowly out of the field of view it suddenly disappears somewhere. The only practical use of this fact that we know of is that some physiologist became quite a favorite in the court of a king of France by pointing this out to him; in the boring sessions that he had with his courtiers, the king could amuse himself by "cutting off their heads" by looking at one and watching another's head disappear.

Figure 35–2 shows a magnified view of the inside of the retina in somewhat schematic form. In different parts of the retina there are different kinds of structures. The objects that occur more densely near the periphery of the retina are called *rods*. Closer to the fovea, we find, besides these rod cells, also *cone* cells. We shall describe the structure of these cells later. As we get close to the fovea, the number of cones increases, and in the fovea itself there are in fact nothing but cone cells, packed very tightly, so tightly that the cone cells are much finer, or narrower
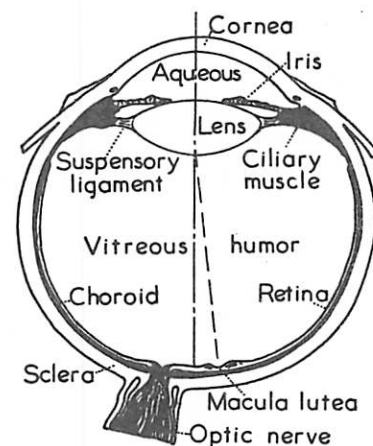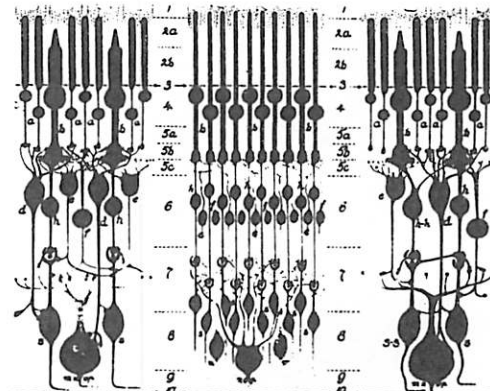
Fig. 35–1. The eye.

Fig. 35–2. The structure of the retina. (Light enters from below.)

here than anywhere else. So we must appreciate that we see with the cones right in the middle of the field of view, but as we go to the periphery we have the other cells, the rods. Now the interesting thing is that in the retina each of the cells which is sensitive to light is not connected by a fiber directly to the optic nerve, but is connected to many other cells, which are themselves connected to each other. There are several kinds of cells: there are cells that carry the information toward the optic nerve, but there are others that are mainly interconnected "horizontally." There are essentially four kinds of cells, but we shall not go into these details now. The main thing we emphasize is that the light signal is already being "thought about." That is to say, the information from the various cells does not immediately go to the brain, spot for spot, but in the retina a certain amount of the information has already been digested, by a combining of the information from several visual receptors. It is important to understand that some brain-function phenomena occur in the eye itself.

35–2 Color depends on intensity

One of the most striking phenomena of vision is the dark adaptation of the eye. If we go into the dark from a brightly lighted room, we cannot see very well for a while, but gradually things become more and more apparent, and eventually we can see something where we could see nothing before. If the intensity of the light is very low, the things that we see have *no color*. It is known that this dark-adapted vision is amost entirely due to the rods, while the vision in bright light is due to the cones. As a result, there are a number of phenomena that we can easily appreciate because of this transfer of function from the cones and rods together, to just the rods.

There are many situations in which, if the light intensity were stronger, we could see color, and we would find these things quite beautiful. One example is that through a telescope we nearly always see "black and white" images of faint nebulae, but W. C. Miller of the Mt. Wilson and Palomar Observatories had the patience to make *color* pictures of some of these objects. Nobody has ever really seen these colors with the eye, but they are not artificial colors, it is merely that the light intensity is not strong enough for the cones in our eye to see them. Among the more spectacular such objects are the ring nebula and the Crab nebula. The former shows a beautiful blue inner part, with a bright red outer halo, and the latter shows a general bluish haze permeated by bright red-orange filaments.

In the bright light, apparently, the rods are at very low sensitivity but, in the dark, as time goes on they pick up their ability to see light. The variations in light intensity for which one can adapt is over a million to one. Nature does not do all this with just one kind of cell, but she passes her job from bright-light-seeing cells, the color-seeing cells, the cones, to low-intensity, dark-adapted cells, the rods. Among the interesting consequences of this shift is, first, that there is no color, and second, that there is a difference in the relative brightness of differently colored objects. It turns out that the rods see better toward the blue than the cones do, and the cones can see, for example, deep red light, while the rods find that absolutely impossible to see. So red light is black so far as the rods are concerned. Thus two pieces of colored paper, say blue and red, in which the red might be even brighter than the blue in good light, will, in the dark, appear completely reversed. It is a very striking effect. If we are in the dark and can find a magazine or something that has colors and, before we know for sure what the colors are, we judge the lighter and darker areas, and if we then carry the magazine into the light, we may see this very remarkable shift between which was the brightest color and which was not. The phenomenon is called the *Purkinje effect*.

In Fig. 35–3, the dashed curve represents the sensitivity of the eye in the dark, i.e., using the rods, while the solid curve represents it in the light. We see that the peak sensitivity of the rods is in the green region and that of the cones is more in the yellow region. If there is a red-colored page (red is about 650 mμ) we can see it if it is brightly lighted, but in the dark it is almost invisible.
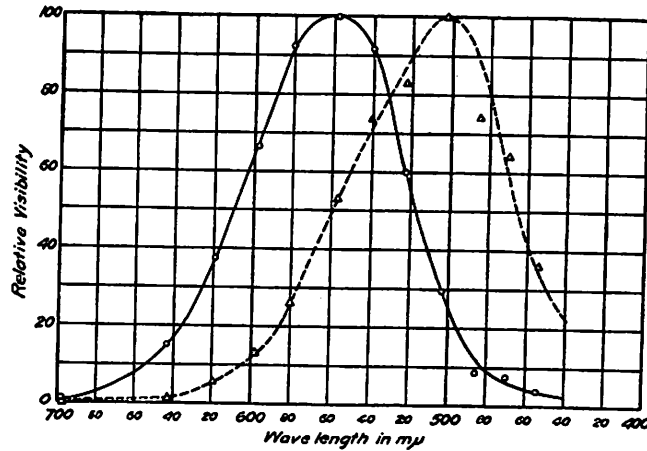
Fig. 35–3. The spectral sensitivity of the eye. Dashed curve, rods; solid curve, cones.

Another effect of the fact that rods take over in the dark, and that there are no rods in the fovea, is that when we look straight at something in the dark, our vision is not quite as acute as when we look to one side. A faint star or nebula can sometimes be seen better by looking a little to one side than directly at it, because we do not have sensitive rods in the middle of the fovea.

Another interesting effect of the fact that the number of cones decreases as we go farther to the side of the field of view is that even in a bright light color disappears as the object goes far to one side. The way to test that is to look in some particular fixed direction, let a friend walk in from one side with colored cards, and try to decide what color they are before they are right in front of you. One finds that he can see that the cards are there long before he can determine the color. When doing this, it is advisable to come in from the side opposite the blind spot, because it is otherwise rather confusing to almost see the color, then not see anything, then to see the color again.

Another interesting phenomenon is that the periphery of the retina is very sensitive to motion. Although we cannot see very well from the corner of our eye, if a little bug moves and we do not expect anything to be moving over there, we are immediately sensitive to it. We are all "wired up" to look for something jiggling to the side of the field.

35–3 Measuring the color sensation

Now we go to the cone vision, to the brighter vision, and we come to the question which is most characteristic of cone vision, and that is color. As we know, white light can be split by a prism into a whole spectrum of wavelengths which appear to us to have different colors; that is what colors are, of course: appearances. Any source of light can be analyzed by a grating or a prism, and one can determine the spectral distribution, i.e., the "amount" of each wavelength. A certain light may have a lot of blue, considerable red, very little yellow, and so on. That is all very precise in the sense of physics, but the question is, what color will it appear to be? It is evident that the different colors depend somehow upon the spectral distribution of the light, but the problem is to find what characteristics of the spectral distribution produce the various sensations. For example, what do we have to do to get a green color? We all know that we can simply take a piece of the spectrum which is green. But is that the *only* way to get green, or orange, or any other color?

Is there more than one spectral distribution which produces the same apparent visual effect? The answer is, definitely *yes*. There is a very limited number of visual effects, in fact just a three-dimensional manifold of them, as we shall shortly see, but there is an infinite number of different curves that we can draw for the light that comes from different sources. Now the question we have to discuss is, under what conditions do different distributions of light appear as exactly the same color to the eye?

35–3

The most powerful psycho-physical technique in color judgment is to use the eye as a *null instrument*. That is, we do not try to define what consitutes a green sensation, or to measure in what circumstances we get a green sensation, because it turns out that this is extremely complicated. Instead, we study the conditions under which two stimuli are *indistinguishable*. Then we do not have to decide whether two people see the same sensation in different circumstances, but only whether, if for one person two sensations are the same, they are also the same for another. We do not have to decide whether, when one sees something green, what it feels like inside is the same as what it feels like inside someone else when he sees something green; we do not know anything about that.

To illustrate the possibilities, we may use a series of four projector lamps which have filters on them, and whose brightnesses are continuously adjustable over a wide range: one has a red filter and makes a spot of red light on the screen, the next one has a green filter and makes a green spot, the third one has a blue filter, and the fourth one is a white circle with a black spot in the middle of it. Now if we turn on some red light, and next to it put some green, we see that in the area of overlap it produces a sensation which is not what we call reddish green, but a new color, yellow in this particular case. By changing the proportions of the red and the green, we can go through various shades of orange and so forth. If we have set it for a certain yellow, we can also obtain that same yellow, not by mixing these two colors but by mixing some other ones, perhaps a yellow filter with white light, or something like that, to get the same sensation. In other words, it is possible to make various colors in more than one way by mixing the lights from various filters.

