EXCHANGE THRESHOLDS FOR GREEN TESTS

ADAM REEVES
Institut fuer Arbeitsphysiologie an der Universitaet Dortmund, Ardeystrasse 67, D4600 Dortmund 1, F.R.G.

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Abstract—Thresholds for detection of foveal \( \pi_4 \)-detected 522 nm, 1 deg, 200 msec test flashes rise by up to 0.4 log units just after a \( \pi_4 \)-equated “exchange” field has been substituted for the adaptation field, and take 60-90 sec to recover. This effect is not changed by an intense blue auxiliary field, and varies with the difference between adaptation and exchange field wavelengths as if only inputs from long-wavelength (LW) cones are involved. The effect can be virtually eliminated by adaptation to a background which alternates at 15 Hz between selected \( \pi_4 \)-equated long- and short-wavelength fields, which suggests that the LW cones exert their effect at a red-green opponent site.

INTRODUCTION

Thresholds mediated by a pathway whose sensitivity is controlled by a single class of cones must remain undisturbed by the exchange of one background light for another, if the two background lights produce identical quantum catches in those cones, and if the Principle of Univariance (Rushton, 1972) is applicable (Rushton et al., 1973; Mollon and Polden, 1977, p. 228; Sirovich and Abramov, 1977). Stiles's psychophysically defined \( \pi_4 \) mechanism has a field spectral sensitivity \( \pi_4 \) that, after suitable corrections, closely resembles the absorbance spectrum of the middle wavelength (MW) cones measured between about 470 and 620 nm (Bowmaker et al., 1978, 1980). Thresholds mediated by \( \pi_4 \) obey Stiles's Field Displacement Law (Stiles, 1939, 1953), except perhaps at very long wavelengths (670 nm; Sigel, 1979); and can show field additivity (Stromeyer and Sternheim, 1981). These results suggest that under \( \pi_4 \) measurement conditions, in which tests are flashed on a steady adapting background, thresholds are controlled by MW cones alone, except perhaps at very long wavelengths. If so, it is possible to equate backgrounds for their quantum effects on MW cones by “equating them for \( \pi_4 \)” (choosing backgrounds on which thresholds of tests mediated by \( \pi_4 \) are equal). In turn, it seems reasonable to expect that in the dynamic conditions of the exchange experiment, thresholds would continue to be determined only by MW cones. In this case, an exchange between \( \pi_4 \)-equated backgrounds should leave undisturbed the thresholds of a test detected by \( \pi_4 \).

This expectation was tested in the first experiment, and was not confirmed. Rather, thresholds rose after the exchange, taking about one min to recover to their prior values. The contribution of long-wavelength (LW) cone responses to the effect was shown by measurements of the “spectral response”. (That short-wavelength (SW) cone responses are probably not involved was supported by the finding that an intense blue auxiliary field did not change the amount by which thresholds rose). That the LW cones have their effect at a red-green opponent site was suggested by the final experiment.

METHODS

Apparatus

The three channel Maxwellian view system described previously (Reeves, 1981) was modified so that, with the aid of crossed polarizers, the adaptation field provided by channel 1 could be exchanged for a different field in channel 2 (the “exchange field”). The exchange was accomplished within 1 msec (with a ripple not exceeding 0.06 log units) by moving a strip of polaroid near a nodal point in the adaptation beam. The two channels provided concentric 3.7 deg fields with a tiny (about 2') black dot mounted centrally to aid fixation. The source was a tungsten halogen lamp, rated at 100 W and 6.6 A, and slightly under-run at 14.8 V. Field wavelength was controlled with manually adjusted Barr and Stroud type SS2 interference filters (bandwidths at half-maximum between 9 and 13 nm). The two channels were equated for \( \pi_4 \) separately in each session (see Procedure), by adding appropriate (calibrated) neutral density filters to channel 2.

A foveal test light of wavelength 522 nm (bandwidth 16 nm) was provided by a Schott type DAL interference filter in the third channel. Test duration (200 msec) was controlled by digital logic and a Vincent Uniblitz shutter with rise and fall times less than 2 msec. Test diameter was 1 deg.

A 20 deg auxiliary field could be added with a beam-splitter (between M6 and L14, in Reeves, 1981, Fig. 1). This field was lit by a 12 V car headlamp bulb driven by an unregulated power supply, filtered with suitable heat absorbing glass, and provided with a wavelength of 443 nm (bandwidth 16 nm) with a Schott type DAL interference filter.
Finally, the observer adapted for 30 sec to the field in channel 2, and then a steady threshold on that field was obtained. (Pilot work established that longer re-adaptation periods were not needed.) The two steady thresholds were expected to be equal, as the intensities of the two fields had been equated for $\Pi_a$ on that basis.

