

Opponent Processes as a Model of Neural Organization

LEO M. HURVICH *University of Pennsylvania*

DOROTHEA JAMESON *University of Pennsylvania*¹

On an occasion such as this one we have an opportunity to pull back from the trees, the underbrush, and thorny bullweed to raise again, in case it has been lost sight of, the central question of visual perception: Why do things look as they do? Because they are what they are? No, because we are what we are.

Some of you will surely recognize the question as one raised precisely in those words by Kurt Koffka (1935). Without getting embroiled in the specifics of the mind-body problem and its many proposed resolutions—it was the subject of a recent major article in *Science* by Globus (1973)—it seems clear to us that the answer to the broad question “Why do things look as they do?” will be given in an informative way only when the principles of neural organization are known. To describe more specifically what we mean by this, we shall ask you to bear with us while we review first the opponent process principles of neural organization in relation to our own earlier work in color and brightness perception, remind you of some of the more recent electrophysiological data that are particularly relevant to these principles, and then discuss briefly the way in which the same principle of spatial neural organization can be shown to account for very different visual phenomena.

The phenomena of visual perception can be approached in a variety of ways, and they are well

summarized in Koch's (1959) volumes on the study of psychology and Floyd Allport's (1955) volume on theories of perception, as well as in the many monographs that explicate a particular theoretical approach. For example, there is Graham's (1965) S-R approach, Gibson's (1966) view of perception as a direct apprehension of the invariants of distal stimulation, Helson's (1964) broadly unifying principle of adaptation level, Hebb's (1949) cell-assembly concept, approaches that emphasize motivational aspects, directive state, the transactional view, and so on. But for a long time, views of visual perception could be roughly divided into either of two camps that might be described as mosaic versus Gestalt, point-for-point image representation versus field representation, or elementistic or wholistic. Moreover, if what is given in the neurophysiology is a response mosaic that reflects each transitory change in the stimulus mosaic, there is obviously much cognitive decoding and resynthesis to be done on route from stimulation to perception. The elementalists consequently often stressed the importance of learning as the crucial process whereby the meaningless mosaic of sensory elements could be interpreted as the meaningful forms, outlines, and solid objects of the real visual world. The Gestalt approach to perception, on the other hand, was more compatible with a relatively greater stress on nativism, if nativism here is interpreted as an inherent physiological organization into delimited fields of higher nervous activity that lead directly to figure percepts. So the difference in point of view with respect to elementalism versus Gestalt also carried over into a difference in emphasis with respect to empiricism versus nativism. Conceptual differences of this sort also had their parallels in the rival views of the mechanism of color vision, and these existed long before the formal warfare between the Structuralists and Gestaltists was declared.

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Requests for reprints should be sent to Leo M. Hurvich, or Dorothea Jameson, Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, Pennsylvania 19174.

On the one hand, all of the phenomena of color vision were considered to be interpretive resyntheses of three elementary fundamental sensations that were attributable to three kinds of retinal receptors and their associated nerve fibers; on the other hand, these same phenomena were considered to be attributable to a visual response mechanism whose fundamental properties and principle of organization could be inferred directly from the properties observable in the phenomena themselves.²

Consider, for example, the simplest of afterimage phenomena. Figure 1 shows the bust of a young girl; if you fixate rigorously on a single spot, for instance, the tip of her nose, and then shift fixation to a uniform field, the girl will reappear as an afterimage. You have all seen afterimages of this sort. Elementary texts seem to favor a stimulus that will generate an American flag, or a photograph that will give us W. C. Fields resplendent in top hat. But most of you may not have seen this particular afterimage because the figure comes from the estate of Goethe and was probably painted by him. It appears in a recent American edition of Goethe's monograph on color theory that was translated and edited by Herb Aach (1971) after Mattaei's German edition.

Goethe, as most of you know, was fascinated by visual color phenomena, and although he was mistaken about some of the physical principles involved in producing different kinds of colored stimuli, he had some sharp insights into the principles inherent in the perceptual effects. The negative afterimage he illustrated with this figure suggests, by its very name, the principle of response rebound of opposite quality. When a primary pattern of sustained stimulation has built up one mode of response in the visual system and the stimulus is then suddenly removed, the consequence is a different mode of response, one that is opposite to, or the negative of, the initial response.

Obviously, an opponent physiological rebound is not the only way to account for a negative afterimage that is projected on a uniformly illuminated surface, and elementalists feel quite comfortable with the explanation that the phenomenon results from what is called *local adaptation* or *fatigue* of the retinal receptors.³ If the cone receptors are



Figure 1. Black and white photograph of Goethe's figure for colored afterimage. (For color plate, see Aach, 1971.)

first selectively desensitized by the different wavelengths contained in the different parts of the primary stimulus that is imaged on the retina, then only those receptors that have not been desensitized or bleached can respond to the homogeneous white light of the projection surface, hence the negative afterimage. Other characteristics of afterimage phenomena, which are best summarized as manifesting an oscillatory pattern of opposite effects that tend to damp out in time, make it difficult to avoid postulating an organization of antagonistic neural processes that wax and wane in temporal alternation as the system returns to equilibrium. These oscillatory events tend not to be featured in accounts that emphasize localized receptor bleaching to explain the occurrence of negative afterimages.

The mosaic of receptors hypothesis is still less comfortably accommodated to the phenomena of simultaneous contrast, which demonstrate another principle of neural organization. Just as the negative afterimage can be seen as an instance of *opponent temporal organization*, namely, primary response followed by opposite rebound, simultaneous contrast can be seen as an instance of *opponent spatial organization*, namely, a primary response in one spatial location inducing an opposite response in an adjoining neural region. These spatially opponent effects can, of course, be seen in strictly achromatic patterns, as in Figure 2, where

² A discussion of these views in their historical context can be found in Hurvich (1969).

³ Brown (1965) reviewed such explanations in some detail and also discussed a number of specific photochemical hypotheses that have been advanced to account for afterimage effects.

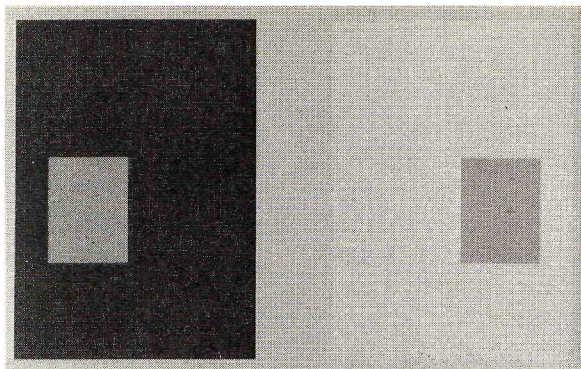


Figure 2. Achromatic contrast illustration. (Pattern from Albers, 1963, Plate IV-2.)

the gray on the right looks darker than that on the left only because of the luminance difference between the light surround on the right and the darker one on the left.

