Sampling in spatial vision

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The human visual system is capable of making spatial discriminations with extraordinary accuracy. In normal foveal vision, relative position, width or size can be judged with an accuracy much finer than the size or spacing of even the smallest foveal cones. This remarkable accuracy of spatial vision has been termed 'hyperacuity'[1]. Almost a century ago Ewald Hering proposed that the accuracy of Vernier acuity could be accounted for by averaging of discrete samples along the length of the lines comprising the targets[2]; however, the discovery that Vernier acuity of a few arc seconds could be achieved with dots has rendered the nature and role of sampling in spatial discrimination unclear[3]. We have been investigating the sampling of spatial information in central and peripheral vision (the perifovea) of normal human observers and in observers with strabismic amblyopia. Our results, presented here, show that peripheral vision and central vision of strabismic amblyopes differ qualitatively in their sampling characteristics from those of the normal fovea. Both the periphery and the central visual field of strabismic amblyopes demonstrate marked positional uncertainty which can be reduced by averaging of spatial information from discrete samples.

In the first experiment highly practised observers judged whether a test line presented briefly bisected the interval between two continuously viewed reference lines. The lines were composed of discrete samples (dots), each approximately 1 arc min and separated by inter-sample spaces of variable extent. We varied both the number of dots comprising each line and the inter-space size. The inset in Fig. 1 shows an example of a stimulus in which each line comprised five samples. The vertical separation of the lines was chosen to be optimal for each observer based on preliminary testing (see Table 1, column 2). A signal detection methodology was used to obtain thresholds for this spatial discrimination[4]. Figure 1*a* shows for two normal observers that foveal thresholds improved only slightly as the number of samples increased from 1 to 5. Additional samples beyond 5 had no further effect on thresholds and with even a single sample, thresholds were smaller than the inter-cone spacing (~30 arc s in the fovea).

Figure 1*b* shows results at 2.5° in the lower visual field; the data differ both quantitatively and qualitatively from those of the fovea. First, the threshold for a single sample is higher by more than a factor of 10. The threshold for a single sample (in the absence of spatial averaging) may provide an estimate of the intrinsic positional uncertainty of the visual system. What is of special interest here is that the threshold for a single sample is much larger than the inter-cone spacing at 2.5° (~70 arc s), suggesting that it is the cortical sampling grain rather than the cone mosaic which limits position discrimination in the periphery. Second, in the periphery, adding samples has a strong effect on bisection thresholds. For an 'ideal detector' that is limited by the spatial sampling grain, the positional uncertainty would be reduced in proportion to the square root of the number of independent samples; for the log–log axes of Fig. 1 this would mean a slope of −0.5. A flatter slope (like that of the fovea) would indicate that sparseness of sampling was not the factor limiting spatial discrimination. A higher slope would indicate an effect on the visibility of the targets by luminance summation. Table 1 gives the parameters for the fits to all the data in Fig. 1 (broken lines). While the results for the fovea are not compatible with a slope of −0.5, those for the periphery are consistent with a decrease in threshold proportional to $\sqrt{n}$ (n is the number of discrete samples) up to $n = 10$. Beyond this, adding more