Results are the means of four such thresholds taken in different sessions. Absolute thresholds for the 522 nm test were also measured after 2 min dark adaptation, with the aid of tiny fixation points located 1 deg above and below the test. Mean absolute thresholds did not vary by more than 0.1 log units for A.R. and 0.2 log units for A.W. from one session to the next.

**RESULTS**

Thresholds rise after exchanging 496 and 626 nm fields

That exchange thresholds are clearly higher than steady thresholds is shown in Fig. 1, for two well-practiced color-normal observers, A.R. (O), the author, aged 33, and A.W. (.), aged 24. Data on the left of the figure are log thresholds averaged over four sessions and plotted relative to the mean absolute threshold. Symbols 496, 626 and ↔ on the abscissa identify steady thresholds on the 496 and 626 nm fields, and exchange thresholds, respectively. Solid lines connect steady and exchange thresholds obtained at the same field intensities (the intensity of the 496 nm adaptation field is given in the legend: at 496 nm, 0 log ergs equals 11.4 log quanta). Steady thresholds are equal on the two fields as expected. Exchange thresholds rise by about 0.4 log units at each of the background intensities tested.

Dashed horizontal lines connect the steady thresholds to the appropriate positions on the curve at far right, which is Stiles's $\pi_a$ branch positioned correctly on the abscissa of log ergs·deg$^{-2}$·sec$^{-1}$ for the 496 nm field. Points are mean thresholds from two sessions for each observer. (Stiles's $\pi_a$ lies above $\pi_s$ at low intensities of the 496 nm field, but converges to $\pi_s$ above 3.0 log ergs·deg$^{-2}$·sec$^{-1}$.)

Results (not plotted) for the opposite direction of exchange, that is, adaptation to 626 nm followed by an exchange to 496 nm, were within 0.08 log units of those plotted for the symmetrical adaptation conditions shown in Fig. 1.

These results show that for all intensity levels and both directions of exchange, exchange thresholds rise about 0.4 log units above steady thresholds. This clearly disconfirms the expectation that steady and exchange thresholds should be equal (see Introduction).

**Small changes in intensity: a control**

It is possible that the rise in exchange threshold reflects an imperfect $\Pi_a$ equation between the 496 nm and 626 nm fields. To control for this possibility, the intensity of the exchange field was varied in steps of
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Fig. 1. Steady and exchange thresholds for observers A.R. (○) and A.W. (●). Left panel: log thresholds of a 522 nm 1 deg, 200 msec, foveal test, presented on a steady 496 nm field (496 on the abscissa), or on a steady 626 nm field (626), or 64 msec after the exchange of a λ4-equated 626 field for the 496 field (●). Continuous straight lines connect thresholds at the same intensities of the 496 nm field (−3.6, −3.1, and −2.5 log ergs·deg−2·sec−1). Right panel: steady thresholds of the same 522 nm test on a 496 nm field whose intensity is given on the abscissa: the solid curve is Stiles's π4 branch. Horizontal dashed lines connect steady thresholds obtained at the same field intensities to aid the eye.

0.1 log units from 0.2 to +0.2 log units relative to the π4 equation. For adaptation both to 496 and to 626 nm, at the three intensities shown in Fig. 1, variations in exchange field intensity altered all of A.R.'s steady and exchange thresholds by less than 0.2 log units. In particular, the mean exchange threshold was always at least 0.4 log units higher than the mean steady threshold. It is therefore unlikely that the main results could be explained on the assumption that the π4 equation was inexact.

Time-course

Figure 2 shows for both observers the time-course of the threshold after an exchange from 496 to 626 nm (unfilled symbols), or of an exchange from 626 to 496 nm (filled). As before, background intensities were chosen so that the steady thresholds would be 0.8 log units above absolute threshold. These thresholds were obtained by a tracking method in which the observer continuously moved the neutral density wedge in order to keep the test flash just visible. The test was flashed once every second, and the symbols shown are means over each successive 5 sec. averaged over the four records obtained by each subject in each adaptation condition. (Additional results showed that the time from exchange to presentation of the 200 msec test was varied between 64 and 520 msec, exchange thresholds remained about 0.4 log units above the steady thresholds. These thresholds are connected to those in Fig. 2 by dotted lines on the far left of the plot.)

