

by Floyd Ratliff
June 1972

We see contours when adjacent areas contrast sharply. Surprisingly, certain contours, in turn, make large areas appear lighter or darker than they really are. What neural mechanisms underlie these effects?

Contours are so dominant in our visual perception that when we draw an object, it is almost instinctive for us to begin by sketching its outlines. The use of a line to depict a contour may well have been one of the earliest developments in art, as exemplified by the "line drawings" in the pictographs and petroglyphs of prehistoric artists. We see contours when there is a contrast, or difference, in the brightness or color between adjacent areas. How contrast creates contours has been thoroughly studied by both scientists and artists. How the contour itself can affect the contrast of the areas it separates has been known to artists for at least 1,000 years, but it is relatively new as a subject of scientific investigation. Although the psychophysiological basis of how contrast enables the visual system to distinguish contours has been studied for the past century, it is only in the past few years that psychologists and physiologists have started to examine systematically the influence of contour on contrast.

You can readily observe how the visual system tends to abstract and accentuate contours in patterns of varying contrast by paying close attention to the edges of a shadow cast by an object in strong sunlight. Stand with your back to the sun and look closely at the shadow of your head and shoulders on a sidewalk. You will see a narrow half-shadow between the full shadow and the full sunlight. Objectively the illumination in

the full shadow is uniformly low, in the half-shadow it is more or less uniformly graded and in the full sunlight it is uniformly high; within each area there are no sharp maxima or minima. Yet you will see a narrow dark band at the dark edge of the half-shadow and a narrow bright band at its bright edge. You can enhance the effect by swaying from side to side to produce a moving shadow.

These dark and bright strips, now known as Mach bands, were first reported in the scientific literature some 100 years ago by the Austrian physicist, philosopher and psychologist Ernst Mach. They depend strictly on the distribution of the illumination. Mach formulated a simple principle for the effect: "Whenever the light-intensity curve of an illuminated surface (whose light intensity varies in only one direction) has a concave or convex flexion with respect to the abscissa, that place appears brighter or darker, respectively, than its surroundings" [see bottom illustration on next page].

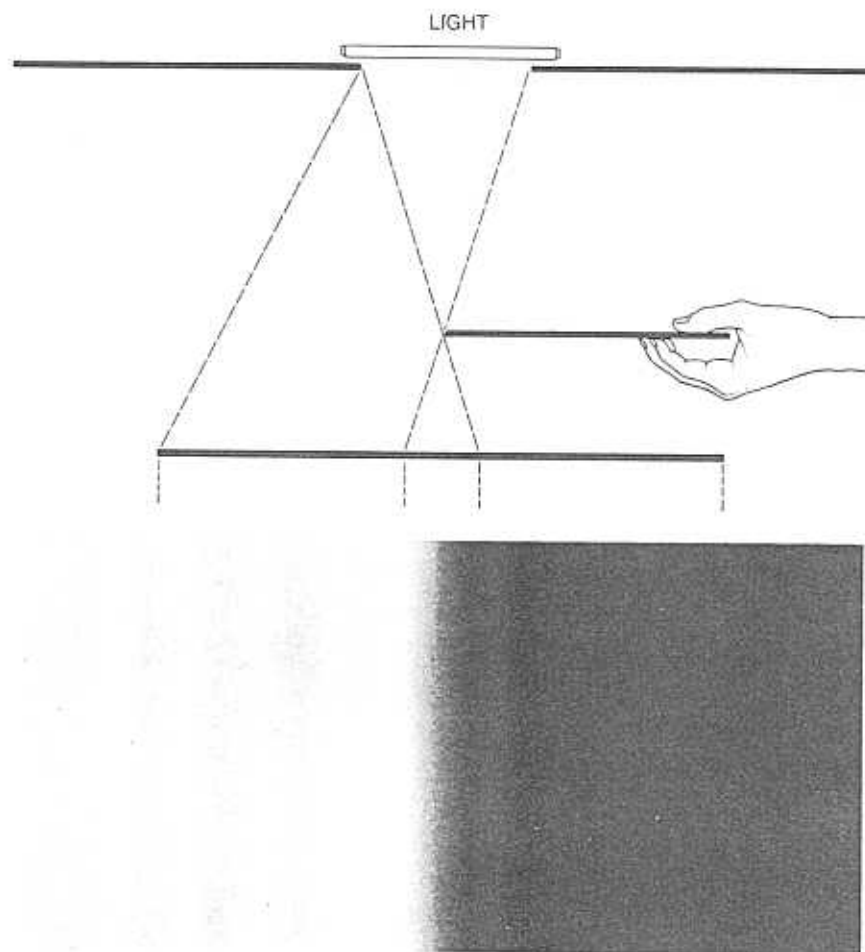
The basic effect can be demonstrated by holding an opaque card under an ordinary fluorescent desk lamp, preferably in a dark room. If the shadow is cast on a piece of paper, part of the paper is illuminated by light from the full length of the lamp. Next to the illuminated area is a half-shadow that gets progressively darker until a full shadow is reached. Ideally the distribution of light should be uniformly high in the bright area, uniformly low in the dark area and

smoothly graded between the bright and the dark areas [see top illustration on next page]. If you now look closely at the edges of the graded half-shadow, you see a narrow bright band at the bright edge and a narrow dark band at the dark edge. These are the Mach bands. Their appearance is so striking that many people will not believe at first that they are only a subjective phenomenon. Some will mistakenly try to explain the appearance of the bands by saying they are the result of multiple shadows or diffraction.

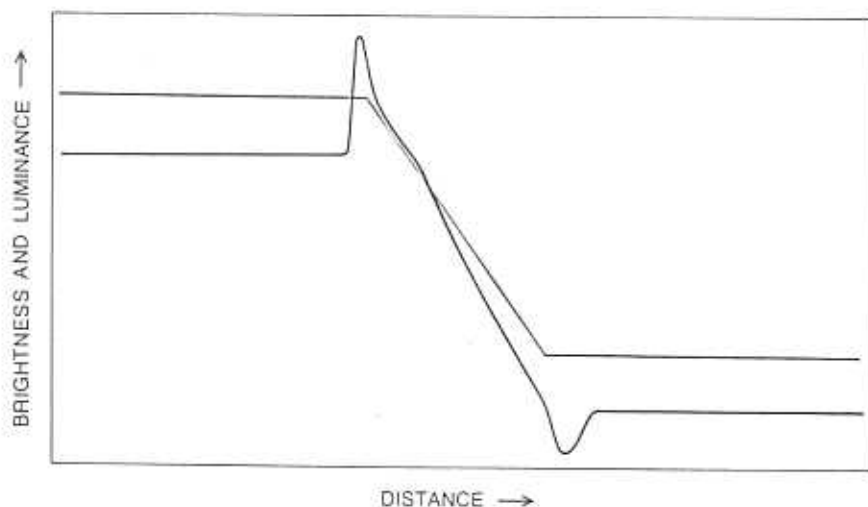
Exact psychophysical measurements of the subjective appearance of Mach bands have been made by Adriana Fiorentini and her colleagues at the National Institute of Optics in Italy. Their technique consists in having an observer adjust an independently variable spot of light to match the brightness of areas in and around the Mach bands. In general they find that the bright band is distinctly narrower and more pronounced than the dark band. The magnitude of the effect, however, varies considerably from person to person.

Since Mach bands delineate contours we expect to see, only a careful observer, or someone who has reason to objectively measure the light distribution at a shadow's edge, is likely to realize that the bands are a caricature of the actual pattern of illumination. Artists of the 19th-century Neo-Impressionist school were unusually meticulous in their observations, and this was reflected in much of their work. A good example is Paul Signac's "Le petit déjeuner." In this painting there are numerous contrast effects in and around the shadows and half-shadows. Particularly striking is how some of the shadows are darkest near their edges and quite light near

NEO-IMPRESSIONIST PAINTER Paul Signac was a meticulous observer of the contrast effects in shadows and half-shadows. On the opposite page is a portion of his "Le petit déjeuner" (1886-1887). Note how the shadow is darker near the unshaded tablecloth and lighter next to the dark matchbox. Similar effects can be found in other shadows. The effects change when the painting is viewed from various distances. The painting is in the Rijksmuseum Kröller-Müller at Otterlo in the Netherlands and is reproduced with its permission.



MACH BANDS can be produced with light from an ordinary fluorescent desk lamp (*upper illustration*). Place a sheet of white or gray paper on the desk and the light about a foot or so above it. Covering the ends of the lamp, which usually are not uniformly bright, may enhance the effect. Turn out the other lights in the room and hold an opaque card an inch or less above the paper. Various positions should be tried for optimum results. Note the narrow bright line and the broader dark line at the outer and inner edges of the half-shadow; these are the Mach bands. The lower illustration is a photograph of a half-shadow produced by the method described. The reproduction of the photograph does not retain all the characteristics of the original because of losses inherent in the reproduction process.



