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Spatial sensitization of increments and decrements: A border-contrast process and a net-excitation process

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Abstract

We investigated the spatially local factors that adjust the sensitivity of the human visual system within a small patch of visual space. A very small adapting field was varied in diameter to map out the strength and extent of the spatially local processes that adjust sensitivity for both increments and decrements. The results demonstrated antagonistic center/surround adaptation regions with a decremental test probe comparable to those demonstrated previously for incremental probes (Westheimer, G., 1965. Spatial interaction in the human retina during scotopic vision, *Journal of Physiology 81*, 812–894; Westheimer, G., 1967. Spatial interaction in human cone vision, *Journal of Physiology 190*, 139–154) implying comparable antagonistic adaptation regions in the ON and OFF channels. In addition to spatial interactions based on light adaptation, we report a weaker effect that is based on the location of a border (luminance edge) and is governed by the contrast of this edge. Finally, we show that these effects are elicited by both highly localized edges (1′ ring pairs) and radial lines (Ehrenstein figure) as well. We conclude that both a border-contrast mechanism and a net-excitation mechanism govern the spatially local adaptation of the visual system and that this view fits well with the behavior of single units reported previously. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The spatial interactions between an incremental test probe and a nearby bright adapting background are well documented (Crawford, 1940; Westheimer, 1965, 1967). Westheimer demonstrated that while a small concentric adapting field raises test threshold (desensitization), slightly larger backgrounds act in an antagonistic fashion, increasing sensitivity to the test probe. This pattern has been taken to suggest a correspondence of the spatial interactions of adaptation to the center/surround organization of receptive fields. This 'sensitization effect' or 'Westheimer effect' has been investigated extensively, with numerous authors similarly concluding that the desensitization-sensitization function can be accounted for by the center-surround characteristics of retinal cells (Teller, Andrews & Barlow, 1966; McKee & Westheimer 1970; Tulunay-Keesey & Vassilev, 1974; Tulunay-Keesey & Jones 1977; Ransom-Hogg & Spillmann, 1980; Hayhoe, 1990). Indeed, a version of this test has been used to assess the functional integrity of specific retinal layers of patients with various retinal disorders (Enoch, 1978). There is also direct physiological support from single-cell studies in ganglion cells (Essock, McCarley, Sinai, Khang, Lehmkuhle, Krebs & Yu, 1997) as well as LGN cells (Essock, Lehmkuhle, Frascella & Enoch, 1985). This effect is modeled well by simply considering the effect of the background field as light integrated over a difference-of-Gaussians mechanism profile (Essock & Krebs, 1992; Essock et al., 1997). Yu and Essock (1996a, b) have proposed that the bulk of the desensitization-sensitization effect is indeed retinal, but that cortical factors also serve to impart additional, probably inhibitory, influences on the measured test probe response and the inferred spatial parameters. The cortical contribution has been underscored by results from amblyopes and dichoptic testing (Yu & Levi, 1997).

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Implicit in the traditional account of the Westheimer function is the idea that the sensitivity of the cell (or a composite mechanism such as a small group of cells) is based on its net-excitation level, determined by the summed response of the antagonistic center and surround components (Teller, 1980). For example, when a bright background fills the receptive field center of an ON-center cell, the net-excitation of the cell is high, which, in turn, renders the cell less able to detect the additional light of the test probe. This is sometimes viewed as reflecting Weber's law behavior (or an increase in signal to noise ratio), or due to response compression in a gain-setting mechanism. When the bright background is enlarged, the adapting light is thought to encroach upon the surround, whose antagonism thereby inhibits the cell lowering its net-excitation level making the test probe easier to detect, in effect 'sensitizing' the cell. Although it was rarely, if ever, made explicit, one would presume that an analogous account would govern the behavior of OFF-center units where a dark background would first desensitize then sensitize the response of an OFF-center cell to a decremental test probe as background diameter was increased.[1]

Problems with the net-excitation account exist in both the psychophysical literature and in the physiological literature. First, some (Lennie & MacLeod, 1973) have suggested that it is the presence of a nearby border that causes the desensitization–sensitization effect. They claim that due to small eye movements this border creates a region of local transient activity and that these localized transients raise threshold when the border is near the test probe, but not when the border is farther from the test probe. This conjecture is at odds with the report that when the background is replaced by an edge (a pair of 1′ rings, one dark, one light) test threshold is unaffected by the position of this edge (Westheimer, 1967). Stabilized backgrounds have been used to evaluate the influence of local transients from a nearby border on increment threshold and the results have consistently shown that sensitization is indeed reduced, but still present, with the amount of the reduction varying among these studies (Tulunay-Keesey & Vassilev, 1974; Tulunay-Keesey & Jones, 1977; Hayhoe & Smith, 1989). That a border alone would result in some magnitude of desensitization-sensitization is inconsistent with a strict net-excitation account.[2]

In the physiological literature, two studies (Essock et al., 1985; Cleland & Freeman, 1988) have shown that ON and OFF cells respond comparably (rather than oppositely) to a given background configuration and are therefore inconsistent with the net-excitation account. Since incremental tests are detected at threshold by the ON-system, and decremental tests are detected by OFF-system (Schiller, Sandell & Maunsell, 1986; Schiller, 1992; Dolan & Schiller, 1989, 1994), the mediation of the detection of an incremental test on a bright background would be by ON units and the detection of a decremental test on a dark background would be by OFF units. Thus, a bright background of a size corresponding to the receptive field center would excite ON-center cells and raise thresholds for an incremental test probe flashed in its center, but detection of a decremental test probe would presumably be by OFF-center cells which would not be excited greatly by the bright central background. That is, the net excitation model predicts that increasing the diameter of a bright background would cause desensitization followed by sensitization for incremental tests (ON channel) but not for decremental tests (OFF channel). However, ON- and OFF-center X-cells have been shown to respond comparably to a test probe of matching polarity (incremental and decremental, respectively) as the diameter of a bright adapting background was increased (Essock et al., 1985; Essock et al., 1997). Desensitization followed by sensitization in both ON and OFF X-cells as the diameter of a bright background was increased was observed. Likewise Cleland and Freeman (1988) found that ON and OFF cat ganglion cells responded comparably when a given polarity of adaptation field stimulated their receptive fields. These studies suggest that the local mechanisms setting sensitivity can be independent of whether the center and background polarity match and that the existence of these mechanisms is not restricted to one channel (ON or OFF). Furthermore, these studies indicate that the net-excitation receptive-field account of the effects of local adaptation observed in the Westheimer paradigm is not consistent with important aspects of single cell recordings, although single cells (ganglion and LGN cat X-cells) do demonstrate comparable spatial interactions between an incremental test probe and a bright adapting background as in the original psychophysical studies.

The current study addressed the issue of the behavior of local adapting mechanisms as revealed in the Westheimer paradigm. Specifically we investigated: (1) the spatial interactions in the OFF channel; (2) the validity of the net excitation account; and (3) the role that a

[1] We assume that it is activity in the ON neurons that mediates the behavioral detection of incremental test stimuli at threshold and activity in the OFF neurons that mediates the behavioral detection of decremental test stimuli at threshold. The basis for this is several studies demonstrating that blocking (by APB) the activity of the ON-pathway decimates the ability of the monkey to behaviorally detect incremental test stimuli, completely disrupting this ability at lower contrasts (Dolan & Schiller, 1989,1994). By extension, decremental stimuli are presumed to be detected behaviorally at threshold by the OFF system (Schiller, 1992; Dolan & Schiller, 1994).

[2] Except when the transition between the bright and dark rings is placed such that it perfectly coincides with the zero-crossing between the center and surround, in which case a small effect may be expected (see Discussion).

nearby border, whether physical or subjective, plays in the Westheimer paradigm response. First, we demonstrate the existence of an OFF channel analogue to the Westheimer function which displays this type of antagonistic spatial interactions for a decremental test probe on a dark adapting background. Second, we test the net excitation explanation directly by using mixed polarity conditions where increments are tested on dark backgrounds and decrements are tested on bright backgrounds, and we find sensitization in both cases that is contrast dependent. Third, we show that the effects of a border can be relatively large depending on the polarity and positioning of the border. Finally, we show that a localized edge or the border created in a subjective-contour figure (Ehrenstein) can also cause desensitization and sensitization in some conditions.

