

## BEHAVIOURAL DETERMINATION OF THE CONTRAST SENSITIVITY FUNCTION OF THE EAGLE *AQUILA AUDAX*

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(Received 25 September 1979)

**Abstract**—The results of behavioural experiments determining contrast sensitivity functions (CSFs) for the eagle *Aquila audax* and man at two low luminances are compared. At 20 cd/m<sup>2</sup> the shapes of the CSFs are similar: both species show a peak in sensitivity with attenuation of higher and lower spatial frequencies. The human is more sensitive at all frequencies and up to one hundred times more sensitive at low frequencies. The relatively poor performance of the eagle under these conditions may result from its adaptation to achieve high resolution in conditions of high luminance and contrast. At 2 cd/m<sup>2</sup> the eagle no longer shows attenuation of low frequencies. This result is discussed with reference to lateral inhibition.

### INTRODUCTION

That falconiformes (eagles, falcons and hawks) can recognise small objects at large distances is so widely believed as a result of casual observations of their behaviour that it is incorporated into metaphor and legend in many cultures. This proposition is supported by examination of photoreceptor density in the fovea (Rothen-Duvigneaud, 1919; Polyak, 1941), ophthalmoscopic examination (Shlaer, 1972) and, most convincingly, by behavioural observations of a kestrel's ability to discern 100% contrast square-wave gratings (Fox *et al.*, 1976). These three observations indicate that, in optimum conditions, a falconiforme can discern a maximum spatial frequency about three times higher than can a human.

Apparently, survival in the natural habitat of the eagle has required it to adapt its visual system to achieve high spatial resolution. For this reason, they are important and interesting subjects in the study of vision. So far, however, only one aspect of their visual performance—their resolution limit—has been investigated. In this study we investigate the sensitivity to contrast of the Australian wedge-tail eagle *Aquila audax* (Fig. 1). Contrast sensitivity functions (CSFs—defined as the reciprocal of the threshold contrast required for the detection of a sine wave grating of a given spatial frequency) were determined at two low luminances† for the eagle and, for comparison, the same function of the human visual system was measured under the same conditions.

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† As the spectral sensitivity of the eagle's eye is unknown it may be argued that radiometric rather than photometric units of brightness are more appropriate. We chose the latter to allow comparison with the human performance.

### METHODS

#### Subjects

The eagle subject, LB, was taken from an eyrie at about 2 weeks of age and subsequently hand-reared in an open-air aviary. The bird was occasionally flown outside the aviary. He was approximately 18 months old when testing began.

The human subject, AC, was an unpaid volunteer who wore glasses to correct for optical astigmatism and refractive errors. She was 34 yr old when tested and had no previous experience as a psychophysical observer.

#### Apparatus

Stimulus patterns were stationary vertical sine-wave gratings of various spatial frequencies and contrasts. The gratings were generated on the screens of two Tektronix 604 monitors with green phosphors (P31—peak wavelength approximately 520 nm). Spatial frequency (i.e. the number of complete luminance distributions subtended in one visual degree) and contrast (i.e.  $\{I_{\max} - I_{\min}\} / \{I_{\max} + I_{\min}\}$  where  $I_{\max}$  and  $I_{\min}$  refer respectively to the brightest and dimmest parts of the intensity distribution) could be varied continuously and independently. The fidelity of the gratings was measured by sampling the output of the displays with a light meter and optical system (whose convolution width was smaller than the screen spot size) mounted on a differential micrometer stage. The deviation of the intensity function from the sinusoidal was always less than -11 db. For a fuller description see Reymond (1979).

Average luminance of both screens was kept constant for each experiment. Each screen was centred in a rectangular perspex frame, 25 × 22 cm illuminated

from behind with lamps. This light was filtered to nearly match the colour and luminance of the displays. The displays,  $12.7 \times 10$  cm, were viewed from a distance of 3 m and subtended a visual area of  $2.0 \times 1.8^\circ$ . The laboratory was illuminated by two strips of incandescent lights with an overall illumination slightly lower than that of the displays.