What we have just discovered may be expressed analytically as follows. A particular yellow, for example, can be represented by a certain symbol Y, which is the "sum" of certain amounts of red-filtered light (R) and green-filtered light (G). By using two numbers, say r and g, to describe how bright the (R) and (G) are, we can write a formula for this yellow:

$$Y = rR + gG. \tag{35.1}$$

The question is, can we make *all* the different colors by adding together two or three lights of different, fixed colors? Let us see what can be done in that connection. We certainly cannot get all the different colors by mixing only red and green, because, for instance, blue never appears in such a mixture. However, by putting in some blue the central region, where all three spots overlap, may be made to appear to be a fairly nice white. By mixing the various colors and looking at this central region, we find that we can get a considerable range of colors in that region by changing the proportions, and so it is not impossible that *all* the colors can be made by mixing these three colored lights. We shall discuss to what extent this is true; it is in fact essentially correct, and we shall shortly see how to define the proposition better.

In order to illustrate our point, we move the spots on the screen so that they all fall on top of each other, and then we try to match a particular color which appears in the annular ring made by the fourth lamp. What we once thought was "white" coming from the fourth lamp now appears yellowish. We may try to match that by adjusting the red and green and blue as best we can by a kind of trial and error, and we find that we can approach rather closely this particular shade of "cream" color. So it is not hard to believe that we can make all colors. We shall try to make yellow in a moment, but before we do that, there is one color that might be very hard to make. People who give lectures on color make all the "bright" colors, but they never make *brown*, and it is hard to recall ever having seen brown light. As a matter of fact, this color is never used for any stage effect, one never sees a spotlight with brown light; so we think it might be impossible to make brown. In order to find out whether it is possible to make brown, we point out that brown light is merely something that we are not used to seeing without its background. As a matter of fact, we can make it by mixing some red and yellow. To prove that we are looking at brown light, we merely increase the brightness of the annular

background against which we see the very same light, and we see that that is, in fact, what we call brown! Brown is always a dark color next to a lighter background. We can easily change the character of the brown. For example, if we take some green out we get a reddish brown, apparently a chocolatey reddish brown, and if we put more green into it, in proportion, we get that horrible color which all the uniforms of the Army are made of, but the light from that color is not so horrible by itself; it is of yellowish green, but seen against a light background.

Now we put a yellow filter in front of the fourth light and try to match that. (The intensity must of course be within the range of the various lamps; we cannot match something which is too bright, because we do not have enough power in the lamp.) But we *can* match the yellow; we use a green and red mixture, and put in a touch of blue to make it even more perfect. Perhaps we are ready to believe that, under good conditions, we can make a perfect match of any given color.

Now let us discuss the laws of color mixture. In the first place, we found that different spectral distributions can produce the same color; next, we saw that "any" color can be made by adding together three special colors, red, blue, and green. The most interesting feature of color mixing is this: if we have a certain light, which we may call X, and if it appears indistinguishable from Y, to the eye (it may be a different spectral distribution, but it *appears* indistinguishable), we call these colors "equal," in the sense that the eye sees them as equal, and we write

$$X = Y. \tag{35.2}$$

Here is one of the great laws of color: if two spectral distributions are indistinguishable, and we *add to each one* a certain light, say Z (if we write $X + Z$, this means that we shine both lights on the same patch), and then we take Y and add the same amount of the same other light, Z, *the new mixtures are also indistinguishable:*

$$X + Z = Y + Z. \tag{35.3}$$

We have just matched our yellow; if we now shine pink light on the whole thing, it will still match. So adding any other light to the matched lights leaves a match. In other words, we can summarize all these color phenomena by saying that once we have a match between two colored lights, seen next to each other in the same circumstances, then this match will remain, and one light can be substituted for the other light in any other color mixing situation. In fact, it turns out, and it is very important and interesting, that this matching of the color of lights is not dependent upon the characteristics of the eye at the moment of observation: we know that if we look for a long time at a bright red surface, or a bright red light, and then look at a white paper, it looks greenish, and other colors are also distorted by our having looked so long at the bright red. If we now have a match between, say, two yellows, and we look at them and make them match, then we look at a bright red surface for a long time, and then turn back to the yellow, it may not look yellow any more; I do not know what color it will look, but it will not look yellow. Nevertheless *the yellows will still look matched*, and so, as the eye adapts to various levels of intensity, the color match still works, with the obvious exception of when we go into the region where the intensity of the light gets so low that we have shifted from cones to rods; then the color match is no longer a color match, because we are using a different system.

The second principle of color mixing of lights is this: *any color at all can be made from three different colors*, in our case, red, green, and blue lights. By suitably mixing the three together we can make anything at all, as we demonstrated with our two examples. Further, these laws are very interesting mathematically. For those who are interested in the mathematics of the thing, it turns out as follows. Suppose that we take our three colors, which were red, green, and blue, but label them A, B, and C, and call them our *primary* colors. Then any color could be made by certain amounts of these three: say an amount a of color A, an amount b of color B, and an amount c of color C makes X:

$$X = aA + bB + cC. \tag{35.4}$$

Now suppose another color Y is made from the same three colors:

$$Y = a'A + b'B + c'C. \tag{35.5}$$

Then it turns out that the mixture of the two lights (it is one of the consequences of the laws that we have already mentioned) is obtained by taking the sum of the components of X and Y:

$$Z = X + Y = (a + a')A + (b + b')B + (c + c')C. \tag{35.6}$$

It is just like the mathematics of the addition of vectors, where (a, b, c) are the components of one vector, and (a', b', c') are those of another vector, and the new light Z is then the "sum" of the vectors. This subject has always appealed to physicists and mathematicians. In fact, Schrödinger wrote a wonderful paper on color vision in which he developed this theory of vector analysis as applied to the mixing of colors.

Now a question is, what are the correct primary colors to use? There is no such thing as "the" correct primary colors for the mixing of lights. There may be, for practical purposes, three paints that are more useful than others for getting a greater variety of mixed pigments, but we are not discussing that matter now. *Any three differently colored lights whatsoever** can always be mixed in the correct proportion to produce *any color whatsoever*. Can we demonstrate this fantastic fact? Instead of using red, green, and blue, let us use red, blue, and yellow in our projector. Can we use red, blue, and yellow to make, say, green?

By mixing these three colors in various proportions, we get quite an array of different colors, ranging over quite a spectrum. But as a matter of fact, after a lot of trial and error, we find that nothing ever looks like green. The question is, *can* we make green? The answer is yes. How? *By projecting some red onto the green*, then we can make a match with a certain mixture of yellow and blue! So we have matched them, except that we had to cheat by putting the red on the other side. But since we have some mathematical sophistication, we can appreciate that what we really showed was not that X could always be made, say, of red, blue, and yellow, but by putting the red on the other side we found that red plus X could be made out of blue and yellow. Putting it on the other side of the equation, we can interpret that as a *negative amount*, so if we will allow that the coefficients in equations like (35.4) can be both positive and negative, and if we interpret negative amounts to mean that we have to *add* those to the *other side*, then any color can be matched by any three, and there is no such thing as "the" fundamental primaries.

We may ask whether there are three colors that come only with positive amounts for all mixings. The answer is no. Every set of three primaries requires negative amounts for some colors, and therefore there is no unique way to define a primary. In elementary books they are said to be red, green, and blue, but that is merely because with these a *wider range* of colors is available without minus signs for some of the combinations.

35–4 The chromaticity diagram

Now let us discuss the combination of colors on a mathematical level as a geometrical proposition. If any one color is represented by Eq. (35.4), we can plot it as a vector in space by plotting along three axes the amounts a, b, and c, and then a certain color is a point. If another color is a', b', c', that color is located somewhere else. The sum of the two, as we know, is the color which comes from adding these as vectors. We can simplify this diagram and represent everything on a plane by the following observation: if we had a certain color light, and merely doubled a and b and c, that is, if we make them all stronger in the same ratio, it is the same color, but brighter. So if we agree to reduce everything to the *same light intensity*, then we can project everything onto a plane, and this has been done in Fig. 35–4. It follows that any color obtained by mixing a given two in some pro-

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* Except, of course, if one of the three can be matched by mixing the other two.

portion will lie somewhere on a line drawn between the two points. For instance, a fifty-fifty mixture would appear halfway between them, and 1/4 of one and 3/4 of the other would appear 1/4 of the way from one point to the other, and so on. If we use a blue and a green and a red, as primaries, we see that all the colors that we can make with positive coefficients are inside the dotted triangle, which contains almost all of the colors that we can ever see, because all the colors that we can ever see are enclosed in the oddly shaped area bounded by the curve. Where did this area come from? Once somebody made a very careful match of all the colors that we can see against three special ones. But we do not have to check *all* colors that we can see, we only have to check the pure spectral colors, the lines of the spectrum. Any light can be considered as a sum of various positive amounts of various pure spectral colors—pure from the physical standpoint. A given light will have a certain amount of red, yellow, blue, and so on—spectral colors. So if we know how much of each of our three chosen primaries is needed to make each of these pure components, we can calculate how much of each is needed to make our given color. So, if we find out what the *color coefficients* of all the spectral colors are for any given three primary colors, then we can work out the whole color mixing table.

An example of such experimental results for mixing three lights together is given in Fig. 35–5. This figure shows the amount of each of three different particular primaries, red, green and blue, which is required to make each of the spectral colors. Red is at the left end of the spectrum, yellow is next, and so on, all the way to blue. Notice that at some points minus signs are necessary. It is from such data that it is possible to locate the position of all of the colors on a chart, where the x- and the y-coordinates are related to the amounts of the different primaries that are used. That is the way that the curved boundary line has been found. It is the locus of the pure spectral colors. Now any other color can be made by adding spectral lines, of course, and so we find that anything that can be produced by connecting one part of this curve to another is a color that is available in nature. The straight line connects the extreme violet end of the spectrum with the extreme red end. It is the locus of the purples. Inside the boundary are colors that can be made with lights, and outside it are colors that cannot be made with lights, and nobody has ever seen them (except, possibly, in after-images!).