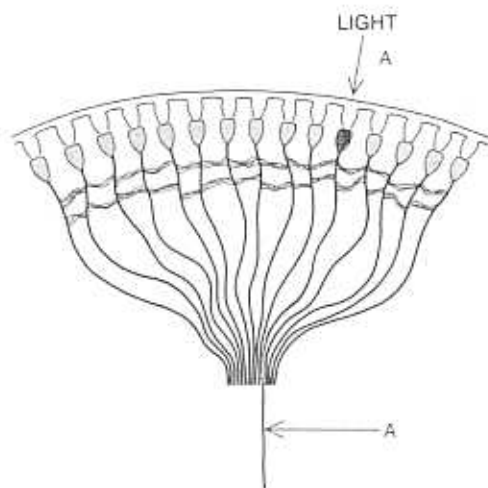
OBSERVED BRIGHTNESS CURVE obtained by psychophysical measurements (*black line*) has two sharp flections, one corresponding to the bright band and the other to the dark band. Measurement of actual luminance (*colored line*) across a half-shadow region reveals that the effect lies in the eye of the beholder and is not an objective phenomenon.

the object casting the shadow. Where Signac saw contrast he painted contrast, whether it was objectively present in the original scene or not. The effects we see in his painting depend of course partly on what Signac painted and partly on how our own eyes respond to contrast. When we view Signac's painting, our own eyes and brain further exaggerate the contrast he painted. As a result the painting appears to have even more contrast than the original scene could have had.

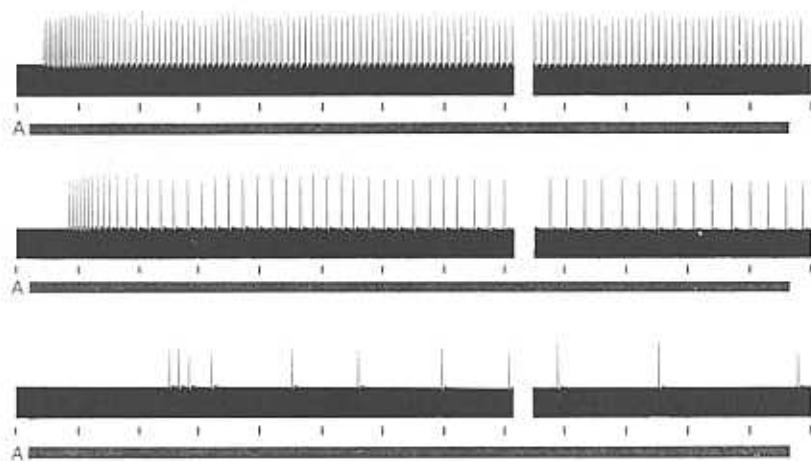
Without precise physical and psychophysical measurements it is difficult to tell how much of the contrast we perceive is objective and how much is subjective. Adding to the confusion is the fact that the subjective Mach bands can seemingly be photographed. All the photograph does, however, is to reproduce with considerable fidelity the original distribution of light in a scene, and it is this distribution of light and dark that gives rise to the subjective Mach bands. Moreover, the photographic process can itself introduce a spurious enhancement of contrast. Edge effects that closely resemble Mach bands can arise as the film is developed. Unlike Mach bands, they are an objective phenomenon consisting of actual variations in the density of the film, and the variations can be objectively measured.

On many occasions scientific investigators have mistaken Mach bands for objective phenomena. For example, shortly after W. K. Röntgen discovered X rays several workers attempted to measure the wavelength of the rays by passing them through ordinary diffraction slits and gratings and recording the resulting pattern on film. Several apparently succeeded in producing diffraction patterns of dark and light bands from which they could determine the wavelength of the X rays. All, however, was in error. As two Dutch physicists, H. Haga and C. H. Wind, showed later, the supposed diffraction patterns were subjective Mach bands.

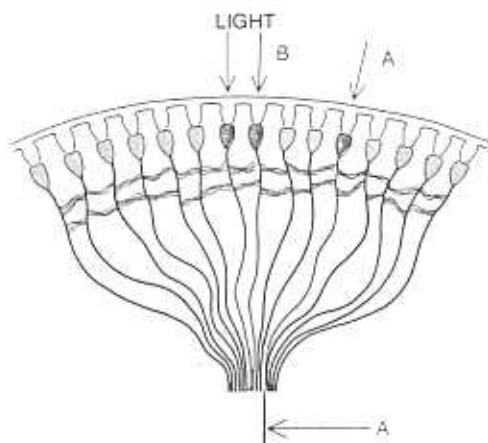
As early as 1865 Mach proposed an explanation of the subjective band effect and other contrast phenomena in terms of opposed excitatory and inhibitory influences in neural networks in the retina and the brain. The means for direct investigation of such neural mechanisms did not become available, however, until the 1920's, when E. D. Adrian, Y. Zotterman and Detlev W. Bronk, working at the University of Cambridge, developed methods for recording the electrical activity of single nerve cells. The basic excitatory-inhibitory principle



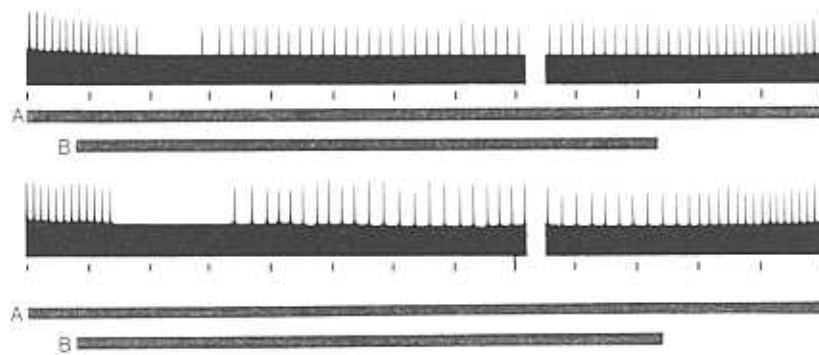
RATE OF DISCHARGE of nerve impulses produced by steady illumination of a single receptor, *A*, in the eye of the horseshoe crab *Limulus* is directly related to the intensity of the light. The nerve fibers from the receptor are separated by microdissection and connected to an electrode from an amplifier and a recorder.



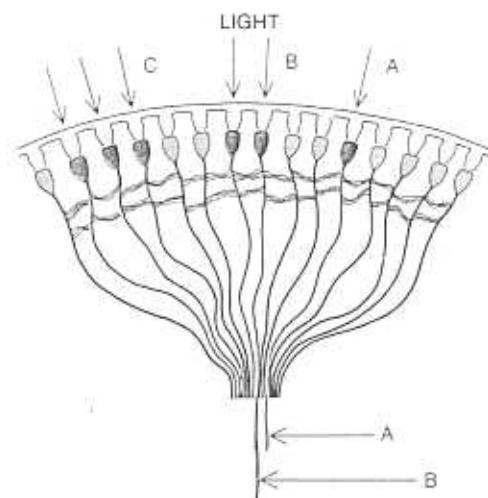
The top record shows the response of *A* to steady, high-intensity light. The middle record shows the response to light of moderate intensity, and the lower record the response to low-intensity illumination. Duration of the light signal is indicated by the colored bar. Each mark above the colored bar indicates one-fifth of a second.