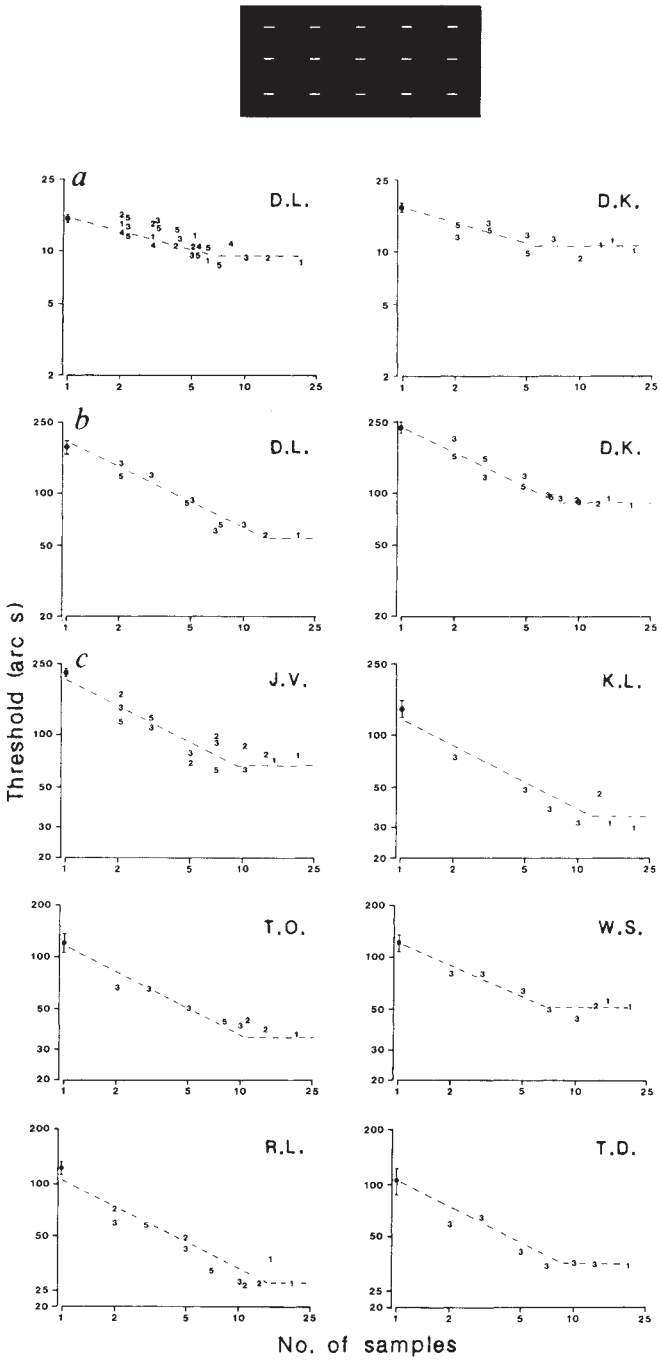

Fig. 1 Top, a schematic diagram of the 3-line bisection stimulus, with each line composed of five samples (that is, dots ~1 arc min) each separated by 2 arc min. The observer's task was to judge the vertical position of the briefly flashed test line (middle line) relative to the bisection point. The vertical separation between the reference lines and bisection point was optimized for each panel and is given in Table 1. Bisection thresholds equivalent to the signal detection parameter, $d' = 0.675$ (75% correct), are based on 250–600 trials per point, and are plotted as a function of the number of samples for normal foveal vision (*a*), peripheral vision (*b*) and the central field of strabismic amblyopes (*c*). The numbers in each graph represent the sizes of the inter-space intervals in arc min. Each graph has been fitted with two lines. Thresholds decrease as the number of samples increases to ~5 for foveal vision and 10 for peripheral and amblyopic vision. A slope of −0.5 (that is, thresholds proportional to the square root of the number of samples) provides a reasonable fit for the data of the periphery and of the strabismic amblyopes. A shallower slope, −0.3, provides a good fit to the foveal results (see Table 1).

Table 1 Parameters for the fits to the data in Fig. 1

Condition	Verical separation (min)	Observer	Snellen acuity	Threshold for a single sample (arc s) (y_0)	Asymptotic no. of samples (x_A)	Slope (r)
Normal fovea	3	D.L.	6/4.5	16.4±0.80	7.8±1.7	−0.29±0.04*
	3	D.K.	6/5	17.4±0.65	5.4±1.3	−0.30±0.04*
Periphery (2.5°)	12.4	D.L.	6/21	191.6±11.3	11.1±2.0	−0.48±0.04
	12	D.K.	6/22	233.5±10.6	9.5±0.9	−0.43±0.04
Strabismic amblyopia†	10	J.V.	6/24	219.8±25	5.3±0.9	−0.66±0.11
	5	T.D.	6/8	97.7±10.5	7.0±1.4	−0.52±0.08
	6.7	R.L.	6/12	110.8±8.1	10.0±2.6	−0.58±0.09
	12	T.O.	6/10	104.7±8.3	11.6±2.6	−0.43±0.06
	5	K.L.	6/12	114.8±17.5	16.2±7.8	−0.50±0.07
	10	W.S.	6/13.5	117.5±9.1	7.2±1.7	−0.42±0.07