#### *Psychophysical method*

The task used to generate the contrast sensitivity functions was a forced-choice visual discrimination test. Subjects were required to choose between two simultaneously presented stimuli, the positive stimulus was a grating of various spatial frequencies and contrasts and the negative stimulus was a blank field of the same overall luminance as the grating. Stimuli were presented on the screens (C) shown in Fig. 2.

The psychophysical method used in both experiments was the same. This method was based on an up-down-transformed response method which allows for reliable stimulus estimates of various percentage points on a psychometric response curve (Wetherill and Levitt, 1965). The particular procedure adopted tracked the 71% positive probability contrast threshold for each spatial frequency tested. In practice, this was achieved by presenting each test grating once or twice: a correct response consisted of two consecutive positive scores and an incorrect response was a positive followed by a negative score or a single negative score. To test any spatial frequency ascending and descending staircases, each composed of ten contrasts, were used. Changes in steps of contrast ranged between 0.03 to 0.05 log units. Ascending and descending staircases for all spatial frequencies tested in each experiment were randomly interleaved to help eliminate subjective bias effects (Cornsweet, 1962). Each successive presented contrast of a particular spatial frequency depended on the subject's response to the preceding contrast for that frequency. For a descending staircase, when the response was correct, the subsequent presentation was a grating, the contrast of which had been reduced by a fixed amount. When the response was incorrect the next presentation was a grating the contrast of which had been increased by a fixed amount. Similarly, in an ascending staircase, after an incorrect response the next presentation showed a grating of higher contrast. If the response was correct the next presentation was a grating of lower contrast. In this way the presented contrasts for each spatial frequency approached the subject's threshold and then crossed and re-crossed this threshold. Every time the staircases changed direction an estimate of threshold was obtained. Testing for each spatial frequency continued until twelve measurements of threshold had been obtained. To reduce variability due to guessing and training effects, only the last eight measures were averaged to produce the threshold estimate.

Selection of spatial frequency, contrast and left/right position for each test grating were controlled by

a PDP 8/e computer, and the displays were manually adjusted by the experimenter.

#### *Determination of the contrast sensitivity functions at 20 cm/m<sup>2</sup>*

CSFs for the eagle and human subjects were determined at an average luminance of 20 cd/m<sup>2</sup>. Contrast sensitivities of eight different spatial frequencies, i.e. 3.5, 5.0, 7.5, 10, 15, 20, 25 and 30 cycles per visual degree (c/deg) were estimated using the psychophysical method described above.

Before each daily test session (60–80 min), subjects were dark adapted for 10 min. Only natural pupils were used and head and eye movements were not restricted in any way. LB stood on a long perch to view the stimuli while AC was comfortably seated in a chair. Response time was not limited.

#### *Eagle*

Pretraining consisted of teaching LB to fly from the starting perch (A) to a visible food reward (4–7 g of steak, rabbit or chicken) located on one of the two choice perches (B) and then back to the starting perch (see Fig. 2). After LB became accustomed to receiving his daily food allowance (150–200 g) in this way training on the discrimination task began.

Initially, a high-contrast (0.6–0.8) coarse grating was used as the positive stimulus, and the food reward was placed visibly near the grating. Later, finer gratings were introduced and the food was hidden in a food cup fastened to the back of each choice perch. The trial began when a white blind obscuring the two screens was raised. When LB was about to fly the displays were switched off to ensure that he could not change his decision on the basis of changes in spatial frequency with distance (P31 is a fast fade phosphor, it decays to 1% in 250  $\mu$ sec). Some considerable time was spent during training to find the appropriate contrast range to test each spatial frequency. Testing did not begin until LB scored at least 95% of the trials correctly, for ten consecutive training periods.