These spatially opponent effects are equally obvious and important in the organization of the hue-coding system. In the colored original of Figure 3, the two X figures appear in two differently colored surrounds. Although the Xs are spectrally identical retinal stimuli, the different qualities of response induced in the crossed lines by the different surround activities give rise to qualitatively different percepts of two differently colored Xs. An elementalists who is incurably biased against the concept of opponent neural organization to explain spatial contrast has, for his explanation, the choice either of very rapid local adaptation together with eye movements that will cause the surround to desensitize the focal area, or else he must resort to a cognitive unconscious inference hypothesis. In this specific case, it would mean unconsciously assuming that the two sides of the figure are illuminated by lights that are different on the left and on the right. One can usually work out the necessary inferences to come up with a cognitive account of such contrast effects, but it sometimes comes out sounding more like a Watergate cover story than an explanation.

Just to keep the record straight, we have no doubt that there are many situations in which what we see is strongly influenced by what we think is out there, but the universally observed phenomena of simultaneous contrast require something more than that kind of explanation.

If we consider a little more closely the specific character of the oppositions evident in both afterimage and contrast phenomena, they can be itemized very simply: What is light in the primary

image is dark in the afterimage and vice versa, what is blueish in the primary image is yellowish in the afterimage and vice versa, and what is reddish in the primary image is greenish in the afterimage and vice versa. Similarly in the simple contrast situation, the figure in the lighter surround looks darker than the same figure in the darker surround, the figure in the bluer surround looks yellower than the same figure in the yellower surround, and the figure in the redder surround looks more greenish than the one in the greener surround. What we have listed are three pairs of visual qualities that show mutual opposition within each pair: white versus black, blue versus yellow, and red versus green.

Figure 4 describes the appearance of a spectrum with as economical a vocabulary as possible. Starting on the left at the shortest visible wavelengths, around 400 nanometers, we see violet or reddish blue; moving from left to right toward longer wavelengths, the reddishness diminishes until we see simply blue in the vicinity of 475 nanometers; beyond this there is increasing greenness and diminishing blueness and we see simply green near 500 nanometers. Toward longer wavelengths yellowness enters in increasing proportion relative to green, and when we reach approximately 580 nanometers the spectral light appears simply yellow. Orange, or more economically stated, yellow-red, comes in at wavelengths longer than 580 nanometers. The red increases relative to yellow at still longer wavelengths, but spectral light never quite becomes uniquely red out to the long-wave limit of the visible spectrum at about 700 nanometers.

Note that to describe the hues of the spectrum we need the hue names *red*, *yellow*, *green*, and *blue*,

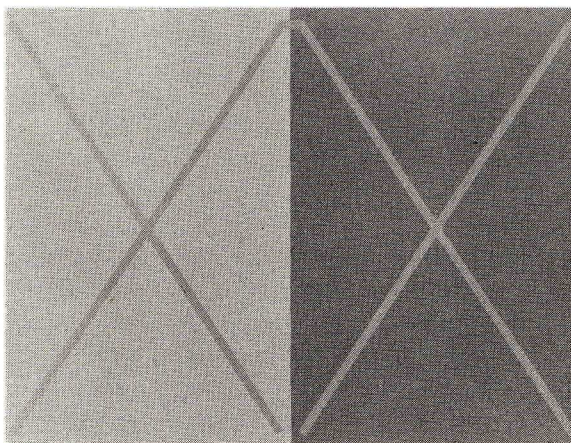


Figure 3. Black and white photograph of colored pattern that illustrates hue contrast. (For color illustration, see Albers, 1963, Plate VI-3.)

but also note that if we are to include all aspects of the spectral light qualities we would, for example, further characterize the yellow near 580 nanometers as more whitish than, say, the very slightly yellowish red at the spectral extreme. The achromatic whitishness or blackishness of each color appearance is a descriptive component just as necessary as the single or binary hue names. Note further that the hue descriptions include the binary pairs red-blue or green-blue but never yellow-blue, also yellow-green or yellow-red but never green-red. Thus, in the simple description of hue qualities we find that yellow and blue are mutually exclusive, as are red and green. This is, of course, true for all colored objects and is not restricted to the spectral light situation. The opponent character evidenced in this property of mutual exclusiveness has the same paired characteristics as the opposition observable in both afterimage and contrast phenomena. What we see does indeed seem to be trying to tell us something about the way the visual nervous system is functionally organized. Moreover, the opponent or mutually exclusive characteristics of the hue qualities themselves suggested the principle of measurement by which the qualitative descriptions that we have just itemized could be subjected to precise psychophysical measurement and expressed as quantitative spectral functions (Jameson & Hurvich, 1955). This psychophysical measurement procedure was a hue cancellation or *bucking* technique. The relative strength of a given hue elicited by spectral stimuli of a series of different wavelengths was estimated by determining the variable energy required at a fixed wavelength that elicited the opposite hue in order for the effects of the two mutually opponent hue processes to precisely cancel each other. For example, we measure how much "yellow" is generated by each of a series of different spectral wavelengths between 500 and 700 nanometers by determining how much energy of a 480-nanometer blue-generating stimulus is necessary to just balance out each of the yellows. The results of this

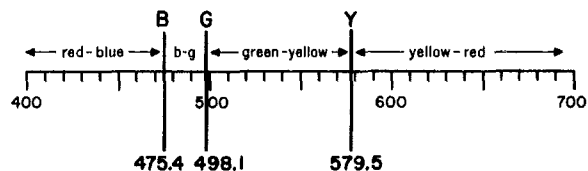


Figure 4. Description of hues of spectrum with loci of unique hues determined experimentally for one individual. (From Hurvich & Jameson, 1951.)

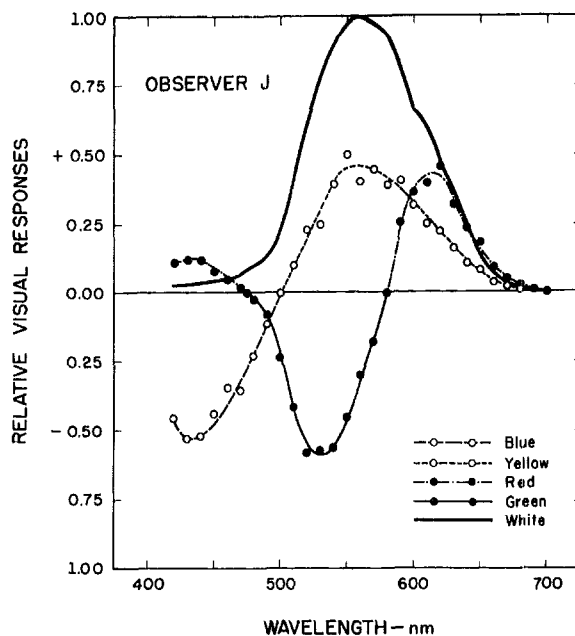


Figure 5. Psychophysical measures of chromatic and achromatic responses. (From Jameson & Hurvich, 1955.)

experiment for one observer are shown in Figure 5. These are old data which were published in the *Journal of the Optical Society* in 1955, and we show them here simply as basic data for human color vision against which we can compare some of the electrophysiological findings that have emerged from various laboratories, first for fish and then for a variety of animals up through the macaque monkey.

