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Author

Westheimer, Gerald

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The On-Off Dichotomy in visual processing: From receptors to perception

Gerald Westheimer
Division of Neurobiology
University of California
Berkeley, CA 94720-3200

Author's Address
Gerald Westheimer
144 Life Sciences Addition
University of California
Berkeley, CA 94720-3200

Tel: (510) 642-4828
Fax: (510) 643-6791

gwestheimer@berkeley.edu

Abstract

Vision scientists long ago pointed to black and white as separate sensations and saw confirmation in the fact that in the absence of light one perceives the visual field as gray against which the negative after-image of a bright light appeared blacker. The first recordings from optic nerve fibers in vertebrates revealed ON and OFF signals, later associated with separate streams, arising already at the synapse between receptors and bipolar cells. These can be identified anatomically and physiologically and remain distinct all the way to the lateral geniculate nucleus, whose fibers form the input to the primary visual cortex. The dichotomy has been probed by electro-retinography and analyzed by means of pharmacological agents and dysfunction due to genetic causes. The bi- rather than a unidirectional nature of the retinal output has advantages in allowing small signals to remain prominent over a greater dynamic range.

The two streams innervate cortical neurons in a push-pull manner, generating receptive fields with spatial sensitivity profiles featuring On and Off subregions. Manifestations of the dichotomy appear in a variety of simple visual discriminations where there are often profound threshold differences in patterns with same-polarity as compared with mixed contrast-polarity components. But even at levels in which the spatial, contrast and color attributes have already been securely established and black and white elements participate equally, a categorical difference between blackness and whiteness of a percept persists. It is an opponency, akin to the ones in the color domain, derived from the original ON and OFF signals and subsequently bound with the other attributes to yield a feature's unitary percept.

Keywords

Retina, visual cortex, contrast polarity, center-surround antagonism, black/white opponency, visual discrimination thresholds, perceptual grouping.

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1. Introduction

That the sensation of black is not the same as absence of light is one of the central tenets of Hering's teaching (Hering, 1874). Even before that, many authors commented on the fact that in complete darkness the experience is not that of black but of gray (within which sometimes floating clouds could be distinguished) leading to phrases such as "intrinsic light of the retina" or "eigengrau" (Goethe, 1808, Helmholtz, 1860, Purkinje, 1823).

Hering was quite explicit in differentiating between the physics of a situation and the corresponding perceptual experience. To be sure, energy impinging on the retina is proportional to that emitted by the source. But when viewing a sequence of stimuli progressively increasing in light intensity from a piece of black velvet to the disk of the sun, it is equally justified, so argued Hering, to regard this as a decrease in black as an increase in white. Hering took his point of departure by looking at the afterimage of a bright patch. Even when all light is excluded from reaching the retina, the negative afterimage appears distinctly darker than unaffected regions of the visual field. Hering proceeded to postulate that the sensations of black and white, though experienced within a single continuum, are separate, each going from zero to full intensity in opposite directions as the gray scale is traversed, maintaining an approximately equal level at an intermediate gray.

As the understanding of the physics of light came to permeate vision science, it supplanted the subjective view of a bidirectionality of sensation from gray to black on one side, and from gray to white on the other. The equipment and experimental procedures utilized in vision experiments helped this trend. One generated stimuli by turning light sources on, by delineating patterns in white on black, and, especially as cathode-ray tube monitors supplanted optical bench setups, by regarding blackness as the null or zero setting, and whiteness the active, positive one. Soon the systems-theoretical bent lent an air of inevitability to the use of targets that, instead of having a distinct polarity, were distributed in extent and modulated in amplitude around an intermediate light level. Contrast came to be specified by Michelson's formula

$$(I_{max} - I_{min}) / (I_{max} + I_{min})$$

which masks the distinction between stimulus and background, instead of the earlier Weber fraction, $\Delta I / I$, for which the ratio between stimulus and background light levels can unambiguously be positive or negative. As a result a qualitative, possibly categorical, difference between black and white sensations was downplayed or ignored.

In the meantime, physiological experiments on animal preparations pointed the other way. Of interest are those on vertebrates. One of the earliest recordings from the incoming visual stream, the optic nerve of the frog, reported that some fibers fired nerve impulses when a light was switched on, and others when it was switched off, with little activity during steady illumination (Hartline, 1935, Hartline, 1938). Apart from the demonstration of the transient nature of nerve signals dedicated to vision – and later the

spatial sensitivity profile, the receptive field, soon to dominate such studies – the experiment highlighted the importance of up or down direction of the light change, and indeed the words ON and OFF responses entered the vocabulary at the time. When microelectrode recording from single neurons in the mammal became possible, the ON and OFF properties were associated with retinal ganglion cells of cats, with the additional significant observation that each type had a concentric antagonistic organization (Kuffler, 1953). Cells, both those showing an ON or an OFF response in the center of their receptive fields, manifested a change in the opposite direction in a concentrically arranged surround. In a contemporaneous study Barlow was able to show that this kind of arrangement also occurred in the frog, that is, enlarging the diameter of a circular light stimulus leads first to an increase in cell response and, once the stimulus exceeds the center and invades the surround, a decrease, and that this holds for OFF cells as well as ON cells (Barlow, 1953).

In all these studies, reference is also made to an ON-OFF cell type, but in those early days it could not be convincingly demonstrated that these were a separate class of cells or the result of stimulus situations in which light directed into the receptive field overlapped the two zones, instead of being strictly segregated in a portions stimulating only the center or only the surround.

In what follows, attention is restricted to the non-chromatic aspect of vision with, it is hoped, no loss of generality, just as it is possible at some level to examine its spatial aspects while leaving motion aside.

2. RETINA

A. Source of ON/OFF divide – Internal retinal Circuitry

Traditionally, the retina, being an outlying isolated piece of nervous tissue sharing essential properties with the brain proper, has been the first venue for detailed analyses of neural circuitry and so it was in connection with the ON-OFF dichotomy originally discovered in optic nerve fibers. The photochemical and cellular light transduction stages in the retina in vertebrate photoreceptors, the rods and cones, were shown to fit in with the physicalist view of light exchange of electro-magnetic energy: photon absorption is absent in complete darkness and increases with increasing light levels. That is to say, photon capture and the entrained photoreceptor activation increase from none in darkness to the maximum in the brightest light. Curiously, however, vertebrate photoreceptors respond by increasing hyperpolarization with increasing light capture, in contradistinction to the typical sense cell where the stimulus acts to depolarize the cell membrane. Because the release of transmitter substance increases with cell depolarization, photoreceptor cells have the strange property of releasing less transmitter substance the more light activation they experience. Regardless of this detail, the conclusion is that activity within and communication from the primary light sensory cell undergo a gradual change in a single direction as the range from dark to bright is traversed. There are no

separate ON and OFF photoreceptors; all photoreceptors release glutamate, and in decreasing doses as their light activation increases.

The dichotomy under consideration here appears at the very next stage of processing. The photoreceptor signals represented by the release of the glutamate neurotransmitter (in decreasing quantity with increasing light level) are directed principally to the next tier of cells, the bipolar cells which exist in two flavors: “about half of the units hyperpolarize to central illumination, while the other half depolarize” (Werblin & Dowling, 1969). Those showing an increase in excitation with increase in glutamate concentration, i.e., that are activated by a decrease in light are called OFF bipolar cells, and are now known to express the ionotropic glutamate receptor molecules at their synaptic ending, which respond to glutamate by opening cation channels, thus depolarizing the cell. On the other hand, those with a response in the opposite direction, i.e., increasingly activated by decreases in glutamate release consequent to onset of light, are called ON bipolars. The receptor molecule on their surface at the synapse with the rods or cones is the mGluR6 metabotropic receptor (Duvoisin, Morgans & Taylor, 2005) which is coupled to a pathway causing cation channels to close and thus, through this inhibitory influence, producing an inverted signal.

