

HIGHER ORDER COLOR MECHANISMS

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Abstract—Evidence supporting the existence of higher order color mechanisms, that is, ones beyond the previously identified second stage mechanisms is presented. This evidence includes a reanalysis of the data of Krauskopf *et al.* [*Vision Res.* **20**, 1123–1131 (1982)] on the desensitizing effects of viewing chromatically modulated fields, new experiments on a generalized version of the “transient tritanopia” experiment of Mollon and Polden [*Phil. Trans. R. Soc. Lond.* **278**, 207–240 (1977)] and results on the relationship between discrimination and detection of brief color changes.

Color vision Transient tritanopia Discrimination and detection Opponent mechanisms

INTRODUCTION

Krauskopf *et al.* (1982) found that thresholds for detecting changes in color were selectively elevated after viewing isoluminantly modulated fields. When only the inputs to the long wavelength sensitive (R) cones and the middle wavelength sensitive (G) cones were modulated by the habituating field, thresholds for detecting isoluminant changes in color were raised for all test colors except those which varied only the inputs of the short wavelength sensitive (B) cones. Conversely, when the habituating field only modulated the B cones, thresholds for all isoluminant changes in color were raised except those for which only the R and G cone inputs varied. Thresholds for all isoluminant changes in color were raised after viewing a field modulated in any other direction. These facts were taken as support for the idea that there are only two major second stage chromatic mechanisms.

Subsequently, Derrington *et al.* (1984) recorded the responses of individual cells in the lateral geniculate nucleus of the macaque to modulations in different directions in color space. The color space they used to represent the stimuli (Fig. 1) had two isoluminant axes identical to those identified as cardinal by Krauskopf *et al.* (1982), and a luminance axis. This space is an extension of the representation sug-

gested earlier by MacLeod and Boynton (1979). The most saturated colors lie on the rim of the isoluminant plane. A stimulus at 0° appears reddish, one at 90° appears greenish yellow, one at 180° appears greenish and one at 270° appears purplish.

Each LGN cell responded best when the stimuli were modulated in one direction and failed to respond at all to stimuli modulated in orthogonal directions. In general, the response was proportional to the cosine of the angle between the stimulus direction and the direction of maximal excitation. All parvocellular neurons have color opponent center-surround receptive fields. Two classes of units were found, one which responds best to isoluminant modulation near the constant R&G axis while the other responds best to isoluminant modulation near the constant B axis of Fig. 1.

The possibility of another set of adaptable mechanisms at yet a higher level of the visual system tuned to many directions about the color circle was raised by Krauskopf *et al.* (1982) to account for evidence of residual selective desensitization after viewing fields modulated in directions intermediate to the cardinal directions. In this paper, we present additional evidence supporting to the existence of higher level mechanisms. This evidence includes a reanalysis of the data of Krauskopf *et al.* with a new method, new data on a generalized version of the “transient tritanopia” experiment of Mollon and Polden (1977) and some results of the relation of discrimination and detection of color changes.

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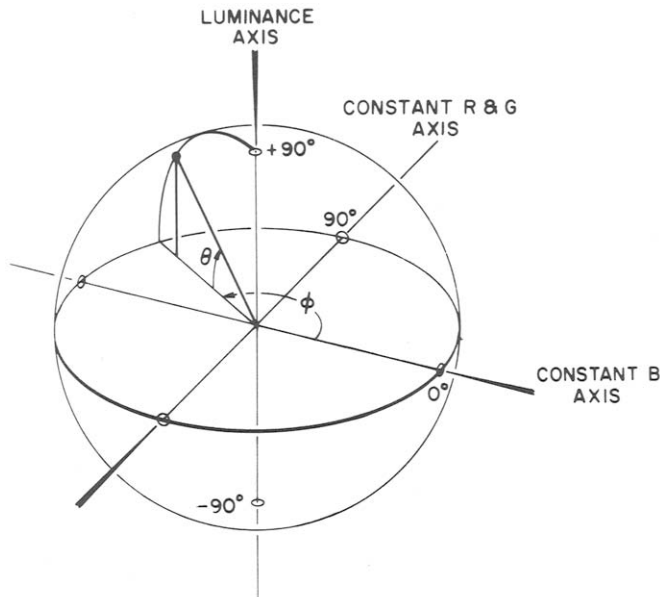


Fig. 1. Chromaticity space in which the "constant B" and "constant R&G" axes define an isoluminant plane, centered on the white point. The constant B axis is assigned the direction 0°, the constant R&G axis, 90°. Stimuli at 0, 90, 180 and 270° appear reddish, greenish-yellow, greenish and purplish, respectively. The third axis passes orthogonally through the isoluminant plane at the white point. The direction of any line that passes through the white point is specified by its *azimuth* (which can take values between 0 and 360°) and its *elevation* (which can take values between -90 and 90°, which appear as decrement and increments in luminance respectively). The color space can be thought of as a sphere with the white point at its center.