These psychophysical functions not only provide a more precise description of color appearances, but also, since they are quantitative expressions of the three qualitative variables basic to color vision, they permit the derivation of other basic quantitative data of color vision such as the three-variable color-mixture data, wavelength discrimination data, and so on. Such derived functions, compared with independent data measured in various other laboratories, were published many years ago in the *Journal of the Optical Society* (Hurvich & Jameson, 1955) and summarized in the *Psychological Review* (Hurvich & Jameson, 1957).

Figure 6 is a schematic diagram of the conceptual model developed to show how the three paired color variables of the quality-coded neural response system are related to the cone receptors in which the initial spectrally selective light absorption takes place. At the time that this model was developed, the spectral absorptions of the three kinds of cone

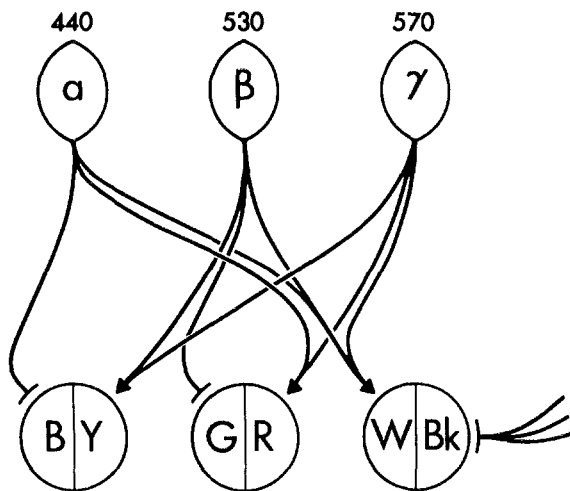


Figure 6. Schematic diagram of relations between cone absorptions and opponent response processes.

receptors were not independently known, and their absorption characteristics had to be inferred on the basis of psychophysical data together with specific assumptions about the bleaching characteristics of visual pigments. We now have more information both about bleaching properties and about the spectral absorptions of the cone photopigments (Dartnall, 1972). This information comes from a technique known as retinal reflection densitometry (Rushton, 1958; Weale, 1957), which measures light reflected back from the whole retina before and after bleaching, and also from a technique known as microspectrodensitometry, which can measure, at least approximately, the spectral absorptions of isolated, individual retinal cones (Brown & Wald, 1963, 1964; Marks, Dobbie, & MacNichol, 1964). It is on the basis of this independent evidence from the discipline of visual photochemistry that the three kinds of cones, labeled here alpha, beta, and gamma, are specified as containing photopigments whose absorption maxima occur approximately at 450, 530, and 570 nanometers, respectively (Jameson & Hurvich, 1968). Note that in this model there is no suggestion that the receptors themselves provide the color coding. Rather, the color coding is assumed to be associated with the neurophysiological events at the opponent process level (Jameson, 1972). This level is organized, according to the model, in three kinds of paired processes. Within each pair, one response mode is labeled positive and one negative to indicate their opposite physiological characteristics and to accord with their opponent and mutually exclusive perceived characteristics. Which mode of response is

considered positive and which negative is immaterial. The plus and minus signs are used as conventions to indicate oppositeness of response mode and also to express the property that the ultimate net neural response is determined by the algebraic sum of the signed arousal inputs from the excited receptors to which each neural system is functionally related. Thus, if the incident light on a given part of the retina is heavily weighted in short-wave energy, it will be absorbed more strongly by the short-wave alpha receptor than by the beta or gamma receptor, and the signed input from the more strongly excited alpha receptor will be greater than the combined inputs from the less strongly excited beta and gamma receptors which are of opposite sign. Consequently, the net response of the blue-yellow color-coded neural system will be signed as a blue response. If the nature of the light stimulus is changed so that it is now more heavily weighted in energy from the long-wave region of the spectrum, then it will be less strongly absorbed by the alpha receptor than by the beta and gamma receptors, the signed input from the less strongly excited alpha receptor will be less than the combined inputs from the more strongly excited beta and gamma receptors which are of opposite sign, and the net response of the blue-yellow color-coded neural system will now be signed as a yellow response. So the model leads us to expect that, even if we were red-green blind and lacked the red-green opponent response mechanism entirely, we would still retain some spectral color discrimination because the hue-coded response of one sign for short wavelengths would switch to one of the opposite sign for longer wavelengths. Congenital protanopes and deuteranopes and normal vision in the retinal periphery are instances of this kind of reduced color vision (Hurvich, 1972, 1973; Moreland, 1972).

How might this bimodality of response be expressed in the electrical responses of individual nerve cells? The first discovery of wavelength-specific neurophysiological response in individual cells of the retina was made by Gunnar Svaetichin (1956) in the isolated fish retina. And this vertebrate, unlike the cat, is known to have good color discrimination. The responses took the form of graded changes in dc potentials that varied in magnitude from one wavelength to the next, and in some cells showed a reversal in polarity of response, from hyperpolarizing potentials at short wavelengths to depolarizing responses at longer wavelengths, or vice versa. Figure 7 shows such records from Svaetichin's work. These results have

been confirmed many times, in the retinas of many species and by different investigators in many different laboratories (Abramov, 1972). The electrical potentials are thought to be responses of the horizontal cells of the retina (Svaetichin & MacNichol, 1958), and they are often referred to as S-potentials in recognition of Svaetichin's early recordings. To illustrate the complexity of the retinal network, Figure 8 shows a diagrammatic cross section from the recent work of Dowling and Boycott (1966) with the rods and cones at the top, horizontal cell sending its processes laterally in the layer between the receptors and the different kinds of bipolar cells, and amacrine cells also sending their processes laterally between the layer of the bipolars and the different types of ganglion cells,

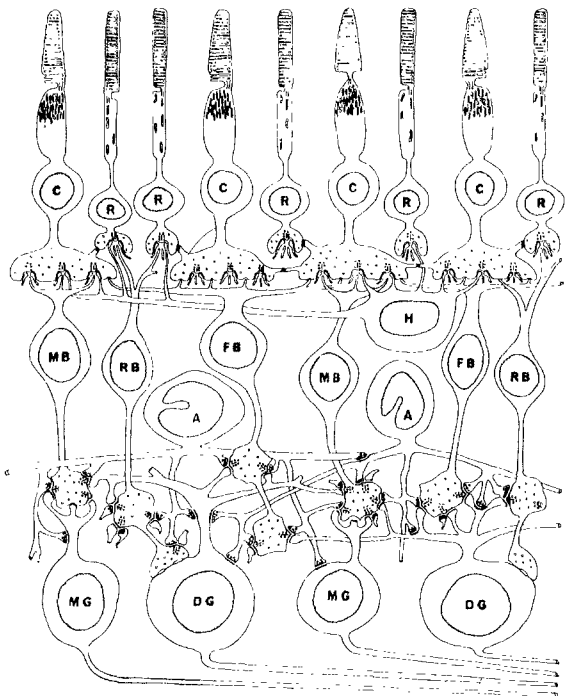


Figure 8. Summary diagram of the contacts among retinal cells of various types. (R, rod; C, cone; MB, midget bipolar; RB, rod bipolar; FB, flat bipolar; H, horizontal cell; A, amacrine cell; MG, midget ganglion; DG, diffuse ganglion. After Dowling & Boycott, 1966.)

