Field Additivity of the Middle-wavelength Cone Pathway Under Various Test and Field Configurations

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The field additivity of the M-cone pathway was measured with psychometric functions at 10 times absolute threshold on monochromatic fields and their mixtures. Observers detected a 500 nm test on 530 or 610 nm fields, and a 530 nm test on 481 or 622 nm fields. For both sets of wavelengths, field additivity held with the 1 deg test, 10 deg field condition which defines II-4 and with the 3.6 min arc test on a 8.6 min arc field used to isolate the M fundamental by Stockman (1983) Ph. D. thesis, Trinity College, Cambridge University, Cambridge. Sub-additivity occurred for a 1 deg test on a 1 deg field, a condition for Foster’s “spectral sharpening” which may evince opponency.

Human color vision  Field additivity  M-cones  Spatial configuration  Opponency

INTRODUCTION

In the elegant two-color increment threshold technique of Stiles (1939, 1949), a test spot of fixed size, duration, and wavelength, is brought to threshold on a large, steady, monochromatic adapting field. The field spectral sensitivity curve plots, against field wavelength, the energy in each adapting field required to bring to threshold a test of a criterion radiance. All such fields form an equivalent set in that they produce the same response (threshold visibility) to exactly the same test stimulus. Just as long as the transfer characteristics of the detection mechanism are independent of the adaptive states of other mechanisms (adaptive independence), and the same mechanism detects the test at all field wavelengths (mechanism isolation), equivalence implies that the transfer characteristics of the detection mechanism, including non-linearities, probability summation, and the like, cannot affect the shape of the field spectral sensitivity curve. If the shape is independent of the choice of test parameters, adaptive independence and isolation are supported, and the curve represents a true mechanism spectral sensitivity whether the mechanism reflects encoding by single or multiple classes of photoreceptors. [Thus the II mechanisms were called mechanisms to emphasize their operational rather than physiological status (Stiles, 1953).] Stiles demonstrated shape independence (the “displacement laws”) by systematically varying test wavelength and energy for fixed test duration and size.

If adaptive independence and mechanism isolation hold true, one can query whether mechanism sensitivity to monochromatic (i.e. pure) fields can be used to predict sensitivity to desaturated fields. We therefore asked how pairs of equivalent pure fields, when mixed, might affect sensitivity. The simplest possibility is field additivity: the effect of any field or mixture of fields on test threshold is controlled by mechanisms that are linear combinations of the excitations of various classes of receptors. When a proportion (p) of one pure field is mixed with (1-p) of another, field additivity implies that thresholds on the mixed field should be equal to those on the two pure fields. Thus, equivalence of pure and mixed fields may be used as a check of field additivity. The following experiments used equivalence to test the middle wavelength pathway for field additivity under II-4 and related conditions. We argue that conditions for mechanism isolation can be found (see Discussion), and we do not reject adaptive independence as II-4 obeys Stiles’s displacement laws (Stiles, 1953; Sigel & Brousseau, 1982; see Reeves, 1982a).

The radiances of the pure fields used in the current experiments were chosen so that the criterion increment threshold would be 10 times absolute threshold (Stiles’ “field point!”). At the field point, Stiles’s II-4 (middle-wavelength) mechanism was earlier shown to be field additive (Reeves, 1987), as was Stiles’ long-wavelength mechanism, II-5 (Sigel & Pugh, 1980). When the middle- and long-wavelength mechanisms are tested at intensities somewhat above the field point, i.e. in Stiles’ (1953) II-4’ and II-5’ regions, the field spectral sensitivity changes

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and field additivity is violated (Wandell & Pugh, 1980; Stomeyer & Sternheim, 1981). Pugh and Kirk (1986) concluded that \( \Pi - 4 \) itself was not field-additive, as Kirk (1985) had found that the field spectral sensitivity of \( \Pi - 4 \) changed in shape when an additional field of fixed wavelength and intensity was added to the main field. However, Kirk’s added field drove threshold up by 0.4 log units, into the \( \Pi - 4' \) region. One advantage of the equivalence method is that all thresholds can be obtained at the field point.