METHOD OF ANALYSIS

The new method of analyzing the data of Krauskopf *et al.* (1982) uses Fourier methods to average the effects of an habituation stimulus over several test stimuli. Derrington *et al.* (1984) found that the response of macaque LGN cells to sinusoidally modulated stimuli is proportional to the cosine of the angle between the stimulus direction and the direction of maximal response. Let us assume that the desensitizing effects of viewing modulated fields occur within mechanisms that have the sensitivities of the parvocellular cells of the macaque and that the degree of desensitization is a monotonic increasing function of the response of the mechanisms. Assume further that the signals to be detected are some summative function of the signals conveyed by the two mechanisms. If the habituation stimulus is modulated along the direction of maximal response for one of the mechanisms, e.g. along the constant B axis, thresholds for detecting test stimuli at 0 and 180° will be raised most, thresholds for stimuli at 90 and 270° will not be raised at all, and thresholds for stimuli at other directions will be raised intermediate amounts. Similarly, if the

habituation stimulus is modulated along the constant R&G axis thresholds for detecting test stimuli at 90 and 270° will be raised maximally, thresholds for test stimuli at 0 and 180° will not be elevated at all and thresholds for stimuli at other directions will be raised by intermediate amounts.

When the habituation stimulus is modulated in intermediate directions, both transmission channels will be desensitized and thus thresholds will be raised for all test stimuli. The precise form of the variation in threshold elevation with test stimulus angle also depends on the specific model of signal summation, but certain qualitative predictions will be independent of the model assumed. Krauskopf *et al.* (1982) found that desensitization is a monotonic increasing function of the amplitude of the habituation stimulus. Since the relative effects of the habituation stimuli on the two mechanisms vary inversely with one another as the habituation angle is varied, there must be some direction at which the desensitizing effects of the habituation stimulus are equal as measured by the changes in thresholds of tests in the two cardinal directions. With this habituation stimulus thresholds

must be raised equally for all test stimuli no matter what response functions one assumes for the mechanisms unless it is further assumed that the response functions are significantly and specially altered in *shape* by habituation. All other habituation stimuli must desensitize one of the mechanisms more than the other, in which case thresholds for detection of stimuli along one cardinal axis will be raised more than those along the other cardinal axis and thresholds will be raised an intermediate amount for stimuli in the intermediate directions. Thus, as the habituation direction is varied around the color circle, from one cardinal axis to the next, the maximum of the threshold elevation remains fixed at one cardinal axis until the habituation direction which results in uniform threshold elevation, at which point there is no maximum, then the maximum of the threshold elevation shifts suddenly to the other cardinal axis. What is critical to our conclusions is that the maximum should remain fixed, which, if both mechanisms contribute to detection of stimuli at angles intermediate to the cardinal directions, must be true for all plausible response functions.

Some of the data from Krauskopf *et al.* (1982) are replotted in Fig. 2. The threshold elevations for the case of the 90–180° habituation stimulus show the expected undulations with test direction, while those of the case of the 45–225° habituation stimulus are more or less independent of test direction. It is difficult to discern much more about the overall pattern of the effects from this figure.

However, much of the structure of the results can be captured by a Fourier analysis of the threshold elevations as a function of test color direction for each habituation angle. The theory that desensitization occurs within two mechanisms that precede the detection mechanisms

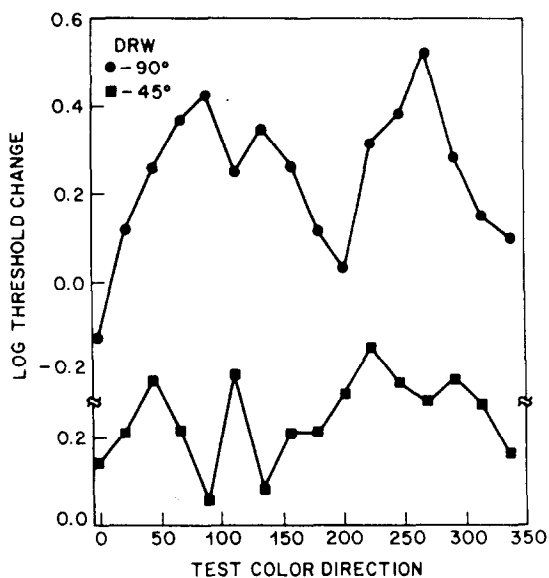


Fig. 2. Changes in log thresholds as a function of test angle. Upper curve for habituation stimuli varying in the 90–270° cardinal direction. Lower curve for habituation stimulus varying in the 45–225° direction.