Although retinal circuitry is quite complicated, the basic organizational principle, entrained by this bifurcation of the originally unipolar stream onto reciprocally activated ON and OFF paths, is maintained and conveyed out of the retina by the final output, viz. the ganglion cell axons which become the optic nerve fibers:

B. Antagonistic pairing in the domain of brightness.

When the retina is exposed to a uniform field, ganglion cells discharge impulses at a rate of a score or so per second but they fall into two classes as regards their light response. Those fed by ON bipolar cells and manifesting a burst of additional impulses for a brightening light pulse are the ON ganglion cells and are responsible for the ON burst discovered in the frog by Hartline in the 1930's. The members of the other class respond with a burst when a small spot is suddenly dimmed and are called OFF ganglion cells. Ignoring the complications associated with the temporal transients for which there is yet another overlaid internal retinal circuitry, and of the non-stationarity due to prominent adaptational effects, changes in light level are signaled by two reciprocally activated paths, one for increases and the other for decreases in light. In each case this is superimposed on a steady low-level “spontaneous” firing in the absence of specific stimuli, which can thus experience increases on delivery of the relevant stimulus (light for an ON cell or darkening for an OFF cell), as well as inhibition on delivery of the opposite stimulus (e.g. darkening for an ON cell, light for an OFF cell), see Fig. 1.

C. Spatial antagonism.

Each of the two classes of ganglion cell also exhibits a spatial antagonism, in that a ganglion cell, whether ON or OFF, has its activation reduced when its relevant stimulus

is extended from the center of its receptive field into a concentric spatially surrounding zone. Thus an ON ganglion cell will fire briskly when the center of its receptive field is brightened but less so when the stimulation also extends into its surround. This spatial antagonism has the important property of dropping out in dim illumination (Barlow, Fitzhugh & Kuffler, 1957).

According to the current teaching of physiology, all the properties of an ON-center retinal ganglion cells in photopic vision are generated, at least in the mammal, entirely through intra-retinal circuitry involving bipolar cells of only the ON variety, and the equivalent statements holds for OFF ganglion and bipolar cells (Fig.2). The strong support for this view comes from experiments with the pseudo-neurotransmitter, APB (Schiller, 1992), which competitively binds to and hence inactivates the synapse between Receptors and ON bipolar cell synapse, while leaving the OFF stream unaffected.

D. Abnormalities of Genetic Origin

Relevant also are two abnormalities now identified as having a genetic origin, the congenital stationary nightblindnesses types 1 and 2 (CSNB1 and CNBS2). In the first there is a mutation of a gene, NYX, whose protein product *nyctalopin* is involved in the pathway through which glutamate acting on the mGluR6 metabotropic receptor at the ON bipolar cell synapse controls Ca^{++} channels (Morgans, Ren & Akileswaran, 2006). Because in the first instance the rods communicate only through ON bipolar cells (Waessle, 2004), affected patients have no rod vision, but because the cone ON bipolar cells also do not function, there are deficits in photopic vision as well. Electroretinography has revealed a similarity between the effect of APB, which is a competitive inhibitor of glutamate at these mGlu5R receptors, and the CSNB1 syndrome (Khan, Kondo, Hiriyanna, Jamison, Bush & Sieving, 2005).

In CSNB2 a different protein is malfunctioning, the *CANAI1F* Ca^{++} channel (Morgans, 2001) which seems to be involved in glutamate release at the rod/rod-bipolar synapse. Some patients with this condition have fully functional cone vision (Allen, Zito, Bradshaw, Patel, Bird, Fitzke, Yates, Trump, Hardcastle & Moore, 2003) but it is possible that cone pathways may not always be spared (Bech-Hansen, Naylor, Maybaum, Pearce, Koop, Fishman, Mets, Musarella & Boycott, 1998, Strom, Nyakatura, Apfelstedt-Sylla, Hellebrand, Lorenz, Weber, Wutz, Gutwillinger, Ruther, Drescher, Sauer, Zrenner, Meitinger, Rosenthal & Meindl, 1998). The situation is complicated by the existence of several subtypes of both ON and OFF bipolar cells.

E. Other Pathways

One cannot leave a survey of retinal processing, however brief and schematic, without mention of its immense intricacy and subtlety that have been ignored here. The overlaid temporal properties – transient versus sustained firing, adaptation -- have already been referred to. In some species there is even movement selectivity. The structural and functional divisions subserving color discrimination fill many additional

chapters (Masland, 2001, Waessle, 2004). So does the magnocellular/parvocellular dissociation.

Finally, there is one recent development that is pertinent to this study: the existence, even in the mammal, of a separate pathway utilizing a small number of simple light-level detectors in the retina containing the photopigment *melanopsin*. The output is purveyed directly to non-cortical structures in the central nervous system, and has been implicated in pupil responses and in the setting of diurnal rhythms and the photoentrainment to the day/night, light/dark cycle (Berson, 2003, Freedman, Lucas, Soni, von Schantz, Munoz, David-Gray & Foster, 1999, Van Gelder, 2003).

3. PRIMARY VISUAL CORTEX

A. Input to the Cortex

Quite early on, it was confirmed that the retinal ON/OFF organization also applies to cells in the lateral geniculate body (Hubel & Wiesel, 1961) whose axons provide the principal visual afferents to the primary visual cortex. Hence it was evident, from neurophysiological recording of the frog and cat, later demonstrated even in the alert primate, that the ON-OFF dichotomy is present in the visual stream from the retina to the first input stage of the primary visual cortex (Fig. 3).

More recent work from the anesthetized cat preparation (Hirsch, 2003) has revealed that ON and OFF geniculate neurons with corticopetal axons receive inhibitory inputs from the opposite stream of matching retinotopic location through a local circuit. This would have the functional significance of potentiating the ON/OFF divide in the cellular signals, in a kind of push-pull operation, while maintaining their spatial specificity.

B. Receptive Fields.

Receptive fields of neurons in the primary cortex of the cat and primate have always been described as having subregions. In the original report (Hubel & Wiesel, 1961) it is stated that some subregions are excited at light onset and others inhibited at offset. Later it could be seen that this corresponded to subdivisions which are activated respectively by raising or lowering light stimulation with respect to the background. The exact spatial profile of the receptive field, whether edge, bar, or multi-lobed with odd or even symmetry, seems to vary from cell to cell, as also whether such a specific stimulus needs to be in just a single location in the visual field (simple cell) or can be in a range of locations (complex cell). The substrate for this arrangement is a sophisticated spatial deployment of elements of the incoming ON and OFF streams originating in the retina (Alonso, Usrey & Reid, 2001). In reports of recent experiments utilizing advanced analytical methods, the interdigitation of the ON and OFF subregions of receptive fields of neurons in the primary visual cortex has been subjected to detailed study both in the primate (Mata & Ringach, 2005) and cat (Martinez, Wang, Reid, Pillai, Alonso, Sommer & Hirsch, 2005, Priebe & Ferster, 2005). Input from each stream reaches spatially adjoining zones to generate a receptive field profile containing two kinds of subregions.

The two streams operate in the same push-pull fashion that is also evident in the lateral geniculate nucleus: in the regions activated by light increases, the ON fibers excite and the OFF fibers inhibit, and the reverse applies where the activation is caused by a light reduction (see Fig. 4).

The circuitry required to bring about the specific response property of each neuron is quite subtle but it implies that the cells would respond and yield signals with their characteristic signature so long as they receive at least some input from either stream, a conclusion supported by experiments in which the ON stream was selectively inactivated in the primate by injection into the eye of the substance APB. There were only mild deficits in performance such as flicker, visual and stereoscopic resolution, and grating orientation discrimination (Dolan & Schiller, 1994, Schiller, Sandell & Maunsell, 1986).

