and the subsequent maintenance of normal connectivity in the mammalian central visual pathway.

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Electrophysiological correlates of hyperacuity in the human visual cortex

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The human visual system is capable of detecting a vernier misalignment with extraordinary accuracy. Since this remarkable precision in spatial localization is better than can be naively predicted by simple optical or anatomical considerations it has been termed a hyperacuity[1]. So far no single neurone model seems capable of accounting for hyperacuity[2], and the retinal image might require reconstitution in a finer grained form in the visual cortex[3]. We report here an electrophysiological correlate of hyperacuity recorded from the human visual cortex. The amplitude of the visually evoked potentials (v.e.ps) elicited by the appearance of a vernier offset varied systematically with the magnitude of the offset. Extrapolation of the function relating v.e.p. amplitude and log offset to zero voltage resulted in an electrophysiological estimate of vernier acuity that was similar to the observer's psychophysical threshold.

The stimuli in these experiments were repetitive vernier patterns generated on the monitor of a small computer, and are shown schematically in Fig. 1 (top). Specifically, the stimulus consisted of five bright horizontal lines, each composed of three segments, presented on a dark background. Initially all of the line segments were aligned. The appearance of the vernier offset was introduced by displacing the outer line segments downward; after 350 ms the outer line segments were returned to their original aligned position (disappearance). In this manner, the appearance of the stimulus changed from colinearity of the line segments, to non-colinearity without changing the mean luminance of the display.

The observer's electroencephalogram (EEG) was amplified (10^5 times with a pass band of 0.3 to 100 Hz), and time-lock averaged in synchrony with the appearance of the vernier offset. Figure 1 shows the responses elicited by offsets of different magnitudes for two observers. The v.e.p. elicited by the vernier offset was characterized by a positive going wave with an onset roughly 100–110 ms after the appearance of the vernier offset. The response was quite reliable (Fig. 1), and the amplitude of the positive deflection varied systematically with the magnitude of the offset. It is well known that accelerated motion (displacement) of a pattern across the retina can evoke scalp potentials[4]. Therefore, in order to demonstrate a visually evoked potential correlate of vernier acuity, it is important to ensure that the responses obtained were not evoked by displacement (motion) of the retinal image. To control for this displacement artefact, we recorded responses elicited by an equal displacement of all the line segments moving together. Psychophysically, the human observers' sensitivity to unreferenced motion is 7 to 10 times poorer than their sensitivity to a vernier offset[5]. Thus, as expected, in the present study the displacment of all of the line segments by 40 s was subthreshold, and resulted in an evoked potential which could not be distinguished from noise (Fig. 1, bottom right). In contrast, a vernier offset of 40 s resulted in a robust and reliable response. Therefore, we conclude that in the range of vernier offsets near threshold (10 to 50 s) displacement artefacts do not contribute to the responses. It is also of interest that the waveforms elicited by the vernier display differ from those elicited by other patterned stimuli. For comparison, responses elicited by the appearance/disappearance of a 15 cycle per degree square wave grating recorded under the same stimulus and recording conditions are shown for observer K.B.S. (Fig. 1, bottom left). The responses elicited by the appearance of the pattern differ from the vernier v.e.p. in showing an early negative deflection and shorter peak latencies. It is interesting that the waveforms elicited by the appearance of a vernier offset

Table 1 V.e.p. vernier thresholds obtained with two different electrodes

Observer	V.e.p. threshold (arc s) Right to midline electrode	Left to midline electrode	Psychophysical threshold† (arc s)
K.B.S.	8.1	7.2	7.5
B.W.Z.	15.4	10.5	16.6
D.M.L.*	8.15	7.15	6.3
R.E.M.*	9.3	10.75	13.6

*Mean of two threshold estimates.
† 75% seen (yes/no method of constant stimuli). The false alarm rate was 4 to 9%.

are reminiscent of the waveform elicited by another type of hyperacuity stimulus, stereopsis. Regan and Spekreijse recorded visually evoked potentials elicited by the appearance of a change in depth[6]. The waveforms of their v.e.ps were elicited by disparities much larger than the offsets used here, but are at least qualitatively similar to those shown in Fig. 1.

The v.e.p. amplitude varies systematically with the magnitude of the vernier offset. When the amplitude is plotted as a function of log offset (Fig. 2), the results are well fit (correlations were always greater than 0.93) by a line of the form $Y = M \log (X/X_0)$ for X greater than X_0 and $Y = 0$ for X less than X_0. Campbell and Maffei[7] have used the method of extrapolation to zero voltage to obtain an electrophysiological contrast 'threshold' estimate. Our electrophysiological estimate of vernier threshold, X_0 (shown by the intercept of the line with the abcissa) has a standard error of about 20% (shown by the horizontal error bar), and is in reasonable agreement with the psychophysical estimate of threshold (shown by the arrow for each observer). Table 1 summarizes the 'v.e.p. vernier thresholds' obtained with two different electrode configurations (shown in Fig. 1). Psychophysical thresholds were also obtained for each of the four observers. A yes–no method of constant stimuli with feedback in which the stimulus was presented with one of four offsets (including blanks) was used to obtain psychometric functions for vernier detection. Interpolation to the 75% seen level provided a psychophysical estimate of threshold, which is also shown in Table 1.

