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QUALITY OF THE PRIMATE PHOTORECEPTOR LATTICE AND LIMITS OF SPATIAL VISION

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Abstract—Quantitative analysis of a primate photoreceptor lattice shows that the foveal lattice is a highly regular hexagonal structure with a positional correlation length of at least 130 photoreceptors. This result indicates that the photoreceptor lattice is not sufficiently disordered to prevent aliasing in the fovea, but rather could provide the metric with which the visual system determines spatial separation even for tasks involving hyperacuity.

Photoreceptor lattice Hyperacuity Aliasing

INTRODUCTION

There is a growing recognition that the photoreceptor lattice must play a fundamental role in spatial vision (Williams and Collier, 1983; Miller and Bernard, 1983; Yellott, 1982; Hirsch and Hylton, 1982). The question of how accurately the photoreceptors are placed in the lattice then becomes of considerable importance, and two quite different views of the consequences of imperfections in the lattice have been proposed. We have recently presented evidence suggesting that spatial intervals are measured by counting points in a cortical lattice which is derived from the photoreceptor lattice. From this point of view, the photoreceptor lattice is the basic geometrical instrument for measuring distances and any randomness in the spacing of photoreceptors will limit the accuracy with which the measurements can be made.

A conflicting view suggesting that randomness in the photoreceptor lattice is desirable as an anti-aliasing mechanism has also recently been proposed (Yellott, 1982). Actually this argument requires not random (unknown) errors in position but rather an irregular lattice formed of photoreceptors whose individual positions must be accurately known. If the photoreceptor positions had truly random (unknown) errors large enough to prevent aliasing, serious degradation of the high frequency content of an image would occur (French *et al.*, 1977). Thus if the photoreceptor lattice were highly disordered one would be left with the question of exactly how the positions of the individual photoreceptors were determined by the visual system.

To study the question of photoreceptor lattice quality we have analyzed the foveal cone mosaic from an adult primate (*Macaca fascicularis*) using an electron micrograph of a section taken tangent to the external limiting membrane (ELM) close to its scleral side (Miller, 1979). Our analysis is based on measurements of the positions of the centers of about 100 cone inner segments in the central fovea (Fig. 1).

This lattice was chosen for analysis rather than that published by Polyak (1957) and studied by Yellott (1982) because the Polyak lattice is a photograph of a whole mount that appears to be focused near the level of the outer segments. The outer segment locations are irrelevant for positional analysis since the outer segments are basically light guides for photons that enter the cones at the inner segments. The outer segments may also be subject to substantial positional distortion since they are embedded in a semifluid extracellular matrix. In contrast, the positions of the inner segments are fixed at the ELM by desmosomes, after which they taper and increase in refractive index to become light guides, providing the mechanism by which the cones form separate optical channels. Thus the inner segment at the ELM is the spatial aperture of the cone for its photon catching function and its position specifies cone location for the purpose of image reconstruction. We further note that the Miller lattice displays clearly higher spatial quality than the Polyak lattice. Given the unlikelihood of accidentally introducing order into an initially disordered lattice, the more orderly lattice must be more representative of the intact retina.

RESULTS

Figure 2(a) is a histogram of the distances between the centers of all pairs of photoreceptors in our

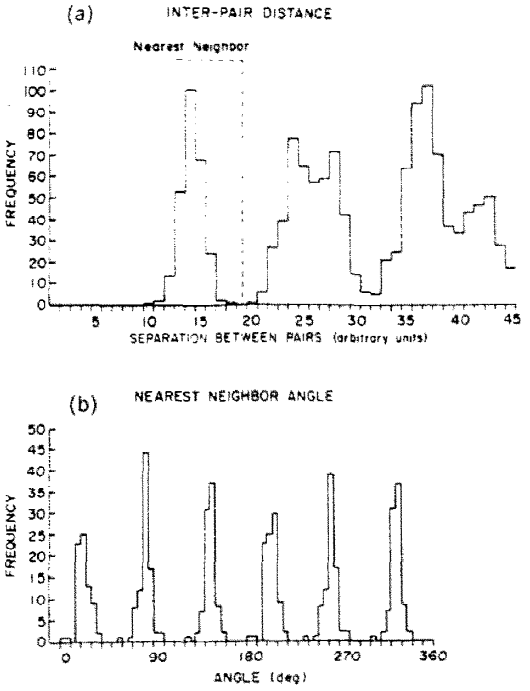

Fig. 2. (a) Histogram of distances between all pairs of photoreceptors in the sample shown in Fig. 1. The first peak shows the distribution of distances between the centers of nearest neighbors. (b) Histogram of all angles between the horizontal axis and the lines connecting the center of each photoreceptor to the center of its nearest neighbors. The six peaks demonstrate a high quality hexagonal lattice.