predicts that the modulation of the second harmonic, i.e. its amplitude divided by the average threshold elevation should have large values when the habituation stimulus varies along the cardinal axes and should be zero for habituation stimuli that are at some particular intermediate angle between cardinal directions. Furthermore, the peak of the second harmonic should be at 0° when the habituation stimulus is along the Constant B axis, and remain at 0 until 45° where it should be indeterminate as the modulation drops to zero, and then shift to 0° for habituation stimuli from 45 to 135° and so on. The first harmonic should not exist, while the value of higher harmonics will depend on the rules relating desensitization to the amplitude of the habituating stimulus and on the rule of signal summation in the detector mechanism.

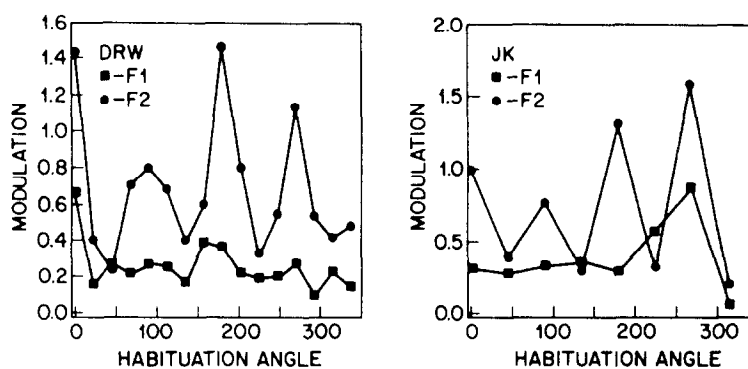


Fig. 3. Modulation (amplitude/mean threshold change) of first and second harmonic as a function of habituation angle.

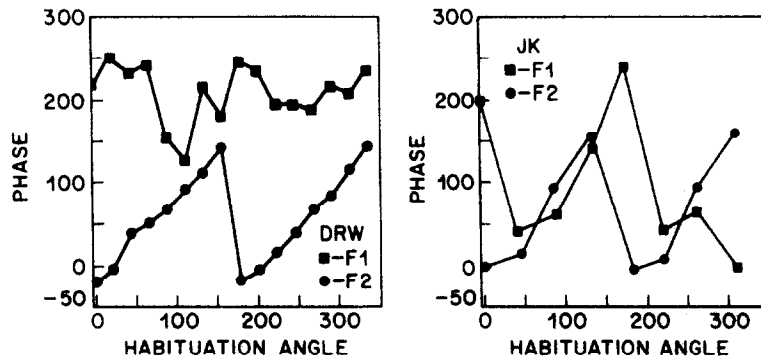


Fig. 4. Phase of first and second harmonic as a function of habituation angle. Phase is plotted so that its value corresponds to the azimuth in color space of the first peak of the sinusoid fitted to the data.

The results of applying this method to the data of Krauskopf *et al.* (1982) are illustrated in Figs 3 and 4. For both observers the fundamental modulation is small and is not dependent on habituation angle in any systematic way, while, as expected, the modulation of the second harmonic has peaks at 0, 90, 180 and 270° (Fig. 3).

The phase of the fundamental and the second harmonic are plotted in Fig. 4 as a function of the direction of the habituation stimulus. In this plot, phase is expressed in terms of the position of the peak of the sinusoid implicitly fitted to the data. Thus, for example, a "phase" of the second harmonic of 90° implies that the best fitting second harmonic component through the data has maximal threshold elevations for test stimuli at 90° and at 270° in azimuth in color space.

The phase of the fundamental doesn't vary in a systematic way, but that of the second harmonic does not agree with the predictions made above. Rather it follows the direction of the stimulus quite precisely even when the modulation falls to small values. This method of portraying the results makes clear regularities that are hardly discernible in the plots of Krauskopf *et al.* (1982). For example, it is quite clear that the phase of the second harmonic varies for J.K. as well as that for D.R.W., a conclusion that could not easily be drawn from the representation of the same data in their paper.

Before discussing the significance of these results in detail, let us consider the results from a new experiment, a generalized version of "transient tritanopia". Mollon and Polden (1977) applied this term to the elevation in the threshold for detecting short-wavelength test flashes when long-wavelength backgrounds are turned off. This phenomenon has been attributed to a change in the sensitivity of the second

stage mechanism that conveys the signals from the B cones. It is recognized that the background and the change in background may have effects on other mechanisms, and that the test might be detected through different mechanisms under different conditions within the experiment. We have attempted to minimize these problems.

