this butterfly can distinguish between the aqueous extracts of two such similar strains of a plant species which does not, in nature, serve as a host. It seems that the major deterrent factors are in the volatiles emanating from these solutions; however, after steaming the extract, there remain non-volatile elements (which have not been identified) in the residue, which influence the ovipositing behaviour of the butterfly. It is therefore interesting to find that the large white can distinguish between two very similar cannabinoids (differing from each other only by a ring closure which changes a substituted terpinoid (CBD) into a dibenzopyran (THC). Although present in small quantities these probably constitute two of the non-volatile repellents in the plants, and the relative unattractive nature of the THC could contribute to the greater repulsive qualities of the Mexican strain.

It is difficult to determine whether the initial choice of a leaf is made after merely a close approach or a rapid or brief contact. It will be seen (Table 2) that out of 26 trials the Mexican extract leaf was only once selected for ovipositing before the Turkish extract leaf. Recognition of a leaf sprayed with CBD and THC occurred after, rather than before 'touch down'.

The tendency for females to lay larger batches (containing more eggs than the controls) on certain CBD-treated leaves (Table 4) suggests that there may be an ovipositing stimulant, but not an attractant, in this substance. There is no doubt that several different factors contribute to the production of large egg batches, quite apart from the age and past history of the females concerned.

The few results we obtained with Mexican steamed extract in 1979 (Table 2) differed from those of other years. Thus, after heating and steaming, the residue retained much of its original repellent quality. Possibly the THC concentration was higher. Moreover, the spring had been exceptionally cold, and in an unheated greenhouse all the plants suffered. Indeed it would be surprising if the secondary plant substances—always disconcertingly variable[1,4]—were similar in all respects to those found in the previous crops.

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A curiosity of light adaptation

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By standard psychophysical procedures[1] it is possible to arrange that visual discriminations depend only on signals originating in the violet-sensitive receptors of the eye. A person's vision then shows several characteristic properties: differential sensitivity is lower than when the green- and red-sensitive cones contribute to detection, spatial and temporal resolution is poorer, and a number of anomalies of adaptation reveal themselves[1-9], including the saturation that we have demonstrated when violet targets are presented on steady blue or violet adapting fields[10]. 'Saturation' refers to the empirical finding that as the intensity (I) of the short-wavelength field increases, the threshold intensity (ΔI) for detecting a violet target rises much more rapidly than is described by Weber's law ($\Delta I/I = $ constant). These earlier results (replicated here; see Fig. 2, right-hand data), were obtained in what would conventionally be regarded as equilibrium conditions, in that thresholds were measured after 4 min of adaptation to the steady field. Here we examine a very odd aspect of the phenomenon: the threshold reaches its saturated state only after passing through a much lower value[11,12].

Figure 1 shows (for 3 observers) the time course of the threshold for a 436-nm target during the first 3 min after the onset of a composite adapting field. The latter consisted of a 440-nm component of $10^{10.6}$ quanta s^{-1} deg^{-2} and a 575-nm component of $10^{11.7}$ quanta s^{-1} deg^{-2}. The second, yellow, component would traditionally be termed an 'auxiliary field' (ref. 1, p. 198); it serves to suppress the red- and green-sensitive cones. The left-most data points of Fig. 1 represent the threshold 1 s after the onset of the composite field; the threshold is elevated relative to its dark-adapted value (not shown). Thereafter the threshold falls (as would normally be the case during the first few seconds of light adaptation), passes through a minimum, and then rises with remarkable speed.

For observers J.D.M. and D.D. the function at its steepest has a slope of 1 dB s^{-1}. To record accurately these rapid changes in sensitivity we have revived a special psychophysical method described by Cornsweet and Teller[23]. An ordinary staircase procedure[12], such as is traditionally used to track a changing threshold, would require a very large step size if it were to track faithfully the extremely rapid changes seen in Fig. 1; but then the precision of the estimate at any given delay (Δt) would be low. The modified procedure (called here the 'method of a thousand staircases') is designed to obviate this difficulty. In the present example, the observer receives 13 exposures to the adapting fields, each exposure, or run, lasting 3 min and successive runs being separated by 15-min intervals to allow the visual system to recover. During each run, test flashes (and accompanying warning tones) are presented at 3-s intervals. On the first run of the series the test flashes are all presented at the same intensity and the observer indicates by pushbuttons whether he has seen each flash. The response corresponding to each value of Δt is stored by the computer that controls the experiment. On the next run the computer adjusts the intensity of the flash at a given Δt according to the response previously given at that Δt but independently of responses given earlier in the current run. The new response at each Δt is now stored and is used to determine the flash intensity at that Δt on the third run; and so on. The adjustments between runs are made according to the rules for a single staircase[13], but what is unusual is that a large number (here 60, but in principle unlimited) of staircases are being maintained concurrently, each staircase corresponding to a single Δt. The final thresholds plotted in Fig. 1 are based on the intensity levels visited at a given Δt in the last eight runs.

