fore) failed to affect the subsequent morphine-induced rotation. Pretreatment with noradrenalin (50 μg in the MRF), however, attenuated the subsequent morphine-induced rotation. Pretreatment with carbachol (10 μg in the MRF) potentiated and with atropine (10 μg in the MRF) attenuated the morphine-induced rotation. These results suggest that the mechanism underlying morphine-induced rotation is different from that following application of dopaminergic agonist or antagonist in unilaterally nigroneostriatal lesioned animals, and involves a complex interaction between cholinergic and noradrenergic mechanisms (*5*).

The rotation behavior following morphine microinjection in the MRF appears to have two components: (i) a heightened arousal, with the rat being hyper-responsive and making vigorous "runs" to escape from previously neutral auditory and visual stimuli, and (ii) an impaired ability to move the ipsilateral hind limb, so that the net effect is a pivot, or rotation. [We observed that the ipsilateral fore and hind limbs were often hypotonic and showed a loss of placing reflex (*6*).]

Circus movement and head turning have been reported following MRF lesions; these were contralateral to the side of lesion (*7*). Electrical stimulation in the ventromedial MRF elicited an ipsilateral turning of the head and body (*8*); however, contralateral turning has also been reported. This rotatory behavior, however, appears to be of a different kind, more similar to type 2, than the bursts of rapid rotations with one leg as a pivotal point seen in our studies. Thus, it seems unlikely that the effect of morphine here is similar to that of electrical stimulation.

Hyper-responsivity to previously neutral, mild auditory and visual stimuli was previously reported (*9*) following morphine microinjections in the midbrain periaqueductal gray matter (PAG). The hyper-responsivity took the form of explosive bursts of repetitive, rapid leaps, sometimes as high as 60 cm. In contrast, morphine microinjection into the MRF resulted in animals oriented in a horizontal (rather than vertical) plane, and the rotating animals never exhibited any leaps. Nevertheless, the hyper-responsivity to mild stimuli seen following morphine microinjection in both the PAG and the MRF suggests a common neural pathway or mechanism of action for this stimulatory action of morphine. Since the MRF is known to be an "activating" system, it is not surprising that the morphine action here is to lower the threshold for sensory-motor systems. In the PAG-injected animals, the hyper-responsivity to previously neutral auditory and visual stimuli was accompanied by a profound analgesia to painful stimuli (pinches, pinpricks, and hot and cold stimuli). However, in the MRF-injected animals, no analgesic action of morphine could be detected. Thus, the two effects of morphine, hyper-responsivity to mild stimuli and analgesia to painful stimuli, appear to be dissociable effects of morphine, and site specific.

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Falcon Visual Acuity

Abstract. *Grating acuity, the ability to resolve high-contrast square-wave gratings, was measured in a falcon and in humans under comparable conditions. This behavioral test of falcon acuity supports the common belief that Falconiformes have superb vision—the falcon's threshold was 160 cycles per degree, while the human thresholds were 60 cycles per degree. Falcon acuity, however, was much more dependent on luminance, declining sharply with decreases in luminance.*

The belief that falcons and hawks possess extraordinary visual acuity is deeply ingrained in language and thought. It arises in part from reports of awesome feats of visual prowess based on casual observation under national conditions. More substantial evidence is provided by the anatomy of eye and retina, where a number of features facilitating acuity are present. The most notable of these is a cone density substantially greater than in the human retina (*1–3*), which implies visual acuity superior to that of humans, yet provides no basis for quantitative prediction. Recently R. Shlaer (*4*) succeeded in measuring retinal image quality in a live bird, the African serpent eagle, and conservatively deduced that its visual resolution would be 2 to 2.4 times greater than that of humans. Shlaer noted that a more definitive answer requires behavioral testing.

We report here a behavioral test of falcon visual acuity under conditions that permit direct comparison with human acuity; to the best of our knowledge this is the first such test. Our subject was an American kestrel (*Falco sparverius*), a small falcon (approximately 125 g) possessing the essential attributes of larger Falconiformes. The bird was born in the wild and donated to us at about 3 weeks of age. It was reared in our laboratory under conditions afforded a pet. These conditions made the bird, which we named Wulst, quite tame and facilitated testing.