If the adaptation of \( \Pi - 4 \) is only controlled by one class of cones (M cones), equivalence (and hence field additivity) follows directly from the principle of univariance. However, if more than one class of receptors is involved in adapting \( \Pi - 4 \), say L and M cones (Sigel & Brousseau, 1982; Pugh & Kirk, 1986), equivalence follows only if the cone types combine linearly. Sub-additivity (a lower threshold on the combined field), rather than equivalence, may occur if \( \Pi - 4 \) detections are mediated by a non-linear, L/M coded opponent pathway. For example, if the pure fields of opposite hue “polarized” each other (Pugh & Mollon, 1979; Mollon, 1982), then their mixture might partly cancel and be less desensitizing than the pure fields. Any similar model in which sensitivity decreases monotonically with \( |L - M| \) makes this prediction.

In general it is unclear whether detection of incremental flashes involve hue, brightness, luminance, saturation, or any combination of these properties (e.g. Hurvich, 1963). If an additive pathway is dominant at threshold, as suggested for Stiles’ conditions by Mollon (1982), then sub-additivity might only be found above threshold. However, studies of test additivity can show L–M opponency at threshold (Guth, 1967; Guth, Donley, & Marrocco, 1969.) In general, both additive and chromatic pathways may be active, with their relative salience depending on the strength of the test flash (Ingling, 1978). To explore these possibilities, additional field additivity measurements were made with test flashes just above and below threshold.

The spatial, spectral, and temporal parameters defining the test and field were varied in an attempt to study field additivity in conditions of theoretical interest in addition to those employed by Stiles.

Spatial parameters

The stimuli, illustrated in Fig. 1, were large, a 1 deg test on a 10 deg field, as used by Stiles (1953) to define \( \Pi - 4 \); small, a 3.6 min arc test on a 8.6 min arc field, similar to those used by Stockman (1983) to isolate M (and L) action spectra; and coincident, a 1 deg test on a 1 deg field, similar to those used by Foster (1981) to obtain spectral sharpening.

Stockman (1983) chose small stimuli (3 min arc test on a 7–8 min arc field) because, as threshold-vs-radiance (tvr) curves for small tests and fields rise faster than larger ones (Graham & Bartlett, 1940), small stimuli can reveal double-branched tvr curves which are smeared together for large stimuli. Insofar as tvr branches are cone specific, small stimuli will therefore isolate cone mechanisms better than large ones. Stockman (1983) concluded that the sensitization brought about by using

![FIGURE 1. Stimuli. Upper panels; from left to right, large, coincident, and small. Hatching indicates test and field wavelengths (see key) in wavelength sets A, B, and the control (C).](image_url)
a small test on a small background is largely cone specific (McKee & Westheimer, 1970), so test spectral sensitivities measured with small spots should be fundamentals (see Stockman & Mollon, 1986). Cone specificity predicts that the small spot conditions should be field additive, as single classes of cones obey univariance.

Foster (1981) used a steady auxiliary monochromatic light, spatially coincident with the test flash, to produce “spectral sharpening”, the narrowing and shifting apart of Stiles’ II-4 and II-5 field sensitivity curves. To measure field sensitivity, the main 10 deg conditioning field was adjusted in radiance to return a visible test to threshold. Without the auxiliary, field sensitivity closely resembled II-4. A weak auxiliary kept thresholds below II-4, yet the field sensitivity curve shifted to shorter wavelengths and narrowed. Thus, while an additive pathway may mediate detection of the test in II-4 conditions (Mollon, 1982), detection can shift to an opponent pathway in the coincidence condition. This shift may occur because the opponent pathway is less vulnerable to masking by spatially coincident edges than is the additive pathway (Foster & Snelgar, 1983; see also Cole, Stromeyer & Kronauer, 1990). Alternatively, the opponent pathway may have higher temporal acuity, but lower spatial acuity, than the luminance pathway. (Recall that in the coincident condition there is no spatial transient to mark the occurrence of the test flash.) In either case, if detection in the coincidence condition is mediated by the opponent pathway on both pure and mixed fields, and if mixed fields reduce or eliminate polarization (Mollon, 1982), then we should find subadditivity (a lower threshold on the mixed field) in this condition.

