

methods state that for each spatial frequency tested "a threshold was obtained only when the percentage of correct responses extended from 50% to ~90% or more" to allow a psychometric function to be drawn. This suggests the falcon did not respond to criteria for stationary frequency above ~25 cycles-deg⁻¹, so perhaps 25 cycles deg⁻¹ is the appropriate cutoff frequency for the falcon, rather than the extrapolated value. In view of this ambiguity, it is unfortunate that the method of extrapolation was not stated. Irrespective of uncertainty regarding the actual cutoff frequency, it is unnecessary to invoke foveal image magnification to explain falcon acuity because even the higher extrapolated value is below the bird's anatomical cutoff frequency.

This particular falcon, the American kestrel, typically hunts in bright daylight conditions in luminances of $\geq 2,000$ cd m⁻². A simple explanation for the falcon acuity of 40 cycles deg⁻¹, rather than 46 cycles deg⁻¹, when tested at 40 cd m⁻², is that performance was luminance-limited³. The appropriate test of the magnification theory of the fovea is to measure spatial acuity under optimum luminance levels and to compare this behavioural cutoff frequency with that set by the anatomical constraints acting on the bird's eye.

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2. Snyder, A. & Miller, W. *Nature* **275**, 127-129 (1978).
3. Raymond, L. & Wolfe, J. *Vision Res.* **21**, 263-271 (1981).

HIRSCH REPLIES—Dvorak *et al.* assert that since the observed cutoff frequency for the kestrel of 40 cycles deg⁻¹ is less than the 46 cycles deg⁻¹ expected from retinal anatomy, foveal magnification is not necessary. Their argument is flawed because they fail to consider accurately the extent to which low illumination limits kestrel vision.

In my study, human and kestrel cutoff frequencies were found to be nearly identical at moderate levels of photopic illumination, that is, an average of 40 cd m⁻² (ref. 1). This observation is remarkable considering that the kestrel eye is only half the size of the human eye. It has been suggested that two anatomical/optical features of the kestrel eye account for this level of performance: the reduced centre-to-centre spacing of photoreceptors² and the foveal pit which has been hypothesized to serve as an image magnifier³.

The highest cutoff frequency, ν , observed for human at high levels of illumina-

tion is 57-60 cycles deg⁻¹ (refs 4, 5) and is predicted by focal length, F (≈ 17 mm), and centre-to-centre spacing of foveal photoreceptors, d_{cc} (≈ 3 μ m)²:

$$\nu = \frac{F}{d_{cc}\sqrt{3} \times 57.3} \times m$$

However, the observed cutoff for the human observers in this study was only ≈ 40 cycles deg⁻¹ as expected due to the moderate level of illumination^{6,7}. Therefore, the limitation of human cutoff frequency due to illumination was 40/60 or ≈ 0.66 .

Kestrel acuity has been reported to fall off 2.4 times faster than human for levels of illumination below 350 cd m⁻² (ref. 8). The optimal cutoff frequency for kestrel estimated from the above equation (where $F = 9.1$ mm and $d_{cc} = 2$ μ m) is 46 cycles deg⁻¹. Making the conservative assumption that the illuminance limiting factor for the kestrel is the same as for human, the expected cutoff frequency for the kestrel in this experiment is ≈ 0.66 (46 cycles deg⁻¹) or ≈ 30 cycles deg⁻¹; using the kestrel data cited above the expected cutoff is between 28.5 and 29 cycles deg⁻¹. Hence, I propose that foveal magnification boosts the expected cutoff frequency of ≈ 30 cycles deg⁻¹ or less for the moderate level of illumination in this experiment to the observed value of 40 cycles deg⁻¹.

In addition, Dvorak, Mark and Raymond complain that the final data point for the stationary condition in my study was 25 cycles deg⁻¹ and suggest that 'perhaps 25 cycles deg⁻¹ is the appropriate cutoff frequency'. However, as the two functions (stationary and phase changing gratings) merge above 10 cycles deg⁻¹, thresholds were not determined more than once above 25 cycles deg⁻¹. Data points were simply connected with a smooth line and the final observation was at 40 cycles deg⁻¹. Therefore, the 40 cycles deg⁻¹ cutoff frequency is an observed and not an 'interpolated' value.

Their argument for no foveal magnification requires that the observed cutoff frequency of 40 cycles deg⁻¹ was only marginally luminance-limited and, therefore, that 40 cd m⁻² is a nearly optimal level of illumination for the kestrel. As pointed out above, this assumption is not consistent with previous data for either human or kestrel or with previous arguments by Raymond and Wolfe⁹ to account for the very poor visual performance observed for the eagle at an average illumination of 20 cd m⁻².

To summarize, in what is the first published avian MTF study (which characterizes performance of the complete visual system), I reported the surprising finding that the kestrel's spatial frequency cutoff is the same as that of the human for moderate photopic illuminances and pointed out that this finding may be explained by the kestrel's higher receptor packing

density and a magnification factor¹. Dvorak *et al.* contend that the magnification factor is not necessary to explain the data but their argument is only valid, all other things being equal, if the kestrel's fall-off in acuity due to low illumination is much less rapid than that of the human, which seems unlikely. The best available anatomical data of focal length and receptor density alone cannot account for the remarkable visual acuity of birds of prey. Therefore, the magnification factor remains plausible, even though its existence has yet to be confirmed experimentally for birds of prey as it has been for other species¹⁰. Thus, the proposed optical magnification function of the deep fovea³ remains the most likely explanation for the exceptional visual acuity of birds.

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Carbon geodynamic cycle

AN estimate has recently been presented of the rate of exchange of carbon dioxide between the mantle of the Earth and the atmosphere and ocean¹. Basing their argument principally on the concentrations of the stable isotopes of carbon in mid-ocean ridge basalts, Javoy *et al.* arrive at a best estimate of the flux of carbon dioxide from the mantle to the ocean equivalent to 3.9×10^{14} g C yr⁻¹. They suggest that subduction of carbonate sediments carries an equivalent flux of carbon back into the mantle.

This estimate is almost certainly too large, probably by a substantial factor. Carbon is removed from the fluid phase (ocean and atmosphere) and restored to the solid phase (sea floor sediments) principally by reaction with dissolved calcium and magnesium ions to form carbonate minerals. An estimated 13×10^{14} g Ca²⁺ yr⁻¹ or 7.8×10^{14} g Mg²⁺ yr⁻¹ would be needed to neutralize the proposed carbon dioxide flux of 3.9×10^{14} g C yr⁻¹, but rivers carry to the ocean only an estimated 5×10^{14} g Ca²⁺ yr⁻¹ and 1.4×10^{14} g Mg²⁺ yr⁻¹ (ref. 2). Much of this river-borne flux of calcium and magnesium ions is derived from the weather-