Figure 2 places the phenomenon of Fig. 1 in context. Consider first the data to the right. These constitute an increment–threshold function ('threshold-vs-intensity' (t.v.i.) curve) for 436-nm targets presented on a 440-nm field and were obtained in steady-state conditions, in that measurements at each intensity of the field were preceded by 4 min of adaptation to the field. A fixed yellow (575 nm) auxiliary field of $10^{11.2}$ quanta s^{-1} deg^{-2} was present throughout. The broken line has a slope of unity and corresponds to Weber's law. The thresholds deviate upwards from this line, showing the operational saturation described earlier. At the highest intensity of the 440-nm field, another class of cones becomes responsible for detection[10] and the function flattens. A conventional, random double-staircase procedure[13] was used to obtain these data.

In the central panel of Fig. 2, log threshold is plotted as a function of Δt, with the intensity of the 440-nm field as parameter. These data were obtained by the method of a thousand staircases and they show how the threshold reaches its final 'equilibrium' value. The broken lines project the
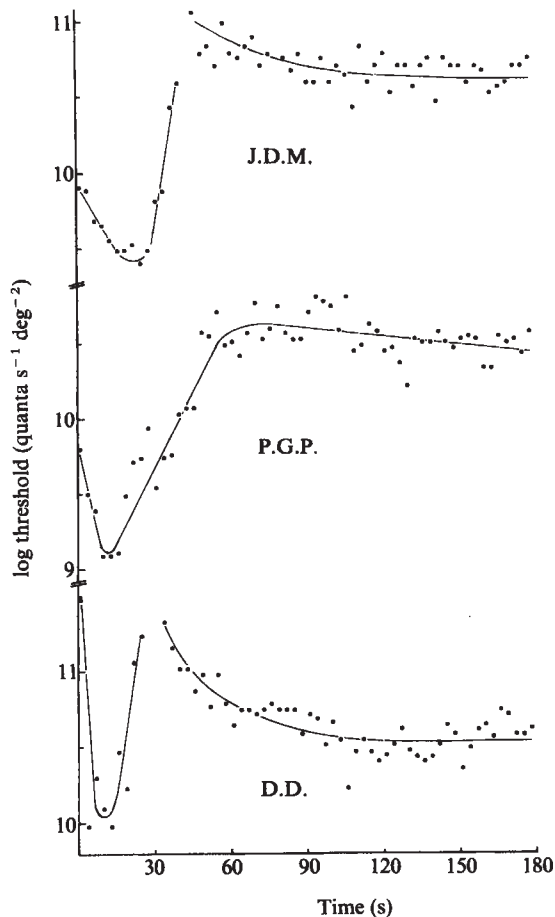
Fig. 1 Variation of log threshold intensity for detecting 436-nm flashes during the first 3 min of adaptation to a composite adapting field consisting of a 440-nm component at an intensity of $10^{10.6}$ quanta s^{-1} deg^{-2} and a 575-nm component at an intensity of $10^{11.7}$ quanta s^{-1} deg^{-2}. (The nominal chromaticity coordinates of this composite field are $x=0.45$, $y=0.47$.) The target flash subtended 1 deg of visual angle, was delivered to the centre of fovea and had a duration of 200 ms; the steady adapting fields were concentric with the target flash and subtended 6.5 deg. Target flashes were presented at 3-s intervals, each being preceded by a warning tone. A period of 2 min of dark adaptation preceded the onset of the fields. The solid lines are interrupted at values of Δt at which insufficient light was available to measure a threshold. Observers are denoted by initials.

asymptotic threshold levels to their rightful places on the t.v.i. curve. The 575-nm field remained the same intensity throughout and was combined in different sessions with different intensities of the 440-nm field.

