Contour and Contrast

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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 psychophysical 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 page 173).

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 page 173). 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 following 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.
Subjective vision is the ability to see in the absence of客观 被o光。While we may not see contrast when we actually view a scene, our visual system can still perceive contrast, either objectively or subjectively. The effects we see in our own paintings depend on our own perceptions of contrast. When we view Signac's painting, we see the contrast as our own eyes respond to contrast. 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 determine 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 photographs show, however, is to reproduce 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 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.

In many occasions, scientific investigators have mistaken Mach bands for objective phenomena. For example, shortly after W. K. Roentgen 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, were 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 Dettlev 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 \( A \).
been demonstrated to be essentially contained 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 it 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 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.
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.
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.
the remaining set, thus increasing their rate of discharge [see bottom illustration on page 174]. 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 motor nerves 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 175].

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.

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.
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 170]. Contours are enhanced; uniform areas are lost. To obtain a xerographic copy of the uniform areas one merely has to put a half-tone 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-OBRIEN 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.
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 it 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 178]. 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 page 177]. 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 correspondence 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 of 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.
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 com-
pres-sion 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 infor-
mation. 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 bright-
ness is actually set by the maxium
and minimum at a contour or discontinui-
ity and is then extrapolated to adjacent
areas can be found in experiments con-
ducted by L. E. Arend, J. N. Buehler
and Gregory R. Lockhead at Duke Uni-
versity. They worked with patterns simi-
lar 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 ap-
parent brightness between each band of
light and its background depended only
on the actual increment in luminance
provided by the band, but that the ap-
parent brightness of the two bands in
relation to each other was determined
by the apparent brightness of the back-
ground. 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 bot-
tom illustration on page 17]. A number
of related phenomena, in which contrast
effects are propagated across several ad-
jacent areas, are under investigation by
Edwin H. Land and John H. McCann at
the Polaroid Corporation. These experi-

JAPANESE INK PAINTING, "Autumn
Moon" by Keisai, has a moon that objec-
tively 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 cover-
ing the moon's edge with string. The paint-
ing, made about 1900, is in the collection
of the late Akira Shimazu of Nara in Japan.
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 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 at left]. Since the effect depends on variations in the depth of the translucent monochome 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.