Figure 2 shows that the effect of an exchange on the threshold of the 1 deg, 200 msec, 522 nm test takes 60-90 secs to die away. There may be some difference between observers and direction of exchange (496-626 nm or the reverse), and an exact picture may well require the sort of forced choice measurements recently made by Maloney and Wandell (1981). However, there is no clear evidence here for an asymmetry due to direction of exchange.

Spectral response

The dependence of the rise in exchange threshold on the wavelength of the exchange field is shown in Fig. 3. The abscissa shows the wavelength of the exchange field. The wavelength of the adaptation field (496 or 626 nm) is indicated by an arrow in each panel. Thresholds are plotted in log units relative to the absolute threshold. Steady thresholds on the adaptation and exchange fields, shown by circles and triangles respectively, are about constant at 0.8 log units above absolute threshold. These thresholds were obtained by a tracking method in which the observer continuously moved the neutral density wedge in order to keep the test flash just visible. The test was flashed once every second, and the symbols shown are means over each successive 5 sec. averaged over the four records obtained by each subject in each adaptation condition. (Additional results showed that the time from exchange to presentation of the 200 msec test was varied between 64 and 520 msec, exchange thresholds remained about 0.4 log units above the steady thresholds. These thresholds are connected to those in Fig. 2 by dotted lines on the far left of the plot.)

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Unfilled squares show thresholds measured 64 msec after the exchange. When the exchange and adaptation fields were equal in wavelength (as marked by

Fig. 2. The time-course of thresholds following an exchange from 496 to 626 (unfilled symbols) or from 626 to 496 (filled), obtained in a continuous tracking task. Thresholds measured by a different procedure did not vary during the first second (as indicated by dotted lines on the far left). The 626 nm field was π4-equated to the 496 nm, −3.1 log ergs·deg−2·sec−1 field.
The results show that the exchange thresholds are influenced by cones other than the M.W. ones. The spectral response curves in Fig. 3 also suggest that short-wavelength (SW) cones have no effect on the exchange thresholds, as the latter vary rather little with wavelength below 536 nm. This hypothesis was tested by adding a steady blue (443 nm) auxiliary field to the background. This field, chosen to selectively desensitize SW cones, should decrease the extent of the rise in exchange threshold if, contra hypothesis, SW cone responses did affect the exchange thresholds. The (uncalibrated) auxiliary field was intense enough to raise the threshold of a violet (427, 16 nm bandwidth) 200 msec, 1 deg test by 1.8 log units above its absolute threshold. It raised the threshold of the 522 nm test by just 0.3 log units. Thus, the auxiliary field produced a strong selective desensitization of the SW cones.

The standard exchange between 496 and 626 nm was performed. The 496 nm field was dimmed by about 0.3 log units from its previous intensity, to ensure that when acting together with the blue auxiliary, the threshold of the 522 nm test would once more be 0.8 log units above absolute threshold. The 626 nm field was also dimmed by 0.3 log units to preserve the 0.8 log units above the absolute threshold. It raised the threshold of a violet (427, 16 nm bandwidth) 200 msec, 1 deg test by 1.8 log units above its absolute threshold. It raised the threshold of the 522 nm test by just 0.3 log units. Thus, the auxiliary field produced a strong selective desensitization of the SW cones.

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The steady and exchange thresholds now obtained by A.R. were within 0.05 log units of those reported in Fig. 3. For observer A.W., steady thresholds were within 0.04 log units of those previously reported, but the exchange threshold rose by only 0.32 log units above the steady threshold, less than the 0.4 log units previously found for this observer. (A.W. experienced some difficulty in setting thresholds in the presence of the auxiliary light, but it is not clear whether this was responsible for the slight decrease in the effect.) These results provide additional support for the hypothesis that SW cone responses do not contribute to the exchange thresholds.

\section*{Red-green opponency}

If the rise in the exchange threshold is due to inputs from LW cones, it is possible that such inputs either sum with or oppose inputs from MW cones at a "second site" in the pathway that detects the 522 nm test. One rather indirect way of distinguishing these possibilities, based on Guth et al. (1976)'s method for studying post-receptoral chromatic adaptation, is to alternate between fields whose wavelengths straddle the "neutral point" of the red-green opponent pathway. At fast alternation rates, such fields should effectively rise for the opponent pathway, so the output of the opponent site should be null. However, alternation should have relatively little effect on the response of a summative site.