sample. There is a very distinct peak corresponding to the nearest neighbor distance (which we call ring 1). The r.m.s. width of the peak (standard deviation of the nearest neighbor distance) is 0.077 times the mean separation between nearest neighbor photoreceptors and drops to 0.070 when the contribution from our measurement error is removed. This is comparable to the maximum tolerable spacing error (0.078) estimated below from human psychophysical results.

Figure 2(b) shows a histogram of the angles between the horizontal axis and the lines connecting the center of each photoreceptor to the center of its nearest neighbors where nearest neighbors are defined as any pair whose center to center separation is less than the maximum nearest neighbor distance shown in Fig. 2(a). This figure shows a well defined set of directions with hexagonal symmetry (60° spacing) which determine the orientation of the lattice, and is consistent with previous qualitative observations of retinal structure (Borwein *et al.*, 1980; Polyak, 1957). (It has been pointed out to us that the packing of the lattice approximates a hexagonal tessellation with the centers of the receptors forming a triangular lattice.)

By specifying the mean nearest neighbor distance and orientation of the lattice we have fully determined the basis vectors for the lattice. (See Kittel, 1971, for a discussion of crystal structure.) We then make the following calculations. For each photoreceptor we take its center to be the origin and use the nearest neighbor distance cut determined from Fig. 2(a) to locate its nearest neighbors. We then measure the difference between expected and actual positions for the photoreceptors just assigned to the ring of nearest neighbors assuming a perfect hexagonal lattice with the basis vectors determined above. The nearest neighbor distance cut is then used again to move out from the nearest neighbors to the ring of second nearest neighbors and again we measure the error in actual position versus the expected position for a perfect hexagonal lattice centered on the original photoreceptor. We continue this process until all photoreceptors have been assigned to some ring and their errors computed. The process is then repeated with a new photoreceptor as the origin.

Figure 3 shows a graph of the variance (mean square error) in relative position as a function of ring number. The data have been normalized so that the mean nearest neighbor photoreceptor distance (ring 1) is 1.0. We plot separately the components of variance parallel and perpendicular to the line which joined the photoreceptor at the origin and the one being tested. The parallel component corresponds to errors in separation while the perpendicular component corresponds to errors in orientation. The variance increases linearly with distance (ring number), consistent with accumulating uncorrelated errors, and the parameters of the best fit straight lines are given in Table 1. Measurement error and jitter in the lattice (discussed below) would lead to a positive y intercept and appear to be small.

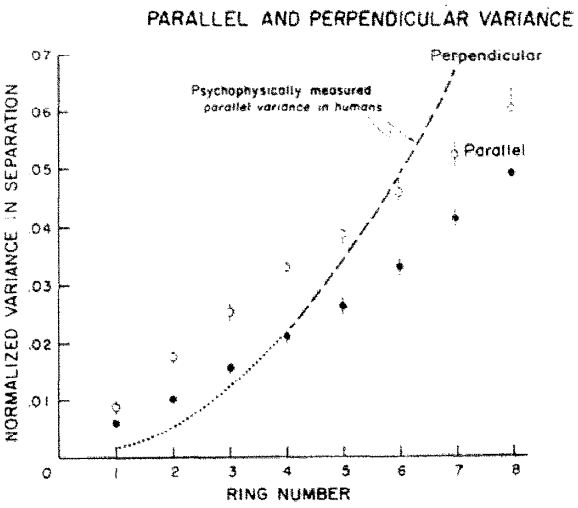

Fig. 3. Variance between expected and actual positions of photoreceptors vs ring number normalized so that the nearest neighbor distance is 1.0. Solid circles correspond to errors in separation (parallel), and open circles correspond to errors in orientation (perpendicular). The curve is a psychophysical estimate of the total parallel variance in spatial interval measurement by humans.