However, according to the essential principle of neural organization, enunciated by Johannes Müller (Müller, 1826), the message conveyed by a neuron, regardless of how it is excited, is fixed and embodied in the structure of its connectivity. Hence, once a neuron in the primary visual cortex is caused to discharge impulses, however fragmentary the components of its total possible input that are involved, it will participate, be it even to a limited extent, in the appropriate manner in the chain of events leading from retinal stimulation to a visual response and to perception.

The ON and OFF dichotomy can thus be placed in perspective. It (a) does not exist in the photoreceptor cells themselves, (b) is incorporated into two separate streams beginning in the inner layers of the retina, through the transmission of signals from the retina to the first stages of cortical visual processing, where then (c) interdigitation and integration takes place to create receptive fields with a variety of spatial profiles.

Though a great deal can be known about the kinds of optimal object light patterns that will activate cells in the primary visual cortex of even an alert, behaving primate, what remains vague is the nature of the contribution of that neuron's firing to the final percept. If a particular cell's receptive field is optimally covered by, say, a bright bar of given location, orientation, width and length, would a firing burst of that cell lead to the perception of such a bar, or perhaps, with a more modest expectation, provide a substantial contribution within an ensemble of kindred cells to the emergence of such a percept? Experiments in which minimal localized stimulation was applied to a cortex have so far provided inconclusive and contradictory. Nor have modern non-invasive techniques of visualizing cortical activity as yet achieved the needed resolution to help with an answer.

In such a situation, it is best to concentrate analysis on the other end of the arc that leads from object presentation to a subject's experience, namely on carefully conducted psychophysical experiments designed, in this particular instance, to elucidate the role of the blackness and whiteness attribute of pattern components and their interaction in the performance of relevant visual tasks. This is not only appropriate if the overall research program is the understanding of the full perceptual process, but it is also a powerful aid in mapping the channeling of visual streams within the neural pathways.

4. ON/OFF dichotomy in visual perception

Evidence for the separation into ON and OFF components in the afferent stream in visual function and perception can be examined according to several criteria.

A. Criterion I: Performance asymmetries between stimulus brightening and darkening, due to differences in processing of the two pathways during their initial stretch of segregation between the outer retina and the visual cortex.

The elimination of ON signals at the retina by APB produces some impairment of contrast detection and resolution in the primate, and this is consonant with reduced, but not absent, input to cortical neurons whose full response capabilities depend on both streams. Data in more sophisticated visual tasks is lacking so far. The congenital night blindness syndrome, whose putative cause is genetic impairment of signals to the ON bipolar cells, has yielded contradictory results when it comes to visual performance, though its effect in abolishing signals from rods seems firm.

The seemingly clear segregation of processing within the retinal ON and OFF streams in the center/surround antagonism would preclude major interaction effects between them, for example where activity in one might impede or potentiate that in the other. However, the two may not operate in exactly the same way. For example, it has been documented that thresholds for light increments are consistently different from those for light decrements (Chichilnisky & Wandell, 1996, Walraven, 1977). This asymmetry has been ascribed to a difference in the rules for adaptation in the ON and OFF pathways, a consequence of the fact that at any adaptation level the range of possible increments is always bigger than the range of decrements.

B. Criterion II. Performance difference, assignable to confluence of ON and OFF pathways in primary visual cortex:

There is abundant evidence of the influence of differences in contrast polarity of patterns, or pattern components, in a variety of visual tasks. In several of these tasks, furthermore, the interaction, or lack of it, between bright and dark stimulus elements is distance-dependent and hence most easily explained by the specific patterning of ON and OFF subregions in the receptive field of neurons in the primary visual cortex (Fig. 5).

Vernier discrimination suffers if one of the abutting lines is white and the other black (O'Shea & Mitchell, 1990), as well as when the alignment task involves black/white edges with oppositely-directed gradients (Levi & Waugh, 1996, Westheimer, 2007). The same applies for separation discrimination (Levi & Waugh, 1996, Levi & Westheimer, 1987) where the deficit decreases with separation, being essentially abolished for a 10 arcmin separation at the fovea (Fig. 6). In a two-dot alignment task when one dot is white and the other black on a gray background, the opposite-polarity deficit exhibits a

similar fall-off with separation (Levi & Waugh, 1996). Three-line bisection behaves in the same fashion (Westheimer, Crist, Gorski & Gilbert, 2001).

The discrimination of the orientation of a line is seriously impaired when it is made up of alternating dark and bright segments (Fig. 7), but the orientation signal of two jointly-exposed lines can be summed when they are about 10 arcmin apart or more in the fovea – although there seems to be the need for strict collinearity (Brincat & Westheimer, 2000, Westheimer & Ley, 1997).

For the detection of contrast differences, data from several studies were summarized by Dresch who concluded that in interactions between neighboring stimuli – for example, potentiation or sensitization – there are contrast polarity influences, depending on the separation (Dresch, 1999).

In a field in which dot pairs with short separation are arrayed in a distinct fashion, e.g., all with radial or circular displacements (Glass patterns), the overall pattern is clearly evident when both members of the pair have the same contrast polarity, both black or white, but the percept is severely impaired when the members of the pairs have opposite contrast polarity (Badcock, Clifford & Khuu, 2005, Glass & Switkes, 1976) Fig. 9. There are indications that the effect is asymmetrical. Neither the putative processing apparatus nor the interaction distances provide certainty at this juncture whether the task fits into the present category or whether it should really be included among those discussed below, i.e., where interaction takes place between pattern elements that have already been fully articulated.

In experiments using random-dot cinematograms to study global motion processing, Edwards and Badcock concluded that ON and OFF signals remained separate at a beginning stage of motion detection because no motion is seen when a dot changed contrast polarity during a stroboscopic displacement. But at a higher levels of the motion processing there was sub-threshold summation of white and black dots, implying that at that stage integration of information from the two streams had taken place (Edwards & Badcock, 1994).

The interaction between components of a stroboscopic stimulus pair is, however, somewhat more nuanced. A line changing contrast polarity when it is suddenly displaced can indeed generate a stroboscopic movement, but for some temporal and spatial intervals this movement is in the reverse direction, the so-called inverse phi phenomenon (Anstis, 1970). A modern viewpoint of the cortical mechanism of movement detection (Adelson & Bergen, 1985) as validated by intracellular recording in mammalian cortical neurons (Priebe & Ferster, 2005) makes this readily understood: the temporal sequence of two stimuli with the same contrast polarity will excite the central lobe of the temporal-spatial receptive field, but excitation can also ensue if the later member of the stimulus pair is of the opposite contrast polarity and has a temporal-spatial location that places it in the (opponent) flanking zone of the receptive field. For this to occur, its displacement needs to be in the opposite direction. This phenomenon thus belongs to the category

where there are spatial (here spatio-temporal) subregions of a unit's receptive field fed by ON and OFF fibers, each contributing according to their own sign to the cell's response.

Size-specific adaptation experiments also suggest segregation of ON and OFF streams as demonstrated in the change of apparent duty cycle of square-wave gratings and bar widths after an observer had been viewing patterns of related but spatially wider configurations (De Valois, 1977).

A single explanation can cover the extensive list of visual tasks in which the responses differ when two or more pattern elements are of like or unlike contrast polarity: their neural locus is at the site where the separate ON and OFF retinal streams converge, most prominently on the primary visual cortex. Such stimuli are, therefore, of particular interest in the elucidation of the mechanism through which the respective discriminations are achieved. They allow the delineation of the distances over which signals are summed in the activation of individual neural units, and hence permit an estimate of the size of the sub-regions of the receptive fields of these units that are covered by the input from each of the streams.