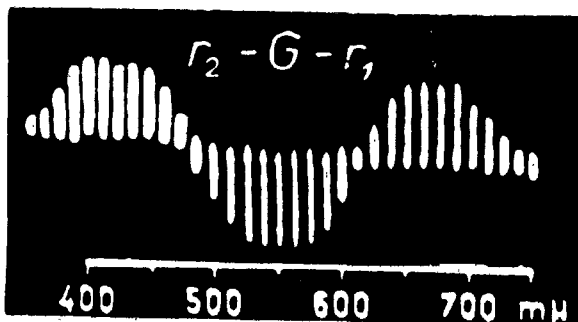
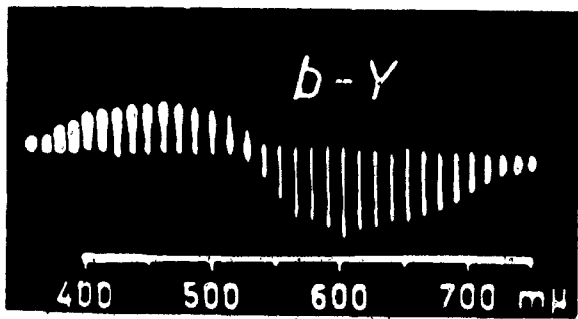
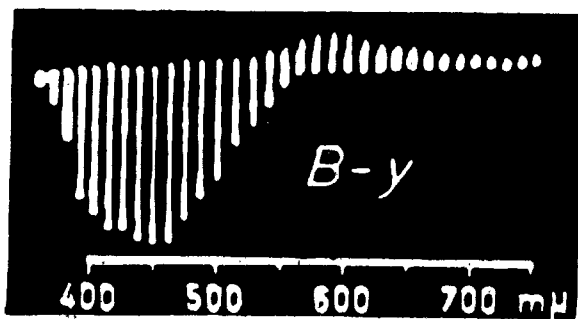


Figure 7. Records showing reversal of polarity of electrical graded potential responses to light stimuli of different wavelengths. (From Svaetichin et al., 1963.)

shown at the bottom of the diagram. At the later neural cell level, that of the ganglion cell, the responses are characterized by spike discharges rather than by graded potential changes alone. Instead of electrical polarity reversals exhibited by the graded potentials, the spectrally opponent responses of ganglion cells are exhibited by spiking discharges versus suppression of spiking discharges. For example, when short-wave light stimulates the retina, there may be spiking at the onset of stimulation and suppression of spiking at stimulus offset, whereas at longer wavelengths there may be suppression of spike discharge at stimulus onset followed by a burst of spikes at stimulus offset, the so-called off-discharge. Spectrally opponent responses of this sort have been recorded from ganglion cells of the fish retina and the retinas of other species as well as from the optic nerve, and from both the lateral geniculate and visual cortex of the monkey (DeValois, 1965; Hubel & Wiesel, 1968; Wiesel & Hubel, 1966). Figure 9 shows records of such responses from the work of DeValois and his co-workers. Compare the response to a 440-nanometer light above with the response of the same cell

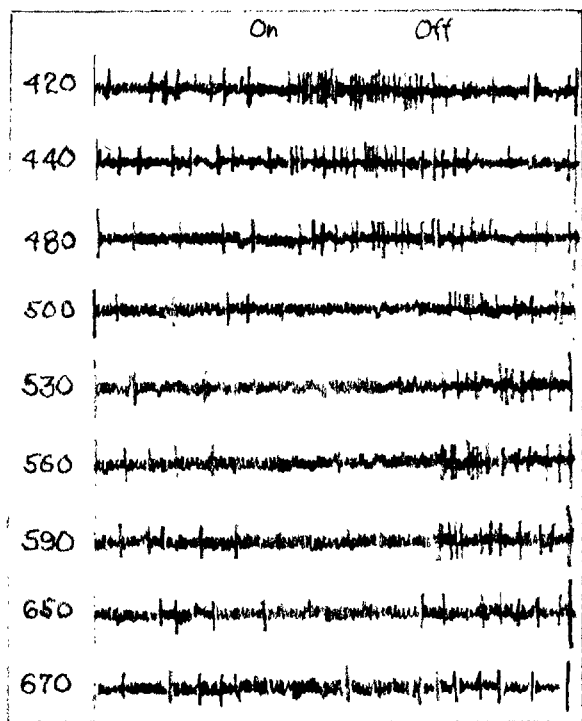


Figure 9. Series of records showing change in response of a spectrally opponent cell in the macaque LGN. (The cell shows on-responses to short wavelengths [420–480 nanometers] and off-responses to the long wavelengths [500–670 nanometers]. This figure is our tracing of a photographic reproduction from DeValois, 1965.)

to 590 nanometers below. These are records from the lateral geniculate body of the macaque monkey, and in these so-called spectrally opponent cells there is a change from spiking to stimulation at short wavelengths to suppression of spontaneous discharge during stimulation and an after-discharge of spikes for stimuli of longer wavelengths.

If we assume that the coding in a cell of this sort is blueness when the cell fires and yellowness when the cell firing is inhibited by stimulation, then we can relate this pattern directly to the negative afterimage phenomena with which we started this discussion. A short-wave stimulus is imaged on the retina, cells with this particular coding fire, and that firing codes blueness. When the stimulus is removed the cell goes into a silent phase, the coding is the opposite of blueness, namely, yellowness or the afterimage hue. And eventually the cell returns to its spontaneous firing rate again. If the stimulus is of a longer wavelength, the cell is silent while the stimulus persists and fires when it is removed. This is consistent with a yellow primary

hue in this instance followed by the blue afterimage hue when the cell again fires at stimulus off, again with the “firing equals blueness” coding. This is not to say that no bleaching or receptor adaptation or desensitization occurs when an afterimage is developed, but rather to say that the neural organization is such that the opponent activities fundamental to hue perception lead, *sui generis*, to opposite aftereffects.