The behaviour of the threshold changes systematically with small changes in the intensity of the 440-nm field. In all cases, the threshold passes through a minimum before rising again, but the more intense the field the earlier the minimum occurs and the steeper the slope of the rising part of the function. The latter trend can be seen in the data of Stromeyer *et al*[12]. Ancillary evidence suggests that for $\Delta t > 45$ s the upper limit to the family of functions in Fig. 2 depends on detection by a recovering long-wavelength mechanism (see also ref. 12, Fig. 14). At the lower field intensities, the functions resemble those given by Augenstein and Pugh[8] for light adaptation to long-wavelength fields alone. The left-most panel of Fig. 2 is discussed below.

Hitherto, we have treated the 575-nm field merely as an auxiliary field, serving to adapt the long- and middle-wavelength cones. If we assume that the spectral sensitivity of the short-wave receptors is approximately that of the

psychological mechanism Π_3 (ref. 1, p. 18), then in our conditions the 575-nm field will contribute never more than 1% to the total number of photons absorbed in those receptors. Yet Fig. 3 demonstrates that this field (and thus probably a signal originating in the long- and middle-wavelength cones) is crucial to the temporal variation in sensitivity. In the control condition of this experiment (solid circles, Fig. 3) the onsets of the fields were simultaneous as before, but in the experimental condition (open circles) the onsets were uncoupled, the onset of the 575-nm field being delayed by 40 s relative to that of the 440-nm field. The delay chosen is equal to a Δt at which the threshold would have passed its minimum if the onsets of the fields had been simultaneous. Yet 40 s of pre-adaptation to the violet field has little effect on the function: the onset of the delayed yellow field finds the threshold close to the value for $\Delta t = 1$ s in the control condition and the threshold then passes through its curious oscillation as before; the rising part of the function is displaced along the abscissa by a delay (47 s) that is slightly greater than the imposed delay of the yellow field. Because it seems to matter only slightly whether or not the retina has been pre-exposed to the 440-nm component, the phenomenon must depend substantially on a signal originating outside the short-wavelength receptors. However, the 440-nm component (and thus, probably, the adaptive state of the violet-sensitive receptors) must be independently important, as variation in its intensity produces the family of functions seen in Fig. 2. The 7-s discrepancy noted in the present results may be attributable to the difference in the adaptive state of the short-wavelength receptors.

We relate the present phenomenon to a general model of the short-wave mechanism[14,15], in which it is supposed that signals originating in the short-wavelength receptors are transmitted only via chromatically opponent pathways[16-18] and that the sensitivity of the psychophysically defined short-wavelength mechanism depends on (1) the adaptive state of the short-wavelength receptors and (2) the balance of short- and long-wavelength signals reaching a chromatically opponent site. A crucial assumption is that a chromatically opponent channel is most sensitive to input perturbations when it is close to the centre of its operating range; as it is 'polarized' (that is, driven to one or other end of its operating range by, for example, a saturated blue or a saturated yellow field), incremental or decremental inputs are increasingly attenuated. In our experiments, yellow fields alter the measured sensitivity to short-wavelength targets primarily by altering the polarization of the opponent site, for they negligibly stimulate the short-wavelength receptors. The violet fields act both at short-wavelength receptors and at the opponent site, but, in the presence of the yellow field, contribute negligibly (<5%) to absorptions in the long- and middle-wavelength cones. Note that the most sensitive state of the opponent channel almost certainly does not correspond to the condition of equal rates of isomerization in the three classes of receptor; there is good evidence that the signal from the violet-sensitive receptors is disproportionately weighted in its contribution to this channel[19].

