

The Influence of Light and Dark
Adaptation on the Effectiveness
of Masking Gratings

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Abstract

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The intended purpose of this research was to study the effect of manipulating the state of light adaptation of the eye on the tuning functions of individual spatial frequency sensitive channels. Using a forward masking paradigm, one of three target frequencies (1.41, 4.0, & 8.0 c/d) was detected either in the presence or absence of a masking grating. The spatial frequency of the masks varied within a three octave range of the target frequency. Two related changes in the data were noted as the luminance level was altered. The absolute amount of masking decreased as the eye became dark adapted and there was, as well, a broadening of the masking effect, primarily at the lower masking frequencies. Instead of describing individual tuning functions, these data were hypothesized to be reflecting the effects of dark adaptation on interchannel inhibition and were interpreted in terms of the attenuation of retinal receptive field surround influences that have been observed in the dark adapted eye.

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The Influence of Light and Dark Adaptation on the Effectiveness of Masking Gratings

Although it is not completely understood how the process of seeing provides us with a spatial representation of the outside world, most visual scientists agree that perception of a visual scene involves an analysis of the complex pattern into simpler elements. Accordingly, researchers have been trying to discern the mechanisms implicated in this analytic process. One of the questions that has received a lot of attention concerns the nature of the basic element(s). In order to provide an historical context for this thesis, literature from relevant neurophysiological and psychophysical reports will be reviewed.

Approximately 20 years ago Lettvin, Maturana, McCulloch & Pitts (1959) found that there are different cells in the frog's optic nerve that increase their rate of firing under particular retinal stimulus conditions (i.e., sustained contrast, moving edges, etc.). From these findings they concluded that the process of encoding certain features (i.e., unique neural representations) is begun in the eye. Hubel and Weisel (1962, 1968) have developed a model of feature detection, based on the response characteristics of cortical cells in the cat and the monkey, that assumes an hierarchical organization of the visual system. Hubel and Weisel (1962) found two groups of cells that differed in terms of the complexity of their receptive fields and

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accordingly referred to them as "simple" and "complex" cells. The receptive fields of the "simple" cells possessed distinct excitatory and inhibitory regions such that when stimulated they either increased or decreased, respectively, the maintained firing rate of the cells. The most effective stimuli for these cells were bars or "slits of light" of a particular width and orientation. According to Sekular (1974), these "simple" cells have often since been referred to as bar, line or orientation detectors. The organization of the "complex" cells was found to be much more elaborate and therefore more difficult to map out. These "complex" cells showed the characteristics of the "simple" cells (i.e., orientation and width specificity) as well as a response preference for movement in a particular direction. The properties of these "complex" cells were proposed to reflect synaptic interactions among several "simple" cells, where the receptive fields of the afferent cells were assumed to have identical axis orientation but different retinal positions. Apart from "simple" and "complex" cells, Hubel and Weisel (1968) found lower and higher order "hypercomplex" cells in the striate cortex of the monkey that were responsive to the length of the "slit of light" and would decrease their rate of firing whenever the stimulus was extended in length beyond a critical value. Some of the higher order "hypercomplex" cells were also sensitive to movement in two directions.

According to Thomas (1970), the feature detection model

holds that each detector system responds optimally when stimulated by a pattern fulfilling the appropriate parameters (i.e., orientation, position, width, etc.). Given that the output of a particular detector is determined by the sum of light falling within its receptive field, the selectivity of the detector is determined by the characteristics of its receptive field (i.e., size, linear versus non-linear spatial integrating properties, etc.). Hubel and Weisel (1968) suggested that the prime functions of the striate cortex are the elaboration of "simple" cortical fields from geniculate cells, "complex" from "simple" and "hypercomplex" from "complex" cells and in this way outlined their model of the hierarchical organization of feature detectors in the visual system.

Two aspects of Hubel and Weisel's hierarchical model have recently received a lot of attention and as a result the feature detection model has been somewhat undermined (De Valois & De Valois, 1980). One issue addresses the question of whether there is any physiological evidence to substantiate an hierarchical organization, with sequential processing of increasingly complex stimuli by increasingly more complex cells. Findings such as those reported by Stone (1972), of shorter response latencies in complex cells and evidence suggesting parallel processing rather than sequential ordering of cells are incompatible with the notion of simpler cells mapping onto more complex cells.

The second issue that needs to be dealt with in order

to substantiate the feature detection model is whether cells in the visual system actually behave as feature detectors. The spatial frequency filter model, proposed by Campbell and Robson (1968) is an alternative model of the visual system which holds that spatial frequencies, rather than features, become the critical stimuli to be detected. It is based on the mathematical theorem of Fourier analysis which proves that any periodic waveform of f frequency can be represented by the sum of a series of sine-waves including the fundamental f frequency and its harmonics (integer multiples of the fundamental frequency). Accordingly, the square-wave illustrated at the bottom of Figure 1 can be approximated by summing a finite number of the sinusoidal harmonic components. This model, according to Georgeson (1979), assumes that any image focussed on the retina can be thought of as a complex pattern of light and dark regions. The resulting waveform of a cross-sectional plot of the distribution of luminance over space would, according to the spatial frequency filter model, be Fourier analyzed. Each of the resulting components could be described by a sinusoidal luminance distribution of a particular spatial frequency. Spatial frequency in this context is typically expressed as the number of cycles (i.e., peak plus trough) per degree (c/d) of visual angle. Based on the system's sensitivity to individual spatial frequencies it would differentially transmit a wide range of spatial frequencies. A unique set, determined by different phase

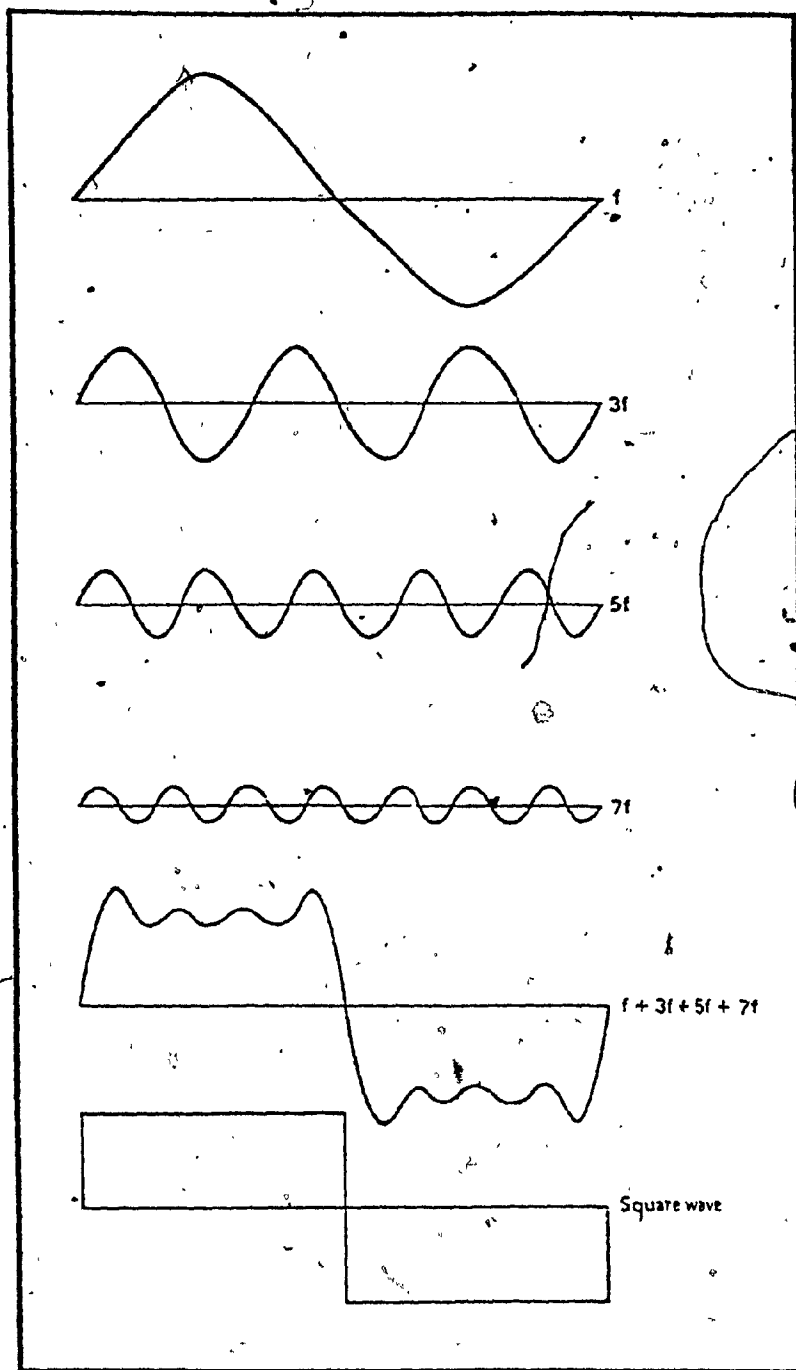


Fig.1 Approximation of a square-wave grating by summing a finite number of sinusoidal components. (after Kaufman, 1974).

relations, would be associated with unique retinal images.

Understanding the concept of differential transmission of particular spatial frequencies presume familiarity with the term gain. According to Georgeson (1979), gain is the ratio of output intensity to input intensity. When it is greater than one, it represents amplification and similarly, when it is less than one, it represents attenuation. The relative gain at different spatial frequencies, measured by the transfer function, describes the differential transmission of the visual system. Using different sinusoidal test gratings, each with a sinusoidal luminance distribution of a particular spatial frequency, the transfer function of the eye can be defined. Contrast sensitivity over a range of spatial frequencies is used as a measure of the relative gain of the visual system. According to Campbell and Robson (1968), the variation in sensitivity over a range of spatial frequencies is reflected in the contrast sensitivity function (CSF) with the reciprocal of the threshold contrast necessary for detection of the grating serving as the measure of sensitivity. Although according to Braddick, Campbell, and Atkinson (1978), the idea of using grating stimuli of varying spatial frequency dates back to Ernst Mach in 1866, Schade (1956) was the first to measure the CSF in the human visual system.

Regarding the issue of whether or not cells in the visual system behave as feature detectors, rather than responding to spatial frequencies, the selective sensitivity

of cells for bars versus spatial frequency gratings best assesses this question (Tyler, 1978). As Albrecht, De Valois & Thorell (1980) explained however, there is physiological evidence that cortical cells can be driven either by bars or sinusoidal gratings and these findings lend support to both the feature detection model and the spatial frequency filter model. Therefore they tried to determine which model would best describe the cells' activity. Looking at the response of single cells in the striate cortex of the monkey and the cat to bars and gratings that had been equated in terms of width and contrast, Albrecht et al (1980) found that both "simple" and "complex" cells responded more vigorously to spatial frequency. There was also evidence of finer tuning for spatial frequency. Whereas these cells responded almost uniformly across bar width they were selectively sensitive to particular spatial frequencies.

Apart from the above-mentioned neurophysiological evidence of the visual system's sensitivity to spatial frequency, support for the spatial frequency filter model of visual processing is also evident in human psychophysical research. As already mentioned, according to Fourier theory any waveform can be thought of as the sum of a number of sine-wave components. Campbell and Robson (1968) found that the contrast threshold for detecting a middle to high spatial frequency square-wave grating could be predicted based upon knowledge of its Fourier components and the CSF of the visual system. Seeing as there is an attenuation in

contrast sensitivity for spatial frequencies above 3 c/deg., Campbell and Robson (1968) predicted and found that detection of a square-wave grating could be determined primarily by the system's sensitivity to its fundamental component. This prediction was based on the higher amplitude of the fundamental frequency compared to that of the harmonic components. A multiple-channel model of the visual system might be useful for interpreting this finding. Detection of a square-wave grating occurred when one of its harmonic components was at, or above, its threshold contrast. Given the higher amplitude of the fundamental frequency, it is most likely that it will be the first to reach its threshold contrast. Another factor that predisposes the fundamental frequency of a middle to high spatial frequency square-wave grating to be critical for detection is its lower spatial frequency. Given that the band-pass characteristic (greater sensitivity to middle frequencies) of the CSF shows a rapid attenuation in contrast sensitivity to high spatial frequencies, it is once again more likely that the lower spatial frequency fundamental component will be the first to reach its threshold contrast. The multiple-channel model is useful in explaining some of Campbell and Robson's (1968) additional findings as well. For example, they found that a low contrast square-wave grating was indistinguishable from a sine-wave grating until the contrast of the grating was increased to the point that the third harmonic component of

the square-wave grating was at its own threshold. According to Campbell and Robson, a multiple-channel model of the visual system provides a better explanation of this finding. The multiple-channel model assumes a Fourier-like analysis of the input stimulus into sinusoidal components but contends that individual channels are responsive to the various components. Given that the mechanism which is detecting the fundamental component is less sensitive to the higher harmonic frequencies, it seems that the square-wave quality of the grating becomes apparent only when another mechanism "tuned" to the harmonic component has reached its threshold. Accordingly they suggested that the CSF reflects the envelope of sensitivities of a number of separate spatial frequency channels as opposed to describing a single spatial frequency filter.