C. Criterion III. Contrast polarity of individual features and perceptual grouping.

Even though the majority of perceptual tasks can be carried out equally when the pattern is shown in black or white, there are situations in which the visual performance differs depending on whether the association is between elements of like or unlike contrast polarity.

When an observer responds equally to stimuli that are black on white or white on black, one may suppose that processing levels are involved beyond those at which ON and OFF signals have already converged and their respective subregions have been organized into spatially elaborate receptive fields. Nevertheless the blackness or whiteness attribute is retained and remains available for further stages of perceptual processing..

Indeed at the very beginning of the Gestalt thinking, Mach (Mach, 1886) tried to exemplify what he meant by Gestalt (and he used that word) in a figure where the same letter of the alphabet was shown twice, side by side, one black on white and the other white on black (Fig. 8, left and middle panels): what was common to the two was their Gestalt, Mach explained. By the same argument, the two differed in what he called "color." The configurations' form may be the same, but in addition each has as an integral part, immediately and categorically associated with it, the attribute of blackness or whiteness. In more general situations when one views an assembly of black and white pattern elements on a gray background, the blackness or whiteness attribute of each is preserved along with those for location, orientation or form – it pops out instantaneously. Yet, in the binding operation for joining elements, each individually well-articulated, into a perceptual entity, black and white constituents are by no means

interchangeable (Fig.8, right). This holds to a varying extent also for (Fig. 9) grouping of isolated components in the formation of Glass patterns and (fig. 10) the development of contour salience(Li & Gilbert, 2002).

The perception of form depends in part on the relative location and orientation of parts and here again contrast polarity enters as a factor. Geometrical-optical illusions, being specific aberrations that afford a glimpse into the assembly operations resulting in the appearance of configurations, can be examined with respect to their susceptibility to mixing of contrast polarity. These illusions are unfortunately not a uniform group, but in at least some of them the magnitude of the perceptual error depends on whether the configurations are made up entirely with lines of the same contrast polarity or not (Fig. 11).

By the same token, situations in which contrast polarity does not matter can occasionally afford insight. The central apparatus of visual acuity still needs full elucidation; hence it is an important pointer that “crowding” of visual acuity letters, where closely-adjacent bars impair performance, seems to be largely indifferent to whether the contrast-polarity of the letter and the masking elements is the same or not (Ehrt & Hess, 2005).

The neural basis of stereopsis continues to fascinate and here also, contrast polarity issues enter, as was emphasized already by Helmholtz in the plates included in his *Physiological Optics* and has emerged as an analytical probe in more recent studies (Cumming & Parker, 1997).

5. Benefits of ON/OFF bifurcation

The retinal recoding that produces strong and active signals in optic nerve fibers both for increases as well as for decreases in incident light can be interpreted as having benefits at two levels of visual processing, first by making the initial signals for small light changes more conspicuous, and, secondly, by accenting and segmenting contrast polarity of visual elements for purposes of perception

A. Conspicuity of impulse responses over large dynamic range.

Setting the discharge frequency of retinal output neurons at a non-zero level during steady light stimulation becomes an option once adaptation (in part even photochemical in origin) decouples the neural state from the magnitude of the invariant incident light intensity, and thus allows both increases and decreases in light to be represented by equivalent changes in impulse rates. Because there is always a greater range of possible light increases than decreases, the maintained steady-state discharge frequency would have to be quite high to allow a good range of signal levels in both the up and the down directions. It is presumably for this reason that a second analogous system with sign-inversion has evolved, assuring that at least one of them provides a well-defined signal. In principle, a single ON channel can convey the needed information and it is telling that the sign inversion needed for spatial surround antagonism in constructing retinal center/surround receptive fields is provided not by an opponent-stream signal but by inhibitory interaction arising from the same-polarity stream.

The well-known phenomenon of *successive contrast*, in which a sudden change in light intensity gives a strongly contrasting experience is a manifestation of this organization. When a step increase of light is presented to the eye, the ON retinal ganglion cell will respond with an additional burst superimposed on their sputtering spontaneous activity, and the OFF ganglion cell's spontaneous activity will be briefly silenced. This pattern is maintained in the LGN cells that become the cortical input. It has been shown that the visual field representing on the retinal surface is seamlessly tiled by overlapping ON and OFF ganglion cells (Waessle, Peichl & Boycott, 1981) and superposition of their inputs ensures that this is the case also for neurons in the primary visual cortex (Martinez et al., 2005). This push-pull effect explains how the retinal ON and OFF dichotomy, associated as it is with overlap at the retina and accurate superposition in the cortex, can act to enhance the magnitude of the cortical signal to a temporal light change. The case for a darkening pulse is equivalent, with a reversal of the roles of the ON and OFF ganglion cells.

Most studies in the visual cortex have been devoted to the spatial profile of the receptive fields, showing that there is a convergence and spatially meaningful ordering of retinal ON and OFF inputs in the interest of building up the spatial profile characteristic to the cell. Though both are needed for optimum results, nevertheless the cell will generate a signal to one alone, illustrating that, just as ON-OFF interaction is not necessary for center/surround antagonism in the retina, so it is quite possible that similar spatial differentiation within receptive fields could be achieved by suitable circuitry involving just one of these streams.

B. Contrast-polarity as a feature label

As is obvious from inspection of Figures 8-11, contrast polarity is an immediate and compelling perceptual property of a feature. The difference in character between features with positive and negative contrast is a great advantage in the articulation of forms and objects in the perceptual process. But receptive fields of neurons in the primary visual cortex arise through a confluence of ON and OFF signals onto their subregions, so that each cell can no longer be regarded as belonging to either the ON or the OFF stream, as is the case for the preceding neurons. That is not a problem so long as the units are assumed to represent detectors or templates with particular spatial profiles, such as a Gabor patch. That single isolated features have a well-defined darkness or whiteness label, on the other hand, requires operations in which information on this attribute, which is fully contained in earlier visual stages, be conserved and ultimately bound with output from other processes to yield the unitary percept. Regardless of how it is implemented, there is something categorical in the way, against a gray background, black and a white targets present themselves. The difference is qualitative, not just quantitative as would be the case if merely a photon count per unit of space and time were being performed.

C. Pathways, channels, streams, parallelism and opponency.

The substantive words -- opponency, push-pull, sign-inversion -- used to characterize the ON-OFF divide raise the question whether the widely-used term *channel* applies here.

It is now accepted that visual attributes are processed in parallel. By this is meant that the signals arising from the transduction of light in the receptors are, at some stage, divided and used in separate circuit modules, to extract different aspects of the original retinal image. When the operation of one module excludes the use of the signal on which it operates from use in another module, one refers to these as channels. The capture of photons by a photopigment in, say, a blue cone precludes their use by another pigment and converts them into the blue cone's proprietary signal. Ideally, then, signals in different channels are orthogonal, even though their input acceptance domain may overlap (as the absorption spectra of the photopigment). Nor does the channel hypothesis preclude interaction between outputs of the individual channels.

It is true that ON and OFF signals are derived from the same original source and travel along separate pathways. However, because they share a dimension, differing only in the direction in which it is coded, the word channel does not properly fit. From this standpoint it is better to refer to them as "pathways" or "streams" and avoid the words "channel" and "parallel" with their deeper connotation of non-overlapping processing domains.

On the other hand, in the realm of perception, the categorical difference between black and white cannot be denied. As reported by an observer, a black letter and a white letter, both on a gray background, exhibit a fundamental difference, not just in the degree of their grayness.

