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RESEARCH NOTE

IMAGE SAMPLING PROPERTIES OF PHOTORECEPTORS: A REPLY TO MILLER AND BERNARD

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Abstract—Miller and Bernard argue that photoreceptor sampling occurs at the inner rather than outer segments. Foveal inner segments form a lattice-like array that should create visible Moiré patterns when frequencies above 60 c/deg are image by interferometry. Despite a checkered past, this prediction is confirmed by recent experiments. Extrafoveally, frequencies above the nominal Nyquist limits of the cones are routinely present in the retinal image. Spectral analysis shows that the inner segments there form optimally irregular sampling arrays that avoid Moiré distortion by scattering supra-Nyquist frequencies into broadband noise. Thus it appears that topological disorder in the receptor mosaic prevents aliasing outside the fovea—the only place it could occur in normal vision.

Photoreceptors   Image sampling

Miller and Bernard (1984) argue on optical grounds that the effects of retinal image sampling by photoreceptors should be analysed in terms of inner segment size and spacing instead of the corresponding outer segment parameters used by Yellott (1982). I find their argument persuasive. This note explains its impact on the analysis offered in my 1982 paper and outlines my current understanding of the aliasing problem.

Yellott (1982) dealt with two puzzles: (1) the fact that normal extrafoveal vision is not plagued by Moiré distortion despite a large mismatch between retinal image spatial bandwidth and the nominal Nyquist limits implied by extrafoveal cone density; and (2) the fact that apart from Byram (1944), studies of foveal acuity for interference fringes have generally reported limits on the order of 60 c/deg (LeGrand, 1937; O'Brien, 1951; Westheimer, 1960; Campbell and Green, 1965). If the foveal cones form a spatially regular sampling array one would expect much higher limits, because frequencies above 60 c/deg should alias back to detectable lower frequencies.

Since outer segment diameters are too small to support an explanation of either puzzle in terms of contrast reduction due to integration over receptor apertures, I sought solutions based on topological disorder in the receptor mosaic. Spectral analysis of a section of human foveal outer segments indicated an optimally disorderly sampling scheme, whereby spatial frequencies above the nominal 60 c/deg Nyquist limit implied by foveal cone density would be scattered into broadband noise, instead of aliasing back to specific low frequencies, while frequencies below that limit would largely escape masking by sampling noise. This result seemed to explain puzzle (2).

It also offered a potential explanation of puzzle (1), but no spectral analysis of extrafoveal receptor arrays had been made at that time. Now such an analysis has been made for sections of rhesus cones ranging from the parafovea to the far periphery (Yellott, 1983). The results indicate that throughout the extrafoveal retina the cones form optimally random sampling arrays that avoid aliasing by scattering spectral energy from supra-Nyquist frequencies into broadband noise. The signature of this sampling scheme is a "desert island" power spectrum consisting of a spike at the origin surrounded by a circular noise-free island whose radius is always twice the nominal Nyquist frequency implied by local cone density. The sections used in that analysis allow one to visualize the spatial arrangement of both outer and inner segments, and the degree of spatial disorder is the same for both. Extrafoveal inner segment diameters are too small to prevent aliasing by integration over the receptor aperture: e.g. in the parafovea, where the nominal Nyquist frequency is 15 c/deg, inner segment dimensions (diameter approximately 1.2 min visual angle) imply that a 30 c/deg grating retains 60% of its original contrast. Thus regardless of whether image sampling effectively occurs at the inner or outer segment level, it appears that spectral scattering by an irregular sampling array is the major factor that prevents aliasing outside the central fovea. In other words, one can accept Miller and Bernard's argument and still conclude that topological disorder provides a solution to puzzle (1).

Puzzle (2) now appears in quite a different light. Here Miller and Bernard's argument implies not only increased high frequency attenuation due to integration over a larger receptor aperture, but also—and far more critically—a dramatic increase in the spatial regularity of the effective sampling array. Miller's (1979) striking photomicrograph of *M. irus* foveal inner segments, and comparable sections from *M. mulatta* published by Borwein *et al.* (1980), clearly show that in the center of the primate fovea the inner segments approximate a perfect hexagonal lattice. Miller and Bernard's analysis shows that integration over inner segment apertures still leaves substantial post-sampling contrast for spatial frequencies in the range 60–150 c/deg. It follows that there should be substantial aliasing of spatial frequencies at least an octave beyond the 60 cycle Nyquist limit of the foveal cones, and it seems inevitable that this aliasing should be visible when the optics of the eye are bypassed by interferometry.

That prediction is not supported by the literature on interference fringe acuity. Of the studies cited above, only Byram (1944) explicitly reported detection of spatial contrast in interference fringes at frequencies well above 60 c/deg. He saw "curved and broken lines" up to 150 c/deg. Westheimer (1960), also using pre-laser methods, explicitly contradicted Byram: his observers saw fine lines "which disappeared into the background as spatial frequency was increased beyond the threshold" (around 52 c/deg). Campbell and Green (1965), using laser interferometry, reported curious qualitative effects (scintillation, brightness enhancement, desaturation) at very high frequencies, which they characterized as well described by Byram, but reported spatial contrast sensitivity functions vanishing around 60 c/deg. Legrand (1937, 1957) and O'Brien (1951) also reported interference fringe acuity limits on the order of 60 c/deg.

This conflict with the bulk of the psychophysical literature would seem to argue against Miller and Bernard's hypothesis. However, Williams (1983) has recently begun a study of high frequency contrast sensitivity using a refined interferometer that eliminates laser speckle. His preliminary results agree well with Byram's. In particular, he can detect frequencies up to at least 130 c/deg in the central 20 min of the fovea, and their appearance seems consistent with aliasing by a sampling array having the degree of spatial regularity displayed by Miller's section of Macaque inner segments. This result provides critical evidence that Miller and Bernard's waveguide arguments are valid *in vivo*. If receptor sampling took place at the outer segments, as assumed in Yellott (1982), frequencies above 60 c/deg might well be discriminable from uniform fields, but because of the spatial disorder of the outer segments their appearance should be that of broadband noise rather than periodic Moiré patterns.

Thus the solution to puzzle (2) now appears to be a matter of psychophysical methodology rather than retinal anatomy—the bulk of the literature notwithstanding, it seems that spatial frequencies above 60 c/deg are visible in the form of their low frequency aliases when they are artificially imaged on the fovea by interferometry.

Altogether then, it seems one can now give a sensible account of the design principles underlying cone geography throughout the primate retina. In normal vision the retinal image is optically band-limited to 60 c/deg, which is also the nominal Nyquist limit implied by the density of the centermost cones. Since these cones are optically protected from aliasing they can afford to form a regular close-packed lattice, and so they do at the level of their inner segments. This has two advantages: it allows noise-free image reconstruction via Shannon's sampling theorem, and it maximizes quantum catch. Outside the foveola, cone density must fall off to make room for rods. But retinal image bandwidth cannot decrease so quickly, because it is determined by fixed optical components. Consequently photopic vision outside the foveola would necessarily suffer from aliasing if the cones remained regularly arranged. So they don't: instead they assume an optimally irregular arrangement that avoids Moiré distortion of high frequencies and minimizes sampling noise for low frequencies—an arrangement whose spectral signature is a desert island power spectrum. (The transition from foveolar regularity to parafoveal disorder is nicely illustrated by Fig. 16 in Borwein *et al.*, 1980, which shows tangential sections of inner segments across the fovea for both *M. irus* and *M. maccaca*.) Of course there is some irony in the fact that this spectrum was first observed in a place where it now appears to be visually irrelevant, i.e. in an analysis of foveolar outer segments.

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