has been observed (14). Cells of Chlorella vulgaris, however, require much longer periods of sonication to be ruptured, and the released cell walls are quite resistant to further disintegration. Thus Chlamydomonas walls are more susceptible to mechanical rupture than Chlorella walls are, though the thickness of their walls is nearly the same [21 nm for Chlorella (15) compared to 19 nm for C. reinhardtii (16)]. This weakness of the wall may be correlated with the fact that Chlamydomonas maintains its osmotic balance via energy-expending contractile vacuoles, rather than via wall pressure as in more advanced plant types. Although the weak walls of Chlamydomonas appear to lack cellulose (16), this does not mean that the absence of cellulose is the cause of the weak wall. Coenocytic algae such as Codium (17) also lack both cellulose and contractile vacuoles but possess relatively rigid walls that contain hydroxyproline (12). Therefore it seems possible that the changeover from hydroxyproline heterooligosaccharides to homooligosaccharides marks a fundamental evolutionary transition from wall organization which was mechanically weak to a wall organized in such a way (a highly cross-linked covalent network) as to provide sufficient tensile strength to balance internal and external osmotic pressures. Experimental proof of this hypothesis awaits further study.

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- 8. It is possible that hydroxyproline glycosides other than those listed are present in small amounts, as trace amounts of xylose and mannose were present when glycosides A, B, and C were hydrolyzed. However, these trace amounts cannot be considered constituents of the listed glycosides for they are always present in less than 1/5 molar equivalent to 1 molar equivalent of hydroxyproline.
- 9. The elution positions of Hyp-Ara, and Hyp-Ara4 are within the same range that peaks

Hyp D to Hyp G occupy. The presence of trace quantities of $Hyp-Ara_3$ and $Hyp-Ara_4$ might account for the somewhat higher than expected yields of arabinose in peaks Hyp D to Hyp G. There can be only trace amounts of Hyp-Ara₃₋₄, however, because subst quantities of them would lower the Gal however, because substantial Hvp molar ratios and any large amount of Hyp-Ara₄ would appear as Hyp-Ara₃ in the mixture of Hyp glycosides released from Hyp D and E. Such a glycoside was not released in any detectable amount.

10. Mild acid hydrolysis of glycosides B to G released these Hyp glycosides. Quantitative analysis of each glycoside indicates a tentasequence for each oligosaccharide; the present data do not exclude a branched structure. In a few cases, where no sugar is indicated, trace amounts (less than 5 percent of the total sugar present) appeared on paper chromatograms. These traces probably arose from sugars actually present and undergoing epimerization as a result of the acidic conditions. Glycosides are listed in the order they eluted from the column, from largest to smallest. The percentages of total hydroxyproline give an indication of the relative lability of the terminal glycoside bond to acid hydrolvsis

- 11. The theoretical molar ratios of this glycoside can only be tentative because the glycoside eluted with the void volume of the column, and this fraction may contain free sugars released during alkaline hydrolysis. Hence released during alkaline hydrolysis. Hence the exact sugar content is not yet known, but the elution position of this glycoside on a Sephadex G-25 column indicates a molecular weight consistent with this empirical
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An Eagle's Eye: Quality of the Retinal Image

Abstract. The optical quality of a living eagle's eye was determined by an ophthalmoscopic method. The performance of the eye was substantially better than that reported for humans, but did not confirm some of the wilder claims made for such birds.

Although man has assigned to himself the highest niche in the order of evolution, many lower forms may surpass human abilities in certain aspects of sensory performance. For instance, almost any lower vertebrate is thought to have a keener sense of smell, bats and dogs to be sensitive to a wider range of auditory frequencies, cats and owls to have better visual performance under low levels of illumination, and hawks and eagles to possess keener vision. The last of these assertions is supported largely by anecdotal evidence, and by microscopic examination of bird retinas. Rochon-Duvigneaud estimated that the density of cones in the central fovea of the hawk reaches 1 million per square millimeter. (1), which may be compared with perhaps 147,000 per square millimeter in the center of the human fovea (2). Both Rochon-Duvigneaud and Polyak surmised that the visual acuity of the birds of prey surpassed that of man, but they did not offer quantitative estimates (1, 3-6). However, Walls (7) states that in the central fovea an eagle could reach acuities eight times that of man!

Walls's claim is undoubtedly exaggerated-the human visual system becomes diffraction limited and reaches its maximum performance at a pupil diameter of 2.3 to 2.4 mm (8, 9). The cutoff frequency of a perfect optical

system is directly proportional to the diameter of its entrance pupil. A bird would therefore require a pupil at least 18.4 mm in diameter to be theoretically capable of fulfilling Walls's expectations, a dimension which is beyond the capability of even the largest birds of prey (3-5, 10).

The size and organization of the eagle eye does suggest that its resolving power is extremely high, but the retinal mo-



Fig. 1. Three selected linespreads measured external to the eagle's eve. Except for small errors introduced by source and slit width differences, these waveforms may be compared directly to the external linespreads obtained for the human eye by Campbell and Gubisch (8).