Methods

We modified the original transient tritanopia experiment in an effort to reduce the effects of receptor adaptation and to confine the conditioning and test stimuli to a single plane in color space, specifically the isoluminant plane. In contrast to the original transient tritanopia experiments the thresholds were always measured on the same background, a mid-white. They were first measured with the background constant. Subsequently, thresholds were measured 200 msec after a 1.0 sec step change in the background in some direction in the isoluminant plane.

We used a computer controlled laser color mixer (Krauskopf *et al.*, 1981). This system allows rapid and precise variation of stimuli within the portion of color space defined by its primaries: a 632 nm He-Ne laser, a 514 nm Argon laser, and a 442 nm He-Cd laser. The field was originally set at mid-white of about 500 td. The test target was a disc 2° in diameter. The stimuli were gaussian pulses, total duration 600 msec with a sigma of 150 msec. Threshold amplitudes were measured using a staircase procedure for stimuli which varied in eight directions away from the mid-white within the isoluminant plane: 0°, 45°, etc.

Results

Logarithmic changes in threshold are plotted for tests in different isoluminant color directions

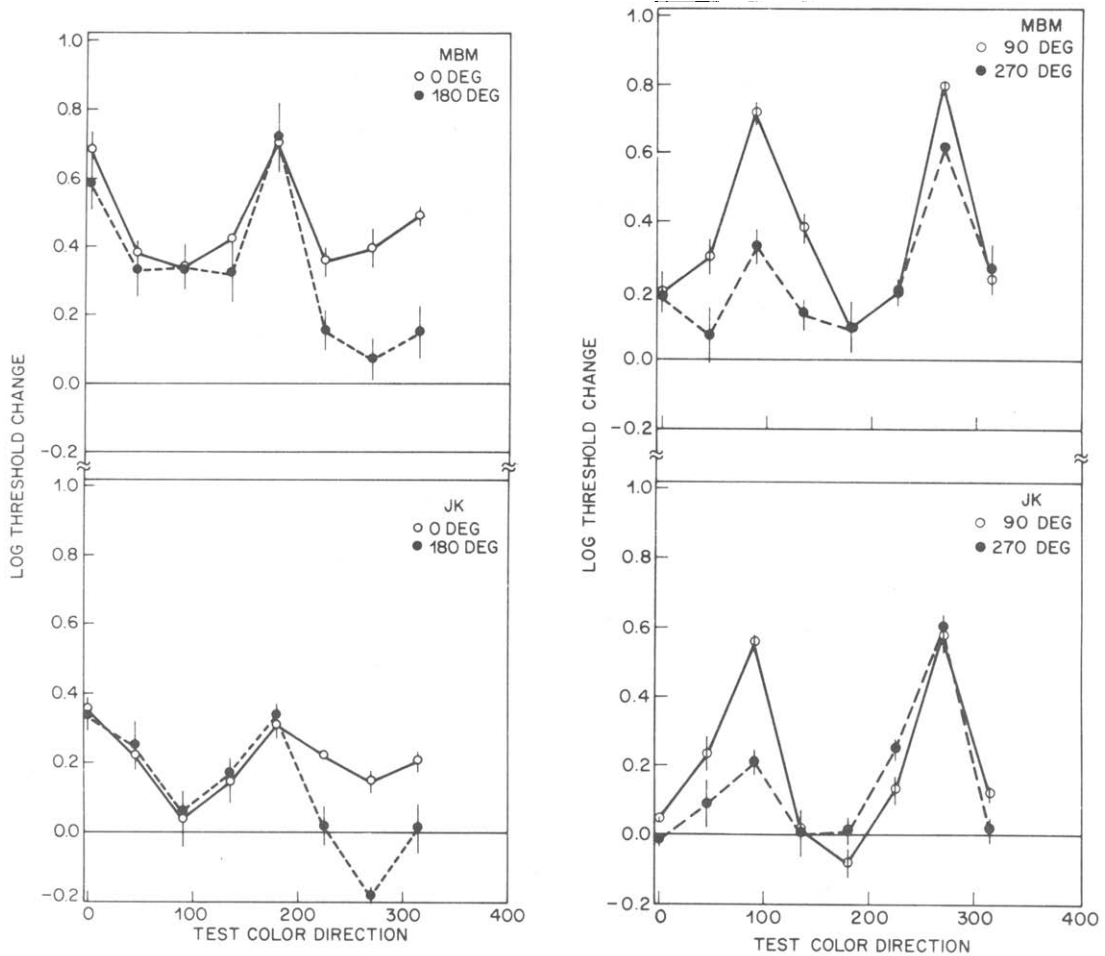


Fig. 5. Changes in log threshold as a function of test color direction for conditioning stimuli in cardinal directions.