35–5 The mechanism of color vision

Now the next aspect of the matter is the question, *why do colors behave in this way?* The simplest theory, proposed by Young and Helmholtz, supposes that in the eye there are three different pigments which receive the light and that these have different absorption spectra, so that one pigment absorbs strongly, say, in the red, another absorbs strongly in the blue, another absorbs in the green. Then when we shine a light on them we will get different amounts of absorptions in the three regions, and these three pieces of information are somehow maneuvered in the brain or in the eye, or somewhere, to decide what the color is. It is easy to demonstrate that all of the rules of color mixing would be a consequence of this proposition. There has been considerable debate about the thing because the next problem, of course, is to find the absorption characteristics of each of the three pigments. It turns out, unfortunately, that because we can transform the color coordinates in any manner we want to, we can only find all kinds of linear combinations of absorption curves by the color-mixing experiments, but not the curves for the individual pigments. People have tried in various ways to obtain a specific curve which does describe some particular physical property of the eye. One such curve is called a *brightness curve*, demonstrated in Fig. 35–3. In this figure are two curves, one for eyes in the dark, the other for eyes in the light; the latter is the cone brightness curve. This is measured by finding what is the smallest amount of colored light we need in order to be able to just see it. This measures how sensitive the eye is in different spectral regions. There is another very interesting way to measure this. If we take two colors and make them appear in an area, by flickering back and forth from one to the other, we see a flicker if the frequency is too low. However, as the frequency increases,
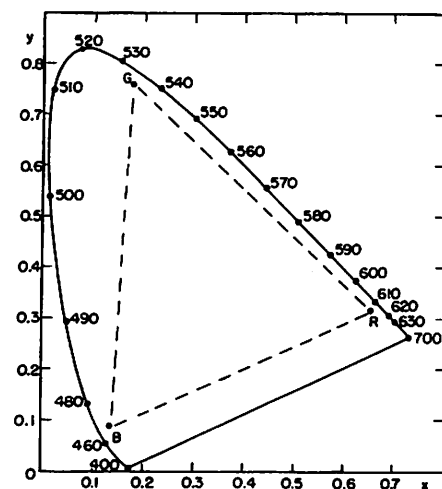

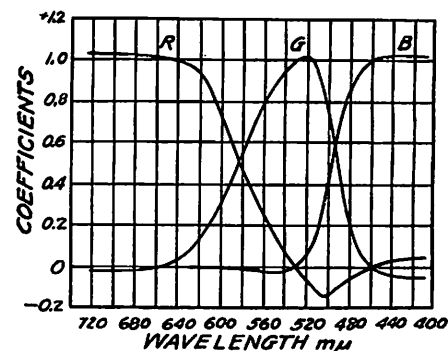Fig. 35–4. The standard chromaticity diagram.

Fig. 35–5. The color coefficients of pure spectral colors in terms of a certain set of standard primary colors.

the flicker will ultimately disappear at a certain frequency that depends on the brightness of the light, let us say at 16 repetitions per second. Now if we adjust the brightness or the intensity of one color against the other, there comes an intensity where the flicker at 16 cycles disappears. To get flicker with the brightness so adjusted, we have to go to a much lower frequency in order to see a flicker of the color. So, we get what we call a flicker of the brightness at a higher frequency and, at a lower frequency, a flicker of the color. It is possible to match two colors for "equal brightness" by this flicker technique. The results are almost, but not exactly, the same as those obtained by measuring the threshold sensitivity of the eye for seeing weak light by the cones. Most workers use the flicker system as a definition of the brightness curve.

Now, if there are three color-sensitive pigments in the eye, the problem is to determine the shape of the absorption spectrum of each one. How? We know there are people who are color blind—eight percent of the male population, and one-half of one percent of the female population. Most of the people who are color blind or abnormal in color vision have a different degree of sensitivity than others to a variation of color, but they still need three colors to match. However, there are some who are called *dichromats*, for whom any color can be matched using only *two* primary colors. The obvious suggestion, then, is to say that they are missing one of the three pigments. If we can find three kinds of color-blind dichromats who have different color-mixing rules, one kind should be missing the *red*, another the *green*, and another the *blue* pigmentation. By measuring all these types we can determine the three curves! It turns out that there *are* three types of dichromatic color blindness; there are two common types and a third very rare type, and from these three it has been possible to deduce the pigment absorption spectra.
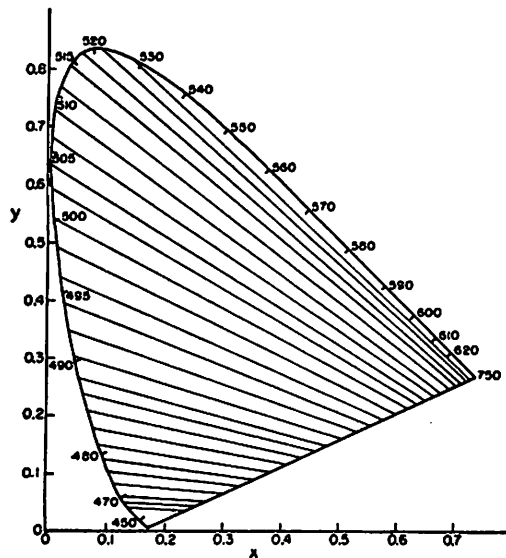
Fig. 35–6. Loci of colors confused by deuteranopes.
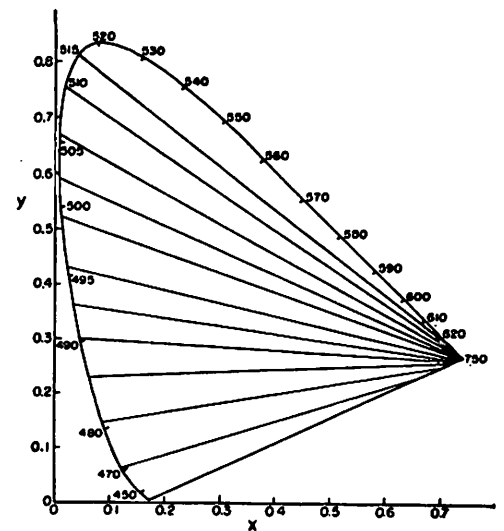
Fig. 35–7. Loci of colors confused by protanopes.

Figure 35–6 shows the color mixing of a particular type of color-blind person called a deuteranope. For him, the loci of constant colors are not points, but certain lines, along each of which the color appears to him to be the same. If the theory that he is missing one of the three pieces of information is right, all these lines should intersect at a point. If we carefully measure on this graph, they *do* intersect perfectly. Obviously, therefore, this has been made by a mathematician and does not represent real data! As a matter of fact, if we look at the latest paper with real data, it turns out that in the graph of Fig. 35–6, the point of focus of all the lines is not exactly at the right place. Using the lines in the above figure, we cannot find reasonable spectra; we need negative and positive absorptions in different regions. But using the new data of Yustova, it turns out that each of the absorption curves is everywhere positive.

35-8

Figure 35-7 shows a different kind of color blindness, that of the protanope, which has a focus near the red end of the boundary curve. Yustova gets approximately the same position in this case. Using the three different kinds of color blindness, the three pigment response curves have finally been determined, and are shown in Fig. 35-8. Finally? Perhaps. There *is* a question as to whether the three-pigment idea is right, whether color blindness results from lack of one pigment, and even whether the color-mix data on color blindness are right. Different workers get different results. This field is still very much under development.

Fig. 35-8. The spectral sensitivity curves of a normal trichromat's receptors.

35-6 Physiochemistry of color vision

Now, what about checking these curves against actual pigments in the eye? The pigments that can be obtained from a retina consist mainly of a pigment called *visual purple*. The most remarkable features of this are, first, that it is in the eye of almost every vertebrate animal, and second, that its response curve fits beautifully with the sensitivity of the eye, as seen in Fig. 35-9, in which are plotted on the same scale the absorption of visual purple and the sensitivity of the dark-adapted eye. This pigment is evidently the pigment that we see with in the dark: visual purple is the pigment for the rods, and it has nothing to do with color vision. This fact was discovered in 1877. Even today it can be said that the color pigments of the cones have never been obtained in a test tube. In 1958 it could be said that the color pigments had never been seen at all. But since that time, two of them have been detected by Rushton by a very simple and beautiful technique.

The trouble is, presumably, that since the eye is so weakly sensitive to bright light compared with light of low intensity, it needs a lot of visual purple to see with, but not much of the color pigments for seeing colors. Rushton's idea is to *leave the pigment in the eye*, and measure it anyway. What he does is this. There is an instrument called an opthalmoscope for sending light into the eye through the lens and then focusing the light that comes back out. With it one can measure how much is reflected. So one measures the reflection coefficient of light which has gone *twice* through the pigment (reflected by a back layer in the eyeball, and coming out through the pigment of the cone again). Nature is not always so beautifully designed. The cones are interestingly designed so that the light that comes into the cone bounces around and works its way down into the little sensitive points at the apex. The light goes right down into the sensitive point, bounces at the bottom and comes back out again, having traversed a considerable amount of the color-vision pigment; also, by looking at the fovea, where there are no rods, one is not confused by visual purple. But the color of the retina has been seen a long time ago: it is a sort of orangey pink; then there are all the blood vessels, and the color of the material at the back, and so on. How do we know when we are looking at the pigment? *Answer:* First we take a color-blind person, who has fewer pigments and for whom it is therefore easier to make the analysis. Second, the various pigments, like visual purple, have an intensity change when they are bleached by light; when we shine light on them they change their concentration. So, while looking at the absorption spectrum of the eye, Rushton put *another* beam in the whole eye, which changes the concentration of the pigment, and he measured the *change* in the spectrum, and the difference, of course, has nothing to do with the amount of blood or the color of the reflecting layers, and so on, but only the pigment, and in this manner Rushton obtained a curve for the pigment of the protanope eye, which is given in Fig. 35-10.