2. General methods

2.1. Observers

Ten observers participated in the experiments. Six of the ten were naive as to the purpose of the experiments. Eight were experienced psychophysical observers. All had normal acuity (20/20 or better) with any needed correction. Ages ranged from 20 to 41 years of age. Informed consent was obtained from all subjects.

2.2. Apparatus and Stimuli

The stimuli were generated by a PC-based computer graphics system, VisionWorks (Vision Research Graphics) (Swift, Panish & Hippensteel, 1997). The monitor (Image Systems) had a custom phosphor (P104) and components which allowed a maximum luminance of 300 cd/m^2. Luminance was linearized over 32 767 steps by the graphics system. The spatial resolution of the monitor was 1024×512 pixels and the pixel size was 0.28 mm horizontal $\times$ 0.41 mm vertical. Frame rate was 117 Hz. The viewing distance was 3 m for Experiment 1 ($0.3 \times 0.5'$ pixels) and 5.64 m for all other experiments in the study ($0.17 \times 0.25'$ pixels). Antialiasing methods were used to optimize the luminance distributions of the edges of the stimulus patterns (i.e. the luminance of pixels at the edge of a pattern were weighted by the percentage of the pixel covered by the pattern; Swift et al., 1997). Viewing was binocular with natural pupils for all experiments. The test stimulus was a 1.5′ test probe and was presented either as an increment or a decrement. Viewing was always foveal. This test probe was presented for a 100 ms duration (with an abrupt onset and offset) and superimposed on a background whose size and shape changed from experiment to experiment. The dependent measure was the intensity of the test probe at threshold relative to the intensity of the background on which it appeared (i.e. positive for an incremental probe, and negative for a decremental probe) on a log scale. Specifically, the value plotted is $\log(\Delta L + L) - (\log L)$, or equivalently, $\log((\Delta L + L)/L)$, where L is the background luminance and ΔL is the change in luminance needed to detect the test probe.

In Experiments 1 and 2, the background field was a disk, which was varied in diameter in different conditions. In some conditions, the luminance of the background disk was fixed and the luminance of the monitor screen surrounding the disk was made either brighter or darker than the disk to create a 'dark' background or a 'bright' background, respectively, relative to the surround. Bright and dark backgrounds were made in this way so as to not confound local adaptation level as set by the intensity of the background with whether the background was a decrement or increment field. In some control conditions in Experiment 2 the surround intensity was held constant and the background's luminance was altered to create the bright or dark backgrounds.

In Experiment 3 the background disk was replaced with either a ring or a subjective contour. This was done to test the effects of a nearby border. The subjective contour was created by presenting an Ehrenstein figure with eight radial lines. These conditions allowed the possibility of testing the effects of a real and an induced border without the background creating a mean luminance change (see below).

2.3. Procedure

A successive two-alternative forced-choice (2AFC) procedure was used. Two 1.4 s intervals were marked by two tones of different frequencies and separated by a short (12 ms) interstimulus interval (ISI). The background field was presented in each of the two temporal intervals as well as during the ISI. On each trial, the 100 ms test probe was presented in the middle of one of the two intervals (selected at random). Another tone provided feedback for incorrect responses. Each staircase consisted of eight reversals. In the practice phase of the staircase (the first four reversals), each correct response decreased the magnitude of the increment or decrement by one step (7.5 cd/m^2), and each incorrect response increased the magnitude of the increment or decrement by three steps (22.5 cd/m^2). The experimental phase consisted of the last four reversals which were averaged to obtain a threshold estimate. During this phase of the staircase, test intensity was decreased in magnitude by one step (1.9 cd/m^2) for a correct response and increased three steps (5.7 cd/m^2) for an incorrect response. Threshold estimates were then averaged over 5–6 days (i.e. staircases) for each subject.

3. Experiment 1: the sensitization effect in the OFF channel

The Westheimer function has been widely demonstrated under a number of different conditions, however an incremental test probe and a bright background have almost always been used (but see Westheimer & Wiley, 1970; Lennie & MacLeod, 1973; Wyatt, 1972). Whether the same type of spatial interactions for a decremental test probe centered on a dark background exist was tested in Experiment 1. Traditionally, the net-excitation, receptive field explanation has been applied to results in the Westheimer paradigm in terms of the ON channel. Here we show that the same pattern of desensitization followed by sensitization occurs in the OFF channel as well when tested with a decrement test and a background of like polarity.

Fig. 1 shows the average results from two observers for both the standard Westheimer paradigm (incremental test probe on a bright background, Fig. 1(a) and the present OFF-channel version (decremental test probe on a dark background, Fig. 1(b). For the bright background condition, the circular background was set to 119 cd/m^2 on a surround (monitor screen) of 49 cd/m^2, and in the dark background condition, the circular background was set to 119 cd/m^2 on a surround of 189 cd/m^2. Thus, the background flux was equated in the bright and dark conditions by using changes in the surround intensity to create the fixed (70 cd/m^2) luminance steps of the background (another condition reported below equated screen intensity). On the dark background the magnitude of the decrement required to see the probe (plotted as a negative luminance difference, or decrement, in Fig. 1(b) first increases, then decreases, as background diameter is increased, analogous to the increase and decrease in the magnitude of the increment threshold (plotted as positive in Fig. 1(a). That is, just as an increment must be brighter to be seen on a 6′ background compared to a 13′ background, a decrement must be darker to be seen on a 6′ background than on a 13′ background. For both the decrement-on-dark and increment-on-bright functions, the peak and plateau branches occur at roughly equivalent background sizes.

In most of the conditions that follow, only three background sizes were tested, 3, 6, and 13′; the three sizes best suited to show the critical points in the functions. Fig. 2 shows the results from several additional observers for both the increment-on-bright and the decrement-on-dark conditions. The background was again held constant at 119 cd/m^2 and the surrounding screen was changed to create background luminance step sizes of 84 and 100 cd/m^2. Desensitization followed by sensitization can be seen for both step sizes in both conditions and is of a similar magnitude as in Fig. 1.[3] The results shown in Fig. 2(b) reflect the same sort of spatial interaction in the OFF channel as occurs in the ON channel and are consistent with the net excitation theory directly extended to the OFF channel. That is, the magnitude of the decrement required for a decremental test probe to be seen on a background that strongly activates the center of a receptive field should first increase, then decrease, if governed by the net output of the detecting unit. In Experiment 2 the polarity of the test and background were mismatched in order to test the net excitation, receptive field explanation directly.

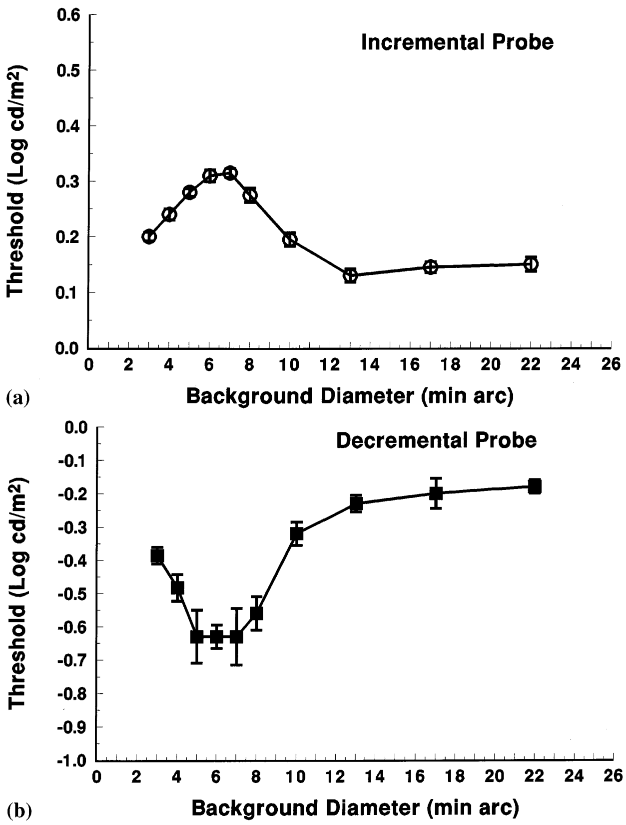


Fig. 1. Average thresholds as a function of background diameter from two subjects for (a) an incremental (1.5′) test probe superimposed on a bright background pedestal and (b) a decremental test probe superimposed on a dark background. Background pedestal step size was 70 cd/m^2 in both cases (see text). Both conditions show that threshold (whether increment threshold or decrement threshold) first increases in magnitude, then decreases as background diameter is increased. Error bars show the average SEM for the two observers.