What of the spatial contrast phenomena that show qualitatively similar effects? If we first put these contrast phenomena into the perspective of the conceptual model, we can then see how the model (Figure 10) relates to the detail seen in electrophysiological studies of individual nerve cells. In looking earlier at the schematic of the conceptual model we considered only what might be called the vertical interrelations, namely, those between the receptor units and the opponent neural response pairs. What the model assumes, in essence, is that specific lateral interconnections exist such that activities aroused in a given paired system, whether in a blue–yellow system, a red–green system, or a white–black system, both influence and are reciprocally influenced by ongoing activities in corresponding adjacent and surrounding neural systems. This influence is assumed in the model to be both mutual and opponent, that is, if, say, blue, or blueness-coded, activity is ongoing in one functional unit of the blue–yellow system, opposite, namely, minus or yellow, activity is induced in adjacent functional units of the same coding. The same mechanism operates, according to the model, in the opponent red–green system, where redness activity

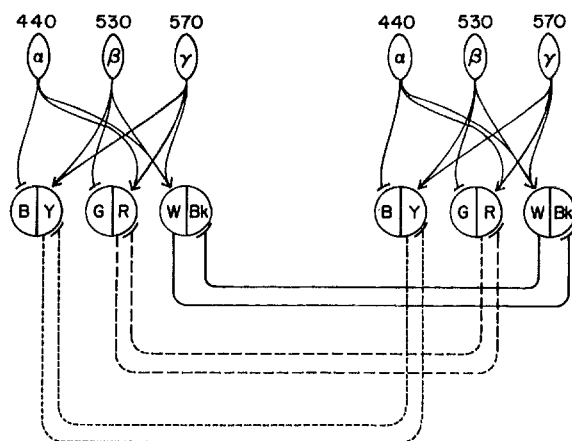


Figure 10. Schematic diagram of model illustrated in Figure 6 expanded to include representation of reciprocal lateral influences at the opponent process level.

induces greenness activity in neighboring units, and vice versa, and in the opponent white-black system. The achromatic white-black system differs from the hue-coded opponent pairs only with respect to symmetry of arousal. There is no external stimulus to excite blackness directly. In terms of what we called the vertical interrelations, all three types of cone activities arouse activities of common sign in the achromatic system and the code is "whiteness." The oppositely signed blackness response comes about only indirectly as an aftereffect of the direct focal stimulation of the retina, or through the system of laterally induced opponent activities. It is the lateral, opponent, induced activities that are, we believe, responsible for the phenomena of simultaneous contrast. Since the conceptual model has been developed in a quantitative way that also expresses these lateral opponent effects in equation form, we have been able to derive quantitative psychophysical functions to express the amount of hue and brightness contrast effect produced for a variety of stimulus parameters. Again we are referring here to theoretical derivations long published and compared with psychophysical measures from both our own and various other laboratories (Jameson & Hurvich, 1964). There is one set of psychophysical functions contained in that paper that we would like to remind you of because it makes an additional point about the mechanisms of visual perception and a basic principle of neural organization to which we have not yet alluded.

When we think of visual contrast effects, usually the first examples that come to mind are effects that we would have to describe as nonveridical. A gray paper in a light surround tends to look black; a gray paper in a green surround tends to look red, and so on. On the other hand, there are all the phenomena of perceptual constancy which attest to the veridicality of our perceptions of objects despite the changes that their retinal images undergo with changes in illumination, and so on. Is it possible that the same visual mechanism that causes surfaces of *constant* characteristics to appear to *vary* in their perceived color and brightness can also bring about the approximate constancy of object appearances? We believe the answer to be very importantly yes.

Figure 11 shows the extent to which the model predicts that brightness constancy will result by the action of the opponent lateral induction processes that account for simultaneous contrast. The stimulus situation to which the figure refers is a visual pattern consisting of a number of different re-

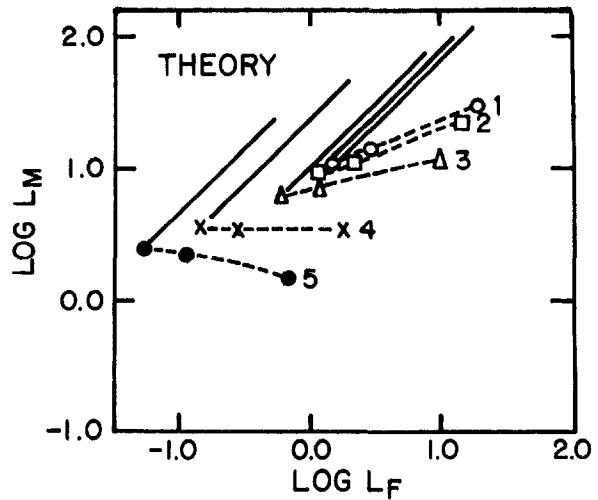


Figure 11. Theoretical predictions of brightness changes with changes in illumination level of a five-element pattern. (Solid lines, —, indicate photometric predictions; dashed lines, - - -, indicate visual predictions based on opponent spatial interaction model [Jameson & Hurvich, 1964].)

flectances that might be described as varying in appearance from near white to very dark gray, and viewed at three different levels of illumination. The amount of light reflected from each part of the pattern increases in the same proportion as the level of illumination is increased, and, if the eye were simply a photometer, then the matching luminance, plotted on the ordinate, would simply increase for each different area in the pattern in direct proportion to the increase in overall illumination, plotted on the abscissa. This photometric prediction is shown by the family of straight lines with a slope of one that are drawn in Figure 11. Each different symbol in the graph refers to an area of different reflectance in the pattern. The equations that embody the opponent spatial interaction concept predict, however, that the changes in apparent brightness will be much less than those that would be recorded by a photometer. The visual predictions are shown by the dashed lines. The pattern as a whole will not show perfect constancy, although a particular area within it may, in this case the area numbered 4 and represented by the Xs in the graph. The departures from constancy are predicted to be such that the pattern will be a little more contrasty, a little sharper, if you will, at the higher levels of illumination. The experimentally measured matching luminances are shown in Figure 12. Here you can see the increase in

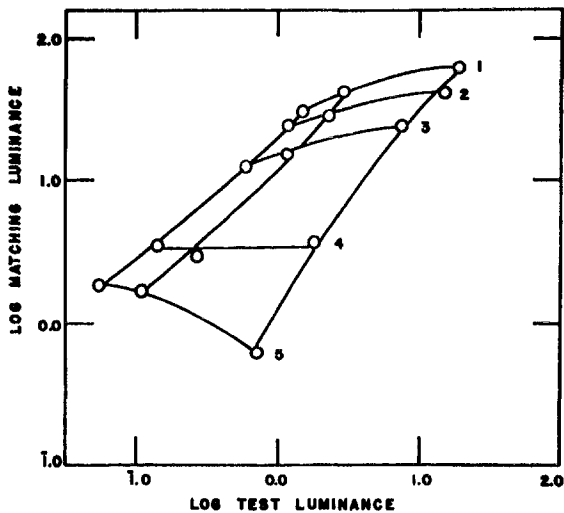


Figure 12. Matching luminance data for apparent brightness changes with changes in illumination level of a five-element pattern. (From Jameson & Hurvich, 1964.)

gradient from left to right between the darkest and lightest areas at the different illumination levels.