The second curve in Fig. 35-10 is a curve obtained with a normal eye. This was obtained by taking a normal eye and, having already determined what one pigment was, bleaching the other one in the red where the first one is insensitive. Red light has no effect on the protanope eye, but does in the normal eye, and thus one can obtain the curve for the missing pigment. The shape of one curve fits beautifully with Yustova's green curve, but the red curve is a little bit displaced. So perhaps we are getting on the right track. Or perhaps not—the latest work with deuteranopes does not show any definite pigment missing.
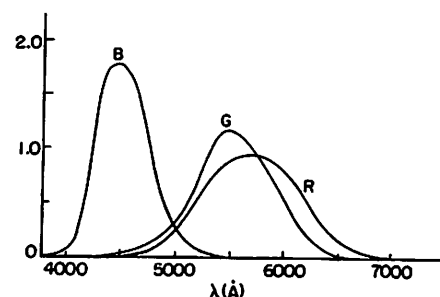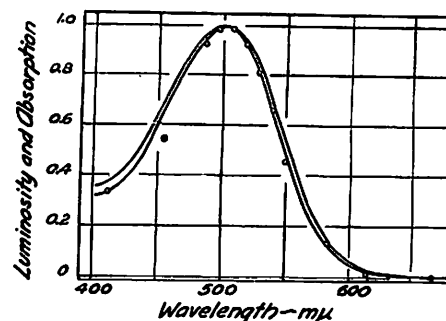

Fig. 35-9. The sensitivity curve of the dark-adapted eye, compared with the absorption curve of visual purple.
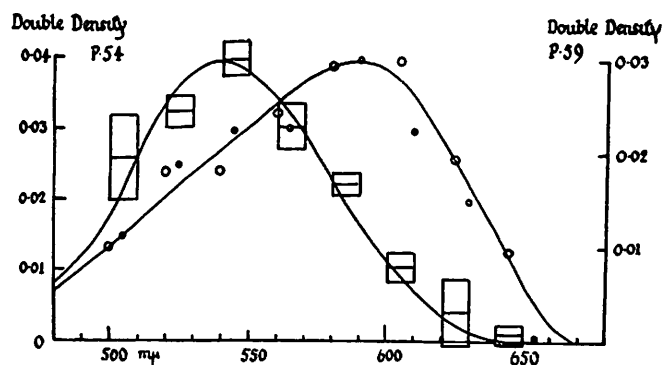
Fig. 35–10. Absorption spectrum of the color pigment of a protanope color-blind eye (squares) and a normal eye (dots).

Color is not a question of the physics of the light itself. Color is a *sensation*, and the sensation for different colors is different in different circumstances. For instance, if we have a pink light, made by superimposing crossing beams of white light and red light (all we can make with white and red is pink, obviously), we may show that white light may appear blue. If we place an object in the beams, it casts two shadows—one illuminated by the white light alone and the other by the red. For most people the "white" shadow of an object looks blue, but if we keep expanding this shadow until it covers the entire screen, we see that it suddenly appears white, not blue! We can get other effects of the same nature by mixing red, yellow, and white light. Red, yellow, and white light can produce only orangey yellows, and so on. So if we mix such lights roughly equally, we get only orange light. Nevertheless, by casting different kinds of shadows in the light, with various overlaps of colors, one gets quite a series of beautiful colors which are not in the light themselves (that is only orange), but in our *sensations*. We clearly *see* many different colors that are quite unlike the "physical" ones in the beam. It is very important to appreciate that a retina is already "thinking" about the light; it is comparing what it sees in one region with what it sees in another, although not consciously. What we know of how it does that is the subject of the next chapter.

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Mechanisms of Seeing

36–1 The sensation of color

In discussing the sense of sight, we have to realize that (outside of a gallery of modern art!) one does not see random spots of color or spots of light. When we look at an object we see a *man* or a *thing*; in other words, the brain interprets what we see. How it does that, no one knows, and it does it, of course, at a very high level. Although we evidently do learn to recognize what a man looks like after much experience, there are a number of features of vision which are more elementary but which also involve combining information from different parts of what we see. To help us understand how we make an interpretation of an entire image, it is worth while to study the earliest stages of the putting together of information from the different retinal cells. In the present chapter we shall concentrate mainly on that aspect of vision, although we shall also mention a number of side issues as we go along.

An example of the fact that we have an accumulation, at a very elementary level, of information from several parts of the eye at the same time, beyond our voluntary control or ability to learn, was that blue shadow which was produced by white light when both white and red were shining on the same screen. This effect at least involves the knowledge that the background of the screen is pink, even though, when we are looking at the blue shadow, it is only "white" light coming into a particular spot in the eye; somewhere, pieces of information have been put together. The more complete and familiar the context is, the more the eye will make corrections for peculiarities. In fact, Land has shown that if we mix that apparent blue and the red in various proportions, by using two photographic transparencies with absorption in front of the red and the white in different proportions, it can be made to represent a real scene, with real objects, rather faithfully. In this case we get a lot of intermediate apparent colors too, analogous to what we would get by mixing red and blue-green; it seems to be an almost complete set of colors, but if we look very hard at them, they are not so very good. Even so, it is surprising how much can be obtained from just red and white. The more the scene looks like a real situation, the more one is able to compensate for the fact that all the light is actually nothing but pink!

Another example is the appearance of "colors" in a black-and-white rotating disc, whose black and white areas are as shown in Fig. 36–1. When the disc is rotated, the variations of light and dark at any one radius are exactly the same; it is only the background that is different for the two kinds of "stripes." Yet one of the "rings" appears colored with one color and the other with another.* No one yet understands the reason for those colors, but it is clear that information is being put together at a very elementary level, in the eye itself, most likely.

Almost all present-day theories of color vision agree that the color-mixing data indicate that there are only three pigments in the cones of the eye, and that it is the spectral absorption in those three pigments that fundamentally produces the color sense. But the total sensation that is associated with the absorption characteristics of the three pigments acting together is not necessarily the sum of the individual sensations. We all agree that yellow simply *does not* seem to be reddish green; in fact it might be a tremendous surprise to most people to discover that light is, in fact, a mixture of colors, because presumably the sensation of light
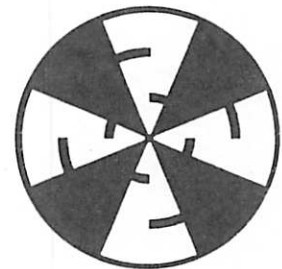
Fig. 36–1. When a disc like the above is spun, colors appear in only one of the two darker "rings." If the spin direction is reversed, the colors appear in the other ring.

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* The colors depend on speed of rotation, on the brightness of illumination, and to some extent on who looks at them and how intently he stares at them.

is due to some other process than a simple mixture like a chord in music, where the three notes are there at the same time and if we listen hard we can hear them individually. We cannot look hard and see the red and the green.

The earliest theories of vision said that there are three pigments and three kinds of cones, each kind containing one pigment; that a nerve runs from each cone to the brain, so that the three pieces of information are carried to the brain; and then in the brain, anything can happen. This, of course, is an incomplete idea: it does no good to discover that the information is carried along the optic nerve to the brain, because we have not even started to solve the problem. We must ask more basic questions: Does it make any difference *where* the information is put together? Is it important that it be carried right up into the brain in the optic nerve, or could the retina do some analysis first? We have seen a picture of the retina as an extremely complicated thing with lots of interconnections (Fig. 35–2) and it might make some analyses.

As a matter of fact, people who study anatomy and the development of the eye have shown that the retina is, in fact, the brain: in the development of the embryo, a piece of the brain comes out in front, and long fibers grow back, connecting the eyes to the brain. The retina is organized in just the way the brain is organized and, as someone has beautifully put it, "The brain has developed a way to look out upon the world." The eye is a piece of brain that is touching light, so to speak, on the outside. So it is not at all unlikely that some analysis of the color has already been made in the retina.

This gives us a very interesting opportunity. None of the other senses involves such a large amount of calculation, so to speak, before the signal gets into a nerve that one can make measurements on. The calculations for all the rest of the senses usually happen in the brain itself, where it is very difficult to get at specific places to make measurements, because there are so many interconnections. Here, with the visual sense, we have the light, three layers of cells making calculations, and the results of the calculations being transmitted through the optic nerve. So we have the first chance to observe physiologically how, perhaps, the first layers of the brain work in their first steps. It is thus of double interest, not simply interesting for vision, but interesting to the whole problem of physiology.

The fact that there are three pigments does not mean that there must be three kinds of sensations. One of the other theories of color vision has it that there are really opposing color schemes (Fig. 36–2). That is, one of the nerve fibers carries a lot of impulses if there is yellow being seen, and less than usual for blue. Another nerve fiber carries green and red information in the same way, and another, white and black. In other words, in this theory someone has already started to make a guess as to the system of wiring, the method of calculation.