for conditioning stimuli in the cardinal directions in Fig. 5. Results for the two observers are presented to allow the assessment of reliability. The condition most similar to the original transient tritanopia experiment is when the step is in the 90° direction and the test is in the 270° direction. In this case the threshold elevations were 0.8 and 0.6 log unit for the two observers. Large threshold elevations were also observed for 270° tests after conditioning with 270° steps, and for 90° tests following 90° steps. Curiously, threshold elevations were much greater for 270° tests both observers than for 90° tests following 270° steps. Thresholds are little changed for tests at 0 and 180° . The general trend of the results is quite similar to those of Krauskopf *et al.* (1982). The plots for 0 and 180° conditioning steps also show selective desensitization at the conditioning directions. The effects are generally smaller and the selectivity does not appear as pronounced.

Results for conditioning steps at 90° and 315° are plotted in Fig. 6. If the results presented earlier we would expect the curves to be flat, but some of the curves have a shape similar to those of Fig. 5. To get a more compact expression of the results we submitted the data to a Fourier analysis, the results of which are presented in Figs 7 and 8.

These plots were generated by the same methods as were Figs 3 and 4. The results for the two observers agree quite well, even in respect to those features which we don't understand. The modulation of the first harmonic is generally smaller than that for the second, but curiously both observers have large values for conditioning pulses at 180 and 270° . Both observers show three peaks in the values of the modulations of the second harmonic. Although the modulation for 0° conditioning pulses is larger than that for 315° conditioning pulses, it is smaller than that for 45° conditioning pulses.

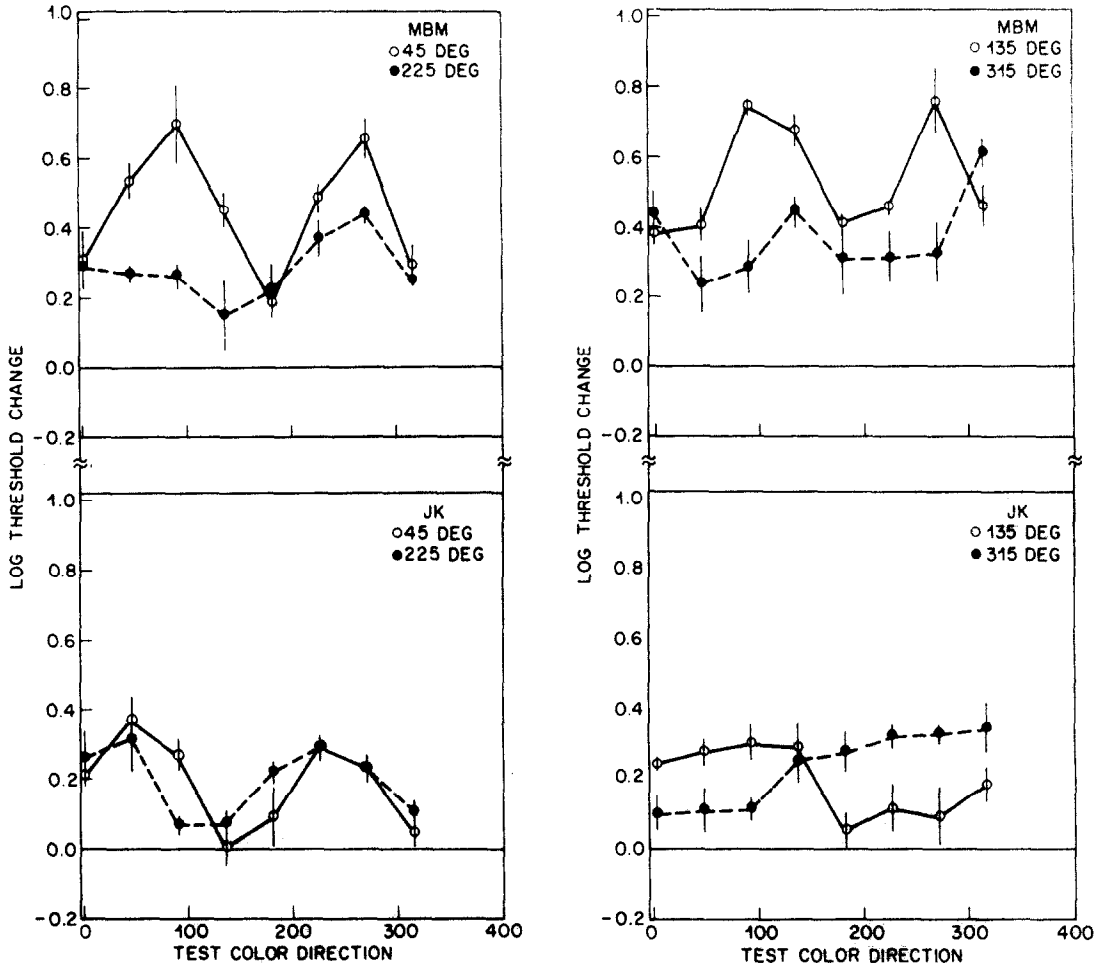


Fig. 6. Changes in log threshold as a function of test color direction for conditioning stimuli in noncardinal directions.

