Why is the retina capable of resolving finer detail than the eye's optical and neural systems?

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Abstract—It is established that the resolving power of the eye accords with that predicted by diffraction theory. Campbell and Green (J. Physiol. 181, 576–593, 1965) and Campbell and Gubisch (J. Physiol. 186, 558–578, 1966) demonstrated that the eye exhibits nearly diffraction-limited performance at 2 mm pupil diameter, resolving up to approximately 60 cyc deg⁻¹. However, Williams (Vision Res. 25, 195–205, 1985) has demonstrated that foveal receptors can respond at up to 200 cyc deg⁻¹, in agreement with measured receptor separation (Hirsch and Curcio, Vision Res. 29, 1095–1101, 1989). The obvious question is: why is there such an apparent mismatch between the eye’s optics and receptors? It is shown that the change in optical energy distribution corresponding to 1 just noticeable difference of defocus has the form of a difference of Gaussians, for which the contrast sensitivity function peaks at 16 cyc deg⁻¹, with a bandwidth from 0 to approximately 70 cyc deg⁻¹. The reason for the even higher-density packing of receptors, in the fovea, appears to be the need to allow the different colour-response cones to be spatially inhomogeneous without excessive aliasing. Prompted by this analysis, some data of Williams (1985) are re-examined, leading to a mapping of the averaged aperture-sensitivity of foveal cones, and demonstrating the reason for the diffuse cutoff of the postulated defocus channel.

1. INTRODUCTION

There has been a recent resurgence of interest in the way in which the retina samples the image formed by the optical system of the eye. Following the results of Byram (1944), and Campbell and Green (1965), using interference fringes formed directly on the retina, it was established that the eye optics are diffraction limited at 2 mm pupil aperture, and that the retina is potentially capable of resolving much finer detail than the optics can provide. Williams (1985) described, in considerable detail, the appearance of Moiré patterns generated by beating interferometrically generated gratings against the receptor mosaic, which has the (local) form of an hexagonal close-packed array (Hirsch and Curcio, 1989). Such patterns were liminally visible to two of his observers at up to 200 cyc deg⁻¹, which is more than three times the normal optical resolution limit. As the title of this paper suggests, the primary aim is to discover why the retinal receptor array appears to oversample the optical image by such a large margin.

Various suggestions have been advanced to explain the discrepancy, which implies some redundancy in the neural pathways. For instance, Yellott (1982) suggested that the foveal cones might be sampled irregularly in order to prevent aliasing. Miller and Bernard (1983) advanced an alternative argument, that foveal aliasing up to 150 cyc deg⁻¹ is attenuated by averaging over the cone aperture, which argument was later accepted by Yellott (1984). He pointed out that spatial frequency analysis
of the cone inner segment arrays demonstrated irregular sampling that scatters aliasing effects into broadband noise. An analysis by Bossomaier et al. (1985) examined other possible effects of irregular sampling by identical cones, and concluded that regularity was demanded by the high-accuracy positional information required during tracking in predatory attack. The effect, on aliasing, of having two and three different types of foveal cone has recently been explored by Williams et al. (1990). That approach, which has been extended here, demonstrates why the retinal mosaic is apparently denser than it need be.

The next aim of this paper is to record a novel, indirect method for determining the contrast sensitivity of a postulated neural focus-monitoring channel, and to compare the relative contributions of the neural and optical contributions to the overall point spread function (PSF). The method used differs from that of Blommaert et al. (1987), and proceeds by linking optical PSF variation to visual discrimination. The data to be used in this paper were obtained in the course of some experiments which unequivocally related wavefront aberration (i.e. the deviation from the ideal spherical form of light emerging from the eye lens) to discrimination ability by means of an optical quality metric known as the Strehl ratio, at least for good quality imagery (Burton and Haig, 1984, Haig and Burton, 1987). This ratio, the principle of which was first enunciated by Strehl (1895), is defined as the ratio of the peak intensity of the measured (aberrated) PSF, to the equivalent unaberrated PSF. This is now a simple measurement to make, and easy to compute, which makes it an extremely useful metric for the testing and prediction of eye/instrument performance. The new interpretation placed on these data reveal the form of a spatial frequency bandpass characteristic curve, which cuts off between 60 and 70 cyc deg⁻¹, and which could provide a means of mediating focus control. The diffuse termination of the cutoff frequency, discovered by the new method, suggested a different form for the individual cone aperture sensitivity function. A fresh examination of some data published by Williams (1985), while demonstrating foveal aliasing, then leads directly to a new mapping of the cone aperture sensitivity, which reveals a smooth termination at the receptor boundary.

2. THE RESOLUTION LIMIT

Miller and Bernard (1983) were able to show that spatial frequencies above approximately 60 cyc deg⁻¹ are visible only as their equivalent low-frequency aliases. This frequency is just less than the Nyquist limit imposed by the centre-to-centre spacing of the cones in the central fovea, as verified by Hirsch and Curcio (1989) using a human retina, which appeared to display a good approximation to the ideal hexagonal close-packed array, having a cone spacing of 0.0087 deg. Hirsch and Curcio were unable to explain the lack of correspondence between cone spacing and resolution acuity in the foveal centre. Their rationale for the mismatch was that the optical image at the foveal centre was somehow poorer than it should be, or that there is some inefficiency in the neural processing. It has already been pointed out (Bossomaier et al., 1985) that significant sampling irregularity is unlikely, on the basis that it seriously increases the chances of interpolation error.

One possible reason why the optical resolution appears not to match the neural resolution is that there exist three different types of cone, having different chromatic sensitivities. If each type of cone is taken in isolation, the closest separation of any two