When eagles are food deprived below their free-feeding body weight they exhibit a condition known as "yarak" (Hamerstrom, 1970). In this condition birds are unpredictable, dangerous and difficult to handle. Consequently it was decided not to deprive LB to any great extent. However, it takes two weeks of total food deprivation before Wedge-tails lose weight (Gerry Olsen, personal communication). So it was possible to keep the eagle deprived enough to perform for a food reward though free-feeding body weight was maintained. Motivation to perform was gauged firstly from the eagle's reaction to the experimenter and the experimental situation. It became apparent that LB performed best when he was nearly satiated in that he spent more time attending to the stimulus displays before making a decision. Also motivation to perform was assessed from his scores on a series of pre-test trials.



Fig. 1. The Australian Wedge-tail Eagle, *Aquila audax*.

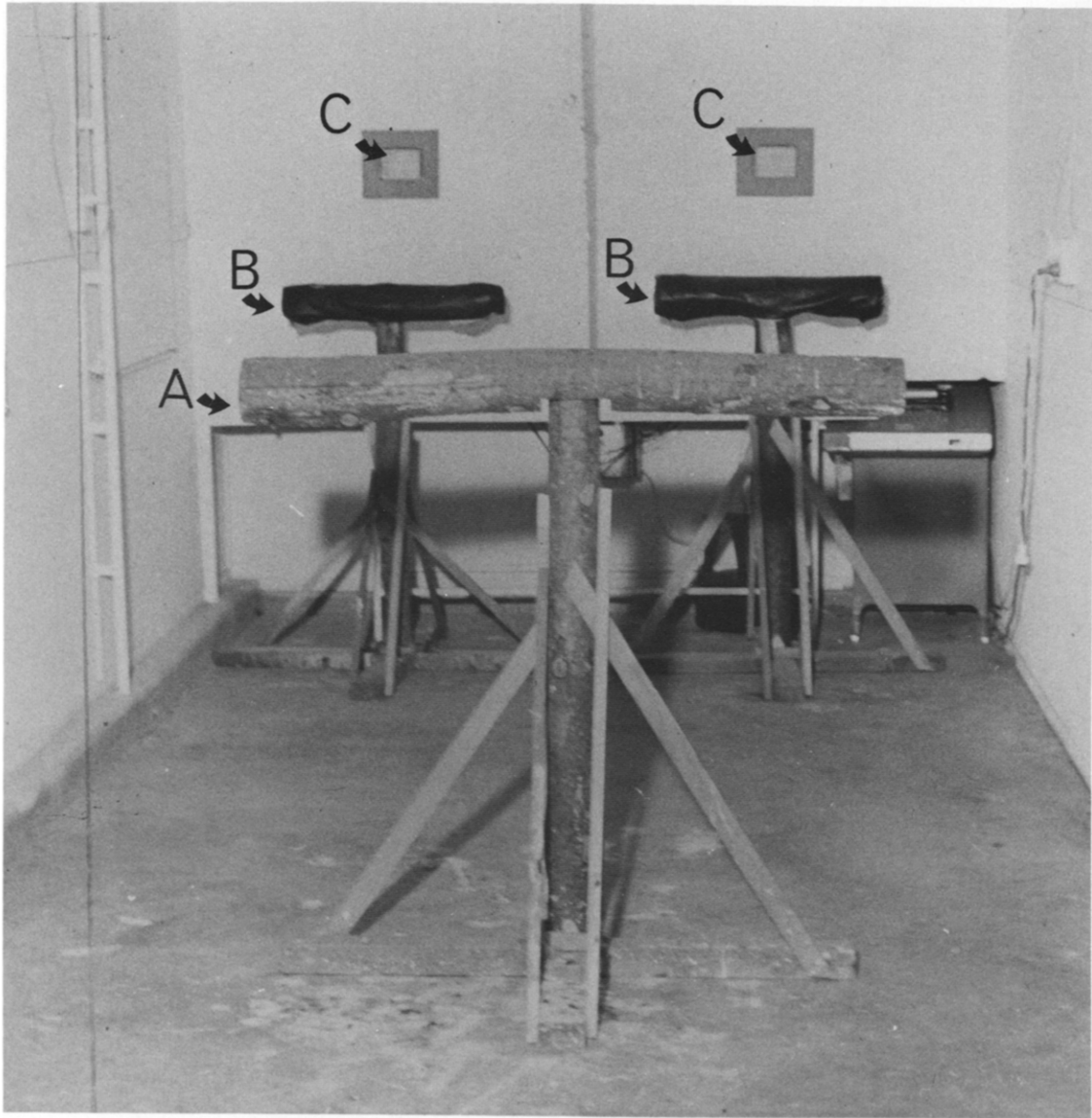


Fig. 2. The experimental arrangement used to test the subjects; when the human was tested the perch was replaced with a chair. (A) starting perch; (B) choice perches; (C) display screens.