[3] The magnitude cannot be compared directly across Figures 1 and 2 as different observers were used. In addition, the threshold in the increment-on-bright condition shown in Figure 2 for the 100 cd/m^2 step size occurred for some subjects at approximately the limit of the amount of light producible by the monitor, most likely resulting in a small underestimation of threshold.

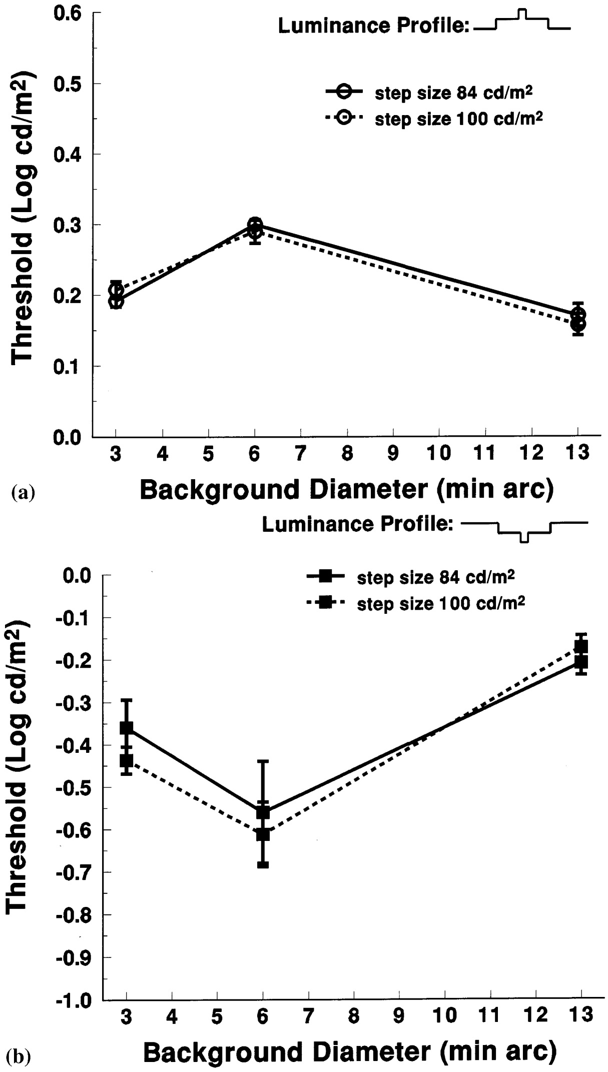


Fig. 2. (a) Increment and (b) decrement thresholds as in Fig. 1 for three background diameters for pedestal step sizes of 84 and 100 cd/m^2. Mean thresholds and SEMs are plotted for the three and four subjects, respectively.

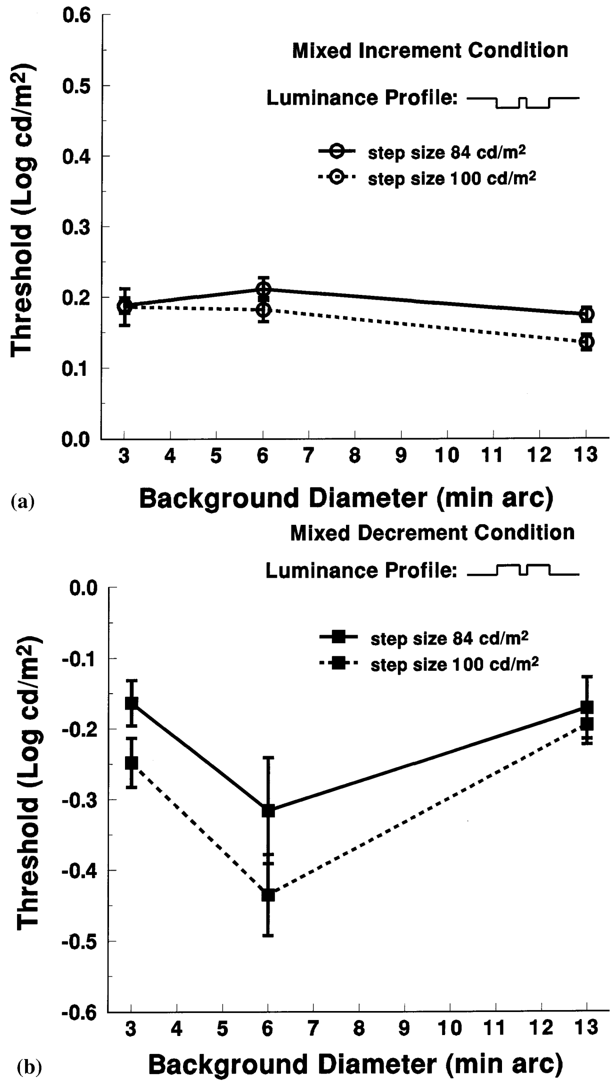


Fig. 3. Average thresholds for (a) an incremental test probe superimposed on a dark background (mixed increment condition) for two luminance step sizes when the background luminance was held constant (119 cd/m^2), and (b) a decremental test probe superimposed on a bright background (mixed decrement condition) for two luminance step sizes on the same background luminance (119 cd/m^2).

4. Experiment 2: testing the net-excitation explanation

The results of Experiment 1 demonstrated initial desensitization of the test probe followed by sensitization when the polarity of the test matched that of the background. The net excitation model would presume that this reflects center/surround antagonism in both the ON channel and the OFF channel with net excitation determining probe sensitivity on a background of the polarity appropriate to excite the center of the unit detecting the increment probe (ON center) or decrement probe (OFF center). In Experiment 2, we tested this account by using the opposite polarity background; a configuration which would not be expected to cause increased, then decreased, excitation as the background diameter was increased. For example, with a bright probe presented on a dark background, the ON-channel units that detect the bright probe would not be strongly excited by the dark background, particularly at the smaller diameters.[4] Thus in the mixed polarity case, an increase in threshold magnitude then decrease, could not be explained by the net-excitation model.

The mixed-polarity cases were first tested by holding the luminance of the background constant at 119 cd/m^2 and varying the luminance of the surrounding screen to produce the ‘bright’ and ‘dark’ backgrounds (as in Experiment 1). However, here we tested the increment on the dark background and the decrement on the

[4] Similarly, if the light of the surround outside of the dark background is considered as a bright annulus, little excitation of an ON-center antagonistic unit would be expected.

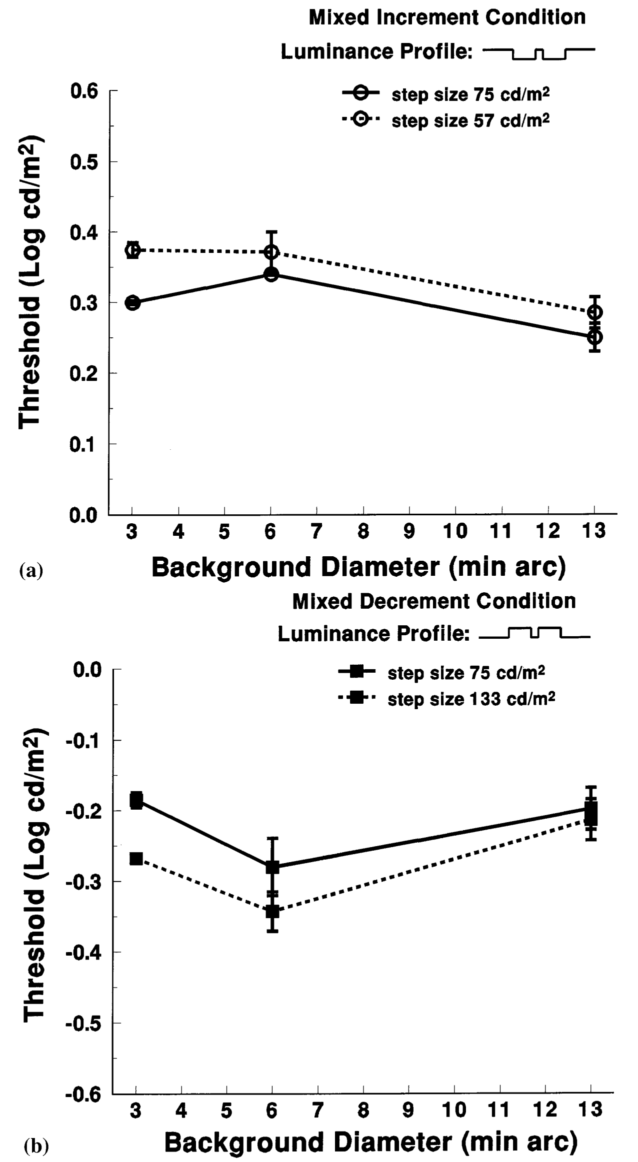


Fig. 4. (a) Increment thresholds on a dark background, and (b) decrement thresholds on a bright background for additional subjects under different step sizes when the surrounding screen was held constant and the background luminance was varied.