Values were obtained by nonlinear regression of the form $\log y = \log y_0 + r \log x$ for $x < x_A$ and $y = \log y_0 + r \log x_A$ for $x \geq x_A$ where y is the threshold in arc s and x is the number of samples. The SAS statistical package was used. Fitting all the data with a second model, where x is the length of samples plus inter-spaces, gave a significantly worse χ^2 value: 226 as opposed to 172 ($p < 0.025$, F test with 127 d.f.). Errors represent 1 standard error. All observers were carefully refracted and wore appropriate spectacle corrections if necessary. Extensive practice was given before the actual data collection. D.L. is an author. Snellen acuity (75% correct) was derived from crowded Davidson-Eskridge charts (6/6 corresponds to a 60-arc s feature). * Not consistent with a slope of −0.5 at the 0.000001 level, whereas all the other data are consistent with a slope of −0.5 at the 0.05 confidence level. † Each of these observers has a constant unilateral strabismus of early onset and reduced acuity in an otherwise healthy eye.

samples has no additional effect on thresholds. The effect of adding samples is not simply explained by luminance summation, as making a single sample seven times brighter in a control experiment did not improve the bisection threshold.

The spatial vision of strabismic amblyopes has previously been compared to that of the normal periphery[5–7]. The data shown in Fig. 1*c* for the amblyopic eyes of six strabismic amblyopes bear a remarkable similarity to the results for the normal periphery (Fig. 1*b*). For each of the strabismic amblyopes, as in the normal periphery, position uncertainty is high with only one sample, and thresholds improve in proportion to the square root of the number of discrete samples. Table 1 also shows Snellen acuity for each observer. For the amblyopic eyes and the periphery, the threshold for one sample is approximately equal to Snellen acuity. In foveal vision, on the other hand, the threshold for one sample is about three times better than Snellen acuity (that is, a hyperacuity). Interestingly, the non-amblyopic eyes of strabismic amblyopes were similar to those of the normal observers. For example, J.V., a highly experienced observer who had the most severe amblyopia, showed a threshold with one sample of 19.0±0.9 arc s and a slope of −0.24±0.1 with his preferred eye.

A second experiment was performed in order to verify our sampling hypothesis and to determine whether information is sampled only along the length of the lines of the target (that is, orthogonal to the discrimination cue) as originally suggested by Hering[2]. Here, the observers' task was to judge whether the separation between two small boxes was larger or smaller than the standard (12.4 arc min) separation[8]. Each box was actually composed of four tiny dots, illustrated schematically in the inset in Fig. 2 (stimuli 1 and 4). In this experiment, we manipulated the distances between the four dots comprising each of the two boxes. When they were close together (10 arc s) and thus unresolved, they represented a single (bright) sample. When the dots were all separated so that they could be resolved (1.2 arc min for the normal fovea; 2.4 arc min for peripheral and amblyopic vision) they provided four discrete samples. By this device the total luminance of each box stimulus was balanced and was approximately 20 times the observers' detection threshold. Figure 2*a* shows the separation discrimination threshold for unresolved (one sample) and resolved dots (four samples). For the normal fovea (Fig. 2*a*) thresholds for the two conditions were identical. For a strabismic amblyopic eye (Fig. 2*b*) and for the normal periphery (Fig. 2*c*), thresholds improved noticeably for the resolved dots. We have confirmed these observations on other observers and at different separations. We anticipated that increasing the number of samples from one to four would result in a twofold decrease in threshold (equal to $\sqrt{4}$). However,

