

DETECTION/DISCRIMINATION IN THE LONG-WAVELENGTH PATHWAYS

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Abstract—We apply the simultaneous detection/discrimination method to the mechanisms mediating detection of long- and middle-wavelength test lights. The results suggest the following: (1) a test light detected by a signal initiated primarily in the long-wavelength receptors will be ultimately detected by different sets of nerve cells, depending upon the background illumination. (2) The discriminability of two test lights depends upon their duration, even when the lights are equated (at threshold) for visibility.

INTRODUCTION

The simultaneous detection/discrimination method is an empirical approach to the isolation and identification of the neural pathways of detection. The method was introduced to study detection mechanisms in pattern and orientation selective mechanisms (Nachmias and Weber, 1975; Tolhurst and Dealy, 1975; Thomas and Gille, 1979; Watson and Robson, 1981). It has also been applied to color (Kirk, 1981; Krauskopf, 1978; Rollman and Nachmias, 1972). We use it to examine conditions under which two test lights, identical except for wavelength, are detected by a single detection-pathway.

THEORY

Assumptions

The following is a set of assumptions about the structure and properties of detection-pathways that allow us to make inferences about them.

We define a collection of receptors and subsequent neurons as constituting a detection-pathway if they have the following functional property: the information available to the subject from the collective response of the detection-pathway elements can be characterized by a positive, continuous, real-valued function of time. We refer to this property as *unidimensionality*.

If two test lights are detected by a single detection-pathway the subject can discriminate them only by the time-course of the detection-pathway's response. When measuring detection/discrimination of incremental test lights of equal duration, we will make the stronger assumption that subjects cannot make use of time-course information. Instead, we suppose the subject's decision may be characterized as depending upon a single, real number—a decision statistic—computed from the detection-pathway's response to the stimulus (see Green and Swets, 1966 for such a

model). A detection model in which the subject bases his detection and discrimination responses only on the peak value of detection-pathway responses is one of many models that satisfy this assumption. If responses are based only upon the value of a single decision statistic, then equating lights for threshold visibility removes any basis for discriminating two test lights.

Finally we assume that the detection-pathway responses is linear with respect to small perturbations. This assumption permits us to calculate the test sensitivity of the detection-pathway.

Based upon these assumptions we conclude that if two test lights can be as accurately discriminated as they are detected, then they are detected by different detection-pathways. If discrimination performance is significantly worse than detection performance, we infer the lights are detected by the same detection-pathway.

Two comments on the assumptions

First, we state unidimensionality separately from the stronger assumption that the decision is based upon a single, real number in order to emphasize that, although we need the stronger assumptions here, the detection/discrimination method may be utilized with the weaker assumptions of unidimensionality and small signal linearity. If small signal linearity holds, test lights that are small sinusoidal modulations will cause a sinusoidal detection-pathway response, leaving only phase differences as a potential source of discrimination. By randomly varying the signal onset time with respect to the tones marking the trial intervals, this cue becomes unusable for the subject.

Second, physiological pathways may signal with two polarities, such as would be the case on an opponent-colors channel; this would provide sufficient information for discrimination, in violation of the assumptions for a detection-pathway. This observation does not pose a severe problem for the listed

assumptions since it is still possible to test the hypothesis that two detection-pathways reflect the action of separate physical mechanisms rather than opposite polarities of a single mechanism by means of a test mixture experiment, because when the test lights are of long-duration, the visibility of the mixture of these two test lights must be less than the visibility of either light, alone. Thus, the test mixture experiment can serve as an aid in deciding whether two lights are discriminable based upon opposite polarities of a single pathway or detection via two pathways.

METHODS

Stimuli

The experiments were performed on a three channel, Maxwellian view system. Two of the channels were used for the test lights (1.1 deg diameter spots, 13 msec duration in some experiments, 300 msec in others). The third channel was used for the steady, adapting background (10.8 deg diameter).

The light source for the Maxwellian view was a tungsten, quartz-iodine bulb, rated at 6.6 A, under-run between 6.0 and 6.4 A. The power supply was a d.c. supply, rated up to 10 A, and stable to within 1% r.m.s. error.

The maximum intensities of each channel was calibrated before each experimental session by means of a photodiode (United Detectors Technology, Pin 10-DP) amplifier, voltmeter combination. The photodiode-amplifier-voltmeter combination had been calibrated against a thermopile and precision voltmeter. The thermopile had been calibrated against a source traceable to the National Bureau of Standards. The gross adjustments of the beam intensities were made with neutral density filters. The calibration values of the filters were measured in our laboratory with our own light measurement system. These agreed closely with the manufacturer's (Melles Griot). During the experiment the intensities of the test lights were controlled by positioning neutral density wedges—mounted on computer driven stepping motors—in each of the test beams.