bright background. Results are shown in Fig. 3. Indeed, consistent with the net-excitation model, clear sensitization is not apparent for the incremental test probe on a dark background ('mixed increment' condition, Fig. 3(a)). However, for the decremental test probe on a bright background ('mixed decrement' condition, Fig. 3(b), the results show a strong desensitization-sensitization curve, and thus are inconsistent with predictions based on the net excitation theory.

To control for any influence of the difference in the intensity of the surrounding screen, we also tested these mixed-polarity conditions with the background step formed by changing background intensity and holding

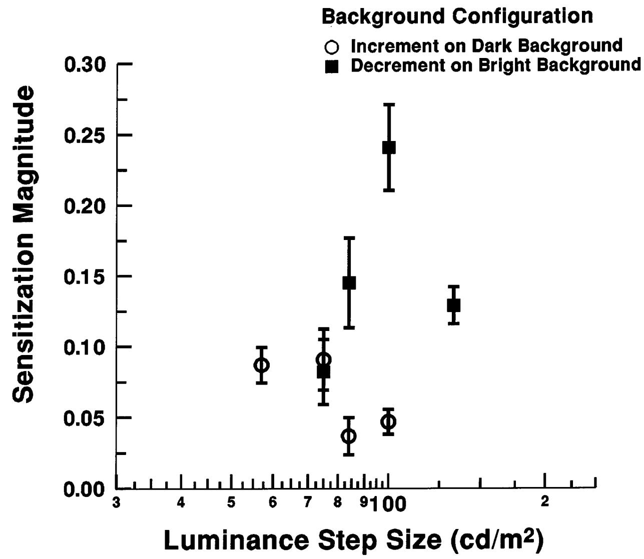


Fig. 5. The sensitization magnitude (6′ threshold − 13′ threshold) plotted as a function of luminance step size (between background disk and surround) for the mixed conditions.

screen (surround) intensity fixed.[5] Fig. 4(a,b) show the results using two step sizes for a mixed-increment configuration and a mixed-decrement configuration, respectively. Comparing the magnitude of the increment

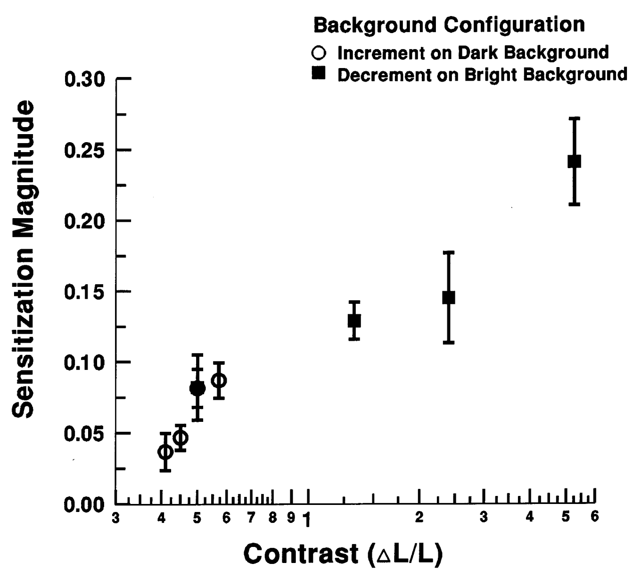


Fig. 6. The sensitization magnitude plotted as a function of Weber contrast of the background on the surround.

[5] We assume that whether the ON or OFF system detects a given test probe is determined by the properties of the probe, and that changes in the luminance of the background do not affect which system detects a given probe. For example, results by Dolan and Schiller (1989) show that regardless of the luminance of the background upon which an incremental test stimulus appears, detection of incremental stimuli is mediated by the ON-system across all photopic background luminances.

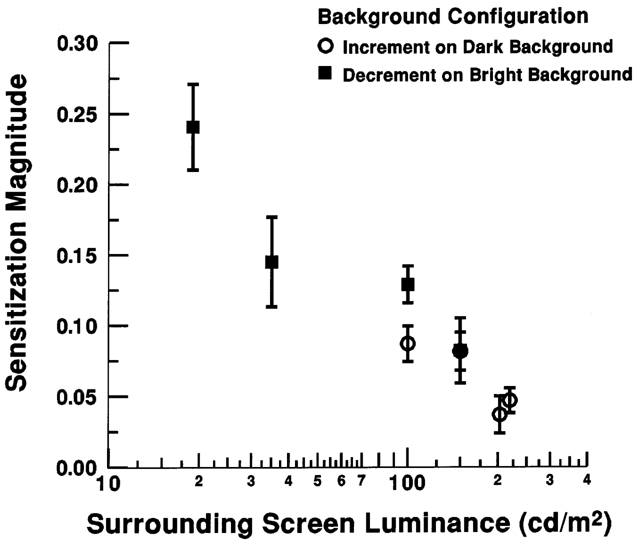


Fig. 7. The sensitization magnitude plotted as a function of the surrounding screen luminance.

or decrement at 6′ to that at 13′ shows that sensitization is now seen for both conditions in both cases (about 0.1 log unit in the reverse decrement condition and a little less in the reverse increment condition). Differences between these conditions (Fig. 4), and the mixed-polarity conditions shown in Fig. 3 include differences in the luminance of the surrounding screen, the luminance difference between the background and surround (the ‘step size’), and relatedly, the contrast between the background and surround. We investigated which of these stimulus differences could explain the apparent differences between the results shown in Figs. 3 and 4 by plotting the data according to step size (Fig. 5), and contrast (Fig. 6), defined as $|L_{\text{Background}} - L_{\text{Surround}}|/L_{\text{Surround}}$, respectively. The magnitude of the sensitization effect (threshold magnitude for the 13′ background condition subtracted from that of the 6′ condition) was plotted for both the reverse increment and reverse decrement cases. It can be seen (Fig. 5) that there is no relation $r = 0.28$, $P = 0.54$) between background step magnitude and magnitude of sensitization while a clear relation exists (Fig. 6) for background contrast and magnitude of sensitization $r = 0.95$, $P = 0.001$). Thus, background contrast appears to govern sensitization magnitude in the mixed-polarity conditions in a fairly direct fashion.