The concept of multiple channels in the human visual system is supported by the early electrophysiological evidence presented by Enroth-Cugell and Robson (1966) which suggests that individual ganglion cells in the cat's retina have CSF with varying band-pass characteristics. The selective spatial frequency sensitivity of the individual cells was attributed by these authors to be due to the different size diameters of their receptive fields. More recently, single cells higher in the mammalian visual pathway have also been demonstrated to be selectively sensitive to spatial frequency (e.g., Maffei & Fiorentini, 1973; Schiller, Finlay & Volman, 1976; Glezer, Kostelyanets

& Copperman, 1977; Maffei, 1978; De Valois, Albrecht & Thorell, 1978; Andrews & Pollen, 1979; Albrecht, De Valois & Thorell, 1980,)

There also exists psychophysical evidence of multiple spatial frequency channels in the human visual system. Three common psychophysical techniques used in the study of spatial frequency channels are the adaptation, subthreshold summation and masking paradigms. Selective adaptation, the reduction in sensitivity to one stimulus resulting from prolonged exposure to another, is the paradigm that was used by Blakemore and Campbell (1969). These authors found that instead of an overall attenuation in contrast sensitivity, the contrast thresholds for a limited spectrum of spatial frequencies (with a bandwidth of one octave at half amplitude centered on the adapting frequency) were elevated after adaptation to a particular spatial frequency grating. From this they concluded that the adapting grating primarily depressed the sensitivity of some channel that could be described by a limited spatial frequency range. The bandpass characteristic of the tuning function of the channel responsive to the adapting frequency revealed the sensitivity of that channel to neighbouring frequencies. Blakemore and Campbell suggested as well, that the channels sensitive to spatial frequency might reflect the properties of spatially sensitive neurons in the human visual system similar to those demonstrated by Enroth-Cugell and Robson (1966) to exist in the cat.

The way in which superimposed, subthreshold stimuli summate is a technique that was first employed by Sachs, Nachmias, and Robson (1971) to help define the characteristics of spatial frequency channels. These authors presented complex gratings (formed from two different, simultaneously presented spatial frequency gratings) at different contrast levels. When the simple grating components were close in spatial frequency, they could be presented and detected as a complex grating at contrast levels lower than the individual thresholds. The principle underlying this paradigm is that if two stimuli are processed by the same channel then the combined input might exceed the detection threshold of the responsive channel. If the stimuli are processed by different channels then there would be no signal summation and subsequently the stimuli would not be easier to detect.

Stromeyer and Julesz (1972) studied spatial frequency selectivity by measuring the detection threshold of a target grating when presented alone or when masked by a noise band of varying width and spatial frequency. When a number of one-octave-wide bands of noise were used to mask different spatial frequency targets, spaced at 0.5 octave intervals, they found that the magnitude of masking decreased as the target frequency became more remote from the noise band cutoffs. In addition, when comparing masking functions for gratings with noise bands varying from +0.5 to +2.0 octaves centered on the grating, maximum masking was found generally

to occur when the noise band was ± 1.0 octave of the grating. Unfortunately, as De Valois and De Valois (1980) point out, the bandwidth characteristics of the channels determined in these different studies vary as a function of the method used in measurement. They strongly recommend that physiological estimates of channel bandwidth in the cat and the monkey, based on recordings from single cells in area 17 be taken into account.

Thus far it seems that there is substantial support for a multiple-channel model of spatial frequency analysis. Another issue that has consequently been raised is whether or not the analysis is global. This question of global analysis is concerned with whether spatial activity in cells in the retina is transmitted in a way that enables the brain to perform a Fourier synthesis, producing what Thomas (1975) refers to as a neural image. Maffei and Fiorientini (1972) found that dichoptic presentation of the fundamental and third harmonic components of a square-wave grating appeared the same as a square-wave grating when viewed under normal monocular conditions. Consequently they suggested that the brain was able to both Fourier analyze and synthesize. However, according to Graham (1979) there is no evidence of neurons in the brain that are capable of performing a strict Fourier analysis and synthesis. The evidence presented earlier of spatial frequency sensitive cells in the visual pathway does however, support the view of a localized Fourier analysis. According to Braddick (1980), it would be

pointless for the visual system to analyze the visual field as a whole when generally we are trying to recognize particular objects within a visual array.

It is known that our ability to perceive the details of objects, as well as other aspects of spatial vision, depends upon our contrast sensitivity at different spatial frequencies (Campbell & Maffei, 1974). It is also known that the state of light adaptation influences overall contrast sensitivity. It has been well established (i.e., Patel, 1966; Van Ness & Bouman, 1967; Campbell & Robson, 1968) that at low luminance levels the sensitivity of the human visual system to both sine and square-wave gratings is attenuated. An additional finding is that the peak sensitivity, measured with the CSF, shifts toward the lower spatial frequencies. Assuming, as suggested by Campbell and Robson (1968) that the CSF measures the envelope of sensitivities of multiple channels that are selectively sensitive to specific spatial frequencies, one way of conceptualizing the effects of lowered luminance is to view it as the differential attenuation of the sensitivities of given channels to the frequency to which they are most sensitive.

A question that remains unanswered has to do with the changes in sensitivity that occur within a channel, as a result of dark adaptation, to spatial frequencies other than the optimal stimulus. In other words, what effect does the level of light adaptation have on the tuning functions of

individual channels? Although there could be many possible outcomes, one will be elaborated upon here for the purpose of illustration. Perhaps in the dark adapted eye, the sensitivity of the channel to all of the spatial frequencies to which it normally responds is attenuated by a constant proportion. In other words as shown in Figure 2, if the sensitivity of a channel was reduced by a factor of two, original sensitivity to the optimal frequency and all other frequencies would be reduced by a factor of two. This reduction is shown in Figure 2 where channel sensitivity is represented on a logarithmic scale. In such a case the shape of the tuning function of the channel which describes the channel's sensitivity to a range of spatial frequencies, would remain the same. The bandwidth of the tuning function would be reduced, however, due to a reduction in sensitivity that would eliminate any responsiveness to frequencies at the extreme of the channel. This effect is illustrated by the function in Figure 2 drawn with a dashed line. One consequence of attenuating sensitivity by a constant proportion, as hypothesized, is that one should be able to compensate for this loss in sensitivity by increasing the contrast of all of the gratings presented in the dark that they appear to be of the same contrast as those seen in the light. As a result of such a manipulation, the responsiveness of the channel should be identical in both the light and dark adapted conditions, producing tuning functions with similar bandwidths. The dotted line in

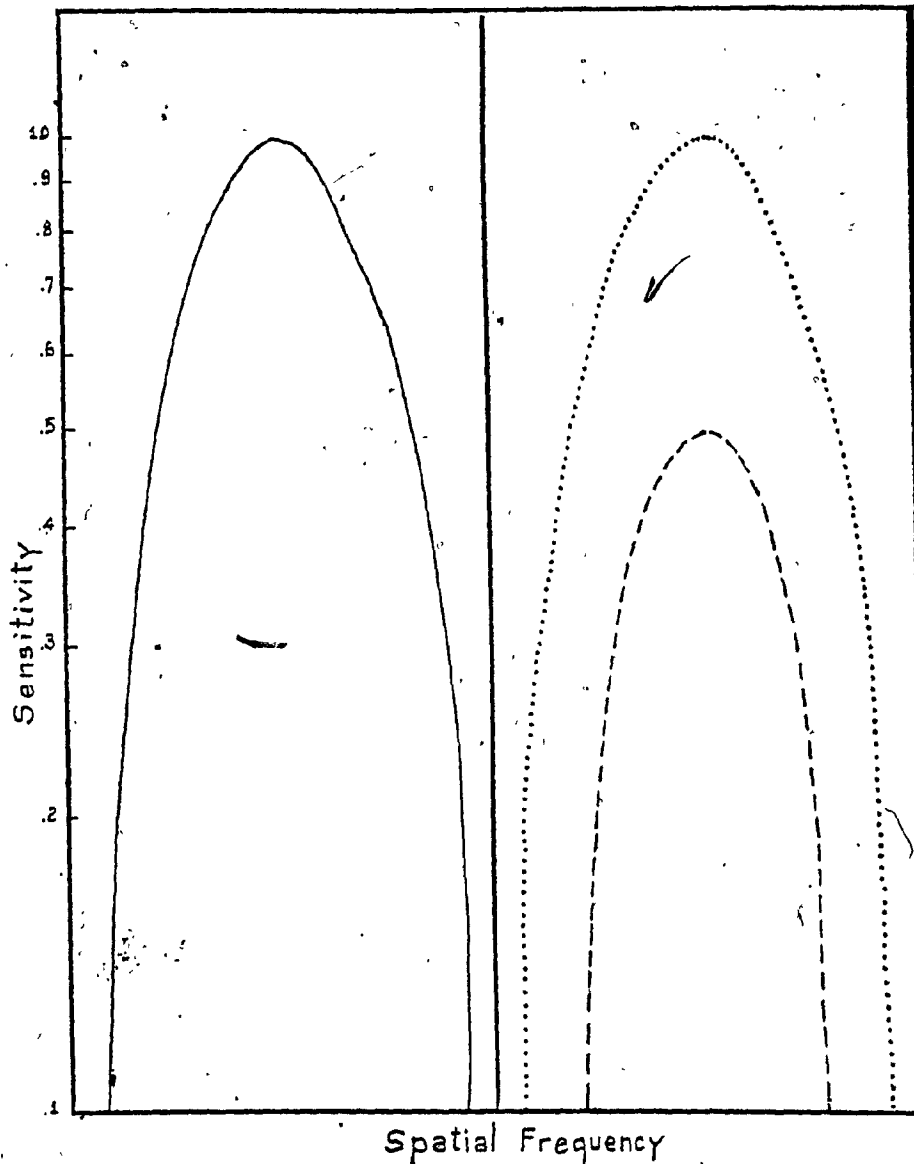


Fig.2 The hypothesized effect of manipulating the level of light adaptation on the tuning function of a spatial frequency channel (solid line is sensitivity in the light, dashed line is in the dark and dotted line, in the dark after a contrast adjustment).

Figure 2 represents the hypothesized effects on a channel's sensitivity after such a contrast adjustment.

Using a variation of Blakemore and Campbell's (1969) adaptation paradigm, the question of possible changes in the shape of the tuning functions was explored. Instead of having observers adapt for an extended period of time to one spatial frequency and then measuring the subsequent effect of adaptation on a range of spatial frequencies in light and dark adapted conditions, a forward masking paradigm was employed. As Legge and Foley (1980) explained, the functions describing threshold elevation as a result of exposure to a masking grating are generally referred to as tuning functions. Braddick et al. (1978) contend that the masking paradigm is thought to reveal individual channels because when there is an interaction between the mask and the target some common mechanism is hypothesized to be processing both stimuli. The differential magnitude of masking produced by a range of masks reflects the sensitivity of the channel detecting the target to the masking frequencies. Use of a masking paradigm over an adaptation paradigm has an advantage in terms of the brief exposure durations typically used. This allows for a much quicker determination of the impact of a range of spatial frequencies on detection of a target grating. In order to evaluate the effect of manipulating the level of light adaptation on the shape of the tuning functions of the spatial frequency channels maximally sensitive to the target

frequencies, two luminance levels were employed.