The method of testing was the classic two-choice discrimination task, where correct and incorrect stimulus pairs are presented simultaneously and the animal selects one member of the pair by moving toward it. Our version of the method required the bird to fly 1.8 m from a starting platform to one of two perches located under 1° square stimulus windows. Selection of the window containing the correct stimulus resulted in a food reward; selection of the incorrect stimulus yielded nothing. The correct stimuli were vertically oriented square-wave gratings transilluminated for 100 percent contrast, while the incorrect stimuli were blank fields of the same mean luminance as the grating (*5*).

We trained Wulst to make discriminations by gradually introducing more complex components of the task after simpler ones had been mastered. The first step was to train him to fly from the starting platform to the perches and then return. Choice discrimination was introduced by presenting a coarse grating

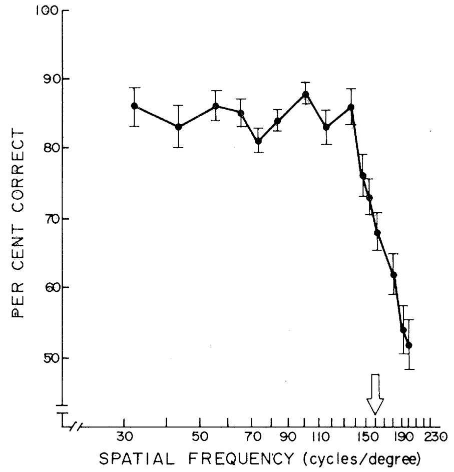

Fig. 1. Percentage of correct choices as a function of spatial frequency. Average luminance was 350 cd/m^2. Confidence intervals correspond to 1 standard error. The arrow indicates the threshold, interpolated from the point halfway between maximum performance and chance performance.

in one window and a blank field in the other. When he selected the grating he received a small piece of beef heart immediately upon landing on the perch. At the end of training Wulst went through the experiment spontaneously, his flight from platform to perch and his return serving to start and stop each trial (*6*).

Testing took place in two sessions per day, each session consisting of about 20 to 25 trials. Spatial frequency was constant within a session and gradually increased over sessions. When discriminations became difficult a staircase procedure was used, with a higher-frequency, more difficult grating followed by a lower-frequency, less difficult grating; repeated shifts up and down the frequency scale produced the discrimination function. During testing, control sessions were frequently introduced in which both stimuli were blank; these sessions produced chance performance, indicating that discrimination was controlled by the grating. Further evidence for grating control was provided by having a group of sessions encompassing a representative range of frequencies and introducing randomly over trials luminance differences between stimulus pairs. Grating position rather than luminance governed performance.

The way Wulst examined each stimulus from the starting platform was instructive, especially when discrimination became more difficult. He examined each stimulus window by rotating his head 45° to the left and right. Selection of a window was signaled by stopping head rotation and aligning head and body perpendicular to the window. Once this alignment occurred no change in selection was ever observed. Others have reported falcons and hawks scrutinizing a stimulus with the head held obliquely and this may be a general characteristic (*3, 7*). It would allow the stimulus to be viewed by the central fovea of each eye, which anatomically is likely to be capable of much higher resolving power than the temporal fovea. It is probable, then, that discrimination performance is based on the resolving power of the central fovea.

Figure 1 shows discrimination performance in terms of the percentage of correct choices as a function of increasing spatial frequency; it is analogous to a frequency-of-seeing curve used in human psychophysics. The large number of data points and the fact that the number of trials contributing to each point varies from 80 to 260 comes about as a by-product of the staircase procedure. Observations from different sessions could be pooled because performance at a particular frequency did not differ significantly across sessions. We believe that using small changes in spatial frequency, together with the practice of not spending more than one session on a very difficult discrimination, acted to maximize performance. Performance at lower spatial frequencies would have reached 100 percent if we had eliminated trials at the beginning and end of the sessions, where seemingly careless errors tended to occur. Threshold frequency was arbitrarily defined by interpolating to the abscissa from the point halfway between chance and maximum performance. This threshold value, 160 cycle/deg, can be compared to the human grating acuity, a visual angle of approximately 30 seconds (60 cycle/deg), obtained by S. Shlaer (*8, 9*). Thus, falcon performance was 2.6 times better than human performance, a ratio reasonably close to the 2.4 predicted by R. Shlaer from the retinal image quality of his eagle. Since Shlaer's eagle is a much larger bird than Wulst, the agreement between optics and behavior may be fortuitous. Yet there is no functional reason why there should be wide variation in the acuity of falcons and hawks when consideration is given to the size of the prey they prefer, their own body size, and the heights at which they fly. The kestrel scans the ground from treetop height and will attack small insects. At 18 m, an object 2 mm long would be twice the threshold. Larger Falconiformes fly at higher altitudes and attack larger prey. At 1500 m, an object 16 cm long would be twice the threshold. Attacks on smaller prey would probably not justify the energy expended.