6. Parallels with other opponencies.

An analysis of the categorical distinction between the two directions of change, white → black and black → white, cannot be decoupled from the consideration of the highly-developed ability to detect contrast differences, which have occupied vision scientists since the days of Weber and Fechner. And here we can return to Hering's idea that the darkest black and the brightest white are in fact just the outermost extremes, the polar opposites, within a single continuum wherein each achromatic level of brightness is an expression of a particular balance point in a twin push-pull mechanism. Although as phrased here this appears to be a static process, there are no difficulties including temporal and adaptation aspects in developing this viewpoint further. What remains to be elucidated is the connexion of Hering's perceptual black/white opponency with the ON and OFF dichotomy, which has so far been tracked neurophysiologically only from the retina to the primary visual cortex.

Fig. 12 is an updated depiction of the way Hering first presented the black and white opponency in 1874. It has been modified to accommodate the non-linearity that has been demonstrated in signals in the outer retina (Naka & Rushton, 1966, Valeton & van Norren, 1983) where increasing light levels give rise to activity that does not increase in tandem or perhaps logarithmically, but progressively approaches an upper limit. This

saturating non-linearity is here assumed to apply equally to the two sub-systems in their respective directions.

Comparison with the chromatic attribute offer themselves, in particular since the Hering concept of red-green and blue-yellow opponency has gained validity in neurophysiological thinking and the topic under discussion is exactly the black-white opponency that Hering proposed as a companion to his chromatic ones. How much there is in common between the way a feature's labels in the chromatic dimensions and along the black/white continuum are developed remains to be explored, though making the pattern elements in Figs 8 -11 equiluminant heterochromatic instead of black and white seems, at first glance, to make little difference. However, the spatial perception of patterns created with black/white contrast are not always equivalent to those with equiluminant color contrast (see, e.g., the Kitaoka illusion) although they are in many visual illusions (Li & Guo, 1995).

The open question then concerns the neural circuit from which the qualitative distinction between sensations of black and white in achromatic features with pronounced negative and, respectively, positive, contrast polarity emerges. The retinal ON-OFF bifurcation is employed to generate spatially differentiated cortical receptive fields which, viewed as a whole, do not obviously retain the ON and OFF label, though it is possible that such neurons exist in these two flavors. An attractive alternative is to posit that one apparatus (probably in the primary visual cortex) serves to sift and recode the retinal information for purposes of elaborating shape and form and contour, with parallel mechanisms not only for movement and perhaps depth, but also for color – all this with the need for binding signals for each of these attributes to allow for the emergence of a unitary percept. If Hering's usual prescience is eventually confirmed, the continuum which has black and white as its poles will be found to be subserved by a circuit separate from that which generates the spatially diverse receptive fields in the primary visual cortex and more akin to that for chromaticity. And its source surely cannot exist apart from the retinal ON/OFF dichotomy any more than that of color from the retinal signals encoded from the red, green and blue cones.

7. Future Directions

That black and white are seen as antagonists rather than end-points in a single continuum preceded visual science as a discipline and, surviving the physicists' teaching of a monotonic rise in energy absorption and photochemical activity with increasing incident light levels, received underpinning from the discovery of separate ON and OFF signals in the retina.

The dichotomy has its origin at the very first synapse in the visual system where receptor signals are transmitted to the next tier of retinal cells; the molecular events here are only

beginning to be unraveled and several steps intervening between the change in receptor cell membrane and the opening of ion channels in the bipolar cells remain to be elucidated, specifically the operations associated with the ionotropic and metabotropic glutamate receptors where genetic intervention has and should continue to provide clues.

In view of the complex and deeply intertwined circuitry of the retina, the apparently sharp dissociation between ON and OFF streams in this structure seems surprising and may need further probing, especially since it is being questioned not only in *necturus* (Pang, Gao & Wu, 2007) but also in the mouse (Renteria, Tian, Cang, Nakanishi, Stryker & Copenhagen, 2006). In the same vein, the full separation of pathways into the cortex, drawn schematically in Fig. 3, may have to be revised, in particular since subtle interaction in the LGN has already been reported.

The most intriguing question relates to the provenance of the perceptually distinct attributes of black and white. Their opponent nature is at least of the same kind as that of yellow vs. blue and red vs. green, even though the intermediate stages of gray seem to have more unity than the spectral intermediates. How are the signals threaded through the cortex so as to allow the emergence of such a categorical distinction while they at the same time converge to operate in a push-pull fashion in the generation of receptive fields with spatially antagonistic sub-regions? And if there is indeed a separate elaboration of blackness and whiteness via subsidiary pathways, what are the similarities and differences to those responsible for the chromatic attributes?

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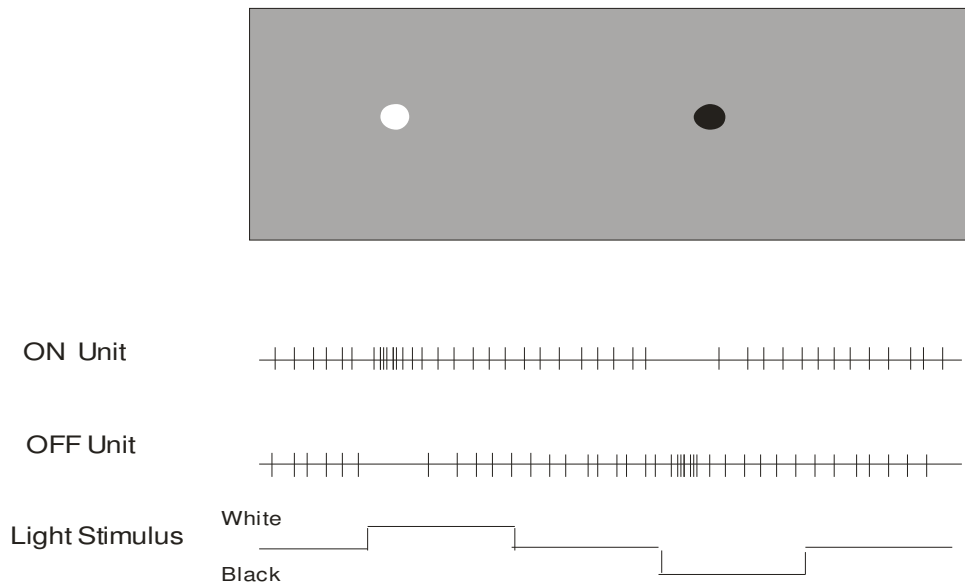


Fig. 1. Schematic illustration of ON and OFF retinal ganglion cell discharges when white and dark stimuli are delivered to the centers of their receptive fields (redrawn from Schiller, 1992). Bursts occur in On cells for white and in OFF cells for black, and there is brief cessation of firing in the reverse situation. Surround stimulation yields an inverse pattern, but the center/surround antagonism is engendered by excitatory and inhibitory interaction separately within each stream and not by superposition of ON and OFF signals.

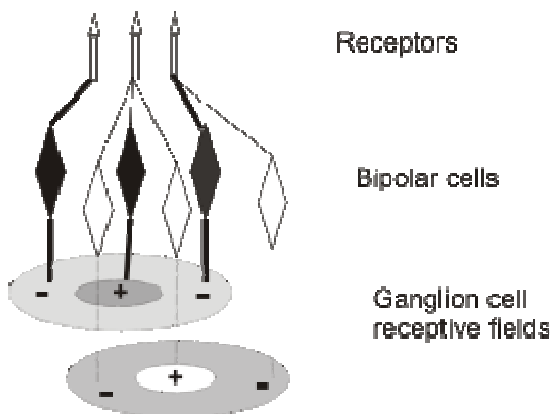


Fig. 2, Schema of channeling of ON and OFF signals in retina from receptors via bipolar cells, creating center/surround structure of ganglion cell receptive fields separately for the ON (open symbols and light lines) and OFF (closed symbol and heavy lines) systems. Adjacent region cause surround antagonism by inhibitory interaction, but in each case this takes place within its stream. The more complex interconnection within the retina involving horizontal and amacrine cells has been ignored in this sketch.