SCIENCE, VOL. 176

920

saic is only one element of the visual system. Lacking is information on behavioral performance and on the properties of the image. Below I report an attempt to measure the quality of the retinal image formed by an eagle's visual optics.

The methodology was that of Campbell and Gubisch (8) with minor modifications. A straight wire tungsten lamp (G.E. No. 1872) was 1 m from the eye, with its axis oriented vertically. At this distance it subtended 0.29 minute of arc horizontally and was masked to subtend 30 minutes vertically. The natural pupil was used, the lamp being viewed through an aperture 12 mm in diameter and a +1 diopter eye lens. The image formed on the retina becomes in turn a source which is reimaged exterior to the eye. By way of a pellicle beam splitter and a scanning mirror, this second image projected onto an analyzing slit 1 m from the eye which subtended 0.35 by 30 minutes of arc. The scanning mirror was pivoted about a vertical axis, and when driven electromechanically by a sawtooth waveform caused the external image to move across the analyzing slit. The scan covered 80 minutes of arc and was performed once every 2 seconds. The light entering the slit was detected by an EMI 9558B photomultiplier (S-20 photocathode) and was displayed continuously on a Brush Mark 280 rectilinear chart recorder. The resultant waveforms represent the linespread function of the subject eye degraded by a second passage through the optics, by the source and slit widths, and by scattered light. The source lamp was run at 6 volts d-c, which gave a color temperature of about 3000°K. Ignoring the spectral property of the eagle's fundal reflection, the product of the source and photocathode gives a spectral response curve with 95 percent of its area between 400 and 760 nm and a broad peak at 600 nm.

The subject, obtained on rental from a local pet store, was identified as an African Serpent Eagle, *Dryotriorchis spectabilis*, a medium-sized eagle with large head and eyes (11). The bird weighed 1.33 kg and was in vigorous good health, although it had sustained some superficial injuries and feather loss in capture and transit. The eagle was gently wrapped in a large towel, and once properly restrained, it remained relaxed during the procedure. Measurements were made by simply holding the animal up to the eyepiece



Fig. 2. Spatial contrast transfer functions for the visual optics of the eagle, computed from the corresponding external linespread functions in Fig. 1. Relative contrast transmission is plotted against spatial frequency in cycles per degree. The dashed line is the performance of a diffraction-limited system in 600-nm light with a round entrance pupil 6 mm in diameter (13). The thin solid line is redrawn from Campbell and Gubisch (8) to illustrate the best human performance (2.4-mm pupil diameter). These curves indicate the amount by which an optical system attenuates the contrast of a sinusoidal grating at different spatial frequencies. High frequencies correspond to fine gratings, and low frequencies to coarse gratings. The better the performance, the less the system attenuates in the frequency range of interest, or the higher is its contrast transfer. The point at which the transfer becomes zero is termed the cutoff frequency; the higher the cutoff, the better the resolution of an optical system.

for about 5 minutes at a time and letting it look in with one eye. The pupil was observed visually to insure that it remained within the limits of the viewing aperture. Since the apparatus is an autocollimator, small lateral and rotational movements of the eye were canceled out. The hope was that given enough time, a near-optimal combination of fixation and accommodation would occur. Because artifacts and deviations from optimum serve only to broaden the measured linespread, and because the natural pupil was not necessarily at the optimal diameter, such a sampling method will give a conservative estimate of maximum performance.

The diameter of the subject's entrance pupil was determined under recording conditions by replacing the scanning mirror with a 35-mm camera. Kodak 2485 film and MX 642-1 developer were used to photograph the pupil by the light which would ordinarily go to the analyzing slit. To avoid error from light scatter in the emulsion, the resulting image was compared with white disks of different diameters placed at the eyepiece and photographed to the same density. In ten consecutive photographs the pupil diameter varied between 6 and 6.5 mm. Wider variations during recording cannot, of course, be excluded.

The hundreds of linespread functions obtained were sorted by visual inspection, first for symmetry (an indication that nothing changed during the scan), and then for "narrowness." The three narrowest functions are reproduced in Fig. 1. Such a selection procedure is justified because the method used can only approach the best performance of the eye but cannot exceed it. The variations in area under the curves in Fig. 1 probably result from pupil changes or differences in local reflectivity of the retina. All of the best curves were obtained during the first day of experimentation. On the second day the eagle began to defocus, apparently to avoid the very bright light against a dark background, which is perhaps as aversive to birds as it is to humans. By the end of the second day records were coming out practically flat, precluding further observations.

The three selected linespread functions were digitalized with an optical comparator. The corresponding contrast transfer functions T(u) for retinal imagery were then calculated with corrections for source and slit width. Briefly, the procedure involves taking the source, slit, and external linespread functions f(x), g(x), and h(x), respectively, performing the calculation

$$T(u) = \left(\frac{H(u)}{F(u) \cdot G(u)}\right)^{\frac{1}{2}}$$

and normalizing T(0) = 1, where F(u), G(u), and H(u) are the Fourier transforms of f(x), g(x), and h(x). For a justification of this calculation, see (8). Computation was done on a Digital PDP-8, the program first having been tested on waveforms with known Fourier transforms to exclude possible artifacts.