Two experiments were designed for the present study in order to investigate whether, as suggested, the effect of dark adaptation is to attenuate the sensitivity of a channel to a range of spatial frequencies, by a constant proportion. In the first experiment the masking gratings were contrast matched under the highest luminance condition, across spatial frequency so as to ensure equivalent impact on a light adapted system. In this way the differential magnitude of masking across spatial frequency could be attributed to the differential sensitivity of a channel to the spatial frequency masks. Any observed differences in the sensitivity of a channel to particular spatial frequencies across levels of dark adaptation could also be demonstrated by comparing the shapes of the resultant masking functions.

In the second experiment all the masks, across luminance levels, were contrast matched such that they were of equivalent impact regardless of spatial frequency or luminance condition. Given the possibility suggested earlier that the sensitivity of a channel to all spatial frequencies is attenuated by a constant proportion as a result of dark adaptation, this contrast manipulation might be expected to result in identical tuning functions regardless of luminance condition. In other words, the reduction in channel sensitivity would be compensated for by increasing the contrast of the masking gratings such that

the magnitude of a channel's response became identical in the light and dark. If there were any changes in the shape of the masking functions across the luminance conditions, despite the contrast manipulation, differential changes in sensitivity to all the spatial frequency gratings, as a result of a dark adaptation manipulation, could be inferred.

Method

Observers

The author and a male undergraduate student at Concordia University participated in this study. Both had normal, uncorrected visual acuity as measured with the Keystone Stereopsis and Visual Acuity Test.

Apparatus

Following the method of Campbell and Green (1965), vertical sine-wave gratings were generated onto the face of a single beam oscilloscope screen (Tektronix, Model 5403). The display field, 11.5 cm by 14.5 cm, subtended approximately 6.6° by 8.3° of visual angle at a viewing distance of one meter.

A raster was derived from a 1KHz horizontal sweep and a 1MHz vertical saw tooth-wave that was provided by a Tektronix function generator (Model FG 501). The time base of the oscilloscope was synchronized such that the beginning of each horizontal sweep coincided with the same point of the sine wave grating. This was to ensure that the image that was painted onto the screen was identical on each sweep and resulted in a stationary grating. The synchronization was accomplished with the use of an AND gate which was looking for a signal from the time base of the oscilloscope plus a TTL pulse from the function generator producing the sine-wave.

Signals corresponding to the mask and target gratings were provided by two additional Tektronix function

generators (Model FG 501). The output frequency of each function generator was calibrated with a digital volt meter. The contrast of the displayed gratings was calculated from the ratio of maximum luminance minus minimum luminance to maximum luminance plus minimum luminance $\{L(\max) - L(\min)\} / \{L(\max) + L(\min)\}$. The contrast was varied around a mean luminance level. Whenever a grating was not being presented (i.e., between trials), a uniformly lit field was shown on the oscilloscope screen. The mean screen luminance of 10 candelas per square meter (cd/m^2) was established before each testing session with a Spectra spot photometer and was equal to the space-average luminance of any display containing a grating.

A Coulbourn Instruments logic system controlled stimulus duration, intertrial interval (ITI), interstimulus interval (ISI) as well as the presentation of warning tones to signal the onset and offset of the test interval.

An ISI was considered necessary in order to avoid criterion shifts when the target and masking gratings were similar versus different in spatial frequency. As a result, there was extensive pilot work to find a mask contrast and ISI combination that would meet the following criteria: the mask contrast would be high enough to produce maximum masking in the light adapted condition without a) entering the non-linear range of the oscilloscope screen; b) producing an infinite amount of masking at the lower luminance level such that it would be impossible to reach

target threshold.

Taking into account pupillary contraction and dilation in response to changes in field luminance as outlined by Wyszecki and Stiles (1967), neutral density filters of 1.2 and 2.3 log units were employed so that the original 2.1 log troland display could be reduced to 1.1 and 0.1 log trolands, respectively. According to Boynton (1966), this allows for sampling of responses in the photopic, mesopic and scotopic ranges.

Stimuli

The 18 sine-wave masking gratings ranged in spatial frequency, by quarter octave steps, from 0.5 to 11.31 cycles per degree (c/d) of visual angle. The highest spatial frequency used for a given observer was chosen to be the one that could be contrast matched to a standard grating set at a contrast ratio of 0.4. The lower spatial frequency limit was established taking into account the controversy of how many bars are necessary for a stimulus to be considered a grating (i.e., Kelly, 1975; Savoy & McCann, 1975; Van Den Brink & Bilsen, 1975; Estevez & Cavonius, 1976; McCann, Savoy, & Hall, 1978).

The spatial frequencies of the target gratings were 1.41, 4.0, and 8.0 c/d. These target frequencies were chosen so that the masking effect of a range of both higher and lower spatial frequencies could be evaluated. The lowest spatial frequency target was preceded, during an interval containing a mask, by gratings ranging from 0.5 to

3.36 c/d. The 4.0 c/d target was preceded by masking gratings that ranged from 1.19 to 8.0 c/d, and the highest spatial frequency target was preceded by masks that ranged from 2.38 to 11.31 c/d. The target and masking gratings were adjusted so that they would be presented in phase whenever they were identical in spatial frequency. Due to the synchronization procedure mentioned earlier, a common phase relationship was maintained for each combination of the mask and target when they differed in spatial frequency.

Procedure

During pilot work, in order to obtain the correct contrast levels for the masks used in the second experiment, each observer contrast matched all the masks across the three luminance levels. This was accomplished by first matching the 4.0 c/d mask, in each luminance condition with a standard grating of identical spatial frequency whose known physical contrast was 0.4. All 18 masking gratings were then perceptually matched with their appropriate standard in each luminance condition. As previously mentioned, the contrast of the masks as well as the stimulus parameters such as individual ISIs and target and mask durations were determined by the maximum amount of masking that could be thus produced without artifactually increasing the mean screen luminance. It was found during the course of piloting, that given the reduced sensitivity of the visual system to high spatial frequencies, the contrast of

the mask and the target, had to be very high in order to reach or exceed threshold. The contrast of the masks was however chosen so as to not have to enter the non-linear range of the oscilloscope where increases in the contrast of either grating artifactually changed the mean luminance of the screen. Otherwise the observers may have been able to detect the presence of the target during an interval containing a mask by detecting a change in the mean screen brightness. In addition, the luminance profile of the grating could no longer have been accurately described as being sinusoidal.

Based on the above criteria, observer DC showed maximum masking when the targets and masks were 29 msec in duration and the ISI was 70 msec. Similarly, observer MB showed maximum masking with an ISI of 75 msec given 49 msec targets and masks.

During both studies the observers sat in a dark room for approximately five minutes and monocularly adapted to the luminance of a uniformly illuminated screen. Using a forward masking paradigm, the observers were presented with one of the targets either alone or preceded by a masking grating. During an interval containing a mask, the target was preceded by the mask and an ISI that consisted of the presentation of a homogeneously lit field. During an interval that did not contain a mask, the target followed the presentation of a uniformly lit screen whose exposure duration was equal to the time interval of a mask plus the

ISI. Four replications of each possible mask and target combination were obtained for each observer under two luminance conditions. This included four replications where the target was not preceded by a mask.

While all three targets were presented in the highest luminance condition, at the lowest luminance level it was possible only to present the lower spatial frequency targets (1.41 & 4.0 c/d). The 8.0 c/d target was barely detected at the lowest luminance and therefore was presented at an intermediary level (1.1 log trolands).

In order to maintain a constant level of light adaptation during a testing session the luminance levels were blocked. The order of the luminance levels was counterbalanced for the two observers. Practice effects were minimized by blocking the replications within a luminance condition such that all the possible stimulus combinations were exhausted before proceeding to the next replication. The presentation of the mask and target combinations was randomized within a block for each observer.

In the first study the mask contrasts utilized were those established during perceptual matching at the highest luminance level only. In other words, in this study there was no compensation at the lower luminance levels for decreases in sensitivity and the perceptual contrasts of the masks were allowed to float. In the second study the contrasts of the masks were those established during the

perceptual matching across spatial frequency and luminance.

During a trial, target thresholds in the presence or absence of a mask were first crudely estimated by having the experimenter increase the contrast of the target in steps of approximately 0.05 units until the observer indicated that the target was just perceived. After this gross estimation, the thresholds were determined with .005 contrast steps using a modified ascending method of limits. Approximately four catch trials were included during a threshold trial, but not until the observer had indicated that the target had been seen. The reason for this departure from convention was that in the lowest luminance condition, when the target and mask were similar in spatial frequency, it was discovered that insertion of a catch trial prior to threshold would cue the observers that they were approaching their estimated threshold. For this reason and in order to maintain consistency across the luminance manipulations, catch trials were always inserted after an indication on the part of the observer that the target had been perceived.

A typical testing session contained approximately 68 trials so that at least two replications of each mask and target combination could be exhausted. During a trial four catch trials were inserted, where the target was not presented, so as to evaluate the observer's false alarm rate. After each trial the experimenter recorded, from the digital volt meter, a number that was correlated with contrast readings for each of the three target gratings.

Results

Evidence of decreased sensitivity, in the dark, to each of the target frequencies is shown in Tables 1 and 2. Detection thresholds for the target, when it was presented alone, increased as luminance was decreased. Comparing the two tables shows, as well, that detection thresholds for each target, within a given luminance condition and across both experiments, remained relatively stable for both of the observers. Given that the conditions for detecting a target when it was not preceded by a masking grating were identical in both experiments, this consistency in detection threshold suggests that the observer's detection criterion remained stable over time. Looking at tables 1 and 2, might suggest that sensitivity increased in the dark as the target frequency increased. However, it must be remembered that the lowest luminance condition for the 8.0 c/d target was 1.1 log trolands, whereas the lowest luminance level used for the two other targets was 0.1 log trolands. As a result, the thresholds for detecting the three targets in the dark cannot be compared. The observer's detection criterion was also evaluated across all stimulus combinations in terms of his or her false alarm rate. Given that four catch trials were inserted in each threshold estimate, regardless of stimulus combination (i.e., target alone or target with a mask), the false alarm rates for the 1.41 c/d and 4.0 c/d targets were each based on 192 catch trials. Similarly, the false alarm rate for the 8.0 c/d target was based on 160

Table 1

Contrast Thresholds for Each Target Presented Alone

Experiment I

1.41 c/d target

| | 2.1 log trolands | | 0.1 log trolands | |
|----|------------------|------|------------------|------|
| | \bar{X} | S | \bar{X} | S |
| DC | .027 | .006 | .164 | .034 |
| MB | .020 | .004 | .118 | .060 |

4.0 c/d target

| | 2.1 log trolands | | 0.1 log trolands | |
|----|------------------|------|------------------|------|
| | \bar{X} | S | \bar{X} | S |
| DC | .031 | .004 | .346 | .061 |
| MB | .026 | .005 | .193 | .043 |

8.0 c/d target

| | 2.1 log trolands | | 1.1 log trolands | |
|----|------------------|------|------------------|------|
| | \bar{X} | S | \bar{X} | S |
| DC | .025 | .002 | .051 | .005 |
| MB | .015 | .001 | .026 | .003 |

Table 2

Contrast Thresholds for Each Target Presented Alone

Experiment II

1.41 c/d target

| | 2.1 log trolands | | 0.1 log trolands | |
|----|------------------|------|------------------|------|
| | \bar{X} | S | \bar{X} | S |
| DC | .033 | .002 | .177 | .015 |
| MB | .023 | .003 | .148 | .013 |

4.0 c/d target

| | 2.1 log trolands | | 0.1 log trolands | |
|----|------------------|------|------------------|------|
| DC | .041 | .015 | .469 | .011 |
| MB | .029 | .003 | .259 | .035 |

8.0 c/d target

| | 2.1 log trolands | | 1.1 log trolands | |
|----|------------------|------|------------------|------|
| DC | .026 | .001 | .062 | .012 |
| MB | .023 | .006 | .041 | .008 |

catch trials. As seen in Table 3, observer DC hardly ever indicated that the target was perceived when it was not being presented. This low false alarm rate was evident for all the target frequencies, in both luminance conditions and across the two experiments. Observer MB was a little less consistent in her false alarm rate but nonetheless, regardless of experiment, luminance level or target frequency her false alarm rate never exceeded 0.085.