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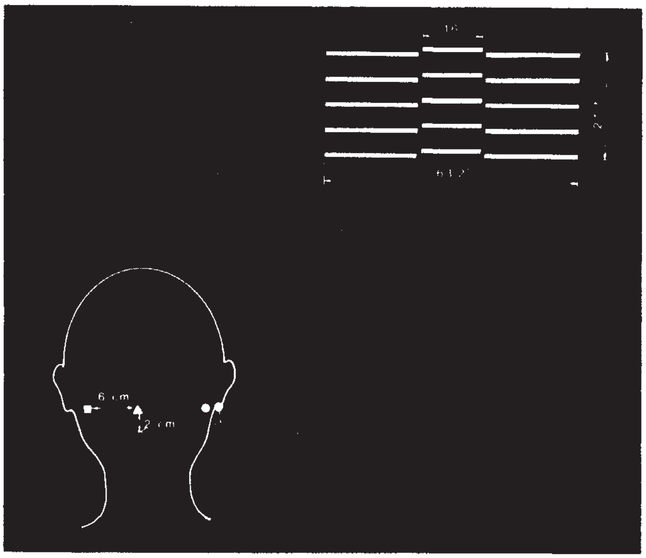
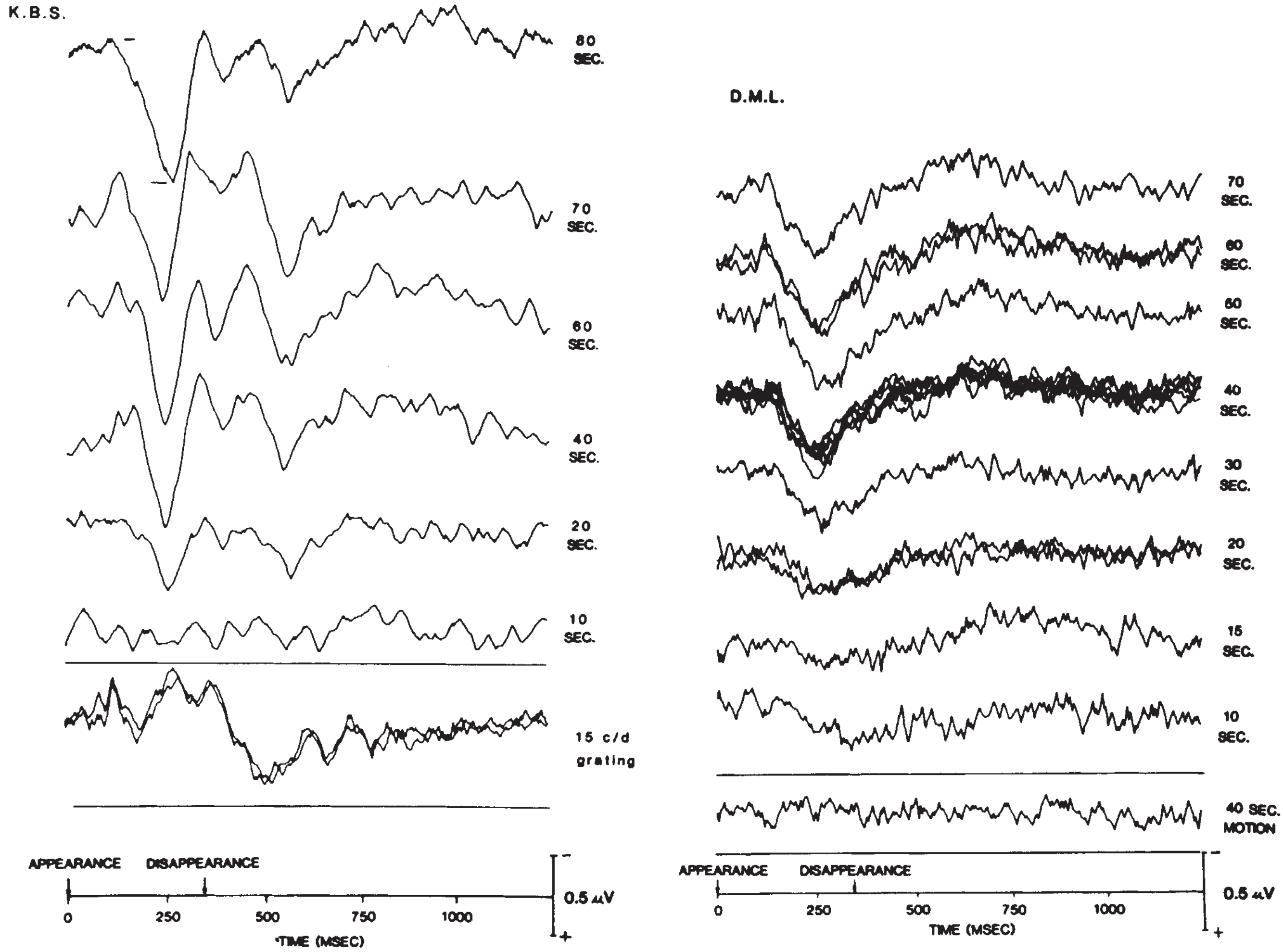
Fig. 1 Top: Schematic illustration of the stimulus and recording conditions. The stimulus, which subtended about 1° by 0.5°, consisted of 5 rows of bright lines each of 3 segments. Before introduction of vernier offset all segments were aligned. Vernier offset was introduced with no change in luminance, by displacing the lateral segments downward (appearance of vernier offset) and back (disappearance of vernier offset) at a rate of 0.71 Hz. The centre segments aided accommodation and fixation. V.e.ps were recorded with a bipolar electrode arrangement. At least two different electrode pairs were used. All the data shown here are for the electrode pair illustrated by the ○ and △ (2 cm above the inion on the midline, and 6 cm to the right). Table 1 also includes results obtained with a second electrode pair (□ and △). For both electrode pairs the midline electrode served as the reference. Bottom: Averaged v.e.ps ($n = 300$) elicited by the appearance/disappearance of vernier offsets ranging from 80 to 10 s of arc are shown for observers K.B.S. (left) and D.M.L. (right). Several examples of repeated runs are shown to demonstrate the reliability of the data. The six traces shown for D.M.L. (40 s offset) were recorded on two different days. The two responses shown for D.M.L. to 60 and 20 s offsets were recorded during the same session. For comparison, v.e.ps recorded in identical conditions in response to the appearance/disappearance of a 15 cycle per degree (120 s per bar) squarewave grating are shown for observer K.B.S. Also shown are the responses recorded to a displacement of all of the line segments (motion) of 40 arc s, for D.M.L. In contrast to the highly visible vernier offset of 40 s, the unreferenced motion was subthreshold and resulted in responses which could not be distinguished from noise.





