75-11,981

SIMON, Lynn Gross, 1944-
COLOR SPECIFIC EFFECTS IN METACONTRAST.

The City University of New York, Ph.D., 1975
Psychology, general

COLOR SPECIFIC EFFECTS IN METACONTRAST

by

LYNN GROSS SIMON

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

1974

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

Dec 19 1974
date

Elizabeth Fehrer
Chairman of Examining Committee

Jan 13. 1975
date

Florence L. Denmark
Executive Officer

Thomas E. Fenton

Elizabeth Fehrer

Eli S. Hellman
Supervisory Committee

The City University of New York

Abstract

COLOR SPECIFIC EFFECTS IN METACONTRAST

by

Lynn Gross Simon

Advisor: Professor Elizabeth Fehrer

The color specificity of metacontrast brightness suppression was examined using monochromatic lights equated for luminance. All stimuli were presented to the near periphery; the entire visual display occurring between two and four degrees horizontal visual angle. The stimuli were made as similar as possible; that is, all fields were equated for luminance, duration and size. Under these circumstances, the metacontrast effect was found to be extremely wavelength specific.

The number of inducing wavelengths was restricted to four stimuli whose wavelengths were chosen to approximate the unique hues of red, yellow, green and blue. Each inducing wavelength was then successively paired with nine test wavelengths in order to measure the spectral extent of the masking due to a given inducing field.

Traditional U-shaped metacontrast functions were obtained only in those chromatic situations in which the test and inducing fields were of identical wavelength. Small

wavelength differences (15-20 nm) between test and inducing fields produced severe flattening of these curves; greater wavelength disparities produced little or no brightness reduction at all asynchronies. For two out of three subjects there was also a marked tendency for these flattened U functions to reach peak masking amplitude at a shorter asynchrony.

In general, the peak amplitude of each masking function appeared to be positively related to the similarity in wavelength between test and mask. The data were therefore plotted as functions relating test wavelength to the magnitude of the brightness suppression maximally achieved with each test-mask pairing. These functions were severely limited in spectral extent. Reductions of 85% to 97% in brightness level were reached when test and inducing fields were of the same wavelength, but the degree of brightness suppression decreased sharply with increasing differences between wavelengths. Each function displayed marked irregularities which were consistent among the subjects.

Since the functions obtained were so narrow, it seemed most appropriate to compare them to the narrow spectral response functions of the opponent color mechanisms. A good agreement was found between the masking data and opponent process functions derived from a situation in which all wavelengths had been equated for luminance. There was also an impressive resemblance in the irregularities characteristic of both sorts of functions.

Accordingly, a model has been constructed which accounts for wavelength specific metacontrast results in terms of opponent process mediation of masking events. It was assumed that since all stimuli were equated for luminance, and each inducing wavelength was close to the locus of a unique hue, the process in the spectrally opponent system which indicates that hue will be the only one strongly affected by the inducing field. Test wavelengths which stimulate the same process will, to a first approximation, be the only ones masked. This severely limits the spectral extent of the metacontrast effect with equal luminance stimuli.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. Elizabeth Fehrer who directed this study and to Dr. Israel Abramov whose support, concern and guidance in the final phases of this dissertation aided greatly in its completion. Special thanks go to Dr. Thomas Frumkes for being so generous with his time and for his helpful insights. I also wish to thank the other members of my committee, Dr. Eric Heinemann and Dr. James Gordon for their advice and critical comments. The assistance of Miss Beverly Malinowsky, Miss Donna Stone and Miss Stephanie Esses who observed unhesitatingly through long hours of difficult concentration, and of Messrs. Walter Del Pellegrino and Al Crump who assisted with the equipment, is greatly appreciated.

Finally I would like to thank my family and friends, most especially my husband Donald, for the support they have given me during this study.

L.G.S.

Brooklyn, N.Y.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

I. INTRODUCTION

It has long been established that the apparent brightness of a lighted source can be altered by manipulation of the visual field which surrounds it (Aubert, 1865; Stigler, 1910; Fry, 1934; Alpern, 1953). Should that light be a brief test flash closely followed in time by a second flash to the same or an adjacent region of the visual field, the apparent brightness of the first stimulus will be substantially reduced. Such alteration in the perceptual brightness, contrast or detection threshold of a stimulus by the subsequent presentation of a second stimulus in close temporal contiguity to it is termed backward masking. However, the more specific term "metacontrast" (Stigler, 1910) is customarily applied to the situation when the stimuli have been placed so as to activate only adjacent, non-overlapping retinal areas.

The term metacontrast does not refer to a single experimental effect but includes many functions, each representing the outcome of an experimental situation in which the visual array satisfies the spatial requirements appropriate to metacontrast. Accordingly, it has become a matter of some concern whether the many functions associated with the term metacontrast represent different manifestations of a single underlying processing mode (Weisstein, 1972), or whether several different processes are being tapped (Kahneman, 1968). It will be shown in great detail later that if only achromatic

stimuli are used in both the test and masking fields, there are not yet sufficient data to decide at what level metacontrast processing occurs. However, the introduction of color to the display should provide additional insight into this problem since it would then become possible to assess the spectral extent of the effect produced by various wavelength manipulations. If all metacontrast situations do not produce functions which display the same spectral characteristics, it may well be that more than one processing mode determines metacontrast masking events. It is the design of the present study to explore wavelength dependencies and specificities in a type of metacontrast masking situation that has not been extensively studied, and to attempt to determine the locus of the effect by comparing the data with the spectral response curves of cells at various levels of the visual system.

1.1 ACHROMATIC DETERMINANTS OF METACONTRAST

The effects of color ought not to be independent of other metacontrast parameters. Consequently the data which result from the manipulation of stimulus dimensions other than color should be examined. Several variables are known to influence metacontrast. Data have been reported for the following: stimulus onset asynchrony (SOA);[1] type of stimulus (homogeneous flash, pattern or letter); angular

[1]Stimulus onset asynchrony (SOA) is the time interval which separates the onset of the test flash from the onset of the inducing or masking stimulus.

separation of test and masking fields; luminance, duration and contrast of the fields; similarity of test and masking contours; and the type of response indicator used. Manipulation of each variable serves to alter either the time course or the magnitude of the effect represented by the masking function.[2] (For reviews of some of these variables see Kahneman, 1968; Weisstein, 1972; Lefton, 1973.)

Metacontrast, it appears, is very much dependent on the exact stimulus situation presented. Nonetheless, it is striking that the results obtained in most metacontrast studies divide reasonably well into two general types. These types have been designated type A and type B metacontrast depending on the overall shape of the function (Kolers, 1962; Kahneman, 1968). In the type A function, the magnitude of the masking effect increases monotonically as the temporal separation between the two flashes is decreased. Peak metacontrast occurs at a stimulus onset asynchrony (SOA) of zero and there is much forward masking, i.e., paracontrast (Fehrer & Smith, 1962; Battersby, Osterreich & Sturr, 1964). In the type B function, some attribute of the appearance of the target increases to a maximum and then decreases as the temporal separation between flashes is decreased. Little or no masking occurs at SOA = 0, forward masking is weak or absent, and the

[2]In this paper the term masking function will refer to the curve which indicates some measure of brightness change in the test stimulus as a function of time between stimuli. Various measures of a decrease in the effectiveness of a visual stimulus have been used, i.e., a reduction in apparent brightness, contrast reduction or a threshold change.

peak backward masking effect is generally found at SOA of 50 - 100 msec. (Alpern, 1953; Fehrer & Smith, 1962; Kolers, 1962).

Lack of systematic manipulation of many of the variables relevant to metacontrast (Lefton, 1973), plus the absence of a specific type A-type B cutoff point, precludes accurate prediction in many specific situations. However, one generalization has been suggested by several authors (cf. Koler, 1962; Kahneman, 1967; Weisstein, 1972; Lefton, 1973) based on the observation that through the years certain stimulus situations and response measures have consistently yielded distinctly type A or type B functions. The proposal put forth strongly suggests that there is one major determinant of metacontrast type; the test/mask stimulus ratios in the dimensions of luminance, contrast and duration. The authors collectively refer to a series of experimental events which appear to produce clear support for their generalization.

The supporting data most often cited are the following. When a substantial imbalance exists between the luminance, duration or contrast of the test and inducing stimuli, a monotonic (type A) rather than a U-shaped (type B) masking function generally results. The set of experimental conditions most often used to achieve the requisite low test/mask ratio in one or several of the dimensions cited is to select an inducing flash of moderate to high value and a test flash approaching threshold. The subject's response task is one of

absolute detection or recognition, and the metacontrast function measures the change in test flash threshold as a function of temporal separation between flashes. The visual array generally used in this context is a disk-annulus or letter-annulus arrangement. On the other hand, the same reviewers have also noted that in those experiments in which the test/mask ratio has been held constant at approximately unity for luminance, duration and contrast, the metacontrast function obtained is characterized by a U-shape. All stimuli are supra-threshold, generally of moderate value, and the visual display is often adjacent rectangles rather than a disk-annulus display. Absolute stimulus detection is inappropriate for this type of situation and either magnitude estimation or a matching technique is used as the response indicator (Kahneman, 1968). Therefore, to the extent that repeated use has correlated each function type with certain sets of operational procedures and response measures, one can set out to produce results which clearly fit one of the two function types.

At first sight the above appears to be an attractive way of systematically classifying a series of heterogeneous experiments. Unfortunately, the generalization proposed by the authors may imply a more precise assumption than is merited by the data currently available. Let us examine the evidence more carefully.

THE STIMULUS VARIABLES

A) Luminance, duration and contrast

Reviewers have used the results cited above to support the assertion that U-shaped functions reflect the time course of metacontrast suppression[3] only in those instances where differences in value between the test and inducing fields is not exceedingly large (cf. Kolers, 1962; Fehrer & Smith, 1962; Fehrer & Raab, 1962; Schiller & Smith, 1966; Kahneman, 1967). However, the majority of the experiments considered were not parametric studies. At most only two or three test/mask ratios have been evaluated. The metacontrast functions obtained in these situations are markedly U-shaped, and the U of the functions becomes more pronounced with an increase in overall luminosity if the same stimulus ratio is maintained between fields (Weisstein & Growney, 1969). Nonetheless, it is clear that these studies cannot specify the total range of test/mask ratios that result in U-shaped functions.

On the other hand, when the luminosity of the masking stimulus exceeds the value of the test field substantially, a monotonic function with peak metacontrast at an SOA of 0 most often results (Fehrer & Smith, 1962; Kolers, 1962; Kahneman, 1967; Weisstein, 1972). These same general effects have been noted for differing test/mask contrast values as

---

[3]Suppression will be used in this paper primarily to denote a reduction in apparent brightness. However, other measures of a decrease in the effectiveness of a visual stimulus (i.e., contrast reduction, threshold alteration) will also at times be referred to as suppression or a suppression effect.

well (Kolers, 1962; contrast is the more appropriate measure when black figures on a white or grey ground rather than light flashes on a dark ground are used). Differences in stimulus field durations also appear to result in effects similar to those obtained when the fields differ in luminance (Kolers & Rosner, 1960; Kolers, 1962; Kahneman, 1967; Weisstein, 1968; Bevan, Jonides & Collyer, 1970). It is not certain whether or not this latter effect is the result of a perfect reciprocity in the time-intensity function associated with metacontrast events.

The relevant question is: do these studies adequately support the proposed generalization? In most instances, studies with low test/mask luminance ratios use detection measures to indicate the masking effect. High test/mask ratio studies customarily employ brightness scaling techniques. Collectively, these studies provide no effective means of resolving a possible confounding between the contribution of stimulus parameters and the contribution of response task in determining the type of function. Threshold measures and brightness assessments are not comparable psychophysical procedures. Therefore to what degree is the presence of a U-shaped function the result of psychophysical procedures rather than of stimulus attributes?

There is limited evidence to suggest that the nature of the response task can be a critical factor. Briefly, it has been found that if one maintains a constant stimulus

configuration and varies only response task, a U-shaped function will result when equal luminance stimuli are monitored for brightness, but a flat function will result when detectability measures such as reaction time or forced choice are used (Fehrer & Raab, 1962; Schiller & Smith, 1966). These findings will be discussed in greater detail later. It should be noted, however, that the change from a rating to a detectability measure is not sufficient to change a U-shaped function to a monotonically decreasing function. The nature of the response task is of great importance, but the confounding of response measure and stimulus values may not be sufficient to destroy the dichotomy based on relative stimulus values.

There appears to be only one parametric study germaine to the issue, i.e., a study in which the nature of the response task has been held constant, but one in which stimulus values have been systematically varied in small steps. The appropriate study by Weisstein is incompletely reported in Weisstein (1972) but it does demonstrate that, using magnitude estimation as the response task, a luminance ratio equal to unity produces U-shaped functions. That U-shape persists as the luminance is decreased by .3 log unit steps until the difference approaches one log unit. For luminance differences exceeding a log unit, the function is clearly monotonic. These data provide support for the notion that while the nature of the response task is important, it is not the sole determinant of

metacontrast function type. The study also specifies the test/mask ratio that corresponds to the transition point between type A and type B curves.

In its gross points, Weisstein's findings are supported by data presented in experiments II and III of Fehrer and Smith (1962). In these last studies several test/mask luminance ratios were used and a single response measure, paired comparison brightness judgments, was maintained. The Weisstein (1972) and Fehrer and Smith (1962) response measures are not directly comparable, but the change from a U-shape to a decreasing monotonic function and the approximate luminance ratio at which this change occurs are strikingly similar for both studies. Of course, the precise point at which the change from a U-shaped to a decreasing monotonic function occurs must depend on the specific parameters of the experimental situation. Nonetheless, both studies support the assertion that luminance ratio is a major determinant of the U-shaped function. Specifically, the inducing luminance may not exceed the test luminance by much more than one log unit if a U-shape metacontrast function is to be obtained.

Unfortunately the problem is not resolved with the clarification of this one point. In order to predict with some degree of certainty that a type B rather than a type A function will result, most reviewers agree that a fair degree of stimulus similarity must exist between the test and masking fields. That is, the value of the stimuli for the three

dimensions of luminance, duration and contrast must be almost the same. Is this assumption valid? The term similarity implies a symmetrical situation; the test and inducing stimuli must be of similar value within specifiable upper and lower limits. We know from Weisstein (1972) and Fehrer and Smith (1962) that the lower limit for luminance "similarity" occurs in the region of one log unit. We do not know from the data just considered if there is a comparable upper limit.

Only one metacontrast study appears to provide data relevant to this particular point. Alpern (1953) detailed the results of a large parametric study using stimuli which were well above threshold. In brief, he found metacontrast to be an inverted U function of SOA. Luminance ratios were not held constant, but the technique he used records the value of the test field as exceeding the value of the inducing stimuli for most matching data.

Figures 3 and 4 of Alpern (1953) clearly indicate that when the test luminance equals or exceeds the luminance of the inducing field, a U-shaped function <u>always</u> results. There is no evidence that a change in function shape accompanies a test/mask luminance difference of more than one log unit if it is the test flash that contains the greater luminance value. Indeed, the U of Alpern's functions become more pronounced at higher test field values.

The results Alpern obtained are not strictly comparable to other metacontrast data. The metacontrast studies

previously considered measure metacontrast by monitoring the suppression effect directly via a change in the threshold or brightness of the test field. Alpern measured the amount of real light which must be added to the test field to overcome the masking or suppression effect. It is unlikely that the positive signal which results from the input of real light to the test patch would sum linearly with the suppression effect due to metacontrast. Alpern's dependent variable is an accurate measure of masking, but it is probably not proportional to the degree of masking as measured in other studies. There are acute problems about the comparability of Alpern's functions to anyone elses at the more extreme brightness values. Moreover, it is not certain that if the method were changed all aspects of Alpern's results would be replicated. Nonetheless, there are no other pertinent data available.

To conclude, the notion of stimulus similarity is not well supported. All available studies show that if the luminance of the test flash is more than one log unit below the luminance of the inducing flash, a monotonic function classified as type A metacontrast will be favored. All other conditions favor U-shaped, type B functions. The stimulus dimensions of contrast and duration appear to follow the general trends specified for luminance except that the cutoff points for the change from type A to type B functions cannot be clearly specified from the data currently available.

B) Size, shape and contour

The stimulus variable of size, shape and contour have also been explored to a fair extent within the metacontrast paradigm. However, the experiments currently available do not allow us to differentiate adequately between each shape related dimension. Accordingly, the discussion to follow will not attempt to separate the studies relevant to each geometric property cited. Metacontrast studies which use the shape aspects of the stimuli as the major parameter are generally of two sorts, studies which use letters or known figure displays in tachistoscopic presentation, and studies which use contoured light flashes set at a constant moderate level. Both types of experiments present data which support similar conclusions.

Fehrer (1966) showed the accuracy of letter identification to be inversely related to the degree of similarity between test and masking stimuli. In a related study Stewart and Purcell (1970) confirmed that the magnitude of the masking effect could be influenced by the relation between target and inducing field configurations. In the latter study several ISI[4] were presented for each condition to show complete masking functions.

---

[4]ISI or interstimulus interval refers to the time which elapses between the offset of the first stimulus (test field) and the onset of the second stimulus (inducing field). Properly speaking, the ISI plus the duration of the first stimulus equals the stimulus onset asynchrony (SOA) referred to in the present study. However, in most tachistoscopic masking studies ISI is usually held constant while duration of the test stimulus varies to obtain a threshold measure. In such studies SOA varies from trial to trial.

Cox and Dember (1970) showed that visual targets became less susceptible to backward masking as the amount of internal contour was increased by the addition of black and white segments to a homogeneous test field. They argued that as the test and masking stimuli became more dissimilar visually by the addition of segments to the target, the target's susceptibility to masking decreased. Pollack (1965) found that not only was contour a relevant variable, but that contour orientation was also important. "Lack of parallelism of inner and outer figure contours (between mask and target figures) inhibits masking as does the presence of angles within the figure to be masked" (Pollack, 1965, p. 370).

Mayzner has attributed these contour as well as several of the shape and size effects to geometric analyzers within the visual system. Similar results have been obtained by him in a related paradigm called sequential blanking (Mayzner et al., 1967; Buchsbaum & Mayzner, 1969). In this technique several of five lines exposed in sequence were completely masked when all lines were of the same height, but these same lines were no longer blanked when line length became unequal. Mayzner and Tresselt (1969), in a similar design, showed that blanking was close to 100% when all five figures possessed the same geometric properties (all squares), but blanking was reduced when the second and fourth squares were foreshortened into trapezoids. The present author (Simon, 1972) has shown similar results using a standard

metacontrast situation. When inducing stimuli were systematically increased in height relative to a constant 2 x 2 inch test field (a square), there was a gradual decrease in the per cent of masking obtained. When the height of the masks reached 12 inches, the two inch square test stimulus was no longer masked at any SOA. However, when this last array was altered by the addition of contour lines to each inducing stimulus so that the added contours replicated the square shape of the test figure within the larger 12 x 2 inch inducing field, the full metacontrast function was restored.

The studies cited above all suggest that the variables related to contour, or more generally shape replication between test and mask, produce a specific set of results under selected conditions. All studies support the generalization that as stimulus similarity decreases, the degree of masking also decreases. However, if the experimental situation used favors U-shape functions, a more specific statement can be made. Under these conditions, any decrease in the geometric similarity of the test and masking stimuli results in a decrease in the amplitude of the U-shape curve itself.

In summary, a consideration of the stimulus variables pertinent to metacontrast makes it clear that one can select an experimental situation which will produce clearly type A or type B metacontrast functions. If test field luminance, duration or contrast values are decreased substantially relative to a constant masking stimulus, a type A rather than a

type B function will be favored. If there is a departure from identity in the dimensions related to stimulus geometry, size, shape, contour and contour replication, a flattened, U-shape function will be observed. The amplitude of the U curve will vary directly with the degree of stimulus similarity, but the point of maximum suppression will remain largely invariant.

THE RESPONSE INDICATOR

As was briefly mentioned, there are several response measures which have become associated with either the type A or type B situation but not both. Situations which generate type A metacontrast functions emphasize an absolute threshold or letter detection task; situations which generate type B functions customarily utilize a magnitude estimation or matching task. The problem is that the measures associated with type B events require an assessment of the stimuli which is substantially different from that associated with type A functions.

The issue becomes a bit more complicated for the type B classification. Both magnitude estimation and brightness matching require the subject to attend to only the brightness aspect of the test stimulus. The apparent brightness of the test field often varies over a wide range from quite bright, to dim, to blackness (reported as phenomenally absent) (Alpern, 1952, 1965; Fehrer & Biederman, 1962; Fehrer & Raab, 1962; Kolers, 1962; Schiller, 1965; Kahneman, 1967).

Nonetheless, even when the target is itself reported as phenomenally absent, subjects have been able to differentiate the presence of the target from a no-target array.

The relation between phenomenal brightness and detectability can be more clearly examined if identical stimulating conditions are used for two different response tasks. Under these conditions, measures which monitor the phenomenal appearance of the target across SOA such as magnitude estimation or matching techniques generate a U-shaped function, but indicators which monitor the detectability of the target remain at or near 100% detection accuracy for all SOA, i.e., a flat function. The invarience of detectability with SOA is evident for both detection by simple reaction time (Fehrer & Raab, 1962) and for detection by forced-choice (Schiller & Smith, 1966). It has been suggested, therefore, that the process represented by the U-shape metacontrast function depends solely on the visual system's response to brightness rather than on detection mechanisms (Weisstein, 1972).

As stated earlier, type A metacontrast functions customarily result from experiments which utilize a detection measure to record changes in the threshold of a test flash as a function of the difference in onset times between target and mask. It is questionable whether the verbal responses used to generate type B functions measure the same processes as do the absolute detection tasks customarily associated with type A curves. Accordingly, it is essential that the

task imposed by the response measure be carefully considered.

In sum, it is necessary when predicting which class of metacontrast functions will result from a particular set of experimental manipulations to consider at least three factors; the test/mask ratio as exemplified by the dimensions of luminance, duration and contrast; the degree of geometric identity as determined by shape, size and contour, and the type of response indicator selected as the dependent variable. Inspection of these factors should enable one to predict, to a first approximation, the masking function to be obtained.

1.2 APPROACHES TO COLOR VISION

The major color theories provide clear implications for both the loci of metacontrast events and for the spectral ranges over which one might expect to obtain metacontrast brightness suppression. Modern theories of color vision largely represent elaborations of earlier color theories, specifically the Helmholtz tri-chromatic and the Hering opponent process models. However, in recent years, there has also been the implication that an updated Helmholtz approach represents a peripheral cone mechanism model, while adaptations of the Hering approach imply a less peripheral excitation-inhibition model. Advocates of each position rely upon physiological mechanisms to explain psychophysical data. Let us consider their explanations.

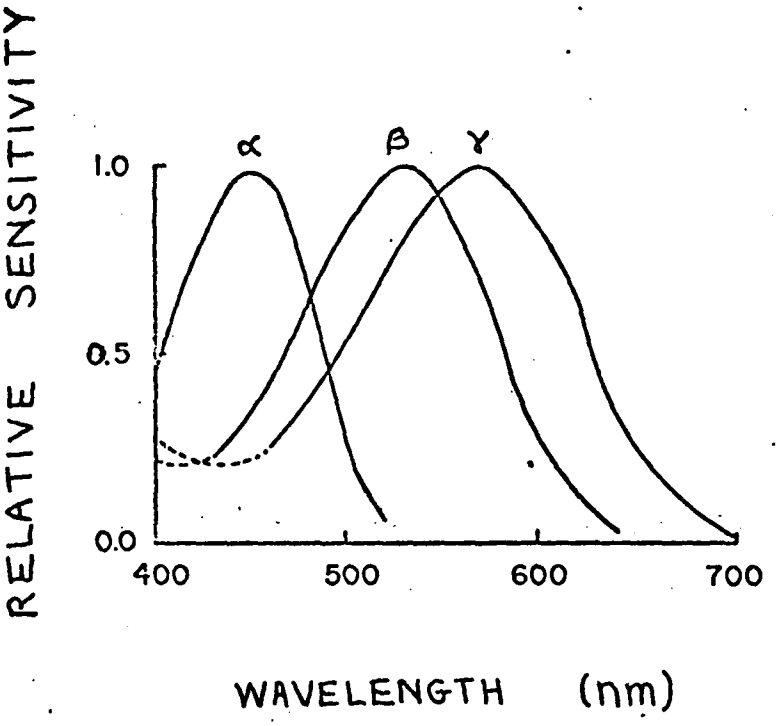
THE TRICHROMATIC APPROACH

The theory of color vision put forth by Helmholtz rests heavily on the principles first enunciated by Thomas Young in 1807. In its refined form, the Helmholtz or Young-Helmholtz approach postulates three hue producing mechanisms, each possessing broad spectral sensitivities and a single response peak (Helmholtz, 1924). The peaks of these mechanisms are spread across the spectrum such that one peak sensitivity falls in the long-wave spectral region, one in the middle-wave region and one in the short-wave region. The hue of a given homogeneous light is determined by the way in which it differentially excites the three mechanisms. That is, homogeneous light excites each kind of mechanism, but the extent of the excitation within a mechanism type depends on wavelength. Helmholtz further postulated that each of the three hue mechanisms can be selectively fatigued. A mechanism strongly stimulated by a red light, for example, will become much fatigued, whereas the green-sensitive and violet-sensitive mechanisms are only feebly stimulated by this same light and therefore display little fatigue. Should white light then fall upon the eye, the green and violet fibers will be relatively more affected than the red-sensitive fibers, yielding the impression of blue-green. This type of argument is put forth as an explanation for the occurrence of successive chromatic contrast, as well as to account for the specifics of each chromatic induction event.

Unfortunately, simultaneous chromatic contrast, now regarded as a similar phenomenon, was not explained using these simple, probably retinal physiological principles. Instead, Helmholtz postulated central factors labeled "inferences" or "errors in judgment" which he assumed to be involuntary, unconscious processes but which were discussed in highly mentalistic "psychic activity" terms. Lateral inhibition was not at this time part of the Zeitgeist.