The duration of each of the stimuli was determined by shutters placed in the separate beams. The shutters consisted of a galvanometer motor with a small flag attached at the shaft and positioned at a focal point within the beam. The position of the motor shaft determined whether the flag interrupted the beam at the focal points or allowed the light to pass on to the observer. With this arrangement, rise and fall times to maximum light intensity were approximately 1.5 msec.

The wavelengths of the three channels were determined by interference filters (Baird-Atomic, halfband about 10 nm) inserted in the beam.

Subjects' heads were fixed in the system by means of a bite bar firmly attached to a vice that could be positioned in three dimensions. The final, focal point

of the system, was centered in the subject's pupil by a second observer, using the Purkinje images. The final focal point of all three beams was 1.5 mm in diameter.

Experimental procedure

Detection/discrimination experiments. On each trial the computer randomly selected one of the two test lights for presentation. A 2×2 forced-choice task was presented the observer who had to respond (1) which interval the test was presented in and, (2) which of the two possible test lights was presented. In early experiments the intensity of the stimulus was determined by a single staircase procedure (Wetherill, 1963). In later experiments the intensity was determined by a double random staircase for each test. Using two staircases reduces problems that arise when one test light is high on the its staircase and the other low, permitting the observer to use brightness differences as a means of identifying the lights. Also, in later experiments, test onsets were delayed relative to the tone indicating the interval onset by a random amount, varying between 0 and 100 msec. This reduces the possibility that latency differences in the signals from the two lights may be used as a means of discriminating the two lights. Several experiments were repeated using the better methods and neither of these changes had any significant effect upon the results.

The staircases for the two tests were controlled by a decision rule based on detection responses alone. The staircase rule was to decrement test intensity 0.1 log unit following 3 correct detection responses, and to increment test intensity following any incorrect detection response. This rule is useful for the detection/discrimination experiments since test intensities remain at detection levels greater than 60% correct detection where the most powerful test of the detection/discrimination hypothesis is possible.

A typical session consisted of 150 trials, a break of a few minutes, and then another 150 trials. The session would last—including set-up time and data collection—about 1½ hr.

Test-sensitivity experiments. Thresholds for the test-sensitivity experiment were measured in a two-alternative, forced choice, staircase procedure. The decision rule for the staircase was that when the observer was correct twice test intensity was decreased 0.1 log unit, whenever the observer made an error test intensity was increased 0.1 log unit. In a single threshold estimate 12 reversals were measured and the mean of the last 10 was used as a threshold estimate. Test sensitivities depend on at least 8 threshold estimates (96 reversals) per test wavelength.

Test-mixture experiments. Thresholds in the text-mixture experiment were also collected using a two-alternative, forced choice procedure. To collect psychometric functions, however, we did not use a staircase. This was because we wanted to make sure we had adequate numbers of observations where the observer was correct with probability near the chance

level. Instead we selected a range of test intensities before the experimental session. A set of 100 forced choice trials, using these intensities, was presented to the observer. The order of test intensities was random: the observer did not know which intensity would be presented. The psychometric functions are averages, pooled across at least 400 trials, measured on different days.

Thresholds to the mixture of the two tests were collected in the same way except that the second, fixed test was added into the variable test. On any day we always measured the psychometric functions of the monochromatic stimuli as well as the test mixture sensitivities.

Data analysis

Detection/discrimination. We have used two methods for analyzing the data. To provide a brief summary of the results it is convenient to graph the probability of a correct wavelength identification as a function of the probability of a correct interval detection (see e.g. Thomas and Gille, 1979). We construct these graphs by pooling data from different sessions and determining the average probability of correct wavelength identification given that the probability of correct interval detection was in the range from 0.50 to 0.59, or 0.60 to 0.69, etc. The probability of correct identification for each range of probability of correct interval detection was weighted by the number of observations that gave rise to it. The weighted averages, usually from three sessions on separate days, are plotted in the figures.

A second method to analyze the data is described by Watson and Robson (1981). In this method the detection and identification data for each of the stimuli are separately fit by a psychometric function. Because of its convenience and to permit comparison with the data of others, we have used the Weibull (1951; Quick 1974) function to fit the data. The equation of the Weibull that is applicable for this task is

$$\text{probability correct} = 0.5 + 0.5 \left\{ 1 - \exp \left[- \left(\frac{I}{\alpha} \right)^\beta \right] \right\}$$

where I is linear intensity. The fits were performed using STEPIT (Chandler, 1965) and the procedure described by Watson (1979).