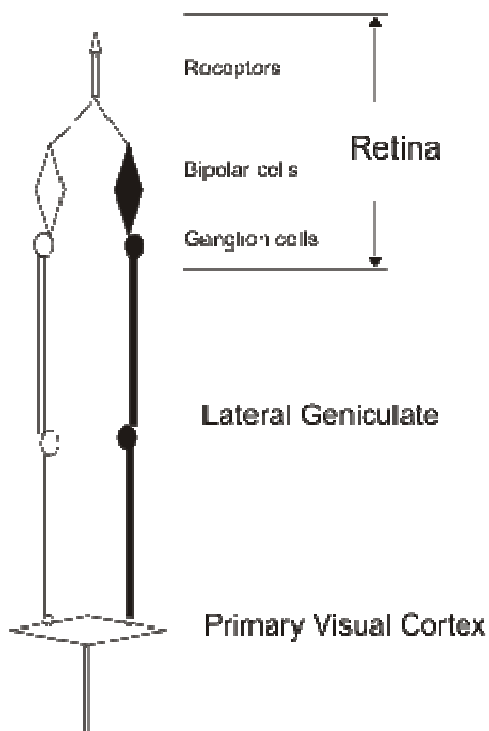


Fig. 3. Schema of On and OFF channeling from receptors to visual cortex. Dichotomy begins at receptor-bipolar cell synapse and is maintained until the two streams converge on neurons in the primary visual cortex, where they generate spatially-differentiated receptive fields. This diagram is highly schematic and does not include some intermediate elements nor reciprocal “push-pull” interactions in the mammalian Lateral Geniculate Nucleus.

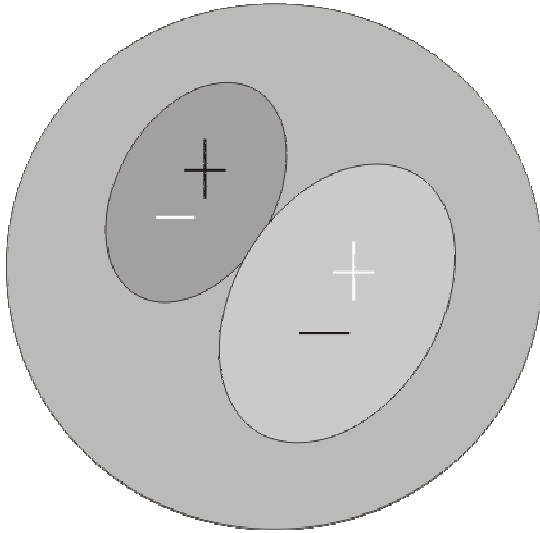


Fig. 4. Convergence of ON and OFF streams onto V1 neurons. The receptive field of this neuron has two sub-regions. The lighter is an ON zone, receiving excitatory contributions from the ON incoming stream (shown as a white +) and inhibitory contributions from the OFF stream (shown as a black -). The reverse applies to the flanking OFF subregion, shown in a darker shade.

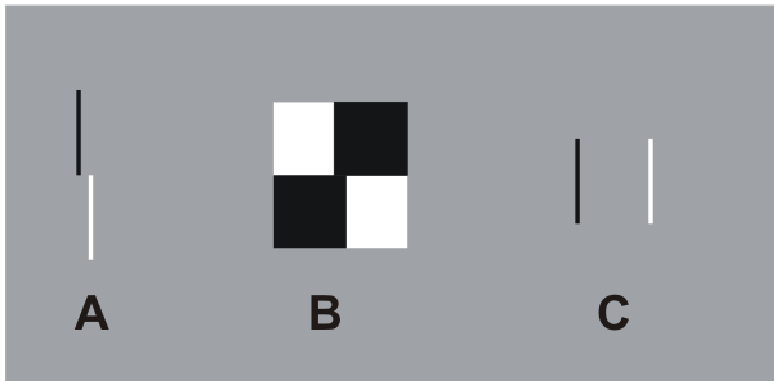


Fig. 5. Patterns in which psychophysical discrimination thresholds depend on contrast polarity of elements. A. Line vernier. B. Alignment of edges with opposite contrast polarity. C. Separation discrimination of two lines.

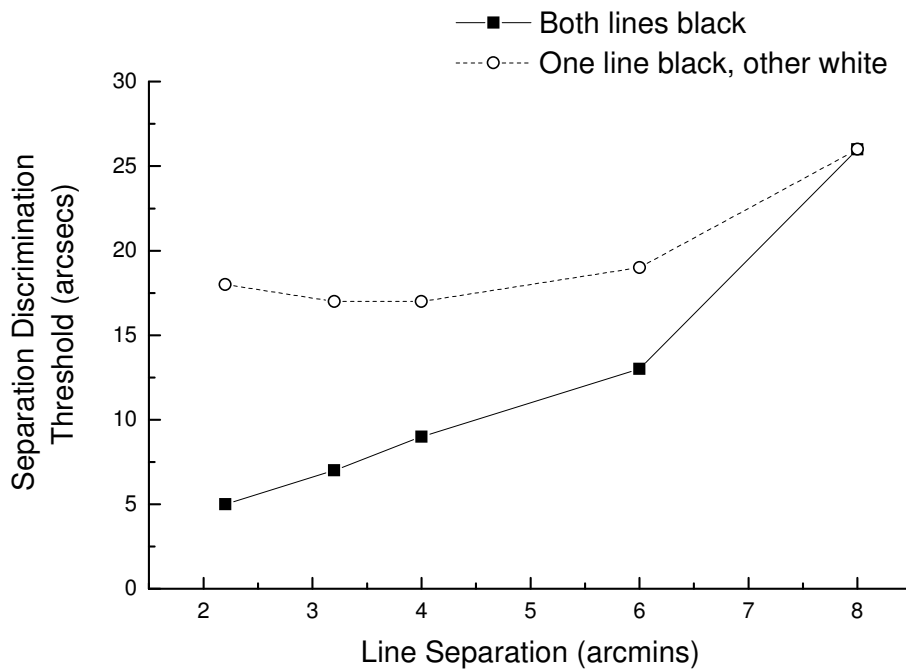


Fig. 6. Thresholds for discrimination of the separation of two parallel lines as a function of their base separation (condition C in Fig. 5). Performance is poorer for mixed contrast-polarity patterns only at short separations. (Redrawn from Levi and Westheimer, 1986).