The modern view of the Helmholtz trichromatic theory is still being revised. Indeed, the most significant alterations appear to be in the details of the spectral characteristics of the three fundamental mechanisms and new insights into how these sensitivity changes are implemented. The red, green and violet spectral curves originally proposed by Helmholtz have been replaced by functions derived from modern photochemical research and are represented by the α, β and γ curves in Figure 1. The shapes of these curves are in accord with the Dartnall nomogram. Dartnall's findings (1953, 1962) show that all known retinal photochemicals have, to the first approximation, the same shape function when quantal absorption is plotted against a frequency scale. Given only the peak absorption wavelength, it is then possible, using the nomogram, to plot a spectral sensitivity curve for each proposed photochemical substance. The particular absorption peaks used in Figure 1 (450, 530 and 570 nm) are based on the work of Marks, Dobelle and MacNichol (1964) and Brown and Wald (1964)

Figure 1. Relative spectral sensitivity of the three hypothetical color mechanisms α, β and γ. Peak sensitivities are at 450, 530 and 570 nm respectively. Solid portion of the curves based on Dartnall's nomogram (1953); dashed portion based on iodopsin (Wald, Brown & Smith, 1955).


RELATIVE SENSITIVITY
1.0
0.5
0.0
α
β
γ
400
500
600
700
WAVELENGTH (nm)

in which difference spectra of single human cones have been measured using microspectrophotometry. The particular peaks chosen should by no means be regarded as the final word on these matters since (1) the number of cones so analyzed is small; (2) the technique of microspectrophotometry contains many technical problems; (3) the results are based on parafoveal cones; and (4) results from the two laboratories differ from one another slightly.[5] Nonetheless, these values are in substantial agreement with the wavelengths of maximum sensitivity obtained from psychophysical measures such as the two-color threshold techniques used by Stiles (1959) and Wald (1964). Moreover the β and γ functions peak close to the estimates of the middle-wave and long-wave pigments as obtained by Rushton (1963, 1965) and Weale (Ripps & Weale, 1963) using the technique of fundus densitometry. Taken together the data lend strong support to the existence at the retinal level of three photolabile substances, segregated into three cone types, which bear absorption peaks in the vicinity of 450, 530 and 570 nm.

As in Helmholtz's earlier approach, loss in sensitivity resulting from exposure to a particular spectral hue is still attributed to a differential effect within the three cone types. However, it is generally acknowledged that although some sensitivity loss is attributable to the actual

[5]For further discussion of the problems of microspectrophotometry, see Liebman, 1972.

bleaching of the cone photopigments by continued exposure to light, Hecht's notion (1934) ascribing adaptation to great amounts of pigment depletion is no longer widely accepted. More recent work has shown that large fluctuations in sensitivity can be accommodated by small or even zero pigment bleaching (Rushton & Westheimer, 1962; Rushton, 1963; Dowling, 1967). Sensitivity changes appear to be of a neural rather than of a strictly photochemical nature. Hence, it would be justifiable, using a modern trichromatic approach, to observe that the spectral sensitivity curves in Figure 1 represent not only photochemical sensitivity but also the initial neural elements of the visual system.

In addition, a further assumption can be made with respect to these most peripheral color mechanisms. As noted earlier, the spectral sensitivity curves represented by α, β and γ possess function peaks which are in good agreement with those obtained using certain psychophysical measures such as the Stiles two-color threshold technique (Stiles, 1959). It is this latter technique which has been used to demonstrate that under selected chromatic situations, each type of color (π) mechanism responds in a manner largely independent of the other mechanism classes. More specifically, if the test thresholds of small monochromatic flashes are determined when these flashes are superimposed on large adapting backgrounds of differing wavelengths, only the mechanism class of greatest sensitivity will determine the test field threshold.

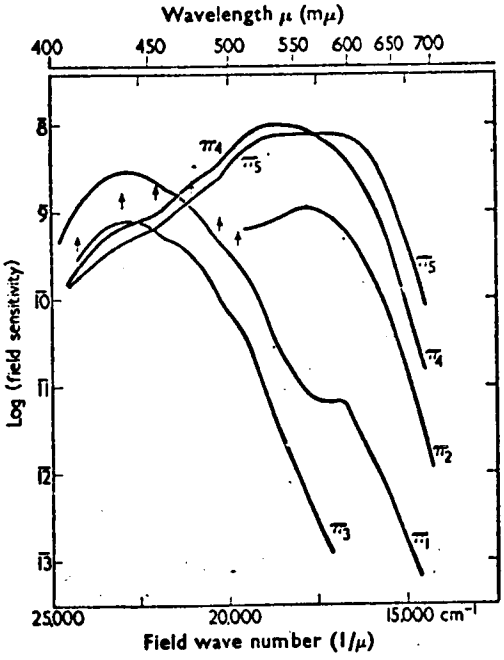
Through the judicious choice of background wavelengths and intensities, it is possible to isolate and identify each $\tilde{\pi}$ mechanism and to specify its spectral characteristics. The Stiles' curves are presented in Figure 2. There are five curves labeled $\tilde{\pi}_1$, to $\tilde{\pi}_5$. Each curve represents the background radiance required to raise the threshold of a test field by a fixed amount (1 log unit above absolute threshold). Note the gross resemblance between Stiles' $\tilde{\pi}_5$, $\tilde{\pi}_4$ and $\tilde{\pi}_1$ and the spectral sensitivity curves γ, β and α depicted in Figure 1. Both set of curves are quite broad and do not differ greatly in spectral characteristics.

The physiological location of the $\tilde{\pi}$ mechanisms is not known, but it is generally assumed that these functions represent the spectral response characteristics of a site central to the cones. However, since the $\tilde{\pi}$ functions strongly resemble cone spectra, it is likely that the processes described by these functions are not far removed from the cones.

Stiles demonstrated that the various $\tilde{\pi}$ mechanisms act more or less independently in increment threshold measures (Stiles, 1959), and the same principle of independence has been extended to include the metacontrast condition where target and surround overlap neither in space nor time (Alpern & Rushton, 1965). It is a small leap, therefore, to assume that under certain conditions it is not only the $\tilde{\pi}$ mechanisms, but also the individual classes of cones, which respond in an independent manner. Consequently, in metacontrast, a sensitivity

Figure 2. Stiles $\tilde{\pi}$ mechanisms. Each curve shows the equal effective field sensitivity for the five mechanisms. The value of -log W_μ is plotted against wavelength (μ); W_μ is the field energy which raises the test threshold to 1 log unit above its absolute value (the tenfold test increment value of W_μ). The abscissa scale is plotted on a wave-number basis so that equal intervals correspond to equal differences of reciprocal wavelength.

The field sensitivity of $\tilde{\pi}_2$ has not been determined for short wavelengths. The whole curve for this mechanism is very approximate; for $\mu < 520 m\mu$ only lower limits (shown by arrows) can be given. (From Marriot, F.H.C. Colour vision: the two-colour threshold technique of Stiles. In The Eye, vol. II, Davson, H. (Ed.), New York: Academic Press, 1962.)


Wavelength μ (mμ)
400
450
500
550
600
650
700
8
9
10
11
12
13
Log (field sensitivity)
π4
π5
π3
π2
π1
25,000
20,000
15,000 cm⁻¹
Field wave number (1/μ)

change in the cone class α should not affect the sensitivity of β or γ. A red inducing field should affect maximally only a red test flash since the red inducing stimuli, via lateral inhibition, will alter only the γ mechanism which mediates sensitivity for red in the test patch. A blue test patch mediated by α or a green test patch mediated by β should be relatively unaffected.

No information as to time constants or spatial parameters is supplied by this theoretical approach. What it does predict, however, is that the range of effect for a particular inducing field should be broad; at least as broad as the spectral sensitivity function which primarily mediates the inducing field color. Since the mechanisms α, β, γ or Stiles' $\tilde{\pi}_1$, $\tilde{\pi}_4$, $\tilde{\pi}_5$, are all broad and overlap extensively, it is unlikely without severe additional assumptions that chromatic metacontrast effects could be extremely wavelength specific, i.e., sharply peaked functions if mediated at the more peripheral levels.

There is, of course, an alternate approach to the three receptor model just discussed which stems from the implications of the Hering induction model.

THE OPPONENT PROCESS APPROACH

Unlike Helmholtz, who based his theory of color vision largely on the facts of three variable color mixture data and color matching experiments, Hering's theory of 1874 began with the psychological aspects of color sensation (Linksz,

1952; Hering, 1964). In the "natural system of color sensations" all colors can be regarded as intermediaries between red, yellow, green, blue, black and white. Several of these sensations are mutually exclusive; yellow as opposed to blue, red as opposed to green and black as opposed to white. However, one quality of a given pair may combine with either quality of each of the other pairs. For example, it is possible to combine blue and green or a red and white but not blue and yellow, green and red or black and white (Hering, 1964).

To account for color sensations, Hering postulated a visual system composed of three retinal substances, each capable of undergoing metabolic change during visual stimulation. Opposing processes termed assimilation and dissimilation (A and D respectively) were assumed to take place in each of the three substances. The ratio of A to D in at least two processes, the black-white and red-green and/or yellow-blue systems determined the color perceived. The various spectral hues were to be considered mixtures of four fundamental hue sensations, red, green, yellow and blue, each coupled with excitation of the black-white dimension. In Hering's system, pure red was considered to be an extra-spectral hue.

The Hering approach accounted for the main facts of successive chromatic contrast by the addition of only one postulate. It was assumed that should a dissimilative process predominate during adaptation, the effectiveness of subsequent

dissimilative stimuli was decreased while the effectiveness of subsequent assimilative stimuli was enhanced and vice versa. By adding the assumption of lateral inhibition as the spatial analog of temporal enhancement, the same reasoning could be made to account for the facts of simultaneous chromatic contrast as well. In short, Hering rejected both Helmholtz's physiological model of successive contrast and his psychological explanation of simultaneous contrast in favor of a theory which accounted for both phenomena in terms of opponent physiological processes. Hering's theory met with little popular success since it was not until the recent advances in neurophysiology that the importance of inhibition as well as excitation became known, and that spectrally opponent responses were actually recorded from single neurons in the visual system (Svaetichin, 1953; McNichol & Svaetichin, 1958; DeValois, 1965; Abramov, 1972). These findings provided the belated evidence needed to show that, in general, Hering's notions were indeed correct.

Nonetheless, prior to the establishment of the general features of human color vision pigments via microspectrophotometry and fundus densitometry, Hurvich and Jameson (1955) modernized and quantified Hering's theory of opponent colors while retaining its essential features.

In 1955 Hurvich and Jameson postulated four[6] receptor

---

[6]In the 1955 version, Hurvich and Jameson state that mathematical consideration of tri-chromatic mixture data permits data transformation to either three or four excitation curves. Both sets of transformations are provided but the accompanying text regards the four receptor system as simpler conceptually for their theory.

substances whose closely overlapping spectral characteristics were linear transformations of the C.I.E. tri-stimulus values. Activities in these four photosensitive materials were assumed to combine to produce paired opponent mechanisms similar to those proposed by Hering. However, by 1968, Hurvich and Jameson reformulated their position to accommodate the new information derived from microspectrophotometry and densitometry techniques. This modification included a tri-receptor stage whose spectral characteristics were similar to those postulated for the tri-chromatic approach elaborated earlier. Their new schema (Hurvich & Jameson, 1968) is presented in Figure 3. The absorption curves of α, β and γ (Figure 3a) show peak sensitivities at 448, 528 and 567 nm and follow the Dartnall nomogram. In Figure 3b, these same pigments are shown attenuated by macular pigment and ocular media to reflect receptor sensitivities for an equal energy spectrum at the cornea. Figure 3c, the final stage, most resembles Hering's scheme and represents the opponent process level. The r-g and b-y curves are analogs of Hering's red-green mediating and blue-yellow mediating substances. The curve labelled "W" corresponds to the "white" process and represents the foveal luminosity function. The r-g, b-y and W functions are weighted linear transforms of α, β and γ, the earlier stage, receptor level functions.

Although the curves in Figure 3c are theoretical constructs, it is important to note that these functions can

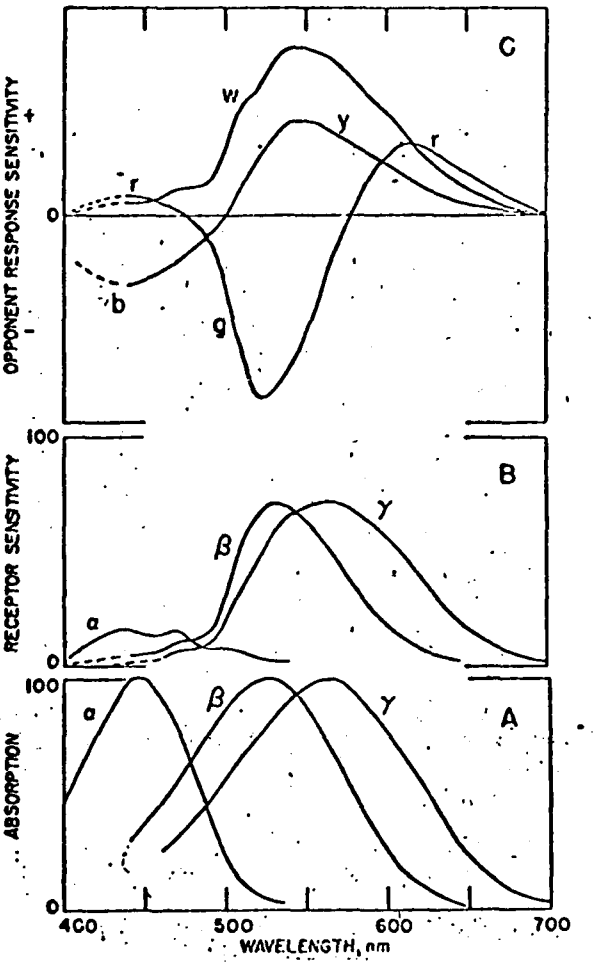
Figure 3. Theoretical curves of the Hurvich and Jameson Opponent Process Color Theory.

(a) Spectral absorption of photopigments

(b) Receptor sensitivities after correction for ocular media and macular pigment

(c) Sensitivities of opponent chromatic and achromatic response mechanisms.

(From Jameson & Hurvich, 1968)


C
OPPONENT RESPONSE SENSITIVITY
+
0
-
w
y
r
r
b
g
100
B
RECEPTOR SENSITIVITY
0
α
β
γ
100
A
ABSORPTION
0
α
β
γ
400
500
600
700
WAVELENGTH, nm

be experimentally derived and validated. The "W" curve represents foveal luminosity and therefore can be derived by any of the standard methods. The opponent chromatic curves have been derived by Hurvich and Jameson (1955) using a complementary cancellation procedure. The determination of these response functions makes it possible to predict quantitatively the spectral hues as products of the relative contributions of the four basic processes. This is done by taking the ratio of each chromatic response to the sum of both chromatic responses at any given wavelength. The term for the function so derived is called the hue coefficient by Hurvich and Jameson. The hue coefficients for red and green are:

$$L = \frac{(/r\text{-}g/)_\lambda}{(/r\text{-}g/+/y\text{-}b/)_\lambda}$$

the corresponding values for yellow or blue are:

$$L = \frac{(/y\text{-}b/)_\lambda}{(/r\text{-}g/+/y\text{-}b/)_\lambda}$$

The sum of L for red-green and for yellow-blue at each wavelength is always unity. Only one response from an opponent pair occurs at any one time, therefore, one value in the numerator and two values in the denominator are always zero. The specifics of the equation depend on the exact wavelength being considered. At wavelengths corresponding to the unique hues, three values in the denominator are zero. Red is regarded as an extra-spectral hue as it was in Hering's earlier approach.

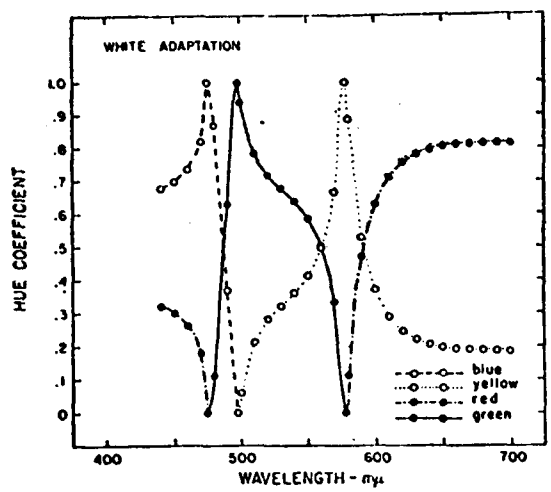
The hue coefficients experimentally obtained by Hurvich and Jameson (1955) are presented in Figure 4. Cursory inspection shows that there are four narrow, sharply peaked curves which overlap, but not so extensively as the curves of Stiles or other tri-chromatic theorists. Successive and simultaneous chromatic contrast are treated by Hurvich and Jameson (1964, 1969) in much the same manner as in Hering's earlier theory. Both effects are considered to be incremental additions to the test (induced) region of activity; the induced activity being opponent to the inducing stimulus hue.

OPPONENT PROCESS AND BRIGHTNESS

The previous sections have examined the two major theoretical approaches to color largely for the purpose of providing a framework within which to consider masking phenomena as a function of wavelength. It is clear from the preceding discussion that the more modern approaches resolve the polemic between the adherents of Helmholtz and Hering respectively by stating that both are partially correct. A Helmholtz-like situation exists at the level of the receptors, whereas subsequent stages of processing follow the lines indicated by Hering. Most current theories postulate two basic systems at the more central stages. One is opponent and is concerned largely with signaling hue; the other is non-opponent, of broad spectral extent, and is concerned

Figure 4. Spectral hue coefficient curves for a standard luminance spectrum (10 mL) presented under white light adaptation conditions.

(From Hurvich & Jameson, 1955)


WHITE ADAPTATION
HUE COEFFICIENT
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
400
500
600
700
WAVELENGTH - mμ
blue
yellow
red
green

largely with luminosity or brightness (Hurvich & Jameson, 1955; De Valois, 1965).

The masking phenomenon which will be considered in this thesis involves primarily changes of brightness. At first glance this would seem to suggest that masking should be mediated either at the very earliest level of the receptors, or by the channel primarily concerned with luminosity--the non-opponent system. Is this valid? If we temporarily exclude peripheral mediation, must we ascribe brightness mediation to only the non-opponent system? Can we demonstrate that in some circumstances opponent channels either contribute to, or are the sole determinants of luminosity, brightness or absolute visual thresholds?

There are several ways in which we can demonstrate that opponent systems may also contribute to the brightness dimension. Consider a few examples. Under most conditions the spectral sensitivity function from a given organism seems to be determined by the non-opponent channel. The evidence is simply that the two sets of spectral sensitivity curves (physiological and psychophysical) agree closely (Granit, 1955; De Valois & Jacobs, 1968). However, there are situations in which this is not necessarily true. In the macaque monkey, spectral sensitivity functions measured as increment thresholds against a bright background, do not resemble the functions produced by the non-opponent cells, but do resemble quite closely a function derived from a combination of

opponent cell responses (Abramov, 1972). Another series of experiments by Guth and by Boynton (Boynton et al., 1964; Guth et al., 1969) has examined interactions between cones or mechanisms in threshold type experiments. The basic experiment runs along the following lines. Thresholds are measured separately for long and short wavelength lights. Then the threshold for short wavelength light might be re-measured in the presence of a background of the long wavelength light. Even if the long wavelength light is itself at, or close to, threshold, it exerts a large influence on the threshold for the short wavelength light. The increment threshold for the short wavelength light is considerably elevated, whereas the increment threshold for long wavelength light on long wavelength light is not. This clearly implies some form of inhibitory interaction between mechanisms most sensitive to long and short wavelength lights respectively. Guth has extended these arguments to show that it is only the opponent processes which are capable of explaining these findings (Guth, 1973). Arguments of this sort strongly suggest that brightness changes can be related to the responses of the opponent channels and are not confined exclusively to the non-opponent system.

IMPLICATIONS FOR METACONTRAST

Since wavelength has in general not been manipulated as a parameter in masking experiments, it is difficult to make specific predictions. However, the following statements

can be made on the basis of information presented earlier in this section. If metacontrast of all types is mediated only at a peripheral level, then one might expect the spectral extents of the masking functions to be broad like those of the cones or π mechanisms. However there would seem to be several good reasons to say that some types of masking are not primarily peripheral events. For example, metacontrast can be obtained dichoptically (Kolers & Rosner, 1960; Battersby, Osterreich & Sturr, 1964; Schiller, 1965; Smith & Schiller, 1966; Schiller & Smith, 1968; Weisstein & Growney, 1969). Moreover, perceptually suppressed stimuli may still elicit behavioral responses (Fehrer & Raab, 1962; Fehrer & Biederman, 1962; Harrison & Fox, 1966; Schiller & Smith, 1966), produce a strong masking effect on a prior stimulus (Pieron, 1935), and exhibit an essentially intact cortical evoked potential (Schiller & Chorover, 1966). If some metacontrast events are central phenomena, then it is possible that their mediation may involve the opponent or non-opponent channels, or both. It is therefore worthwhile to examine the predictions that would follow if it were true that opponent channels were involved.

The predicted masking effects of a unique hue inducing stimulus paired with any chromatic test patch could, in an opponent process approach, be expressed by a curve which represents the action spectrum of the hue mechanism primarily mediating the inducing wavelength. To a first approximation,

the hue coefficient curves of Hurvich and Jameson would be of good predictive value in estimating the masking effects for each inducing field. The action spectrum of a particular opponent mechanism is narrower than in the tri-chromatic approach, hence masking should be more wavelength specific. If one also assumes that a mechanism independence similar to that discussed for the $\tilde{\pi}$ mechanisms is sustained at the opponent induction level, then the capacity for chromatic masking should be governed by the similarity in mechanism activity aroused by the inducing and test field wavelengths within these narrower mechanism bounds. A theoretical approach of this kind also implies that metacontrast (type B) does not take place at the peripheral receptor level but at one or several of the more central opponent process stages.

Let us hold further discussion of these topics until after the data have been presented so that a full and directed analysis of each point can be made. The relevant question, at this time, is whether one or several of the consequences suggested by the various color theories has been supported by data obtained in chromatic metacontrast studies. Accordingly let us briefly review the finding of those metacontrast experiments which use chromatic stimuli.

1.3 COLOR AS A VARIABLE IN METACONTRAST

Until quite recently color had rarely been pursued as a variable in masking, particularly in the metacontrast paradigm. Boroncz in 1911 (as reported by Alpern, 1952) found

evidence for masking with chromatic stimuli but the effect was found to be highly specific to a narrow range of inter-stimulus intervals. Werner's (1935) classic study of contour formation also reported some instances of chromatic masking. Werner found that with figures of the same hue the center disk of a disk-ring array could be made to vanish, but with figures of diverse color the center disk would not vanish. Unfortunately, in both investigations the effects of color differences had been confounded with the differences in brightness contrast between figure and ground making it impossible to isolate the separate effects of these two variables. Nonetheless, it is curious that the variable of color was not widely studied in this context during the years that followed. If one temporarily eliminates the related paradigm called the after-flash effect (Alpern, 1965; Alpern & Rushton, 1965) to be discussed in section 1.4, it was not until 1969, with the publication of Teft's brief article, that an attempt was made to investigate color as the major independent variable in metacontrast. Let us now turn to these recent studies.

In 1969 Teft compared four Munsell hues in a type A backward masking paradigm under conditions of monoptic and dichoptic presentation. Masking stimuli were a series of colored lattice patterns exposed for 200 msec. to similar and adjacent retinal areas to which a letter target (20 msec. above identification threshold) had been exposed 35 msec.

earlier.[7] Both the lattice inducing fields and the letter targets were selected Munsell hues of red, yellow, green and blue which had been equated for saturation and lightness. The dependent variable was a per cent correct measure for letter identification. Teft found a small but statistically significant difference of 4% more masking for monoptic over dichoptic viewing conditions. He concluded that the four hues differed both in terms of their resistance to masking and in their ability to mask other targets. Blue was the most difficult color to mask and was the most effective inducing hue. Yellow was the easiest to mask and the weakest inducing hue.

The mode of data presentation makes it impossible to assess adequately the relation between brightness suppression and similarity in stimulus color. It is obvious that all colors are not equally effective in producing a masking effect even when stimuli have been equated for Munsell lightness and saturation. Color related effects in masking are definitely implied by this study; however, since only four Munsell hues were considered and only a limited masking function summed across all test colors or all masking colors was provided, no firm conclusions about color specificity can be drawn.

---

[7] In metacontrast no retinal overlap between fields is permitted. In Teft's situation some letter configurations produce an overlap with the lattice pattern masking stimulus. This precludes the stricter designation metacontrast rather than backward masking.

One year later, Bevan, Jonides and Collyer (1970) published a metacontrast study dealing with color as the major variable. A tachistoscopic Werner disk-ring display was presented at several asynchronies in the range of 5 to 68 msec. ISI. Test field duration was 18 msec; ring presentation time, 100 msec. As in Teft's study, Munsell papers equated for saturation and lightness were selected from the red, yellow, green and blue spectral regions. The dependent measure was per cent failure to detect the color of the test disk. Findings using this color detection technique in a type A metacontrast paradigm were as follows: (1) complementary colors provided the least masking, (2) identical colors yielded the most masking, and (3) different but non-identical primaries yielded intermediate levels of masking. Oddly the difference between conditions two and three was not statistically significant.

The article clearly favors the interpretation that the degree of metacontrast suppression is dependent on the phenomenal similarity between test and inducing colors. Nonetheless, the precise degree of color specificity required to produce maximum masking effects must remain indeterminate on the basis of these data. The metacontrast functions provided include data for only the four disk colors (test fields) rather than information based on the interaction of both the disk and the ring colors. In addition, the per cent failure to detect measure used by Bevan et al. is strictly speaking

an all or none, absolute detection technique. No verbal response measure is available for reports on partial suppression or darkening effects. Teft's letter identification task, described earlier, similarly lacks provision for demonstrating partial brightness reduction effects. In consequence, neither study supplies sufficient data to determine the degree of chromatic similarity necessary to replicate the classic masking functions, type A or type B. Both studies present only a type A masking situation at one (Teft), or at several (Bevan et al.) ISI. The time course and amplitude of the type B metacontrast function under chromatic conditions is therefore not at all known from these data.

In 1964 Alpern published a brief study whose results were consonant with Bevan's data. Alpern found that when the test and inducing flashes were of the same color, substantially greater suppression effects were observed than when test and inducing flashes were of complementary colors. Although only red (621nm) and green (538nm) were used, the results clearly indicate that, for these wavelengths, metacontrast was greater when color contrast between fields was minimal, i.e., when a red-red or green-green combination was displayed. All stimuli were of equal duration and a complete metacontrast function (eleven SOA) was generated by the matching technique described earlier (p. 10). This was the first study to indicate clearly that brightness suppression functions resemble the classic U achromatic masking curve

only under the conditions of identity in the color of the test and masking stimuli. The quest for a plausible explanation for this selective color masking effect led Alpern, and then Alpern and Rushton, to embark on a series of studies using a related paradigm called the after-flash effect.