However, since background contrast and surround intensity tended to be confounded, an alternative interpretation is that the magnitude of the effect in the mixed-polarity condition is inversely related to surround (screen) intensity (as plotted in Fig. 7, $r = -0.90$, $P = 0.005$). To allow us to choose between these two possibilities (background contrast or surround luminance), we varied the background step size (contrast) while holding the surrounding screen's luminance constant (150 cd/m^2) and measured test probe threshold at the three background diameters. This procedure also provides a direct comparison of the magnitude of the mixed-polarity sensitization in the ON channel (reverse increment) with that in the OFF channel (reverse decrement) (see also Fig. 4). Data from two subjects (shown in Fig. 8(a,b) show that mixed-polarity sensitization increases as a function of background contrast for both the increment and decrement test conditions. Furthermore, since the effect increases as a function of contrast when the surround intensity is held constant, it is background contrast rather than surround intensity that governs the sensitization response. The magnitude of sensitization is consistently a little greater, or increases a little more rapidly, for the mixed-increment

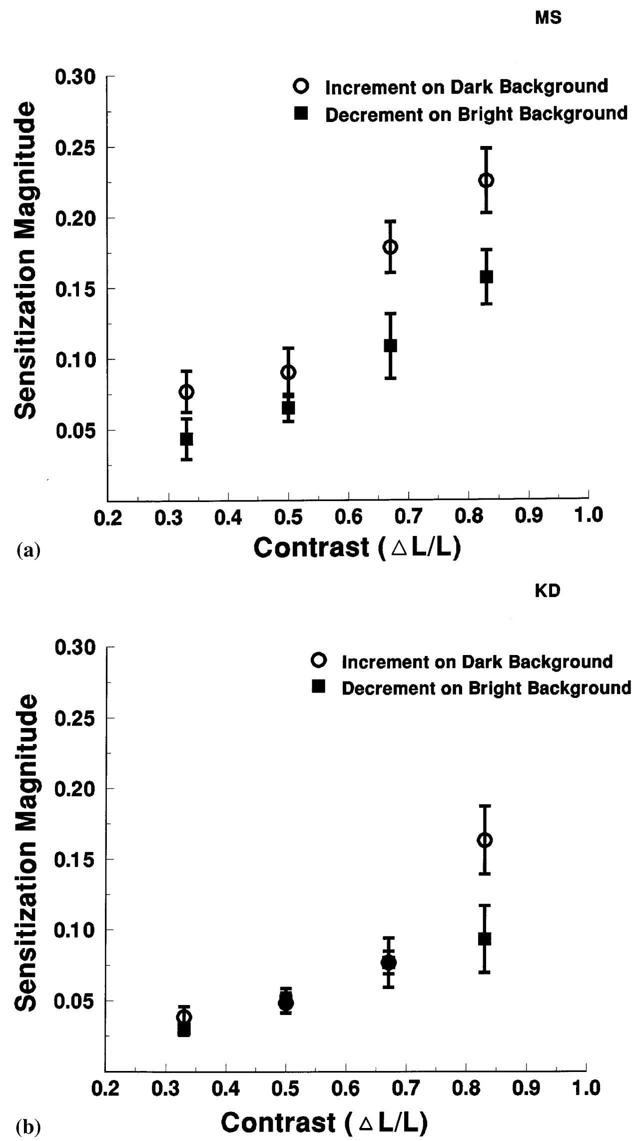


Fig. 8. The effect of background contrast when surround intensity is fixed (150 cd/m^2) on the sensitization magnitude in the mixed polarity conditions plotted for two subjects (a and b).

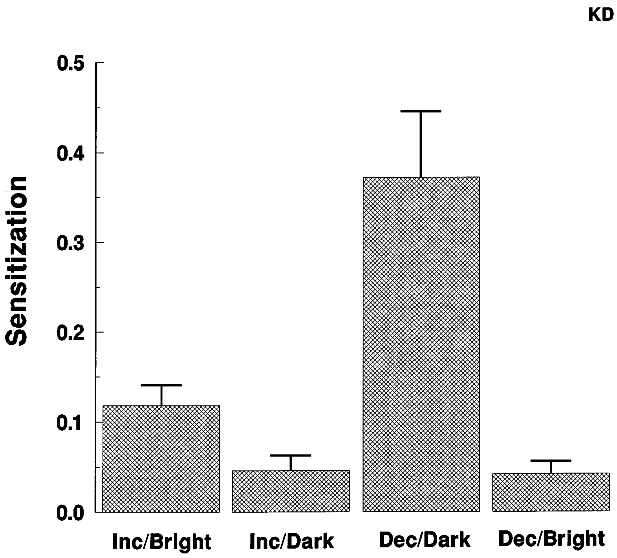


Fig. 9. Sensitization magnitude for one observer compared for all four conditions (incremental test on a bright or dark background and a decremental test on a dark or bright background) when the surround luminance was held constant (150 cd/m^2) and the contrast was fixed (50%).

(ON-channel) condition than for the mixed-decrement test condition. Note that the much larger sensitization effect observed in the mixed-decrement case compared to the mixed-increment case in the prior experiment (Fig. 3), is consistent with the much greater Weber contrast (526 relative to 45%) in that experiment.

Taken together, these results indicate that the sensitization effect has a strong dependence on contrast and that when considered with respect to contrast the basic desensitization–sensitization spatial interactions are obtained with both types of mixed-polarity configuration (decrement-on-bright and increment-on-dark) as well as with the matching-polarity configurations (decrement-on-dark and increment-on-bright). Thus, the net excitation model fails to account for these results: the contrast of the background's edge appears to play a crucial role in this effect, and the light within the background's edge (i.e. the polarity) does not exclusively determine threshold, as often reported previously. Instead, both the contrast of the background's edge and the amount of the appropriate-polarity light in the background (net-excitation) together set threshold. This conclusion that both effects contribute in the matching-polarity case is consistent with the greater magnitude of the effect observed in the matching-polarity condition than in the mixed-polarity condition, as seen in the data for both the increment and decrement test probes when matched for luminance. To compare the mixed-polarity and matched-polarity versions when background contrast was equated, each of the four conditions was retested at a fixed Weber contrast of 50% for two observers. Results (Fig. 9) showed that indeed, in both the ON channel (increment probe) and the OFF channel (decrement probe), the magnitude of sensitization was greater in the matching-polarity case than in the mixed polarity case.

As one final control, we replaced the flashed test with either a rapid-on or a rapid-off sawtooth temporal waveform modulated about the background intensity. This condition ensured that: (1) the test probe consisted exclusively of either incremental or decremental transients, and (2) the test probe itself did not cause a change (however small) in the total luminance in the region covered by the background field. That is, this control condition further assured that the increment probe was detected by the ON pathway and the decremental probe was detected by the OFF pathway in all conditions (Kremers, Lee, Pokorny & Smith, 1993; DeMarco, Smith & Pokorny, 1994). This condition was tested with a test probe with 2 Hz sawtooth temporal modulation in two observers in the same 2AFC paradigm (but with a 2 s test probe presentation centered in 3 s intervals). A background contrast of 50% was chosen (bright background of 50 cd/m^2 on a screen of 33 cd/m^2 and a dark background of 50 cd/m^2 on a screen of 100 cd/m^2). Both mixed- and matched-polarity stimuli were tested with both rapid-on and rapid-off modulation of the test probe. The results of both observers with this sawtooth test probe (Fig. 10) were quite comparable in every way to the results with the 100 ms square-wave flashes (e.g. Figs. 1–4). Indeed, the magnitude of the effect in the four conditions very closely matched the magnitude obtained with the 50% contrast stimuli in the square-wave flash conditions at the same (50%) contrast (see Fig. 8a,b, Fig. 9). This control condition further suggests that the incremental or decremental test probes were indeed detected by the ON and OFF pathways respectively.

5. Experiment 3: the contribution of the background's border

This experiment was concerned with determining the contribution the nearby border itself makes in these variations of the Westheimer paradigm. To do this, we removed the large luminance difference conveyed by the bright or dark background by replacing the disk-shaped background field with an edge of equivalent diameter. Two types of such circular border were investigated: a ring-shaped edge and a subjective disk. The ring-shaped border was created by a pair of contiguous 1′ rings, one bright (240 cd/m^2) and one dark (0 cd/m^2) together forming an edge with no average luminance contribution relative to the surround. For the subjective disk, an Ehrenstein figure made of $1' \times 10'$ radial lines was used to create a subjective edge (and also a subjective disk created from the perceived brightness that fills in from