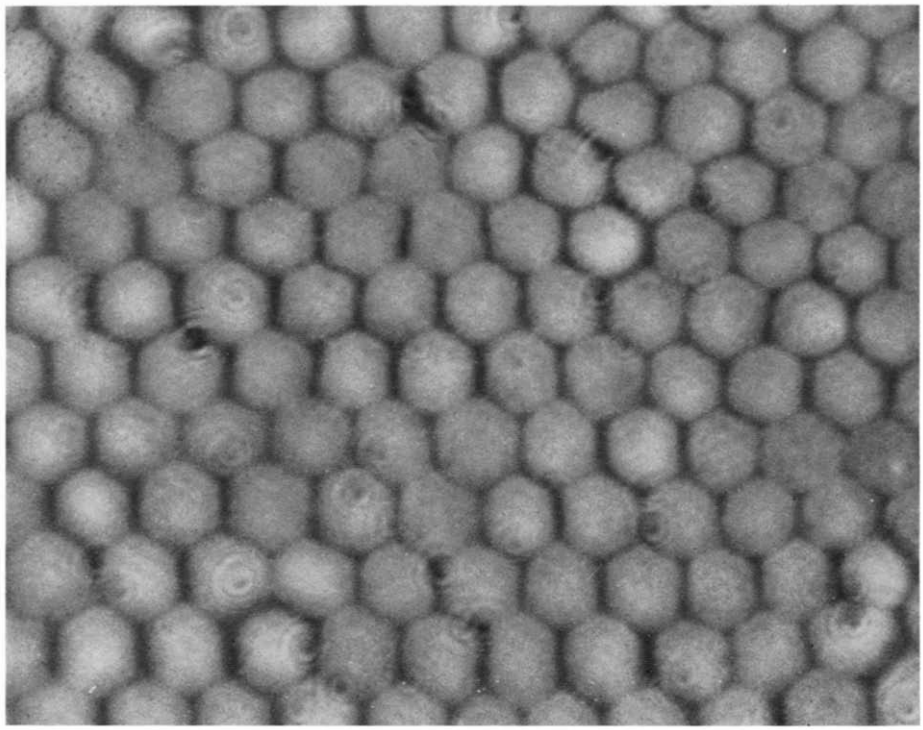

Fig. 1. Cone inner segments at the central fovea in the retina of the monkey, *Macaca fascicularis*, shown in a photograph of a 1 μm thick section tangent to and on the scleral side of the external limiting membrane. Center-to-center distance of cones is 3 μm. From Miller (1979) with permission.

Table 1. Parameters of best fit lines variance[a] vs ring number

Variance	Slope	Intercept	χ^2	d.f.	Conf.
Uncorrected					
Parallel	0.0056 ± 0.0002	0.0001 ± 0.0006	8.89	6	0.18
Perpendicular	0.0075 ± 0.0003	0.0021 ± 0.0009	2.60	6	0.86

[a]Variance is expressed in units of mean inter-neighbor distance squared.

If we define the positional correlation length of the lattice as the distance between two lattice points at which the r.m.s. spacing error equals the lattice spacing, then the correlation length for the parallel component is 178 ± 7 photoreceptors and for the perpendicular component the correlation length is 133 ± 5 photoreceptors.*

LATTICE QUALITY AND LIMITS OF SPATIAL RESOLUTION

Assuming that a *Macaca fascicularis* lattice is comparable to a human lattice, these anatomical results can be compared to human psychophysical results. We have found that changes (Δs) in a spatial interval s can be correctly discriminated by human observers 75% of the time when $\Delta s \sim 0.025 * s$ for a very large range of s, i.e. from greater than 1 deg of visual angle to at least 0.04 deg. (See Hirsch and Hylton, 1982 for details of the measurement procedure.) Assuming a normal response distribution, 75% correct corresponds to 0.68 standard deviations, and the r.m.s. error is 0.025/0.68 or 0.037 times s. Since the psychophysical result is basically a measure of the total parallel (separation) error, it provides an upper limit for the parallel component of photoreceptor spacing error if the photoreceptor lattice is considered as the metric with which spatial intervals are measured.† For the smallest value of s we have been able to test (0.04 deg) the r.m.s. error Δs was about 0.0013 deg or about one sixth of the center-to-center photoreceptor spacing in the fovea. Since this value of s corresponds to a span of about 4.5 photoreceptors, and we naively expect that spacing errors will accumulate proportionally to the square root of distance, the fundamental spacing error between neighboring photoreceptors must not exceed $0.037 * \sqrt{4.5} = 0.078$ times the average photoreceptor spacing. This psychophysical limit in humans is clearly of the same order as the primate lattice error measured above (0.070).