Painters and artists, of course, do not need a model of the spatial interaction in the visual nervous system to represent this effect in their canvases and drawings. If they want to recreate the impression of bright illumination in a drawing or painting, they do so by manipulating their pigments or shading to increase the contrast from one area to the next. And as we know from the impressionists, they also do not need to be told that the same kinds of effects occur in the opponent hue mechanism: In a painting, increasing the yellow of the fully illuminated area and the blue of the shadowed area is quite effective in representing bright sunlight. But our main point here is that the mechanism of lateral interaction, the same mechanism that causes the changes in appearance that we call contrast, also brings about the relative stability with change in overall illumination that we call constancy, or more correctly in terms of our actual perceptions, approximate constancy.

We wish to consider now another aspect of the spatial neural organization that we believe can account for another set of apparently mutually contradictory phenomena, namely, contrast, on the one hand, and reverse contrast, spreading, or assimilation, on the other. To explore this issue we must look more closely at the detail of the opponent spatial organization as revealed in studies of the electrophysiological responses of individual nerve cells in the retina and other visual centers.

We know that when responses are recorded from ganglion cells in the retina, such a single cell responds not simply to punctiform stimuli located within very tiny areas of the retinal image surface, but rather to stimulation within a relatively large area which is known as the receptive field of the cell. Moreover, the receptive field is characterized as eliciting one type of response in the ganglion cell for stimuli that fall in its center of receptivity, say, "on" responses, and an opposite mode of response, in this case spike inhibition during stimulation with subsequent "off" responses for stimuli that impinge on its peripheral, or surround, area of receptivity (Kuffler, 1953).

We know from the electrophysiological work that at the level of the retina, in fish, the ground squirrel, the cat, and other species, the receptive fields have a typical organization into a roughly circular center with antagonistic annular surround. This type of organization is illustrated in Figure 13. Receptive fields with approximately circular center-surround organizations of this sort can also be located in the higher neural centers, in the lateral geniculate of the cat and the monkey, for example, and we know from the extensive work of DeValois and his associates that many geniculate cells also have spectrally opponent or, apparently, hue-cod-

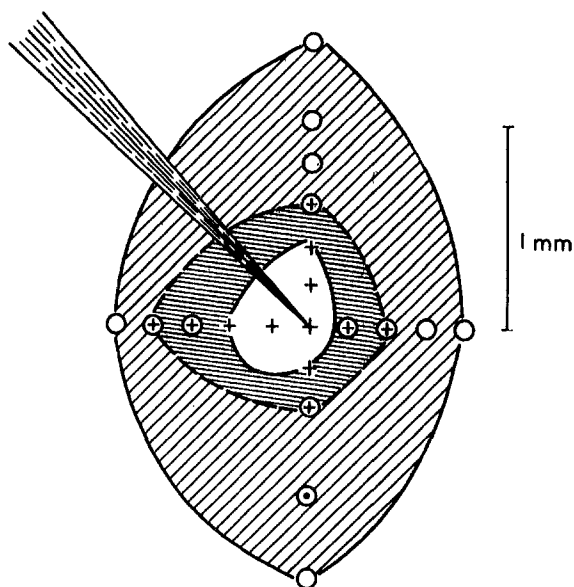


Figure 13. Receptive field map of ganglion cell in cat retina. (Crosses represent on-discharges [central region], circles represent off-discharges [diagonal hatching, peripheral region]. Both on- and off-discharges occur in intermediate region [horizontal hatching]. From Kuffler, 1953.)

ing properties. Most of DeValois' (1965) records were obtained with large or diffuse light stimuli, and thus provide no information on the receptive field characteristics of the individual geniculate cells. The spatial properties of those monkey geniculate cells whose receptive field properties have been explored with stimuli of appropriate dimensions, for example, by Wiesel and Hubel (1966), seem to fall into a number of different classes whose significance is not directly apparent. Arrangements that would properly code both hue and hue contrast would be center versus surround opposition together with wavelength opposition of reversed sign in both center and surround. Cells of this sort have been detected by Hubel and Wiesel (1968) in the monkey only in the visual cortex where the circular center-surround receptive field organization is not typical but where spatial characteristics that are apparently more highly specialized emerge. Rather than pursuing the neurophysiology of line detectors, curvature detectors, and so on, let us consider a diagrammatic representation that illustrates the essence of the opponent spatial organization that emerges from specific relations assumed between groups of retinal receptor units, on the one hand, and single neural visual cells, on the other. The organization diagrammed in Figure 14 represents a cell that shows a spatially opponent receptive field organization but no wavelength specificity with respect to mode of response. Note that the cell is under the influence of activities engendered when light is incident upon and absorbed by a relatively large number of receptors on the retina, that the inputs from those receptors located in the center of the receptive field of such a cell are associated with one mode of response, and that inputs from other receptors located in the periphery of the cell's receptive field are associated with the opposite mode of response in the cell. If the center is excitatory of spike discharge the periphery is inhibitory, and vice versa. The response profile of such an arrangement is shown in the lower part of the figure and is identical to what Békésy (1968) termed the *neural unit* in dealing with Mach band phenomena. Given stimuli of the appropriate dimensions, such an organization is ideally suited to heighten contrast; thus, a weak light falling on the receptors in the center of the receptive field would cause some firing in such a cell, but a stronger light falling on the receptors in the surround of the receptive field would inhibit or diminish the firing rate of the cell. The net response of the cell would then be equivalent to or even less

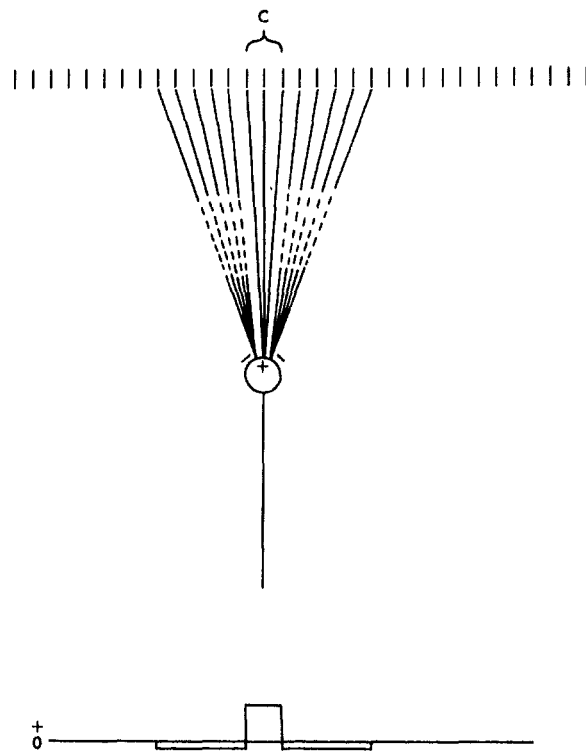


Figure 14. Diagrammatic representation of spatially opponent receptive field organization. (See text.)

than what it might be were there no light at all impinging on the receptors centered in its receptive field. So because of this arrangement, a gray spot centered in a light surround would, in terms of its physiological coding, appear darker or blacker than it would if the response depended on the photometric luminance of the gray spot alone. There are, of course, many such cells whose receptive fields on the retinal surface overlap, but a mathematical analysis of the outcome will, under the circumstances described, lead to the same outcome with respect to heightened contrast that we have just described for the single cell that is under the influence of an organized field of receptor inputs.