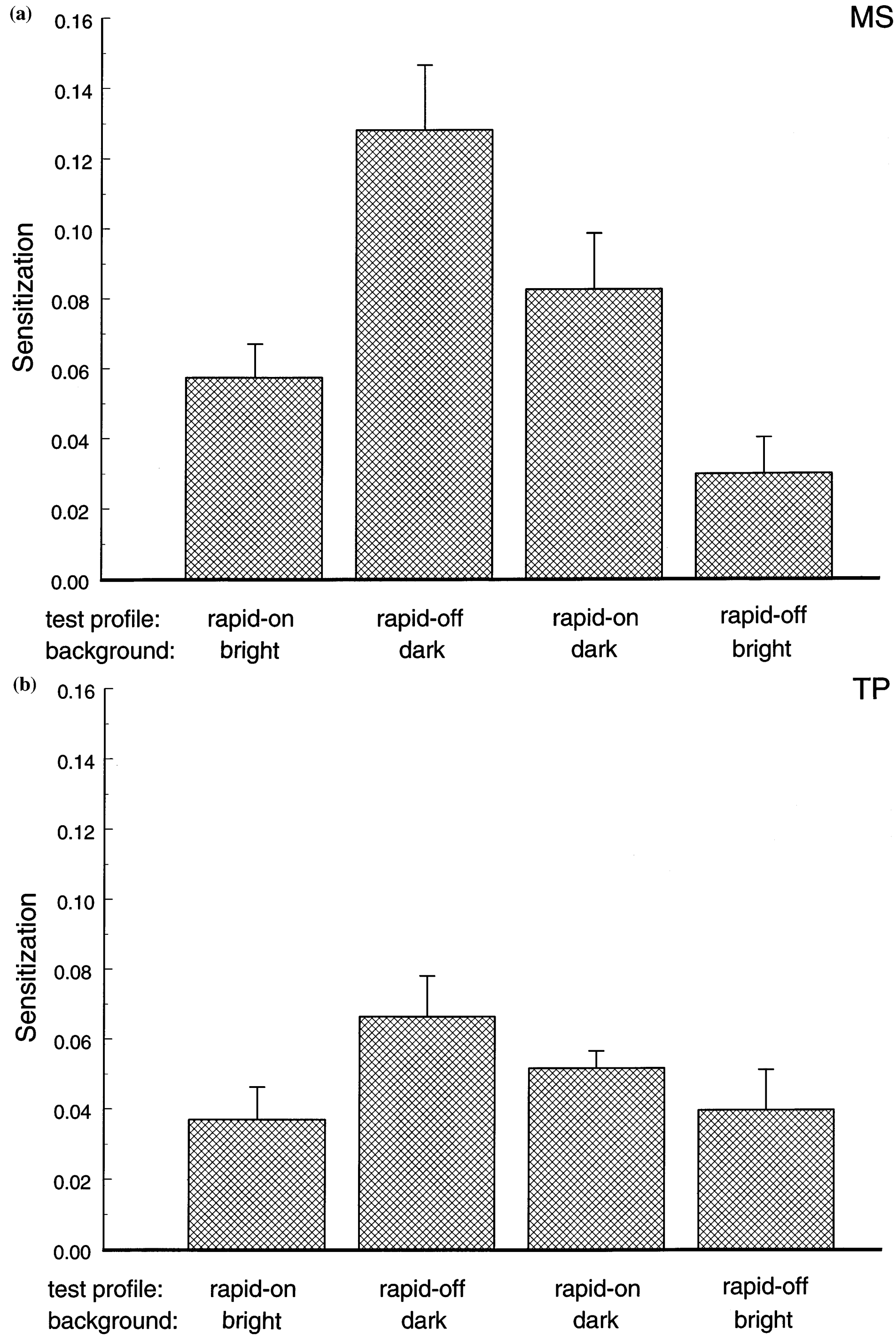


Fig. 10. Sensitization magnitude for the two observers tested with a test probe modulated by a 2 Hz sawtooth temporal waveform The test probe was in either rapid-on or rapid-off phase and presented either on a bright or dark background The rapid-on/dark-background and rapid-off/bright-background conditions are analogous to the mixed-background conditions of other figures and the rapid-on/bright-background and rapid-off/dark-background conditions are analogous to the matching-background conditions.

the subjective contour). Thus, this subjective edge also created a ring-shaped edge with no physical luminance difference inside the edge. For both of these backgrounds then, we were able to test the influence of a nearby border without varying physical luminance across the border.

Westheimer (1967) reported that a comparable ring pair did not affect sensitivity to an incremental test probe, suggesting that the presence of a nearby border was not the governing factor behind the desensitization–sensitization function. However, Lennie and MacLeod (1973) found that an annulus could affect sensitivity (in scotopic conditions) and postulated that it did so by creating transients at the border due to small eye movements. Findings from studies using disk-shaped backgrounds stabilized on the retina in order to eliminate such transients suggest that transients at the edge of a border make either a negligible or partial contribution to the sensitization effect (Tulunay-Keesey & Vassilev, 1974; Tulunay-Keesey & Jones, 1977; Hayhoe & Smith, 1989). From these studies it is still unclear to what degree sensitivity is affected by the presence of a border per se compared to a filled background; particularly in terms of the OFF channel (Experiment 1), and in the mixed polarity cases (Experiment 2) examined here. This issue was addressed in Experiment 3.

The results indicated that neither background configuration, neither the ring pair nor the subjective background, actually acted like a pure edge. Instead, the effect of both of these backgrounds was found to be like the corresponding matched-polarity or mixed-polarity disk-shaped background, yielding the same pattern of results as observed in Experiments 1 and 2 (with the physically bright or dark background disks), but of a lessened magnitude. The results for both of these backgrounds selected to emphasize the edge mechanism can be interpreted within the framework laid out above: that there is both a light-based adaptation mechanism and a weaker contrast-based edge mechanism active.

Results with the ring pair are shown in Figs. 11 and 12. Stronger sensitization was observed when the polarity of the test probe matched that of the inner ring of the ring pair, than when the inner ring polarity is opposite to that of the test probe. For the matched-polarity case, sensitization is about 0.07 log units for increments (Figs. 11 and 12(a) and 0.10 log units for decrements (Fig. 12(b)), and for the opposite-polarity cases sensitization is reduced, but still apparent (about 0.02 log units for most of the five observers tested for increments, shown in Figs. 11 and 12a and about 0.05 log units for decrements, shown in Fig. 12(b)).

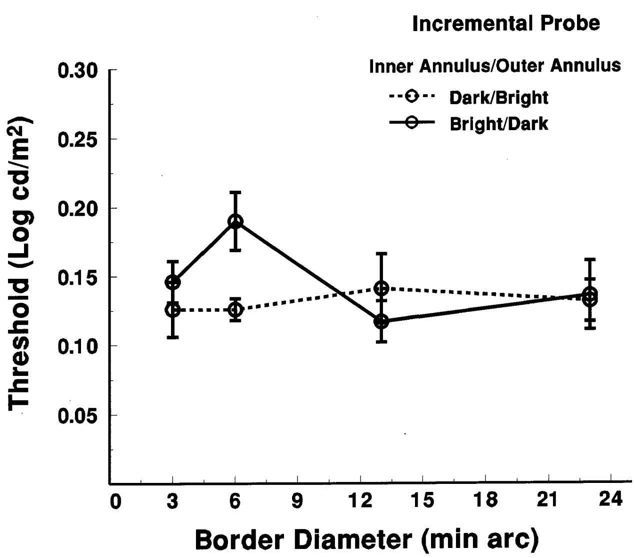


Fig. 11. Average increment thresholds for three subjects when the background was replaced by a pair of concentric bright and dark rings (each 1′ wide), across varied ring diameters In one condition the inner ring was bright (240 cd/m^2) and the outer ring was dark (0 cd/m^2) while in the other condition the intensities were switched, on a screen of 240 cd/m^2.