This argument is shown graphically in Fig. 3 where we have plotted the square of the psychophysical limit $\Delta s = 0.037 * s$ (dashed line) along with the anatomical results. The parallel variance intersects the psychophysical limit slightly below 4 photoreceptors indicating that the photoreceptor spacing error is less than the psychophysically measured total error for spatial separations greater than 4 photoreceptors. That is, the psychophysical measurements do not require a positional accuracy exceeding the photoreceptor lattice accuracy measured above for separations greater than four photoreceptors. Note that the psychophysical limit is only established for separations greater than about 4.5 photoreceptors.

ALIASING

We now turn our attention to the question of aliasing. Figure 4 shows the Fourier transform of our lattice sample along the direction of one of the reciprocal lattice basis vectors; the other basis directions are quite similar. The frequency axis has been normalized to $2/\sqrt{3} \times 1/d$, which is the frequency at which the first tooth of the alias comb should occur for this orientation on a hexagonal lattice. There is clearly quite severe aliasing, with the first two aliases having amplitudes of 0.8 and 0.5 respectively.

Now consider the conditions necessary to prevent aliasing, which depend both on the degree of disorder in the lattice and the size of the reconstruction window, i.e. the number of sample points available simultaneously for reconstructing the image at a

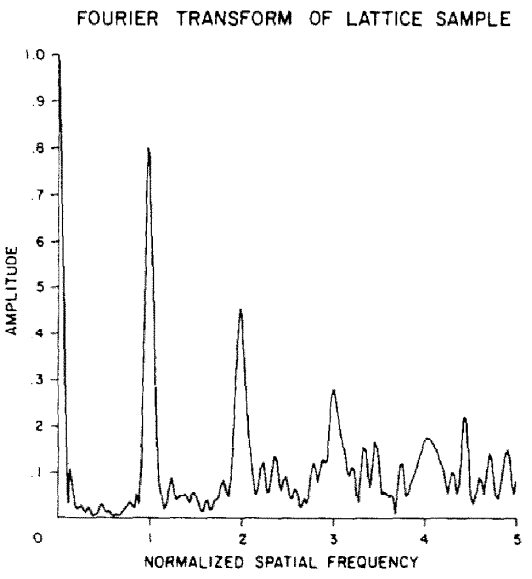

Fig. 4. Fourier transform of the lattice sample. The frequency axis has been normalized to the first frequency at which aliasing is expected.

*We do not understand why the perpendicular variance is greater than the parallel. We suspect it is related to the distortions discussed later. Note that correlation length is a measure of lattice quality and is not related to any actual length.

†We make the assumption that there is no mechanism for measuring the true spatial positions of photoreceptors so that errors in lattice spacing cannot be corrected for. We also assume there is no averaging along the orthogonal dimension (Westheimer and McKee, 1977).

particular point. (We consider only the one dimensional case). Aliasing occurs because a sinusoid of frequency f and a sinusoid of frequency $f + 1/d$, where d is the lattice spacing, have exactly the same values at the sample points. That is, at the sample points given by $x_N = Nd$

$$\exp[i2\pi(f + 1/d)x_N]$$
$$= \exp[i2\pi f x_N]\exp[i2\pi(1/d)(Nd)] = \exp[i2\pi f x_N]$$

and hence the two frequencies are indistinguishable after sampling. However, if there is an accumulated spacing error $\Delta(N)$ over N photoreceptors, the values at $x_N = Nd + \Delta(N)$ for the two sinusoids are

$$\exp[i2\pi f x_N]$$

and

$$\exp[i2\pi f x_N]\exp[i2\pi\Delta(N)/d]$$

respectively, where the effect of the accumulated spacing error has been to introduce an effective accumulated phase shift $\Delta(N)/d$ whose r.m.s. value increases with N. Assume a phase shift of half a cycle is necessary to break the coherence and allow the two frequencies to be distinguished, a condition in reasonable agreement with detailed calculations. Then to prevent aliasing we must have $\sigma(N) \geq d/2$ where $\sigma(N)$ is the r.m.s. value of $\Delta(N)$.