**Spectral parameters**

Two sets of wavelengths were employed. Wavelength set A was composed of a 530 nm test with 481 and 622 nm fields. Combinations of these or similar middle- and long wavelength fields can be inhibitory (Ikeda, 1963; Boynton, Das, & Gardiner, 1966; Guth, 1967; Guth, Alexander, Chumbly, Gillman & Patterson, 1968; Guth et al., 1969; Thornton & Pugh, 1981, 1983). Guth et al. (1968) obtained optimal cancellation using 485 and 635 nm fields of 20 min arc, 45 min arc, and 2 deg diameter. Foster (1981) determined the maximum amount of spectral sharpening from the difference between the sensitivity curves derived from 503 and 621 nm adapting fields. Each had a 619 nm auxiliary that was coincident in size with the test. The greatest difference was produced with a test of 530 nm. Thus, wavelength set A is very close to Foster’s optimum wavelength set. These conditions were thought likely to show opponent interactions, and therefore be subadditive, in the small test and field spatially coincident conditions. In the 1 deg test spot condition field additivity was expected, replicating Reeves (1987) who used nearly the same field wavelengths as set A (480 and 622 nm fields) and a test flash which, though shorter in wavelength (500 nm), was not expected to probe a different mechanism.

Wavelength set B was composed of a 500 nm test with 530 and 610 nm fields. This test wavelength was originally chosen by Stiles (1959) to determine II-4, and should separate II-4 from II-5 adequately (Stiles, 1939, 1953; also Kirk, 1985), although a 460 nm test may isolate M cones a little better. Field additivity was expected in the Stilesian (large spot) condition, as Reeves (1987) had found field additivity in such conditions using a 500 nm test with 530 and 622 nm fields, similar to set B. In general set B provides a conservative test for field additivity, as these wavelengths can stimulate the red-green opponent pathway quite strongly (Werner & Wooten, 1979a, b).

A third wavelength set, composed of a 500 nm test with two identical 622 nm fields, served as a control. Mixing two identical fields ensures no change in thresholds, and thus an additive result, unless there are optical errors or procedural problems. Both observers were run in this control with a 1 deg, 200 msec test flash, using the procedure described for Expt. 2. Results (given in Table 2) showed near perfect additivity and so validated the method.

**Temporal parameters**

Experiment 1 employed two test durations, 200 msec, as used by Foster (1981) and by Stiles (1953) to determine II-4, and 20 msec, as used by Foster (1981) and Stockman (1983). In Expts 2 and 3, only the 200 msec duration was used to facilitate observation of possible sub-additivities. We presumed that the longer duration test is more likely to be detected by opponent than additive pathways (King-Smith & Carden, 1976; Stromeyer, Khoo, Mugggeridge, & Young, 1978; Stromeyer & Sternheim, 1981). Additivity can fail increasingly at longer test flash durations (Ejima & Takahashi, 1988). Moreover, Foster (1981) found spectral sharpening with a 200 msec test flash; sharpening was much reduced, though not eliminated, with a 20 msec test.

**GENERAL METHODS**

**Observers**

The authors (JS and AR) were the two psychophysically experienced observers. JS was a 33-yr-old male with normal vision. AR was a 42-yr-old male, who used his spectacle lens (–3 D) during the experiment to correct his myopia. Observers performed normally on the Farnsworth–Munsell 100-hue test and the Nagel anomaloscope. Some data were confirmed with a third observer in Expt 1 (JA), who was naive but had had considerable practice.

**Apparatus**

A conventional four-channel Maxwellian view provided a 2 mm diameter final image at the pupil of the left eye. The light source was a 150-W xenon arc mercury lamp (Osram XBO) mounted in a Schoeffel housing. The first channel provided a 481 nm (half-bandwidth at half-maximum ± 9 nm) or 530 nm (± 12 nm) field.
or 622 nm (±16 nm) in the control experiment. The second channel provided a 610 nm (±8 nm) or 622 nm (±16 nm) field. A 50% mixture field was produced by combining the two fields and halving the total radiance. A third channel provided the test flash, of 500 (±8 nm) or 530 nm (±8 nm). A variable neutral density wedge under computer control attenuated the test radiance in approx. 0.01 log unit steps. Flash duration (19, 20, or 200 msec) was controlled by a Uniblitz shutter. A fourth channel provided a dim (1 td) white (approximately equal energy) 10 deg auxiliary field for use with wavelength set B. Fixation was aided by four tiny markers located 45 min arc from top, bottom, left and right of center; the markers were black dots on large fields or 2 min arc, 500 nm spots at absolute threshold and when the field was small.