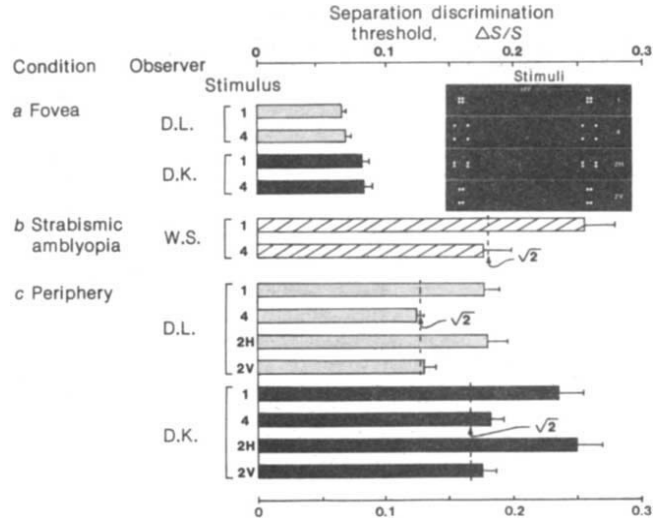

Fig. 2 Inset, a schematic diagram of the stimuli for spatial interval discrimination. In an experimental run, the stimulus (two boxes) was presented briefly with one of five closely spaced separations, centred at 12.4 arc min, and the observer judged whether the spatial interval between the two boxes (SEP in inset) was larger or smaller than the implicit standard. Stimulus feedback was given after each trial. Each box actually comprised four tiny bright dots on a dark background. When the dots were closely spaced (10 arc s) and therefore unresolved, there was only one sample per box (stimulus 1). When the dots were separated by 1.2 arc min (fovea) or 2.4 arc min (periphery and strabismic amblyope) they were seen as four discrete samples (stimulus 4). Separating the dots either only horizontally (2H) or only vertically (2V) resulted in two discrete samples. Threshold, equivalent to $d' = 0.675$, is specified as a fraction of the base separation (12.4 arc min) for unresolved (stimulus 1) and resolved (4) dots for the fovea of two normal observers (*a*), a strabismic amblyope (*b*) and peripheral vision of two observers at 2.5° (*c*). Each threshold is the mean of four counterbalanced runs (125 trials per run). To test which samples were effective in lowering the threshold, the dots were separated either horizontally or vertically. The results show that two samples separated horizontally (2H) were not significantly better than a single sample, whereas two samples separated vertically (2V) were $\sqrt{2}$ better than a single sample in lowering the separation discrimination threshold.

surprisingly, the thresholds were in fact reduced by only $\sim\sqrt{2}$, suggesting that only two of the samples were effective. To test this possibility, we separated the dots either horizontally only or vertically only (stimuli 2H and 2V in the inset), thus providing two samples either in the same direction as the discrimination cue (horizontal separation) or in the orthogonal direction (vertical separation). Horizontal separation gave thresholds identical to that obtained with a single sample whereas vertical separation gave thresholds which were $\sqrt{2}$ better. Thus, the two samples in the direction orthogonal to the discrimination cue each contributed effectively to reducing the threshold. This result is consistent with Hering's hypothesis regarding the averaging of discrete samples and suggests that this process is performed by oriented mechanisms.

Our results show that spatial information is indeed sampled discretely along the length of targets as originally proposed by Hering. In normal foveal vision, this process has a relatively small impact on the accuracy of spatial discriminations, presumably because the fovea has little intrinsic positional uncertainty. Thus foveal thresholds are smaller than a cone diameter. However, in the normal periphery and in the central field of strabismic amblyopes, the addition of spatial samples in the direction orthogonal to the discrimination cue reduces thresholds in proportion to $\sqrt{n}$, as would be expected in an ideal detector with uncorrelated noise at an early stage of visual processing.

In peripheral vision, the high degree of spatial uncertainty with a few samples can be understood on the basis of the anatomy and physiology of the retina and cortex which results in a sparse neural sampling grain[9]. In strabismic amblyopia, we hypothesize that abnormal binocular interactions result in similar neural consequences—that is, a sparse spatial sampling grain as a result of there being insufficient cortical neurones to provide accurate position signals and/or a scrambling of the neural signals[5]. A sparse sampling grain and/or scrambling of neural signals would introduce positional noise which is uncorrelated between stimulus samples in peripheral and strabismic amblyopic vision.