1.4 THE AFTERFLASH TECHNIQUE AND π MECHANISM INDEPENDENCE

In Alpern's 1953 paper (see section 1.1) the dependent variable was the test flash luminance required to match a fixed luminance comparison stimulus as a function of SOA. This produced U shape, type B metacontrast functions. The luminance ratios between test and masking stimuli varied from trial to trial to achieve a match at different SOA, and between the subexperiments conducted at different comparison luminances. It was found that the magnitude of the masking effect increased as the luminance or duration of the inducing flashes was increased relative to a constant comparison flash luminance, or when the general luminance range of the test flash was decreased by decreasing the luminance of the comparison light. Hence from this early work Alpern made the interpretation (in Alpern, 1965) that metacontrast may have been partially the result of an interaction of cones excited by a strong inducing field and rods, or rods plus cones, excited by an initially weak test flash.[8]

[8]This point bears further consideration. In Alpern's technique, metacontrast effects are measured by a null match with the comparison stimulus. To achieve this match the test

A possible explanation based on rod-cone interaction is supported by two specific aspects of the 1953 results as interpreted by Alpern: (1) maximum effects occurred at low test flash luminance levels combined with high afterflash (inducing field) levels, and (2) minimal effects occurred when the test and afterflash were confined to excitation of the rod free fovea. Alpern's explanation at first sight seems plausible. It is known that rod latency is longer than cone latency and that intense stimuli are transmitted more quickly than weak stimuli. It is therefore possible that the neural activity evoked by two lights of substantially different luminance and presented 50 or more msec. apart may either arise simultaneously or at least occur simultaneously at some point in the system. If this were the explanation for metacontrast, even type A metacontrast, it would be an example of the inhibition of rods by cones.

This early and tentative explanation has since been ruled out by Alpern's 1965 study. In the 1965 study, a test threshold vs. background intensity measure rather than a matching technique was used. Alpern used one SOA; 50 msec., a chromatic background of variable intensity and chroma, and a large, intense inducing field which surrounded but did not

---

flash must be raised to a luminance at least equal to and often well above that of the inducing stimuli. The greater the effect produced by higher and higher luminance inducing flashes, the greater the luminance to which the test flash must be raised to achieve a match. Therefore how Alpern interprets this effect as a rod-cone stimulation by the test and inducing fields is not at all clear.

include a small, square test patch of variable chroma. This paradigm was called the afterflash effect although it does qualify as a form of metacontrast because of its spatial arrangement.

Alpern found that if a substantial brightness imbalance was allowed to exist between visual stimuli such that the test field excited only rods, but the more intense afterflashes of various wavelengths excited both rods and cones, those afterflashes of fixed scotopic brightness but different photopic luminance would all raise the test field threshold equally. "Thus it is the excitation only of the rods by the afterflash which raises the rod threshold of the test flash. . . . There is no interaction between rods and cones" (Alpern, 1965, p. 471). In this situation the metacontrast function is determined solely by the scotopic luminosity of the induction stimuli, independent of wavelength, so long as the test field is of a sufficiently low luminance to fall exclusively within the scotopic range.

What then can be predicted for the more common masking situation where both test and inducing stimuli fall above the scotopic luminance range? If the eye is allowed to dark adapt to the point where the cones have fully recovered but the rods retain an elevated threshold, similar metacontrast effects are displayed. "Since in this instance neither flash falls upon an active rod mechanism, the phenomenon demonstrates that cones affect cones as much as rods affect rods"

(Alpern, 1965, p. 471). But does this independence of effect extend to the various types of cones such that a member of a specific cone type interacts only with members of its own class? The studies of Bevan, Jonides and Collyer (1970) and Alpern (1964) give presumptive evidence for an independence of cone or π mechanisms in the masking situation. In both experiments there was a marked increase in the degree of metacontrast produced when test and induction stimuli were identical in hue. Complementary, or at least non-identical hues, produced only limited metacontrast effects. However, it is only in the succeeding study by Alpern and Rushton (1965) that sufficient evidence is presented to firmly support a cone-cone independence model for some metacontrast events.[9]

In the scotopic situation just described the test flash affects only rods and the effects of various colored afterflashes are equivalent provided their scotopic brightness is always the same. However, in the photopic situation the absolute extent of the metacontrast effect depends very much on the dominant wavelengths of both the afterflash and the test flash. Only afterflashes of fixed activation value for a particular mechanism will affect a particular test

---

[9]Again the Alpern and Rushton studies on afterflash were run at only one SOA. In Alpern and Rushton (1965) the test flash was confined to the central fovea and the background intensity was reduced to 0 except for threshold determinations designed to excite exclusively the blue mechanism, π_1 . Presumably this situation would produce a type A function were several SOA to be presented.

flash threshold equally. More precisely, the procedure shows that when afterflashes or inducing fields of different dominant wavelengths are adjusted in brightness so that each activates a particular $\tilde{\pi}$ mechanism equally, each adjusted afterflash will raise to an equal extent the threshold of a test flash activated by that same $\tilde{\pi}$ mechanism. In short, a red, green or blue afterflash will raise the threshold of a red test flash equally if each has been adjusted in brightness so as to excite equally the red mechanism, $\tilde{\pi}_5$. These same inducing fields would not, in like manner, produce equal threshold effects on a green test patch since green threshold flashes stimulate the $\tilde{\pi}_4$, not $\tilde{\pi}_5$ mechanism. If each inducing wavelength is rescaled for equal excitation of the $\tilde{\pi}_4$ mechanism, then each now raises the green test flash threshold equally. An analogous argument can be made for the blue or $\tilde{\pi}_1$ situation. It may thus be concluded that each of the Stiles' color mechanisms acts independently in metacontrast. "If a test flash at threshold excited $\tilde{\pi}_5$, then the afterflash raises this threshold only by stimulating $\tilde{\pi}_5$ in the surround (inducing flash). The extent to which $\tilde{\pi}_4$ and $\tilde{\pi}_1$ are also stimulated is quite irrelevant. Similarly, if the test excites $\tilde{\pi}_4$ or $\tilde{\pi}_1$ at threshold, the afterflash effectiveness depends solely upon the stimulation of $\tilde{\pi}_4$ or $\tilde{\pi}_1$ in the surround" (Alpern & Rushton, 1965, p. 482). The assumption is always that the test flash excites but one receptor mechanism at threshold and that the effectiveness of

subsequent afterflashes is solely dependent on its stimulation of the same receptor mechanism some 50 msec. later.

Unfortunately, no individual data have been provided. If one looks at Stiles' $\tilde{\Pi}_5$ and $\tilde{\Pi}_4$ mechanisms, it is apparent that there is a large overlap between the two functions. At 600 nm, the wavelength selected by Alpern and Rushton as the red test flash, $\tilde{\Pi}_5$, there is sufficient individual variability in the amplitudes of the $\tilde{\Pi}_5$ and $\tilde{\Pi}_4$ functions to cast some doubt as to whether it is definitely $\tilde{\Pi}_5$ and not $\tilde{\Pi}_4$ which is being stimulated by the flash (Abramov, I, personal communication). As Alpern and Rushton provide no individual data, we must hope that the situation is as set forth for individual subjects and that only $\tilde{\Pi}_5$ was stimulated by the 600 nm. input at threshold.

Two additional points should also be considered. (1) When an induction flash is made sufficiently intense, a "critical level" is reached above which a test flash of fixed value can no longer be seen. Alpern and Rushton (1967) show that this "critical level" depends not on the specific wavelength of the afterflash but on the effectiveness of that flash in its ability to excite the same $\tilde{\Pi}$ mechanism activated by the test flash. "If the surround region upon which the contrast (induction) flash falls is first adapted by background or bleaching, its efficacy is reduced so that the 'critical level' (necessary to achieve complete masking of the test stimulus) is raised" (Alpern & Rushton, 1967,

p. 519). The extent of the increase in the log "critical level" equals the increase in the log threshold for seeing the afterflash itself, i.e., the adaptation effect. Hence, if an afterflash is of sufficient intensity after adaptation to generate a signal at or above some critical value within the same mechanism primarily mediating the test hue, partial or even complete metacontrast brightness suppression may still occur. (2) If one first adapts to a background but holds the contrast flash at some fixed intensity, the contrast flash will raise the test field threshold by a fixed amount no matter how far that threshold has already been raised by light adaptation. This is surprising since backgrounds and bleaching usually exert greater effects when the eye is dark rather than light adapted.

Clearly the way an inducing field raises the threshold of a test field in metacontrast is entirely different from the way light adaptation increases threshold. The suppression effect produced by an inducing stimulus inhibits the test signal by interaction at some site central to where adaptation occurs. Adaptation serves to decrease the effectiveness of an inducing stimulus by attenuating the size of its signal going to the next processing level. However, if the inducing stimulus is sufficiently strong after attenuation to surpass the requisite critical value, its ability to completely suppress a test flash of fixed intensity is unimpeded.

In a situation resembling that used to generate a type A function we now have some evidence that the locus of metacontrast events is not at the cones. Since it is Alpern and Rushton who often interchange the words cone and $\tilde{\pi}$ mechanism processing in their discussions of metacontrast and its mediation, it is indeed interesting that within their own studies lies evidence that these suppression effects do not occur at the cones but must be at least at the level of the $\tilde{\pi}$ mechanisms.

The central questions still remain unanswered. At what locus (or loci) in the visual system does metacontrast suppression occur? Do all forms of metacontrast brightness suppression reflect the mediation of a single mechanism type; primary receptors, $\tilde{\gamma}$ mechanisms or opponent processes? Since the various chromatic mechanisms located at either very peripheral or more proximal loci possess response characteristics of differing spectral ranges, the type of mechanism(s) primarily responsible for mediating metacontrast suppression events would influence the hue specificity of the event itself. We now know that color specific effects do occur in metacontrast. In a situation which approximates that used to produce type A functions, the specificity of the metacontrast effect appears to conform to a peripheral mediation approach (Alpern & Rushton, 1965). It therefore remains to be determined whether the type B masking situation will also produce results which favor a peripheral interpretation.

Accordingly let us now turn our attention to the study proposed; its design, rationale and hypotheses.

1.5 THE PROPOSED STUDY

The information available strongly suggests that when chromatic stimuli are used in a photopic metacontrast situation the results will be color specific. Further, we know that in the special situation termed the afterflash effect (Alpern & Rushton, 1965), threshold measures of chromatic test stimuli show the color specificity of the effect to conform to a retinal or at least peripheral interpretation of metacontrast. What must be determined is whether the different sets of experimental conditions within the framework of metacontrast all produce results which favor the same peripheral approach. The choice of a single situation, if sufficiently different from the one selected by Alpern and Rushton (1965), should provide an adequate first step. It is therefore the purpose of this study to examine the chromatic specificity of metacontrast brightness suppression in a situation in which all stimuli have been equated for luminance, i.e., a situation which clearly favors type B rather than type A metacontrast results.

Let us examine the problem more carefully. It should be recalled that Alpern and Rushton (1965) did not vary SOA in their study so that we do not definitely know if their procedure would have produced type A or type B metacontrast functions. We do know, however, that the test/mask ratios

used were low enough to fall within the range of luminance ratios customarily associated with functions classified as type A. (Preliminary work by K. Alexander [referred to in Weisstein, 1972] suggests weak monotonic functions across SOA for an experimental paradigm similar to Alpern and Rushton's (1965) but using more moderate inducing luminances.) We know only that the Alpern and Rushton metacontrast situation produced results whose spectral characteristics bear a strong resemblance to the Stiles' π mechanisms. Indeed, the similarity of their findings to the spectral characteristics of π_1, π_4, and π_5 is so strong that we may assume that the π mechanisms provide the mediation locus for these specific metacontrast events. However, what is not clear is whether the same interpretation is appropriate for other metacontrast situations, specifically, situations which generate U-shaped, type B functions. If the various metacontrast functions classified as type A and type B represent different manifestations of a single underlying processing mode, then the chromatic response characteristics of the mechanisms which underlie Alpern and Rushton's afterflash effect ought to be reflected in the response characteristics which underlie equal luminance, type B metacontrast results as well. This has not yet been demonstrated.

When all fields have been equated for luminance and duration, a U-shape, type B function should result. Previous discussions have demonstrated that type B functions are

easily modified by several sorts of changes in the visual field (see section 1.1). On the basis of the effects noted with other parameters, the predictions of modern color theory, and the data from the afterflash effect, it is justifiable to assume that manipulation of the wavelength composition of the test and masking fields would produce specific modifications in the U function itself. These modifications would probably be manifest as either a decrease in the amplitude of the curve or as a change in the SOA of peak effect. The spectral range over which these modifications take place should allow us to specify the types of cells or processes which mediate type B metacontrast events by the use of correlative assumptions similar to those employed for the afterflash paradigm. If both situations activate primarily the same underlying processes, the spectral range of the changes in the U function should correspond to the spectral extents of the π mechanisms as they do in the afterflash situation. If we presume one underlying mechanism for monotonic and U-shape curves, there must be no metacontrast situation which produces results in which the spectral extents of the functions are different from those found in other metacontrast situations.

It is necessary, therefore, that this study provide two sorts of data; data which demonstrate the manner and extent of the change in the U-shape curve as a function of test and masking wavelength, and data which specify the spectral range over which these modifications take place as

a function of inducing wavelength. The situation selected for examination represents a typical situation within the class of experimental conditions known to produce type B metacontrast functions. All fields have been made as similar as possible, that is, all fields have been equated for luminance, duration and geometric properties. It is believed that this design is sufficiently different from the afterflash technique to favor other processing modes, if appropriate. It is also hoped that the current scheme will minimize possible complex interactions between variables. Only wavelength and SOA will be systematically altered.

The initial problem was to choose a situation in which the underlying color mechanisms could be differentially stimulated by the test and masking stimuli and at the same time satisfy the experimental conditions known to produce type B metacontrast results. Narrow pass filters calibrated for equal luminance would make it possible to have lights of high spectral purity and still retain stimuli which fell within photopic range. However, the number of possible wavelength pairings is quite large. Therefore to reduce the problem to manageable proportions, the number of inducing wavelengths was restricted to four monochromatic stimuli whose wavelengths were chosen to approximate the unique hues of red, yellow, green and blue. Each inducing wavelength could then be successively paired with several test wavelengths in a random order. The various test wavelengths included the four inducing wavelengths.

Clearly the test stimulus would vary in appearance as the spectral composition of the test and inducing stimuli was changed from trial to trial. It was therefore decided that all test stimuli would be monitored for changes in both apparent brightness and color (hue and saturation). Five SOA were selected to demonstrate a complete function for each test-mask wavelength pairing. These SOA were 0, 37, 70, 100 and 150 msec.

The most direct approach toward achieving the stated purposes of this study would be to use chromatic stimuli in a matching method in which a comparison field is adjusted to match the appearance of the test field. Ideally the brightness and color composition of the comparison stimulus would be finely adjustable to the extent that a perfect match could always be made. In practice this is difficult to achieve because of two factors. First, the range of test and inducing wavelengths required is quite wide. This increases the possibility that some of the induced hues observed may be extra-spectral in nature causing imperfect matches to be made. The problem could be solved through the use of negative mixtures (i.e., adding a hue to the test field) but this would introduce an additional operation into the procedure and increase the time needed to complete each match. In addition to these drawbacks, the matching method itself necessitates the use of multiple exposures for each visual array. This is extremely time consuming in a color situation and implies

that the perception is invariant from exposure to exposure. Since the metacontrast situation utilizes brief flashes which might induce a perceptual change in more than one dimension, it is simply not true that there is only the most minor of variances from trial to trial. A given masking situation usually yields reasonably stable results. Nonetheless, if a match is to be perfect for brightness, hue,and saturation, any perceptual variability during the matching process would severely increase the time and difficulty involved in producing phenomenal identity.

An alternative to the classical null method is to use an absolute judgment technique in which subjects are required to make responses that directly reflect their perception of the test stimulus on a particular exposure. Such techniques offer the advantage of eliminating the need to present the visual array repeatedly within a trial. Instead, information is gained about the appearance of each physical stimulus through an absolute judgment procedure which incorporates scaling or fixed category responses along a continuum to evaluate each parameter. There are, of course, many variants of the absolute judgment technique which can be employed. Each offers the advantage of eliminating the use of repetitive viewing within the trial and each utilizes response categories which can be preselected for increased sensitivity in certain dimensions. Experimental objectives can be satisfied by selecting a method which contains ratio scaling, one which

naive subjects can learn easily, and one which possesses sufficient sensitivity to measure small changes in the perception of the stimulus.

Given the advantages of an absolute judgment technique for the study of metacontrast, and support for the reliability and validity of these types of psychophysical techniques in color work (Boynton & Gordon, 1965), it seems the appropriate tool to apply to the specific problems of this experiment. It was decided that all judgment tasks were to be arbitrarily divided into two major spheres; one encompassing the brightness aspect of the array, the second involving the color aspects of hue and saturation. Subjects would be asked to attend to these different stimulus dimensions on separate looks at the same visual array. Responses for apparent brightness utilize a magnitude estimation technique; reports on hue and saturation employ fixed category responses to be described in detail in section 2.2. The independent variables of the study are the wavelength of the test and masking stimuli and stimulus onset asynchrony. The dependent variables are judged brightness and color (hue and saturation). All viewing will be performed under conditions of type B metacontrast masking. All fields will be of equal luminance and duration and will remain constant in physical intensity throughout the study.

It has been mentioned briefly that evidence can be cited to support both a highly peripheral and a more central

processing approach to metacontrast. Therefore the type of theoretical color data which will prove to be the more relevant for prediction of the degree of color specificity associated with an equal luminance metacontrast event will have to wait for an inspection of the spectral extents of the brightness suppression data obtained. Accordingly, this dissertation must begin by making only limited predictions about the data to come. The current study cannot be strong in the rigor of its hypothesis, but it can begin to answer several important preliminary questions. It is the answers to these questions which will generate predictive power. Therefore let me now state both the hypotheses relevant to, and the questions generated by, this work.

HYPOTHESES

1. Wavelength will be an effective metacontrast variable under equal luminance conditions and will produce the classic U-shaped function only with selected wavelength combinations.

2. Homochromatic hue pairings, because they preserve the high degree of stimulus identity present under equal luminance achromatic conditions, will replicate the classic U masking function both in the amplitude of the metacontrast function and in the asynchrony at which peak suppression occurs.

3. Heterochromatic pairings will produce altered metacontrast functions. The modifications in the functions

will be manifest by either a decrease in the amplitude of the masking curve or by a shift in the SOA of peak brightness reduction.

4. A monochromatic inducing field paired with an achromatic test stimulus of the same luminance will produce modifications in the metacontrast function which resemble those produced by heterochromatic pairings of monochromatic lights.

QUESTIONS

1. Will an equal luminance, type B, metacontrast situation be more or less sensitive to wavelength manipulation than is the afterflash effect, a modified type A situation?

2. If the masking functions obtained are of the expected U shape, but the point of maximum suppression does not remain constant across different test-mask hue pairings, what relation do these effects bear to the different cone time constants? What does this imply about the mediation locus?

3. Is the cone-cone independence effect displayed in the afterflash paradigm sustained in an equal luminance metacontrast display?

4. If a mechanism independence is sustained, are the spectral extents of the brightness reduction functions broad or sharply peaked?

5. Do the data clearly support a peripheral cone or $\tilde{\pi}$ mechanism interpretation, or do they favor a more central opponent-process approach, or neither?

How does this relate to the problem metacontrast, one function or many?

We will return to these problems in greater detail in section 4, the discussion.

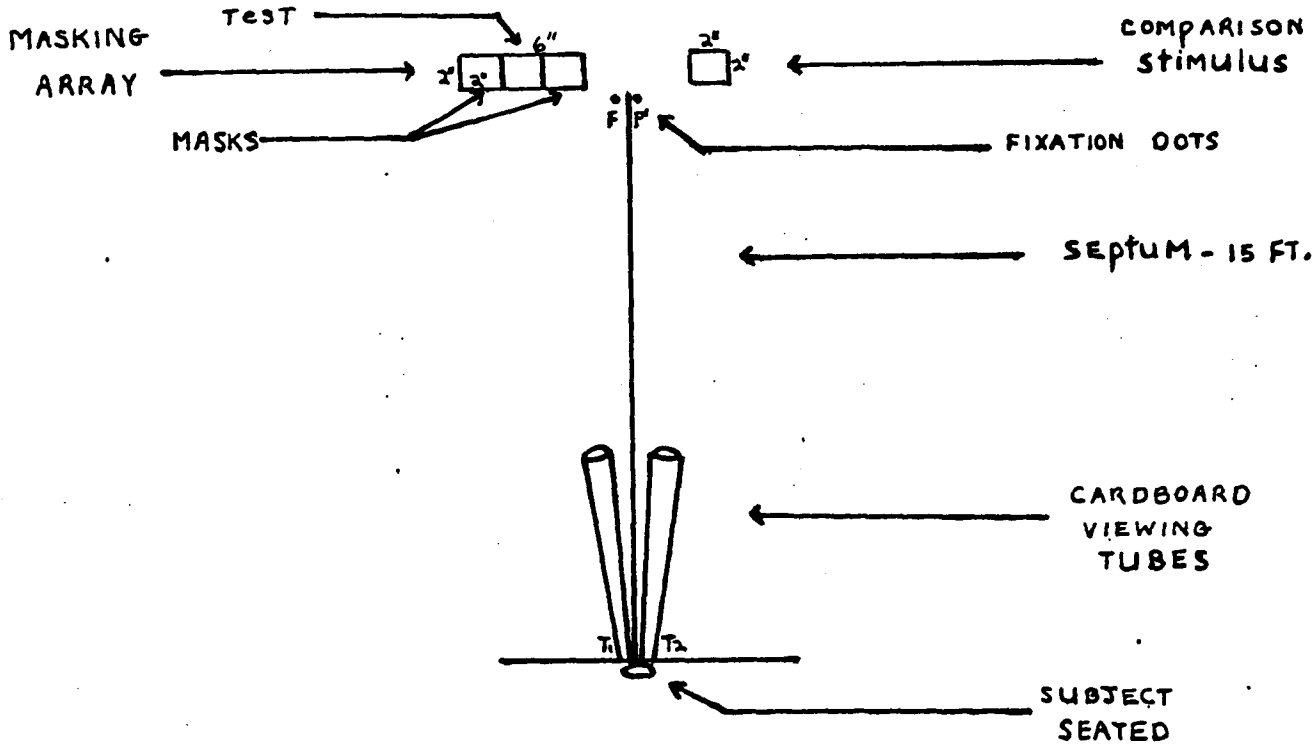
II. APPARATUS AND PROCEDURE

2.1 APPARATUS

The stimulus array and the subject were located in a lightproof room, the subject seated 15 feet in front of the visual display. The portion of the total array to be viewed by each eye was controlled by the use of fixation dots and a septum. E's operating panel and recording sheets were placed in an adjacent room.

The entire visual array was viewed at eye level. That portion of the stimulus display exposed to the left eye was a lighted array composed of three adjacent 2 x 2 inch squares; the right eye viewed a single 2 x 2 inch square comparison stimulus. Since the subject sat in total darkness and was required to use both eyes, it was necessary to provide a fusable binocular fixation point. This was accomplished by using two pin point red lights placed at locations F and F' at either end of a 15 foot long, 3/8 inch thick plywood septum painted black (see Figure 5, p. 65). To further insure against possible visual overlap of the left and right eye views, two cardboard reduction tubes (T_1 and T_2 on Figure 5) were mounted at a convenient eye level via a series of clamps. These tubes allowed an adequate view of the display by each eye and also minimized the effects of stray light.

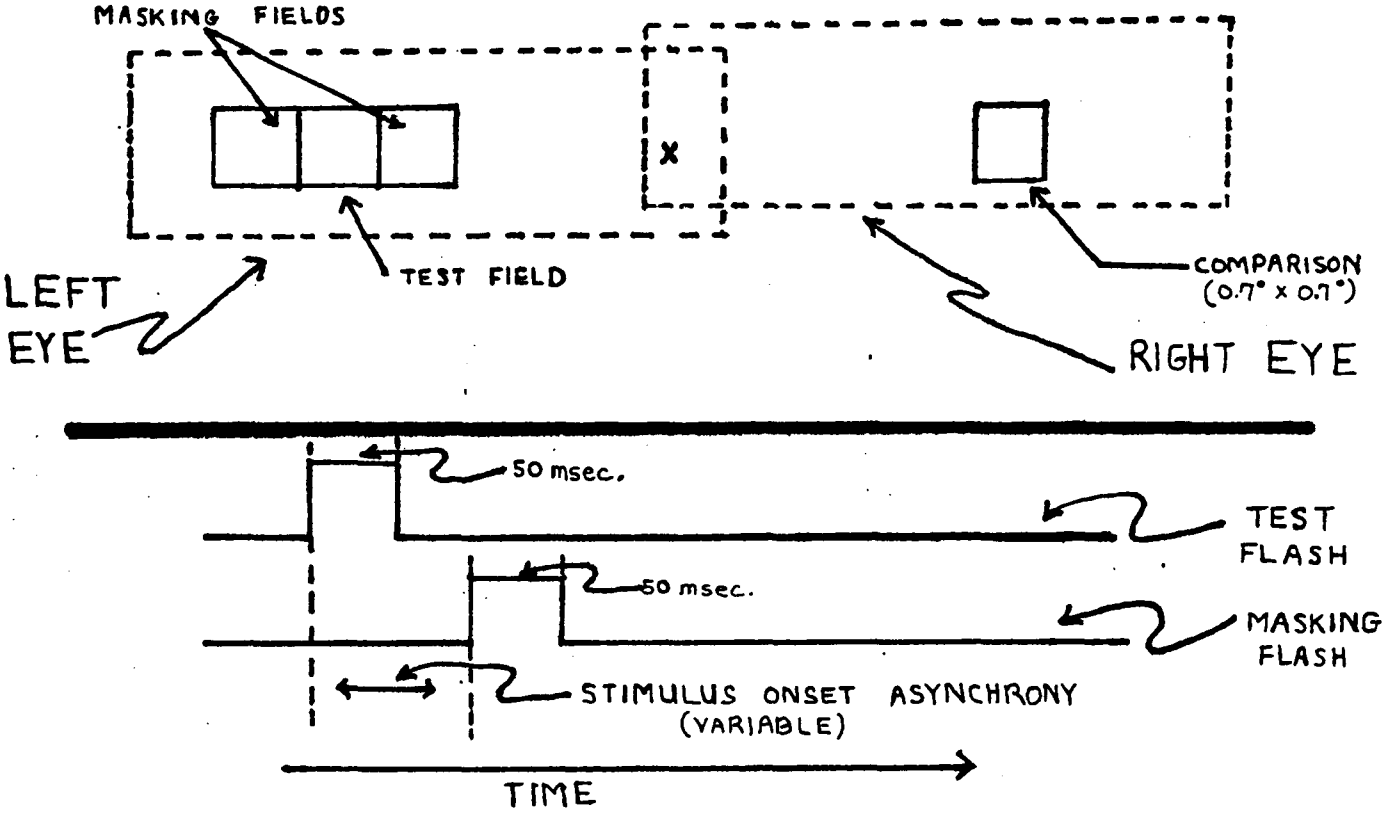
Figure 5. Schematic diagram of stimulus and subject placement within the experimental room.