Field stop diameters were either 200 µm, 5 or 20 mm, to define a field of 8.6 min arc, 1 or 10 deg diameter at the eye. Test stop diameters were either 50 µm or 6 mm (3.6 min arc or 1 deg at the eye). The 50 µm and 200 µm field stops had bevelled edges, to reduce diffraction. All beams were imaged upon a final Maxwellian lens and were centered on the pupil before every run. The positions of the stops were adjusted to ensure that the fields superimposed exactly and that the test spot was at the center of the field. Adjusting the lens position of each monochromatic channel brought each stimulus separately into focus for the observer. A Powell achromatizing lens was tried, but not used, as it did not improve image quality.

Calibration

Stimulus radiances were measured with a silicon photodiode (United Detector Technology PIN-1ODF) calibrated by the manufacturer. All neutral density filters and wedges were calibrated in situ for all test and field wavelengths used. During experiments the radiance of the arc lamp, which was run from a high-quality stabilized power supply (Kepco JQE-36), fluctuated by <1.0% (Schirillo, 1990). The duration of the test flash was checked with an event counter triggered by a photocell with a fast (<1 msec) response.

Procedure

Full TVR curves were not measured, but rather, just the absolute (photopic) thresholds and the increment thresholds at the field point. The absolute threshold was obtained after 6 min dark adaptation. The test radiance was raised 1 log unit above absolute threshold, which placed the test at the field point. The field in Channel I (Field I) was then turned on and adjusted in radiance until the test was returned to detection threshold. The adjustment was done using a yes–no tracking method (see below). After the first few adjustments the steps were small, and changes were made slowly, to permit nearly complete light adaptation. Following the initial adjustment, observers adapted for 3 min. The subject then made even smaller adjustments in field radiance to bring the test as close to threshold as possible, and adapted to the final level for another 3 min.* The field radiance was then left unchanged, and the final test threshold was determined using the yes–no tracking method. Five such thresholds were obtained to determine a mean threshold.

Field I was then replaced by the field in Channel II (Field II), and the field point measurement just described was repeated. If the test threshold differed by more than 0.04 log unit from the threshold on Field I, the computer adjusted the radiance of Field II in an attempt to compensate for the discrepancy, as often as was necessary to ensure that the two fields were equivalent. Next, Field I was turned on again (Field II was left on), and each field radiance was reduced by 0.3 log unit. The observer then adapted for 6 min to the resulting mixed field, before setting the threshold. This procedure for checking field additivity by equivalence has two particular advantages: the adaptive state of the mechanism being tested is almost entirely constant throughout the experiment, and the method depends only on the accuracy with which the 0.3 log unit reduction can be achieved, not on any of the absolute calibrations.

Each condition of spatial configuration and wavelength set was run ten times on each observer. The sequence of conditions was determined pseudorandomly. One run took approx. 50 min. Up to three runs were done in a day, separated by breaks of at least 1 hr.

Yes–no tracking method. A computer-controlled yes–no tracking method provided an estimate of the threshold. Observers were instructed to respond “yes” to the detection of any change in intensity, hue, or saturation perceived anywhere in the area of the test flash. Test radiance was increased after a “no” response and decreased after a “yes” response. The step size, initially 0.32 log units, was doubled if the observer’s responses were the same for three consecutive trials, and otherwise halved. Observers could push a no-judgment key to repeat the flash. A trial terminated upon reaching a step size of 0.02 log unit. When applied to the field, the tracking algorithm was the same except that test intensity was unchanged; rather, a “no” response decreased field radiance and two successive “yes” responses increased field radiance.

The two-alternative forced choice constant stimulus method. Seven levels of test radiance were chosen within a 0.36 log unit range to bracket the test threshold (Crawford & Pirenne, 1954) in steps of 0.06 log unit. In each two-alternative forced-choice trial, a 40 msec tone signalled the onset of each of two 300 msec intervals in which the flash might, with equal probability, occur. Test intensity was changed to a new level after every five

*The long (6 min) adaptation times required for each field should be sufficient to reach a steady state of adaptation and overcome any adaptational hysteresis in the red-green opponent system (Stiles, 1953; Reeves, 1982b, c). It also ensures that the small (8.6 min arc dia) fields have sufficient time to adapt the foveola despite small eye movements.
TABLE 1. Log increment thresholds (re absolute threshold) and associated standard deviations for a 530 nm test on a 622 nm field, a 481 nm field, or the mixture of the two fields, in various conditions