As well as the programmed stimulus presentations, non-randomised trials were included in the test sessions. During training LB learnt the correction procedure adopted to avoid the development of side preferences, so during testing every incorrect trial was followed by an easy grating presented on the correct side for the last trial. The eagle was also monitored for position preferences by the introduction of two blank screens. Twice a left preference was apparent. When this occurred testing was suspended and training sessions, using coarse gratings, reintroduced until it was lost. One one occasion when all the discriminations became difficult, the eagle's discriminatory behaviour appeared to break down, i.e. he no longer fixated the display windows and flew as soon as the blind was raised. To overcome this problem, easy discriminations were again reintroduced and thereafter only one in every four stimulus responses used a test stimulus, the other three used easy gratings. Non-randomized trials were not included in the results.

One hundred training and testing sessions (between 35 and 50 trials) were required to generate the contrast sensitivity function at this luminance.

#### Human

To facilitate comparison between the subjects, attempts were made to equate the procedure adopted to test the human to that used to test the eagle. AC was instructed to give a response for every simultaneous stimulus presentation and was always informed of the correctness of her choice. A training session of 2 hr was required to familiarise her with the appearance of gratings and a total of twelve sessions (approximately 600 trials) were needed to complete testing.

#### Determination of the contrast sensitivity functions at $2 \text{ cd/m}^2$

CSFs for the eagle and human subjects were determined at an average luminance of  $2 \text{ cd/m}^2$  to see if there were any qualitative changes in the features of the CSFs when tested at the lower luminance. Contrast sensitivities of six different spatial frequencies, i.e. 3.5, 5.0, 7.5, 10, 15 and  $30 \text{ c/deg}$  were estimated as above. The lower luminance was achieved by placing a Kodak Wratten neutral density filter (No. 96) in front of each display screen. The surround illumination was lowered to match that of the screens and the background illumination was kept constant, at about  $2 \text{ cd/m}^2$ .

#### Eagle

LB was tested late in the afternoon when the outdoor illumination was low. He was adapted to the laboratory illumination for 10 min prior to testing. It was hoped that in the late afternoon his eyes would not be strongly light-adapted and that dark-adaptation would be rapid (Barlow *et al.*, 1957). Throughout this experiment only 1 in 4 stimulus responses used a test stimulus. Positioning and ordering of the easy

gratings were controlled by the experimenter and these trials were not included in the results. LB was tested for side preferences but none was apparent. Thirty-two sessions were required to complete testing.

#### Human

AC was tested in the morning and adapted for 20 min before testing. Five sessions were required to complete testing.

## RESULTS

Before flying, the eagle looked at each display screen in the same characteristic fashion for both luminances. With easy discriminations he fixated the stimuli binocularly but with difficult discriminations he turned his head to the left or right and fixated monocularly. The eagle is bifoveate and apparently this behaviour, also observed in the kestrel (Fox *et al.*, 1976), allowed the stimulus to be imaged on the less developed temporal (binocular) foveae or on a finer grained nasal (monocular) fovea (Reymond, 1979). The suggestion that the eagle used foveal vision indicates that the bird was operating in its photic range and that the measured contrast sensitivities are those of cone receptive fields, as no rods have been reported in the foveae of diurnal raptors.