The effect of the masks on the channel detecting the target was calculated in such a way as to discount the channel's sensitivity to the target itself. This was accomplished by calculating the difference between the log contrast threshold of the target in the presence of a mask and the log contrast threshold of the target when it was presented alone. In other words changes in the sensitivity to a target as a function of the state of light adaptation of the eye was removed from each measure of the channel's response to the mask.

Functions describing the magnitude of masking for each observer are plotted in Figures 3 through 8. The horizontal dotted line in each graph represents no masking and accompanying data points are ± 1 standard error bars.

Figures 3 through 5 were plotted from the data collected at each target frequency, during the first experiment, where an attempt had been made to achieve equivalence of perceptual impact across spatial frequency in the highest luminance condition only. Figures 6 through 8

Table 3
False Alarm Rates per Target Across Luminance

| | Experiment I | | Experiment II | |
|---------|---------------------|---------------------|---------------------|---------------------|
| | 1.41 c/d target | | | |
| | 2.1 log trolands | 0.1 log trolands | 2.1 log trolands | 0.1 log trolands |
| DC | 0 | .010 | 0 | 0 |
| MB | .005 | .083 | .010 | .031 |
| N = 192 | | | | |
| | 4.0 c/d target | | | |
| | 2.1 log trolands | 0.1 log trolands | 2.1 log trolands | 0.1 log trolands |
| DC | 0 | .016 | .005 | .005 |
| MB | .026 | .042 | .052 | .005 |
| N = 192 | | | | |
| | 8.0 c/d/ target | | | |
| | 2.1 log trolands | 1.1 log trolands | 2.1 log trolands | 1.1 log trolands |
| DC | 0 | .012 | .012 | 0 |
| MB | .038 | .063 | .056 | .047 |
| N = 160 | | | | |

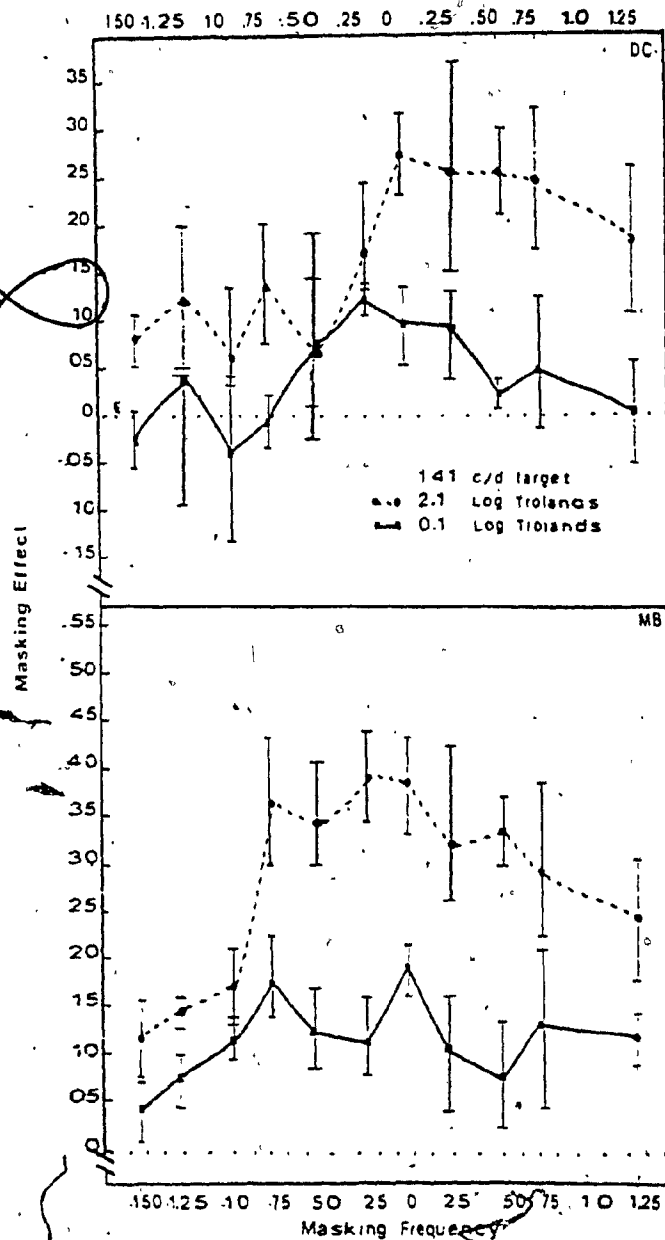


Fig.3 (Exp I) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold (target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

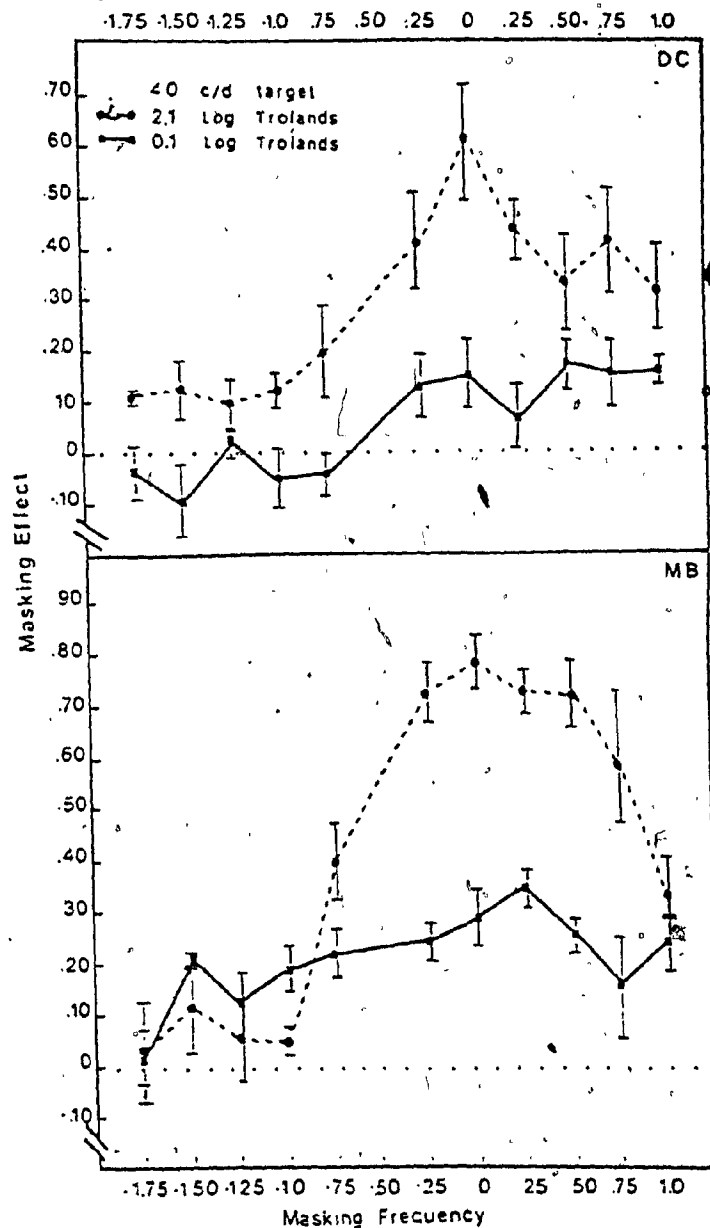


Fig.4 (Exp I) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold (target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

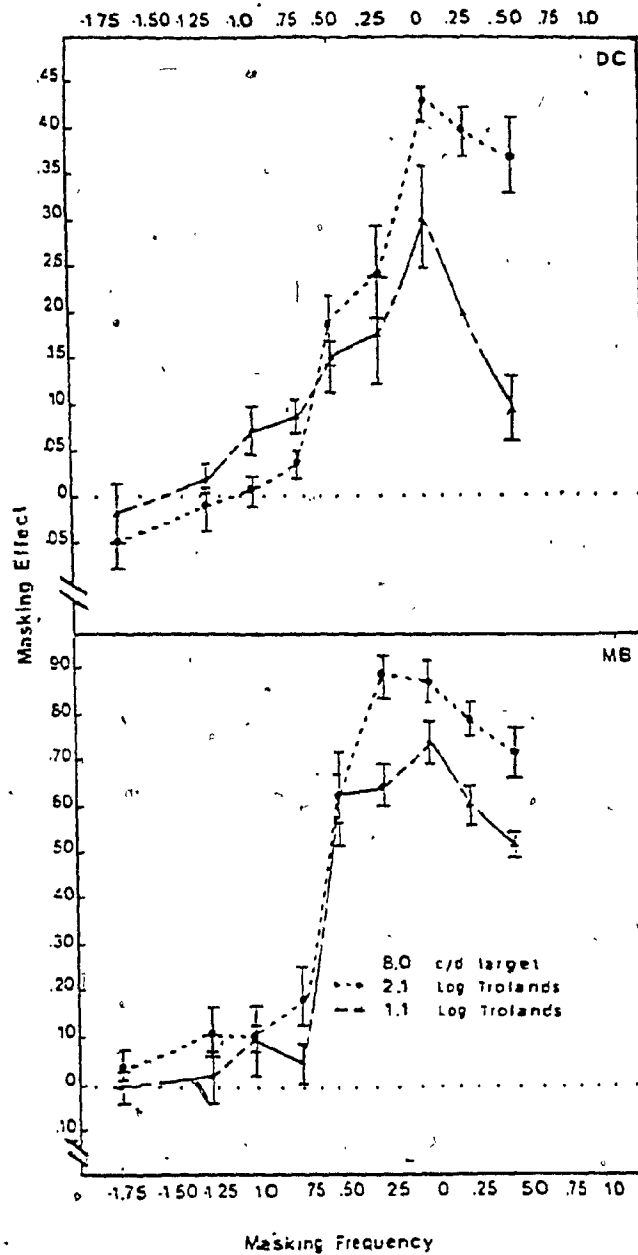


Fig.5 (Exp I) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold (target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

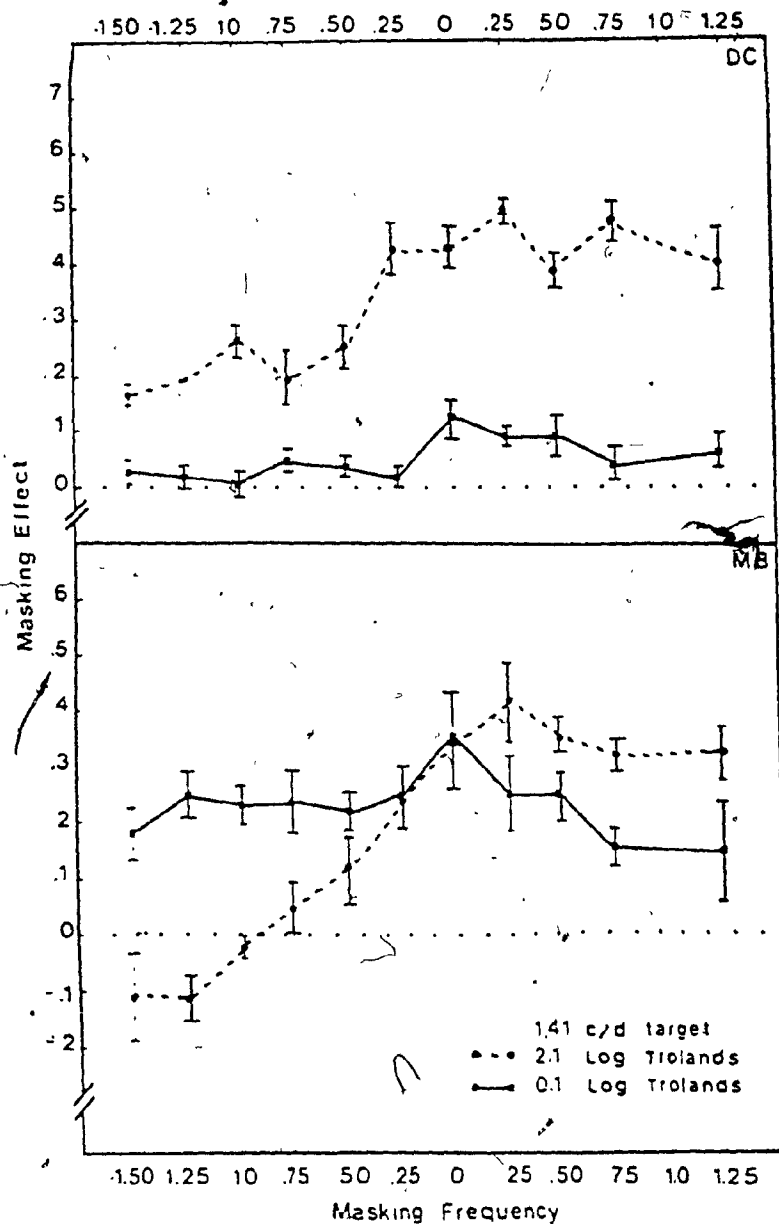


Fig.6 (Exp II) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold (target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