Just as in the reanalysis of the data of Krauskopf *et al.* (1982), the phase of the second harmonic varies with the direction of the conditioning pulse (Fig. 8). A novel feature of these results is that the phase of the first harmonic directly follows the azimuth of the conditioning pulse.

Once again, it can be seen that the use of Fourier methods to summarize the data makes clear trends which are not very well defined in the original plots. That the phase of the second harmonic follows the angle of the habituation stimulus in the present experiments reinforces the conclusion that selective desensitization re-

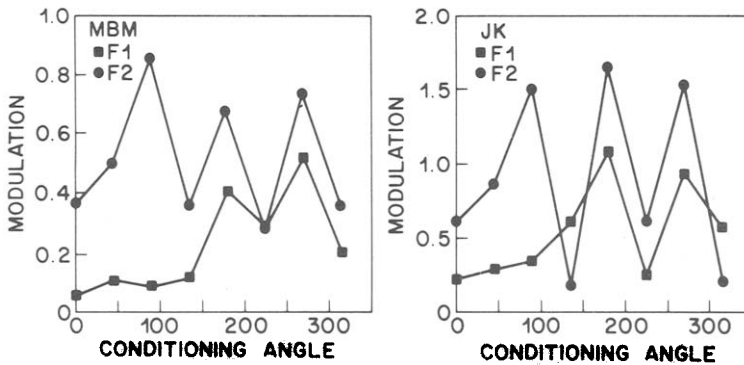


Fig. 7. Modulation (amplitude/mean threshold change) of first and second harmonic as a function of conditioning angle.

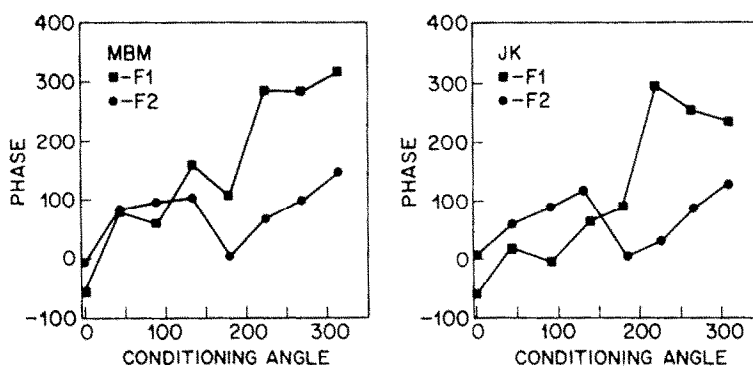


Fig. 8. Phase of first and second harmonic as a function of conditioning angle. Phase is plotted so that its value corresponds to the azimuth in color space of the first peak of the sinusoid fitted to the data.

sults from viewing stimuli modulated in any direction. One likely explanation of these results is that the procedures used in these experiments desensitize not only the second stage mechanisms but higher level mechanisms as well. The next experiment provides very different evidence for the existence of such higher order mechanisms.

DISCRIMINATION AND DETECTION

This experiment tests the hypothesis that changes in color within the isoluminant plane are detected by independent mechanisms maximally sensitive within each of the cardinal directions, and insensitive to changes in orthogonal cardinal directions. In order to test this hypothesis we make a further assumption, namely the validity of Muller's doctrine of Specific Nerve Energies, or in modern terms, that the detectors are labeled lines.

According to Muller, the sensation we perceive is determined by the nerves which respond to a stimulus and not by the stimulus *per se*. In the present context stimuli varying along a particular cardinal direction should always generate sensations of the same quality because they are always detected by the same mechanism, but stimuli falling along radii between the cardinal directions should vary in appearance, since they would be detected sometimes by one mechanism, sometimes by another and sometimes by both of these mechanisms. Therefore, stimuli falling along cardinal directions should be perfectly discriminable from one another, while intermediate stimuli, though equally separated in color space should sometimes be confused with one another since they are sometimes detected by the same mechanism.