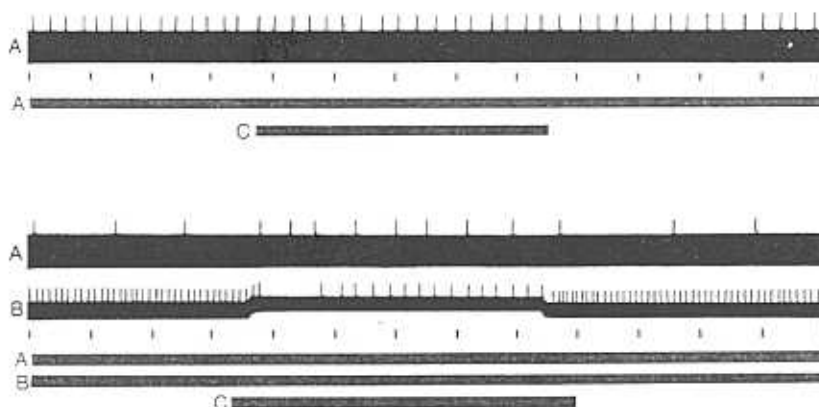
INHIBITION of receptor, *A*, steadily exposed to moderate illumination is produced when neighboring receptors, *B*, are also illuminated. The beginning and the end of the records show the initial and final rate of impulses by *A*. The colored bars indicate duration



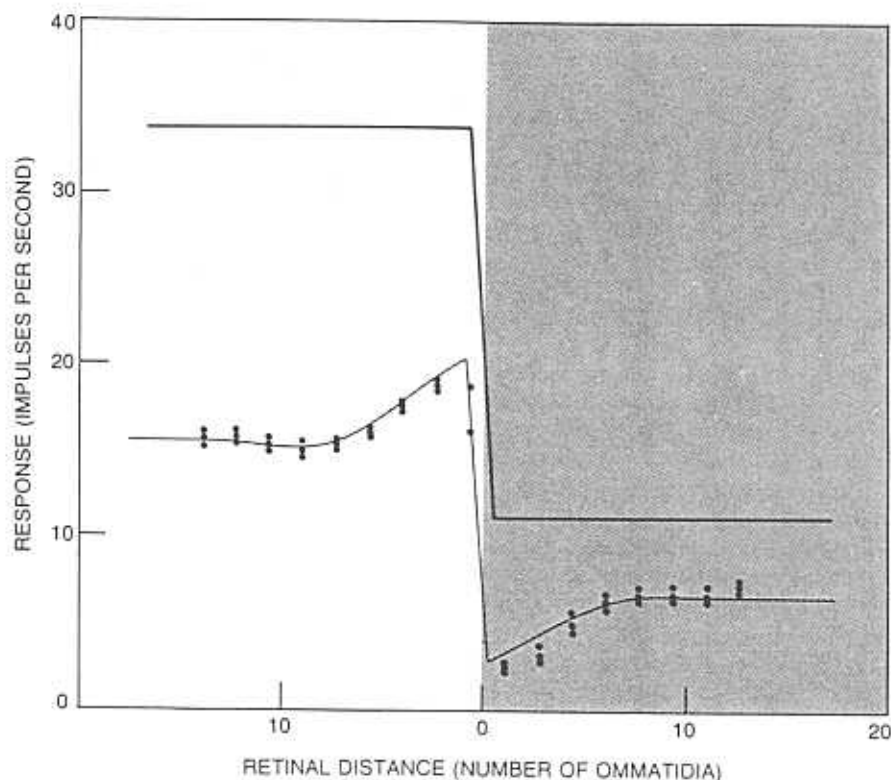
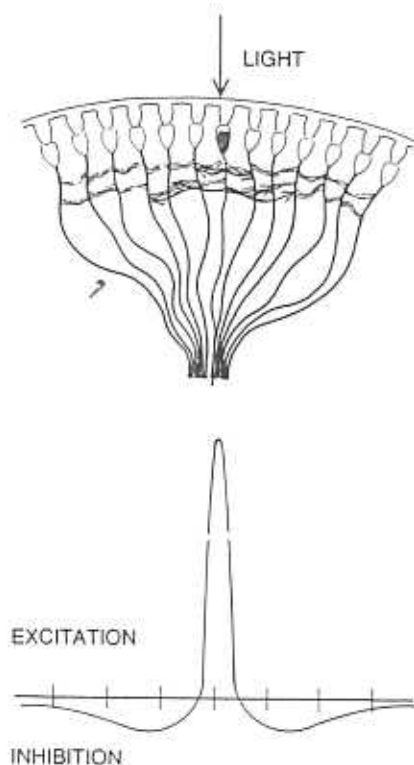
of light signals. The upper record shows the effects on *A* of moderate-intensity illumination of *B*. The lower record shows the effect on *A* of high-intensity illumination of *B*. The stronger the illumination on neighboring receptors, the stronger the inhibitory effect.



DISINHIBITION of receptor *A* occurs when the inhibition exerted on it by the *B* receptors is partially released by illuminating the large area *C*. The upper record shows that *A*'s activity is not affected when *C* also is illuminated because of the distance between

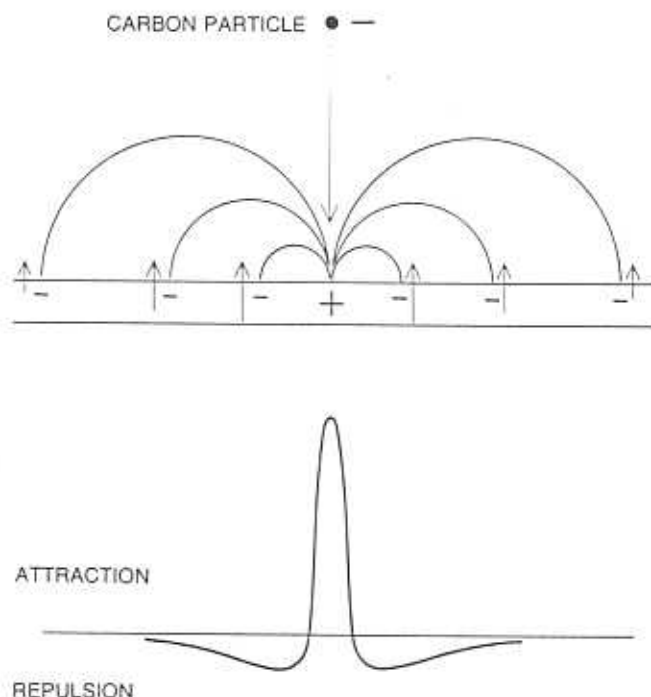


them. The first part of the lower record shows the inhibitory effect of *B* on *A*, then the inhibition of *B* when *C* is illuminated and the concomitant disinhibition of *A*. When the illumination of *C* stops, *B* returns to a higher rate of activity and resumes its inhibition of *A*.



LATERAL INHIBITION in the eye of the horseshoe crab is strongest between receptors a short distance apart and grows weaker as the distance between receptors increases. Below the eye section is a graph of the type of excitatory and inhibitory fields that would be produced by the illumination of a single receptor. The colored line in the graph on the right shows what the retinal response

would be to a sharp light-to-dark contour if lateral inhibition did not occur. The points on the graph show responses actually elicited by three scans of the pattern across the receptor in an experiment by Robert B. Barlow, Jr., of Syracuse University. The thin line shows the theoretical responses for lateral inhibition as computed by Donald A. Quarles, Jr., of the IBM Watson Research Center.



EDGE EFFECT in xerographic copying is the result of the shape of the electrostatic field (which is quite similar to that of the "neural" field in the top illustration) around a single charged point on the xerographic plate (upper left). The first panel on the right shows



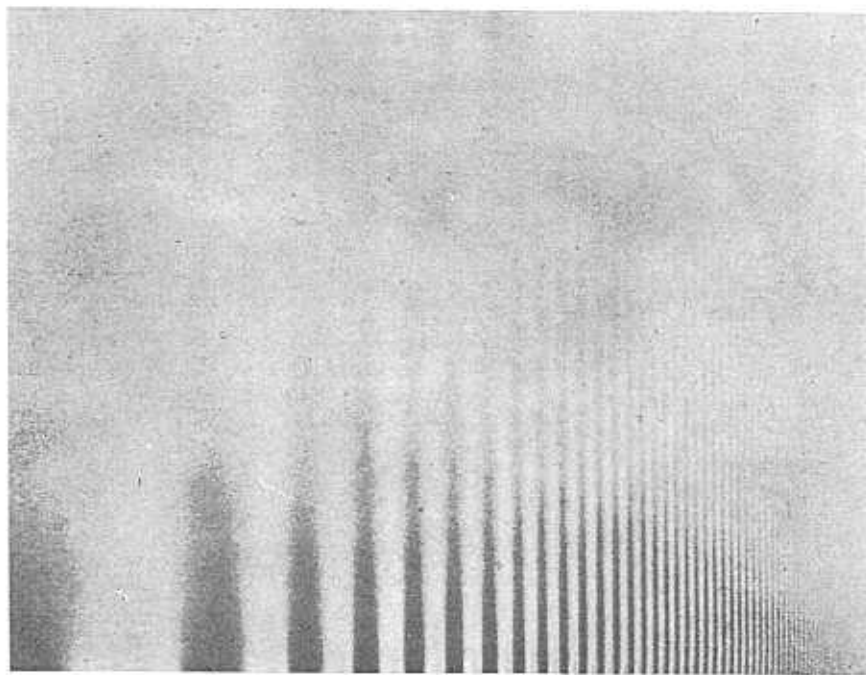
the original pattern. The middle panel shows a Xerox copy of the original. Note how contrast at the edges is greatly enhanced. The bottom panel shows a Xerox copy made with a halftone screen placed over the original so that the pattern is broken up into many dots.

has been demonstrated to be essentially correct in experiments that H. K. Hartline and I, together with our colleagues, have carried out over the past 20 years.