In preliminary analyses of the data we allowed both α and β to vary freely. The values of β did not vary systematically with α and were generally near 3.0. For convenience, therefore we use the approximation that β is 3.0 in all conditions.

If β is constant across conditions, then the α estimates for detection and identification will be equal when the lights are perfectly discriminable. We may summarize the discriminability of the two lights at threshold by computing the difference of the logarithms of α for detection and identification for each stimulus and averaging these two differences. Values near zero indicate discriminability equal to detect-

ability, while large values indicate that discrimination occurs only when the stimuli are above threshold.

RESULTS

Detection/discrimination upon a 580 nm background field

We plot the simultaneous detection/discrimination data for test lights detected against a 580 nm back-

OBSERVER: JS
 $\mu = 580 \text{ nm}$
 $(10.07 \text{ log quanta deg}^{-2}\text{sec}^{-1})$
 $\lambda_1 = 670 \text{ nm}$

○ = 13 msec
 ● = 300 msec

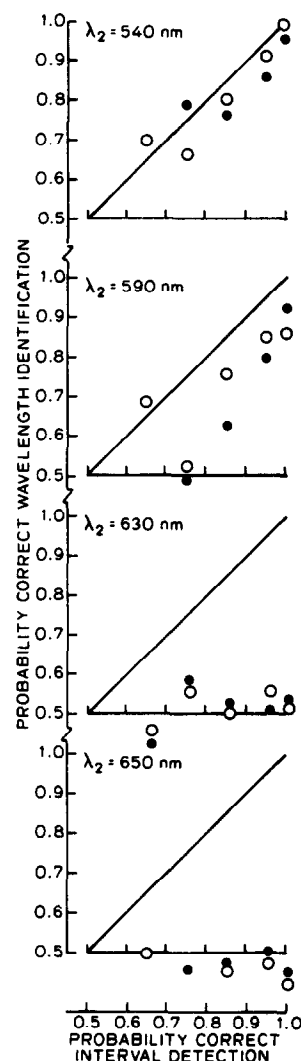


Fig. 1. The probability of correctly identifying the wavelength of a comparison light from a standard, 670 nm test light as a function of the probability of correctly identifying the temporal interval of occurrence of the test lights. The wavelength of the comparison light is indicated in each, separate panel. The filled symbols refer to test durations of 300 msec, the unfilled symbols to test durations of 13 msec. The data are for observer J.S. on a 10.8 deg. 580 nm field. The line drawn in each panel is the 45 deg line.

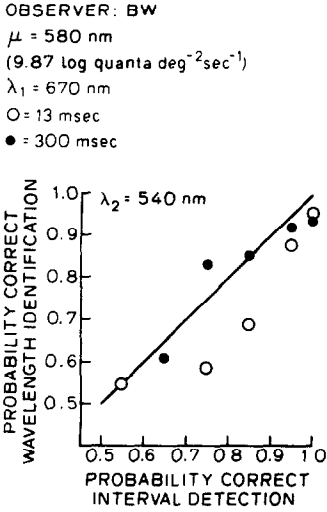


Fig. 2. As Fig. 1 but for observer B.W.

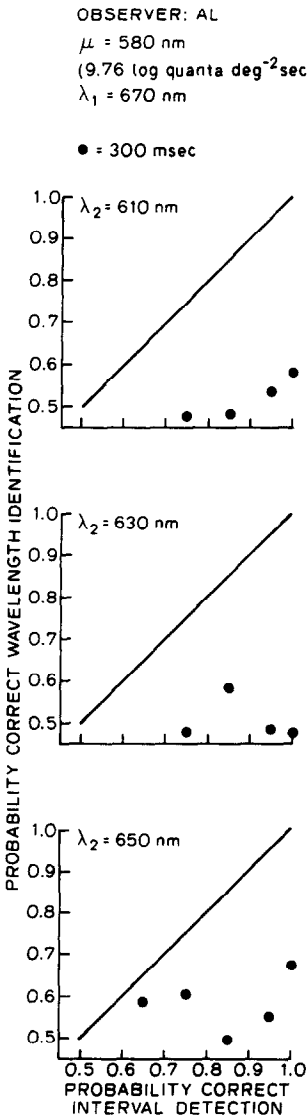


Fig. 3. As Fig. 1 but for observer A.L.

ground at $9.87 \text{ log quanta deg}^{-2} \text{ sec}^{-1}$ in Figs 1-3. The probability of correctly identifying the test flash wavelength is plotted as a function of the probability of correctly detecting the interval in which the test flash occurred.