The problems we are trying to solve by guessing at these first calculations are questions about the apparent colors that are seen on a pink background, what happens when the eye is adapted to different colors, and also the so-called psychological phenomena. The psychological phenomena are of the nature, for instance, that white does not "feel" like red and yellow and blue, and this theory was advanced because the psychologists say that there are *four* apparent pure colors: "There are four stimuli which have a remarkable capacity to evoke psychologically simple blue, yellow, green, and red hues respectively. Unlike sienna, magenta, purple, or most of the discriminable colors, these simple hues are unmixed in the sense that none partakes of the nature of the other; specifically, blue is not yellowish, reddish, or greenish, and so on; these are psychologically primary hues." That is a psychological fact, so-called. To find out from what evidence this psychological fact was deduced, we must search very hard indeed through all the literature. In the modern literature all we find on the subject are repeats of the same statement, or of one by a German psychologist, who uses as one of his authorities Leonardo da Vinci, who, of course, we all know was a great artist. He says, "Leonardo thought there were five colors." Then, looking still further, we find, in a still older book, the evidence for the subject. The book says something like this: "Purple is reddish-blue, orange is reddish-yellow, but can red be seen as purplish-orange? Are not red and yellow more unitary than purple or orange? The average person, asked to state which

Neural Responses

Photochemical Absorptions

$$y-b = k_1(\beta+\gamma-2\alpha)$$
$$r-g = k_2(\alpha+\gamma-2\beta)$$
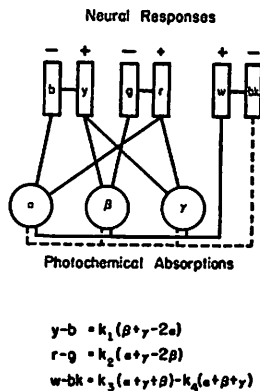$$w-bk = k_3(\alpha+\gamma+\beta)-k_4(\alpha+\beta+\gamma)$$

Fig. 36–2. Neural connections according to an "opponent" theory of color vision.

colors are unitary, names red, yellow, and blue, these three, and some observers add a fourth, green. Psychologists are accustomed to accept the four as salient hues." So that is the situation in the psychological analysis of this matter: if everybody says there are three, and somebody says there are four, and they want it to be four, it will be four. That shows the difficulty with psychological researches. It is clear that we have such feelings, but it is very difficult to obtain much information about them.

So the other direction to go is the physiological direction, to find out experimentally what actually happens in the brain, the eye, the retina, or wherever, and perhaps to discover that some combinations of impulses from various cells move along certain nerve fibers. Incidentally, primary pigments do not have to be in separate cells; one could have cells in which are mixtures of the various pigments, cells with the red and the green pigments, cells with all three (the information of all three is then white information), and so on. There are many ways of hooking the system up, and we have to find out which way nature has used. It would be hoped, ultimately, that when we understand the physiological connections we will have a little bit of understanding of some of those aspects of the psychology, so we look in that direction.

36–2 The physiology of the eye

We begin by talking not only about color vision, but about vision in general, just to remind ourselves about the interconnections in the retina, shown in Fig. 35–2. The retina is really like the surface of the brain. Although the actual picture through a microscope is a little more complicated looking than this somewhat schematized drawing, by careful analysis one can see all these interconnections. There is no question that one part of the surface of the retina is connected to other parts, and that the information that comes out on the long axons, which produce the optic nerve, are combinations of information from many cells. There are three layers of cells in the succession of function: there are retinal cells, which are the ones that the light affects, an intermediate cell which takes information from a single or a few retinal cells and gives it out again to several cells in a third layer of cells and carries it to the brain. There are all kinds of cross connections between cells in the layers.

We now turn to some aspects of the structure and performance of the eye (see Fig. 35–1). The focusing of the light is accomplished mainly by the cornea, by the fact that it has a curved surface which "bends" the light. This is why we cannot see clearly under water, because we then do not have enough difference between the index of the cornea, which is 1.37, and that of the water, which is 1.33. Behind the cornea is water, practically, with an index of 1.33, and behind that is a lens which has a very interesting structure: it is a series of layers, like an onion, except that it is all transparent, and it has an index of 1.40 in the middle and 1.38 at the outside. (It would be nice if we could make optical glass in which we could adjust the index throughout, for then we would not have to curve it as much as we do when we have a uniform index.) Furthermore, the shape of the cornea is not that of a sphere. A spherical lens has a certain amount of spherical aberration. The cornea is "flatter" at the outside than is a sphere, in just such a manner that the spherical aberration is less for the cornea than it would be if we put a spherical lens in there! The light is focused by the cornea-lens system onto the retina. As we look at things that are closer and farther away, the lens tightens and loosens and changes the focus to adjust for the different distances. To adjust for the total amount of light there is the iris, which is what we call the color of the eye, brown or blue, depending on who it is; as the amount of light increases and decreases, the iris moves in and out.

Let us now look at the neural machinery for controlling the accommodation of the lens, the motion of the eye, the muscles which turn the eye in the socket, and the iris, shown schematically in Fig. 36–3. Of all the information that comes out of the optic nerve A, the great majority is divided into one of two bundles (which we will talk about later) and thence to the brain. But there are a few fibers, of
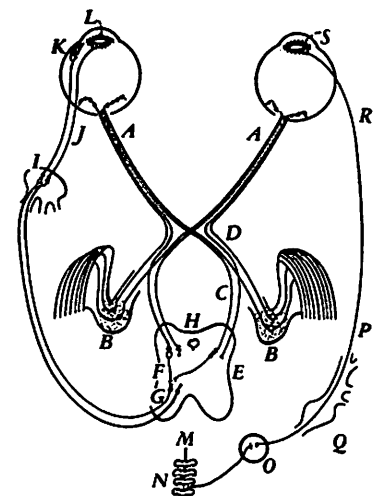

Fig. 36–3. The neural interconnections for the mechanical operation of the eyes.

Fig. 36–4. The neural connections from the eyes to the visual cortex.

interest to us now, which do not run directly to the visual cortex of the brain where we "see" the images, but instead go into the mid-brain *H*. These are the fibers which measure the average light and make adjustment for the iris; or, if the image looks foggy, they try to correct the lens; or, if there is a double image, they try to adjust the eye for binocular vision. At any rate, they go through the mid-brain and feed back into the eye. At *K* are the muscles which run the accommodation of the lens, and at *L* another one that runs into the iris. The iris has two muscle systems. One is a circular muscle *L* which, when it is excited, pulls in and closes down the iris; it acts very rapidly and the nerves are directly connected from the brain through short axons into the iris. The opposite muscles are radial muscles, so that, when the things get dark and the circular muscle relaxes, these radial muscles pull out. Here we have, as in many places in the body, a pair of muscles which work in opposite directions, and in almost every such case the nerve systems which control the two are very delicately adjusted, so that when signals are sent in to tighten one, signals are automatically sent in to loosen the other. The iris is a peculiar exception: the nerves which make the iris contract are the ones we have already described, but the nerves which make the iris *expand* come out from no one knows exactly where, go down into the spinal cord back of the chest, into the thoracic sections, out of the spinal cord, up through the neck ganglia, and all the way around and back up into the head in order to run the other end of the iris. In fact, the signal goes through a completely different nervous system, not the central nervous system at all, but the sympathetic nervous system, so it is a very strange way of making things go.

We have already emphasized another strange thing about the eye, that the light-sensitive cells are on the wrong side, so that the light has to go through several layers of other cells before it gets to the receptors—it is built inside out! So some of the features are wonderful and some are apparently stupid.

Figure 36–4 shows the connections of the eye to the part of the brain which is most directly concerned with the visual process. The optic nerve fibers run into a certain area just beyond *D*, called the lateral geniculate, whereupon they run out to a section of the brain called the visual cortex. Notice that some of the fibers from each eye are sent over to the other side of the brain, so the picture formed is incomplete. The optic nerves from the left side of the right eye run across the optic chiasma *B*, while the ones on the left side of the left eye come around and go this same way. So the left side of the brain receives all the information which comes from the left side of the eyeball of each eye, i.e., on the right side of the visual field, while the right side of the brain sees the left side of the visual field. This is the manner in which the information from each of the two eyes is put together in order to tell how far away things are. This is the system of binocular vision.

The connections between the retina and the visual cortex are interesting. If a spot in the retina is excised or destroyed in any way, then the whole fiber will die, and we can thereby find out where it is connected. It turns out that, essentially, the connections are one to one—for each spot in the retina there is one spot in the visual cortex—and spots that are very close together in the retina are very close together in the visual cortex. So the visual cortex still represents the spatial arrangement of the rods and cones, but of course much distorted. Things which are in the center of the field, which occupy a very small part of the retina, are expanded over many, many cells in the visual cortex. It is clear that it is useful to have things which are originally close together, still close together. The most remarkable aspect of the matter, however, is the following. The place where one would think it would be most important to have things close together would be right in the middle of the visual field. Believe it or not, the up-and-down line in our visual field as we look at something is of such a nature that the information from all the points on the right side of that line is going into the left side of the brain, and information from the points on the left side is going into the right side of the brain, and the way this area is made, there is a cut right down through the middle, so that the things that are very close together right in the middle are very far apart in the brain! Somehow, the information has to go from one side of the brain to the other through some other channels, which is quite surprising.

The question of how this network ever gets "wired" together is very interesting. The problem of how much is already wired and how much is learned is an old one. It used to be thought long ago that perhaps it does not have to be wired carefully at all, it is only just roughly interconnected, and then, by experience, the young child learns that when a thing is "up there" it produces some sensation in the brain. (Doctors always tell us what the young child "feels," but how do *they* know what a child feels at the age of one?) The child, at the age of one, supposedly sees that an object is "up there," gets a certain sensation, and learns to reach "there," because when he reaches "here," it does not work. That approach probably is not correct, because we already see that in many cases there are these special detailed interconnections. More illuminating are some most remarkable experiments done with a salamander. (Incidentally, with the salamander there is a direct crossover connection, without the optic chiasma, because the eyes are on each side of the head and have no common area. Salamanders do not have binocular vision.) The experiment is this. We can cut the optic nerve in a salamander and the nerve will grow out from the eyes again. Thousands and thousands of cell fibers will thus re-establish themselves. Now, in the optic nerve the fibers do not stay adjacent to each other—it is like a great, sloppily made telephone cable, all the fibers twisting and turning, but when it gets to the brain they are all sorted out again. When we cut the optic nerve of the salamander, the interesting question is, will it ever get straightened out? The answer is remarkable: yes. If we cut the optic nerve of the salamander and it grows back, the salamander has good visual acuity again. However, if we cut the optic nerve and *turn the eye upside down* and let it grow back again, it has good visual acuity all right, but it has a terrible error: when the salamander sees a fly "up here," it jumps at it "down there," and it never learns. Therefore there is some mysterious way by which the thousands and thousands of fibers find their right places in the brain.