Vernier thresholds depend critically upon the relative distances between the features of the stimulus[1]. This property of vernier acuity is also evident in the v.e.p. Figure 3 shows how the v.e.p. amplitude varies as a function of offset magnitude for three different conditions, with the features abutting, separated by 7.5 min or with no reference lines (displacement). The psychophysical thresholds obtained in identical conditions are shown by the arrows, and are in good agreement with the electrophysiological estimates. This dependence of the v.e.p. amplitude on the proximity of the stationary reference is similar to that recently reported by Zemon and Ratliff[8] which they interpreted as a demonstration of lateral interactions.

We conclude that the responses obtained in these experiments were elicited by the appearance of the relative positional information in the vernier stimulus introduced by breaking colinearity. To our knowledge, this is the first report of evoked potentials elicited by such localized changes in the appearance of a stimulus. This is of particular interest since the v.e.p.

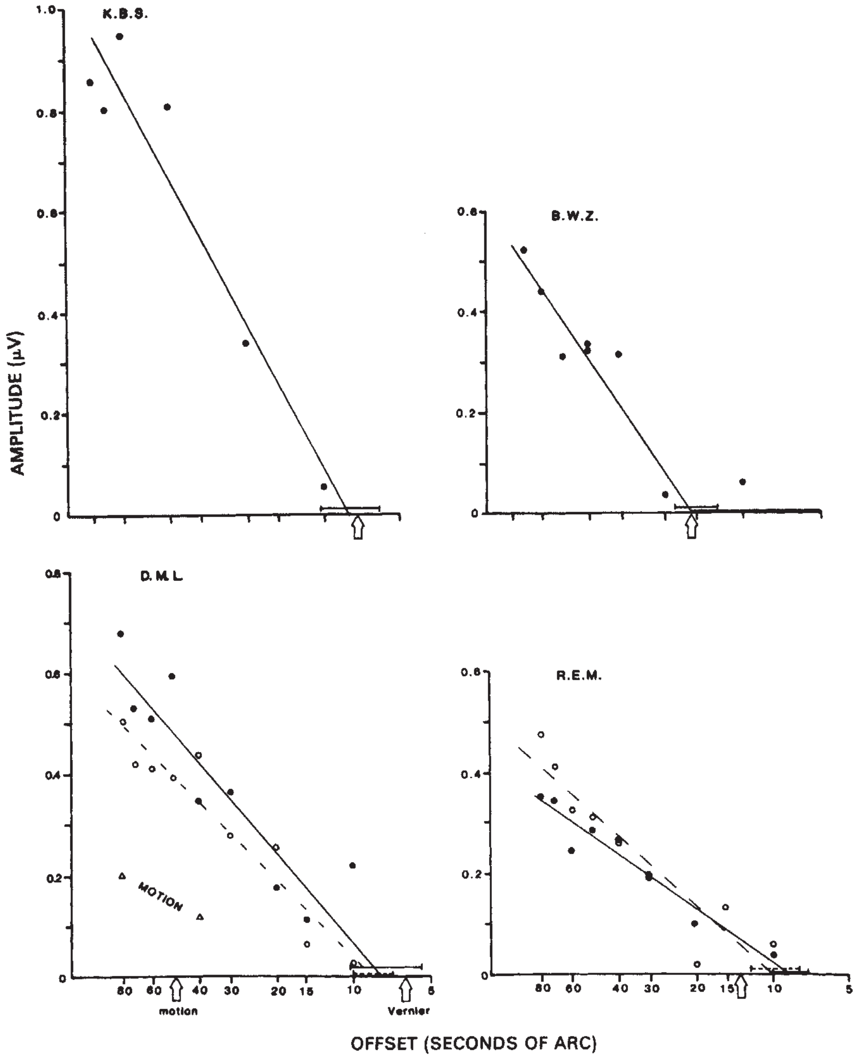
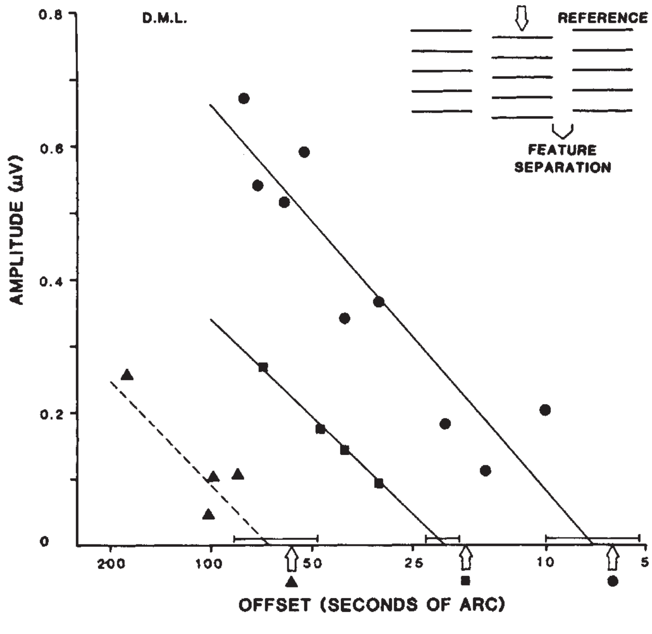


Fig. 2 The peak-to-trough amplitude of the early components elicited by the appearance of the offset (shown by the horizontal lines on the top record of K.B.S. in Fig. 1) are plotted as a function of the magnitude of the offset. Note that offset is plotted on a logarithmic scale for each of the four observers. The lines were fit to the data by nonlinear regression. The v.e.p. vernier threshold was given by the parameter X_0 of the nonlinear