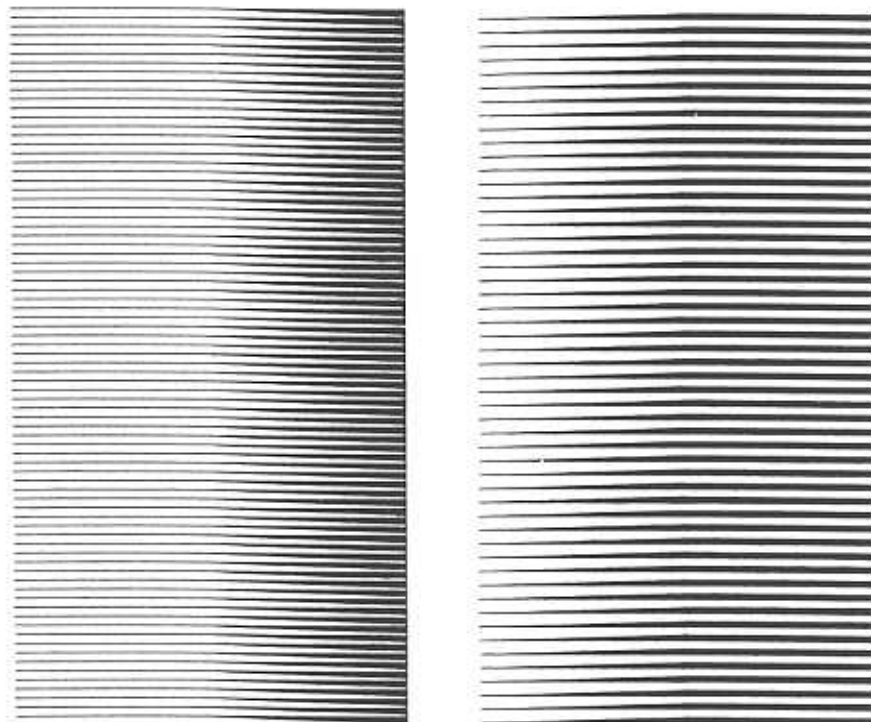
We measured the responses of single neurons in the compound lateral eye of the horseshoe crab *Limulus*. (The animal also has two simple eyes in the front of its carapace near the midline.) The lateral eye of the horseshoe crab is comparatively large (about a centimeter in length) but otherwise it is much like the eye of a fly or a bee. It consists of about 1,000 ommatidia (literally "little eyes"), each of which appears to function as a single photoreceptor unit. Excitation does not spread from one receptor to another; it is confined to whatever receptor unit is illuminated. Nerve fibers arise from the receptors in small bundles that come together to form the optic nerve. Just behind the photoreceptors the small nerve bundles are interconnected by a network of nerve fibers. This network, or plexus, is a true retina even though its function is almost purely inhibitory.

Both the local excitatory and the extended inhibitory influences can be observed directly. A small bundle of fibers from a single receptor is separated by microdissection from the main trunk of the optic nerve and placed on an electrode. In this way the nerve impulses generated by light striking the receptor can be recorded. Weak stimulation produces a low rate of discharge; strong stimulation produces a high rate. These responses are typical of many simple sense organs.

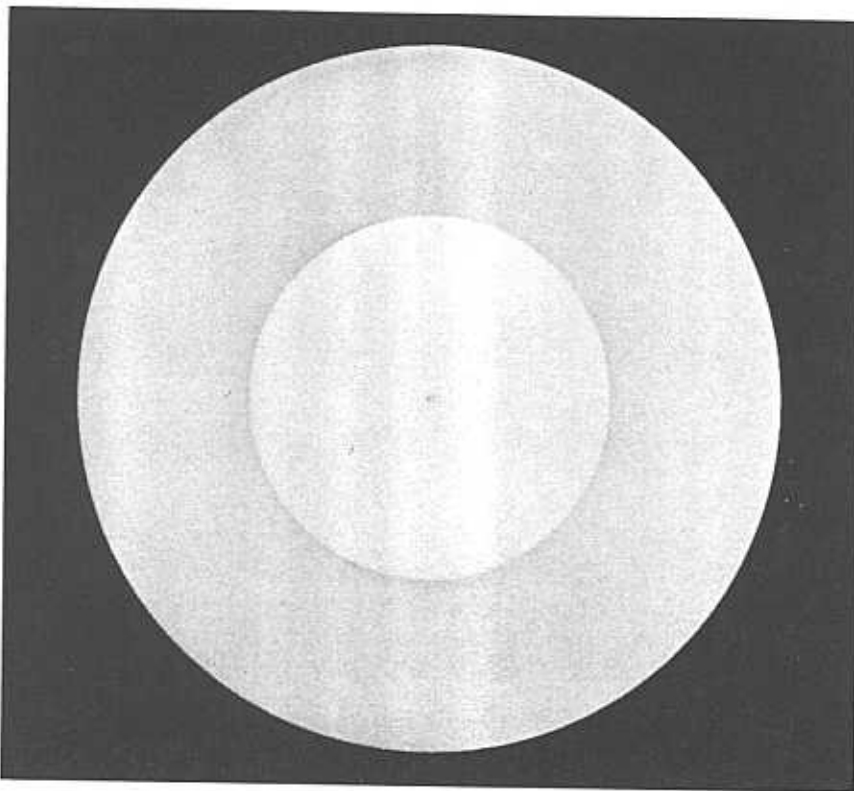
In addition to the excitatory discharge there is a concomitant inhibitory effect. When a receptor unit fires, it inhibits its neighbors. This is a mutual effect: each unit inhibits others and in turn is inhibited by them. The strength of the inhibition depends on the level of activity of the interacting units and the distance between them. In general near neighbors affect one another more than distant neighbors, and the stronger the illumination, the stronger the inhibitory effect. We discovered that such an organization can produce a second-order effect that we call disinhibition. If two sets of receptors are close enough together to interact, they inhibit each other when both sets are illuminated. Now suppose a third set of receptors, far enough away so that it can interact with only one of the two sets of receptors, is illuminated. The activity of the third set will inhibit one set of the original pair, which in turn reduces the inhibition on



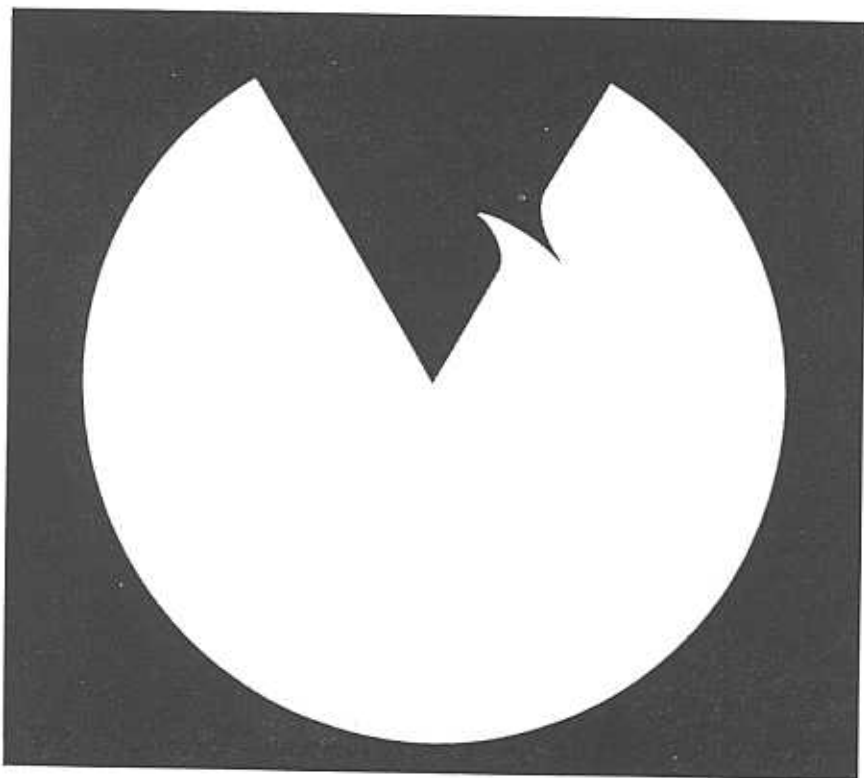
FILTER produced by lateral inhibition at low spatial frequencies and the lack of resolving power of the retina at high spatial frequencies causes intermediate spatial frequencies to be the most distinctly seen. The width of the vertical dark and light bands decreases in a logarithmic sinusoidal manner from the left to the right; the contrast varies logarithmically from less than 1 percent at the top to about 30 percent at the bottom. The objective contrast at any one height in the figure is the same for all spatial frequencies, yet the spatial frequencies in the middle appear more distinct than those at high or low frequencies; that is, the dark lines appear taller at the center of the figure. The effects of changes in viewing distance, luminance, adaptation and sharpness of eye focus can be demonstrated by the viewer.