MASKING ARRAY
TEST
6"
2"
2"
2"
COMPARISON STIMULUS
MASKS
F
F'
FIXATION DOTS
SEPTUM - 15 FT.
CARDBOARD VIEWING TUBES
T1
T2
SUBJECT SEATED

The main stimulus assembly consisted of two fluorescent lamps; one U-shaped, the second linear. Both lights were housed in a single rectangular box which had been divided by wooden septa into three adjacent rectangular cells. The front of each cell was formed by a sheet of 2 x 2 inch milk glass for even light diffusion. The total display presented a horizontal visual angle of 2 degrees to the subject's left eye. A second stimulus box had been constructed to serve as a comparison stimulus for the right eye. It consisted of a similar tubular lamp enclosed within a small rectangular box. The housing contained a 2 inch square aperture which was covered with milk glass to form a lighted 2 x 2 inch cell. The comparison display provided a horizontal visual angle of .66 degrees. All stimuli were presented to the near periphery; the entire visual display occurring between the viewing angles of 2 to 4 degrees horizontal visual angle (see Figure 6, p. 68).

A given stimulus lamp consisted of a cold cathode fluorescent tube placed at the rear of each housing. This lamp type was used in both the three lighted cells of the left assembly and the single cell of the comparison stimulus. All lamps were of the mercury vapor type coated with a calcium halo phosphor. The lamp in the center cell of the left assembly (the test square) was flashed by one circuit and the two flanking cells (the masking stimuli) were flashed together by an independent circuit. Regulated power supplies were

Figure 6. (Top) Fused binocular view of the appearance of the stimulus array.
(Bottom) Sequence of events for each trial.


MASKING FIELDS
X
LEFT EYE
TEST FIELD
COMPARISON (0.7° x 0.7°)
RIGHT EYE
50 msec.
TEST FLASH
50 msec.
MASKING FLASH
STIMULUS ONSET ASYNCHRONY (VARIABLE)
TIME

used throughout. When flashed, each lamp provided a reasonably rectangular pulse of light, the chief departure occurring at offset because of phosphor persistance.

All stimuli were 50 msec. in duration. The right comparison cell was synchronized to flash simultaneously with the 50 msec. test flash. The test and comparison stimuli were always flashed before the masks except when the SOA was zero (see Figure 6, bottom, p. 68).

Spectral stimuli were presented to the left eye only. This was accomplished by the snug placement of narrow pass interference filters against the milk glass diffusing surface of the left visual array. The filters were held firmly against the surface via a series of rubber coated pins which protruded from the wooden surface of the housing which surrounded the milk glass. This allowed for both independent manipulation of the filters used to form each color pairing and for a minimum of play in the filter placements. (Note: At a viewing distance of 15 feet it was not necessary to collimate the light between the source and the interference filter.) The filters used for the display were narrow band, 2 inch square, glass interference filters of the Baird Atomic standard 100 and 150 Angstrom series. Maximum bandwidth at half peak transmission was 100Å ± 20Å or 150Å ± 20Å. This information was verified using the Cary Recording Spectrometer Model 14 CM. The filters selected for use had the following peak wavelengths: 470, 510, 578, 630, 615, 590, 555, and 540

nanometers. Filters produced by Baird Atomic will pass approximately the same energy when placed in front of a light source having an equal energy spectrum. The source used, however, was fluorescent not incandescent. (For spectral energy distribution curve, see Appendix, p. 156.) Moreover, since the human eye will not respond with equal sensitivity to all wavelengths, each filter was modified by the addition of neutral density filters to yield an equal luminance spectrum according to the CIE standard observer curve. All modifications were accomplished with the aid of a Prichard Photometer, model number 298 (see Appendix, p. 158 for Prichard Photometer luminosity function). Luminance measured at the filter surface was made to fall within the range of .22 to .26 ft.L. This range is approximately 1 to 1.5 log units above chromatic threshold and 1.5 to 2.75 log units above absolute threshold for each of the subjects as determined by a method of limits. Once set, this low luminance level was held constant throughout the study.

The right comparison display was always an unmodified cell assembly. However, since no interference filters were used, the overall luminance output was much too great. Neutral density filters were therefore slipped between the fluorescent tube and the diffusing surface in order to bring the general light levels to within the .22-.26 ft.L. range. Fine adjustments could then be accomplished during the psychophysical matching procedure to be described in section 2.2.

2.2 PROCEDURE

The experimental procedure was organized to determine the effects of two parameters: wavelength and stimulus onset asynchrony. The major dependent variable was the apparent brightness of the test stimulus under equal luminance field conditions. A second look at each stimulus was also presented to monitor the accompanying hue and saturation changes. It was assumed that with the proper selection of wavelengths, the standard U function associated with type B metacontrast would be demonstrated as a function of SOA only with certain wavelength pairings. The choice of wavelengths and SOA was based on pilot data accumulated prior to this study. The five SOA selected were used throughout the experiment for each test-mask wavelength pairing until a total of 20 trials at each SOA for each color pairing condition was achieved. The five SOA selected were: 0, 37, 70, 100 and 150 msec. stimulus onset asynchrony.

A meaningful investigation of the principal parameter, wavelength, depended on an adequate sampling of the innumerable wavelength combinations possible between test and inducing fields. Pilot data indicated that some pairings reproduced the classic U-shaped achromatic curve as a function of SOA, while other pairings yielded substantially different results. It was therefore decided that four test-mask color categories plus a control would be used. The four types selected were: (1) test and inducing fields approximated the

unique hues of red, yellow, green or blue and each pairing was composed of the same wavelength; (2) test and inducing fields were composed of substantially different wavelengths but each wavelength approximated a unique hue; (3) inducing fields approximated the unique hues, test fields deviated from these hues to a small degree, i.e., masks-red (630nm), test-orange (615 or 590nm); (4) inducing fields were unique hues but the test field was a neutral light of the same luminance. The control condition consisted of three neutral fields whose luminance was within the same photopic range. The wavelengths selected for use were the following:

Unique hues	Intermediate hues
red - 630 nm.	red-yellow - 615 nm.
yellow - 578 nm.	yellow-red - 590 nm.
green - 510 nm.	yellow-green - 555 nm.
blue - 470 nm.	green-yellow - 540 nm.

The number of color pairings which resulted was 29. This required 9 1/2 weeks of laboratory time for the main experiment for subjects who were scheduled five days per week for one hour per day.

It was obvious that the subjects chosen must not only be well practiced in their task but also willing to return frequently to the laboratory. Three female subjects were used throughout the study; two 19-year-old undergraduates (who participated in the earlier pilot study) and one 28-year-old graduate student. Each subject was tested for possible color impairments using the Dvorine pseudo-isochromatic

plates. Following this, all subjects were given several practice sessions in both magnitude estimation and the color naming procedure.

PRACTICE

Day One.--Each practice session was initiated by five minutes of dark adaptation, after which the center cell of the left assembly was presented in synchrony with the comparison stimulus. On practice day one, the subject was requested to match these lights for brightness using a method of limits technique. Specifically the task was to match the test stimulus alone, constant in brightness, to the comparison field which could be varied in brightness. The comparison stimulus was always a white light, but the left assembly's test square could be any one of the four unique hues. In practice yellow was the first unique hue presented since this was the easiest for the subjects to match with the white light. The other three hues appeared in a random sequence. Ascending and descending series were presented until a maximum of five matches per color were completed. This exercise was necessary to teach the subjects to perform cross-color brightness assessments both as part of the experimental procedure to follow and to facilitate the learning of the more difficult cross-color magnitude estimation task to be described below.

The second step was to teach the magnitude estimation task. Only the center stimulus of the left assembly was presented to the left eye while a comparison stimulus of

variable brightness was shown to the right eye. The square presented to the left eye served as a modulus arbitrarily assigned a brightness value of ten. Again the primary hue chosen for initial training was yellow. Two additional color matches were obtained to compute the average dial setting for the comparison stimulus when it was subjectively equal to the test stimulus. The task was then changed to magnitude estimation and the subjects were requested to rate the brightness of the comparison stimulus exposed to the right eye according to the following directive:

> Now I am going to keep the square on the left at a constant brightness which will remain at the same intensity as your earlier matches to yellow. I'd like you to call this constant a standard brightness of 10. I am going to vary the right square in intensity from bright to dim. I want you to assign a number to the right light according to its relative brightness when compared to the square on the left. If it is twice as bright as the left square, call it a 20. If it is half as bright call it a 5. If it matches the stimulus on the left, call it a 10 and so on. You may use any number you think appropriate to express the brightness. Any questions?

This procedure was continued until either thirty preselected comparison settings were rated for brightness or until the hour was up; whichever came first.

Day Two.--On day two, subjects were again dark adapted for five minutes. As on day one, several brightness matches were made between a yellow test square and the white comparison stimulus. After two or three matches were easily completed, twenty new intensity settings of the comparison stimulus were exposed. Again the colored test square

presented to the left eye served as a modulus of ten. The variable comparison stimulus presented to the right eye was rated as on day one using the magnitude estimation technique. On completion of these twenty trials, one additional match was requested between the test field and the comparison stimulus. The brightness scale reading of the comparison field was recorded on this match and the comparison temporarily fixed at that brightness level. (Note: Calibration of the comparison stimulus was in arbitrary units.) The comparison stimulus would now serve as the modulus for the next step. Since there was no provision for varying the physical brightness of the left array, any variation in brightness must be ascribed to the action of the inducing fields of the left array. Accordingly, all three squares of the left array were then introduced into the practice session at each of the five preselected SOA. The subjects were instructed to rate only the brightness of the center test square relative to the comparison stimulus and to ignore as much as possible the two flanking squares. The task proceeded with great difficulty. Subjects needed constant reminders to keep their eyes on the fixation dot. Many repetitions of a particular presentation were allowed since there was a great deal of involuntary eye movement. At the end of one hour the session was terminated.

Day Three.--On day three, the color naming scheme was explained, discussed, and illustrated via a Munsell color book (for details see p. 78). The subjects were then dark

adapted for five minutes. Two brightness matches between the white comparison stimulus and the colored test square were obtained and the mean of the two ratings was computed. This fixed the brightness level of the comparison stimulus for that session. That brightness level was then arbitrarily set equal to ten for the magnitude estimation task on that day. With the modulus level fixed, the flanking squares of the left stimulus assembly were activated along with the center test square and the subjects began to rate the test square on the left, relative to the comparison modulus on the right as they had on day two. Observations were made at fifteen second intervals to allow for fading of the primary after-images. The particular wavelength pairings selected for practice day three varied with the subject but only the unique hues were presented. (To facilitate rapid learning, the introduction of non-unique hues was delayed until the main experiment.) On day three much time was spent with each wavelength pairing. Each of the five preselected SOA were presented three times in a randomized order so that fifteen brightness judgments could be made for each test-mask wavelength combination. However, beginning on day three, each SOA was presented not once but twice per trial, each occasion separated by the customary fifteen second interval. In all, thirty flashed presentations were rated within each randomized block of fifteen trials. For the first presentation of each pairing within a trial only brightness was rated, for the second presentation hue and saturation were specified.

Early sessions displayed a huge practice effect associated with the ability to keep the eyes effectively fixated for several seconds. Two of the three subjects were not naive in their ability to perform the required visual task. About the middle of day three they began to provide consistent data, their ratings became stable, and we were able to complete four different wavelength pairings within the one hour practice session. It was decided that further practice days would serve no purpose. The third subject, however, was totally naive. It was found necessary to add two additional practice days in order to bring her performance level to that of the other subjects.

THE EXPERIMENT

The procedure utilized for a given session was essentially the same as that already described under practice day three. Each session began with five minutes of dark adaptation, after which the center cell of the left assembly was presented in synchrony with the comparison stimulus. Using the method of limits, the subject was requested to match these lights; one colored, one white, for brightness. The mean of two such matches was computed and this fixed the luminance level of the comparison stimulus for that session. The experiment then began. A given test wavelength was selected for use in the brightness matching, magnitude estimation and color naming tasks. This test wavelength was paired with each of the four unique hue inducing fields in a randomized

block design. Four blocks of fifteen trials per block were presented so that sixty brightness and sixty hue and saturation responses were recorded per one hour session. It was found that brightness ratings of three and below represented trials in which the test field was so dark that no color response could be accurately provided. Accordingly, stimuli were not presented a second time for hue and saturation reports. The procedure continued in this manner with fifteen second intervals between presentations until four blocks per session were completed.

Verbal Report.--Verbal reports were obtained in the same manner as during the third practice day.

Magnitude Estimation.--In the magnitude estimation task subjects were asked to rate the relative brightness of the test flash using the comparison stimulus as a modulus of ten (see earlier description, p. 76).

Color Naming - Hue.--Subjects were requested to name the hue restricting their categories to red, yellow, green, blue or neutral. If the color was an intermediate hue such as orange, it could be designated as red-yellow or yellow-red; the dominant hue name specified first. The estimated per cent of each color composing that hue was designated as "A," more red than yellow in a red-yellow; "B," equally red and yellow; or "C," more yellow than red.

Color Naming - Saturation.--Saturation information was provided on a sliding scale of five to one. Five denoted full

saturation; three, as much color as no color; and one, just the merest hint of color. Total desaturation was called neutral.

It must be noted that all estimates of hue and saturation were made relative to a modulus color which was defined as the color of the test field when presented in isolation. A separate presentation of the test flash alone was therefore provided upon request or when five trials had passed; whichever occurred sooner.

ADDITIONAL PROCEDURES

When the main experiment had been totally completed, two additional procedures were implemented; a threshold procedure and a truncated 655 nm series. The first was undertaken to determine each subject's absolute and chromatic thresholds at each wavelength used in the study; the second to compare the masking functions which result from 655-630 nm and 630-630 nm pairings.

The threshold measures were simply determined using a standard method of limits procedure for each absolute threshold, and a modified method of limits using only the ascending phase for determination of each chromatic threshold. The center field of the left array, presented in total darkness, was used to obtain all threshold measures. The requisite changes in the luminosity of this field were accomplished by the manual addition of neutral density filters to each interference filter package in 1/10 log unit steps. Each

absolute and chromatic threshold represents the mean of two separate determinations.

Some weeks after the completion of the threshold determinations, several additional sessions were presented to assess the masking effects obtained when a 655 nm (red) test stimulus was paired with 630 nm inducing stimuli. The procedure used was essentially a repetition of that employed during the main experiment. Three randomized blocks, each consisting of three trials at each of five SOA, were presented. The first block was to obtain a brightness function for the 630-630 nm pairing typical of that day's performance, the second block was the 655-630 nm test-mask pairing, and the third block was another 630-630 nm series for comparison. This required one experimental session for each subject.

III. RESULTS

3.1 BRIGHTNESS SUPPRESSION EFFECTS

Metacontrast studies which use stimuli equated for luminance are generally presented at a brightness level well above that of the present experiment. Figure 7, which presents per cent brightness reduction vs. SOA in msec. confirms the presence of the customary U-shaped function at a low photopic level. The masking function is clearly U-shaped, its peak is located at 70 msec. SOA for all observers, and all observers produce similar inverted U curves.

Figures 8 through 10 are designed as chromatic analogs to the white light masking functions of Figure 7. Each figure presents data for a separate observer. Per cent brightness reduction (based on the mean of the judged brightness ratings) is again plotted on the ordinate as a function of SOA (in msec.). Each of the four separate quadrants presents all brightness data obtained with a particular wavelength inducing field.

By comparing Figure 7 with Figures 8 to 10, it becomes evident that when test and inducing fields are paired homochromatically, the masking function is similar to that produced in the achromatic situation. Thus, for example, maximum brightness reduction generally reaches levels of 85% or greater at SOA of 70 msec., 70% or greater at SOA of 37 msec., but all functions descend rapidly to 10% or less at other SOA

Figure 7. Individual masking functions obtained using white light stimuli under conditions of low photopic luminance (.24 ft. L.). The ordinate represents per cent reduction in brightness; the abscissa, stimulus onset asynchrony in msec. The achromatic metacontrast functions were plotted individually for each of three subjects; S.E., D.S., and B.M., but have been combined on a single set of coordinates for comparison purposes. Each data point represents the mean result of 20 replications.

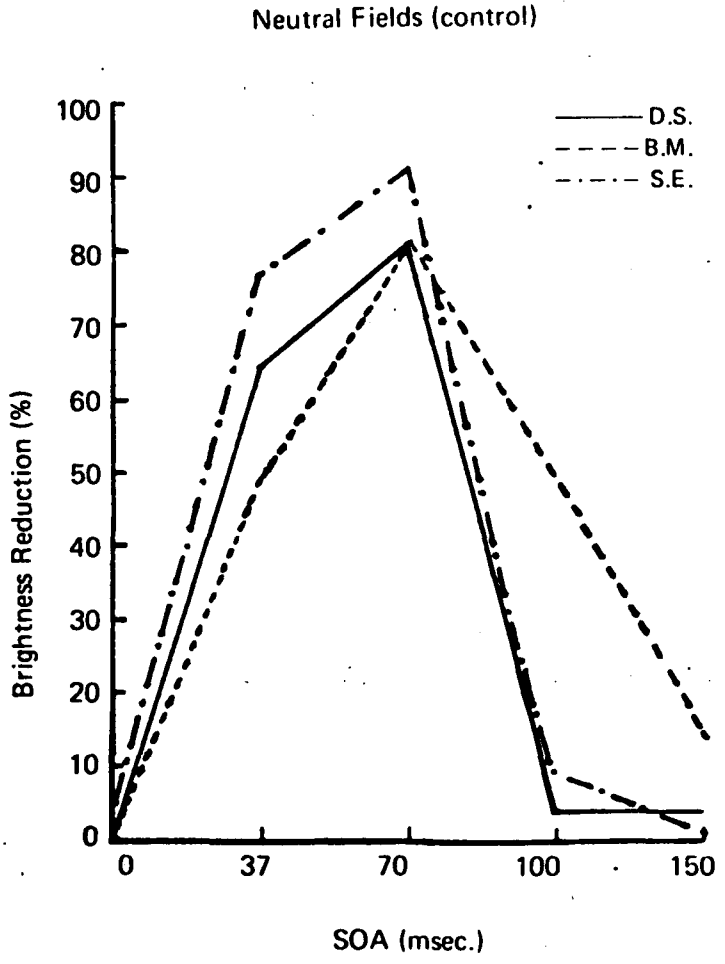

Neutral Fields (control)
D.S.
B.M.
S.E.
Brightness Reduction (%)
100
90
80
70
60
50
40
30
20
10
0
0
37
70
100
150
SOA (msec.)

Figure 8. Brightness reduction functions obtained under chromatic masking conditions for subject S.E. The ordinate represents per cent brightness reduction; the abscissa, stimulus onset asynchrony in msec. The figure is divided into four quadrants, each denoting the pairing of a single masking wavelength with each of several test wavelengths. Each masking stimulus approximates the wavelength of one of the four unique hues as defined by Hurvich and Jameson (1955). Masking stimuli are: top left quadrant--blue, 470 nm; top right--green, 510 nm; bottom left--yellow, 578 nm; bottom right--red, 630 nm. Each data point represents the mean result of 20 replications.

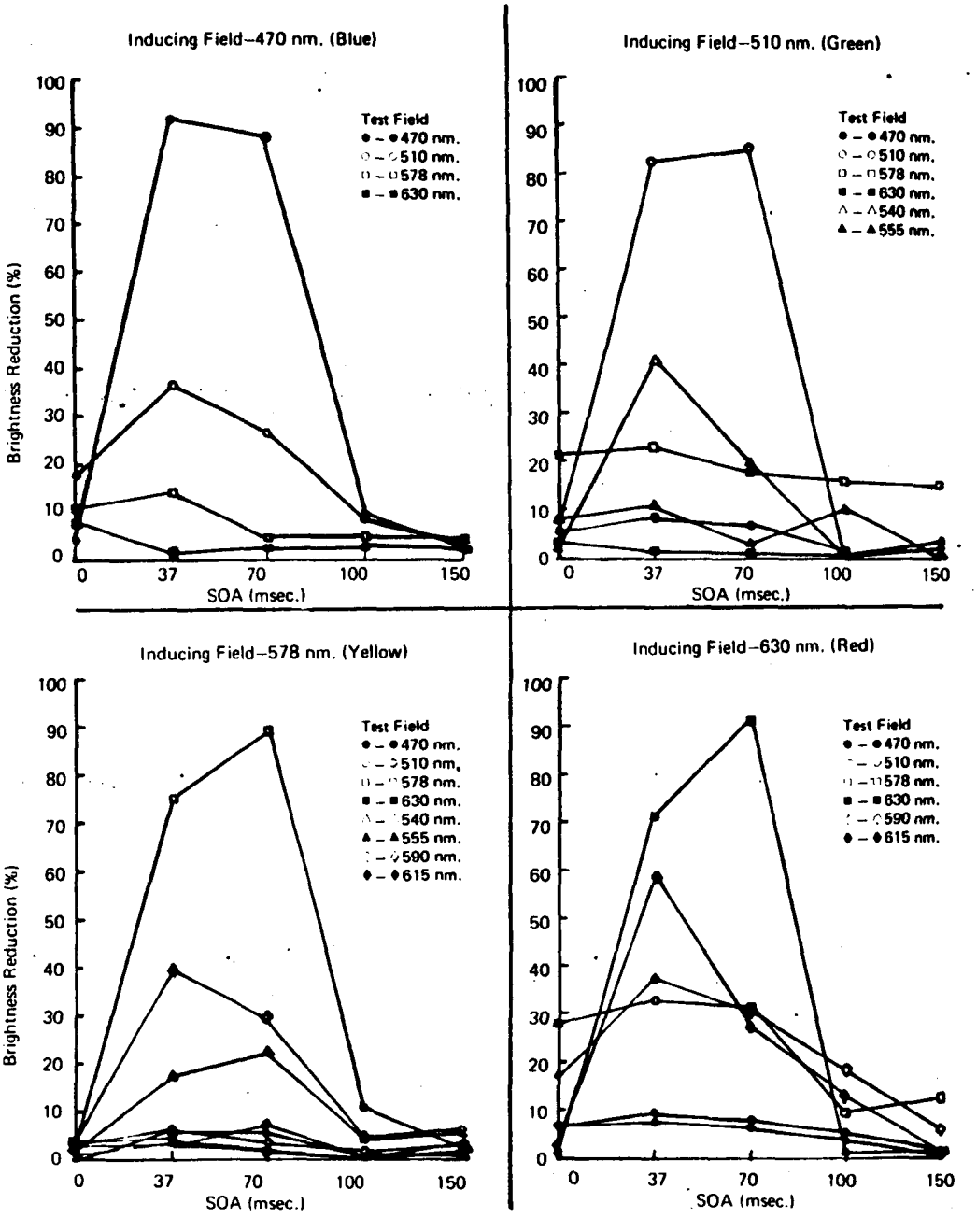

Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
Brightness Reduction (%)
SOA (msec.)
0
37
70
100
150
10
20
30
40
50
60
70
80
90
Test Field
● – ● 470 nm.
○ – ○ 510 nm.
□ – □ 578 nm.
■ – ■ 630 nm.
Δ – Δ 540 nm.
▲ – ▲ 555 nm.
◇ – ◇ 590 nm.
◆ – ◆ 615 nm.

Figure 9. Brightness reduction functions obtained under chromatic masking conditions for subject B.M. For details see legend for Figure 8.