The particular fields used were chosen on the assumption that MW and LW cone responses are proportional to \( \pi_4 \) and \( \pi_5 \) respectively, both in steady and in dynamic conditions. Although this assumption is not critical, it allows for an illustrative calculation. Alternation between \( \Pi_A \)-equated 496 and 588 nm fields, which are intense enough to raise test threshold 0.8 log units above the absolute threshold, changes \( \pi_5 \) from 0.16 log units less, to 0.15 log units more, than theunchanging level of \( \pi_4 \) (using values for Stiles' average observer: Wyszecki and Stiles, 1967). When these fields are alternated at a rate well above the time-constant of the second site, the time-integrated output will be zero (within 3\%) if the site is subtractive, but will be equal (within 3\%) to the level produced by steady adaptation to the 496 nm field if it is summative.

It is now assumed that the second site may be polarized during adaptation (e.g. Wandell and Pugh, 1980; Reeves, 1981), and that such polarization is a necessary condition for the rise in the exchange threshold. On these assumptions, the second of which is so far unsupported, exposure to fast alternation of the 496 nm and 588 nm fields during adaptation should eliminate the rise in exchange thresholds, if the site is opponent, but have virtually no effect if it is summative.

To test these alternatives the experiment shown in Fig. 1 was re-run exactly as before, except that during the 4 min adaptation period the background alternated at 15 Hz between \( \Pi_A \)-equated 496 and 588 nm
fields. After adaptation, the test phase of the experiment was run just as before.

Results for both observers (not plotted) showed that steady thresholds were equal on the two backgrounds, and were very close to those previously obtained. The exchange thresholds, however, averaged only 0.03 log units higher than the steady thresholds for A.R., and 0.06 log units higher for A.W., in sharp contrast with the 0.4 log unit elevation seen in Fig. 1. Thus alternation virtually eliminated the threshold rise in the exchange condition. This was so for both test durations and for the same background intensities as shown in Fig. 1.

The spectral response measurements shown in Fig. 3 were re-run by both observers, with the 496 nm "adaptation" field alternated at 15 Hz with the exchange field during the 4 min adaptation period (Otherwise, the experiment was repeated exactly.)

Results are plotted in Fig. 4 in the same format as in Fig. 3. They show, as before, that alternation virtually eliminated the threshold rise normally obtained after an exchange to 588 nm. At shorter exchange wavelengths, there was also little or no threshold elevation. At longer exchange wavelengths some threshold elevation occurred. Results are expected on previous arguments, because the LW cone response differs from the stable MW cone response to a greater extent at long wavelengths than at short, and so the time-integrated response of the opponent site should no longer be zero. (e.g. for an exchange between 496 and 626 nm, \( \pi_g \) varies from \(-0.16\) to \(+0.48\) log units relative to the unchanging level of \( \pi_d \)).

**DISCUSSION**

If the steady and exchange thresholds of the 522 nm test were determined by MW cone responses alone, they would be equal on the assumptions given in the Introduction. However, exchange thresholds rise up to about 0.4 log units above the steady thresholds, and do so over a range of test intensities (0.4, 0.8 and 1.2 log units above absolute threshold). They take about 1 min to recover. This effect is of about the same size as, but much longer lasting than, the rise in exchange thresholds reported for \( \pi_s \) (Sternheim et al., 1977; but see Reeves, 1982).

The threshold rise following the exchange of \( \Pi_{c}=\text{equated backgrounds appears to be due to transient inputs from LW cones, which act to desensitize the green-sensitive pathway (}\pi_g\text{ in the steady state). In addition, it appears that SW cones responses are not involved, as shown by the lack of effect of the intense blue auxiliary field. However, is not known whether MW or LW cones mediate detection after an exchange: LW cones would do so, if an exchange desensitized the green-sensitive pathway sufficiently. As SW cone effects on the green-sensitive pathway would not be measurable in conditions in which LW cones mediated the exchange thresholds, the evidence that SW cone responses did not affect the exchange thresholds per se does not imply that the green-sensitive pathway is uninfluenced by SW cone responses to all the exchanges.**

The fact that the threshold rise can be reduced or eliminated by alternation between appropriate short- and long-wavelength backgrounds throughout adaptation, suggests that exchange thresholds are raised only if inputs from LW cones polarize a red-green opponent site during adaptation (Reeves, 1981)—perhaps the site identified by Wandell and Pugh (1980) in the pathway that detects 1 deg, 200 msec, long-wavelength tests. Such polarizing inputs presumably do not influence steady-state thresholds, if \( \pi_g \) is in fact field-additive. One model in which a "pseudo-pigment", such as \( \pi_g \) may be, could show field additivity and yet fail to produce unchanging thresholds in the exchange experiment, is given by Strovich and Abramov [1977, section 5(b)].

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