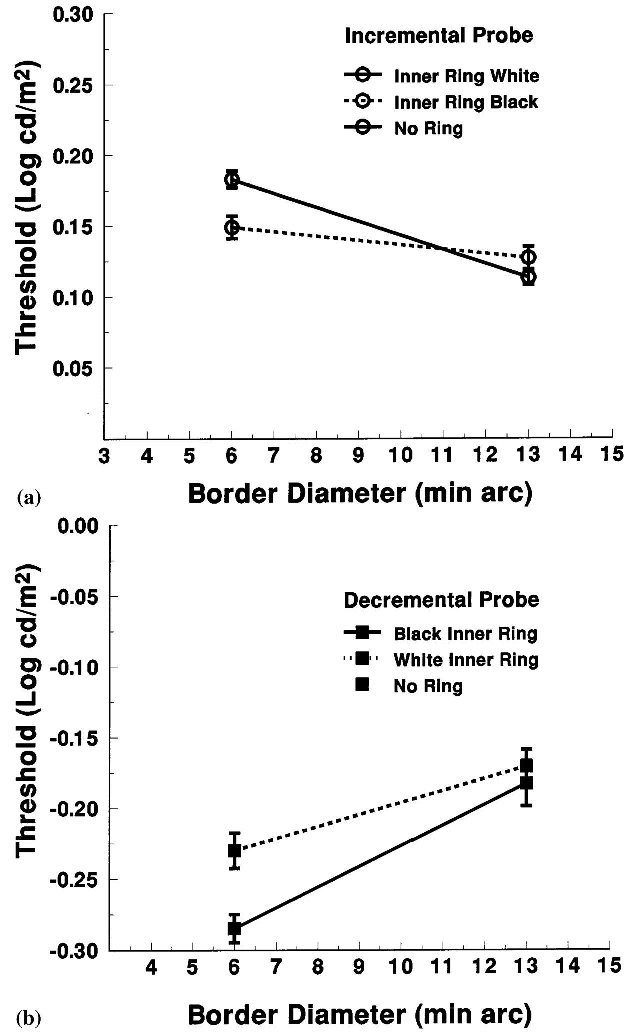


Fig. 12. (a) Increment and (b) decrement thresholds averaged from two subjects for the ring background configuration. Mean threshold when no background was present is present is indicated by the isolated symbol plotted. Intensity of the surround was 150 cd/m^2.

These findings of greater sensitization when the polarity of the inner ring matches the polarity of the test (Figs. 11 and 12, solid lines) than when it is opposite (dashed lines) are accountable within a net-excitation model if the spatial distribution of background light is thought to be assessed very accurately across space. For example, a ring-pair straddling a receptive field's zero-crossing would slightly excite the unit when the polarity of the inner ring matches the test, but not when the inner ring is opposite to the test. When the entire ring pair falls within the center (or within the surround), the effect of the ring pair would be negligible. Thus, the finding of some sensitization with ring pairs with a matched-polarity inner ring is consistent with the net-excitation model if the adaptation process is assumed to be sensitive to placement within 1′ and to give measurable differences. Indeed, this has been shown to be the case in prior studies (Yu & Essock, 1996a,b). This interpretation suggests that the results reported by Westheimer (1967) for a ring pair were obtained for an opposite-polarity configuration of an increment test and a dark inner ring (the actual polarity was not stated in the original paper). In the case when the inner ring does not match the polarity of the test probe (Figs. 11 and 12, dashed lines), a highly localized (i.e. 2′) edge exists and the small, but consistent, sensitization (dashed lines) can be attributed to the contrast-based edge mechanism as in the prior experiments (cf. Fig. 8).[6] We conclude that a part of the sensitization observed with ring-pair backgrounds is due to the edge mechanism (dashed lines) and that part is due to the net-excitation mechanism (the difference between the dashed lines and the solid lines) and thus the effect of the ring-pair background is very analogous to that of the disk-shaped physical backgrounds.

Finally, we replaced the background with an Ehrenstein figure which created a subjective contour of a circle as the background field (i.e. subjective contours appeared between the real contours of the ends of the radial lines). In this way we were able to test the effect of a subjective border and the associated disk of induced brightness (or darkness) inside the ends of the 1′ wide radial lines (10′ long) used in the figure. That is, as is typical of subjective contours, when black radial lines are used, a subjective disk is seen which is slightly brighter than the surrounding screen and, conversely, when bright lines are used to create the figure the subjective disk is seen as slightly darker than the surrounding screen. We also used lines consisting of a pair of contiguous lines (each $0.5 \times 10'$), one bright and one dark line placed side by side, to control for the mean luminance difference. Such a pattern tends to create a subjective circle that stands out

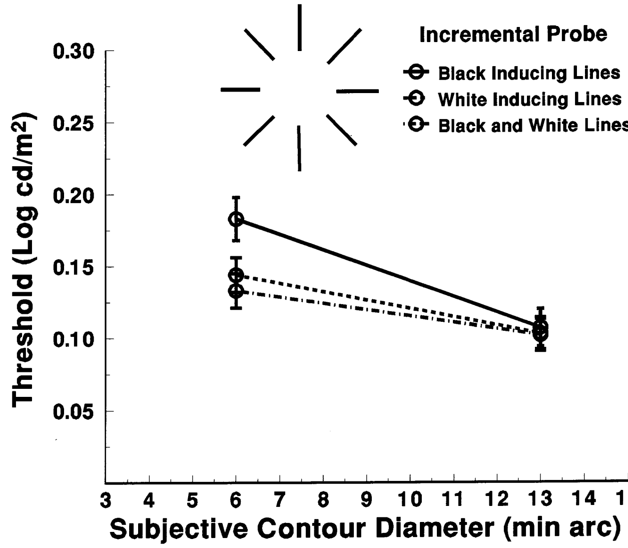
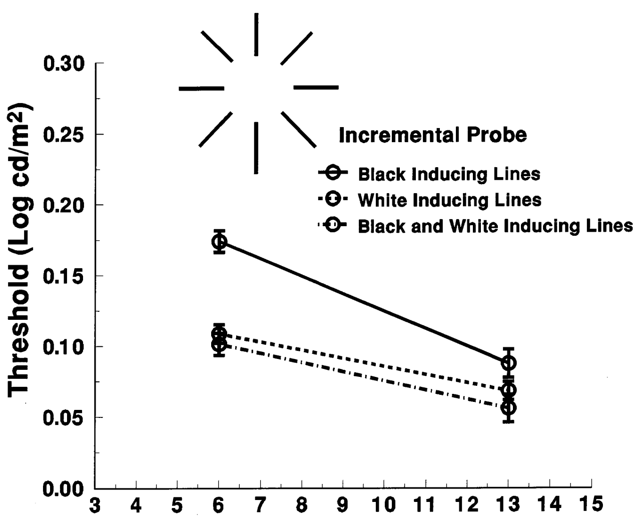
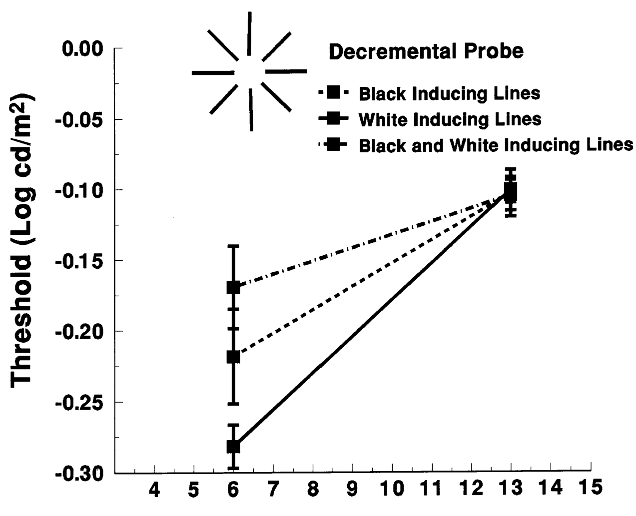


Fig. 13. Average increment thresholds for three subjects when the background was induced by a subjective contour created of $1 \times 10'$ radial lines (Ehrenstein figure) either 224 or 0 cd/m^2 on a screen of 119 cd/m^2.



(a)



(b)

Fig. 14. (a) Increment and (b) decrement thresholds for another subject when the test probe was centered on an Ehrenstein figure created by 1′ white, black, or both types (0 5′ each, 1′ total) of radial lines of 300 or 0 cd/m^2 on a screen of 150 cd/m^2.

[6] Furthermore, this edge-effect may account for the ‘anomalous desensitization’ reported by Wyatt (1972) for an increment test on a dark annulus under scotopic conditions, as well as the sensitization that may be evident in that study.

in depth and was not seen as brighter or darker.[7] A number of studies have shown that illusory contours influence increment and decrement thresholds (Coren & Theodor, 1976; Dresp & Bonnet, 1991; McCourt & Paulson, 1994; Jory, 1987), but these prior studies used relatively large figures, ranging from a 26′ diameter Ehrenstein figure to a 3.25° Kanizsa square. These prior studies found that thresholds were typically raised near the illusory border, but in the present application we were interested in testing the influence when the illusory figure was on the same scale as the local spatial interactions investigated in this study.