MACH BAND PHENOMENON created with horizontal lines is shown here. In the illustration at left the black lines are a constant thickness from the left side to the midpoint and then thicken gradually. When the illustration is viewed from a distance, a vertical white "Mach band" appears down the middle. In the illustration at right the horizontal black lines are a constant thickness from the right side to the midpoint and then thin out. When viewed from a distance, the illustration appears to have a vertical black band down the middle.



CRAIK-O'BRIEN EFFECT (this example is known as the Cornsweet illusion) is the result of a specific variation of luminance at the contour, which makes the outer zone appear slightly darker even though it has the same luminance as the inner zone. The effect here is less than in the original because of difficulty in reproducing the actual intensity relations.



RAPID ROTATION of this disk will create the Cornsweet illusion. The white spur creates a local variation near the contour between the two zones that causes the apparent brightness of the inner zone to increase. In the same way the dark spur creates a local variation that causes the outer zone to appear darker. Except in the spur region the objective luminance of the disk when it is rotating is the same in both the inner and the outer region.

the remaining set, thus increasing their rate of discharge [see bottom illustration on page 11]. Following the discovery of disinhibition in the eye of the horseshoe crab, Victor J. Wilson and Paul R. Burgess of Rockefeller University found that some increases in neural activity (called recurrent facilitation) that had been observed in spinal motoneurons in the cat were actually disinhibition. Subsequently M. Ito and his colleagues at the University of Tokyo observed a similar type of disinhibition in the action of the cerebellum on Deiter's nucleus in the cat.

The spatial distribution and relative magnitudes of the excitatory and inhibitory influences for any particular receptor unit in the eye of *Limulus* can be represented graphically as a narrow central field of excitatory influence surrounded by a more extensive but weaker field of inhibitory influence [see top illustration on page 12].

As Georg von Békésy has shown, the approximate response of an inhibitory network can be calculated graphically by superimposing the graphs for each of the interacting units, each graph scaled according to the intensity of the stimulus where it is centered. The summed effects of overlapping fields of excitation (positive values) and inhibition (negative values) at any particular point would determine the response at that point. In the limit of infinitesimally small separations of overlapping units, this would be mathematically equivalent to using the superposition theorem or the convolution integral to calculate the response. In fact, these inhibitory interactions may be expressed in a wide variety of essentially equivalent mathematical forms. The form Hartline and I used at first is a set of simultaneous equations—one equation for each of the interacting receptor units. Our colleagues Frederick A. Dodge, Jr., Bruce W. Knight, Jr., and Jun-ichi Toyoda have since that time expressed the properties of the inhibitory network in a less cumbersome and more general form: a transfer function relating the Fourier transform of the distribution of the intensity of the stimulus to the Fourier transform of the distribution of the magnitude of the response. This in effect treats the retinal network as a filter of the sinusoidal components in the stimulus, and can be applied equally well to both spatial and temporal variations. The overall filtering effect of the *Limulus* retina is to attenuate both the lowest and the highest spatial and temporal frequencies of the sinusoidal components.

It has long been known that spatial and temporal filtering effects of much the same kind occur in our own visual system. The main characteristics of the spatial "filter" can be seen by viewing the test pattern devised by Fergus W. Campbell and his colleagues at the University of Cambridge [see top illustration on page 13].

Even without considering the filter-like properties of neural networks it is possible to see how the subjective Mach bands can be produced by the interaction of narrow fields of excitation and broad fields of inhibition. Near the boundary between the light and dark fields some of the receptors will be inhibited not only by their dimly lit neighbors but also by some brightly lit receptors. The total inhibition of these boundary receptors will therefore be greater than the inhibition of dimly lit receptors farther from the boundary. Similarly, a brightly lit receptor near the boundary will be in the inhibitory field of some dimly lit receptors and as a result will have less inhibition acting on it than brightly lit receptors farther away from the boundary. Because of these differential effects near the boundary the response of the neural network in the *Limulus* retina will show a substantial maximum and minimum adjacent to the boundary even though the stimulus does not have such variations.

Opposed excitatory and inhibitory influences can mediate some highly specialized functions in higher animals. Depending on how these opposed influences are organized, they can detect motion, the orientation of a line or the difference between colors. No matter how complicated the visual system is, however, the basic contrast effects of the excitatory-inhibitory processes show up. For example, recent experiments by Russell L. De Valois and Paul L. Pease of the University of California at Berkeley show a contour enhancement similar to the bright Mach band in responses of monkey lateral geniculate cells. The simple lateral inhibition that produces contrast effects such as Mach bands may be a basic process in all the more highly evolved visual mechanisms.

Contrast phenomena are by no means found only in the nervous system. Indeed, contrast is found in any system of interacting components where opposed fields of positive (excitatory) and negative (inhibitory) influences exist. Whether the system is neural, electrical, chemical or an abstract mathematical model is irrelevant; all that is needed to

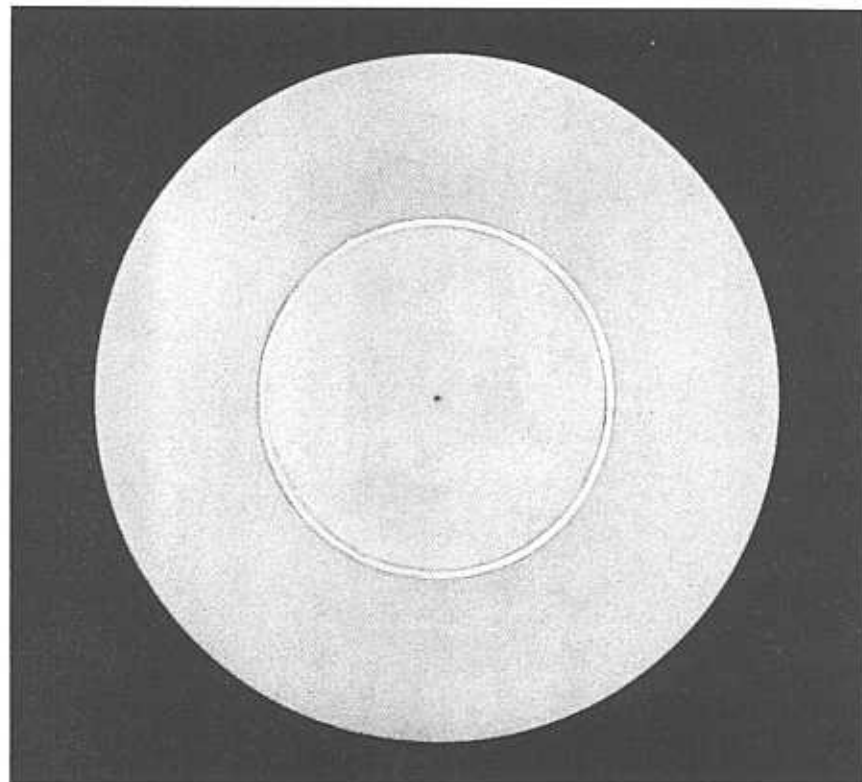
produce a contrast effect is a certain distribution of the opposed influences. A familiar example is the contrast effect in xerography. The xerographic process does not reproduce solid black or gray areas very well. Only the edges of extended uniform areas are reproduced unless some special precautions are taken. This failing is inherent in the basic process itself. In the making of a xerographic copy a selenium plate is first electrostatically charged. Where light falls on the plate the electrostatic charge is lost; in dark areas the charge is retained. A black powder spread over the plate clings to the charged areas by electrostatic attraction and is eventually transferred and fused to paper to produce the final copy.