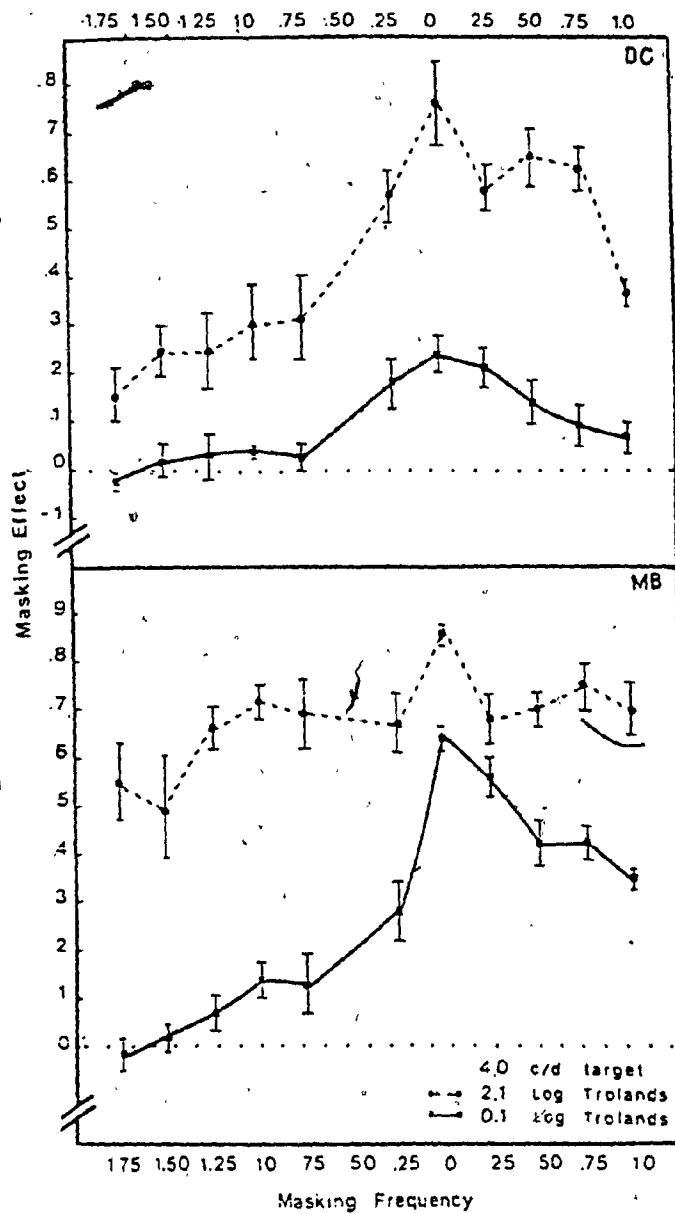


Fig.7 (Exp II) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold (target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

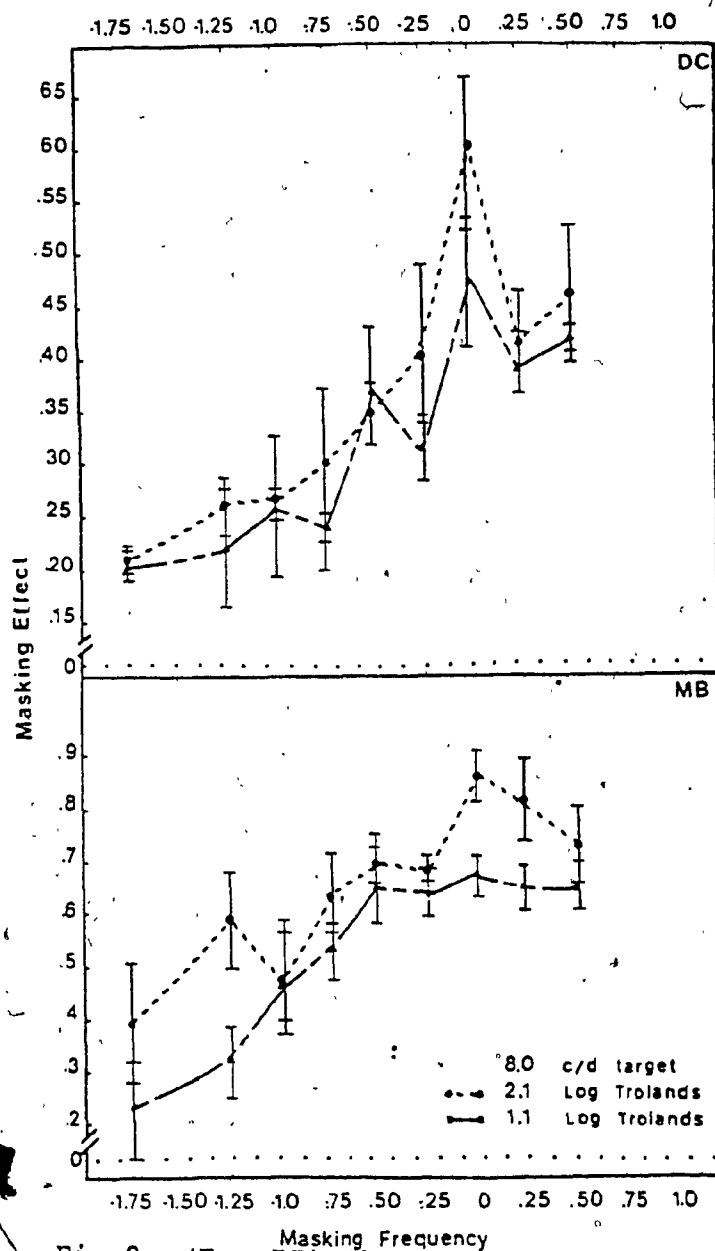


Fig.8 (Exp II) The magnitude of masking is expressed as log contrast threshold (target with mask) - log contrast threshold₀(target). Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

were plotted from the data collected during the second experiment where the masks were contrast matched across spatial frequency as well as luminance.

Highest Luminance Condition

Experiment 1.

Looking at the highest luminance condition (function represented by the solid circles) in Figure 3, observer DC showed maximum masking when both the target and mask were 1.41 c/d. Similarly observer MB showed maximum masking at a spatial frequency only .25 octaves lower than the target frequency. The masking functions, for the lowest spatial frequency target, for both observers, were somewhat asymmetrical, showing more of a masking effect at the remote frequencies higher, compared to those lower, than the target. In addition to the asymmetry, the amount of masking did not reach zero at either extremes of the function for both observers.

In Figure 4 the band-pass characteristics of the masking functions are a little more obvious, particularly for observer MB. Both observers showed maximum masking when the target and mask were both 4.0 c/d. Once again the absence of a masking effect was not evident for observer DC. However, observer MB showed no masking at frequencies 1 octave below the target. Whereas observer DC showed the suggestion of a secondary peak in the masking function at a spatial frequency .75 octaves above the target frequency, observer MB continuously showed less masking as the

frequencies of the mask exceeded that of the target.

Unfortunately the masking effects for an 8 c/d target, shown in Figure 5, look a bit incomplete. Due to the difficulty in perceptually matching masking gratings higher than 11.31 c/d in spatial frequency to the 0.4 standard, the masking effect includes masking frequencies up to, only .50 octaves above the target frequency. Nonetheless, for both observers, maximum masking occurred when the target and mask were similar in spatial frequency. It was also possible to obtain a response that showed an absence of masking, for both observers, at frequencies approximately 1 octave lower than the target.

Experiment 2.

Figure 6 shows that maximum masking occurred for both observers when the mask was .25 octaves higher than the target frequency. However, this data point was not significantly different from the masking effect obtained at the target frequency for either observer. At both extremes of the masking function, for observer DC, there was still evidence of a masking effect. Observer MB showed no masking for frequencies approximately .75 octaves lower than the target frequency and in fact showed a facilitation effect at the two lowest spatial frequency masks. MB also continued to show a masking effect as high as 1.25 octaves above the target. In this experiment as well, there was a noticeable asymmetry in the function for the 1.41 c/d target of each observer, favoring masking at the higher spatial

frequencies.

In Figure 7 maximum masking was evident for both observers at 4.0 c/d, when the target and mask frequencies coincided. Masking effects also continued to be evident for each observer, at both extremes of the function. In fact the masking function for observer MB appeared almost flat. Once again Observer DC showed the suggestion of a secondary peak, this time when the masking frequency was .50 octaves higher than the target frequency.

Although the masking effect in Figure 8 appears incomplete for the 8.0 c/d target, maximum masking was evident at 8.0 c/d, where the target and mask frequencies were identical. The low spatial frequency masks continued to exert an effect even when they were as remote as 1.75 octaves lower than the target frequency.

Given that the mask contrasts used in the light adapted conditions were identical across the two experiments, a similarity in the functions would be expected. In both experiments there tended to be an asymmetry in the masking function of the 1.41 c/d target, favoring masking at the higher spatial frequencies. The observers showed maximum masking at the same points across the two experiments. Two findings that were not replicated across experiments, both showed up in observer MB. One was the facilitation effect observed during the second experiment at the low spatial frequencies when detecting the 1.41 c/d target in the high luminance condition. The other anomalous finding was the

flat appearance of the masking function of the 4.0 c/d target in the light adapted condition of the second experiment.

Lowest Luminance Condition

Experiment 1.

The functions described by the connected squares in Figures 3 to 5 represent the lowest luminance condition (0.1 log trolands). In the first experiment the contrast of the masking gratings had not been perceptually equated across luminance conditions. Figure 3 shows that maximum masking occurred at a frequency .25 octaves lower than the target for observer DC. However, this data point is not significantly different from the one observed at the target frequency. Maximum masking occurred at the target frequency (1.41 c/d) for the other observer. When comparing the two luminance conditions, the magnitude of peak masking was reduced at the lower luminance condition, for both observers.

Similarly, as seen in Figure 4, the magnitude of peak masking was reduced for both observers in the lower luminance condition. Observer DC showed maximum masking at the target frequency and at a frequency .50 octaves higher than the target. Observer MB showed the suggestion of maximum masking frequency (4.0 c/d). Absence of a masking effect was evident for both observers at the lower spatial frequencies. Observer DC showed no masking at frequencies lower than .75 octaves from the target, whereas no masking

was evident only at the lowest spatial frequency for observer MB. Both observers continued to show masking effects at a frequency 1.0 octave higher than the target.

Figure 5, showing incomplete masking functions for an 8.0 c/d target, reflects the reduction in peak masking when the display was 1.1 log trolands only in the data from observer MB. As shown, maximum masking occurred when the target and mask were similar in spatial frequency. Masking effects were absent for both observers at frequencies 1.25 octaves lower than the target.

The reduction in magnitude of masking is seen in the data of observer DC in Figure 6. Although both observers showed maximum masking at the target frequency (1.41 c/d), the masking functions for the .1 log troland display appear flat.

In Figure 7 there is clearly a marked reduction in the magnitude of masking for both observers in the dark adapted condition. Both observers continued to show maximum masking at the target frequency. Although both observers showed no masking at the lower spatial frequencies, there continued to be a masking effect at frequencies one octave above the target.

Figure 8, showing incomplete masking functions for an 8.0 c/d target, similarly reflects the reduction in peak masking when the display was 1.1 log trolands. Masking effects were still evident for both observers at frequencies 1.75 octaves lower than the target.

The main point to be noted about these data from both experiments is the tendency towards more masking in the highest luminance condition, with the possible exception of the highest spatial frequency target.