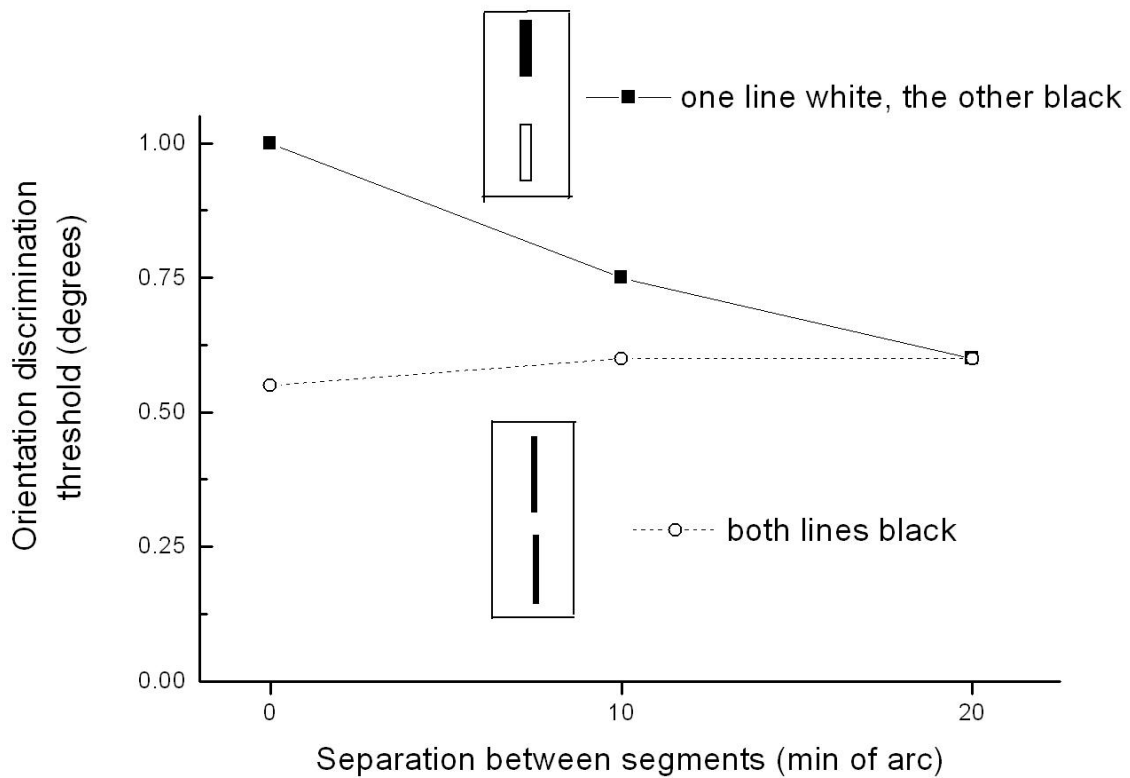


Fig. 7. The stimulus, shown in the inset boxes, consists of a collinear pair of lines, each 10 arcmins long, whose members were either both black, or one white and the other black. Data show thresholds for the discrimination of the orientation of the whole configuration, as a function of the inner separation of the lines. Difference in the contrast polarity of the two lines matters only when there is little or no separation between them. Foveal observation. Redrawn from Brincat and Westheimer (2000).

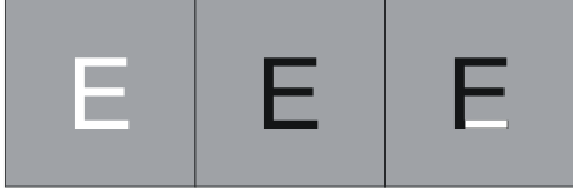


Fig. 8. Mach (1886) pointed out that a letter is perceived as having the same “Gestalt” regardless of whether it is black or white. The configuration as a whole, however, does not survive mingling of the contrast-polarity of its components.

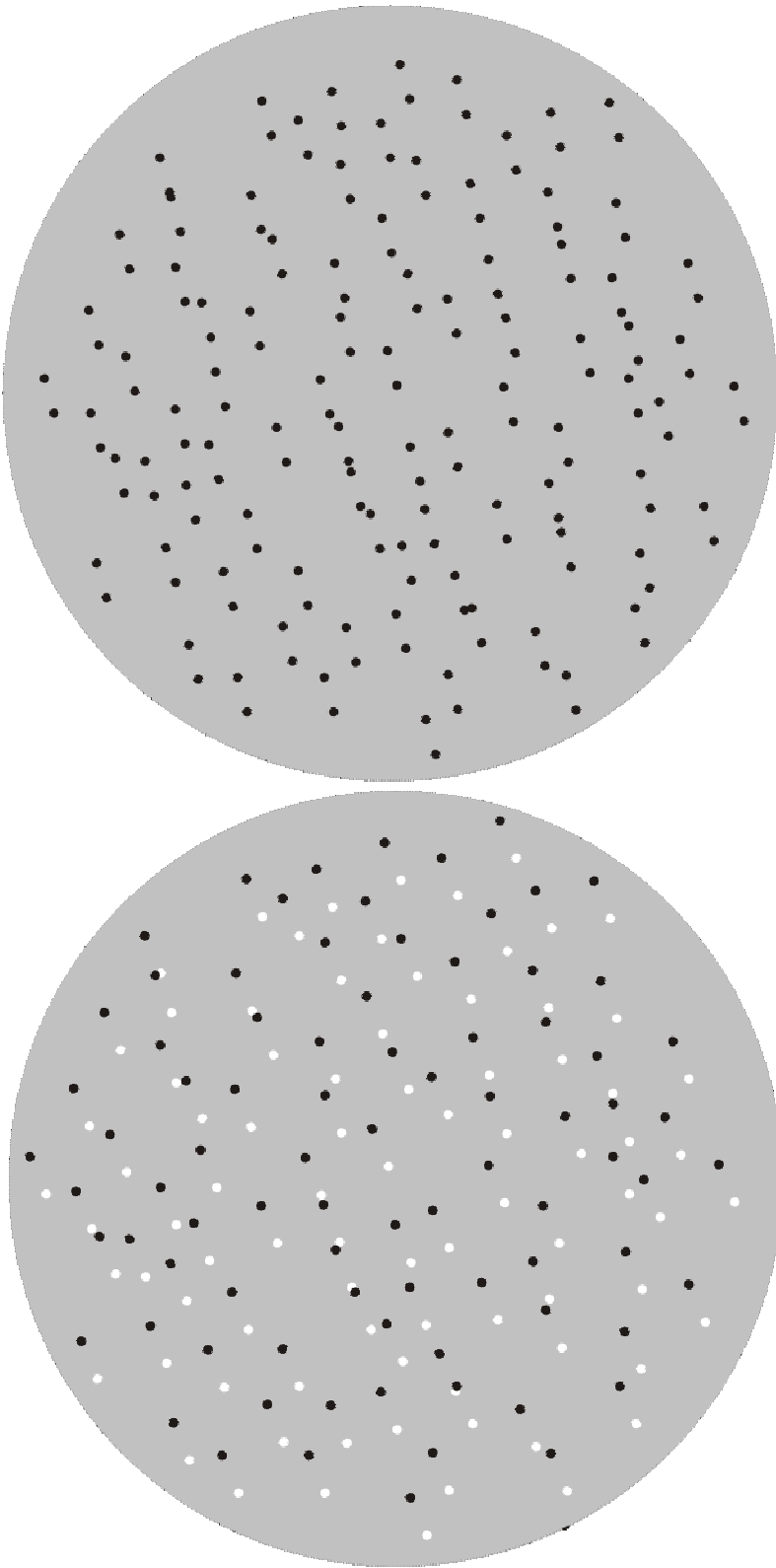


Fig. 9. The Glass pattern formed by duplicating each dot with a displacement is easier to discern when the duplicates have the same contrast polarity (top) than the opposite contrast polarity (lower).