Results for subjective backgrounds induced by the radial lines (Figs. 13 and 14) are very comparable to the other results when viewed with respect to the polarity of the test probe and the model of joint effects from the net-excitation and edge mechanisms. When the polarity of test probe matches the polarity of the induced disk (solid lines plotted in Figs. 13 and 14) greater sensitization is obtained than when they are mismatched (dashed lines). For the matched-polarity condition sensitization was 0.09 log units for an increment and 0.18 log units for a decrement, and for the opposite polarity condition sensitization was 0.04 log units for increments and 0.11 log units for decrements. Thus, the Ehrenstein figure background appears to produce results very similar in pattern and magnitude to the results with the 1′ paired rings, suggesting both a small net-excitation effect (the difference between the solid and dashed lines) and a small edge-based effect (dashed lines). However, both of these small effects obtained with the Ehrenstein figure may stem from the difference in average luminance between the surrounding area that contains the black or white radial lines and the central area which is physically bright or dark relative to the average luminance of the surround (e.g. dark radial lines at a 6′ separation, in effect, make a bright 6′ background). That is, these effects are comparable to those obtained with the 1′ rings which also produced only a small average luminance difference between the center and the surrounding region. The results with the Ehrenstein figure made with paired black and white lines more conclusively indicate that a subjective contour may create a small effect (Figs. 13 and 14, dash-dotted line compared to dotted lines). However, the ends of the radial lines could be viewed as contributing real edges to the circular boarder (i.e. real edges with a subjective edges in between).

[7] An examination of the Fourier transforms of the stimuli demonstrated that bright or dark lines alone had some power similar to that for a real disk, but that this was not apparent in the spectrum of the black/white paired lines.

6. General discussion

These results demonstrate that a decrement test probe is first desensitized, then sensitized, as the diameter of a dark background is increased. This effect is at least as great in magnitude, and is of a similar spatial scale as the conventional Westheimer function in which a bright adapting field reveals center/surround spatial interactions about an incremental test probe. Since detection of decrement spots are thought to be mediated by OFF-center neurons (Schiller et al., 1986; Dolan & Schiller, 1989, 1994), we feel that we have demonstrated an OFF-channel analog to the Westheimer paradigm that reveals local spatial properties of the perceptual OFF channel. The spatial scale of these OFF-channel interactions is comparable to the ON channel to a first approximation, but are presently being examined in more detail. This effect is consistent with the idea that the net excitation level of the detecting unit (or cell) is inversely related to the unit's ability to detect an additional increment/decrement. That is, whether a unit is an ON-center unit detecting an increment test, or an OFF-center unit detecting a decrement, high activity results in lowered sensitivity to an additional small test stimulus. One possible distinction between the ON and OFF channels is that plotted as we have done here, the magnitude of the sensitization effect is consistently larger in the decrement probe (OFF-channel) case, with this difference apparent in all disk, ring and subjective contour cases.

The present results also demonstrate a second effect that causes nearby desensitization and surrounding sensitization. This effect is driven by the edge of the adapting background per se, and is based on contrast (rather than, for example, the flux in the background). This effect is obtained even if the polarity of the test and background do not match and thus is unrelated to any process based on net excitation. The magnitude of this effect is smaller than that seen in the matching polarity cases (increment-on-bright and decrement-on-dark). We assume that this border-contrast effect is present in the matching polarity cases as well as in the mixed-polarity cases, and therefore suggest that the larger effect observed in the same-polarity case is due to the combination of both effects: the border-contrast effect and the net-excitation effect. Furthermore, such an account fits well with the observed behavior of single neurons (Essock et al., 1985, 1997), explaining the paradox outlined in the Introduction. Specifically, even in a stimulus condition that would be inconsistent with a net-excitation process, a neuron would be expected to still show the sensitization effect when test conditions were appropriate for the generation of the boundary-contrast effect (i.e. a mixed-polarity decrement-on-bright background for an OFF-center cell; Essock et al., 1985). This two-process account of the sensitization effect also accounts for the residual sensitization effect observed with a stabilized border (see Introduction) as this is a condition that may preclude an edge-based process (the border-contrast effect), but not the net-excitation effect, resulting in a reduced effect.

Our test conditions with a subjective background or with rings (a pair of bright and dark narrow contiguous rings) help to explain the nature of these two mechanisms. Both configurations produce a small, but consistent, effect which is largest when the polarity of the test and background (induced or inner-ring) match, but is still apparent at the opposite polarity. That is, these stimuli behave in the same way as the full disk backgrounds indicating that both the Ehrenstein-figure backgrounds and ring pairs drive these mechanisms in the same way, albeit at less strength.

That a 1′ ring-pair acts as a weak filled-disk background may at first seem puzzling since if the ring-pair is considered more globally (e.g. averaged over a 2′ wide window) no luminance difference exists. The ring-pair has been viewed as a pure edge in this sense, that is, that no mean luminance difference exists (Westheimer, 1967). However, the data reported here, as is typical for this paradigm, are highly spatially dependent and accurate to an extent such that a 1-min difference of background diameter or position makes a large difference in sensitivity (Yu & Essock, 1996a,b). Considering the high resolution of this test paradigm, it is apparent that paired 1′ rings would provide a relevant spatial luminance contribution and should not be considered as an edge with no effective luminance contribution. Indeed, the present results show that an inner ring of matching polarity causes a bigger effect (i.e. due to both the border-contrast and net-excitation effects) than the opposite polarity case (due only to the border-contrast effect).

The existence of a number of adaptation and gain control mechanisms has been indicated at a number of levels in the visual system (Shapley & Enroth-Cugell, 1984). Hayhoe (1990) has demonstrated that the sensitization observed in the standard increment-on-bright Westheimer paradigm appears to be due to a subtractive mechanism. This spatially local mechanism serves to 'discount the background' on which a stimulus appears and is thought to be related directly to retinal center/surround antagonism (Hayhoe, 1990). Thus, the 'net-excitation' model seems consistent and essentially equivalent to this view of subtractive adaptation mechanisms.

The second, boundary, process that we have demonstrated here, is governed by contrast and thus fits with the notion that the visual system strives to code the visual world in ratios (contrast) in order to discount luminance variations due to illumination differences (Shapley & Enroth-Cugell, 1984). Thus the boundary-contrast process appears to change the gain within both the ON and OFF pathways based on proximity to an edge of a given contrast. Such a process may have some utility by serving to perceptually smooth an image, suppressing (desensitizing) objects or noise occurring just next to a strong edge.

We suggest that together these two processes, the border-contrast and net-excitation processes, account for the single-unit studies that were so similar to the present results, including the results with mixed-polarity stimuli (Essock et al., 1985, 1997). This indicates that both the net-excitation and border-contrast processes are likely to be first organized at the retinal level. However, the border-contrast process seems closely related to processes revealed with grating patterns that are presumed to be organized at the cortical level (Bowen & Wilson, 1994; Makous, 1997). The boundary-contrast retinal process may provide the substrate for these presumably cortical processes. Recently, Makous (1997) has described an account of the sensitization effect that is based on spatial frequency specific masking. His model fits well with a polarity-insensitive mechanism like the border-contrast mechanism, but can not explain the polarity-specific nature of the net-excitation mechanism (i.e. under such a model results for the mixed- and matching-background conditions should not differ). If viewed strictly as a cortical process, the model also can not explain the existence of the sensitization effect in pre-cortical single-units, nor can it explain the findings of different scaling (E_2) values for the center and surround processes that suggest different levels (i.e., retinal and cortical) of organization (Yu & Essock, 1996b). We conclude that: (1) the sensitization effect is best viewed as mediated by two processes, a net-excitation adaptation process and a boundary-contrast gain process, (2) these two processes are first organized at a retinal level (Essock et al., 1997), but have spatial profiles that are modified at the cortical level (Yu & Essock, 1996b; Yu & Levi, 1997), and (3) the border-contrast process appears to be related to spatial frequency specific properties of cortical sensitivity adjustment processes (Bowen & Wilson, 1994; Makous, 1997).

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