regression. The horizontal error bars show ±1 s.e. of the v.e.p. threshold. For comparison, psychophysical thresholds (75% detection level) are indicated by the arrows. For observers D.M.L. and R.E.M., two sets of data are shown. The results shown by the filled symbols and solid lines are with a repetition rate of 0.71 Hz. The data shown by the open symbols and dashed lines were obtained with a higher repetition rate (1.42 Hz) for R.E.M. For D.M.L., the open symbols and dashed lines were obtained in response to the appearance of a vernier offset for 350 ms every 1,400 ms (0.71 Hz) followed 700 ms later by a displacement of all of the line segments (motion) of the same magnitude.

Fig. 3 Fine spatial localization depends strongly on the proximity of the reference features. In order to determine whether this property of vernier acuity is reflected in the v.e.p., responses elicited by the displacement of the *central* line segments were recorded, while the lateral (reference) line segments were separated at various distances from the central test lines. V.e.p. amplitudes as a function of the magnitude of the offset for no feature separation (●), 7.5, minute separation (■), and with no reference lines, (▲) are shown for D.M.L. The lines are fit to the data by regression. The open arrows show the psychophysical thresholds obtained under the same conditions.



provides a new tool for investigating hyperacuity. In addition, it seems likely that these, and other hyperacuity stimuli, may provide a very sensitive technique for the investigation of anomalies of spatial vision[9].

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