Extrapolating the results above shows that the parallel variance $\sigma^2(N)$ will not reach $d^2/4$ for N less than 45. Thus to avoid aliasing we must always use a sample length of at least 45 photoreceptors, which corresponds to a reconstruction window containing over 20 complete cycles of sinc (x). We regard such a long range interpolation (nearly 0.4 deg) as very unlikely.

SOURCES OF ERROR AND LIMITATIONS OF THE ANALYSIS

While these results establish that the photoreceptor lattice is highly accurate, there is a potential problem with the data that may have caused the degree of error to be severely overestimated. Close inspection of the lattice in Fig. 1 leaves the impression that the lines formed by nearest neighbor photoreceptors are not perfectly straight but rather possess a slight degree of curvature. Numerical analysis confirms that this is indeed the case and that the lattice is systematically distorted. Further, these systematic errors contribute substantially to the increase in variance with distance shown in Fig. 3. If these distortions were introduced in the preparation process they should be removed from the data, and one might even argue that, regardless of origin, systematic errors are correctable and should not be included in this analysis.

We have attempted to correct for this problem in a number of ways and conclude that systematic distortion accounts for roughly half of the slope in Fig. 3 while decreasing the ring 1 variances only slightly. (Jitter in the lattice is then significant.) We estimate that with the systematic distortions removed, the correlation lengths may be as much as 400 for the parallel and 200 for the perpendicular components respectively, with the psychophysical limit intersecting the parallel variance at about 2.5 photoreceptors. Thus we believe the above estimates of correlation length are conservative.*

We note that the results presented here apply directly to measurements over spatial intervals less than some tens of photoreceptors since we only analyzed a section of about 10 × 10 photoreceptors. However, the psychophysical measurement of the total variance rises as the square of separation (i.e. the r.m.s. error is a constant fraction of the distance being measured) while the photoreceptor position variance is only rising linearly over the section we analyzed. As long as the photoreceptor variance rises less rapidly with distance than the psychophysical variance over long spans the error contributed by photoreceptor spacing will be negligible. (The measurement of large distances actually requires considerations that are beyond the scope of this paper.) We also assume inhomogeneities in the lattice are unimportant, perhaps requiring that the position measurement always be done in a sufficiently restricted region of the retina.

OTHER FORMS OF IMAGING ERROR

In addition to the kinds of random spacing errors discussed above which lead to a finite correlation length we can distinguish two other kinds of randomness. The first is jitter in the lattice which occurs if each point in perfect lattice is given a random deviation from its expected position. Since jitter does not build up over distance it will not contribute to the slope of the variance vs distance function but only contributes to the y intercept and appears small when the curvature of the lattice is neglected (see Table 1). The other form of error we consider is topological disorder in the mapping from retina to cortex, which is quite distinct from the essentially geometric disorder considered previously. If we think of the cortex as receiving a bundle of fibers originating from the retina with each fiber identified only by a number, then topological disorder occurs when a sequentially numbered sequence of fibers is not monotonic in space due to random cris-crosses in the fiber bundle. This effectively causes the apparent positions of two photoreceptors to be erroneously interchanged. Such

*We find that after correcting for curvature the variance vs ring number function is still consistent with a straight line, but the y-intercept is no longer consistent with zero. This could be interpreted as the sum of a constant variance due to jitter in the lattice plus accumulating uncorrelated errors. However, the exact values of the slope and intercept depend significantly on the form of the curvature correction, and so we adopt the conservative approach and apply no corrections.

mapping errors could cause severe problems for image reconstruction, but given the long correlation lengths estimated for the retina there is probably no significant topological disorder at the retinal end of the bundle, and it is conceivable that in general such errors are eliminated during the formation of the visual pathways (Rakic and Riley, 1983).