This problem of how much is wired in, and how much is not, is an important problem in the theory of the development of creatures. The answer is not known, but is being studied intensively.

The same experiment in the case of a goldfish shows that there is a terrible knot, like a great scar or complication, in the optic nerve where we cut it, but in spite of all this the fibers grow back to their right places in the brain.

In order to do this, as they grow into the old channels of the optic nerve they must make several decisions about the direction in which they should grow. How do they do this? There seem to be chemical clues that different fibers respond to differently. Think of the enormous number of growing fibers, each of which is an individual differing in some way from its neighbors; in responding to whatever the chemical clues are, it responds in a unique enough way to find its proper place for ultimate connection in the brain! This is an interesting—a fantastic—thing. It is one of the great recently discovered phenomena of biology and is undoubtedly connected to many older unsolved problems of growth, organization, and development of organisms, and particularly of embryos.

One other interesting phenomenon has to do with the motion of the eye. The eyes must be moved in order to make the two images coincide in different circumstances. These motions are of different kinds: one is to follow something, which requires that both eyes must go in the same direction, right or left, and the other is to point them toward the same place at various distances away, which requires that they must move oppositely. The nerves going into the muscles of the eye are already wired up for just such purposes. There is one set of nerves which will pull the muscles on the inside of one eye and the outside of the other, and relax the opposite muscles, so that the two eyes move together. There is another center where an excitation will cause the eyes to move in toward each other from parallel. Either eye can be turned out to the corner if the other eye moves toward the nose, but it is impossible consciously or unconsciously to turn both eyes *out* at the same time, not because there are no *muscles*, but because there is no way to send a signal to turn both eyes out, unless we have had an accident or there is something the matter, for instance if a nerve has been cut. Although the muscles of one eye can certainly steer that eye about, not even a Yogi is able to move *both* eyes out freely
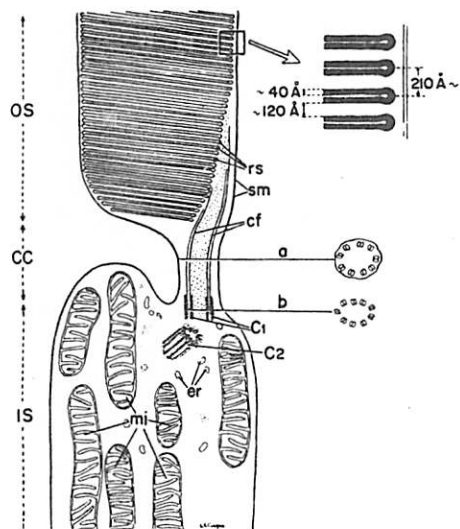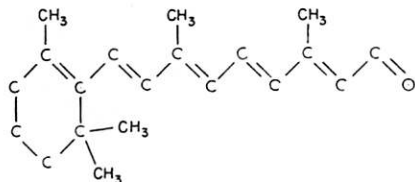
under voluntary control, because there does not seem to be any way to do it. We are already wired to a certain extent. This is an important point, because most of the earlier books on anatomy and psychology, and so on, do not appreciate or do not emphasize the fact that we are so completely wired already—they say that everything is just learned.

36–3 The rod cells

Let us now examine in more detail what happens in the rod cells. Figure 36–5 shows an electron micrograph of the middle of a rod cell (the rod cell keeps going up out of the field). There are layer after layer of plane structures, shown magnified at the right, which contain the substance rhodopsin (visual purple), the dye, or pigment, which produces the effects of vision in the rods. The rhodopsin, which is the pigment, is a big protein which contains a special group called retinene, which can be taken off the protein, and which is, undoubtedly, the main cause of the absorption of light. We do not understand the reason for the planes, but it is very likely that there is some reason for holding all the rhodopsin molecules parallel. The chemistry of the thing has been worked out to a large extent, but there might be some physics to it. It may be that all of the molecules are arranged in some kind of a row so that when one is excited an electron which is generated, say, may run all the way down to some place at the end to get the signal out, or something. This subject is very important, and has not been worked out. It is a field in which both biochemistry and solid state physics, or something like it, will ultimately be used.

This kind of a structure, with layers, appears in other circumstances where light is important, for example in the chloroplast in plants, where the light causes photosynthesis. If we magnify those, we find the same thing with almost the same kind of layers, but there we have chlorophyll, of course, instead of retinene. The chemical form of retinene is shown in Fig. 36–6. It has a series of alternate double bonds along the side chain, which is characteristic of nearly all strongly absorbing organic substances, like chlorophyll, blood, and so on. This substance is impossible for human beings to manufacture in their own cells—we have to eat it. So we eat it in the form of a special substance, which is exactly the same as retinene except that there is a hydrogen tied on the right end; it is called vitamin A, and if we do not eat enough of it, we do not get a supply of retinene, and the eye becomes what we call *night blind*, because there is then not enough pigment in the rhodopsin to see with the rods at night.

The reason why such a series of double bonds absorbs light very strongly is also known. We may just give a hint: The alternating series of double bonds is called a *conjugated* double bond; a double bond means that there is an extra electron there, and this extra electron is easily shifted to the right or left. When light strikes this molecule, the electron of each double bond is shifted over by one step. All the electrons in the whole chain shift, like a string of dominoes falling over, and though each one moves only a little distance (we would expect that, in a single atom, we could move the electron only a little distance), the net effect is the same as though the one at the end was moved over to the other end! It is the same as though one electron went the whole distance back and forth, and so, in this manner, we get a much stronger absorption under the influence of the electric field, than if we could only move the electron a distance which is associated with one atom. So, since it is easy to move the electrons back and forth, retinene absorbs light very strongly; that is the machinery of the physical-chemical end of it.

36–4 The compound (insect) eye

Let us now return to biology. The human eye is not the only kind of eye. In the vertebrates, almost all eyes are essentially like the human eye. However, in the lower animals there are many other kinds of eyes: eye spots, various eye cups, and other less sensitive things, which we have no time to discuss. But there is one other highly developed eye among the invertebrates, the *compound* eye of the insect. (Most insects having large compound eyes also have various additional simpler eyes as well.) A bee is an insect whose vision has been studied very carefully. It is

Fig. 36–5. Electron micrograph of a rod cell.

Fig. 36–6. The structure of retinene.

easy to study the properties of the vision of bees because they are attracted to honey, and we can make experiments in which we identify the honey by putting it on blue paper or red paper, and see which one they come to. By this method some very interesting things have been discovered about the vision of the bee.

In the first place, in trying to measure how acutely bees could see the color difference between two pieces of "white" paper, some researchers found they were not very good, and others found they were fantastically good. Even if the two pieces of white paper were almost exactly the same, the bees could still tell the difference. The experimenters used zinc white for one piece of paper and lead white for the other, and although these look exactly the same to us, the bee could easily distinguish them, because they reflect a different amount in the ultraviolet. In this way it was discovered that the bee's eye is sensitive over a wider range of the spectrum than is our own. Our eye works from 7000 angstroms to 4000 angstroms, from red to violet, but the bee's can see down to 3000 angstroms into the ultraviolet! This makes for a number of different interesting effects. In the first place, bees can distinguish between many flowers which to us look alike. Of course, we must realize that the colors of flowers are not designed for *our* eyes, but for the bee; they are signals to attract the bees to a specific flower. We all know that there are many "white" flowers. Apparently white is not very interesting to the bees, because it turns out that all of the white flowers have different proportions of reflection in the *ultraviolet*; they do not reflect one hundred percent of the ultraviolet as would a true white. All the light is not coming back, the ultraviolet is missing, and that is a color, just as, for us, if the blue is missing, it comes out yellow. So, all the flowers are colored for the bees. However, we also know that red cannot be seen by bees. Thus we might expect that all red flowers should look black to the bee. Not so! A careful study of red flowers shows, first, that even with our own eye we can see that a great majority of red flowers have a bluish tinge because they are mainly reflecting an additional amount in the blue, which is the part that the bee sees. Furthermore, experiments also show that flowers vary in their reflection of the ultraviolet over different parts of the petals, and so on. So if we could see the flowers as bees see them they would be even more beautiful and varied!

It has been shown, however, that there are a few red flowers which do *not* reflect in the blue or in the ultraviolet, and *would*, therefore, appear black to the bee! This was of quite some concern to the people who worry about this matter, because black does not seem like an interesting color, since it is hard to tell from a dirty old shadow. It actually turned out that these flowers were *not* visited by bees, these are the flowers that are visited by *hummingbirds*, and hummingbirds *can* see the red!

Another interesting aspect of the vision of the bee is that bees can apparently tell the direction of the sun by looking at a patch of blue sky, without seeing the sun itself. We cannot easily do this. If we look out the window at the sky and see that it is blue, in which direction is the sun? The bee can tell, because the bee is quite sensitive to the *polarization* of light, and the scattered light of the sky is polarized.* There is still some debate about how this sensitivity operates. Whether it is because the reflections of the light are different in different circumstances, or the bee's eye is directly sensitive, is not yet known.†

It is also said that the bee can notice flicker up to 200 oscillations per second, while we see it only up to 20. The motions of bees in the hives are very quick; the feet move and the wings vibrate, but it is very hard for us to see these motions with our eye. However, if we could see more rapidly we would be able to see the motion. It is probably very important to the bee that its eye has such a rapid response.