Were it the case that one could detect a light at the same intensity as it becomes possible to identify its wavelength, then the data points would fall on the identity line, sketched on the figures. To the extent that the data points fall below the line, the observer can detect the test light before being able to accurately discriminate its wavelength from the constant 670 nm wavelength.

First, observe that in this background wavelength discriminability does not depend importantly on the

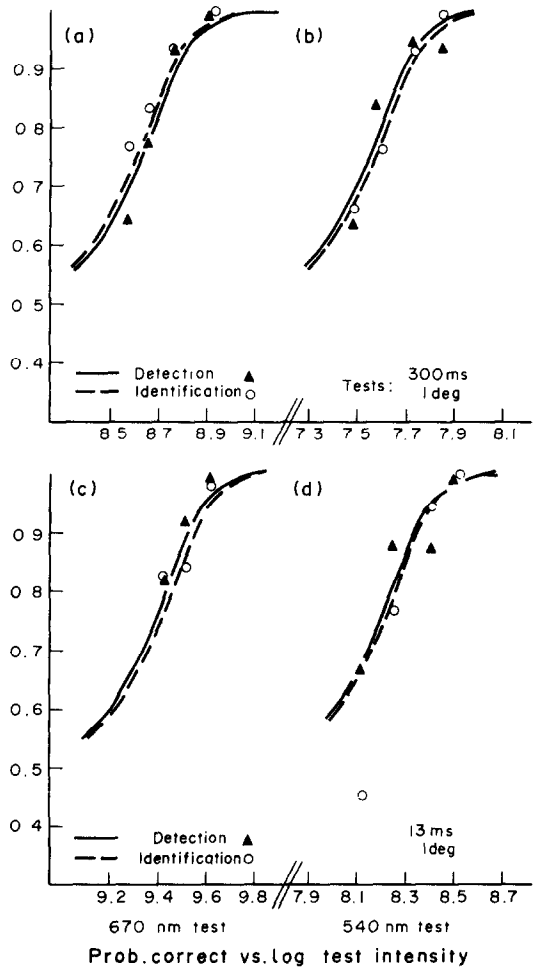


Fig. 4. (a and b) The probability of correct detection (filled symbols) and identification (unfilled symbols) of 300 msec test flashes upon a 10.8 deg , 580 nm , $9.87 \text{ log quanta deg}^{-2} \text{ sec}^{-1}$ background for a 670 nm test flash (circles) and 540 nm test flash (squares). The intensity axis is $\text{log quanta deg}^{-2} \text{ sec}^{-1}$. The smooth curves fit through the data are best-fitting Weibull functions with a $\text{log } \alpha$ values of 8.673 (670 nm detection), 8.640 (670 nm identification), 7.611 (540 nm detection), 7.623 (540 nm identification). (c and d) As Figs 4 (a and b) except the test duration is 13 msec. $\text{log } \alpha$ of the Weibull functions are 9.433 (670 nm detection), 9.475 (670 nm identification), 8.273 (540 nm detection), 8.294 (540 nm identification).

duration of the test flash (Figs 1 and 2). The 13 msec and 300 msec tests at different wavelengths are discriminated equally well when equated for probability of detection. As we will see shortly, this is not true for all background wavelengths.

Second, upon this background there is a wide range of test wavelengths—extending down to nearly 590 nm—that are indistinguishable from a 670 nm test light at increment threshold (Figs 1 and 3). For both long and short duration test flashes and for all three observers, discrimination performance is approximately equal to detection performance when the second test wavelength is at 540 nm.

Figure 4 shows the probability of detecting and discriminating the 670 nm and 540 nm 300 msec test flashes against the 580 nm background. The smooth curves are the best-fitting Weibull functions, constrained to have a β of 3.0. Figure 4 (a and b) is the probability of correctly identifying 300 msec tests, and 4(c and d) is the probability of correctly identifying 13 msec tests. If discrimination is as good as detection, the curves fit to the discrimination data and the curves fit to the detection data will have equal, average values of α .

For both duration test flashes the α estimates for detection and identification differ by very small amounts, the average of the differences being 0.007 log units for the long-duration lights and 0.043 log units for brief-duration lights.