It should be emphasized here, however, that the outcome of any such spatial arrangement depends very strongly on the dimensions of both the pattern of stimulation on the retina and the receptive field sizes relative to that pattern. Thus, for example, adjacent retinal areas of stronger and less strong illumination that are of very small dimensions such that the adjacent differences in illumination fall not in the center and surround of the receptive field, respectively, but well within, say, the circumscribed central area, will produce no enhancement of re-

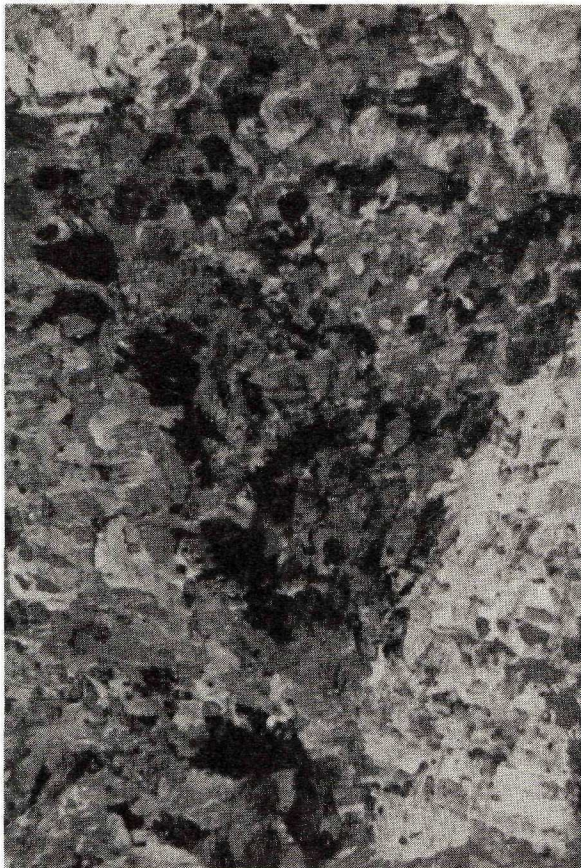


Figure 15. Black and white rendering of highly magnified colored detail from Seurat's "Grande Jatte."

sponse differences, but rather they will produce a summated response in the cell. Moreover, an image grain of the sort envisaged here, where the spatial dimensions are very small relative to the dimensions of the receptive fields of the cells responding to the related receptor inputs, will fail to be re-



Figure 16. Black and white rendering of Seurat's "Grande Jatte."

solved at all by such an assembly of visual cells. The perception will be one of uniformity, or of perfect spatial light mixture. Outside of the laboratory, we are probably most aware of such spatial light mixture when we view a pointillist painting at a sufficiently remote distance. On approaching closer to such a painting we begin to resolve the variegated texture of the painted surface, and if we get too close the perception becomes one of an abstract array of differently colored dots or blobs. (Figure 15 is a black and white rendering of a colored detail.) This is a greatly magnified detail of the "Grande Jatte" by Seurat, who, as you know, exploited the spatial light-mixture effect in the development of his very finely structured pointillist technique. A photograph of the full painting is shown in Figure 16.

In view of the crucial nature, with respect to the perceptual outcome, of the dimensions of the receptive fields of visual cells relative to the dimensions of the stimulus pattern imaged on the retina, information about the dimensions of receptive fields of individual cells becomes highly relevant to any conceptual modeling intended to handle contrast and mixture phenomena. From the electrophysiological evidence available for the visual system of the monkey, two general findings about these dimensions can be stated. One is that the diameters of the receptive field centers are smallest near the fovea and tend to increase in size as distance from the fovea increases. The other finding, equally important, is that for any given region of the retina there is a very appreciable spread in the measured diameters of the receptive field centers. Figure 17, from Hubel and Wiesel's work (1960), provides the evidence for both of these statements.

We have seen that, depending on the diameter of the receptive field, for a given pattern of stimulation on the retina, there is a physiological basis for either accentuation of contrast, or mixture and failure of visual resolution. But given the range of receptive field sizes even for cells responding to the same part of the retina, we should anticipate that the responses of some cells would lead to one kind of perception and the responses of other cells would lead to the other. We have, in fact, perceptions that we can readily interpret as the outcome of precisely such a physiological organization, in the visual phenomena called *assimilation*, the Bezold spreading effect, or sometimes, reversed contrast.⁴

⁴ For colored illustrations of this effect, see Evans (1948, Plate XI opposite p. 192).

These are phenomena in which a repetitive pattern is clearly resolved against a differently colored background, and yet the hue or lightness of the pattern seems to be more like the background color, or vice versa, as if the pattern and background were mixing with each other to some extent, rather than contrasting with each other. If the resolution of the pattern as distinct from its background is being carried out by the responses of visual cells with small receptive fields, while at the same time cells with receptive fields too large to provide such resolution are responding to the same parts of the stimulus pattern imaged on the same part of the retina, then the phenomenon of mixture or assimilation of pattern and background at the same time that it is clearly resolved loses its mystery (Jameson & Hurvich, 1972). We shall report on some quantitative aspects of this problem in the near future, but the effect is a large one and easily demonstrated. The pattern shown in Figure 18 is, in the original, printed in three colored inks, namely, a red, a green, and a blue. Separate hues are seen in each of the center bull's-eye and annulus patterns, but they can appear to be mixed in the easily resolved horizontal stripes.

A number of other visual phenomena can also be related to these receptive field size variations. Thomas (1970) considered some of them in a recent review article, and they are unquestionably at the base of the many effects that can be shown to be frequency specific (Blakemore & Campbell, 1969), since spatial frequency is a special case of variation in image size. Moreover, some organization of cells with common spatial properties must be assumed if we are to explain the various specific adaptation phenomena that are variants of the McCollough effect, which McCollough (1965) originally demonstrated as a specificity that conjoined hue, size, and orientation. The way in which such highly specific cellular receptive field organizations can arise at the cortical level through inputs of systems of cells with shared hue and dimensional properties would require a whole additional exposition. Hubel and Wiesel (1965) worked out a detailed schema for achromatic cells for the cat cortex, and a similar scheme works out for the human or monkey cortex if we add the necessary additional variable of hue specialization with its bimodal opponent properties.