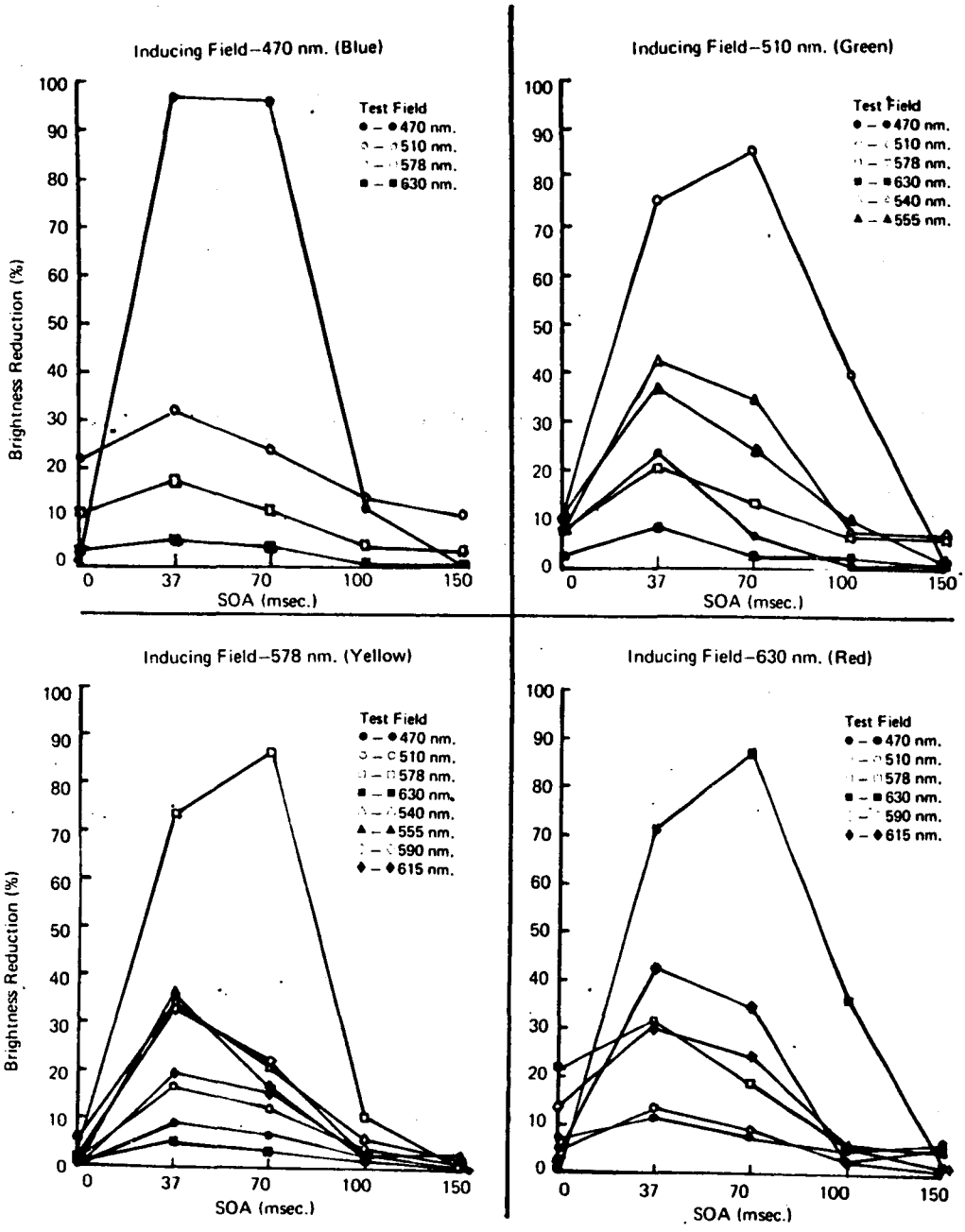
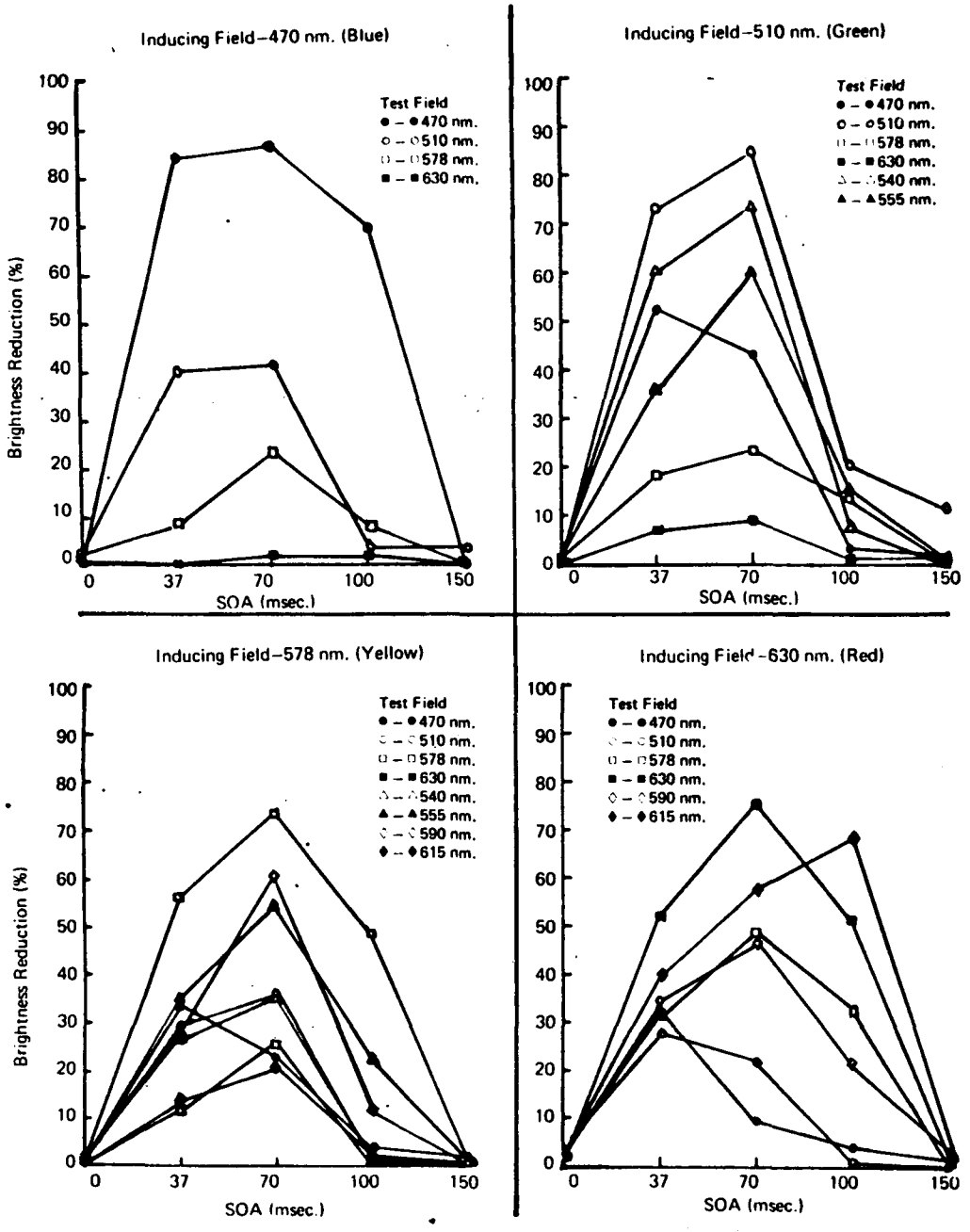

Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
Brightness Reduction (%)
SOA (msec.)
0
37
70
100
150
10
20
30
40
50
60
70
80
90
100
Test Field
● – ● 470 nm.
○ – ○ 510 nm.
□ – □ 578 nm.
■ – ■ 630 nm.
◇ – ◇ 540 nm.
▲ – ▲ 555 nm.
▽ – ▽ 590 nm.
◆ – ◆ 615 nm.

Figure 10. Brightness reduction functions obtained under chromatic masking conditions for subject D.S. For details see legend for Figure 8.

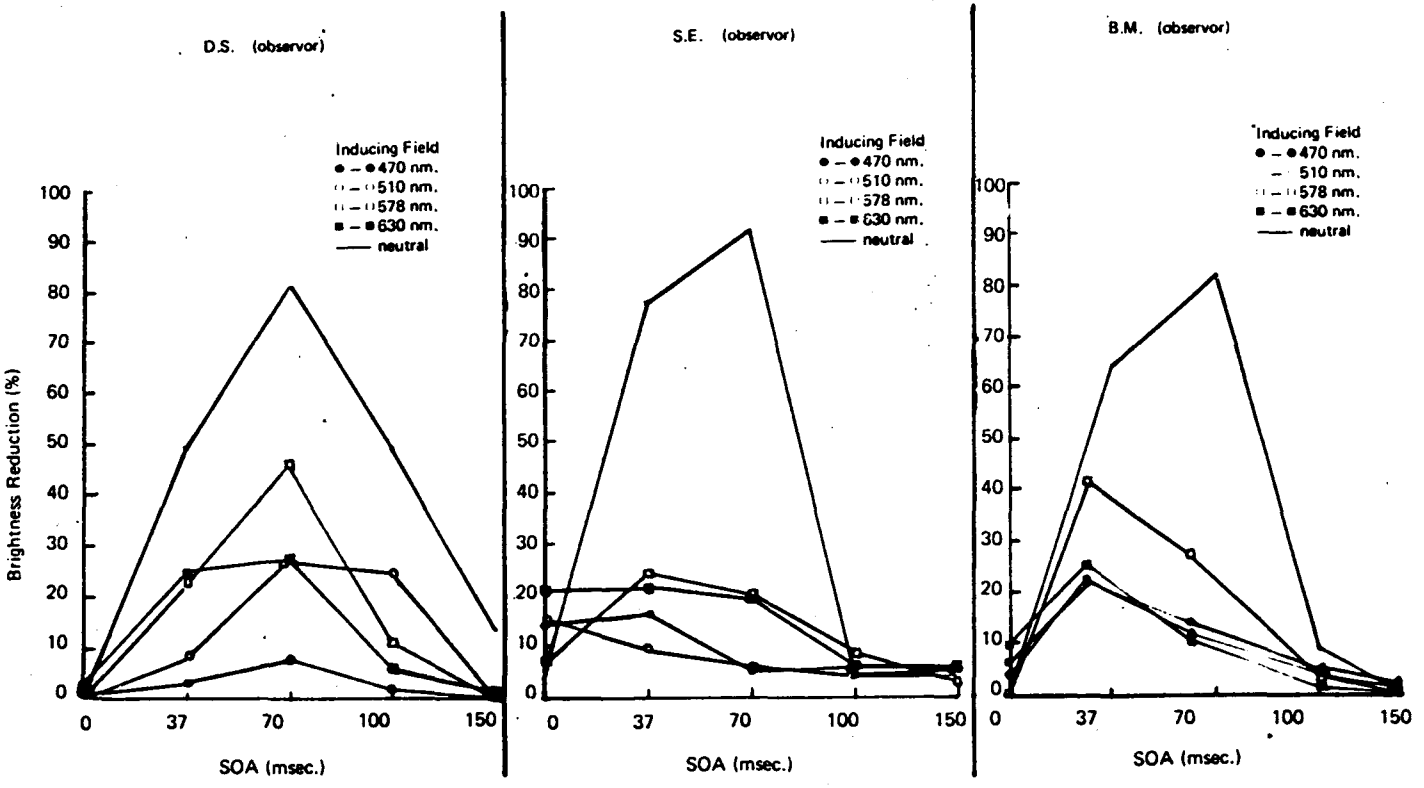

Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
Brightness Reduction (%)
SOA (msec.)
0
37
70
100
150
Test Field
● – ● 470 nm.
○ – ○ 510 nm.
□ – □ 578 nm.
■ – ■ 630 nm.
△ – △ 540 nm.
▲ – ▲ 555 nm.
◇ – ◇ 590 nm.
◆ – ◆ 615 nm.

values. With heterochromatic pairings, functions consistent across subjects are again obtained with two major differences. (1) Heterochromatic pairings produce considerably less brightness reduction at most SOA values; particularly at the 37, 70 and 100 msec. intervals. In general, the greater the wavelength difference between test and inducing flashes, the smaller the masking effect. (2) In heterochromatic situations, peak masking tends to occur at the 37 msec. as opposed to the usual 70 msec. SOA value. This tendency is most clear for subjects S.E. and B.M. (Figures 8 and 9); least so for subject D.S. (Figure 10). In all instances the major trends of the data remain consistent among the subjects although the actual levels of brightness reduction vary somewhat among observers. Subject D.S. tends to display broader metacontrast functions than her colleagues.

Figure 11 presents the brightness data obtained using chromatic inducing fields paired with an achromatic test stimulus. Under mixed chromatic-achromatic conditions the brightness reduction effects are essentially the same as those produced with heterochromatic pairings. Three distinct changes can be noted relative to an entirely achromatic function. (The achromatic functions appear as the top curves for each observer.) (1) Masking is severely reduced. For two observers peak masking drops to around 50% of the achromatic level; 65% for observer S.E. (2) The level of peak masking shows greater variability among the subjects. (3) For two of

Figure 11. Brightness reduction functions obtained when neutral test stimuli are paired with chromatic or achromatic inducing stimuli. The ordinate represents per cent brightness reduction; the abscissa, stimulus onset asynchrony in msec. The top curve indicates the achromatic masking function for each subject; the lower curves display the function obtained when unique hue inducing stimuli are paired with a white light test patch. Left coordinates, observer D.S.; middle coordinates, observer S.E.; right coordinates, observer B.M.

Test Field–Neutral



three subjects there is a consistent shortening of the SOA of peak masking. The rank order of inducing wavelengths in producing a peak brightness reduction effect is first yellow, then green, red, and blue.

In order to emphasize the effects of wavelength independent of SOA, some of the data presented in Figures 8, 9, and 10 have been selected for further analysis. For each test-mask pairing, the brightness reduction value at peak masking and the SOA at which it occurred was noted. The maximum per cent brightness reduction was then plotted as a function of test stimulus wavelength without regard to differences in peak masking asynchrony. For example, in the upper right quadrant of Figure 8, the homochromatic 510 nm pair exhibits peak masking (85.5% brightness reduction) at an SOA = 70 msec. The heterochromatic pairs depicted in this same quadrant show lower masking amplitudes and these peaks occur at 37 rather than 70 msec. SOA. The pairing of each test field (630, 578, 470, 540, 555 nm) with the same 510 nm inducing field produces peak brightness reduction values of 2.5%, 8%, 44% and 11% respectively. It is these masking values which were plotted as a function of test stimulus wavelength to form the upper right quadrant of Figure 12. The same procedure was then repeated for each of the four inducing wavelengths to generate the solid line functions presented for each subject in Figures 12-14.

Figure 12. Maximum brightness reduction as a function of test wavelength for subject S.E. The solid lines plot maximum brightness reduction (on the left ordinate) as a function of the wavelength of the test field in nm (along the abscissa). The dotted function plots mean saturation at peak masking (on the right ordinate) as a function of wavelength along the same abscissa. The figure is divided into four quadrants, each denoting the pairing of a single unique hue masking wavelength with each of several test stimuli. Top left quadrant, blue 470 nm; top right, green 510 nm; bottom left, yellow 578 nm; bottom right, red, 630 nm.

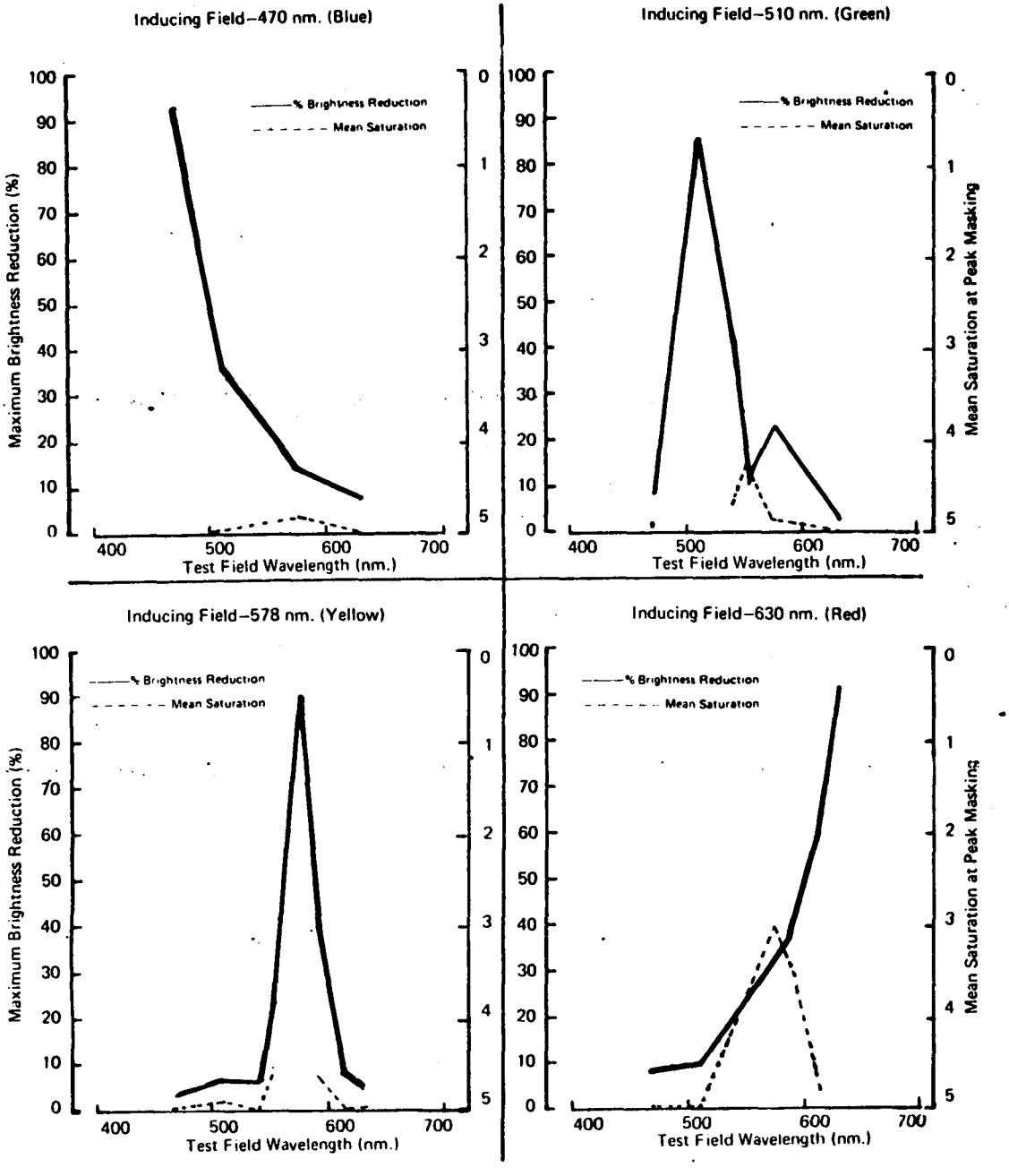

Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
% Brightness Reduction
Mean Saturation
Maximum Brightness Reduction (%)
Mean Saturation at Peak Masking
Test Field Wavelength (nm.)
400
500
600
700
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5

Figure 13. Maximum brightness reduction as a function of test wavelength for subject B.M. For details see legend for Figure 12.

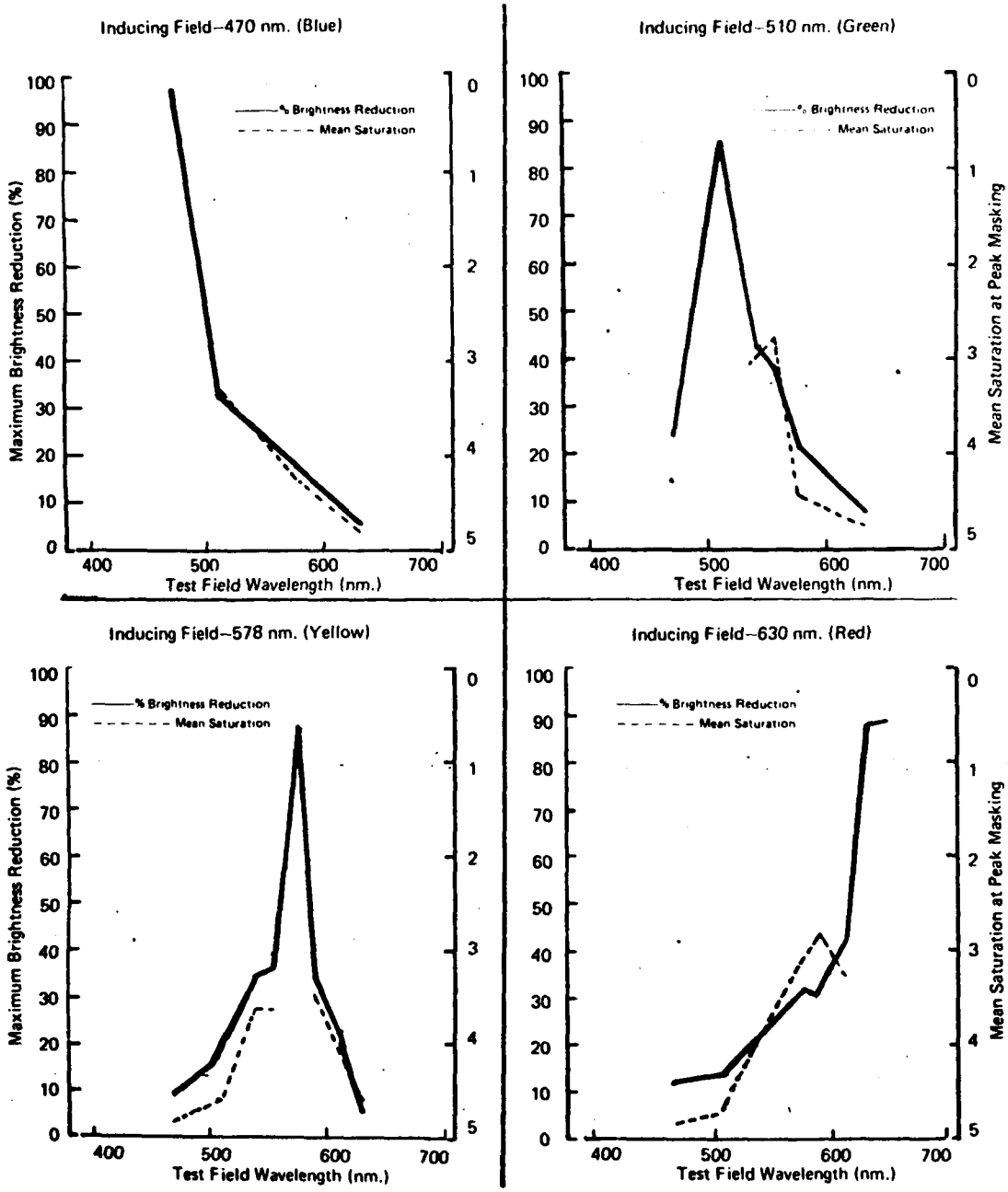
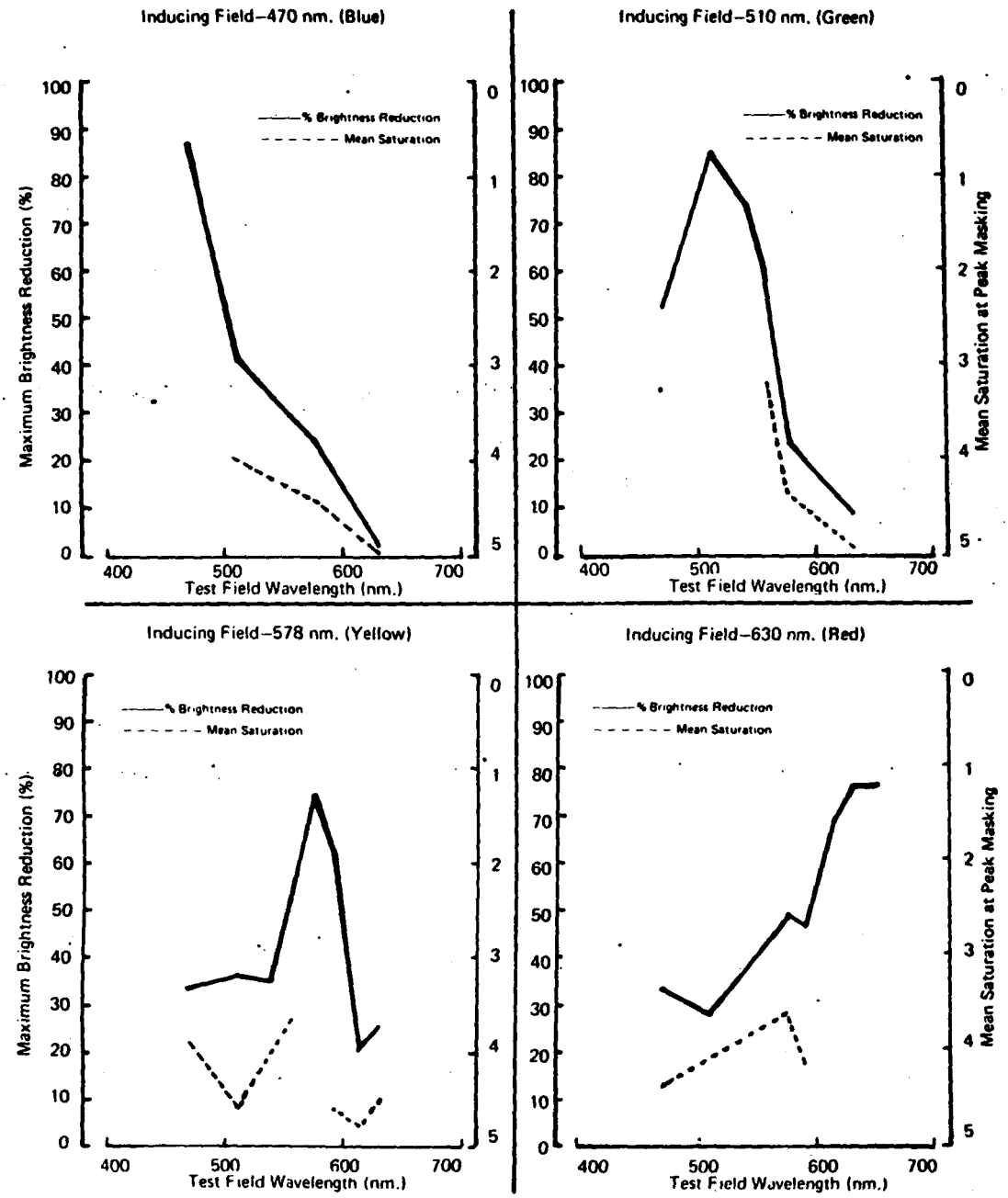

Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
% Brightness Reduction
Mean Saturation
Maximum Brightness Reduction (%)
Mean Saturation at Peak Masking
Test Field Wavelength (nm.)
100
90
80
70
60
50
40
30
20
10
0
400
500
600
700
1
2
3
4
5

Figure 14. Maximum brightness reduction as a function of test wavelength for subject D.S. For details see legend for Figure 12.


Inducing Field–470 nm. (Blue)
Inducing Field–510 nm. (Green)
Inducing Field–578 nm. (Yellow)
Inducing Field–630 nm. (Red)
% Brightness Reduction
Mean Saturation
Maximum Brightness Reduction (%)
Mean Saturation at Peak Masking
Test Field Wavelength (nm.)
400
500
600
700
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5

The functions thus obtained are generally similar in shape for all subjects. Figures 12-14 show peak brightness reduction (on the ordinate) as a function of test field wavelength (along the abscissa) for individual observers. Each curve displays only one distinct peak representing the test-inducing pair at which greatest masking occurs. In all instances this pairing corresponds to the situation in which the test and inducing fields are of the same wavelength. From each peak the curves decline sharply in amplitude as the distance in nm. between test and masking stimuli increases. The functions are quite regular for ungrouped data.