To summarize, within a region near detection threshold, upon a 580 nm background, observers are monochromatic for wavelengths within the range of 600–670 nm. We take this as evidence that varying the test wavelength within this range does not force detection by a new mechanism. Under these viewing conditions, wavelength discriminability does not greatly depend upon the duration of the test flash.

Simultaneous detection/discrimination upon a 650 nm background

The wavelength of the background light strongly affects the pattern of results in the simultaneous detection/discrimination task. There are two qualitative differences, illustrated in Figs 5–8. First, the wavelength at which discrimination from the 670 nm test light first becomes possible changes as the background wavelength changes. Whereas on the 580 nm background 630 nm test light were not discriminable from 670 nm lights at thresholds, they are somewhat discriminable upon a 650 nm background.

Second, there is a measurable difference in detection/discrimination performance between the 13 msec test flashes and the 300 msec test flashes. The 300 msec test lights are easier to discriminate at threshold than the 13 msec test lights. This effect is fairly marked for the discrimination between the 630 and 670 nm tests and is also measurable for discrimination of a 540 nm test light from the 670 nm test.

In Fig. 8a and b we plot the psychometric functions for 300 msec test flashes and in Fig. 8c and d those for

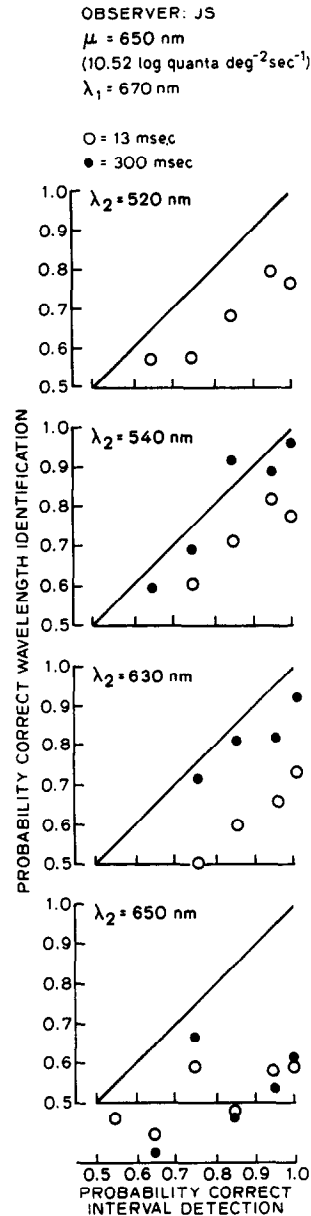


Fig. 5. As Fig. 1 except the background wavelength has been changed to 650 nm with intensity indicated on the graph.

13 msec test flashes. While the average difference in α between detection and discrimination is about 0.073 log units for the 300 msec test flashes, it is 0.434 log units for the 13 msec test flashes. This confirms the impression from the summary data that the 13 msec test flashes are not well discriminated from one another, even for wavelengths as different in supra-threshold appearance as the 670 and 540 nm test flashes.

To summarize, upon an intense 650 nm field observers are monochromats at increment threshold only in the long-wavelength region above 650 nm. We therefore conclude that upon this background test lights below 650 nm are detected—at least in part—by

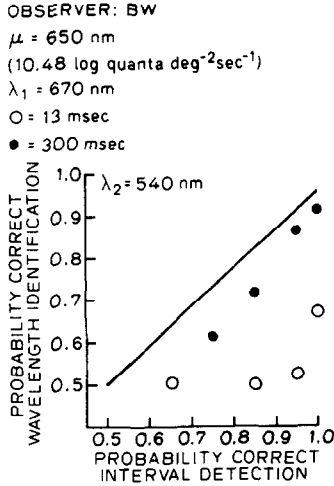


Fig. 6. As Fig. 5 but for observer B.W.