Normalized Data

The data have been replotted in Figures 9 through 14 in order to compare the shapes of the functions across the luminance conditions. Figures 9 through 11 represent data from the first experiment and Figures 12 through 14 represent the data from the second experiment. Each function, representing the range of masking effects within a luminance condition for a specific target, has been normalized to its point of maximum masking. This was accomplished by taking the antilog of the difference of the masking effect at any mask frequency and the masking effect at the point of maximum masking. The shapes of the curves remained the same after this manipulation but the functions were shifted along the Y-axis such that the point of maximum masking was at 1.0 for each function. Unconnected data points are those which showed no significant masking (refer back to Figures 1-6). The horizontal dotted line in each of these graphs represents the level of masking to which each point is being compared. Accompanying data points are ± 1 standard error bars.

Experiment 1.

In Figure 9 it is obvious, particularly for observer MB, that the masking functions for a 1.41 c/d target were

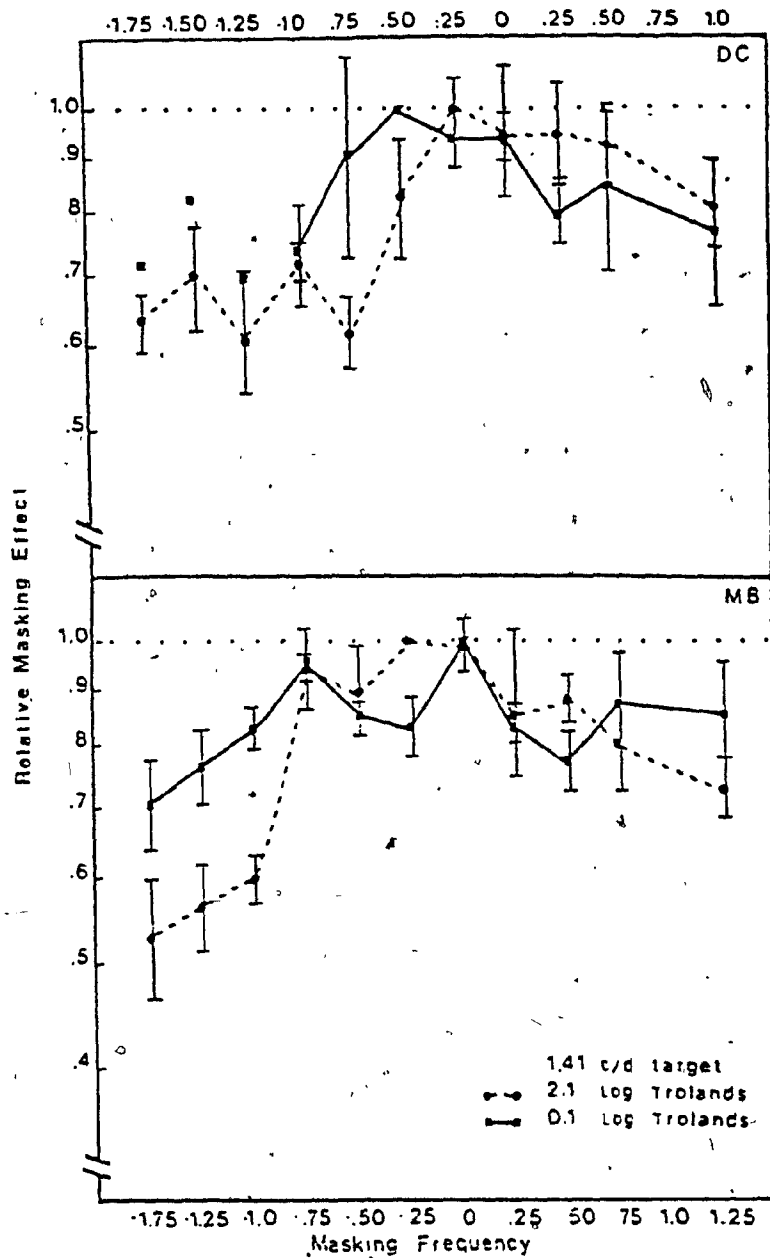


Fig.9 (Exp I) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

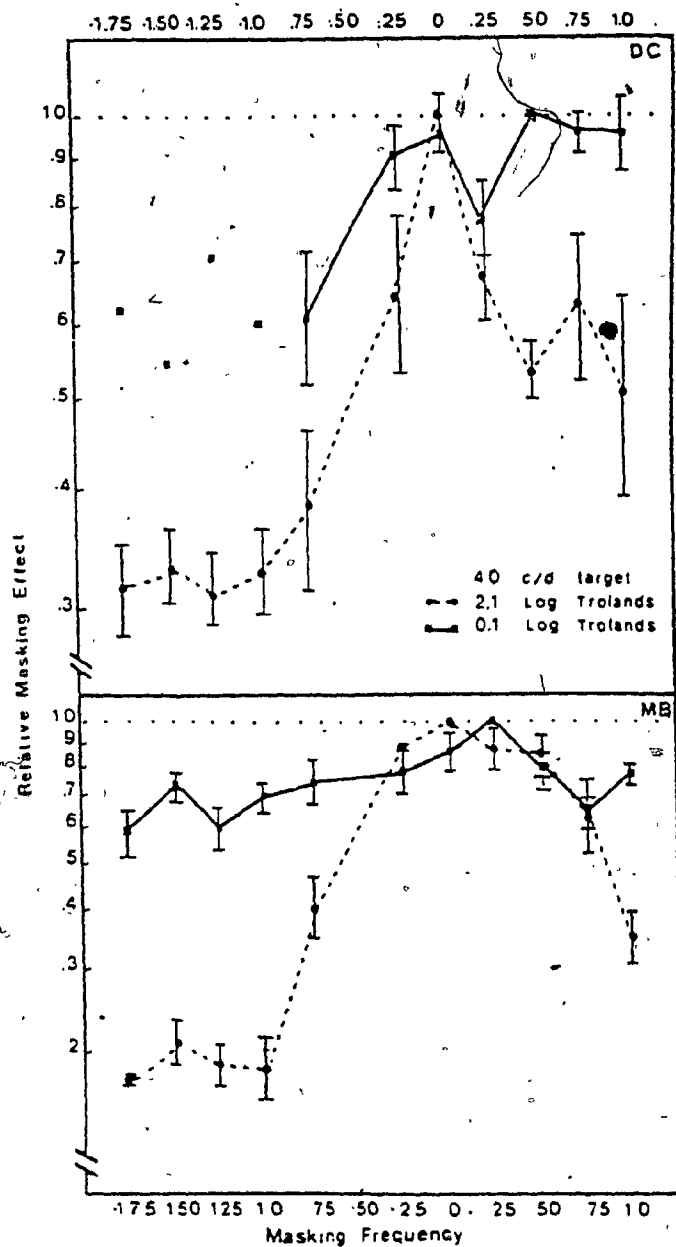


Fig.10 (Exp I) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

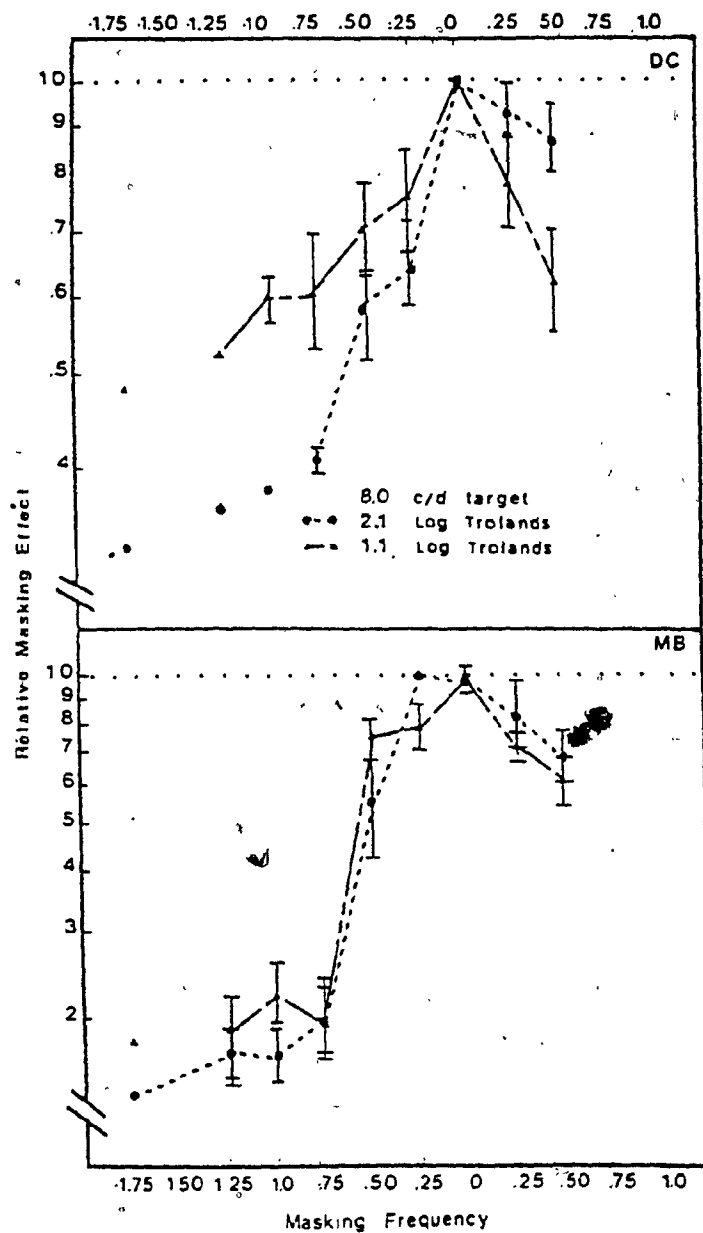


Fig.11 (Exp I) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

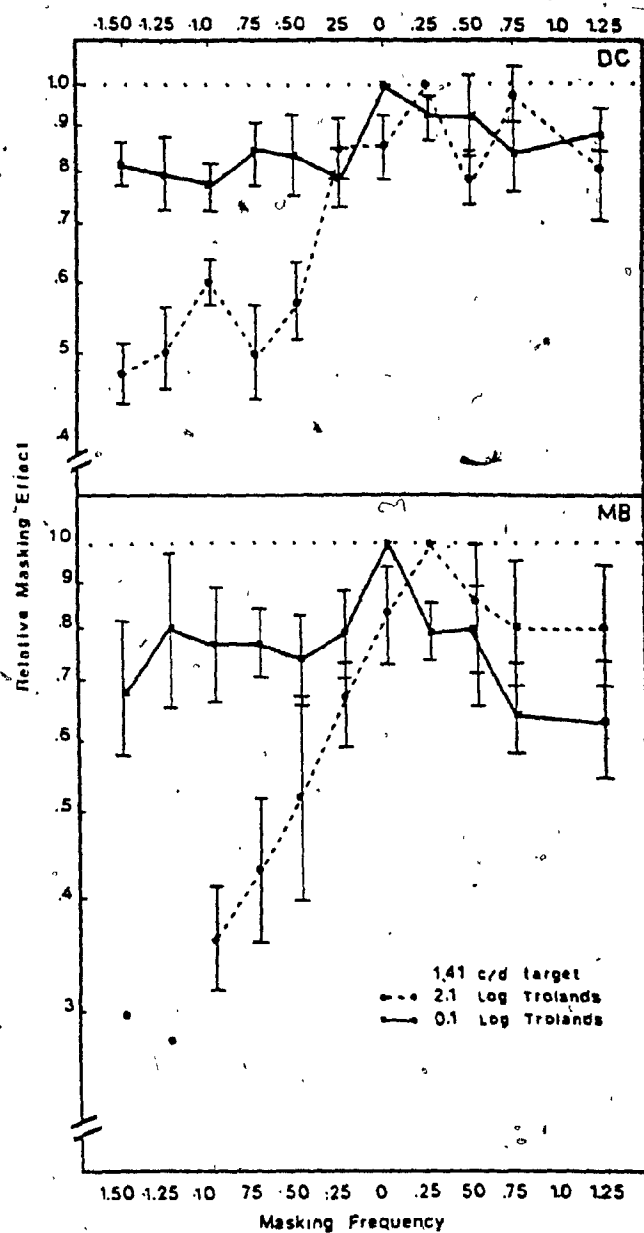


Fig.12 (Exp II) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

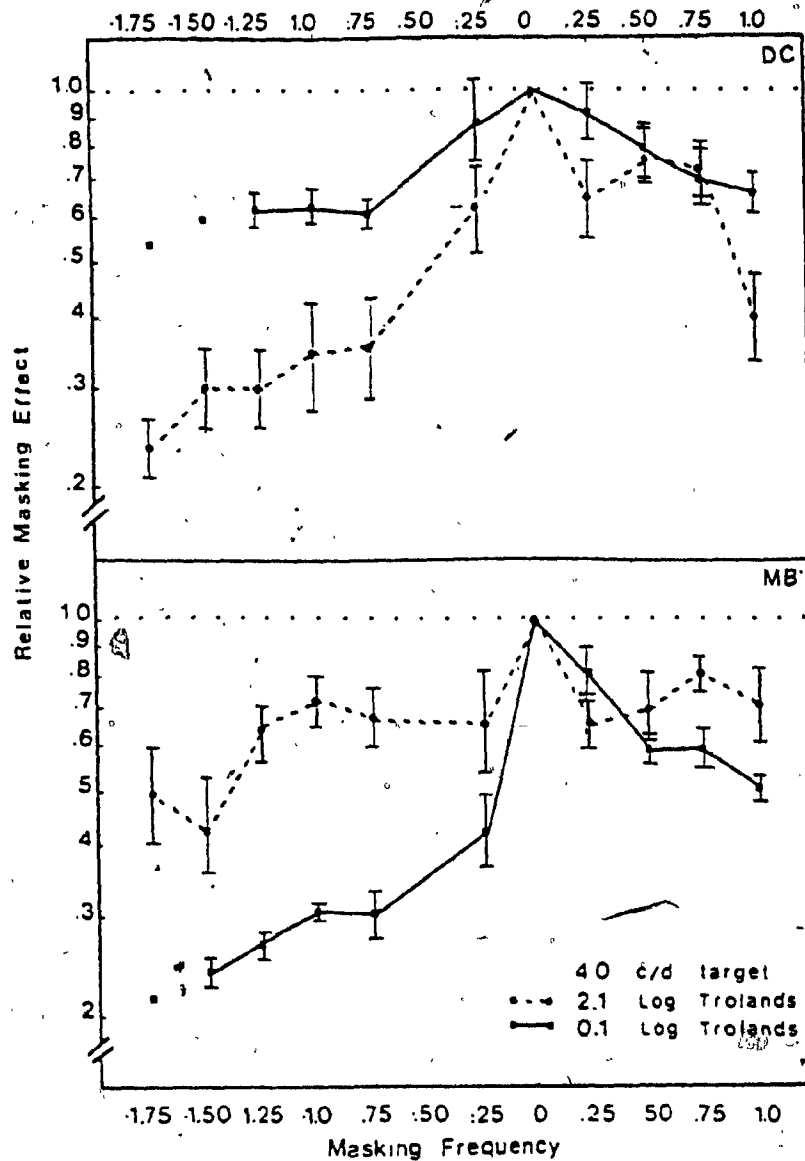


Fig.13 (Exp II) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

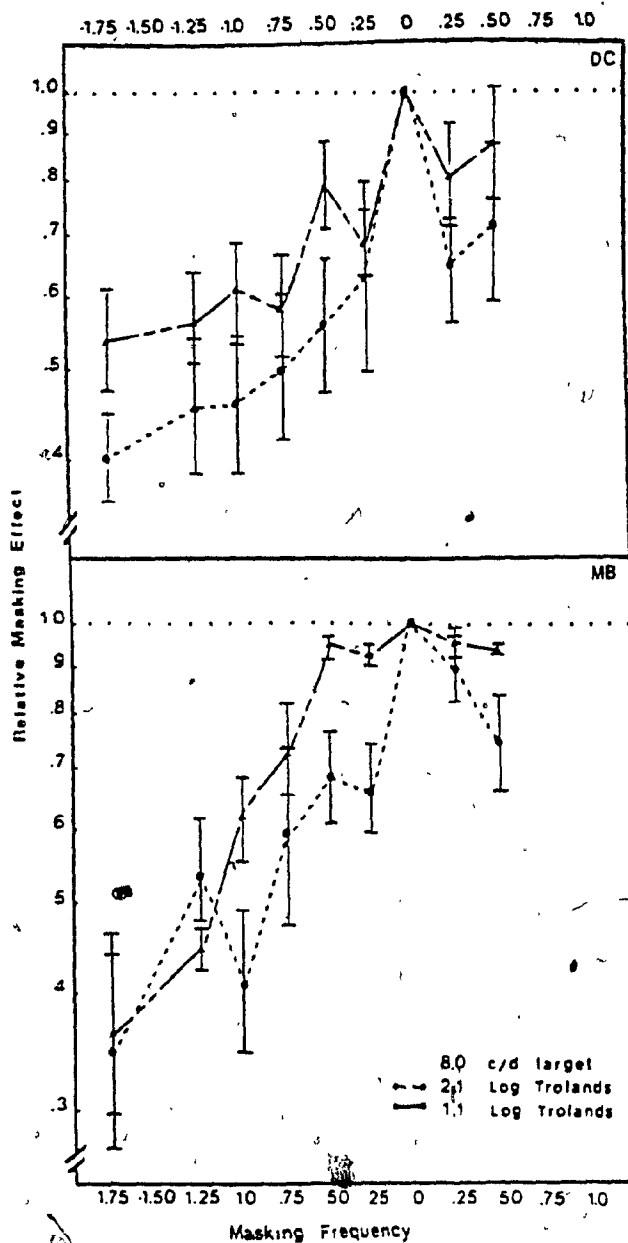


Fig.14 (Exp II) The magnitude of masking across frequencies has been normalized to the point of maximum masking within each function. Masking frequency is expressed in terms of its displacement in octaves from the target frequency.

broadener in the lower luminance condition. In the lower luminance condition the low spatial frequency masks produced greater masking relative to the peak amount of masking in that condition.

In Figure 10 the broadening of the masking function for a 4.0 c/d target is once again evident at the low luminance level, for both observers. This effect was particularly obvious at the lower spatial frequencies for observer MB. Observer DC showed a lot of masking at all the spatial frequencies.

In Figure 11, most evident for observer DC, the lower spatial frequencies again produced greater masking relative to the peak amount of masking in that condition.

Experiment 2.

As previously stated, in Figures 12 through 14 the contrast of the masks had been perceptually matched across luminance level in order to compensate for the decreased contrast sensitivity in the dark adapted eye.

Figure 12 shows the low pass characteristics of the masking functions in the dark adapted eye for both observers detecting a 1.41 c/d target.

Figure 13 shows a general broadening of the masking function of the data from observer DC. When observer MB detected the 4.0 c/d target, relatively less masking at the lower spatial frequencies was shown in the lowest luminance condition. However, this was probably a spurious finding given that the masking function for this observer at 4.0 c/d

was unusually flat in the light adapted condition (refer back to Figure 7).

As seen in Figure 14, observer DC showed relatively more masking at the low spatial frequencies in the lower luminance condition (1.1 log trolands). This effect was not particularly evident however, when observer MB was detecting the 8.0 c/d target.

Given that no masking was sometimes evident at the lower spatial frequencies for all three targets in the dark adapted condition, particularly for observer DC, it may seem that channels narrowed in the dark. However, it is obvious from all of these functions that when masking did occur, the lower spatial frequencies produced relatively greater masking effects in the dark adapted state. To summarize the effects of normalization then, the primary finding that emerged from the data was that masking functions were broader in a low luminance condition, especially at masking frequencies lower than the target frequency.

Discussion

The present investigation set out to examine the changes, due to dark adaptation, in the shape of the tuning functions of spatial frequency channels in the human visual system. Before evaluating such changes however, it is necessary to determine whether or not individual tuning functions have in fact been described. As already mentioned, Legge and Foley (1980) explain that the functions describing threshold elevation as a result of exposure to a masking grating are generally referred to as tuning functions. Let us assume, for the sake of simplicity, a peak detection model as described by Graham (1977), which contends that stimulus detection occurs whenever the response of at least one channel has reached its criterion threshold. Let us also assume that the channel maximally responsive to the target frequency responds to other spatial frequencies as well, only to differing extents. Exposure to different suprathreshold spatial frequency masks should therefore have an impact on the channel detecting the target and differentially elevate the contrast threshold of the target. The band-pass characteristic of the tuning function describing contrast elevation of the channel most responsive to a target frequency should reveal the sensitivity of that channel to neighboring frequencies.