Methods

The stimuli were generated by the laser color mixer. As before the field was maintained at a white of about 500 td between test pulses which were gaussian pulses 600 msec in duration, $\sigma = 100$ msec. Discrimination and detection performance was assayed simultaneously by means of a two-interval, two-alternative forced choice procedure. In any session stimuli in a pair of directions 90° apart were used. They were either cardinal pairs: 0 and 90° , 90° and 180° , 180° and 270° , and 270° and 0; or intermediate pairs: 45° and 135° , 135° and 225° , 225° and 315° and 315° and 45° .

The first step in any session was to find the approximation detection thresholds for each of the pair of changes in color using a yes-no staircase procedure. The stimuli used in the main part of the experiment were set at -0.2 , -0.1 , 0.0 , 0.1 and 0.2 log units with respect to these thresholds. One of these stimuli was presented in either the first or the second of two 600 msec intervals separated by 200 msec. Each stimulus of a pair was presented 25 times at each level in the first interval and 25 times in each level in the second interval in a session. The observer pressed one of two buttons to indicate in which interval he thought the stimulus was delivered and one of a second pair of buttons to indicate which of the two stimuli he thought had been presented. The observer always knew which pair was being presented and had an opportunity to see them at supraliminal levels in the beginning of the session.

Results

A nice feature of the two interval-two alternative procedure is that the estimates of the detection and discrimination probabilities are derived from the same stimulus presentations. If

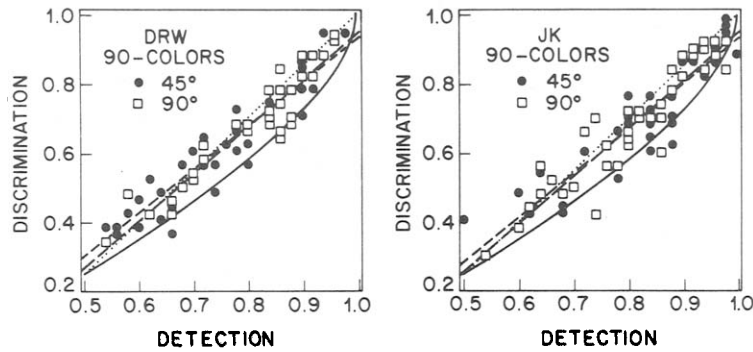


Fig. 9. Fraction correct discrimination vs fraction correct detection for cardinal pairs (squares) and intermediate pairs (circles). Dotted line is the prediction for perfect discrimination of all detected stimuli. Solid line is the prediction on the assumption that detection and discrimination are mediated by independent detectors within cardinal channels. Dashed lines are least squares fits to results. Long dash—90° (cardinal) stimuli, short dash—45° (intermediate) stimuli.

one chooses to assume a threshold model for detection one can predict the discrimination frequencies directly from the detection frequencies. Therefore, we have plotted our results in the form of scatter plots of fraction correct discrimination vs fraction correct detections as shown in Fig. 9. Each point plots the results for one member of a stimulus pair averaged over trials in which it was presented in the two intervals. There are thus 40 points per observer for each type of stimulus pair. The dashed lines which run through the data are least square linear fits. The other two lines are predictions from the model presented above. The upper, dotted, line is for the cardinal pairs and is for the case of perfect discrimination. It was derived in the following way. It is assumed that each time threshold is exceeded the observer correctly judges the stimulus interval and, in addition, that he chooses the correct interval on half of the other trials (the standard guessing correction). According to the Mullerian Doctrine every stimulus that actually exceeds threshold should be correctly identified. In addition half of the unseen stimuli that were guessed as occurring in the correct interval will be correctly identified by chance.

Formally, the relations between the probability of the observer choosing the correct interval (P_i) and naming the correct color given the correct interval (P_{CI}) can be derived as follows. First consider the case that the pairs of test stimuli are each detected by separate independent mechanisms. Let P_D be the true probability of detection, i.e. the proportion of trials on which the observer unequivocally knows when the stimulus was presented. On the remaining trials we assume the observer guesses randomly.

Therefore, the observed probability of choosing the correct interval is the probability of detection augmented by correct guesses on half of the trials on which the test is undetected.

$$P_i = P_D + 1/2(1 - P_D) = 1/2 + 1/2P_D.$$

On the Mullerian hypothesis all the truly detected stimuli plus one half of those not detected but judged by chance in the correct interval will be correctly named. Therefore

$$P_{CI} = P_D + 1/2 * 1/2(1 - P_D) = 1/4 + 3/4P_D.$$

But since

$$P_D = 2P_i - 1$$

$$P_{CI} = 1/4 + 3/4(2P_i - 1) = 1/2(3P_i - 1).$$

This equation relates P_{CI} and P_i independent of P_D .