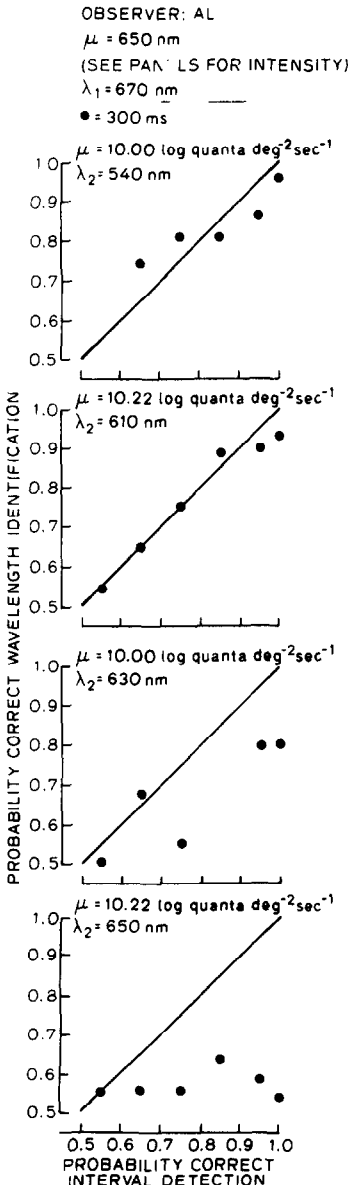
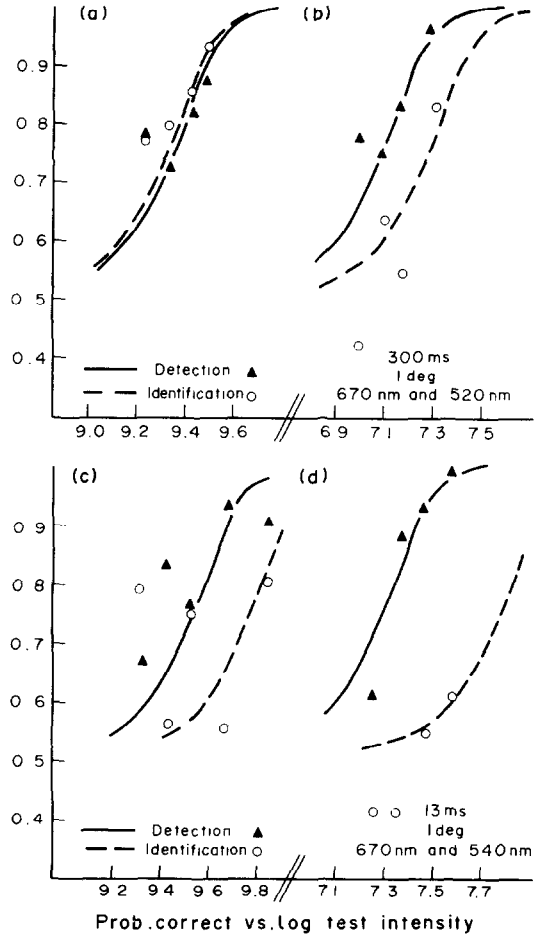


Fig. 7. As Fig. 5 but for observer A.L.



Figs 8. (a and b) As Figs 4 (a and b) except the background has been changed to a 650 nm $10.69 \text{ log quanta deg}^{-2} \text{ sec}^{-1}$ field and the second test light is 520 nm. Log α of the Weibull functions are 9.411 (670 nm detection), 9.358 (670 nm identification) 7.153 (520 nm detection), 7.353 (520 nm identification). (c and d) As Figs 4 (c and d) except the field is 650 nm $10.14 \text{ log quanta deg}^{-2} \text{ sec}^{-1}$. Log α for the Weibull functions are 9.595 (670 nm detection), 9.824 (670 nm identification), 7.363 (540 nm detection), 8.001 (540 nm identification).

a different detection-pathway from lights longer than 650 nm in wavelength. Moreover, on a 650 nm background, discriminability depends upon the test flash duration. No such dependence was evident for the 580 nm background.

Test-sensitivity and test-mixture experiments

The data thus far show that 670 and 650 nm test lights are not discriminable at threshold, whether the measurements are made upon 580 or 650 nm backgrounds. Is it the case that on each of these backgrounds the two test lights are indiscriminable because they are detected by signals from the same class of photoreceptors? In table 1 we show the relative test sensitivities to the 650 and 670 nm tests on 580 and 650 nm backgrounds. The test spectral sensitivities on these two fields are the same within measurement error. The average relative sensitivity