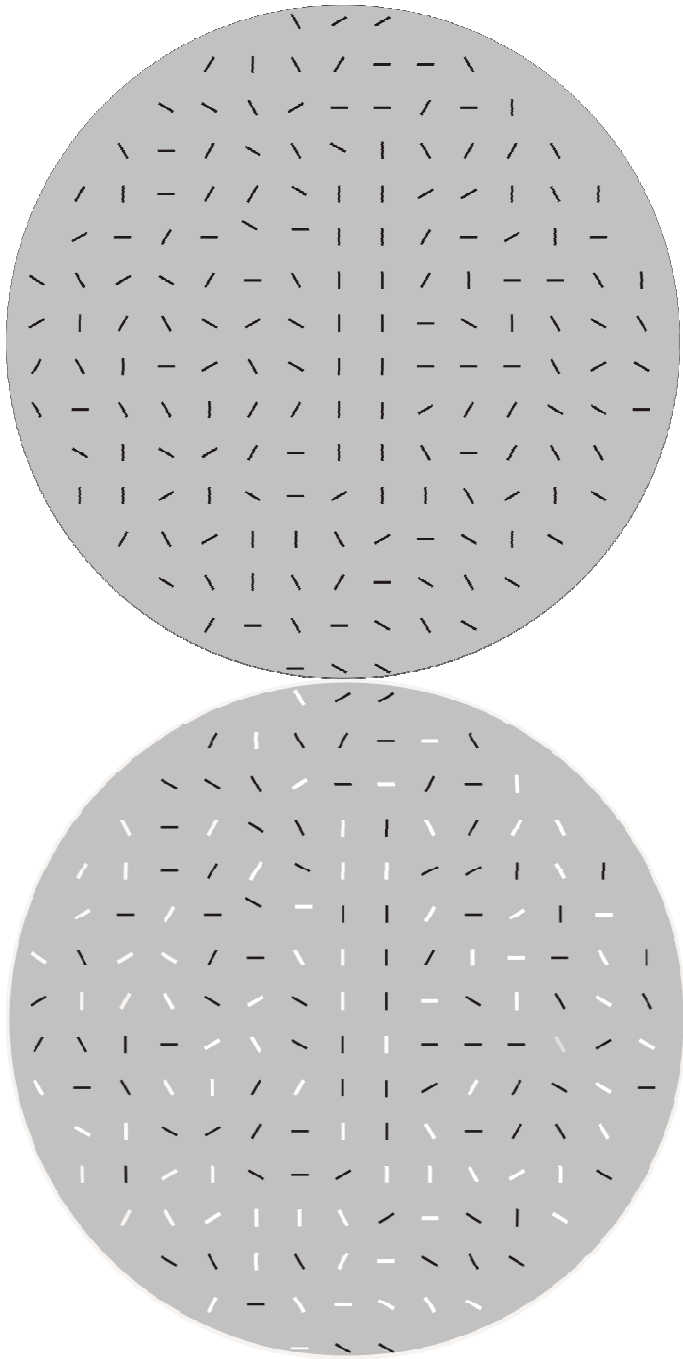


Fig. 10. Contour saliency in a field of same and mixed contrast polarity of elements. Physiological evidence from the primate implicates changes in local connectivity among the neurons in the primary visual cortex in the grouping of line elements in the generation of the percept of a contour, in this case vertical line-pairs arrayed vertically in center of panel(Li & Gilbert, 2002). This appears to be largely robust to the contrast polarity of the line elements.

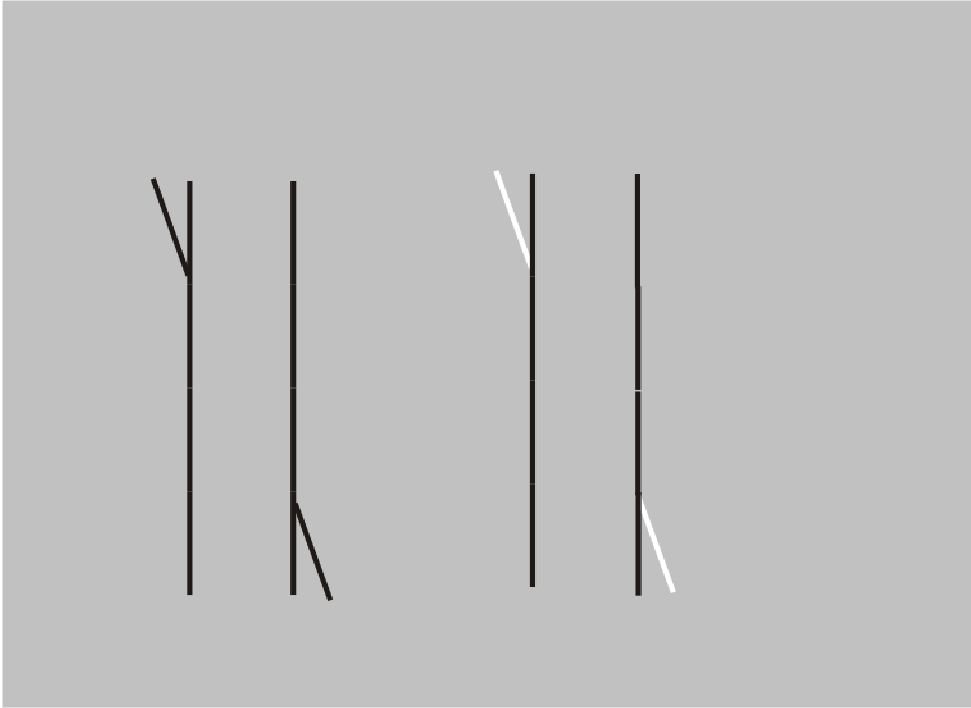


Fig. 11. The apparent misalignment of the transverses in the Poggendorff illusion depends on the contrast-polarity of the line elements of the pattern; the illusion is much weaker when black and white lines are intermingled in the pattern construct.

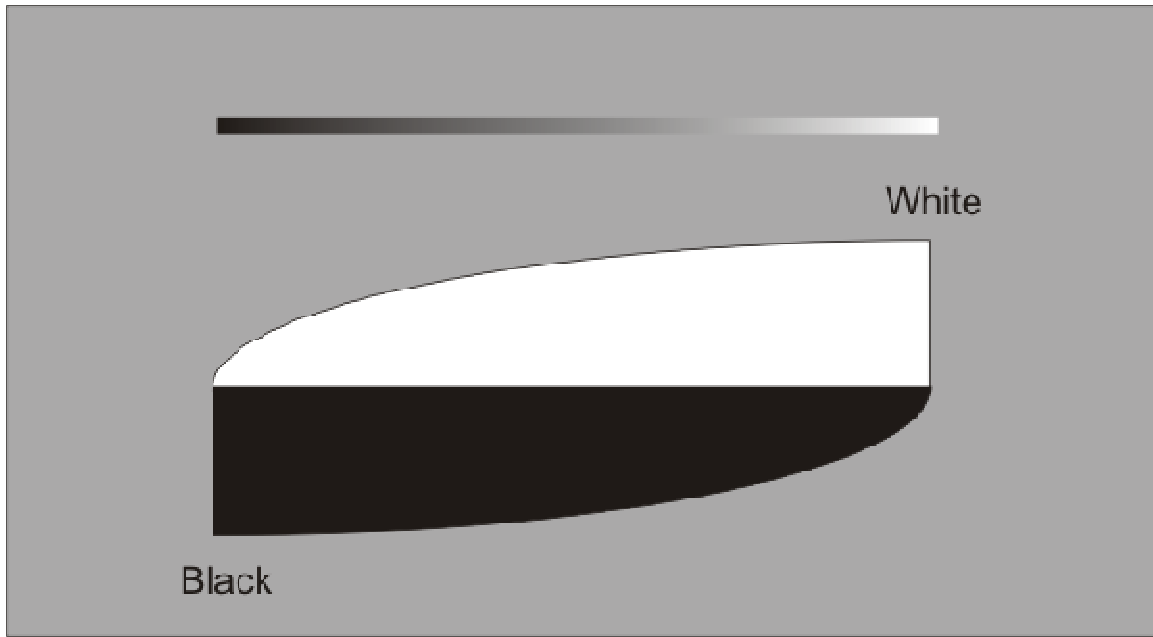


Fig. 12. Modified Hering scheme of black/white opponency. Top: gray scale ranging from full black through intermediate shades to full white. Bottom: Relative contributions of the two antagonistic systems at each gray level. The increasing activity in each sub-system in their respective directions has here been shown with a Naka-Rushton saturating non-linear function (Naka & Rushton, 1966) instead of the linear one in Hering's original (Hering, 1874)