IMPLICATIONS OF ORDERED AND DISORDERED LATTICES

In this section we consider the implications of ordered and disordered lattices for vision. Perhaps the most significant aspect of a highly ordered lattice is that it is capable of providing the geometric information necessary for accurately measuring spatial intervals. As we have shown above, the primate photoreceptor lattice appears to be sufficiently regular to serve as the metric for spatial vision, even for tasks involving hyperacuity, at least over spans of tens of photoreceptors. That is, the distance between two photoreceptors is determined to sufficient accuracy for all spatial tasks simply by counting the number of intervening photoreceptors. Indeed, recent psychophysical results have been interpreted as evidence that the human visual system does in fact measure spatial intervals by counting points in a neural lattice that is derived from the photoreceptor lattice (Hirsch and Hylton, 1982, 1984), and the results presented here suggest that such a scheme is feasible even for the most demanding visual tasks. In the absence of an orderly lattice to provide geometrical information, one would have to postulate the existence of some cortical mechanism capable of determining the distances between all pairs of photoreceptors to the required accuracy, which is not trivial. The existence of an orderly lattice would obviate the need for such a complicated spatial calibration system.

Another potentially advantageous property of a highly regular lattice is that its topological order greatly simplifies the establishment of maps between retina and cortex, whether one-to-one or more complicated. With sufficient regularity at both the retina and cortex, structures at each location could develop independently but achieve congruence relatively easily at some later time. In the simple fiber bundle analogy presented above, this basically requires that the optic nerves maintain nearest-neighbor relationships, which is far simpler than requiring that each fiber must separately seek appropriate end points, or postulating a cortical mechanism capable of an arbitrarily complicated unscrambling. We have recently reported that the orientation dependence of hyperacuity contains a component with hexagonal symmetry, which strongly suggests that the hexagonal packing of photoreceptors is preserved in the cortical mechanisms that underlie hyperacuity (Hirsch and Hylton, 1984).

A final point, which actually does not require a very high degree of geometrical accuracy, is that hexagonal lattices have a higher packing density for round objects than square or random lattices. This has two advantages, as noted by Snyder and Miller (1977). First, the increased number of sample points per unit area leads to an increase in the average Nyquist frequency. Second, the photoreceptors are able to cover a larger portion of the total area, maximizing the photon catch. It is also worth noting that the orientation anisotropies for a hexagonal lattice are actually fairly small and substantially smaller than for a square lattice since the hexagonal lattice is considerably rounder. [The orientation anisotropy is characterized by $1 - \cos(45^\circ) = 0.29$ for a square lattice and $1 - \cos(30^\circ) = 0.13$ for a hexagonal lattice, considerably smaller.]

Now consider the case of a disordered lattice. Yellott (1982) has argued that a disordered lattice has the significant advantage of suppressing aliasing. (As noted above, this argument requires not a lattice of sample points with large unknown errors in position but rather a highly irregular lattice of points whose individual positions must be well known.) However, we do not agree that the suppression of aliasing by an irregular lattice can be of any benefit to vision, at least in the fovea. As discussed below there are other factors in vision which suppress aliasing under normal circumstances anyway, so that aliasing cannot be a major problem in normal vision. More generally, aliasing results from undersampling, and undersampling has serious consequences for vision that cannot be avoided with any sampling scheme. Specifically, hyperacuity requires the ability to interpolate between photoreceptors, and this is impossible unless there is sufficient optical blurring to spread a point image over at least two or three photoreceptors in a row (Barlow, 1979, Westheimer, 1976). The consequences of this blurring in the spatial frequency domain will be to filter out any frequencies high enough to cause aliasing. Thus hyperacuity requires a degree of blurring that will prevent aliasing irrespective of the details of the sampling scheme.

It is also not obvious to us that undersampling with a regular lattice is any more deleterious to vision than undersampling with an irregular lattice. Aliasing *per se* is a symptom of undersampling that is pronounced only if the high frequency content of an image is large and narrowband. However, for images that are not highly peaked in the spatial frequency domain (i.e. not artificially generated gratings) the effect of undersampling is basically to introduce "jaggedness" into the image whether the sampling is regular or irregular. This precludes hyperacuity but has little other effect. The seriousness of the jaggedness will depend on how much of the total power is at high frequencies (above the Nyquist frequency) and whether or not it is highly concentrated. For realistic retinal images the power at high frequencies is apparently neither large nor highly concentrated (Carlson and Cohen, 1978).