In general, Figures 12-14 support the observation that per cent brightness reduction is a function of the separation in nm between test and inducing wavelengths. It is worth noting, however, that the fall-off in degree of masking is not a simple function of the difference in wavelength between fields. There are marked irregularities in the functions. It is evident from visual inspection that the decrease in masking which accompanies increasing wavelength differences is not the same monotonic function for the four inducing wavelengths. Each curve has its own unique set of irregularities and these specific irregularities are replicated in the curves of each of the subjects. The 470 nm (blue) inducing stimulus produces a sharply decreasing function for all subjects. Peak masking at 97% of total (Figure 13) occurs with a homochromatic pairing and the curve declines rapidly in

amplitude as the difference in nm between test and mask increases. The 510 and 578 nm inducing stimuli produce the same general masking trends. However, in the case of the 510 nm function, the curve is asymmetric and there is a definite function shoulder in the 540-570 nm region. The 578 nm function is also asymmetric, but the asymmetry lies in a different spectral region and the curve is somewhat steeper than the other three. The red (630 nm) function is again a sharply decreasing curve, however, there are two interesting points of departure that appear only in this function. The first occurs in the shorter wavelength region. Unique green and blue test stimuli show approximately the same degree of brightness reduction when paired with red inducing fields. This clearly indicates a leveling off of the red masking function at shorter wavelengths. For subject D.S. (Figure 14) there is an actual decrease in masking as the wavelength of the test patch becomes shorter. A second change in the function exists in the long wavelength region. When the 630 nm masking stimuli are paired with either a 655 nm or a 630 nm test field, the same degree of brightness suppression is produced. That is, the function maintains a masking peak which is unaffected by the introduction of a 25 nm difference in wavelength between the test and masking stimuli. This is the only circumstance in which a homochromatic and a heterochromatic pairing produce equivalent results.

The differences among the four masking functions are not minor. Nonetheless, each one is clearly monotonic and should allow us to predict relative brightness suppression as a function of increasing nm separation. In those functions in which enough data points are available for a more reliable curve to be drawn, there is some indication that the functions do approximate linearity over small spectral ranges. Prediction over these smaller ranges is quite accurate. However, when the spectral range becomes large (40 nm or greater), prediction becomes less accurate since the degree to which these functions deviate from linearity as well as from each other becomes more salient.

One further point should be considered. There is a notable lack of reciprocity between many test and inducing wavelengths. That is, one might expect that a blue mask would have the same effect on a green test flash as a green mask has on a blue test flash. This interchangeability of test and masking colors has not been found. In Figure 12, a 470 nm blue inducing field produces 30-40% brightness reduction when paired with a green (510 nm) test patch, but the reciprocal relation between a 510 nm inducing field and a 470 nm test patch produces 10-20% less masking for two of three subjects (S.E. and B.M.). A similar lack of reciprocity is evident for the red-yellow (630-578 nm) pairings for all three subjects. The asymmetries present are unique to each narrow-band masking function. A green flash does not

affect the blue function to the same extent as a blue flash affects the green function. Blue masks green more than green masks blue. It will be shown later that unless the wavelength separation between fields is small so that both colors are largely mediated by the same color mechanism, little reciprocity can occur. If two mechanisms are involved, one for each stimulus, the underlying spectral response functions will be different and their respective irregularities will prevent perfect reciprocity between test and masking colors.

3.2 HUE AND SATURATION EFFECTS

The measurement of hue and saturation change in stimuli undergoing known amounts of brightness suppression shows that the frequency of occurrence and magnitude of these changes is quite small except in those instances where total or nearly total masking has taken place. (These conditions produce an absence of hue and saturation data because the percept is extremely dark and presumably achromatic.) Consequently, the data as outlined in Table I of the Appendix must be regarded as suggestive rather than conclusive since the overwhelming majority of trials displayed little or no color change.

HUE

With these cautions in mind, let us now consider those hue shifts which did occur. It is notable that all hue shifts appeared to be largely uncorrelated with the exact magnitude of the brightness suppression obtained except when the

stimulus appeared extremely dark (judged as 3 or less in brightness). Since the experimental design unfortunately precluded the taking of hue information for very dark stimuli, the trials most likely to display hue changes would be those in which a partial masking or darkening effect was observed. In general, the results indicate that the direction of change was away from the wavelength of the inducing hue. These effects were small and occurred only infrequently.

There are two types of situations which can lead to moderate brightness suppression: (1) exposure at SOAs other than 37 or 70 msec. for many wavelength combinations, and (2) the presentation of heterochromatic pairings which utilize test fields of non-unique hue. Homochromatic pairings produced no hue shifts at all SOA since only one wavelength was present in the visual display. Unique hue heterochromatic pairings produced extremely little masking so that changes in hue were again unlikely at all SOA. Accordingly, it is only those metacontrast situations which resulted from the pairing of non-unique hue test stimuli with the four inducing wavelengths that produced occasional hue shifts. Several examples exist to illustrate the main trend of the data, i.e., a shift away from the wavelength of the inducing color. Test fields of 540 nm and 555 nm paired with a green (510 nm) inducing flash showed a small shift toward yellow 42% and 35% of the times respectively for subject B.M. A red inducing stimulus (630 nm) shifted a 590 nm test flash toward yellow 22% of the

time for observer D.S., while a yellow inducing field shifted 590 nm toward red 30% of the time. Subject B.M. followed the same pattern to a lesser degree for a 615 nm test field. There were only two instances of moderate color induction toward, rather than away from, the inducing wavelength. In both instances an orange stimulus appeared redder when paired with red (630 nm) masking stimuli. (For greater detail see Appendix, Table I, columns 9, 10 and 11.)

SATURATION

Let us now consider saturation changes independent of hue shifts. Limited effects were again shown. The dotted line functions of Figures 12 through 14, plotted as mean saturation at peak SOA (right ordinate) against test field wavelength (along the abscissa), closely parallel the solid line functions, plotted as per cent brightness reduction at peak masking (left ordinate) vs. test field wavelength, for two out of three subjects (Figures 13 and 14). There is a tendency in all cases toward an inverse relation between per cent brightness reduction and mean saturation. As masking increases, mean saturation decreases.

Unfortunately masking under homochromatic conditions was not monitored for saturation at SOA in which the test field appeared extremely dark. It is specifically this condition which produced a huge saturation change. In each saturation function there is a blank spot at the wavelength settings which correspond to the four homochromatic pairings.

Heterochromatic pairings which involved only the four unique hues produced no substantial desaturations with any wavelength combination. Exceptions were minor effects which occurred when a 630 nm (red) inducing field was paired with a 578 (yellow) test flash for all three subjects and some green-blue (510-470 nm) pairings for subjects S.E. and D.S. It was only those heterochromatic pairings which utilized non-unique hue test stimuli (540, 555, 590, 615 nm) that produced moderate desaturation effects. However, even in these instances desaturation was limited. A moderate to large reduction in brightness influenced saturation to only a small degree so that at no time did the mean saturation readings dip below 2.75 on a 5 point scale. (For greater detail concerning these effects for all subjects consult the Appendix, Table I, columns 6, 7 and 8.)

The infrequency and generally small magnitude of the changes which have been recorded for hue and saturation makes it difficult to properly assess the exact nature of the color effects which accompany large fluctuations in apparent brightness. Partly this is caused by a lack of adequate sensitivity in the dependent variable and the absence of color information for trials rated as three and below in brightness, but partly it seems to be the result of a magnitude difference in the response characteristics of the two aspects of the stimulus. While it is true that better methodology might yield less equivocal results, this will not compensate for a basic

difference in the way these two aspects, brightness and color, respond to metacontrast masking events.

IV. DISCUSSION

4.1 THE U-SHAPED FUNCTION

Figure 7 confirms the presence of a U-shaped, type B metacontrast function at a low photopic level. Figures 8 through 10 further indicate that under chromatic conditions similar U-shaped masking functions can be obtained, and that these functions are readily altered by manipulations which introduce a color difference between the test and masking fields. The degree of physical similarity possible in all dimensions in achromatic metacontrast can be duplicated in a chromatic array only with homochromatic pairings. It is noteworthy that these same homochromatic pairings constitute the only chromatic condition that generates U-shaped functions similar to those obtained with an achromatic array. As long as complete dimension identity is maintained, neither the magnitude of the masking function nor the interval at which maximum brightness suppression occurs is appreciably changed by the introduction of color to the array.

Departures from chromatic identity which occur as the result of heterochromatic pairings or chromatic inducing fields paired with white light test stimuli produce marked alterations in the U functions. In these instances there is considerably less brightness reduction at any time interval (i.e., a flattening of the function) as well as a trend in two out of three subjects for the function to peak at the

shorter asynchrony of 37 msec. Both these effects are in accord with qualitative predictions based on the kinds of function modifications observed with other parameters (cf. introduction, section 1.1). However, aside from noting that the various heterochromatic pairings produce modifications in the metacontrast function which resemble, to a degree, those produced by other parametric manipulations, it would be imprudent to assume that there is any common cause underlying these changes.

How then can we begin to analyze the situation? It is evident that there are three aspects of the results which must be explained: (1) the replication of the U-shape achromatic function with homochromatic pairings, (2) the decrease in masking with heterochromatic pairings, and (3) the specificity associated with equal luminance metacontrast events. The first two features are not inconsistent with the cone-cone independence model proposed by Alpern and Rushton (1965) for a different chromatic metacontrast situation (see section 1.4). Let us therefore begin by looking more carefully at the processing of achromatic, homochromatic and heterochromatic masking events at the most peripheral receptor levels.

In achromatic metacontrast, the white lights used for both the test and masking stimuli are often similar in spectral composition. Each achromatic stimulus elicits a specific level of activity within each of the three cone types. If the lights are equated for size, luminance and spectral

composition, the activation pattern produced by the masking stimulus should be identical to the activation pattern produced by the test stimulus. Although different cone cells are activated on two occasions because of spatial factors, the same classes of cones or the same types of mechanisms will be activated to the same extent by both stimulus events.

It is precisely this sort of replication in the cone excitation pattern for two identical events that occurs in the homochromatic masking situation. The only difference is that the dominant wavelength and general luminance level will determine whether it is one, two or three cone types which participate in the mediation of the test and inducing fields. However, since the general rules for mediation by cone types is not changed whether it is one cone type or several cone types which participate, identical events should produce identical consequences. Brightness suppression (masking) may be accomplished at the retinal level as proposed by Alpern and Rushton, or central to this site. Either possibility will not alter the point that at the retinal level at least, achromatic masking events of photopic luminosity and homochromatic hue pairings both produce a replication in the stimulus excitation pattern at the cone or $\tilde{\pi}$ mechanism level. There is nothing at these early visual stages which should prohibit the masking function obtained under homochromatic masking conditions from replicating in all ways the achromatic masking function. As stated earlier, achromatic and

homochromatic masking functions are quite alike in respect to shape of the function, extent of the masking, and point of maximum brightness reduction.

The heterochromatic masking situation differs from the one described above. A dominant wavelength present in the test stimulus but not reproduced in the inducing stimulus will generate an excitatory response pattern which differs to various degrees from the one representing the inducing color. At equal luminance there would be no two wavelengths at a minimum separation of 15 nm which could produce identical cone excitation patterns.

A second factor which must be considered for the heterochromatic situation is the difference in response times associated with each peripheral mechanism. In general, under photopic conditions, the magnitude of these time differences is regarded as small, i.e., 30 msec. or shorter (Frumkes et al., 1973; Krauskopf, 1973; Mollon & Krauskopf, 1973; Goldstein, in preparation). Nonetheless, even small time differences may serve to exaggerate minor differences in the excitation patterns of heterochromatic stimuli to produce heightened stimulus differentiation at the next processing level. It should be briefly mentioned that it is improbable that it is these time differences which are responsible for the shortening in the SOA of peak masking amplitude. Differences in cone response times should be reflected in both an increase and a decrease in the SOA of maximum suppression

with different wavelength combinations. In this study only shortened peak asynchronies were evident.

The arguments presented here do not in any way establish the locus of metacontrast masking; nor do they preclude the possibility that masking may occur at a retinal level. All that is being asserted is that at some peripheral cellular level, probably the cones, adjacent stimuli of the same hue and of equal luminance produce equal physiological events, and that non-identical hues do not produce these equivalent events. Interference effects via lateral inhibition, or any other mechanism one can postulate, may still occur at the next cellular level. However, since the data showed that the hue aspect of each stimulus persists largely unchanged over large fluctuations in apparent brightness, a color signal sufficient to maintain the percept of a particular hue must be preserved at these most peripheral receptor levels. If this were not so, one should observe large color changes. Large hue shifts plainly do not occur (see discussion section 4.4). The simplest assumption, therefore, is that at the peripheral level, the relative excitation pattern is preserved to an extent sufficient for color cueing.

One further point should be added. It is possible that type B metacontrast is the result of an interaction rather than an interference effect (Eriksen & Collins, 1965; Eriksen et al., 1970; see also the "decision neuron" concept of Weisstein's 1968 neuron network model). Metacontrast could be

assumed to be the result of a combination of two signals, the test and the mask, to produce a third signal which differs from either of these inputs. This situation, usually denoted as interaction, is the more likely suppression model here. In an identical size, equal luminance metacontrast event, there are no stimulus latency differences. Hence, it is not likely that an overtake interference hypothesis could be supported in this situation. There is nothing about the data per se to distinguish between these two possibilities. Nonetheless, if we assume a cone-cone independence model (Alpern & Rushton, 1965), we can add the assumption that any cross channel interactions which might occur would probably take place at some locus proximal to the cones or $\tilde{\pi}$ mechanisms since these mechanisms have been shown to act independently for at least some metacontrast situations.

In summary, it appears that the presence of the customary U-shaped metacontrast function under selected chromatic conditions is not inconsistent with a simple peripheral cone or mechanism model. However, there is one important aspect of the data which does not easily conform to such an approach; the extreme narrowness of the spectral extent over which substantial degrees of metacontrast suppression can be achieved. Let us therefore turn to a consideration of this aspect of the data.

4.2 THE SPECTRAL EXTENTS AND IRREGULARITIES OF THE PEAK BRIGHTNESS SUPPRESSION CURVES

Let us assume that the degree of maximum masking produced with each color pairing is predictable from the underlying spectral response curves activated by that pair. If the primary receptors were the appropriate site for the mediation of type B metacontrast suppression, then the peak masking functions should reflect the broad spectral extents characteristic of the cone spectral response curves.

The spectral extents of the peak brightness suppression curves (Figures 12-14) do not conform to a cone or $\widetilde{\pi}$ mechanism approach. Each curve displays one distinct peak representing the color pairing that produces the greatest brightness suppression. In all instances this pairing corresponds to the homochromatic condition. This aspect of the data is in accord with a possible cone or $\widetilde{\pi}$ mechanism approach. However, the critical point is that from each peak the curves decline rapidly in amplitude as the difference in wavelength between test and masking flashes increases. This reduces the spectral extent of each masking function until it becomes severely limited for all but the most minor suppression effects. Clearly such narrow spectral ranges are not easily reconciled with the broad spectral sensitivity functions of the primary receptors. To further complicate matters, cone spectral sensitivity functions must be modified to make them analogous to the present equal luminance situation. These modifications serve only to further flatten each function and make it

still more dissimilar to the sharply peaked curves under consideration.

The divergence between the present findings and the cone spectral response curves is also enhanced by irregularities unique to each peak masking function. According to the Darnall nomogram (1953), each primary photopigment has the same shaped quantal absorption function when plotted as a function of wavenumber. The curves are asymmetrical but all have the same asymmetry. In the current situation, the decrease in the degree of masking was not a simple consequence of the difference in wavelength between test and inducing fields. There were marked irregularities characteristic of each function but no two of them were alike. (For a fuller description see section 3.1.) Recall that there was also a certain lack of reciprocity between test and inducing wavelengths. It was often not possible to interchange the test and inducing wavelengths and still obtain the same per cent reduction in brightness.

If the peak suppression functions were to reflect the action spectrums of the primary receptor types, then the function irregularities which occurred and were replicated among the subjects must remain totally without physiological basis, i.e., an experimental artifact. In view of the cross-subject reliability of these function asymmetries, it is not justifiable to insist that per cent brightness reduction be a linear function of wavelength separation between test and

inducing fields. The departures from linearity within each function and the degree of variability in shape between functions is too compelling to justify an experimental error approach. Indeed, it will become obvious in the next section that these irregularities do in fact occur in a manner consistant with the spectral characteristics of a different class of cells; the opponent process color mechanisms.

4.3 PEAK BRIGHTNESS SUPPRESSION CURVES AND THE OPPONENT PROCESS FUNCTIONS

The narrow spectral extents of each peak suppression curve makes it obvious that test and inducing stimuli which have been equated for luminance do not produce large masking effects over a broad spectral range. Hence it is not plausible in the current situation that the cones which primarily mediate the dominant wavelength of each test and inducing field are the cells that form the locus of suppression in equal luminance metacontrast events. Moreover, the disparity between the obtained data and more inclusive color functions such as Stiles' $\tilde{\pi}$ mechanisms, further serves to emphasize the fact that our data cannot be predicted from any peripheral color response measure. A more central mediation hypothesis must be considered. Further support for a central mediation approach can be derived from the various curve-specific irregularities noted in the current functions. These irregularities are not haphazard in occurrence but they do remain incompatible with expectations based on the Dartnall (1953) nomogram.

It is worth noting that there is good reason why these data should be inconsistent with the cone or $\tilde{\pi}$ mechanism explanation appropriate to the work of Alpern and Rushton (1965). The afterflash or contrast flash paradigm elaborated earlier closely resembles that of type A metacontrast. A large disparity exists between the luminance-duration package delivered for a near threshold test field and the energy package delivered for the high intensity inducing field. This situation was utilized by Alpern and Rushton (1965) to derive threshold measures for each colored test field as a function of increasing afterflash effective intensity on a particular mechanism. Three things must be considered: (1) type A metacontrast displays peak masking at an SOA equal to zero, that is, at simultaneity. To this extent type A resembles simultaneous contrast. (2) In Alpern and Rushton's metacontrast scheme, test and inducing fields were not the same stimuli. There was equivalence of neither shape nor size. A small test stimulus surrounded by a large inducing field mimics the physical situation often associated with simultaneous brightness contrast. (3) Most important, Alpern and Rushton's (1965) test and inducing fields differed dramatically in luminance. All test fields were at threshold, but the inducing stimuli varied from bright to extremely bright. Again, this serves to simulate the conditions for a simultaneous contrast effect. If simultaneous brightness and/or color contrast effects are favored by the stimulus situations

used to produce type A masking, as the SOA of peak suppression would imply, then large brightness and size disparities between stimuli should produce a substantial simultaneous suppression effect. The magnitude of this early blocking activity would effectively preclude the further measurement of lesser interference or interaction effects which might also occur proximal to these loci. Under these conditions, the functions obtained would be broad in spectral extent because it is the cones or $\tilde{\pi}$ mechanisms which are mediating the brightness suppression (Alpern & Rushton, 1965).

Simultaneous contrast effects are not, however, facilitated by the equal luminance metacontrast situation used here. If all fields are equated for luminance, duration and size, there is little peripheral blocking which can occur (Heinemann, 1972). The current situation clearly does not favor a peripherally mediated effect such as the simultaneous brightness suppression noted in type A masking. Suppression effects which are recorded when stimuli are equal in luminance will probably be those which occur central to these loci. That is, the signals which emerge from the receptor level and proceed toward a more central locus will, at a point <u>proximal</u> to the receptors, undergo suppression (masking) effects. The spectral characteristics of equal luminance metacontrast functions should reflect this more central mediation.

The data obtained show narrow spectral functions; functions much narrower than those which should be determined

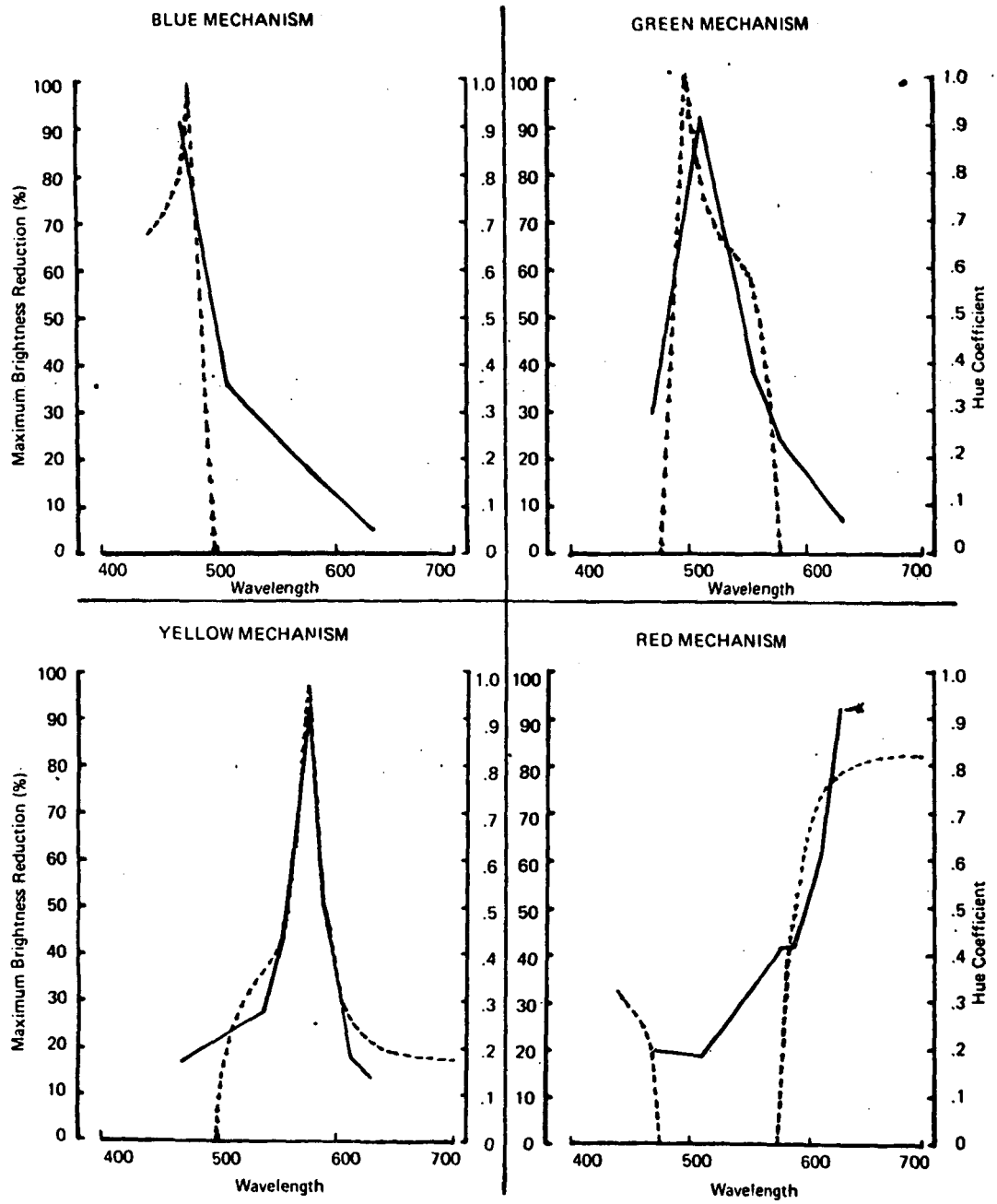
by single receptor classes. The only way in which such narrow spectral functions can be obtained in the visual system is by some form of inhibitory or subtractive interaction between different cone types. Obvious candidates to consider are the responses of the opponent mechanisms. If masking is mediated at the level of opponent processes, then the obtained spectral functions should reflect the degree to which both test and masking stimuli activate the same opponent mechanism class. In order to make such a comparison, we would need to know the spectral responses of the various opponent mechanisms in a situation comparable to the one used in this experiment. That is, we would like to know the spectral response functions of these mechanisms when using monochromatic stimuli of equal luminance.

From the sources cited earlier, it appears that there are four basic opponent processes which mediate, respectively, the phenomenologically unique hues of red, green, yellow and blue. In the present experiment, the masking stimuli were chosen to approximate closely these unique hues and therefore each would activate only one of the basic opponent systems. Thus, to the degree to which masking depends on the activation of the same type of opponent process by both test and mask, one could predict that the spectral ranges of the results would follow the response functions of the particular opponent processes involved. The physiological recordings of De Valois and his co-workers in the macaque lateral

geniculate nucleus (LGN) were obtained using stimuli equated for energy rather than luminance. Since they have also published functions relating response amplitude and light intensity, it would be possible to derive the responses of the opponent channels to equal luminance stimuli. However for human observers there is a more direct route. The opponent process psychophysical data derived by Hurvich and Jameson agree quite well with macaque physiological recordings. Since the Hurvich and Jameson functions were obtained for conditions of equal luminance, it seems more appropriate to make use of them. The curves given by Hurvich and Jameson (1955) for the hue coefficients at any given wavelength represent the relative magnitudes of the responses of the four basic mechanisms to various stimulus wavelengths when they are equated for luminance. I propose, therefore, to compare the brightness reduction functions obtained here, with the hue coefficient functions of Hurvich and Jameson. The assumption underlying this comparison is that when the same opponent process types are stimulated by both test and mask, these processes will interact to a degree proportional to the responses generated in each mechanism class. This will be treated in greater detail in section 4.4. The relevant question now is the extent to which the peak brightness suppression functions resemble the opponent process functions.

Figure 15 plots the maximum brightness reduction curves and the hue coefficient curves on the same set of

Figure 15. Peak suppression responses averaged for three subjects and plotted on the same coordinate as the hue coefficient curves of Hurvich and Jameson (Hurvich & Jameson, 1955). Hue coefficient curves are presented as broken lines; peak suppression curves as solid lines. Responses of individual subjects appear as shape keyed data points. (□ -S.E., O -B.M., Δ -D.S.)


BLUE MECHANISM
GREEN MECHANISM
YELLOW MECHANISM
RED MECHANISM
Maximum Brightness Reduction (%)
Hue Coefficient
Wavelength
400
500
600
700
0
10
20
30
40
50
60
70
80
90
100
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0

coordinates. These functions show that agreement between the obtained data and opponent process spectra is reasonably good for each of the four functions except at a few points. The 578 nm (yellow) inducing wavelength corresponds closely to the locus of the unique hue of yellow as specified by Hurvich and Jameson (1955). In this case agreement between the obtained and theoretical functions is nearly perfect. The green, 510 nm inducing wavelength is 12 nm longer than the Hurvich's unique green. Nonetheless, except for a peak displacement because of this factor, agreement between the functions is quite good. It is interesting to note that even the green function shoulder found in the 520-560 nm region, though washed out by grouping the data, occurs for all individual subjects in approximately the same wavelength region. Unfortunately, the closeness of fit present in the green and yellow functions is less evident for blue. Again the blue inducing wavelength does not fall at the precise point of unique blue, hence a slight peak displacement is evident. More important, however, is that while the blue function shows the least variability among subjects, it is consistently a broader function than the extremely narrow one specified by Hurvich and Jameson. A possible explanation will be given later.