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* The human eye also has a slight sensitivity to the polarization of light, and one *can* learn to tell the direction of the sun! The phenomenon that is involved here is called *Haidinger's brush;* it is a faint, yellowish hourglass-like pattern seen at the center of the visual field when one looks at a broad, featureless expanse using polarizing glasses. It can also be seen in the blue sky without polarizing glasses if one rotates his head back and forth about the axis of vision.

† Evidence obtained since this lecture was given indicates that the eye is directly sensitive.

Fig. 36-7. The structure of an ommatidium (a single cell of a compound eye).

Fig. 36-8. Schematic view of packing of ommatidia in the eye of a bee.

Fig. 36-9. The optimum size for an ommatidium is δ_m.

Now let us discuss the visual acuity we could expect from the bee. The eye of a bee is a compound eye, and it is made of a large number of special cells called *ommatidia*, which are arranged conically on the surface of a sphere (roughly) on the outside of the bee's head. Figure 36-7 shows a picture of one such ommatidium. At the top there is a transparent area, a kind of "lens," but actually it is more like a filter or light pipe to make the light come down along the narrow fiber, which is where the absorption presumably occurs. Out of the other end of it comes the nerve fiber. The central fiber is surrounded on its sides by six cells which, in fact, have secreted the fiber. That is enough description for our purposes; the point is that it is a conical thing and many can fit next to each other all over the surface of the eye of the bee.

Now let us discuss the resolution of the eye of the bee. If we draw lines (Fig. 36-8) to represent the ommatidia on the surface, which we suppose is a sphere of radius r, we may actually *calculate* how wide each ommatidium is by using our brains, and assuming that evolution is as clever as we are! If we have a very large ommatidium we do not have much resolution. That is, one cell gets a piece of information from one direction, and the adjacent cell gets a piece of information from another direction, and so on, and the bee cannot see things in between very well. So the uncertainty of visual acuity in the eye will surely correspond to an angle, the angle of the end of the ommatidium relative to the center of curvature of the eye. (The eye cells, of course, exist only at the surface of the sphere; inside that is the head of the bee.) This angle, from one ommatidium to the next, is, of course, the diameter of the ommatidia divided by the radius of the eye surface:

$$\Delta\theta_g = \delta/r. \tag{36.1}$$

So, we may say, "The finer we make the δ, the more the visual acuity. So why doesn't the bee just use very, very fine ommatidia?" *Answer*: We know enough physics to realize that if we are trying to get light down into a narrow slot, we cannot see accurately in a given direction because of the diffraction effect. The light that comes from several directions can enter and, due to diffraction, we will get light coming in at angle $\Delta\theta_d$ such that

$$\Delta\theta_d = \lambda/\delta. \tag{36.2}$$

Now we see that if we make the δ too small, then each ommatidium does not look in only one direction, because of diffraction! If we make them too big, each one sees in a definite direction, but there are not enough of them to get a good view of the scene. So we adjust the distance d in order to make minimal the total effect of these two. If we add the two together, and find the place where the sum has a minimum (Fig. 36-9), we find that

$$\frac{d(\Delta\theta_g + \Delta\theta_d)}{d\delta} = 0 = \frac{1}{r} - \frac{\lambda}{\delta^2}, \tag{36.3}$$

which gives us a distance

$$\delta = \sqrt{\lambda r}. \tag{36.4}$$

If we guess that r is about 3 millimeters, take the light that the bee sees as 4000 angstroms, and put the two together and take the square root, we find

$$\delta = (3 \times 10^{-3} \times 4 \times 10^{-7})^{1/2}\,\text{m}$$
$$= 3.5 \times 10^{-5}\,\text{m} = 35\,\mu. \tag{36.5}$$

The book says the diameter is $30\,\mu$, so that is rather good agreement! So, apparently, it really works, and we can understand what determines the size of the bee's eye! It is also easy to put the above number back in and find out how good the bee's eye actually is in angular resolution; it is very poor relative to our own. We can see things that are thirty times smaller in apparent size than the bee; the bee has a rather fuzzy out-of-focus image relative to what we can see. Nevertheless it is all right, and it is the best they can do. We might ask why the bees do not develop
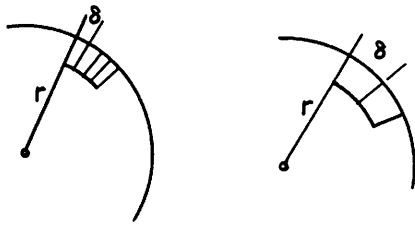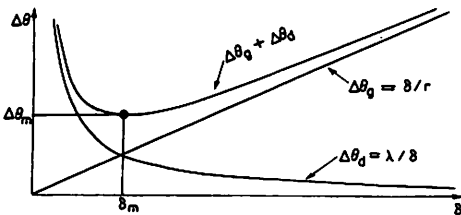
a good eye like our own, with a lens and so on. There are several interesting reasons. In the first place, the bee is too small; if it had an eye like ours, but on his scale, the opening would be about 30 μ in size and diffraction would be so important that it would not be able to see very well anyway. The eye is not good if it is too small. Secondly, if it were as big as the bee's head, then the eye would occupy the whole head of the bee. The beauty of the compound eye is that it takes up no space, it is just a very thin layer on the surface of the bee. So when we argue that they should have done it our way, we must remember that they had their own problems!

36–5 Other eyes

Besides the bees, many other animals can see color. Fish, butterflies, birds, and reptiles can see color, but it is believed that most mammals cannot. The primates can see color. The birds certainly see color, and that accounts for the colors of birds. There would be no point in having such brilliantly colored males if the females could not notice it! That is, the evolution of the sexual "whatever it is" that the birds have is a result of the female being able to see color. So next time we look at a peacock and think of what a brilliant display of gorgeous color it is, and how delicate all the colors are, and what a wonderful aesthetic sense it takes to appreciate all that, we should not compliment the peacock, but should compliment the visual acuity and aesthetic sense of the pea*hen*, because that is what has generated the beautiful scene!

All invertebrates have poorly developed eyes or compound eyes, but all the vertebrates have eyes very similar to our own, with one exception. If we consider the highest form of animal, we usually say, "Here we are!," but if we take a less prejudiced point of view and restrict ourselves to the invertebrates, so that we cannot include ourselves, and ask what is the highest invertebrate animal, most zoologists agree that the *octopus* is the highest animal! It is very interesting that, besides the development of its brain and its reactions and so on, which are rather good for an invertebrate, it has also developed, independently, a different eye. It is not a compound eye or an eye spot—it has a cornea, it has lids, it has an iris, it has a lens, it has two regions of water, it has a retina behind. It is essentially the same as the eye of the vertebrates! It is a remarkable example of a coincidence in evolution where nature has twice discovered the same solution to a problem, with one slight improvement. In the octopus it also turns out, amazingly, that the retina is a piece of the brain that has come out in the same way in its embryonic development as is true for vertebrates, but the interesting thing which is different is that the cells which are sensitive to light are on the *inside*, and the cells which do the calculation are in back of them, rather than "inside out," as in our eye. So we see, at least, that there is no good reason for its being inside out. The other time nature tried it, she got it straightened out! (See Fig. 36–10.) The biggest eyes in the world are those of the giant squid; they have been found up to 15 inches in diameter!
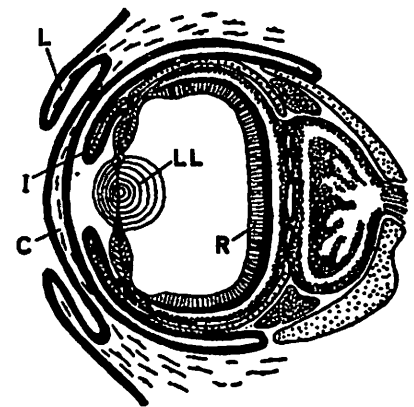

Fig. 36–10. The eye of an octopus.

36–6 Neurology of vision

One of the main points of our subject is the interconnection of information from one part of the eye to the other. Let us consider the compound eye of the horseshoe crab, on which considerable experimentation has been done. First of all, we must appreciate what kind of information can come along nerves. A nerve carries a kind of disturbance which has an electrical effect that is easy to detect, a kind of wavelike disturbance which runs down the nerve and produces an effect at the other end: a long piece of the nerve cell, called the axon, carries the information along, and a certain kind of impulse, called a "spike," goes along if it is excited at one end. When one spike goes down the nerve, another cannot immediately follow. All the spikes are of the same size, so it is not that we get *higher* spikes when the thing is more strongly excited, but that we get *more spikes per second*. The *size* of the spike is determined by the fiber. It is important to appreciate this in order to see what happens next.
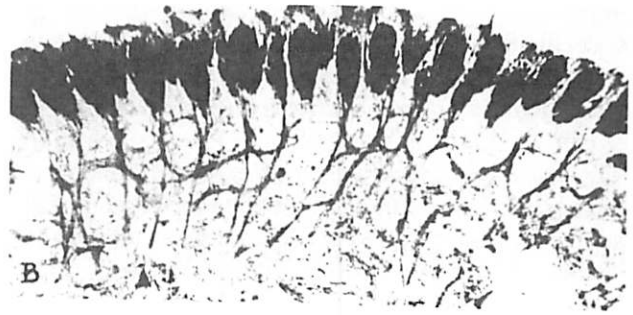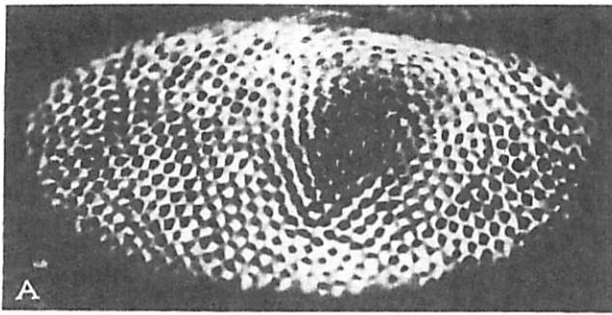
Fig. 36–11. The compound eye of the horseshoe crab. (a) Normal view. (b) Cross section.