As a working hypothesis we suppose that the present phenomenon arises from a temporal variation in the signal delivered to the opponent site from the long- and middle-wavelength cones. A 575-nm field of $10^{11.2}$ quanta s^{-1} deg^{-2} has a troland value of $10^{5.0}$ and will bleach approximately 85% of the pigment in these cones[20]; most of the change in the proportion of unbleached pigment will occur in the first minute after onset of the field[21]. During this time the signal reaching the opponent site from these cones will presumably fall rapidly, owing both to bleaching and to other processes of receptor adaptation (see, for example, ref. 22). The photo-sensitivity of the short-wavelength cones is not known but our calculations suggest that they will not be substantially bleached by our 440-nm field. So we assume that during light adaptation to our composite field the signal from the long- and middle-wavelength cones is changing more rapidly than
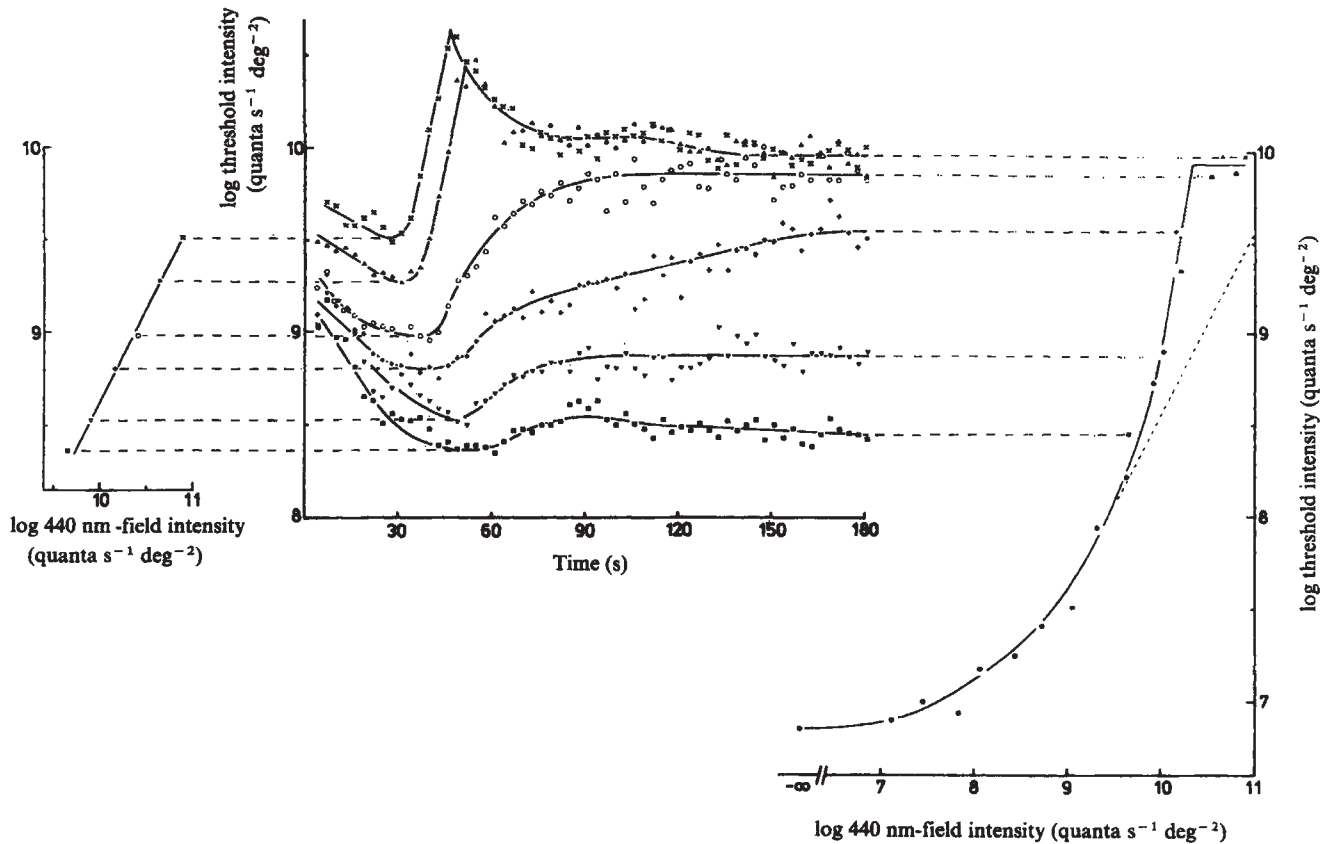
Fig. 2 Right-hand side: a conventionally obtained increment–threshold function for 436-nm test flashes presented on steady 440-nm fields of increasing intensity. A 575-nm auxiliary field of fixed intensity ($10^{11.2}$ quanta s^{-1} deg^{-2}) was present throughout. Thresholds were measured using a randomized double-staircase procedure and the plotted values are based on a sequence of 32 responses obtained between 3.5 and 5.5 min after onset of the composite adapting field, earlier responses being used to place the staircases close to the estimated threshold. Stimulus parameters were as for Fig. 1. Observer: J.D.M. Centre: temporal course of the threshold for detecting 436-nm test flashes during the first 3 min of adaptation to a series of composite fields consisting of a fixed 575-nm component of $10^{11.2}$ quanta s^{-1} deg^{-2} and 440-nm components of intensities: × $10^{10.88}$, ▲ $10^{10.63}$, ○ $10^{10.39}$, + $10^{10.14}$, ▽ $10^{9.88}$, ■ $10^{9.64}$ quanta s^{-1} deg^{-2}. Two experimental sessions were devoted to each of the latter values and the order of sessions was randomized. Left-hand side: minimal thresholds as a function of the log intensity of the 440-nm field. The solid line has a slope of unity.