The lower, solid, curve is the prediction for the intermediate pairs. The difference between the upper and lower curves is due to the ambiguous cases, for example, when detection by the constant-B mechanism alone might have been the consequence of a 45° or a 135° stimulus. For stimuli detectable by one of two mechanisms, a and b , the probability of detection by one or the other or both is given by

$$P_D = P_a(1 - P_b) + P_b(1 - P_a) + P_aP_b$$

where P_a and P_b are the probabilities of detection by each mechanism. Similarly, if P_c is the probability of detection in a third mechanism, then the probability of detection of stimuli which can be detected by either b or c is given by

$$P_D = P_c(1 - P_b) + P_b(1 - P_c) + P_cP_b.$$

The terms $P_b(1 - P_a)$ and $P_b(1 - P_c)$ both refer to cases in which detection is accomplished by the b mechanism alone and thus would be indiscriminable according to the Mullerian doctrine. On half of these trials the observer would therefore guess that the wrong stimulus was presented so P_{CI} in equation (1) is reduced by this amount. For the 45° stimuli P_a equals P_b equals P_c . Therefore

$$P_{CI} = 3/2 - 1/2 - 1/2P_a(1 - P_a)$$

but

$$P_a = 1 - (1 - P_D)^{1/2}$$

and

$$P_D = 2P_I - 1.$$

Thus

$$P_a = 1 - (2 - 2P_I)^{1/2}.$$

Finally

$$P_{CI} = 1/2[P_I + 1 - (2 - 2P_I)^{1/2}].$$

The results for the two observers are in close agreement and for each observer there is little difference between the fitted curves for the cardinal axis and noncardinal axis pairs. The most important question is whether the results with the off-axis pairs can be fit by the lower, solid curve. This fit must be rejected since for J.K. only 7 out of 40 points fall on or below this curve and for D.R.W. only 4 out of 40 points fall on or below this curve. A conventional sign test requires rejection of the null hypothesis at the 1% level when fewer than 11 out of 40 points fall below the line.

Similar experiments in which the stimuli to be detected and discriminated were cardinal pairs 180° apart also produced results well fitted by the perfect discrimination line. On the other hand, when the stimuli were increments and decrements in luminance, discrimination was significantly imperfect, confirming Krauskopf (1980).

DISCUSSION

The finding that the phase of the second harmonic follows the direction of the habituation stimulus in the reanalysis of the results of Krauskopf *et al.* (1982) and the direction of the conditioning stimulus in the generalized transient tritanopia experiment rules out the notion that desensitization occurs solely within independent second stage opponent mechanisms.

Additional desensitization in higher order mechanisms maximally sensitive in noncardinal directions could account for phase following. The existence of such higher order mechanisms is supported by the nearly perfect discrimination of non-cardinal, as well as cardinal, pairs of colors at detection threshold.

The phase of the first harmonic follows the phase of the conditioning stimulus in the generalized transient tritanopia experiment. This is consistent with the existence of fatigable mechanisms which respond more to changes in one direction with respect to the white point in color space than to their complementaries. Such mechanisms may also account for the selective effects on thresholds of habituating with fields modulated in a sawtooth fashion in time, and for the imperfect discrimination of increments and decrements in luminance (Krauskopf, 1980; Krauskopf *et al.*, 1982).

On the other hand, the greater selectivity when the habituation stimulus is in a cardinal direction seems to imply desensitization within mechanisms having the sensitivity of parvocellular LGN neurons (Derrington *et al.*, 1982). The psychophysical desensitization must be due to processes in pathways beyond the combination of signals from the different classes of cone receptors. Otherwise thresholds for detecting changes in color would be raised by viewing fields modulated in luminance, as well as by viewing fields modulated isoluminantly. In addition, no sign of fatigue is found in the responses of lateral geniculate neurons, so the desensitization must occur at a higher level than the LGN. Viewing a modulated field in one eye raises thresholds for color changes detected in the other eye, also implying a more central locus of the desensitizing process (Krauskopf *et al.*, 1982). Our working hypothesis is that desensitization occurs at a cortical level, both in some fatigable mechanisms which receive inputs only from single classes of parvocellular neurons and in other neurons that receive inputs from the two types of parvocellular neurons cells and are maximally sensitive to different isoluminant colors distributed about the color circle.

The similarity of the results of the analysis of the generalized transient tritanopia and habituation experiments suggests that they have a common explanation. The habituation stimulus has a time-averaged value precisely equal to that of the field upon which thresholds are measured. The system is not unbalanced by the procedure. The explanation of transient tritanopia and

related phenomena offered by Pugh and Mollon (1979) in terms of the dynamics of second stage processes does not seem applicable to the desensitizing effects of sinusoidally modulated fields. On the other hand, the phenomena of transient tritanopia and the related effects of transients reported by Augenstein and Pugh (1977) seem explicable in terms of desensitization of central neurons induced by activity.

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