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Generation of end-inhibition in the visual cortex via interlaminar connections

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To understand the mechanisms by which the receptive field properties of visual cortical cells are generated, one must consider both the thalamic input to the cortex and the intrinsic cortical connections. In the cat striate cortex, layer 4 is the main recipient of input from the lateral geniculate nucleus, yet the cells in that layer possess several receptive field properties that are distinct from the geniculate input, including orientation specificity, binocularity, directionality and end-inhibition, the last of which allows cells to respond to edges of a restricted length[1-4]. These properties could be generated by connections within the layer, by its input from the claustrum[5] or by the massive projection that layer 4 receives from layer 6 (refs 6-9). In the present study, we attempted to determine the functional role of the layer 6 to layer 4 projection by reversible inactivation of layer 6 using the inhibitory transmitter γ-aminobutyric acid (GABA). After inactivating layer 6, cells in layer 4 lost end-inhibition. Cells in layer 2+3, which receive their principal input from layer 4, were similarly affected. The elimination of end-inhibition was specific, other receptive field properties, such as direction selectivity or orientation specificity, remaining intact.

Recordings were made in cats maintained on sodium thiopental anaesthesia, paralysed with succinylcholine and artificially respirated with 100% oxygen. At the start of an experiment virtually all of the cells in layers 2, 3 and 4 were end-inhibited to some degree. The oxygen helped maintain the proportion of end-inhibited cells, which otherwise tended to decline during the experiment. The animals' electrocardiogram, electroencephalogram, temperature and expired CO_2 concentration were continuously monitored. A small hole was drilled in the skull above the visual cortex, and the dura and pia opened. To study the role of the layer 6 to 4 pathway, we inactivated layer 6 by injecting GABA and examined the effect of this treatment on the receptive field properties in layers 2 to 4. A similar approach has been used in other systems with inhibitory transmitters or analogues, local anaesthetics or cobalt[10-12]. The advantage of GABA is that it affects cells and not afferents and the effects are reversible. In initial experiments to determine the area inactivated by GABA injections of various amounts and concentrations, the micropipette was placed about 300 μm below the layer 5/6 border and a second tungsten electrode, laterally displaced at various distances from the first electrode, was advanced to approximately the same laminar position as the micropipette. The entrance into layer 6 was recognized by the appearance of cells possessing long receptive fields in this layer[3]. After the penetrations, electrolytic lesions were made to verify the placement of the electrodes histologically and to determine the horizontal displacement between the two electrodes. We found that a 0.1-μl injection of 10 mM GABA inactivated an area of ~700 μm in diameter. The inactivation lasted for several minutes and was always reversible.

Having established the conditions for blockade of the activity of layer 6 cells, we recorded from cells in layers 2+3 and 4 while the GABA pipette was in a corresponding topographical position in layer 6. Figure 1 shows response histograms of a simple cell in layer 4. When tested with a stationary flashing bar, the cell's receptive field consisted of a separate 'on' region flanked by two antagonistic 'off' regions. The cell was end-inhibited: its response to a long bar (8°) was reduced by 54% compared with its response to a bar of optimal length (1°). An injection of 0.1 μl of 10 mM GABA in layer 6 had no effect on the cell's response to the short bar, but greatly increased its response to the long bar, so that end-inhibition was completely eliminated. This blockade was reversible, for 3 min after GABA injection the cell's response was again reduced over 50% by end-inhibition.

Cells in the superficial layers showed similar effects to those seen in layer 4. Figure 2 shows response histograms of a layer 2+3 cell with a complex receptive field, 0.5°×1.5° in size, and on-off responses to a stationary flashing bar. The cell responded briskly when a bar of optimal length (0.5°) was moved across its receptive field, but the response was reduced by 58% when