The electrostatic attraction of any point on the plate is determined not by the charge at that point alone but by the integrated effects of the electrostatic fields of all the charges in the neighborhood. Since the shapes of the positive and negative components of the individual fields happen to be very much like the shapes of the excitatory and inhibitory components of neural unit fields in the retina, the consequences are much the same too [see bottom illustration on page 20]. Contours are enhanced; uniform areas are lost. To obtain a xero-

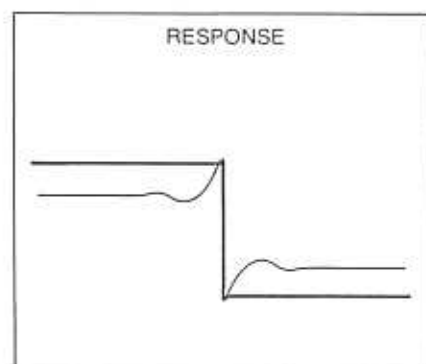
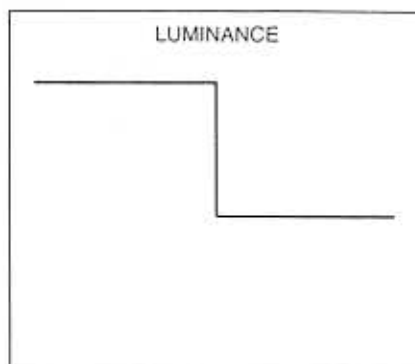
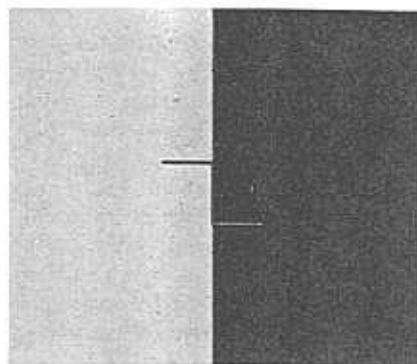
graphic copy of the uniform areas one merely has to put a halftone screen over the original. The screen breaks up the uniform areas into many small discontinuities, in effect many contours.

Similar contrast effects are seen in photography and in television. In photography a chemical by-product of the development process at one point can diffuse to neighboring points and inhibit further development there, causing spurious edge effects; in television the secondary emission of electrons from one point in the image on the signal plate in the camera can fall on neighboring points and "inhibit" them, creating negative "halos," or dark areas, around bright spots. The similarity of the contrast effects in such diverse systems is not a trivial coincidence. It is an indication of a universal principle: The enhancement of contours by contrast depends on particular relations among interacting elements in a system and not on the particular mechanisms that achieve those relations.

How a contour itself can affect the contrast of the areas it separates cannot be explained quite so easily. This effect of contour on contrast was first investigated by Kenneth Craik of the University of Cambridge and was described in

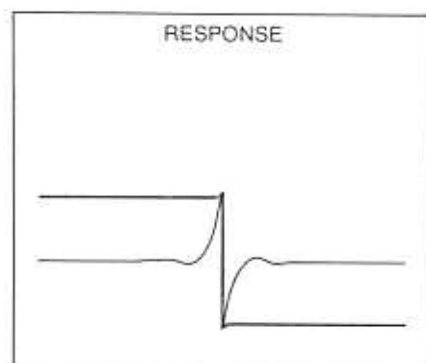
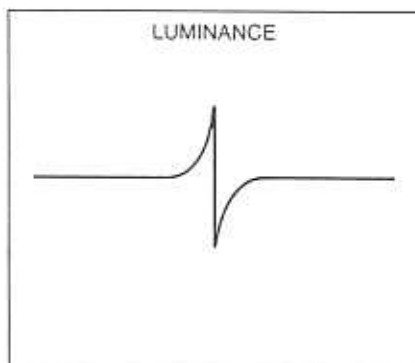
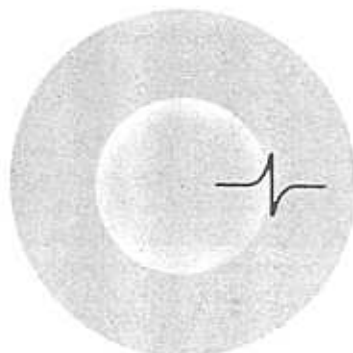


SOURCE OF CRAIK-O'BRIEN EFFECT can be demonstrated by covering the contour with a wire or string. When this is done, the inner and outer regions appear equally bright.



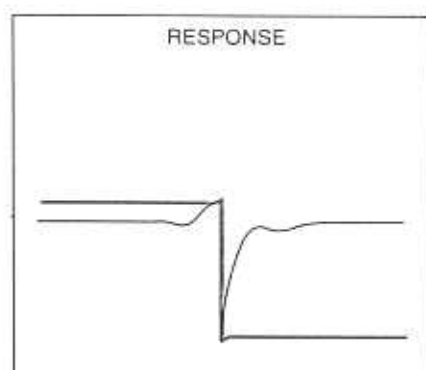
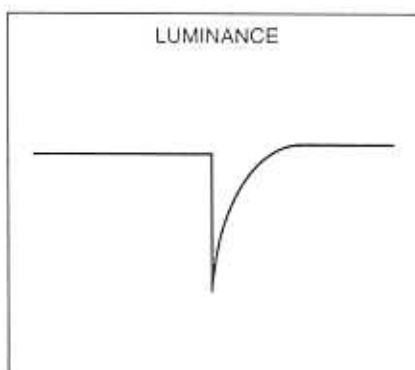
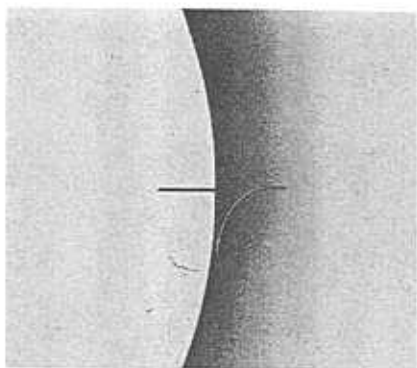
STEP PATTERN of illumination (*left*) also has a step-pattern luminance curve (as measured by a photometer) across the contour. A computer simulation of the response of the *Limulus* eye to the pattern (*black curve at right*) shows a maximum and a minimum

that are the result of inhibitory interaction among the receptors. The colored curve at right shows how the pattern looks to a person; the small peak and dip in the curve indicate slight subjective contrast enhancement at the contour known as "border contrast."



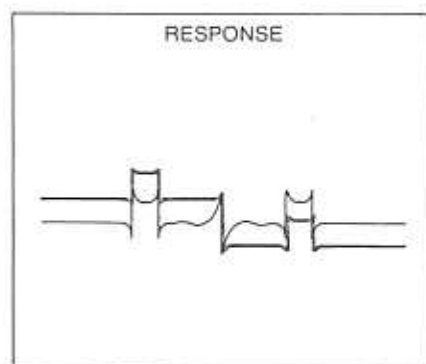
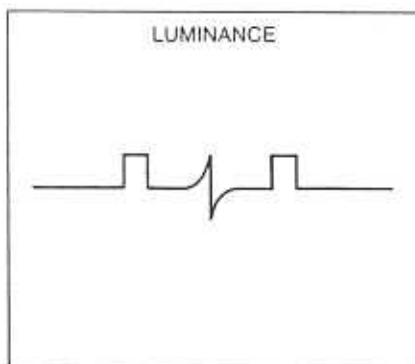
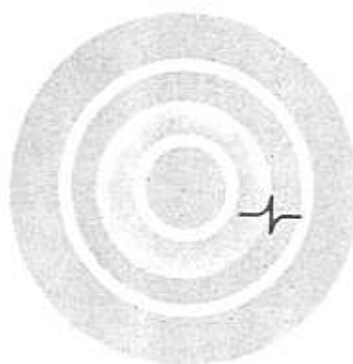
LUMINANCE on both sides of the Craik-O'Brien contour is the same but the inside (here simulated) is brighter. The human visual

system may extrapolate (*colored curve*) from the maximum and minimum produced by inhibitory processes (*black curve at right*).



DARK SPUR between areas can create brightness reversal. Objectively the area at left of the contour is darker than the area at far right, but to an observer the left side (here simulated) will appear

to be brighter than the right side. This brightness reversal agrees with the extrapolation (*colored curve*) from the maximum and minimum produced by inhibitory processes (*black curve at right*).



TWO BANDS OF LIGHT of equal intensity are superimposed on backgrounds of equal luminance separated by a Craik-O'Brien

contour. The lights add their luminance to the apparent brightness (*colored curve*) and one band appears brighter than the other.

his doctoral dissertation of 1940. Craik's work was not published, however, and the same phenomenon (along with related ones) was rediscovered by Vivian O'Brien of Johns Hopkins University in 1958. The Craik-O'Brien effect, as I shall call it, has been of great interest to neurophysiologists and psychologists in recent years.