Figure 36–11(a) shows the compound eye of the horseshoe crab; it is not very much of an eye, it has only about a thousand ommatidia. Figure 36–11(b) is a cross section through the system; one can see the ommatidia, with the nerve fibers that run out of them and go into the brain. But note that even in a horseshoe crab there are little interconnections. They are much less elaborate than in the human eye, and it gives us a chance to study a simpler example.

Let us now look at the experiments which have been done by putting fine electrodes into the optic nerve of the horseshoe crab, and shining light on only one of the ommatidia, which is easy to do with lenses. If we turn a light on at some instant t_0, and measure the electrical pulses that come out, we find that there is a slight delay and then a rapid series of discharges which gradually slow down to a uniform rate, as shown in Fig. 36–12(a). When the light goes out, the discharge stops. Now it is very interesting that if, while our amplifier is connected to this same nerve fiber, we shine light on a *different* ommatidium nothing happens; no signal.
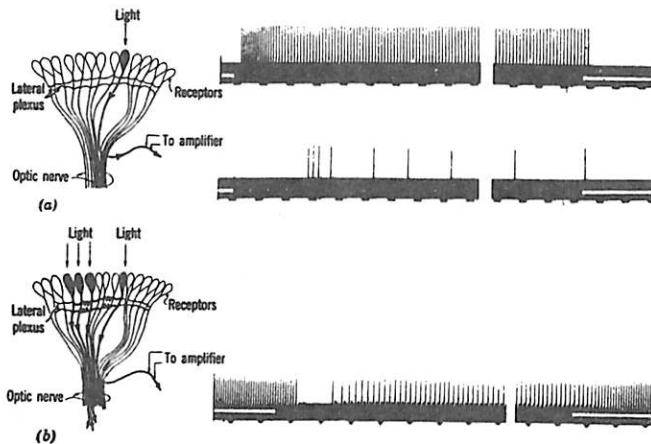

Fig. 36–12. The response to light of the nerve fibers of the eye of the horseshoe crab.

Now we do another experiment: we shine the light on the original ommatidium and get the same response, but if we now turn light on another one nearby as well, the pulses are interrupted briefly and then run at a much lower rate (Fig. 36–12b). The rate of one is inhibited by the impulses which are coming out of the other! In other words, each nerve fiber carries the information from one ommatidium, but the amount that it carries is inhibited by the signals from the others. So, for example, if the whole eye is more or less uniformly illuminated, the information coming from any one ommatidium will be relatively weak, because it is inhibited by so many. In fact the inhibition is additive—if we shine light on several nearby ommatidia the inhibition is very great. The inhibition is greater when the ommatidia are closer, and if the ommatidia are far enough away from one another, inhibition is practically zero. So it is additive and depends on the distance; here is a first example of information from different parts of the eye being combined in the eye itself. We can see, perhaps, if we think about it awhile, that this is a device to *enhance contrast* at the edges of objects, because if a part of the scene is light and a part is black, then the ommatidia in the lighted area give impulses that are

inhibited by all the other light in the neighborhood, so it is relatively weak. On the other hand, an ommatidium at the boundary which is given a "white" impulse is also inhibited by others in the neighborhood, but there are not as many of them, since some are black; the net signal is therefore stronger. The result would be a curve, something like that of Fig. 36–13. The crab will see an enhancement of the contour.

The fact that there is an enhancement of contours has long been known; in fact it is a remarkable thing that has been commented on by psychologists many times. In order to draw an object, we have only to draw its outline. How used we are to looking at pictures that have only the outline! What is the outline? The outline is only the edge difference between light and dark or one color and another. It is not something definite. It is not, believe it or not, that every object has a line around it! There is no such line. It is only in our own psychological makeup that there is a line; we are beginning to understand the reasons why the "line" is enough of a clue to get the whole thing. Presumably our own eye works in some similar manner—much more complicated, but similar.

Finally, we shall briefly describe the more elaborate work, the beautiful, advanced work that has been done on the frog. Doing a corresponding experiment on a frog, by putting very fine, beautifully built needlelike probes into the optic nerve of a frog, one can obtain the signals that are going along one particular axon and, just as in the case of the horseshoe crab, we find that the information does not depend on just one spot in the eye, but is a sum of information over several spots.

The most recent picture of the operation of the frog's eye is the following. One can find four different kinds of optic nerve fibers, in the sense that there are four different kinds of responses. These experiments were not done by shining on-and-off impulses of light, because that is not what a frog sees. A frog just sits there and his eyes never move, unless the lily pad is flopping back and forth, and in that case his eyes wobble just right so that the image stays put. He does not turn his eyes. If anything moves in his field of vision, like a little bug (he has to be able to see something small moving in the fixed background), it turns out that there are four different kinds of fibers which discharge, whose properties are summarized in Table 36–1. Sustained edge detection, nonerasable, means that if we bring an object with an edge into the field of view of the frog, then there are a lot of impulses in this particular fiber while the object is moving, but they die down to a sustained impulse that continues as long as the edge is there, even if it is standing still. If we turn out the light, the impulses stop. If we turn it on again while the edge is still in view, they start again. They are not erasable. Another kind of fiber is very similar, except that if the edge is straight it does not work. It must be a convex edge with dark behind it! How complicated must be the system of interconnections in the retina of the eye of the frog in order for it to understand that a convex surface has moved in! Furthermore, although this fiber does sustain somewhat, it does not sustain as long as the other, and if we turn out the light and turn it on again it does *not* build up again. It depends on the moving in of the convex
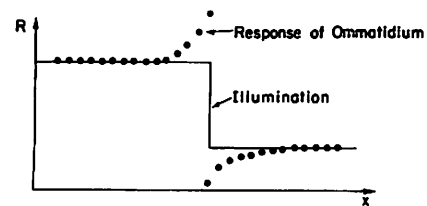

Fig. 36–13. The net response of horseshoe crab ommatidia near a sharp change in illumination.

Table 36–1

Types of response in optic nerve fibers of a frog

Type	Speed	Angular field
1. Sustained edge detection (nonerasable)	0.2–0.5 m/sec	1°
2. Convex edge detection (erasable)	0.5 m/sec	2°–3°
3. Changing contrast detection	1–2 m/sec	7°–10°
4. Dimming detection	Up to $\frac{1}{2}$ m/sec	Up to 15°
5. Darkness detection	?	Very large

surface. The eye sees it move in and remembers that it is there, but if we merely turn out the light for a moment, it simply forgets it and no longer sees it.

Another example is change-in-contrast detection. If there is an edge moving in or out there are pulses, but if the thing stands still there are no pulses at all.

Then there is a dimming detector. If the light intensity is going down it creates pulses, but if it stays down or stays up, the impulse stops; it only works while the light is dimming.

Then, finally, there are a few fibers which are dark detectors—a most amazing thing—they fire all the time! If we increase the light, they fire less rapidly, but all the time. If we decrease the light, they fire more rapidly, all the time. In the dark they fire like mad, perpetually saying, "It is dark! It is dark! It is dark!"

Now these responses seem to be rather complicated to classify, and we might wonder whether perhaps the experiments are being misinterpreted. But it is very interesting that these same classes are very clearly separated in the anatomy of the frog! By other measurements, after these responses had been classified (*afterwards*, that is what is important about this), it was discovered that the *speed* of the signals on the different fibers was not the same, so here was another, independent way to check which kind of a fiber we have found!

Another interesting question is from how big an area is one particular fiber making its calculations? The answer is different for the different classes.

Figure 36–14 shows the surface of the so-called tectum of a frog, where the nerves come into the brain from the optic nerve. All the nerve fibers coming in from the optic nerve make connections in various layers of the tectum. This layered structure is analogous to the retina; that is partly why we know that the brain and retina are very similar. Now, by taking an electrode and moving it down in succession through the layers, we can find out which kinds of optic nerves end where, and the beautiful and wonderful result is that the different kinds of fibers end in different layers! The first ones end in number 1 type, the second in number 2, the threes and fives end in the same place, and deepest of all is number four. (What a coincidence, they got the numbers almost in the right order! No, that is why they numbered them that way, the first paper had the numbers in a different order!)

We may briefly summarize what we have just learned this way: There are three pigments, presumably. There may be many different kinds of receptor cells containing the three pigments in different proportions, but there are many cross connections which may permit additions and subtractions through addition and reinforcement in the nervous system. So before we really understand color vision, we will have to understand the final sensation. This subject is still an open one, but these researches with microelectrodes and so on will perhaps ultimately give us more information on how we see color.
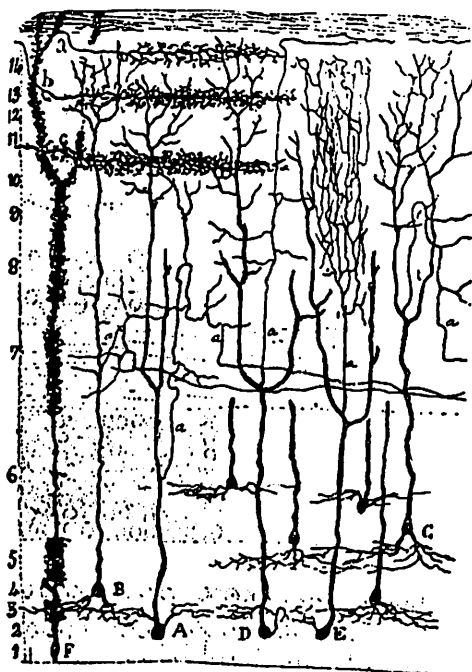

Fig. 36–14.   The tectum of a frog.

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