In Fig. 3 the log of contrast sensitivity (or, equivalently, minus the log of the contrast threshold) is plotted against the log of spatial frequency for the human and eagle subjects, at average luminances of  $20 \text{ cd/m}^2$ . Table 1 lists the average contrast sensitivities of the eagle and human for all spatial frequencies tested at

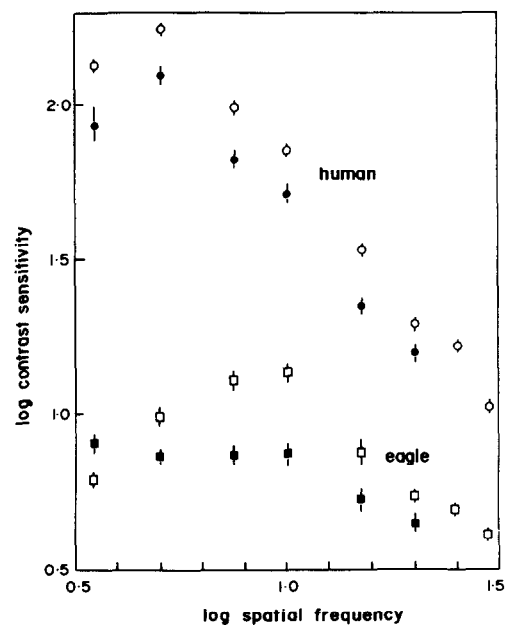


Fig. 3. Contrast sensitivity functions of the eagle (squares) and human (circles) at  $20 \text{ cd/m}^2$  (open) and  $2 \text{ cm/m}^2$  (filled). Error bars represent  $\pm$  the standard error.

Table 1. Average contrast sensitivities of the eagle and human subjects for all spatial frequencies tested at average luminance of 20 cd/m<sup>2</sup> and 2 cd/m<sup>2</sup>

$$\text{Error} = \frac{1}{\text{A.C.T.} - \text{S.E.}} - \text{A.C.S.}$$

A.C.T. = average contrast threshold

S.E. = standard error

A.C.S. = average contrast sensitivity

		Luminance 20 cd/m <sup>2</sup>		Luminance 2 cd/m <sup>2</sup>		Spatial frequency (c/deg)					
		3.5	5.0	7.5	10.0	15.0	20.0	25.0	30.0		
Eagle (LB)	6.17 ± 0.284	9.80 ± 0.713	12.82 ± 1.266	13.65 ± 1.029	7.50 ± 0.888	5.53 ± 0.319	4.95 ± 0.012	4.10 ± 0.093			
Human (AC)	134.00 ± 4.218	172.41 ± 9.736	96.15 ± 5.163	70.42 ± 1.675	33.33 ± 0.855	19.41 ± 1.201	16.50 ± 0.386	10.52 ± 0.320			
Eagle (LB)	7.21 ± 0.664	7.25 ± 0.326	7.37 ± 0.695	7.37 ± 0.695	5.21 ± 0.315	4.41 ± 0.375					
Human (AC)	8.516	9.210	6.388	7.54	1.660	0.083					

Contrast Sensitivity

both luminances. At the higher luminance the forms of the CSFs are similar for both species: both show a peak in sensitivity with attenuation of higher and lower frequencies. The eagle's sensitivity is greatest at 10 c/deg and the human's at 5 c/deg. The human is more sensitive at all spatial frequencies and up to one hundred times more sensitive at low spatial frequencies. Moreover, for any contrast less than about 0.2, *the human is always able to resolve higher and lower spatial frequencies than the eagle.*

At the lower luminance of 2 cd/m<sup>2</sup> the shape of the CSF for the human is similar to that at 20 cd/m<sup>2</sup>. Sensitivity is greatest at 5 c/deg and then declines for lower and higher spatial frequencies. The effect of the lower luminance is simply to uniformly decrease sensitivity across the range of spatial frequencies tested.

The form of the CSF of the eagle at 2 cd/m<sup>2</sup> is qualitatively different: there is no longer a distinct peak in sensitivity. The contrast threshold is constant from 3–10 c/deg and sensitivity is decreased for higher spatial frequencies. (We do not necessarily ascribe significance to the apparently higher sensitivity measured at 3.5 c/deg at this lower luminance, since a subsequent experiment indicates that a learning effect is involved: the lower luminance experiment was performed at a later date, when LB was more experienced in this procedure. Such an effect would have increased variability in the measurements rather than change the forms of the CSFs, since spatial frequencies were presented in random sequence for each luminance tested).