that from the short-wavelength cones. The opponent site passes from being polarized in the yellow direction to being polarized in the other direction and the threshold, correspondingly, falls, passes through a minimum, and then rises again.

A further feature of the parametric results of Fig. 2 (central panel) is compatible with the hypothesis outlined above. The minima of the several functions should correspond to instants at which the opponent site is in the same (maximally sensitive) state. Differences between the minimal thresholds must then depend only on variations in sensitivity at more distal sites in the channel that carries the signal. In the left-most panel of Fig. 2 we plot the minima against the intensity of the 440-nm field: these values, unlike the asymptotes (right-most panel), obey Weber's law closely. As Weber's law (whatever its ultimate explanation) characterizes the threshold for large achromatic targets presented on bright steady fields, it is the behaviour that might be predicted when we hold constant the state of the opponent site. In other experiments we have held constant the 440-nm component of the field and varied the 575-nm component: in this case the minimum threshold, though reached at different values of Δt, varies little in its absolute value, as would indeed be predicted if (1) sensitivity at the distal site is predominantly set by the 440-nm component and (2) the minima represent equivalent states of the opponent site.

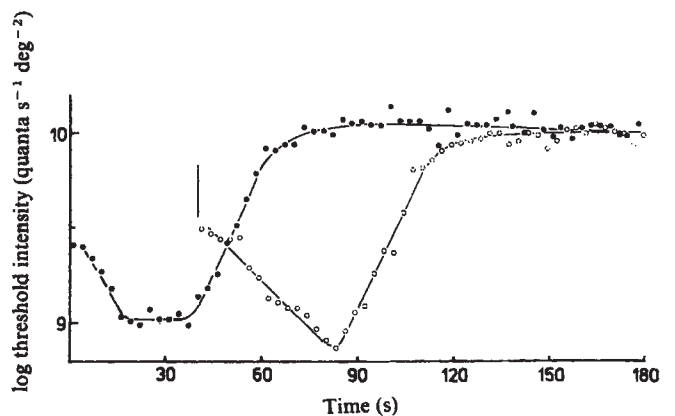Is   the   hypothesis   supported   by   the   observer's

Fig. 3 Solid points: variation of log threshold intensity for detecting 436-nm test flashes during the first 3 min of adaptation to a composite adapting field consisting of a 440-nm component at an intensity of $10^{10.4}$ quanta s^{-1} deg^{-2} and a 575-nm component at an intensity of $10^{11.2}$ quanta s^{-1} deg^{-2}. Observer: J.D.M. Open points: results obtained when the onset of the 575-nm component of the field was delayed by 40 s. All points are plotted relative to the time of onset of the 440-nm component of the field. The onset of the delayed yellow field is indicated by a vertical bar.

phenomenological experience? Assuming that it is the central region of the field that is most relevant, the CIE chromaticity coordinates of the composite fields used for the measurements of Fig. 2 range from $x = 0.47$, $y = 0.50$ to $x = 0.36$, $y = 0.32$; but these chromaticities are not a good guide to the appearance of intense stimuli in transitional conditions. Formal phenomenological reports were obtained in separate runs in the conditions of Fig. 2. At onset, all fields were 'dazzlingly' bright and they varied in hue from 'yellow' to 'pale violet' according to the intensity of the 440-nm field. In all cases, after about 10 s, the field darkened strikingly and turned a grey or slate blue colour. After 60 s the colour was always pinkish, and, after 120 s, greyish. The sudden darkening always occurred a few seconds before the independently measured loss of sensitivity, and the value of Δt at which it occurred varied less with field intensity than did the point of minimum threshold. We therefore hesitate to relate the phenomenology to the processes, probably retinal, revealed by the sensitivity measurements; and the reader will have noticed that throughout this article we have avoided the term 'blue–yellow opponent channel'.