OTHER FACTORS THAT FORESTALL ALIASING

We have shown that the photoreceptor lattice is not sufficiently disordered to prevent aliasing in the fovea. However, the following mechanisms will prevent aliasing under most usual conditions.*

(a) The Nyquist frequency is higher than usually estimated. Many papers in the vision literature state that if the cone spacing is 1/120 deg, then aliasing sets in above a spatial frequency of $1/2d = 60$ c/deg (e.g. Yellott, 1982) which is uncomfortably near the foveal optical cutoff frequency, also approximately 60 c/deg (Campbell and Green, 1965). Unfortunately this is incorrect and follows from a failure to analyze sampling in two dimensions. In the two-dimensional case the Nyquist frequency depends on orientation† and ranges between $2/\sqrt{3}$ and $4/3$ times $1/2d$ for a hexagonal lattice, depending on orientation, significantly above the optical cutoff frequency.

(b) The classical analysis of aliasing has a domain of applicability basically limited to a single still picture. The assumption that the visual system has available only a single sampling of the image is questionable. Binocular vision potentially doubles the spatial sampling frequency, and eye motions generate successive independent spatial samples which could be used to resolve aliasing ambiguities when integrated over time.

Yellott (1982) and others (Snyder, 1982, Westheimer, 1982) have noted that point (a) does not hold in parts of the periphery where there is apparently a severe mismatch between optical cutoff frequency and cone sampling frequency. Actually, undersampling by a factor of nearly 2 can be tolerated if one is only interested in low frequencies, a reasonable description of the periphery (Green, 1970). Consider an optical cutoff frequency of 60 c deg and a one dimensional sampling frequency of 70 c deg (Nyquist frequency of 35 c deg). The lowest frequency that can be introduced by aliasing is $|60-70| = 10$ c/deg. By forming appropriately shaped receptive fields one can introduce a neural cutoff frequency of 10 c/deg, eliminating all components above this frequency, aliased or otherwise. However the peripheral undersampling is apparently by a factor of 4 which cannot be eliminated this way (Snyder, 1982; Yellott, 1982; Jennings and Charman, 1981; Osterberg, 1935). Combined with point (b) above, this suggests that, assuming that the peripheral lattice has sufficient regularity, the most sensitive test for aliasing would involve stabilized or very brief monocular gratings in the periphery.

CONCLUSION

We have quantitatively analyzed the spatial quality of a primate foveal cone lattice. We find that it is a high quality hexagonal lattice with a correlation length of at least 130 photoreceptors over spans of tens of photoreceptors. We find that there is not sufficient disorder in the foveal lattice to prevent aliasing. Rather the photoreceptor lattice seems to be constructed with sufficient accuracy so that it can serve as the fundamental metric for spatial vision even in hyperacuity tasks. This suggests there is no need for any visual mechanism to measure the true photoreceptor positions and the burden of spatial calibration falls on the developmental processes involved in the formation of the photoreceptor lattice. The measurements reported here combined with our previous psychophysical results suggest a model of spatial vision in which the photoreceptor lattice is the sole geometrical element with all other elements being topological.

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*Byram (1944), Campbell and Green (1965), and recently Williams (1983 personal communication) have reported that high contrast spatial frequency gratings above the Nyquist frequency appear "wavy", "splotchy", or "scintillating" and change their shape and position. These visual effects are probably due to aliasing under very special conditions and on a lattice which is curved, imperfect, and non-stationary.

†The one dimensional analysis of aliasing shows that aliasing will be avoided if the spatial frequency content of an image is restricted to the interval along the spatial frequency axis between $-1/2d$ and $1/2d$, where d is the spacing of the sample points. The Nyquist limits, the frequencies at which aliasing sets in, are the end points of this interval, $\pm 1/2d$. In two dimensions spatial frequencies are vectors, not scalars. The corresponding result is that aliasing will be avoided if the 2-dimensional spatial frequency content is restricted to a polygon around the origin in the spatial frequency plane. This polygon is a square for a square lattice and a hexagon for a hexagonal lattice with the perpendicular distance from the origin to the sides being $1/2d$ and $1/\sqrt{3}d$ for the square and hexagonal lattices respectively. The Nyquist limit is the boundary of the polygon, and the magnitude of the Nyquist frequency depends on orientation. We also note that aliasing in two dimensions introduces simultaneous ambiguities into both the magnitude and orientation of an undersampled grating, since two-dimensional aliasing involves subtracting spatial frequency vectors, not magnitudes. (See Goodman, 1968, for a discussion of sampling in two dimensions).

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