<table>
<thead>
<tr>
<th>Spatial configuration</th>
<th>Flash duration (msec)</th>
<th>Subject</th>
<th>Log test intensity ± log SD</th>
<th>Additive +</th>
<th>Subadditive -</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>622 nm</td>
<td>481 nm</td>
<td>Mixture</td>
</tr>
<tr>
<td>1 deg test</td>
<td>200</td>
<td>JS</td>
<td>1.03 ± 0.026</td>
<td>1.03 ± 0.031</td>
<td>1.02 ± 0.037</td>
</tr>
<tr>
<td>10 deg fields</td>
<td>19</td>
<td>JS</td>
<td>1.01 ± 0.014</td>
<td>1.01 ± 0.011</td>
<td>1.02 ± 0.020</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>AR</td>
<td>0.94 ± 0.028</td>
<td>0.95 ± 0.040</td>
<td>0.94 ± 0.035</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>AR</td>
<td>0.96 ± 0.032</td>
<td>0.97 ± 0.043</td>
<td>0.97 ± 0.038</td>
</tr>
<tr>
<td>1 deg test</td>
<td>200</td>
<td>JS</td>
<td>1.01 ± 0.029</td>
<td>1.01 ± 0.036</td>
<td>0.93 ± 0.061</td>
</tr>
<tr>
<td>1 deg fields</td>
<td>19</td>
<td>JS</td>
<td>1.02 ± 0.018</td>
<td>1.02 ± 0.019</td>
<td>0.99 ± 0.043</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>AR</td>
<td>1.01 ± 0.028</td>
<td>1.01 ± 0.032</td>
<td>0.92 ± 0.059</td>
</tr>
<tr>
<td>3.6 min arc test</td>
<td>200</td>
<td>JS</td>
<td>1.06 ± 0.046</td>
<td>1.07 ± 0.049</td>
<td>1.09 ± 0.063</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>JS</td>
<td>1.05 ± 0.036</td>
<td>1.04 ± 0.031</td>
<td>1.07 ± 0.041</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>AR</td>
<td>1.02 ± 0.036</td>
<td>1.03 ± 0.044</td>
<td>1.00 ± 0.061</td>
</tr>
</tbody>
</table>

trials, according to a pseudo-random order. A total of 20 trials was collected for each test intensity in each condition and session. Over sessions, 1400 trials were run for each probability of seeing curve, many more than the 500 trials needed to avoid skew (Maloney, 1990).

EXPERIMENT 1

In this experiment field additivity was tested with set A wavelengths (a 530 nm test with 481 and 622 nm fields). The three spatial configurations (see Fig. 1) were: large, a 1 deg test on a 10 deg field, as used to define II-A; small, a 3.6 min arc test on a 8.6 min arc field, and coincident, a 1 deg test on a 1 deg field. An additional small-spot coincident condition was run for observer JS, in which an 8.6 min arc test was flashed on an 8.6 min arc field. The yes-no tracking method was used by observers JS, AR, and JA.

Results

Thresholds on the two pure fields were within 0.04 log units of each other, as required by the procedure. The question of concern is whether thresholds on the mixed fields are equal to the average of those on the pure fields. If so, the fields are equivalent and field additivity is demonstrated. We ask this question for each of the spatial configurations in turn.

Large (1 deg test, 10 deg field). Thresholds for both the 200 msec and the 19 or 20 msec test flash were field additive (Table 1): thresholds on the mixed field did not differ from those on the pure fields, 481 and 622 nm, for either observer (JS, $t_{df-9} = 2.39, P < 0.05$; AR, $t_{df-9} = 2.27, P < 0.05$) (Table 1); the effect was confirmed in JA. Thus these thresholds were mildly subadditive. In addition, the standard deviations of the thresholds on the mixed field were greater than those on either pure field for both JS ($t_{df-9} = 4.13, P < 0.001$) and AR ($t_{df-9} = 3.96, P < 0.001$). All observers felt it was harder to set the threshold when the background was desaturated. Thresholds for the 19 msec test flash, however, showed field additivity for JS ($t_{df-9} = 0.87, n.s.$), the only subject run in this condition.