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Visual acuity is better for letters in rows than in columns

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The spatial resolving capacity of the visual system is usually measured with charts containing letters of different sizes displayed in horizontal rows or, less often, in vertical columns. Although previous studies suggest that acuity may not be equal for these two arrangements[1-7] it is implicitly assumed in clinical tests that orientation of an array of letters is of no consequence to the measurement. The work reported here shows that this assumption is incorrect. While undergoing an examination in an eye clinic, I noticed that letters of a given size seemed more difficult to identify when they were arranged in vertical compared with horizontal arrays. Subsequently, I tested a group of subjects using letters presented pseudo-randomly with different inter-letter spacings, in rows or columns. Subjects were required to identify letters from left to right or from top to bottom in each isolated row or column. A significantly higher number of errors was made for letters in columns than for those in rows. The effect does not depend on order or direction of letter presentation, and it is not found when acuity determinations are made using a non-letter test symbol. To explore the conjecture that the effect could be associated with previous experience, two additional groups of subjects were tested. First, bilingual Chinese, whose first language is read in both horizontal and vertical arrays, were tested using Chinese characters and English letters. Second, acuity determinations were made with young children who could identify letters but did not read. In each case, acuity was not significantly different for horizontal or vertical presentations, a finding consistent with the notion that learning may influence the development of visual resolution.

The tests were carried out with slides containing pseudo-random combinations of eight letters— E, H, R, N, O, X, D and V—arranged in groups of columns or rows. Each letter appeared once at a given inter-letter separation (see below). The slides were mounted in frames for use in a standard vision chart projector. Before the tests, the refractive condition of each subject was carefully determined. Subjects were rejected if

a visual anomaly or considerable refractive error was found. Using appropriate ophthalmic lenses if required, subjects monocularly viewed letters that each initially subtended an anticipated threshold level of 4 arc min at the eye. (A 7.1-mm letter viewed at 20 ft subtends 4 arc min and if correctly read, an acuity of 20/15 is indicated.) Letters were presented in a column or row and all eight letters were shown at each of five inter-letter separations (2, 4, 8, 16, and 32 arc min). For each subject, the zoom lens on the projector was adjusted so that letters were small enough to be near threshold, as estimated by approximately 75% correct identification. Letters of all separations were then systematically presented in columns or in rows and subjects were asked to identify them from top to bottom or from left to right, respectively. Half of the subjects were tested using columns followed by rows and the other half were tested in the reverse order. No differences were found related to order of presentation. Ten letters were used at each inter-letter spacing, but only the inside eight were scored to avoid possible complications of edge effects at the ends of each row or column.

Results for 11 subjects, given in Fig. 1a, show that for both columns and rows, the error rate increases with decreased separation between letters, as could be anticipated from previous work[8]. However, in addition, the mean error rate is clearly higher for columns than for rows of letters and the overall difference is highly significant ($\chi^2 = 26.12$, $P = 0.0062$).

What can account for this difference in acuity between horizontal and vertical arrays of letters? An optical explanation of the effect can be ruled out immediately. The subjects used did not have high amounts of ocular astigmatism, and the moderate or small astigmatic errors found were of both vertical and horizontal types. In either case, these errors were fully corrected with lenses. Furthermore, when grating test targets are used to determine acuity, no differences are found between vertical and horizontal orientations[9,10]. This applies also to laser-created interference-fringe gratings for which the effect of the eye's optics are essentially bypassed[10].

One must therefore propose an alternative explanation for the effect found here and an obvious possibility is that the development of visual acuity for arrays of letters is associated with learned patterns of reading. Specifically, because we learn to read rows of letters, finest acuity develops correspondingly for horizontal displays. Because we also learn to read from left to right, acuity may be superior for this direction compared