Despite other existing theories that explain the different types of masking paradigms, according to Breitmeyer and Ganz (1976), the current consensus holds that

hypothesized integration mechanisms are involved in forward masking. An explanation of the integration hypothesis provided by Kahneman (1968), contends that the closer the mask and target are presented in time the less recovery there should be from the loss in sensitivity induced by the mask. The limiting time interval separating the onsets of the target and the mask, to produce masking, is determined by the temporal integrating properties of the system. This implies that masking effects will be most evident when the response to the mask and target presentation are mixed as if they had been presented simultaneously. The consequent suggestion of an incongruence in psychological and physical time was also recognized by Kahneman (1968). Therefore, the extent to which masking will occur within a spatial frequency channel will depend not only on both stimuli being processed by a common mechanism, but in addition, on the extent to which both the mask and the target are present in the same psychological moment or in what Boynton (1961) refers to as "one discrete time frame". According to Breitmeyer and Ganz (1976), forward masking may be attributed to peripheral and/or central integrating mechanisms. Masking produced by intrachannel inhibition and understood in the context of peripheral integration assumes that the persisting sensory response to the mask obscures the target because both stimuli are analyzed by a common mechanism. Central integration is thought to produce masking by adding noise to the spatial frequency synthesizing

process.

The temporal properties of the eye have been shown to be affected by light adaptation. Barlow (1958), in a human psychophysical study, found that as the area of a test stimulus or the intensity of a background field increased (both resulting in increased light adaptation), temporal summation was reduced. Similarly, Owen (1972) found that luminance, area and duration of a stimulus at threshold are interdependent.

Given the reduction in temporal integration as a result of light adaptation, one would expect to find less of a masking effect as mean retinal illuminance increased. This expectation would be based on the reduced probability of the mask and target stimuli occurring within the same "time frame".

Corroboration of the empirical findings of the effect of light adaptation on the temporal integrating properties of the eye is available from the phenomenological observations of the participants in the present investigation. Both observers remarked that the criterion for establishing the presence of a target during an interval containing a mask differed in the light and dark adapted conditions. Although this brings up the issue of shifts in judgemental criterion that will be discussed later, it is necessary to point out that in the highest luminance condition the observers reported that they detected the presence of the target by noticing a flash after

presentation of the mask. In the lowest luminance condition however, when the spatial frequencies of the mask and target were dissimilar, both observers reported that their decision regarding the presence of the target was often based on detecting a complex grating. It was as if the two stimuli had perceptually overlapped during a single integrating period.

Similar evidence of longer temporal integrating periods in the dark adapted state was indicated by the observers reports describing their threshold criterion when the mask and target were of identical spatial frequency. In the highest luminance condition both participants reported that the detection of a flash following presentation of the masking grating indicated the presence of a target. Whereas, in the lowest luminance condition it was impossible to detect a flash and the observers reported that they relied on the perception of an increase in mask contrast when detecting the target.

Given increased temporal integration in the dark adapted eye, one would have expected to find greater masking in the dark as compared to the light adapted condition. This prediction is based on the assumption that the channel detecting the target would have less "psychological" time to recover from exposure to the mask. As seen in the results of the present investigation however, most masking was evident in the light adapted condition. This finding suggests that temporal integration, per se, was not playing

a role in producing the observed masking effects. Consequently, it might be that the functions observed in the present study were not the tuning functions of individual channels.

Before further considering the possibility that the functions revealed in the present studies were not reflecting the properties of individual channels selectively sensitive to particular spatial frequencies, a discussion regarding the shifts in judgemental criterion might be appropriate. Long ISIs were chosen in the highest luminance condition to ensure that the observers would be able to detect the target by noticing a flash after the mask presentation, regardless of the spatial frequency of the mask.