Small coincident (8.6 min arc test, 8.6 min arc field). Thresholds for the 200 msec test flash were field additive. Neither the thresholds ($t_{df-9} = 0.74, n.s.$) (Table 1), nor their standard deviations ($t_{df-9} = 0.63, n.s.$), differed for JS, again the only subject run.

In sum, results with a 19 or 20 msec were additive. Results with the 200 msec test were sometimes subadditive, but as the effect was small, a better method was thought necessary to pursue it.

EXPERIMENT 2

In Expt 2, the same wavelengths (Set A, a 530 nm test with 481 and 622 nm fields) and spatial configurations were used as in Expt 1, except that the small (8.6 min arc) coincident condition was abandoned as alignment was precarious. The stimulus duration was 200 msec. The same yes-no tracking method was used as before to obtain an initial threshold, but the two-alternative forced-choice/constant stimulus method was then used to develop a psychometric function around the initial threshold estimate, and so refine the measurements made in Expt 1.

Results

Results are plotted in Figs 2-4 as the percentage of trials in which an observer correctly reported the interval in which the test occurred, ranging from chance (50%)
to perfect (100%). The abscissae are test radiances relative to absolute threshold, so 1.0 is the field point.

The experimental procedures again ensured that the two pure fields were equivalent, as the yes-no thresholds on them were both at the field point, but in addition the psychometric functions on the two fields did not differ statistically. This permitted a data reduction in which a single psychometric function could be estimated from the percent correct detections obtained on both the pure fields. This mean pure function was compared with the psychometric function obtained on the mixed field. As the linear regression fits were excellent on both pure and mixed fields (Figs 2-4), the psychometric functions could be characterized by their slopes and 75% correct points (given in Table 2), without requiring more complex curves to be fit.

**Large stimuli** (1 deg test, 10 deg field). Accuracy was the same on the pure (622 and 481 nm) and mixed fields, showing additivity at all test intensities. Results are shown for observers JS and AR in Fig. 2(a). The slope

![Graphs showing percent correct report of a 530 nm test as a function of log test radiance, obtained on 481 and 622 nm fields (averaged together, pure) and their mixture (mixed).](image)

FIGURE 2. Percent correct report of a 530 nm test as a function of log test radiance, obtained on 481 and 622 nm fields (averaged together, pure) and their mixture (mixed). (a) 1 deg 200 msec test on a 10 deg field. (b) 3.6 min arc, 200 msec test on an 8.6 min arc field. (c) 1 deg, 200 msec test on a 1 deg field. The left of each pair of panels shows data for observer JS; the right for AR.
of the psychometric function on the pure fields (solid symbols) was similar to that on the mixed field (open symbols); the ratios of these slopes were 0.95 for JS and 0.98 for AR.

**Small stimuli** (3.6 min arc test, 8.6 min arc field). These results were almost completely additive at all test intensities. The slopes on the pure and mixed fields were similar to each other [Fig. 2(b, c)], but not identical; their ratios were 0.97 for JS and 0.90 for AR.

**Coincident stimuli** (1 deg test, 1 deg field). Results for both observers [Fig. 2(c)], show sub-additivity. The slopes on the pure curves were steeper than on the mixed field, by a factor of 1.38 for JS and 1.35 for AR. The difference in detection was greater at the low test intensities. Above threshold the two curves drew closer together, approaching additivity.

**EXPERIMENT 3**

Experiment 3 was run in the same way as Expt 2, except that wavelength set A was replaced by set B (a 500 nm test with 530 and 610 nm fields). The dim (1 td) 10 deg white field was added to prevent rod intrusions when measuring the threshold of the 500 nm test (Stiles, 1949). The results of Expt 3 paralleled those of Expt 2 for both observers (Table 2).
Results

Large stimuli (1 deg test, 10 deg field). For AR the mean slope on the pure fields were similar to the slope on the mixed field curve [Fig. 3(a)], the ratio of the two being 1.09. By inspection, his thresholds do not appear to deviate from additivity. However, the slope ratio for JS was 1.24. Figure 3(a) shows that JS thresholds were close to additive except at the lowest two intensities, where they were sub-additive.

Small stimuli (3.6 min arc test, 8.6 min arc field). The results for JS [Fig. 3(b)] and AR [Fig. 3(b)] were additive at all test intensities. The pure and mixed slopes were similar (ratios being 0.94 for JS and 0.90 for AR).