One of the general points that we should like to emphasize about the visual system is that the system is organized by means of opponent processes to yield a general tendency toward reestablishing equilibrium whenever the balance of the system is

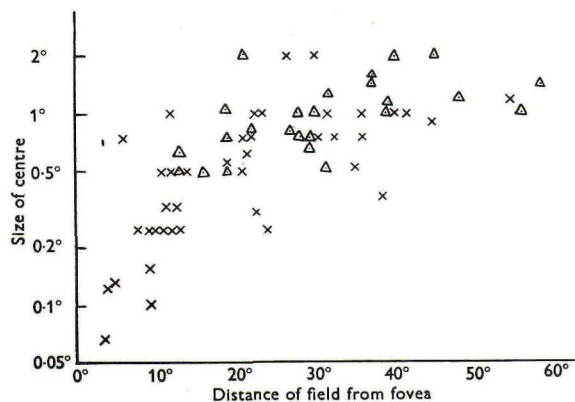


Figure 17. Diameters of receptive field centers in degrees (logarithmic scale), plotted against distance in degrees of each field from the fovea. (X, on-center units; Δ , off-center units. From Hubel & Wiesel, 1960.)

disturbed by stimulation. Thus, the light stimulation that is followed by a back reaction, which can be observed phenomenally in afterimages, is more correctly understood as stimulation of one state, which state itself acts as an internal stimulus for the arousal of the opposite neural process. If the stimulation were to continue unchanged in time, the two opponent processes would cancel each other in time, and there would be no phenomenal experience except the negative one of disappearance—fixed images disappear. So the opponent neural organization is an equilibrium-seeking device, but this equilibrium seeking is itself thwarted by an opponent system of another sort, namely, the efferent system to the muscles that under normal conditions keeps the eyes in motion so that the retinal image cannot be still even in a motionless external

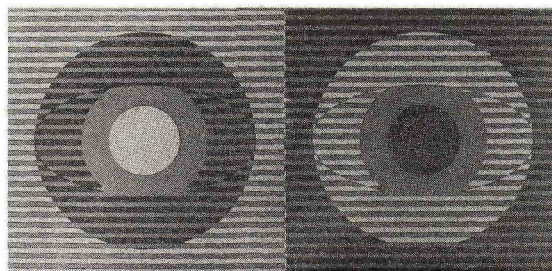


Figure 18. Black and white photograph of colored pattern that shows both contrast and assimilation. (See text. Colored original by David L. Burke Design Corporation for Scott, Foresman Publishers.)

environment. Similarly, the opponent center-surround organization of the receptive fields of nerve cells that serve so well to accentuate border contrast, produce Mach bands, and so on, are ideally organized to turn off when the retina is presented with a spatially homogeneous field of stimulation, or Ganzfeld. A visual field that contains no spatial gradients contains no spatial information, and hence nothing is lost by an opponent organization of the neural system that gives a net response of zero when the information content is zero, even though, in terms of light quanta, there may be an appreciable amount of stimulus energy flooding the retina.

It is the equilibrating effect of the opponent processes during continued stimulation and the release of the strong back-reaction when the primary stimulus is suddenly removed that Solomon has found especially enlightening in relation to a totally different class of phenomena. What Solomon and Corbit (1973) were concerned to understand were sequences of emotional states, or animal behaviors that imply emotional states, and they found the opponent process concept a fruitful one to pursue in their attempts to relate a variety of behaviors associated with learning, habituation, and addiction. As one example from the animal learning area, dogs given shock react with a set of responses that typically suggest a state of unpleasant emotional arousal. When shock terminates, another set of responses occurs that imply what might be called pleasurable relief or perhaps even joy. With longer periods of exposure to the shock stimulus, the intensity of the initial, unpleasant-affect behavior diminishes, but what might be called the relief syndrome after shock termination shows no comparable decrement in the intensity of its expression. The failure of the primary response and the after-effects to build in intensity or wane together seems paradoxical at first, but it follows naturally if, by analogy with the visual situation, what is happening during the primary stimulation is (a) a direct response appropriate to the direct stimulus and (b) an opponent neural response that builds in time in such a way as to restore the system to a new equilibrated state. In the visual situation the image fades more or less during continued exposure of the eye, but the afterimage seen when the eye is relieved from the continued stimulation increases in strength with the duration of the primary stimulus, just as the dog who whimpers less with continued exposure to shock still wags his tail at least as vigorously when the noxious stimulation is termi-

nated. For many other examples, and the potential application of the opponent process concept to the problem of drug addiction, we can better refer you to Solomon and Corbit (1973).

The opponent principle can be seen as operating not only as between states of nervous activity and between inputs at the cellular receptive field level, but also as between areas of the brain that seem to be mutually and reciprocally related in the control of specific behavior. Sprague (1966) discovered such an organization in the control of visually guided behavior in the cat. In this instance, removal of a large area of visual cortex on one side of the brain resulted in functional blindness in a large part of the animal's visual field. Additional removal of more brain tissue from the superior colliculus on the opposite side of the brain had the surprising result, not of increasing the visual disability, but rather of restoring to a large extent the functional efficacy of the presumably blind part of the visual field. And it is not hard to find the general principle of balanced control also operating in the behavior of human patients who have suffered serious brain damage. A case that we personally observed this past spring gave evidence of an aphasic *anomia*—loss of ability to produce names of familiar objects and persons—after severe temporal lobe damage. During the acute recovery stage, the patient talked volubly and excessively, and the anomia was extreme. As time passed and the spontaneous verbal speech flow diminished, the anomia also began to show marked improvement. As Oscar Marin, the clinical neurologist in the case pointed out to us, it was as if the recovery of an inhibitory control in the regulation of the speech behavior was necessary to restore the quality of the output and to release the verbal retrieval processes once again.

By citing these few examples from the recent literature and from our own recent observations, we hope we have not given the impression that we believe the principle of opponent processes to be a newly discovered one in behavior or in physiology. We are, of course, well aware of the history of this general concept in human thought, whether in Hegelian philosophy, the dialectical materialism of Marx and Engels, Pavlovian excitation and inhibition, Sherrington's reflex control of muscle antagonists, matter and antimatter in contemporary physics, or the fundamental Yin and Yang principle that permeates the Oriental point of view. A general principle, universally applied, easily becomes a useless cliché. But our point here is that

the opponent process concept, used as a guiding principle in analyzing specific aspects of particular psychological phenomena, may continue to provide the most useful key to the behavior of the nervous system, as it has already proved to do in the analysis of particular visual phenomena.

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Editorship Nomination

The APA Publications and Communications Board invites nominations for the editorship of the *Journal of Counseling Psychology* for the term running 1976 through 1981. In order to provide a year of overlap with incumbent Ralph Berdie in 1975, the Board will appoint an editor-elect this year. Members wishing to suggest candidates should prepare a brief statement of one page or less in support of each nomination and mail no later than March 1, 1974, to Anita DeVivo, Executive Editor, APA Journals, 1200 Seventeenth Street, N.W., Washington, D.C. 20036.