Keeping ISI constant across luminance levels, the mask and target gratings were often integrated in the lowest luminance condition such that it was no longer feasible for the observers to rely on the criterion of a flash as an indication of the target's presence. Instead, in the dark, when the spatial frequencies of the mask and the target were very similar, the observers had to detect an increment in mask contrast and this made the detection task subjectively much more difficult. Given that temporal integrating periods are longer in the dark adapted eye and to the extent that the two identical grating stimuli are presented in one temporal integrating period, the observer's task was to make an absolute contrast judgement. Had there been complete

integration it would have been impossible for an observer to detect the target at all unless one grating was presented alone to serve as a comparison. Clearly, there was no evidence of perfect integration because there was a target contrast that allowed the observer to detect the contrast increment. Nonetheless, it was for this reason that catch trials were inserted only after the target had been detected. When the frequencies of the mask and target were dissimilar, detection in the dark adapted state involved the perception of a complex grating. From this one might extrapolate that there was an increase in central integration in the lower luminance condition.

Assuming that task difficulty adds noise to the detection process, as the detection task increased in difficulty there should have been an elevation in threshold detection. Predictions based on the shifts in judgemental criteria across luminance, as well as spatial frequency in the lowest luminance condition should have resulted in functions very different from those that were obtained. As the eye became dark adapted the increased difficulty in detecting a contrast increment should have produced an increase in the magnitude of peak masking. Conversely, as the detection became easier in the dark when detecting a target after presentation of a mask remote in spatial frequency, less masking should have occurred. In other words, based on the shifts in judgemental criteria, one would have predicted a much more narrow tuning function in

the dark with an exaggerated estimation of peak masking.

The present findings then are in contradiction to what one would predict both from the shifts in judgemental criteria and the effects of dark adaptation on intrachannel integration. Given that overall contrast sensitivity is known to be reduced in the dark adapted eye and therefore sensitivity to the target as well as the masking frequencies would be attenuated, one might have predicted identical, overlapping functions in the different luminance conditions. Had there been an increase in the magnitude of masking in the dark it may have then been possible to attribute this effect to the shifts in judgemental criteria. Similarly, based on the assumption that the magnitude of forward masking can be attributed to the extent of integration and that the shift in the observers' judgemental criteria in the lower luminance conditions was evidence of increased central integration, greater masking effects would have been expected in the dark adapted condition. It was therefore necessary to generate alternative hypotheses to account for the data. One possibility, given the shifts in judgemental criteria across luminance, is that the two functions cannot be considered to be reflecting the same sensory event of masking and therefore should not be compared. In the second experiment however, the contrasts of the masks had been perceptually matched across luminance conditions so it might be assumed that they had an equivalent sensory impact on the system, regardless of the

state of light adaptation. Given that the overall trends of greater masking in the light and broader functions in the dark were replicated in the second experiment, it seems that manipulating the level of light adaptation was producing a systematic change in the masking effect.

An alternative hypothesis is that the resultant masking effects were primarily due to interchannel inhibition. Instead of revealing the tuning functions of channels that were centered on the target frequencies, the overall responsiveness of the system might be reflected in the present data. Given the suprathreshold quality of the masking gratings it is likely that what was in fact being measured was the response of neighboring channels (Tolhurst, 1972) and their subsequent inhibitory effects on the channel detecting the target.

Inhibitory interactions between spatial frequency channels have been repeatedly demonstrated. Tolhurst (1972) found that adaptation to a square-wave grating did not elevate the detection threshold of the fundamental and third harmonic components as much as would be expected had each component been presented individually as the suprathreshold adapting stimulus. As a result, Tolhurst (1972) suggested that the two spatial frequency channels maximally responsive to each of the components inhibited each other when presented with a square-wave grating and thereby resulted in less of an adaptation effect.

Providing an explanation for the variation in the

bandwidth of the frequency sensitive channels that is observed when different psychophysical techniques are employed, Dealy and Tolhurst (1974) suggested that the threshold elevation effects observed using the adaptation paradigm might be reflecting the broader range of inhibitory interactions between channels rather than the fatiguing effects of prolonged excitation of a particular channel. This contention was supported by their finding that prolonged exposure to spatial frequency gratings that would not be expected to excite a particular channel nonetheless reduced the sensitivity of that channel and resulted in elevated threshold readings.

De Valois (1977) investigated the question of channel independence by examining the effect of adaptation on frequencies significantly removed from the adapting frequency and found evidence of mutually inhibitory relationships among neighboring channels. Adaptation of one channel facilitated the detection of certain spatial frequencies by other channels.

Tolhurst and Barfield (1978) found evidence of disinhibition supporting the contention of interaction between frequency sensitive channels in the human visual system when investigating the effect of adaptation to a single grating on the detection threshold of a variety of spatial frequency gratings. Apart from confirming the earlier findings of Blakemore and Campbell (1969) where threshold was elevated when the testing grating and the

adapting grating were close in spatial frequency, they also found that when the grating frequencies differed by 1-2 octaves threshold was lowered.

Interpreting the present results in terms of interchannel inhibition is consistent with the finding of a decrease in the magnitude of masking in the low luminance condition. It has been well established that contrast sensitivity to all spatial frequencies decreases as the overall state of light adaptation is reduced. For example, Van Nes and Bouman (1966) found that increases in contrast are needed to keep gratings at threshold in low retinal illuminance conditions. The observed decrease in the magnitude of masking in the lowest luminance condition during the present investigation might therefore be explained as a reduction in the inhibitory influence exerted on a target channel resulting from an overall decrease in sensitivity of the system to all the masking frequencies.

The finding that the masking functions were broader in the low luminance conditions can also be explained by the interchannel hypothesis. The overall broadening of the functions in the lowest luminance condition suggests that all of the masking frequencies had more of an inhibitory effect (relative to the point of maximum masking) on the channel detecting the target. An understanding of receptive field organization of ganglion cells in the cat and the changes produced by light adaptation manipulations might be useful for the above interpretation.

Kuffler (1953) found that the basic concentric organization of the receptive field usually contained either an "on" or "off" center, an antagonistic surround and a transitionary area with a combined response. Kuffler also found that the discharge pattern of a cell could be altered by changing the spatial distribution of illumination over the receptive field. In an "on" center cell, for example, entire illumination of the receptive field would result in less of a discharge than illumination at the center alone.

Barlow, Fitzhugh, and Kuffler (1957) found that dark adaptation simplified the organization of retinal receptive fields. They found that the antagonistic surround ceases to exert its influence in the dark adapted eye of the cat.

Given that a) the level of excitation in neighboring channels determines the magnitude of interchannel inhibition; and b) the influence of the often inhibitory antagonistic surround of receptive fields is reduced in the dark adapted eye; perhaps the broadening of the masking function can be interpreted as the result of relatively greater excitatory influence from neighboring channels on the channel detecting the target.

Psychophysical evidence of similar changes in spatial interaction in the human visual system, as a function of the level of light adaptation, was provided by Westheimer (1965, 1967). Based on his findings he attributed the threshold lowering effect of stimulation beyond a critical area to some type of interacting inhibitory response within

the receptive field that was evident only when there was a critical amount of illumination.

Kuffler's (1953) model of the "on" center receptive field can be used to explain the greater tendency for these masking functions to take on low-pass characteristics (relatively greater masking effect in the lowest luminance condition at low spatial frequencies). First of all, the spatial frequency that will produce the maximum response in a ganglion cell, from a light adapted visual system, will be the one that has the most illumination directed on the "on" center and the least amount on the antagonistic surround. Figure 15 shows a cross sectional plot of the illuminance distribution of two gratings, differing in spatial frequency, superimposed over receptive fields in the light and dark adapted eye. As a result of areal summation within the central region of the receptive field, as spatial frequency decreases and more illumination falls onto the "on" center, the greater the excitatory response of the cell. However as soon as illumination "spills" onto the antagonistic surround, the inhibitory response elicited would reduce the discharge of the cell and thus the low spatial frequency limit for that cell would be determined. In the dark adapted eye, as demonstrated by Barlow et al (1957), the influence of the antagonistic surround drops out and therefore there should be no inhibition introduced as the spatial frequency of a grating stimulus decreases beyond the maximal frequency.

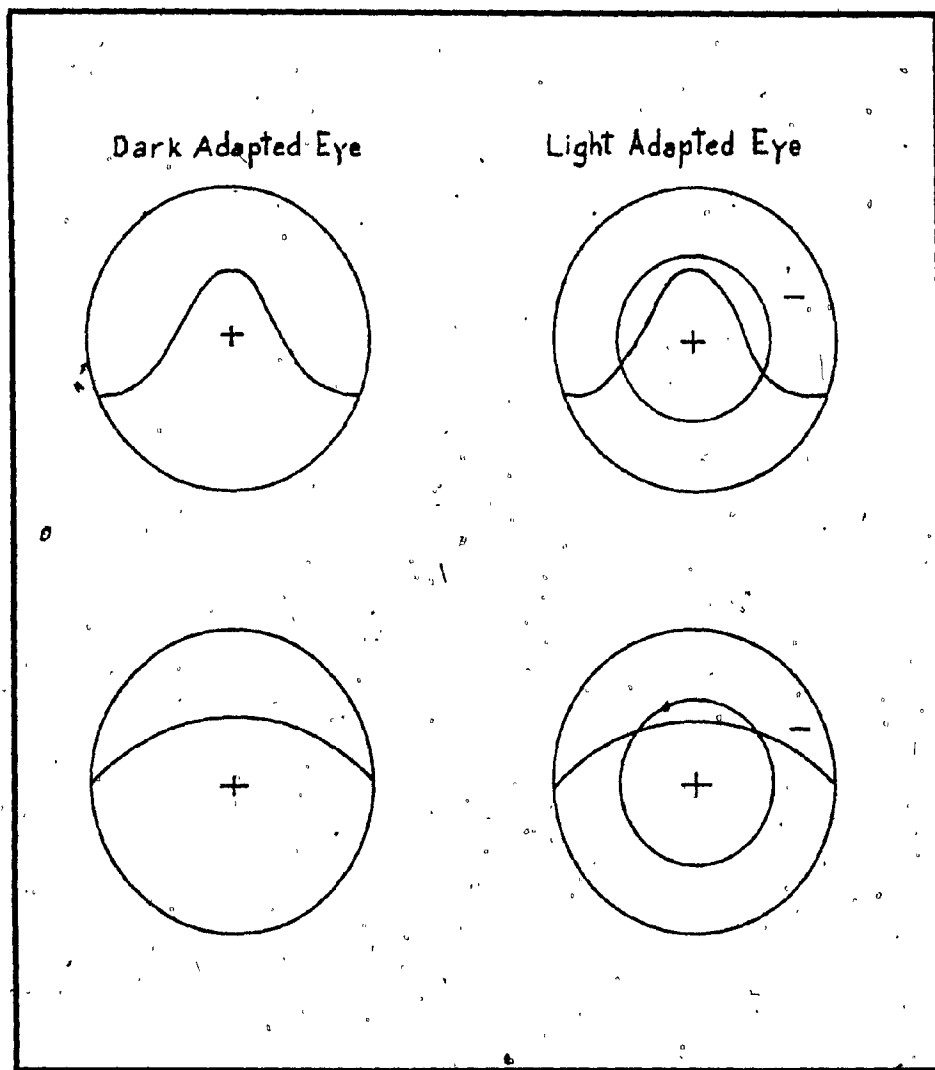


Figure 15. The luminance distribution of a sine-wave grating, differing in spatial frequency, superimposed over a typical "on" center receptive field in the light and dark adapted eye.

The earlier electrophysiological findings of Enroth-Cugell and Robson (1966) substantiate this model of frequency selectivity. These authors found selective spatial frequency sensitivity in ganglion cells from the optic tract of anaesthetized cats. They also found that the individual cells took on low-pass characteristics when illumination was decreased. Enroth-Cugell and Robson (1966) attributed this finding to the disappearance of the influence of the antagonistic surround in the dark adapted eye.

Given the electrophysiological and psychophysical evidence of differential spatial interaction in the visual system resulting from dark adaptation, it is not surprising that in the present investigation there was less of a drop in sensitivity to the low spatial frequency masks.

Although the present study set out to investigate the changes, due to dark adaptation, on the tuning functions of individual spatial frequency channels in the human visual system, that is not what was revealed. Instead, it seems that what was most likely demonstrated was the effect of dark adaptation on interchannel inhibition.

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