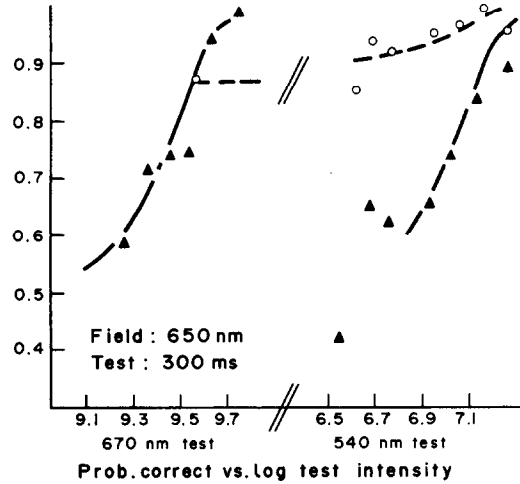
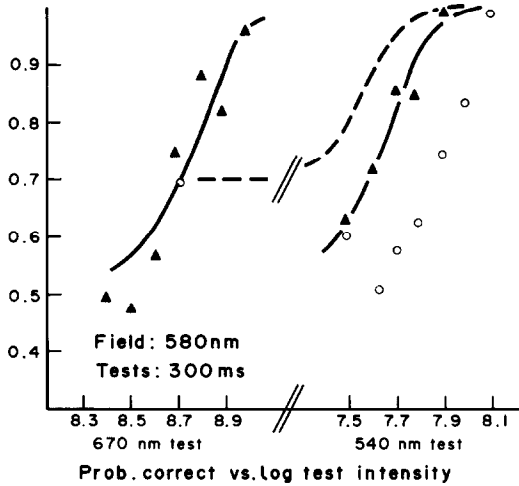


Fig. 9. The left hand panel is the probability of detecting a 670 nm, 300 msec test upon a 580 nm, 9.86 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ background (filled circles). The right hand panel is the probability of detecting a 540 nm, 300 msec test against this same background (filled squares). The open symbols are the probability of detecting a mixture of a 8.76 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ 670 nm test flash and an amount of 540 nm test light indicated on the horizontal axis. The smooth curves through the detection data are Weibull functions with parameters $\log \alpha = 8.69$ and $\beta = 2.45$ for the 670 nm test and $\log \alpha = 7.70$ and $\beta = 2.44$ for the 540 nm test. The dashed curve between the data is the prediction of probability summation from the fitted Weibull functions.

Fig. 10. Conventions as in Fig. 9. The background has been changed to 650 nm 10.69 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ and the 540 nm light has been changed to a 520 nm light. The unfilled symbols are the probability of correct detection for mixtures of a 9.60 log quanta $\text{deg}^{-2} \text{sec}^{-1}$ 670 nm test flash and an amount of 520 nm test light indicated on the horizontal axis. The parameters of the Weibull functions $\log \alpha = 9.54$ and $\beta = 2.26$ for the 670 nm test and $\log \alpha = 7.15$ and $\beta = 1.48$ for the 520 nm test.

for the three observers is quite close to the Smith and Pokorny (1975; tabulated in Boynton, 1980) long-wavelength receptor sensitivity for these wavelengths (0.518) and measurably different from their middle-wavelength receptor sensitivity (0.634). Since on the 580 nm field the test signal is almost certainly detected by a signal originating in the long-wavelength receptors, the similarity of the test spectral sensitivities on the two fields suggests that the 650 and 670 nm lights are detected by a signal either entirely or in large part initiated in the long-wavelength receptors on both fields.

It does not follow, however, that the 670 nm test is detected by the same neural pathway on the 580 and 650 nm fields. As we shall elaborate in the discussion, it is possible that these lights are ultimately detected by different pathways although they are initially signalled by the same receptor class. For example, test lights may be detected by different neural pathways because the change in background illumination causes a shift in post-receptor pathway sensitivities

without reversing the ordering of sensitivity of the receptor classes.

We may illustrate that this is so in the present experiments by comparing the results of test mixture experiments on the 650 and 580 nm backgrounds. The data in Fig. 9 show thresholds to a mixture of 670 nm test flashes and 540 nm test flashes upon a 580 nm field. The smooth curve is the fitted psychometric function and the intervening dashed curve is the prediction of probability summation, based upon the fitted psychometric functions. The open symbols are the results of test mixture where the 670 nm test light, of intermediate intensity (unfilled circle), is mixed with a 540 nm test light, whose intensity is indicated on the horizontal axis at the right. The data are consistent with the cancellative interactions under similar conditions measured by Boynton *et al.* (1964), Guth *et al.* (1969), Stromeyer *et al.* (1978), Kranda and King-Smith (1979) and others.