The red function, at first glance, shows the least apparent concurrence between opponent process and masking data. Nonetheless, these discrepencies can be minimized by

consideration of the inherent differences between the red masking stimulus and the red hue coefficient. The red hue coefficient curve reaches an asymptote at 0.8 rather than 1.0 as do the curves for each of the other unique hues. That is, there is no wavelength which appears uniquely red. A great deal of yellow is always apparent no matter how long the wavelength. This is not inconsistent with our metacontrast findings; it only complicates the issue. When a 630 nm test flash is homochromatically paired with a 630 nm inducing flash, the maximum masking achieved approaches 100%. If both the red and yellow mechanisms participate in mediating the 630 nm test flash hue, they also participate in mediating the 630 nm inducing flash hue. Therefore, although two opponent mechanisms are strongly activated rather than one, masking will be maximal. What is crucial is the fact that the red masking function asymptotes at all. In the main experiment there was no heterochromatic pairing which produced brightness suppression effects equal to those achieved with homochromatic pairings. An asymptote in the red function at wavelengths beyond 630 nm indicates that this area of the spectrum is an important exception to that rule. The red masking function mimics the asymptote of the red opponent function showing that it too ceases to become functionally redder. The major discrepancy between functions lies not at their relative peaks as visual inspection might imply, but at the 510 nm point for the red inducing curve. Partly the inflated placement of

this point is due to one subject (D.S.), and partly it occurs because the 630 nm inducing field is not a unique hue. Two points should be considered. First, the yellow process contributes substantially to the 630 nm inducing flash, and second, the yellow function still produces around 20% brightness suppression at 510 nm. The red masking function shows about the same 20% masking for this point. One plausible explanation for the unexpected level of brightness suppression at this test wavelength is that it is the yellow process, still present, which is mediating the masking effect. To a lesser degree this may also account for some of the masking which occurs at 470 nm, although at 470 nm the red function is beginning to reassert itself. An interesting point is that in the short wavelength region there is a leveling off of the masking function rather than a further decrease in brightness suppression as the difference in wavelength between test and inducing fields increases. Again, in its gross points, this aspect is also consonant with the reactivation of the red opponent process in the short wavelength spectral region.

Similar sorts of considerations can be taken into account when examining the discrepancies between the metacontrast data and each of the other opponent functions. One must note that the inducing wavelengths used here were not necessarily unique hues for each individual subject. The functions of Hurvich and Jameson are representative but are

by no means exact for all observers. For example, Boynton and Gordon (1965) show that the color naming curves for individual subjects, though they agree in general with the opponent process curves used here, do not replicate them exactly. Similar findings were obtained by Gordon, Abramov and Imperato (1973). They, together with Boynton, Schafer and Neun (1964), have also added the information that as one moves away from the fovea, the spectral extent of blue increases. This broadening of the spectral range of the blue process as one moves into the periphery appears to be reflected in the current data as well. All these considerations taken together are probably sufficient to account for the minor discrepancies in Figure 15. The important point is that the present curves are generally as narrow as those of opponent mechanisms and indeed agree closely with them.

To summarize briefly: there is excellent agreement between opponent process data and masking data for the green and yellow mechanisms. The opponent spectral functions are matched both for function shape and for spectral extent except for some low level side shoulders. Blue shows a broader spectral range in the masking function than in the opponent data. This fact remains partially unexplained. Red also shows points of disagreement between the obtained and opponent functions. However, closer inspection of inherent differences characteristic of the two stimulus situations shows this discord to be far less severe than implied by a

first inspection. Agreement between the spectral extents and shapes of each suppression function and its opponent process counterpart clearly indicates that it is the opponent processes which are mediating suppression events.

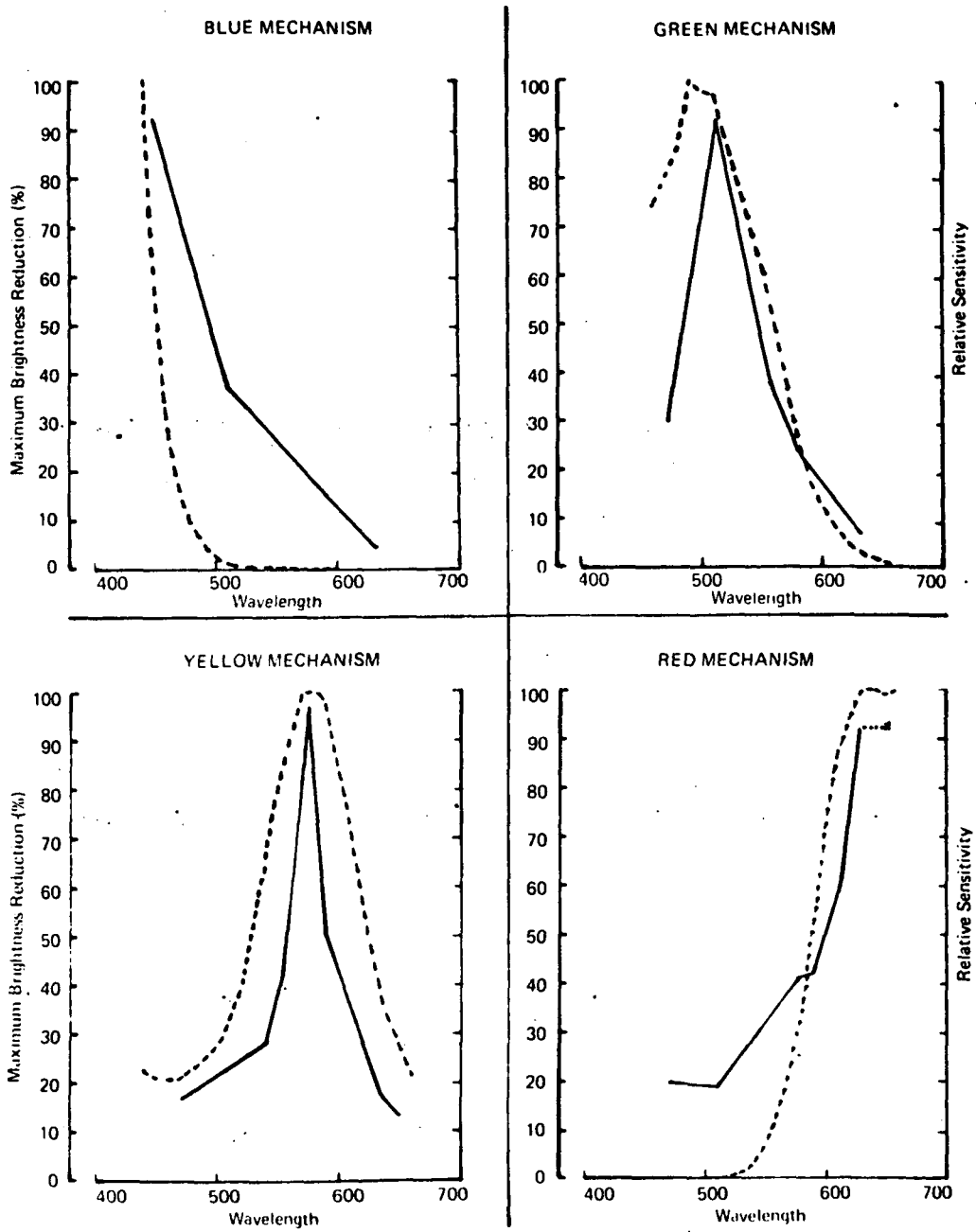
The above conclusion is unusual. The theoretical approaches of both Hurvich and Jameson and DeValois and his co-workers (cf., Abramov, 1972; Abramov & Gordon, 1973) postulate that opponent cells mediate primarily hue. In the present experiments the response measure is a change in brightness. At first glance one might expect that brightness changes would be mediated by the non-opponent processes since these processes are thought to determine the luminosity function. However there is no compelling reason why under certain specific conditions opponent cells cannot contribute to brightness or even be its sole determinant. (It might be noted that in certain situations it is more likely that opponent rather than non-opponent cells underlie the spectral luminosity function; Abramov, 1972.) In any case, from the arguments previously given it seems plausible that under the specific conditions of this experiment a brightness effect is being determined by opponent cells. Indeed the data allow us to go further and assert that non-opponent (broad-band) processes are not contributing at all to brightness suppression. The argument goes as follows. Assume that both opponent and non-opponent mechanisms are involved and that maximal masking occurs when both the test and masking stimuli activate

the same opponent process. Once the wavelength of the test stimulus is sufficiently different from that of the mask, they will no longer activate the same opponent system. However, both must still activate the non-opponent system. Moreover, all the stimuli must activate the non-opponent system to the same degree; the stimuli were all equated for luminance and the spectral sensitivity of the non-opponent cells matches the luminosity function. From these assumptions we would predict that under extreme heterochromatic conditions masking will be less than peak but should reach a limiting plateau. No such plateau is evident. If test and masking wavelengths are sufficiently different, there will be essentially no masking. Such data are in accord with an opponent, not an opponent plus non-opponent, mediation approach. This issue will be discussed further in section 4.4.

One further point should be brought out. It would be interesting to know to what degree one can alter the luminosity ratio between the test and mask and still retain narrow spectral functions. The current study does not address itself to this issue. Nonetheless, Boynton (1956) does provide some relevant data. In an effort to isolate more clearly the spectral sensitivity curves of the cones, Boynton (1956) delevered small, brief, foveal, monochromatic test flashes, 0.05 sec. after the onset of one of several colored adapting stimuli which had been <u>equated</u> for <u>luminance</u>. He used a descending method of limits to obtain test flash thresholds.

This situation differs from type B metacontrast in several ways; fields overlap, the total luminance of the test flash at the time of measurement is slightly greater than that of the inducing stimulus, and the background field preceded rather than followed the test flash as it does in metacontrast. Nonetheless, it is interesting to consider his results because it constitutes the only other study which examines spectral responses to masking when the stimuli are rather similar in luminance and also provides complete response functions. Figure 16 plots the current masking data and Boynton's curves corrected for equal luminosity on the same set of coordinates. The peaks of Boynton's four spectral functions are in good agreement with the peaks of the Hurvich and Jameson functions as well as with my own data. The situation Boynton used was not one of perfect luminance equality, nor were the sizes of his stimuli equal; but then the curves were also not quite so narrow. It is of course possible that forward masking (para-contrast), approximated by Boynton's situation, is not mediated by the same mechanisms as backward masking (metacontrast), but this alternative does not have extensive support. The broadening of these functions relative to those of the pure opponent process functions may represent a slipping toward spectrally broader blocking effects mediated at the primary receptor levels. This could be determined by the luminance and size differences present in Boynton's situation. The thought is certainly intriguing and is totally consonant with

Figure 16. Peak suppression responses averaged for three subjects compared to Boynton's four spectral sensitivity functions corrected for equal luminance. Boynton's theoretical curves are from Boynton, 1956. Solid lines represent the current metacontrast suppression data; broken lines are Boynton's spectral sensitivity functions.


BLUE MECHANISM
GREEN MECHANISM
YELLOW MECHANISM
RED MECHANISM
Maximum Brightness Reduction (%)
Relative Sensitivity
Wavelength
100
90
80
70
60
50
40
30
20
10
0
400
500
600
700

the earlier discussion of why differences between my data and those of Alpern and Rushton are quite reasonable (see also last paragraph of section 4.4).

Let us now consider a possible model to account for equal luminance metacontrast events.

4.4 THE MODEL

Recordings from single cells in the macaque clearly show that there are four types of opponent processes; each maximally activated by wavelengths perceived as red, yellow, green or blue (DeValois, Abramov & Jacobs, 1966). Further, psychophysical tests have shown that the macaque monkey possesses color vision which is essentially identical to that of man (DeValois, 1965; DeValois & Jacobs, 1968). The extensive recordings from primate LGN cells, human chromatic valence and hue coefficient curves (Hurvich & Jameson), and human color naming data (Abramov & Gordon, 1973) all appear to indicate related opponent process results. Consequently, it is now considered quite reasonable to use information gathered about the physiology of the macaque primate species to structure our thinking about human physiology. The model will therefore refer to opponent process lateral geniculate findings as representative of the organization of human visual events although this point has not yet been definitively proven.

The opponent cell types clearly identified for primates are (+r -g), red excitatory, green inhibitory; (+g -r),

(+y -b), and (+b -y). It is believed that the excitatory responses of each of the four opponent cell types signal differences between receptor imputs and should therefore be far more narrow than cone spectral sensitivity functions. Moreover, since each opponent cell type is maximally responsive to a different spectral region, the perceived hue will be signaled by the relative response magnitudes of the various cell types. For example, the percept 'red' is not determined solely by the excitation of the 570 nm photopigment, but by the relative contribution of the appropriate opponent cell type to the total activity in the opponent color system. A hue coefficient curve is defined as the ratio of each chromatic system to the sum of all chromatic responses at a given wavelength. Theoretically then, hue coefficient curves based on psychophysical color data, on macaque LGN recordings or on color naming data should all closely approximate the contribution of each spectrally opponent cell type to the total opponent activity at each wavelength; a sort of action spectrum for each process.[10]

---

[10]These comparisons were made in 1966 by DeValois and his associates. By using the summed absolute deviations from spontaneous response level for paired excitation-inhibition responses for a single color component, each summed deviation could be expressed as a per cent of the total of four sums obtained for all opponent activity at that stimulus hue. The resemblance between color naming data and the physiologically determined opponent cell type contributions was quite strong. See also Abramov (1972) and Abramov and Gordon (1973).

In the present masking situation, the four inducing wavelengths were chosen to approximate each of the unique hues as specified by Hurvich and Jameson. Consequently each inducing wavelength should activate, to a first approximation, only the one process primarily mediating that hue (for greater detail see p. 120). Its ability to mask a test stimulus of the same or different wavelength should clearly depend on the action spectrum of the spectrally opponent cell type expressed as a per cent of the total activity in the entire opponent system. All homochromatic color pairings in the current masking situation involve a replication of response magnitudes within each opponent channel type. Therefore, under homochromatic conditions, the response magnitude within each opponent process activated by the test field will be exactly replicated in the magnitudes and relative contributions to the total opponent system generated by the inducing field. However, because each inducing wavelength approximates a unique hue, most of the spike frequency (response magnitude) representing that wavelength will be confined to one aspect of a single opponent system; let us say green of the red-green system. If, in addition, a process independence similar to the receptor independence found by Alpern and Rushton is sustained at opponent process levels, maximal interference or interaction effects between two stimuli can occur only in the homochromatic situation. When the level of excitation within each opponent system is replicated, masking can be

complete because the excitation level of each independent system is the same on two occasions. This allows total interaction to occur.

On the other hand, in a heterochromatic pairing, test and inducing wavelengths are not identical. Each dominant wavelength generates a different cone excitation pattern which will in turn lead to different response magnitudes within each spectrally opponent mechanism on two occasions. Since the response magnitudes (spike frequencies) within each aspect are different, at peak suppression the interaction effects within some opponent types will be incomplete causing only a partial masking effect. If sufficiently different activation patterns occur among the opponent mechanism types, extremely little masking should result.

Clearly several assumptions are being made. The three most salient assumptions are: (1) opponent channel independence for each aspect of an opponent system in the metacontrast situation, (2) a strict proportionality between the identity of spike frequencies in each channel and the magnitude of the suppression effect, and (3) an absence of any major contribution of the non-opponent system. Let us deal with the last of these issues first.

There is evidence that in addition to the spectrally opponent processes there is a broad band system whose spectral sensitivity matches the luminosity function (DeValois, et al., 1966; DeValois & Jacobs, 1968). This non-opponent system

would be activated equally by all the stimuli in this experiment and should therefore mediate masking over a broad spectral range. As argued earlier, given these experimental conditions the broad band system contributes to only a minor extent. When test wavelength is very different from inducing wavelength, there is very little masking. For some subjects the masking function drops essentially to zero. If in addition to the opponent mechanisms, the broad band, non-opponent system were involved to any appreciable degree, one would expect the masking functions to drop to a plateau level representative of the masking contribution of this system. The data do not really show this. The unusual point about this model is that under equal luminance metacontrast conditions, brightness appears to be mediated by the opponent processes and not by the non-opponent mechanisms. As briefly stated earlier, there is evidence that under certain conditions the opponent cells may be the sole determinant of luminosity. The original simplistic division into brightness and hue channels may not be valid. Indeed, it is inherently unlikely that a simple two channel model is correct. The responses of opponent cells are not determined just by wavelength; they respond just as strongly, in some cases more strongly, than do the non-opponent cells to changes in intensity (DeValois, et al., 1966). In addition, if spectral sensitivity is measured as an increment threshold on a neutral background of high luminance, the function is clearly unlike that of the non-opponent

cells but is closely fit by a function combining the responses of all the opponent cells (Abramov, 1972). In sum, there is adequate precedence to show that under certain conditions brightness can be mediated by the opponent rather than the non-opponent system.

The assumption of opponent channel independence is not as simple to support. What is being advocated is that the mechanism independence found at the receptor level for some types of color situations, including metacontrast, will be sustained among the various channels at the opponent process levels. This notion is not in itself particularly radical since each opponent process is monitoring the difference between two cone channels already responding in an independent manner. What is unusual is that in this situation each member of an opponent process pair acts, to a first approximation, in a manner largely independent of its opponent partner. Green is presumed to act independently of red much as it does to yellow and blue. If one looks at the response distributions of spectrally opponent cells in the macaque, the change from spontaneous rate is much greater for the excitatory than the inhibitory phase. What is being suggested here is that the inhibitory phase covers too small a response range to convey much information. A (+r -g) cell gives substantially greater information about red by its red excitation than a (+g -r) cell, although both contribute to the percept as explained earlier. To this extent, it is reasonable as a

first approximation to assume that each member of an opponent process pair responds independently. The resultant response spectrum for each opponent member type would represent that one cell type alone, not a composite of several opponent mechanisms.

The third assumption, a reasonably strict proportionality between the degree of replication in the spike frequency of each opponent channel class on two occasions and the magnitude of the suppression effect, remains without either physiological support or refutation. What is being advocated here is that if each channel type acts independently, within a channel type the response magnitude characteristic of the first event can be completely blocked by the second event if these magnitudes are equal, or if the magnitude of the second event exceeds that of the first event. If the second event (inducing flash) stimulates a particular type of channel to a lesser degree than does the first event (test flash), only limited brightness suppression will occur. That limit is proportional to the ratio of the response magnitudes stimulated by each visual event. More specifically, if test and masking colors are sufficiently different, in this study different unique hues, then each unique hue activates a different type of opponent channel. No masking can result because, to a first approximation, it is not the same independent type of channel which is being activated by the two stimulus events. However, if the test flash is not a unique hue the

inducing flash would activate only one of the channel types activated by the test flash. Since all stimuli are equated for luminance, the inducing flash must activate that one channel class to a greater degree than does the test flash causing total blocking to occur. Stronger stimulation of one channel type by the unique hue inducing flash must accompany little or no activity by this flash in other active opponent channel classes. The total effect would be a partial masking outcome because in all other types of channels excited by the test flash brightness suppression would be minor or non-existent. The final percept would contain a brightness level proportional to the sum of the residual activity present in all other channels. It is these residual activity levels, summed, which are the peak brightness suppression functions.

Let us also consider the spectral extents of each brightness suppression function. Since each inducing field was chosen to approximate the locus of a unique hue, the process in the spectrally opponent system which indicates that hue will be the only one strongly affected by the inducing field. As test and masking wavelengths become more dissimilar, less and less of the total brightness will be suppressed within the process primarily mediating the inducing color. Since the degree of masking will be closely related to the extent to which the test stimulus activates the same process as does the inducing stimulus, the decrease in per cent masking, or the spectral extent of each masking

function, should characterize the spectral response pattern of each of the four underlying opponent response members.

I submit that in essence the achromatic masking situation is mediated in much the same way as homochromatic masking events. It has already been explained that the two situations are essentially analogous at the early receptor levels. Since the non-opponent system contributes little or nothing to brightness suppression effects under equal luminance chromatic conditions, the arguments presented for the homochromatic situation can be applied to achromatic metacontrast as well. Indeed, a direct analogy based on the preserved identity of the activation patterns elicited by each test and masking stimulus for all mediation stages through opponent process levels can easily be made. One can similarly assert that the results obtained from the pairing of a chromatic inducing field with an achromatic test stimulus of equal luminance supports the same reasoning as does the heterochromatic situation. Both arguments require no further assumptions.

The model presented represents one way of explaining the spectral extents of equal luminance metacontrast events. The extreme narrowness and shape of the peak suppression functions strongly suggests an underlying opponent process mediation. Unfortunately, the exact locus of the metacontrast effect cannot be established from these data. The model presented implies, for simplicity, that suppression

occurs at an early opponent process stage. Let me now state overtly that I do not believe this to be so. Other evidence such as the ability to get both chromatic and achromatic dichoptic metacontrast as well as the ability to elicit an RT to phenomenally dark or absent stimuli, makes it more likely that the actual masking locus is quite central in the visual system; probably at a cortical level. The present data do not preclude a highly central interpretation, they merely provide no further information.

The present study strongly suggests that the cell types which mediate equal luminance metacontrast events are of the opponent process type. This counters the Alpern notion that all metacontrast phenomena are peripheral visual events. (As explained earlier, there is good reason why Alpern's situation and other type A paradigms elicit functions which have a strong peripheral component, while equal luminance, type B situations produce functions which tap higher order processes.) The spectral extents of the curves associated with the type A and type B metacontrast functions indicate that it is very likely that there are two types of brightness suppression subsumed under the term metacontrast. It is possible, however, that these two sorts of metacontrast are not mutually exclusive, and that in many situations both types of processing contribute to the overall brightness suppression. If this were true, one should be able to slide from one type of function, or one mediation locus to another, by the careful

manipulation of luminance ratios between the test and inducing stimuli. The shift from a type B to a type A function should reflect a change from largely opponent process to largely primary receptor mediation of the suppression effect. The sharpness of the transition from one processing locus to another is not certain. Nonetheless, the concept of a transition in the type of mediation which occurs in metacontrast does represent an interesting theoretical prediction from the data.

4.5 HUE AND SATURATION ASPECTS

As we have seen, the broad-band, non-opponent system does not appear to participate in the current situation and it is only the opponent cell types which mediate apparent brightness. It is probable that these same cells also monitor the color aspects of each stimulus. If this were correct, the model proposed would indicate that with homochromatic pairings, hue and saturation should be suppressed at the same time as brightness to produce a total masking response. The data support this prediction completely in that at certain SOA the test flash was often phenomenally absent.

Heterochromatic pairings which involve only the unique hues should also produce minimal hue changes. The luminance and hue aspects of a unique hue test flash are assumed to be mediated largely by a single member of an opponent process pair. An inducing field composed of a different unique hue

should not appreciably affect the activation pattern evoked by the first unique hue. Since the hue percept reflects the relative contributions of all independent opponent channels to the total opponent activity operating at that wavelength, minimal interaction between response patterns implies that the same opponent process will continue to dominate, i.e., to contribute maximally relative to all other opponent processes. In short, there is no cause for a color change. The data also support this aspect of the model.

Heterochromatic pairings which do not involve only the unique hues should produce substantial hue shifts. Since the inducing hue always approximates a unique hue, it activates primarily one type of channel. A non-unique hue test stimulus will activate two types of opponent channels. Since the test flash is followed by the inducing flash, the inducing hue will strongly interact with opponent activity in only one of the two types of channels mediating the test flash hue. Signals present in the other channel types will be unaffected. Again, a hue percept results from the proportional contribution of each channel type to the overall opponent activity present. Since the type of channel which undergoes suppression is the one which mediates the inducing hue, that hue will be effectively eliminated from the final color percept. The reported color should reflect a shift away from the hue of the inducing field. These changes ought to be most effective when there is a small nm difference between test

and inducing wavelengths so that the activation patterns of these stimuli are somewhat similar and independent channel suppression effects are great. To speak loosely, a chartreuse is a yellow-green. If the inducing hue is green and the test stimulus is chartreuse, then the green inducing field effectively removes only green from the stimulus. By negating the green channel, yellow now contributes maximally to the percept, i.e., is the most active remaining channel type. The resultant hue should now appear more yellow. The data do support this prediction, however, the magnitude of the effect is quite small. Any hue shifts which do occur tend to be in the direction away from the inducing hue and occur only in those instances where partial brightness suppression was apparent. The problem is that a brightness suppression effect of 20-40% can coexist with very minimal hue shifts or in most cases no hue shift at all. The overwhelming majority of trials display no hue shifts (see Appendix, Table I, columns 9, 10 and 11). While it is true that the method used to obtain hue information could have been more sensitive (only three categories were allowed per hue), it does not obscure the fact that hue changes were a minor effect compared to modifications in apparent brightness. The model does not account for this discrepency.

The magnitude of saturation changes also appears to be limited. There is a tendency toward an inverse relation between per cent brightness reduction and mean saturation so

that as masking increases, mean saturation decreases. This too is predicted by the general model being considered here. In the models of Hurvich and Jameson and DeValois and his co-workers, the apparent saturation of monochromatic stimuli is proportional to the ratio of the activities evoked in the opponent and non-opponent channels respectively. In the present situation I have argued that the only masking which takes place is mediated by the opponent processes. Thus, if a stimulus pairing produces a reduction in brightness it also produces a reduction in the total chromatic or opponent response. This leaves the total achromatic or non-opponent response unaffected. The result should be a decrease in apparent saturation. This trend does occur in the data, although it appears to be consistent for only two out of the three subjects and the magnitude of the effect is small. Large changes in apparent brightness affect saturation minimally; mean saturation readings never dipped below 2.75 on a 5 point scale.

In sum, the hue and saturation data make two clear points: (1) color information (hue and saturation) is totally suppressed only when brightness suppression is maximal. It is likely that both stimulus aspects are mediated by opponent process activity. (2) If brightness suppression is not maximal, i.e., some portion of the test stimulus remains in the visual percept, then the specific color of that percept (its hue and saturation) is highly stable and tends to remain

unchanged through all SOA. Certainly it can be said that the brightness dimension of these stimuli is far more vulnerable to metacontrast manipulation than are the hue and saturation dimensions. This is not accounted for by the model set forth. However, since the hue and saturation changes which do occur are in accord with predictions based on the opponent process model, the discrepancies in the magnitudes of these two effects may indicate a different opponent processing locus or level for the fixing of color as opposed to brightness information. A more sensitive measure of color change would have to be applied to this situation before a more precise model could be constructed.