#### DISCUSSION

The shapes of the CSFs obtained for the eagle and human at a luminance of 20 cd/m<sup>2</sup> are qualitatively similar, though the sensitivity of the human is greater. The relatively poor performance of the eagle seems contrary to its reputation for super-human vision, and surprising given that Shlaer (1972) estimated that an eye the size of the Wedge-tail's should have a resolving power between 180–216 c/deg. It is necessary, therefore to consider whether this result is spurious, due perhaps to the experimental procedure, or whether it is an accurate reflection of the eagle's visual ability at low luminance.

First, it must be remembered that with all psychophysical studies the quality of the performance depends on how well the problem has been communicated to the subject. Communication with animals is always indirect (in this instance it relied on the technique of operant conditioning) while communication with humans is direct and can be as explicit as required. This difference in communication must place a limitation on the reliability of inter-species comparisons, even when the same psychophysical procedure is used. There is no guarantee, for instance, that the stratagems adopted by LB to resolve or detect gratings were the same as those used by AC. LB's

response time was always shorter than AC's, suggesting that his procedure was simpler, and therefore perhaps less effective in perceiving low contrast. Second, the average wavelength of light used in these experiments was 520 nm. For this wavelength human visual acuity is maximised (Shlaer *et al.*, 1942). It has been suggested that eagles possess intra-ocular filters that absorb these blue-green wavelengths (Wall, 1942). So this choice of wavelength may have rendered the gratings less effective as visual stimuli for the eagle, again resulting in lower contrast sensitivities.

Finally, this particular eagle's poor performance may have been idiosyncratic and peculiar to its particular environmental and developmental history. The eyrie where the eagle was hatched was about 50 m above the ground in an exposed tree on the side of a high mountain. The developing eagle would have had a view extending for kilometers. Comparatively the ground level aviary where it was later housed represents a restricted visual environment. There is an effect of early visual deprivation on visual acuity but the effects of the aviary environment on the eagle's acuity were probably marginal, since even rigorously controlled early visual deprivation produces only slight reductions of acuity (e.g. Muir and Mitchell, 1973.) Also domestication, or the caging of birds, is known to lead to visual defects such as cataracts and myopia (Wood, 1971) which, in turn, impair acuity. But when examined with an ophthalmoscope no abnormalities were apparent in the eagle's eyes.

It seems likely that the most important factor which limited the eagle's performance was the luminance level.

As vertebrate visual systems are unable to process all the information imaged on the retina by the dioptrics of the eye, an animal must adopt a stratagem for processing the most "relevant" information contained in any image. "Relevant" information is presumably determined by the animal's needs in relation to its environment. And, as a general principle, the stratagem adopted must be a compromise between different aspects of visual performance. For example, consider the argument of Snyder *et al.* (1977). High spatial frequency resolution requires a high density of photoreceptors and thus small individual photoreceptors. Since light comprises photons whose individual arrival is random, when small numbers of photons are received (at low luminance levels or with brief exposures) the statistical fluctuations in their number limits the ability of photoreceptors to reliably determine intensity. Thus, at low luminance, the ability of small photoreceptors to distinguish small intensity differences (low contrast) will be more limited by photon noise than will be that of large photoreceptors. This noise can be reduced, and contrast sensitivity enhanced, if individual photoreceptors are "pooled" to form larger photoreceptor fields. However, this increases grain size and decreases resolution. Thus unless there is an unlimited ability to voluntarily pool small photoreceptors, high spatial resolution can only

be achieved at the expense of contrast sensitivity and vice versa.