Coincident stimuli (1 deg test, 1 deg field). Results were subadditive. Slopes on the pure fields were steeper than

TABLE 2. Percent corrects in two-alternative forced-choice at the field points, and slopes of the psychometric functions, on pure and mixed fields

<table>
<thead>
<tr>
<th>Figure</th>
<th>Spatial condition*</th>
<th>Field 1</th>
<th>Field 2</th>
<th>% Correct</th>
<th>Slope</th>
<th>R²</th>
<th>% Correct</th>
<th>Slope</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>2(a)</td>
<td>1 deg test 530 nm test; Mix 78.47 0.88 0.99</td>
<td>61.67 0.96 0.98</td>
<td>2(c) 1 deg test 530 nm test; Mix 76.36 0.69 0.98</td>
<td>62.21 0.57 0.98</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>10 deg fields 481 and 622 nm field</td>
<td>0.95</td>
<td>0.98</td>
<td>10 deg fields 481 and 622 nm field</td>
<td>0.95</td>
<td>0.98</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2(b)</td>
<td>3.6 min arc test 530 nm test; Mix 70.14 0.41 0.97</td>
<td>64.07 0.51 0.98</td>
<td>3(b) 3.6 min arc test 530 nm test; Mix 61.57 0.60 0.98</td>
<td>69.07 0.70 0.99</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>8.6 min arc fields 481 and 622 nm field</td>
<td>0.97</td>
<td>0.90</td>
<td>8.6 min arc fields 481 and 622 nm field</td>
<td>0.56</td>
<td>0.90</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3(a)</td>
<td>1 deg test 500 nm test; Mix 73.11 0.70 0.99</td>
<td>67.86 0.71 0.98</td>
<td>3(b) 3.6 min arc test 530 nm test; Mix 61.57 0.60 0.98</td>
<td>69.07 0.70 0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>10 deg fields 530 and 610 nm field</td>
<td>0.97</td>
<td>0.90</td>
<td>8.6 min arc fields 530 and 610 nm field</td>
<td>0.56</td>
<td>0.90</td>
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<td>3(c)</td>
<td>1 deg test 500 nm test; Mix 73.11 0.70 0.99</td>
<td>67.86 0.71 0.98</td>
<td>4 1 deg test 500 nm test; Mix 68.25 0.93 0.99</td>
<td>62.00 0.95 0.99</td>
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<td>1 deg fields 622 and 622 nm field</td>
<td>0.97</td>
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<td>1 deg fields 622 and 622 nm field</td>
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<td>4</td>
<td>1 deg test 500 nm test; Mix 68.25 0.93 0.99</td>
<td>62.00 0.95 0.99</td>
<td>1 deg fields 622 and 622 nm field</td>
<td>0.97</td>
<td>0.90</td>
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*Flash duration 200 msec.
†Percent correct P(1.0) at the field point (10 x absolute).
‡Percent correct P(x) = 100 (slope) (x - 100) + P(1.0), where x = log test intensity.
§Mix, thresholds on the mixture fields.
¶Pure, average thresholds on the two pure fields.
∥Ration pure slope/mixed slope.
slopes on the mixed field, by a factor of 1.26 for JS [Fig. 3(c)] and 1.39 for AR Fig. 3(c)]. The difference in detection rate was greatest at the lowest test intensities. Above threshold the two curves drew closer together, approaching additivity.

**DISCUSSION**

**Additivity in Stiles’ and Stockman’s conditions**

The results show that the 1 deg test, 10 deg field (Stiles) condition is field additive, confirming Reeves (1987) and providing additional evidence that II-4 is controlled by a linear combination of L and M cones (Pugh & Kirk, 1986). The 3.6 min arc test on a 8.6 min arc field (Stockman’s condition) is also field additive. Stockman (1983) found that adaptive independence holds in these small-spot conditions. Our finding of field additivity is compatible with his hypothesis that such a spatial configuration can be used to estimate the M fundamental. Had we not found field additivity, this hypothesis would have been rejected.