A similar set of measurements for 670 and 520 nm test lights is shown upon the 650 nm background in Fig. 10. In this case the mixture thresholds are approximately consistent with the prediction of probability summation. From these results and the detection/discrimination data we conclude that the 670 and

Table 1. Mean test sensitivities (SEM)

	B.Q.	Observer			Mean
		J.R.	B.W.		
Field	580 nm	0.463 (0.09)	0.509 (0.034)	0.557 (0.032)	0.510 (0.05)
	650 nm	0.490 (0.04)	0.510 (0.059)	0.604 (0.043)	0.535 (0.06)

520 nm test lights on a 650 nm field are discriminated because they are detected by different mechanisms, and not because they cause responses of opposite polarity in a single mechanism.

DISCUSSION

Logical foundations

Were there one detection mechanism that mediated threshold to all wavelengths of light, then no two test lights differing only in wavelength would be discriminable at detection threshold. Rollman and Nachmias (1972), Krauskopf (1978), Kirk (1981) and we have shown that even at detection threshold lights are discriminable. It follows that in order to explain the complete pattern of results at detection threshold more than a single detection mechanism must be involved. The consequence of this for formal theories of detection threshold—where a detection mechanism is characterized by a single real number—is that any complete theory of threshold must include a system of mechanisms where the visibility of lights is represented by more than the value of a single real number.

This point has been made forcefully in several theories of detection threshold that attempt to summarize visibility by vector representations of lights (Guth *et al.*, 1969; Guth *et al.*, 1980; Ingling and Tsou, 1977). Vector theories begin with the well-established representation of lights as vectors. Beyond this, however, in order to make predictions about thresholds and color discrimination, vector theories must make assumptions about the nature of the pooling of information in test mixture and test discrimination experiments. The main assumptions that have been made are the following: the detectability of a mixture of two test lights is a function of their vector sum, while the discriminability between two lights is a function of their vector difference (see Guth *et al.*, 1980 for a concrete theory along these lines). The first of these assumptions is unexceptional as it depends only upon the supposition that the vector representation of the physical mixture of two lights may be described as a vector sum. This is equivalent to the assumption that the quantum absorptions obey small signal linearity (see Krantz, 1975 for a thorough analysis), and is consistent with the known properties of photoreceptor absorptions.

The second assumption—that the discriminability of lights depends upon their vector difference—is more difficult to defend and has been less thoroughly tested. In discrimination experiments the two lights to be compared are not physically mixed. Therefore, the assumption that their discriminability depends upon their vector difference is an assumption about the linearity of the *decision mechanism*, and not the linearity of the physical mechanisms of visual response. There is empirical evidence to suggest that this assumption is problematic (see e.g. Nachmias and Kocher, 1971; Nachmias and Sansbury, 1974; Lasley

and Cohn, 1981). A more complete examination of the basic postulates of vector representations in general is Krantz (1975). Wandell (1982) discusses the application of vector representation to the problem of color discrimination.

The implications of the effects of test duration

A second, theoretical issue concerning theories of color discrimination arises from the observation that the duration of the test flash is a significant parameter in determining the wavelength discriminability of different test lights on the 650 nm background field (Fig. 8d). This observation rules out the hypothesis that wavelength discriminability can be described as a simple functional of the ratio of quantal absorptions in the three photoreceptor classes, ignoring the temporal distribution of the absorptions. The dependence of discriminability upon duration (see also Sigel, 1965) is a complication for line-element models of color discriminability based upon calculations using vector quantities assigned to test lights: the vector assignment rule must take into account not only the number and distribution of quantum absorptions among the photoreceptor classes, but also the timing of these absorptions.

The observation that wavelength discriminability at increment threshold depends upon the temporal parameters of the test light is consistent with the suggestion that differences in the temporal distributions of the test light, like differences in the wavelengths of the test light, affect the relative activity of the detection mechanisms of color vision. Qualitative differences between long and short duration threshold flashes upon intense 650 nm adapting fields have now been observed using several, different experimental measures. Test-additivity results of Boynton *et al.* (1964) and Stiles (1967; 1978) revealed different behavior for long and short duration flashes: long duration flashes failing to be test-additive and short duration flashes being approximately test-additive. A sharp difference in the outcome of shape-invariance and field mixture experiments was also observed when 10 and 200 msec test flashes were used: brief duration test lights were consistent with tests of field-additivity while long duration test lights showed dramatic failures of field-additivity under identical adapting conditions (Wandell and Pugh, 1980a, b).

The discrimination experiments reveal one more difference between brief and long duration test flashes on intense, long wavelength fields. The results are consistent with the suggestion that differences in the temporal characteristics of test lights cause a change in the mechanisms mediating detection of the long-wavelength lights as the background field is changed from 580 to 650 nm (Sternheim *et al.*, 1979; Wandell and Pugh, 1980b).

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