A similar compromise between resolution and sensitivity may obtain in the optics of an eye. A larger eye gives a longer focal length, which results in a larger retinal image. Thus any given photoreceptor spacing subtends a smaller visual angle, and produces a higher resolution. However for a given pupil size, retinal illumination is lowered resulting in lower contrast sensitivity, particularly at low luminance. If a larger pupil is used to increase retinal illumination, aberration may occur to counter any gain in contrast sensitivity (or resolution).

The wedge-tail eagle hunts in broad daylight and from a great height, so high resolution is required. The visual system of this eagle is well adapted to achieve this resolution. Its foveal retinal grain, and presumably subsequent receptive field size, is finer than man's. The diameter of the foveal photo-receptors is about  $2\ \mu\text{m}$  while man's is about  $3\ \mu\text{m}$  (Snyder and Miller, 1978). The axial length of the eagle's eye is larger than that of man's (35 mm as compared to 24 mm) allowing for a longer effective focal length (Reymond, 1979). Under the conditions in which it hunts, i.e. high intensity direct illumination, where shadows give good contrast, the pupil can close down to 5 mm or less, at which diameter the resolution performance of the visual system approaches its diffraction limit (Shlaer, 1972).

Considering this, it is not surprising that the adaptation of the eagle's eye for high resolution has incurred the poor low luminance contrast sensitivity reported here. In both experiments the eagle's pupil was dilated to about 10 mm. Unfortunately, nothing is known of the characteristics of the lens in this eagle, hence we do not know whether the low contrast sensitivity of the eagle at these luminances resulted from the need to sacrifice optical quality, for retinal illumination, or whether performance was limited by the fineness of the eagle's foveal receptive field grain.

It appears the visual system of the eagle has evolved to achieve high resolution, but has sacrificed contrast sensitivity at low luminance. On the other hand primates generally, and presumably the evolving hominids, inhabited forests where illumination is indirect, contrast is low and objects are obscured at large distance. In comparison to that of the eagle, man's compromise favours sensitivity rather than resolution.

The similarity in the shapes of the CSFs at  $20\ \text{cd}\cdot\text{m}^{-2}$  suggests a similar functional organisation of the visual systems. Attenuation of low spatial frequencies is attributed, in human vision, to the lateral inhibitory interactions of the centre-surround organisation of retinal receptive fields. Maximum contrast sensitivity occurs at the lowest frequency at which either the brighter, or dimmer, parts of the grating fall across the centre of a receptive field but do not extend to the antagonistic surround. For frequencies lower than this sensitivity is decreased because the

surround is stimulated and exerts inhibitory effects. (For higher frequencies sensitivity is decreased because of summation in the field.) The low spatial frequency attenuation shown by the eagle at  $20\ \text{cd}\cdot\text{m}^{-2}$  probably also results from lateral inhibition reflecting a similar receptive field organisation. If so, that the eagle showed a contrast sensitivity peak at  $10\ \text{c}/\text{deg}$  and the human at  $5\ \text{c}/\text{deg}$  indicates that the predominant foveal receptive field size of the eagle is smaller than that of the human, at this luminance.

The effects of lateral inhibition disappear at sufficiently low luminance (Barlow *et al.*, 1957) when the sensitivity to noise of this receptive field organization becomes significant (see the discussion in Marcelja, 1979). Thus the absence of attenuation of low spatial frequencies at the luminance of  $2\ \text{cd}\cdot\text{m}^{-2}$  further supports the thesis that the eagle possesses a mechanism for lateral inhibition.

At this lower luminance, humans still attenuate low spatial frequencies. Hence optimal visual performance in the eagle is probably more dependent on luminance than is that of the human. In fact, the observation that avian acuity, in general, decreases rapidly as luminance falls has been noted by a number of researchers (Donner, 1951; Fox *et al.*, 1976; Hodos *et al.*, 1976). To assess optimal visual performance the CSF of the eagle needs to be determined in ecologically characteristic high luminance levels.

*Acknowledgements*—We thank our experimental subjects, Audrey Chapman and Little Bird for their patience; and Bill Bellingham, Michael Cook, Stjepan Marcelja and Richard Mark for their comments on the experimental procedure and manuscript.

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