

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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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-

ing of carbonate minerals³, and so does not contribute to the neutralization of carbon dioxide released from the mantle. Interaction between seawater and sea floor basalts releases a maximum flux of 2×10^{14} g Ca^{2+} yr^{-1} (refs 4, 5) and leads to a net consumption of magnesium ions. So large a flux of carbon dioxide from the mantle to the ocean would therefore imply a geologically rapid accumulation of carbon dioxide in the atmosphere and ocean.

Carbon can be removed from the fluid phase and restored to the solid phase also by the incorporation of reduced organic carbon in sediments. This process is estimated to occur at a rate of 1.2×10^{14} g C yr^{-1} (refs 3, 6), but this flux must be largely cancelled by the rate of oxidation of old organic carbon in sedimentary rocks in order to conserve the oxygen content of the atmosphere.

There are $\sim 4 \times 10^{19}$ g C in the atmosphere and ocean combined³. An unbalanced flux of carbon dioxide from the mantle to the ocean of the magnitude suggested by Javoy *et al.* would therefore lead to a doubling of the carbon content of ocean and atmosphere in a time of only a few hundred thousand years.

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JAVOY *ET AL.* REPLY—We thank Walker for his comments which are very relevant to our article. If one wants to recycle carbon into the mantle through the sediments one has to find carriers which actually belong to the sediments and calcium carbonate is the most obvious, together with organic matter. These are the only recycled species that we have considered in our sedimentary carbon budget. However, we do not think that the values presented by Walker seriously put into question our evaluations for three reasons.

First, any evaluation of geochemical flux is subject to relatively large uncertainties as is the case for our estimates of the mantle carbon flux from the mid-ocean rises ($0.58\text{--}7.2 \times 10^{14}$ g yr^{-1}) and sedimentary carbon flux to the mantle ($2.8\text{--}5.6 \times 10^{14}$ g yr^{-1}). This is also true for Ca^{2+} and Mg^{2+} fluxes from continents or from ocean floor hydrothermalism for which the values given by Walker from his refs 2–5 are true within a factor of 2, but any better precision is doubtful.

However, we shall deal with the values as given and only correct our results because of a remark by Francheteau, who brought to our attention the calculations of Parsons¹: the lithospheric surface created and destroyed is $3 \text{ km}^2 \text{ yr}^{-1}$ and not $4.8 \text{ km}^2 \text{ yr}^{-1}$ as we stated. Hence our results have to be divided by 1.6, giving a mean estimate of 2.44×10^{14} g yr^{-1} for the mantle carbon flux in both directions.

Second, the most important comment to make is that we cannot distinguish between the different carbon sources in the calcium carbonate present in marine sediments: we only know that a certain flux of Ca^{2+} and Mg^{2+} is carried to the oceans from continents and hydrothermal circulations. Taking the estimates given by Walker for calcium alone (7×10^{14} g yr^{-1}) we see that this can recycle 2.1×10^{14} g yr^{-1} of carbon to the sediments. With the addition of sedimentary organic carbon in the proportions given in our paper (one-third of the total sedimentary carbon) we get 3.15×10^{14} g yr^{-1} . In a steady-state model, this recycled carbon comes from the only possible important source external to the exogenous cycle, that is, the upper mantle carbon flux (2.44×10^{14} g yr^{-1}). These two values agree within reasonable limits. The first one is greater, which, in a steady-state model, implies that mantle contributions from sources other than mid-ocean ridges is 7×10^{13} g yr^{-1} .

This type of calculation is similar to those carried out by Craig² and Wickmann³ in their evaluation of the $^{13}\text{C}/^{12}\text{C}$ ratio of mantle carbon, except that they did not calculate the fluxes or postulate recycling into the mantle.

Systematics of basidiomycetes based on 5S rRNA sequences and other data

WALKER and Doolittle¹ have recently suggested a fundamental redivision of the basidiomycetes on the basis of 5S rRNA sequences. They also suggested that certain morphological characteristics “are probably of independent origins” and that there are “contradictory combinations of traits involving reproductive structures and spore germination that traditionally separate the homobasidiomycetes and heterobasidiomycetes”. I intend here to provide support for the basic division they propose, but also to show that there need be no contradictory combinations of traits or traits with independent origins in the basidiomycetes.

I have recently developed algorithms for reconstructing phylogenies from restriction site² or sequence³ data and, more important, for testing alternative phylogenetic hypotheses against one another. For sequence data, a maximum parsimony network is constructed for

Finally, it is worth pointing out that some of the carbon flux from the ridges may be incorporated directly into the mantle oceanic lithosphere, which, in our terminology, belongs to the external cycle.

We believe that continents and sea floor basalts provide enough calcium for the recycling of carbon fluxes into the mantle up to the levels we postulated in our model of the carbon geodynamic cycle. However, we thank Walker for forcing us to explain how our recycling could work.

We should like to take this opportunity to correct three other errors pointed out by Francheteau, whom we thank.

- (1) In ref. 22, read La Jolla and not Paris.
- (2) In ref. 23, read Washington and not Paris.
- (3) Uyeda and Kanamori (ref. 24) speak only of extension and compression but never of strong and weaker distension.

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each variable site assuming a particular phylogeny is true, and then the procedure is repeated for an alternative phylogeny. The difference in the number of mutational events for this particular nucleotide site under the two phylogenies is then used as a score. A similar score is generated for each variable nucleotide in the data set and the resulting scores are used in a Wilcoxon matched-pair signed-rank test.

Figure 1 shows the eight species studied by Walker and Doolittle along with some of their relevant taxonomic and morphological features. Walker and Doolittle concluded that the fundamental split in this group corresponds to the clusters identified on the basis of septal pore type, as indicated in Fig. 1. I tested the significance of this fundamental division and obtained a signed-rank sum of -46 versus the most likely alternative with a sample of 45 non-zero scores. This value is so low it is not listed in the standard tables⁴. Consequently, the rRNA sequence data strongly support the division suggested by Walker and Doolittle.