Field additivity may be indicative of detection by a luminance-sensitive pathway. The luminance pathway might mediate detection of the 3.6 min arc test on a 8.6 min arc field because it has greater acuity than the L/M opponent pathway. The opponent pathway may be favored by larger stimuli under other conditions, but not here as the pure fields were saturated and so may have suppressed the opponent pathway by polarizing it (Mollon, 1982). Detection by the luminance pathway may also have been favored for all these stimuli by the spatial transients produced by the test flashes, which were not blurred.

We found subadditivity with large, coincident stimuli (1 deg test and field), which produce temporal but not spatial transients. Subadditivity is consistent with the opponency inferred from the spectral sharpening found in coincident conditions by Foster (1981). However, Foster (1981) concluded that spectral sharpening occurs for both small or large tests, as long as the auxiliary field is coincident or slightly larger (e.g. a 9 min arc test with up to a 15 min arc auxiliary). If sharpening is due to opponency, one might expect subadditivity in Expt 1 with the 8.6 min arc test on a 8.6 min arc field, but this condition was additive for JS. Moreover, if exact coincidence is not required, one might have anticipated that the 3.6 min arc test on a 8.6 min arc field should violate field additivity, which it did not.* Therefore spatial coincidence may not be sufficient to elicit subadditivity, even though it elicits sharpening. Relatively large spots may also be required.

*Estimations of foveal cone diameters fall between 0.9 and 1.5 min arc (Oesterberg, 1935; Curcio, Sloan, Pucker, Hendrickson & Kalina 1987). Given estimates of optical scatter (Willmer, 1954) and cone center-to-center distances (Cicerone & Nerger, 1989), the 3.6 min arc test used in this study stimulates approx. 27 cones. Given a 2:1 cone ratio in the fovea (Cicerone & Nerger, 1989). approx. 18 long wavelength and 9 middle wavelength cones are hit. So, although these tests and fields are tiny, they are likely to strike both long and middle wavelength cones on every trial.

**Isolation**

Results showing additivity or sub-additivity can only be interpreted in terms of a single mechanism (such as II-4) if isolation holds. An alternative account of our results is by probability summation between two independent detection mechanisms. Suppose that the 500 and 530 nm tests were detected by an M-cone pathway on the long-wave fields but by an L-cone pathway on the short-wave fields. This would violate the assumption of isolation that only a single detection pathway is involved, but it must be considered as a possibility given the close spectral overlap of L and M fundamentals. Especially in wavelength set B, the 481 nm field might suppress the M cones more than the 530 nm test favors them, shifting detection to the L cones.

To test this idea we calculated the effects of probability summation between two independent pathways, given the following plausible (but not unique) assumptions. Even though the pathways mediating detections on the two pure fields are (now) presumed to be different, the experimental procedure made the pure fields equivalent. Thus the chance of detecting a test flash of a particular radiance by the M pathway on the long-wave field (e.g. p) should be the same as the chance of detecting the same test flash by the L pathway on the short-wave field. Report accuracy must then be $p + (1-p)/2$ on each pure field, since on $(1-p)$ of the trials the observer can guess the correct answer half the time. Now, suppose adapting to a mixed field changes the detection rate to kp for each pathway. As the effect of the mixed field is not known a priori, k is unknown. Probability summation implies that the detection rate on the mixed field, say $p*$, should be $p* + 1/2(1-p*)$ when guessing is included. Thus knowing k, one can derive p from report accuracy on a pure field, predict p*, and hence predict report accuracy on the mixed field, at every test radiance. Such “predictions” are vacuous if k is permitted to vary freely with test radiance, but if k is assumed independent of test radiance, it is possible to obtain illustrative predictions. For the large and small spot conditions, the results of which were field additive, a computerized fitting method found values of k for each condition which predicted report accuracy on the mixed field to within measurement error (these values were between 0.6 and 0.7). Thus probability summation between independent pathways can in principle give rise to data which closely resembles field-additivity for a single pathway, even under the restriction that k is constant.

The sub-additivities found in the coincident configuration, however, are unlikely to reflect probability summation. Figure 4 illustrates why. Predictions of report accuracy on the mixed field (with k = 1) are shown by solid triangles for JS [Fig. 4(a)] and AR [Fig. 4(b)]. These do not provide reasonable fits to the mixed field data (open squares). Varying k to best-fit AR’s mixed field data at the lowest two test intensities (k = 0.9) worsened the over-predictions seen in Fig. 4 at the highest test intensities. Varying k to best-fit JS’s mixed field data at
REFERENCES


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