A particular example of this effect, sometimes called the Cornsweet illusion, is produced by separating two identical gray areas with a special contour that has a narrow bright spur and a narrow dark spur [see top illustration on page 14]. Although the two uniform areas away from the contour have the same objective luminance, the gray of the area adjacent to the light spur appears to be lighter than the gray of the area adjacent to the dark spur. When the contour is covered with a thick string, the grays of the two areas are seen to be the same. When the masking string is removed, the difference reappears but takes a few moments to develop. These effects can be very pronounced; not only can a contour cause contrast to appear when there actually is no difference in objective luminance but also a suitable contour can cause contrast to appear that is the reverse of the objective luminance.

With the choice of the proper contour a number of objectively different patterns can be made to appear similar in certain important respects [see illustrations on opposite page]. It is reasonable to assume that in all these cases the dominant underlying neural events are also similar. With the mathematical equation for the response of a *Limulus* eye one can calculate the neural responses to be expected from each type of pattern when processed by a simple inhibitory network. When this is done, one finds that the calculated responses are all similar to one another. Each has a maximum on the left and a minimum on the right. Furthermore, there is a certain similarity between the calculated neural response and the subjective experience of a human observer viewing the patterns: where the computed response has a maximum, the pattern appears brighter on that side of the contour; where the computed response has a minimum, the pattern appears darker on that side of the contour. Indeed, merely by extending a line from the maximum out to the edge of that side of the pattern and a line from the minimum out to the edge of that side of the pattern one obtains a fair approximation to the apparent brightness. This correspon-

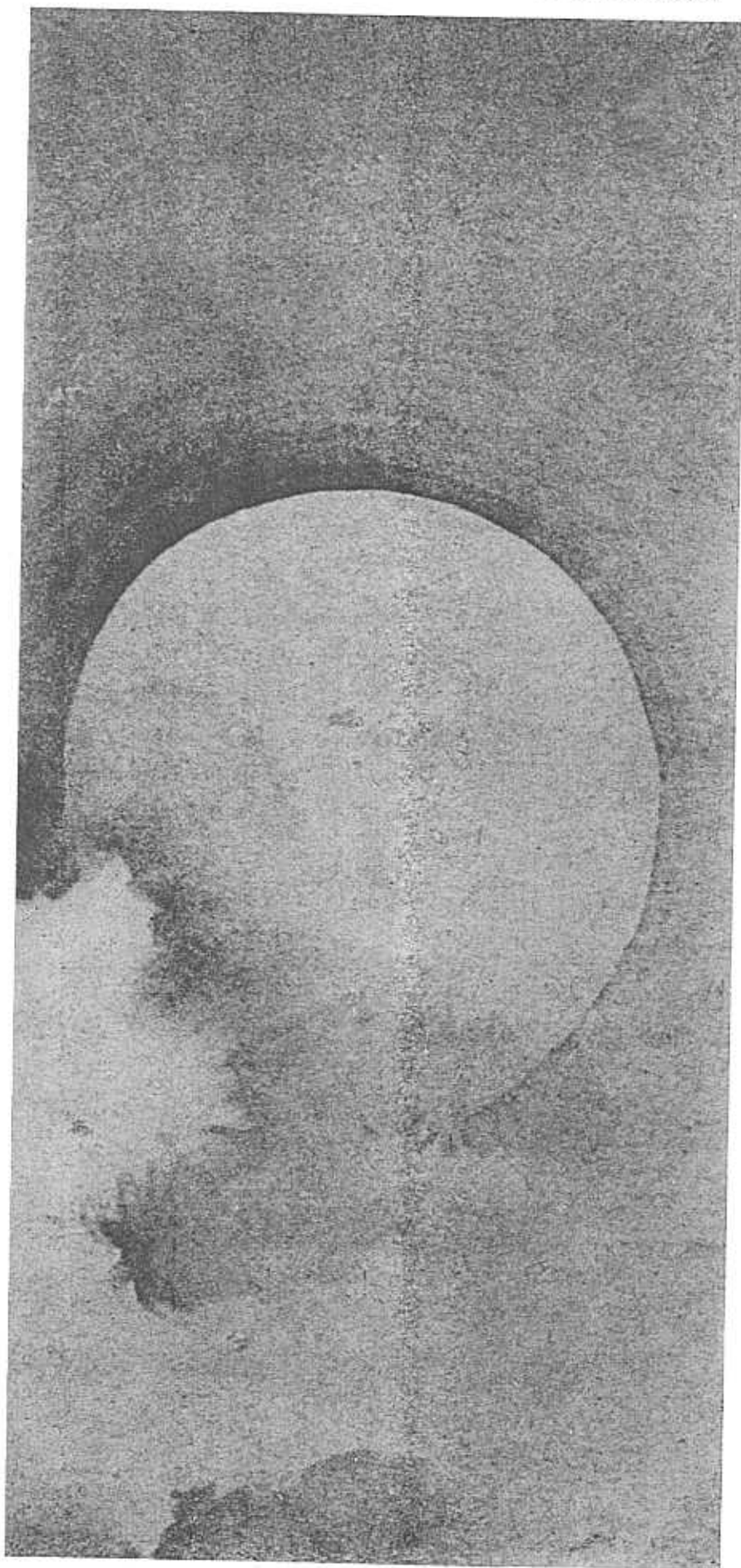
dence suggests that opposed excitatory and inhibitory influences in neural networks of our visual systems are again partly responsible for creating the effect. Even so, much would remain to be explained. Why should the influence of the contour be extended over the entire adjacent area rather than just locally? And why do three distinctly different stimuli, when used as contours, produce much the same subjective result?

The answer to both of these questions may be one and the same. Communication engineers have experimented with a number of sophisticated means of data

compression to increase the efficiency of transmitting images containing large amounts of redundant information. For example, if a picture is being transmitted, only information about contours need be sent; the uniform areas between contours can be restored later by computer from information in the amplitudes of the maxima and minima at the contours. By the same token signals from the retina may be "compressed" and the redundant information extrapolated from the maximum and the minimum in the neural response. Such a process, which was postulated by Glenn A. Fry



KOREAN VASE from the 18th century provides an excellent example of the effect of a dark spur between areas. The moon appears to be brighter than the sky directly below it, but the actual luminance is just the reverse. If only a portion of the moon and an equal portion of the sky about one moon diameter below it are viewed through two identical small holes in a paper so that the dark contour is masked, the moon appears darker than the sky.



of Ohio State University many years ago, could explain the Craik-O'Brien effect.

What the actual mechanisms might be in our visual system that could "decode" the signals resulting from data compression by the retina and "restore" redundant information removed in the compression are empirical problems that have not yet been directly investigated by neurophysiologists. The problem as I have stated it may even be a will-o'-the-wisp; it is possible that there is no need to actually restore redundant information. The maximum and minimum in the retinal response may "set" brightness discriminators in the brain, and provided that there are no intervening maxima and minima (that is, visible contours) the apparent brightness of adjacent areas would not deviate from that set by the maximum or the minimum.

Some evidence that apparent brightness is actually set by the maximum and minimum at a contour or discontinuity and is then extrapolated to adjacent areas can be found in experiments conducted by L. E. Arend, J. N. Buehler and Gregory R. Lockhead at Duke University. They worked with patterns similar to those that create the Craik-O'Brien effect. On each side of the contour they produced an additional band of light. They found that the difference in apparent brightness between each band of light and its background depended only on the actual increment in luminance provided by the band, but that the apparent brightness of the two bands in relation to each other was determined by the apparent brightness of the background. For example, if two bands of equal luminance are superimposed on two backgrounds of equal luminance that are separated by a Craik-O'Brien contour, one of the bands of light will appear brighter than the other [see bottom illustration on page 16]. A number of related phenomena, in which contrast effects are propagated across several adjacent areas, are under investigation by Edwin H. Land and John H. McCann at the Polaroid Corporation. These experi-

JAPANESE INK PAINTING, "Autumn Moon" by Keinen, has a moon that objectively is only very slightly lighter than the sky. Much of the difference in apparent brightness is created by the moon's contour. The extent of the effect can be seen by covering the moon's edge with string. The painting, made about 1900, is in the collection of the late Akira Shimazu of Nara in Japan.

ments lend further support to the general view outlined here.

Of course, the human visual system is far too complex for the simple notion that apparent brightness is determined by difference at contours to be the whole story. Nonetheless, the general idea contains at least the rudiments of an explanation that is consistent with known physiological mechanisms and with the observed phenomena. Several entirely different distributions of illumination may look much the same to the human eye simply because the eye happens to abstract and send to the brain only those features that the objectively different patterns have in common. This type of data compression may be a basic principle common to many different kinds of neural systems.