V. SUMMARY AND CONCLUSIONS

Metacontrast brightness suppression occurs when a test flash is followed by a non-overlapping inducing or masking flash. It is observed that often the brightness reduction obtained is an inverted U-shaped function of stumulus onset asynchrony. The present study was designed to investigate possible wavelength dependencies and specificities in this effect when all stimuli have been equated for luminance and duration; that is, a type B metacontrast paradigm was used. Other than wavelength, the only parameter was the degree of asynchrony in the onset time of the inducing flash relative to the onset of the test flash.

The number of inducing wavelengths was restricted to four monochromatic stimuli whose wavelengths were chosen to approximate the unique hues of red, yellow, green and blue. Each inducing wavelength was then successively paired with several test wavelengths in a randomized block design.

Under these experimental conditions homochromatic pairings produced the greatest per cent brightness suppression. All homochromatic functions were very similar and clearly replicated the U-shape achromatic masking function for both the degree of peak masking achieved and for the asynchrony at which peak suppression occured (70 msec.). Heterochromatic pairings displayed substantial changes in the masking functions. All curves were still roughly U shape,

however, brightness reduction was considerably less at all SOA. Small wavelength differences (15-20 nm) between test and inducing fields produced a severe flattening of the U function; larger wavelength disparities produced little or no masking at all asynchronies. For two of the three subjects there was also a marked tendency for these flattened U functions to reach peak masking at a shorter asynchrony.

Further analysis of the per cent brightness suppression at peak masking revealed that the maximum amplitude of each curve was inversely related to the magnitude of the difference in wavelength between test and inducing stimuli. A plot of these peak amplitudes as a function of test field wavelength was constructed and the spectral extent of the masking obtained with each unique hue inducing field was noted. All curves displayed only one peak which corresponded to the homochromatic situation. From each peak the curves declined rapidly in amplitude as the difference in wavelength between test and masking flashes increased. The functions were severely limited in spectral extent and had marked irregularities which were consistent for all subjects.

The problem was how to interpret these findings. The original intent, based on the work of Alpern and Rushton, had been to relate the results to separate cone mechanisms or perhaps Stiles' $\tilde{\pi}$ mechanisms. However, the spectral sensitivity functions of cones or $\tilde{\pi}$ mechanisms are broad and corrections appropriate to an equal luminance situation

cause these functions to become still broader and flatter. In contrast, the masking functions obtained here are very narrow and sharply peaked.

A reasonable alternative which would permit such narrow functions is to interpret them in terms of spectrally opponent processes. There is good evidence from the work of DeValois and his associates, based on physiological recordings from single cells in the macaque, that there are four types of spectrally opponent processes each maximally activated by wavelengths perceived as red, yellow, green or blue. These responses have been found to be related to the opponent processes derived by Hurvich and Jameson from human psychophysical data. In light of these facts, an opponent process explanation of the masking data has been offered.

Since each inducing wavelength was close to the locus of a unique hue, the process in the spectrally opponent system which indicates that hue will be the only one strongly affected by the inducing field. Test wavelengths which stimulate the same process will, to a first approximation, be the only ones masked. The degree of masking will therefore be closely related to the extent to which the test and inducing stimuli activate the same process. To examine this hypothesis, peak brightness suppression functions have been compared to the spectral responses of the opponent processes in a situation in which all wavelengths have been equated for luminance. Functions which are appropriate to the

requisite set of conditions are provided by the hue coefficient curves of Hurvich and Jameson.

There is good agreement between the masking data and the opponent functions except for a few points. The peak brightness suppression functions display spectral ranges as narrow as those of the opponent processes. There is also an impressive similarity in the irregularities characteristic of both sorts of functions. Together the evidence strongly suggests that in this situation it is opponent processes which are mediating the brightness suppression effect.

Accordingly, a model has been constructed to account for these wavelength specific effects in terms of opponent process mediation of masking events. The interesting feature of both the model and the data is that, under the present conditions, brightness appears to be mediated by opponent processes. Indeed, I have argued that the non-opponent channels do not contribute at all to the findings in this experiment. The model accounts quite well for achromatic, homochromatic, heterochromatic and mixed chromatic-achromatic conditions. It also anticipates most aspects of the hue and saturation data recorded, save for an unresolved discrepancy between the magnitudes of hue and saturation changes relative to the brightness changes observed.

While the present data do not finally resolve the issue of the precise locus of stimulus suppression, the study does provide psychophysical results which are sufficiently

precise to clearly support an opponent process mediation approach for equal luminance metacontrast, and are inconsistent with the Alpern notion that all metacontrast phenomenon are peripheral visual events.

APPENDIX

Table I. Mean Saturation, Hue Shifts and Peak Masking Asynchrony

Inducing Wavelength	Test Wavelength	SOA of Peak Masking			Mean Saturation at SOA of Peak Masking			Hue Shifts at SOA of Peak Masking		
		subject B.M.	subject S.E.	subject D.S.	subject B.M.	subject S.E.	subject D.S.	subject B.M.	subject S.E.	subject D.S.
470 nm	470 nm	37	37	70	not criterion	not criterion	not criterion	none	none	none
	510 nm	37	37	70 & 37	3.25	5.00	4.00	none	none	none
	578 nm	37	37	70	4.25	4.85	4.42	none	10% grn	42% grn
	630 nm	37	flt.fnc	70 & 100	4.80	5.00	4.95	none	5% yel	none
510 nm	470 nm	37	37	37	4.56	4.90	3.24	none	5% blue	none
	510 nm	70	70	70	not cri	not cri	not cri	none	none	none
	540 nm	37	37	70	3.00	4.71	not cri	42% yel	none	none
	555 nm	37	37	70	2.75	4.25	3.20	35% yel 15% grn	none	30% yel
	578 nm	37	37	70	4.45	4.84	4.35	none	none	41% red
	630 nm	37	flt.fnc	70	4.75	5.00	4.90	none	none	none
578 nm	470 nm	37	37	37	4.85	5.00	3.90	none	none	5% grn
	510 nm	37	37	70	4.60	4.90	4.59	none	5% blue	none
	540 nm	37	37	70	3.65	5.00	3.42	none	none	none
	555 nm	37	70	70	3.63	4.85	3.64	none	5% grn	none
	578 nm	70	70	70	not cri	not cri	not cri	none	none	none
	590 nm	37	37	70	3.50	4.65	4.60	none	6% red 6% yel	30% red

Table I (continued)

Inducing Wavelength	Test Wavelength	SOA of Peak Masking			Mean Saturation at SOA of Peak Masking			Hue Shifts at SOA of Peak Masking		
		subject B.M	subject S.E.	subject D.S.	subject B.M.	subject S.E.	subject D.S.	subject B.M.	subject S.E.	subject D.S.
	615 nm	37	70	70	4.15	5.00	4.79	none	none	none
	630 nm	37	37	70	4.60	5.00	4.50	none	none	21% yel
630 nm	470 nm	37	37	37	4.85	5.00	4.33	none	none	none
	510 nm	37	37	37	4.70	5.00	4.05	none	none	none
	578 nm	37	37	70	3.15	3.06	3.56	none	6% red	38% red
	590 nm	37	37	70	2.85	3.50	4.11	100% red	none	22% yel
	615 nm	37	37	70	3.28	4.75	not cri	17% yel	8% yel 53% red	none
	630 nm	70	70	70	not cri	not cri	not cri	none	none	none

Figure 17. Spectral energy distribution curve of Sylvania F40T12 fluorescent lamps. This lamp type was used as the light source for all fields throughout the present study.

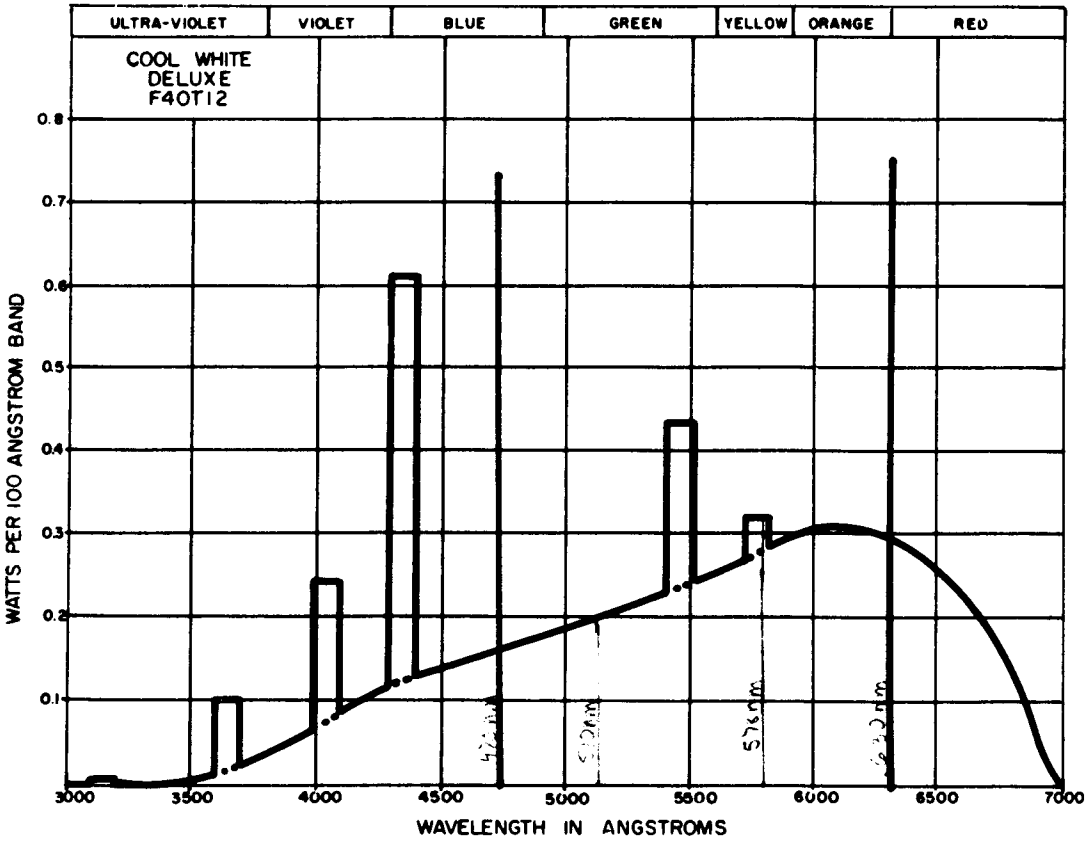
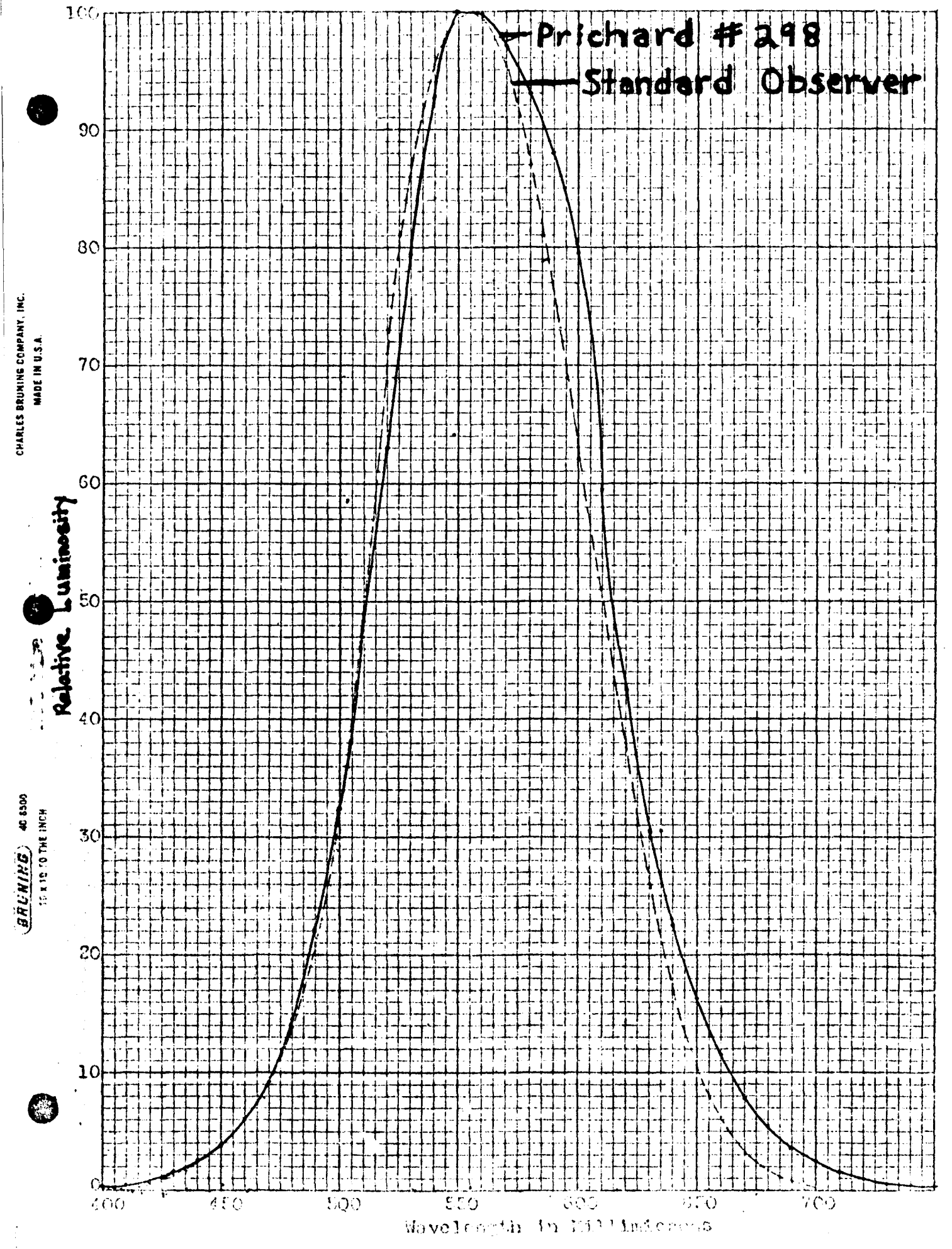

ULTRA-VIOLET
VIOLET
BLUE
GREEN
YELLOW
ORANGE
RED
COOL WHITE
DELUXE
F40T12
WATTS PER 100 ANGSTROM BAND
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
3000
3500
4000
4500
5000
5500
6000
6500
7000
WAVELENGTH IN ANGSTROMS

Figure 18. Prichard Photometer #298 luminosity function compared with the standard observer curve for luminosity. Solid function represents the photometer curve, broken lines are the standard observer curve.

PRITCHARD # 298 Standard Observer Curve



REFERENCES

REFERENCES

Abramov, I. Retinal mechanisms of colour vision. In Handbook of Sensory Physiology, Vol. VII/2, Fuortes, M.G.F. (Ed.). Berlin: Springer-Verlag, 1972.

Abramov, I., and Gordon, J. Seeing. In Handbook of Perception, Vol. III, Carterette, E., and Friedman, M. (Eds.). New York: Academic Press, 1973.

Alpern, M. Metacontrast: historical introduction. Amer. J. Optometry, 1952, 29, 631-646.

Alpern, M. Metacontrast. J. Opt. Soc. Am., 1953, 43, 648-657.

Alpern, M. Relation between brightness and color contrast. J. Opt. Soc. Amer., 1964, 54, 1491-1492.

Alpern, M. Rod-cone independence in the afterflash effect. J. Physiol., 1965, 176, 462-472.

Alpern, M., and Rushton, W.A.H. The specificity of cone interaction in the afterflash effect. J. Physiol., 1965, 176, 473-482.

Alpern, M., and Rushton, W.A.H. The nature of rise in threshold produced by contrast-flashes. J. Physiol., 1967, 189, 519-534.

Aubert, H. Physiologie der netzhaut. Breslau: Morgenstern, 1865. Cited in Pirenne, M. H., Light Adaptation. In The Eye, Vol. II, Davson, H. (Ed.). New York: Academic Press, 1962.

Battersby, W. S., Oesterreich, R. E., and Sturr, J. F. Neural limitation of visual excitability. VII. Nonhomonymous retrochiasmal interaction. Amer. J. Physiol., 1964, 206, 1181-1188.

Bevan, W., Jonides, J., and Collyer, S. C. Chromatic relationships in metacontrast suppression. Psychon. Sci., 1970, 19, 367-368.

Boynton, R. M. Rapid chromatic adaptation and the sensitivity functions of human color vision. J. Opt. Soc. Amer., 1956, 46, 172-179.

Boynton, R. M., and Gordon, J. Bezold-Brücke hue shift measured by color-naming technique. J. Opt. Soc. Amer., 1965, 55, 78-86.

Boynton, R. M., Ikeda, M., and Stiles, W. S. Interactions among chromatic mechanisms as inferred from positive and negative increment thresholds. Vision Research, 1964, 4, 87-117.

Boynton, R. M., Shafer, W., and Neun, M. E. Hue-wavelength relation measured by color-naming method for three retinal locations. Science, 1964, 146, 666-668.

Brown, P. K., and Wald, G. Visual pigments in single rods and cones of the human retina. Science, 1964, 144, 145-151.

Buchsbaum, W. H., and Mayzner, M. S. The effects of line length on sequential blanking. Psychon. Sci., 1969, 15, 111-112.

Cox, S. I., and Dember, W. N. Backward masking of visual targets with internal contours. Psychon. Sci., 1970, 19, 255-256.

Dartnall, H.J.A. The interpretation of spectral sensitivity curves. Brit. Med. Bull., 1953, 9, 24-30.

Dartnall, H.J.A. The photobiology of visual processes. In The Eye, Vol. II, H. Davson (Ed.). New York: Academic Press, 1962.

DeValois, R. L. Analysis and coding of color vision in the primate visual system. Cold Spring Harbor Symposia on Quantitative Biology, 1965, 30, 567-579.

DeValois, R. L., Abramov, I., and Jacobs, G. H. Analysis of response patterns of LGN cells. J. Opt. Soc. Amer., 1966, 56, 966-977.

DeValois, R. L., and Jacobs, G. H. Primate color vision. Science, 1968, 162, 533-540.

Dowling, J. E. The site of visual adaptation. Science, 1967, 155, 242-254.

Eriksen, C. W., Becker, B. B., and Hoffman, J. E. Safari to masking land: a hunt for the elusive U. Perception and Psychophysics, 1970, 8, 245-250.

Eriksen, C. W., and Collins, J. F. A reinterpretation of one form of backward and forward masking in visual perception. J. Exp. Psych., 1965, 70, 343-351.

Fehrer, E. Effect of stimulus similarity on retroactive masking. J. Exp. Psych., 1966, 71, 612-615.

Fehrer, E., and Biederman, I. A comparison of reaction time and verbal report in detection of masked stimuli. J. Exp. Psych., 1962, 64, 126-130.

Fehrer, E., and Raab, D. Reaction time to stimuli masked by metacontrast. J. Exp. Psych., 1962, 63, 143-147.

Fehrer, E., and Smith, E. Effect of luminance ratio on masking. Perceptual and Motor Skills, 1962, 14, 243-253.

Frumkes, T. E., Licht, J. L., and Temme, L. A. Latency of different chromatic mechanisms as measured by perceptual simultaneity. Paper presented to the Association for Research in Vision and Opthalmology, Sarasota, Fla., April, 1973.

Fry, G. A. Depression of the activity aroused by a flash of light by applying a second flash immediately afterwards to adjacent areas of the retina. Amer. J. Physiol., 1934, 108, 701-707.

Goldstein, E. Interaction between color mechanisms in the parafoveal retina. In preparation.

Gordon, J., Abramov, I., and Imperato, J. Color vision in the peripheral retina. Paper presented to the Association for Research in Vision and Ophthalmology, Sarasota, Fla., April, 1973.

Granit, R. Receptors and Sensory Perception. New Haven: Yale Univ. Press, 1955.

Guth, S. L. On neural inhibition; contrast effects and visual sensitivity. Vision Research, 1973, 13, 937-957.

Guth, S. L., Donley, N. J., and Marroco, R. T. On luminance additivity and related topics. Vision Research, 1969, 9, 537-575.

Harrison, K., and Fox, R. Replication of reaction time to stimuli masked by metacontrast. J. Exp. Psych., 1966, 71, 162-163.

Heinemann, E. G. Simultaneous brightness induction. In Handbook of Sensory Physiology, Vol. VII/4, Jameson, D. and Hurvich, L. M. (Eds.). Berlin: Springer-Verlag, 1972.

Helmholtz, H.L.F. von. Treatise on Physiological Optics. (Translated by J.P.C. Southhall.) New York: Dover, 1924.

Hering, E. Outline of a Theory of the Light Sense. (Translated by Hurvich, L. M. and Jameson, D.) Cambridge: Harvard University Press, 1964.

Hurvich, L. M. Hering and the scientific establishment. Amer. Psychologist, 1969, 24, 497-514.

Hurvich, L. M., and Jameson, D. Some quantitative aspects of an opponent-colors theory. II. Brightness, saturation and hue in normal and dichromatic vision. J. Opt. Soc. Amer., 1955, 45, 602-616.

Jameson, D. and Hurvich, L. M. Theory of brightness and color contrast in human vision. Vision Research, 1964, 4, 135-154.

Jameson, D., and Hurvich, L. M. Opponent-response functions related to measured cone photopigments. J. Opt. Soc. Amer., 1968, 58, 429-430.

Kahneman, D. An onset-onset law for one case of apparent motion and metacontrast. Perception and Psychophysics, 1967, 2, 577-584.

Kahneman, D. Method, findings and theory in studies of visual backward masking. Psych. Bull., 1968, 70, 404-425.

Kolers, P. A. Intensity and contour effects in visual masking. Vision Research, 1962, 2, 277-294.

Kolers, P. A., and Rosner, B. S. On visual masking (metacontrast): dichoptic observation. Amer. J. Psychol., 1960, 73, 2-21.

Krauskopf, J. Contributions of the primary chromatic mechanisms to the generation of visual evoked potentials. Vision Research, 1973, 13, 2289-2298.

Lefton, L. Metacontrast: a review. Perception and Psychophysics, 1973, 13, 161-171.

Liebman, P. A. Microspectrophotometry (MSP) of photoreceptors. In Handbook of Sensory Physiology, Vol. VI/B, Dartnall, H.J.A. (Ed.). Berlin: Springer-Verlag, 1972.

Linksz, A. Vision: Physiology of the Eye. Vol. II, New York: Grune and Stratton, 1952.

MacNichol, E. F., Jr., and Svaetichin, G. Electric responses from the isolated retinas of fishes. Amer. J. Ophthal., 1958, 46, 26-46.

Marks, W. B., Dobelle, W. H., and MacNichol, E. F. Visual pigments of single primate cones. Science, 1964, 143, 1181-1183.

Marriot, F.H.C. Color vision: the two-colour threshold technique of Stiles. In The Eye, Vol. II, Davson, H. (Ed.). New York: Academic Press, 1962.

Mayzner, M. S., and Tresselt, M. E. Sequential blanking: a function of geometric analyzers in the human visual system. Psychon. Sci., 1969, 17, 77-78.

Mayzner, M. S., Tresselt, M. E., Adrignolo, A. J., and Cohen, A. Further preliminary findings on some effects of very fast sequential imput rates on perception. Psychon. Sci., 1967, 7, 281-282.

Mollon, J. D., and Krauskopf, J. Reaction time as a measure of the temporal response properties of individual colour mechanisms. Vision Research, 1973, 13, 27-40.

Pieron, H. Le metacontraste. J. Psychol. Norm. Pathol., 1935, 32, 651-652, and 5-24.

Pollack, R. H. Effects of figure ground contrast and contour orientation on figural masking. Psychon. Sci., 1965, 2, 369-370.

Ripps, H., and Weale, R. A. Cone pigments in the normal human fovea. Vision Research, 1963, 3, 531-543.

Rushton, W.A.H. Visual pigments in man. Sci. Amer., 1962, 207, 120-132.

Rushton, W.A.H. A cone pigment in the protanope. J. Physiol. (London), 1963, 168, 345-359.

Rushton, W.A.H. The Ferrier Lecture, 1962. Visual adaptation. Proc. Roy. Soc., Series B, 1965, 162, 20-46.

Rushton, W.A.H., and Westheiner, G. The effect upon the rod threshold of bleaching neighbouring rods. J. Physiol. (London), 1962, 164, 318-329.

Schiller, P. H. Metacontrast interference as determined by a method of comparisons. Perceptual and Motor Skills, 1965, 20, 279-285.

Schiller, P. H., and Chorover, S. L. Metacontrast: its relation to evoked potentials. Science, 1966, 153, 1398-1401.

Schiller, P. H., and Smith, M. C. Detection in metacontrast. J. Exp. Psych., 1966, 71, 32-39.

Schiller, P. H., and Smith, M. C. Monoptic and dichoptic metacontrast. Perception and Psychophysics, 1968, 3, 237-239.

Simon, L. G. Effects of inducing field shape on retroactive masking. Unpublished masters thesis, Brooklyn College, May, 1972.

Stewart, A. L., and Purcell, D. G. U-shaped masking functions in visual backward masking: effects of target configuration and retinal position. Perception and Psychophysics, 1970, 7, 253-256.

Stigler, R. Chronophotische studien uber den umgebungskontrast. Pfluger Archiv. fur die gesamte Physiologie, 1910, 134, 365-435.

Stiles, W. S. Color vision: the approach through increment threshold sensitivity. Proc. Nat. Acad. Sci., 1959, 45, 100-114.

Svaetichin, G. The cone action potential. Acta Physiol. Scand., 1953, 29, Suppl. 106, 565-600.

Teft, W. The effects of stimulus hue on backward masking under conditions of monoptic and dichoptic stimulus presentation. Psychon. Sci., 1969, 16, 287-288.

Wald, G. The receptors of human color vision. Science, 1964, 145, 1007-1016.

Wald, G., Brown, P. K., and Smith, P. H. Iodopsin. J. Gen. Physiol., 1955, 38, 623-681.

Weisstein, N. A. Rashevsky-Landahl neural net: simulation of metacontrast. Psych. Rev., 1968, 75, 494-521.

Weisstein, N. Metacontrast. In Handbook of Sensory Physiology, Vol. VII/4, Jameson, D. and Hurvich, L. M. (Eds.). Berlin: Springer-Verlag, 1972.

Weisstein, N., and Growney, R. L. Apparent motion and metacontrast: a note on Kahneman's formulation. Perception and Psychophysics, 1969, 5, 321-328.

Werner, H. Studies on contour: I. Qualitative analysis. Amer. J. Psych., 1935, 47, 40-64.