The results are shown in Fig. 2, where A, B, and C are the contrast transfer functions for retinal imagery corresponding to the three external linespread functions in Fig. 1. The shapes of the calculated functions suggest a system with a small amount of spherical aberration at different focal settings (12). The dashed line is the performance of an aberration-free system with a round, 6-mm aperture, incoherently illuminated, in 600-nm light (13). The thin solid line, redrawn from Campbell and Gubisch (8), represents the best performance of human visual optics

with a pupil 2.4 mm in diameter. All three avian functions are substantially superior to estimates of maximum human performance (8, 14). When measured by identical methods, human optics at best cut off at approximately 60 cycle/deg (8); the eagle cutoff at 120 cycle/deg (Fig. 2) is twice the human value and may yet improve at smaller pupil diameters.

How superhuman might an eagle's visual acuity be? From published sections of heads of diurnal rapacious birds (5) I estimate the ratio of the width of the skull just posterior to the lateral canthus, to the axial length of the eyeball, to be 2:1. I have measured that skull width on four preserved specimens of Dryotriorchis spectabilis and obtained a mean of 48 mm, which corresponds to an eyeball length of about 24 mm. For the eye of a Golden Eagle 29 mm long, Rochon-Duvigneaud estimated a focal length of 19 mm (10). When this is scaled down, the African Serpent Eagle will have a focal length of 15.5 mm, compared to the human's 17 mm (15). The theoretical resolving power of the retinal mosaic is proportional to the square root of receptor density; from hawk data (1) the ratio to human (2) foveal resolution is then 2.6:1. After correction for optical magnification, this becomes approximately 2.4 : 1. It is impossible to characterize a transfer function by a single number, but on the basis of cutoff frequencies the eagle to human ratio is 2:1. It seems fair to conclude that the visual system of the eagle under test may be capable of from 2.0 to 2.4 times human resolution. On the basis of size the Golden Eagle Aquila chrysaetos might reach 2.4 to 2.9 times, and the Martial Eagle Spizaetus bellicosus, which is reported to have an eye 36 mm long (4), might reach 3.0 to 3.6 times human visual acuity.

In evaluating avian visual performance, certain other factors should be kept in mind. If examined in ordinary (probably tungsten) light, many diurnal birds are somewhat hyperopic (5, 16). When chromatic aberration is taken into account, this refraction will allow birds to accommodate to distant objects in blue light, something an emmetropic human eye cannot do (17). Avian ability to detect objects against the sky should therefore be enhanced. Secondly, the small size of eagle cones with respect to the wavelengths of visi-

ble light (1, 4-6) means that they are inefficient absorbers of radiant energy. Consequently, the photopic visual performance of eagles must fall off very rapidly as luminance decreases.

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 For incoherent monochromatic illumination
- the transfer function of a diffraction limited optical system having a circular aperture is given by:

$$T(u) = \frac{1}{\pi} \left[-\sin\left(2\cos^{-1}\frac{u\lambda}{d}\right) + 2\cos^{-1}\frac{u\lambda}{d} \right]$$

where u is spatial frequency in cycles per radian, λ is the wavelength of the light, and d is the diameter of the entrance pupil.

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Replamineform: A New Process for Preparing Porous Ceramic, Metal, and Polymer Prosthetic Materials

Abstract. The replamineform process (meaning replicated life forms) is a technique for duplicating the microstructure of carbonate skeletal components in ceramic, metal, or polymer materials. The special pore structures of marine invertebrate skeletal materials such as echinoid spines and corals, which are difficult or impossible to create artificially, can thus be copied in useful materials. Of immediate interest is the possibility of using these replicated microstructures in the fabrication of orthopedic prosthetic devices. By means of this technique, prosthetic materials having a controlled pore microstructure for optimum strength and tissue ingrowth may be obtained.

The replacement of damaged body tissue with foreign materials has been an appealing possibility. Sterilized animal bone is seemingly an obvious substitute for human bone, but its use as an implant has been abandoned because of problems with residual organic matter that elicits immunological reactions. Another possible means of repair of fractured bone or damaged joints is the fabrication of prosthetic implants from materials compatible with body tissue and having acceptable mechanical properties. Screws, pins, nails, and other items fashioned from highly polished metal alloys such as Vitallium, for example, have been widely used, but these implants often

cause inflammation and excessive development of fibrous tissue. Corrosion of metal and lack of long-term mechanical attachment are further disadvantages, although attempts to increase the degree of tissue attachment by sintering a layer of metal spheres to the outer surface of the Vitallium have been reported (1). Sintered titanium fiber composites have also been evaluated (2). Other potential prosthetic materials include phosphate bonded alumina (3), and porous ceramics (4). The difficulty in controlling pore size, and more important, the size of the interconnections between adjacent pores, has been a major limitation in the production of porous ceramics (4). We now describe