Even if the cause of the Craik-O'Brien effect is in doubt, the effect itself is incontrovertible. Although the effects of contour on perceived contrast are relatively new to the scientific community, the same effects have long been known to artists and artisans. One can only speculate on how the effects were discovered. Very likely they emerged in some new artistic technique that was developed for another purpose. Once such a technique had been perfected, it doubtless would have persisted and been handed down from generation to generation. Furthermore, following the initial discovery the technique would probably have been applied in other media. In any event such techniques date back as far as the Sung dynasty of China (A.D. 960–1279), and they are still employed in Oriental art. For example, in a Japanese ink painting made about 1900 a single deft stroke of the brush greatly increases the apparent brightness of the moon [see illustration on opposite page]. If the contour is covered with a piece of string, the apparent brightness of the moon diminishes and that area is seen to be very little brighter than its surround.

A similar effect is found in a scene on an 18th-century Korean vase [see illustration on page 17]. Here the moon is actually darker than the space below it. Measurements of a photograph of the vase with a light meter under ordinary room lights showed that the luminance of the moon was 15 foot-lamberts and the space one moon diameter below was 20 foot-lamberts. The contour effect is so strong that the apparent brightness of the two areas is just the reverse of the objective luminance.

The contour-contrast effect can be produced on a ceramic surface by still another technique. This technique was



CHINESE TING YAO SAUCER is an example of the famous Ting white porcelain produced in the Sung dynasty of about A.D. 1000. Although the entire surface is covered with only a single creamy white glaze, the incised lotus design appears brighter than the background because of the incisions, which have a sharp inner edge and a graded outer edge, producing exactly the kind of contour that creates an apparent difference in brightness.

developed more than 1,000 years ago in the Ting white porcelain of the Sung dynasty and in the northern celadon ceramics of the same period. In the creation of the effect a design was first incised in the wet clay with a knife. The cut had a sharp inner edge and a sloping outer edge. The clay was then dried and covered with a white glaze. The slightly creamy cast of the glaze inside the cuts produces the necessary gradient to create the Craik-O'Brien effect. The result is that the pattern appears slightly brighter than the surround [see illustration above]. Since the effect depends on variations in the depth of the translucent monochrome glaze, it is much more subtle than it is in the Japanese painting and in the Korean vase. But then subtlety and restraint were characteristic of the Sung ceramists.

These examples of the effects of contrast and contour from the visual sciences and the visual arts illustrate the need for a better understanding of how elementary processes are organized into

complex systems. In recent years the discipline of biology has become increasingly analytical. Much of the study of life has become the study of the behavior of single cells and the molecular events within them. Although the analytic approach has been remarkably productive, it does not come to grips with one of the fundamental problems facing modern biological science: how unitary structures and elementary processes are organized into the complex functional systems that make up living organs and organisms. Fortunately, however, we are not faced with an either-or choice. The analytic and the organic approaches are neither incompatible nor mutually exclusive; they are complementary, and advances in one frequently facilitate advances in the other. All that is required to make biology truly a life science, no matter what the level of analysis, is to occasionally adopt a holistic or organic approach. It is probably the elaborate organization of unitary structures and elementary processes that distinguishes living beings from lifeless things.

CONTOUR AND CONTRAST

Floyd Ratliff JUNE 1972

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I. SUMMARY

We see contours when there is a contrast in the brightness or color of adjacent areas. That such a contour can influence the contrast of the areas it separates has been known for at least 1,000 years, but it is a relatively new area for scientific investigation. The effects of contour on contrast are readily apparent when one examines a shadow. Next to the illuminated area is a half-shadow that gets progressively darker until the full shadow is reached. Even under ideal conditions, where the distribution of light is uniformly high in the light area, uniformly low in the dark area, and smoothly graded in between, there appears to be a narrow bright band and a narrow dark band at the bright and dark edges of the half-shadow, respectively. The appearance of these so-called Mach bands is so striking that many find it difficult to believe that they are only subjective phenomena.

Ratliff, Hartline, and their colleagues have studied the neural basis of this phenomenon by measuring the responses of single neurons in the compound eye of the horseshoe crab. Each eye consists of 1,000 ommatidia, which function as relatively independent receptor units. Excitation does not spread from one ommatidium to another; the ommatidia are interconnected by a network of nerve fibers, but the function of this network is strictly inhibitory. If a single ommatidium is illuminated and the responses leaving it are recorded, weak stimulation produces a low rate of discharge and strong stimulation a high rate. In addition to these local excitatory effects, there is a concomitant inhibitory effect; when a receptor unit fires, it inhibits its neighbors. The degree of inhibition is inversely related to distance from the stimulated cell, and the stronger the illumination, the stronger the inhibitory effect. The subjective Mach bands are a direct result of these narrow fields of excitation and broad fields of inhibition. Near the boundary between light and dark fields, the receptors in

the dimly lit region will be inhibited not only by their dimly lit neighbors but also by some of the brightly lit receptors. The total inhibition of these boundary cells will thus be greater than for dimly lit cells farther from the boundary. Similarly a brightly lit receptor near the boundary will be in the inhibitory field of some of the dimly lit receptors, and as a result will have less inhibition acting on it than brightly lit receptors farther away from the boundary. Thus the dimly lit part of the border appears darker than it really is, and the border on the bright side appears brighter. The over-all effect of lateral inhibition is thus to accentuate the perception of contours.

It is more difficult to explain how a contour can affect the contrast of the areas it separates. An example of such an effect is the Cornsweet illusion, a specific case of the Craik-O'Brien effect. If two uniformly gray areas on a disc are separated by a special contour composed of a narrow bright spur and a narrow dark spur, when the disc is spun the entire area adjacent to the dark spur appears darker than the area adjacent to the light spur, even though away from the contour the two areas have the same luminance. Why should the influence of the contour extend over the entire area instead of being just local? One possibility is that only the information about contours is transmitted by the retina, and the uniform areas between the contours are restored by extrapolating from the contours. Of course, this notion is far too simple to be the entire story; nonetheless it is consistent with many of the facts that we know about the operation of the visual system. Several entirely different distributions of illumination may look much the same simply because the visual system happens to abstract and transmit only those features that the objectively different patterns have in common. This type of data extraction and compression may be a basic principle common to many different kinds of neural systems.

II. GLOSSARY

carapace — upper shell of the *Limulus* and other animals.

compound eye — an eye consisting of several separate optical systems.

Cornsweet illusion — a specific example of the Craik-O'Brien effect in which a narrow bright spur and a narrow dark spur at the contour between center and surround makes the surround appear darker even though it has the same luminance as the center.

Craik-O'Brien effect — the effect of certain contours on the perception of contrast of the areas that they separate.

Deiter's nucleus — vestibular nucleus situated on the floor of the fourth ventricle.

disinhibition — reduction of the inhibition of a cell when another cell that is causing the inhibition is itself inhibited.

half-shadow — *penumbra*.

lateral inhibition — inhibition of receptors or neurons through the activation of neighboring cells.

Limulus — horseshoe crab.

luminance — the amount of light reflected from a surface, which is largely responsible for the perception of brightness.

Mach bands — the subjective bright and dark bands at the bright and dark edges of a half-shadow.

ommatidia — individual photoreceptor elements which compose the compound eye of some animals.

optic nerve — nerve which transmits visual input from the eye to "higher" brain centers.

petroglyph — a carving on rock; especially a prehistoric rock carving.

pictograph — a pictorial sign or symbol.

plexus — a network of nerve fibers; the *Limulus* ommatidia are interconnected by the lateral plexus.

psychophysical — pertaining to the relation between the physical properties of a stimulus and how it is perceived.

III. ESSAY STUDY QUESTIONS

1. What information in Ratliff's article clearly shows that it is important to make the distinction between the physical and the perceptual properties of objects—for example, between luminance and brightness?
2. Explain how lateral inhibition and the resulting disinhibition leads to an accentuation of borders.
3. What is the physiological basis of Mach bands?
4. Most people assume that their sensory systems give them a faithful representation of the external environment. Discuss in light of Ratliff's article.
5. Ratliff's explanation for the occurrence of Mach bands would have been more convincing if he had shown that horseshoe crabs could perceive them. Discuss.
6. Describe the Cornsweet illusion and the interpretation suggested by Ratliff.
7. Describe how the interactions between contour and contrast have been employed by artists in their work.
8. If Mach bands are completely subjective, how is it that they can be reproduced photographically?
9. The over-all filtering effect of the *Limulus* retina is to attenuate both the lowest and highest spatial and temporal frequencies. Explain.
10. Contrast phenomena exist in any system where opposed fields of positive and negative influence exist. Discuss xerography in light of this concept.

⇒ patterns of disinhibition seem to mediate contours