After testing Wulst at 350 cd/m^2 we measured discrimination at two lower luminance values, 35 and 3.5 cd/m^2, to see how acuity varied with luminance. Human acuity changes moderately over this range of luminance values. In contrast, Wulst's performance was strongly influenced by luminance. Figure 2 compares human and falcon acuity as a function of luminance. One set of the data on humans is replotted from thresholds obtained by S. Shlaer (*8*). The second set is the averaged threshold performance of two observers who viewed gratings in our apparatus (*10*). The difference in slope between lines fitted to the human and falcon discrimination functions is approximately 2.4. The steeper decline in falcon acuity with luminance reduction is consistent with the idea that the cones in the closely packed retinas of falcons and hawks have small diameters and are inefficient absorbers of radiant energy for wavelengths in the visible range. Quantitative formulation of that hypothesis, however, requires measurement of cone diameter, length, alignment, and density, data which are not available (*11*).

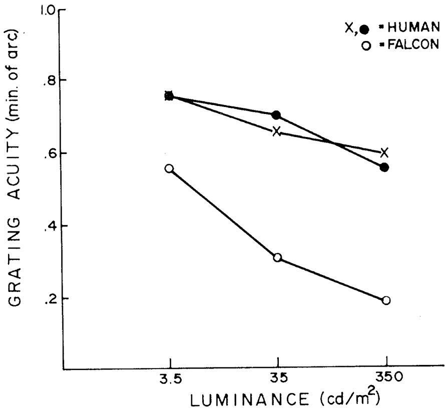

Fig. 2. Human and falcon acuity as functions of luminance. Human acuity measures are (x) data from S. Shlaer (*8*) and (●) averages obtained from two observers with our apparatus. Falcon acuity (○) data are threshold values interpolated from the discrimination performance functions obtained at each of the luminance levels.

What our data do provide is behavioral evidence that falcon acuity is superior to human acuity when tested under comparable conditions. This confirms the belief that falcons and hawks possess keen vision, yet their superiority is not so great as some of the more hyperbolic prior speculations have suggested.

It is difficult to specify all the factors, optical and neural, that may contribute to hyperacuity. Considering the differences between the visual system of the recently evolved mammals and that of the more established vertebrate classes, explanatory concepts derived from studies of mammalian vision should be applied cautiously. Even so, in view of the high grating acuity we have found, it would be surprising if other measures, such as the spatial contrast transfer function, did not also show that falcon vision transcends that of humans.

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5. Gratings of different manufacture, (i) engine-ruled gratings (Ronchi rulings) and (ii) film copies of the engine-ruled gratings, were used. The film gratings were made in order to provide a wider assortment of spatial frequencies. High-contrast film (Kodalith ortho film, type 3) was directly exposed to magnified Ronchi rulings projected by an enlarger, a method that yielded precise control of the number of lines imposed on the film. All gratings, both film and engine-ruled, were examined under a microscope to ensure that contour edges were sharp and that the opaque contours were completely filled. Contrast ($I_{\max} - I_{\min}/I_{\max} + I_{\min}$) measured by a microphotometer was 99+ percent for all gratings. The transparent contours of the engine-ruled gratings passed 7 to 9 percent more light than those of the film gratings. This difference in transmission was corrected by filtering the engine-ruled gratings. As a test of the equivalence of film gratings and engine-ruled gratings, identical spatial frequencies of both kinds were used in different testing sessions; no differences in discrimination performance were found between sessions for any of several frequencies compared in this way. The grating and the blank stimulus were transilluminated by collimated light from two tungsten-halogen lamps. Luminance was controlled by placing appropriate combinations of neutral density filters in the optical paths. Electronic shutters were used to completely block illumination. The gratings and the blank fields were mounted as slides and attached to rotary wheels locked with detents that permitted rapid and repeatable insertion of any desired stimulus combination. The luminance levels of the displays, as seen from the starting platform, were measured before and after each session by a Pritchard photomultiplier photometer and a Salford subjective match photometer.
6. Training followed general methods of operant conditioning with food as reinforcement. The daily food ration was obtained in the testing sessions, one in the morning and one in the late afternoon. The fresh beef heart used as a reward is not a complete diet for falcons. To supplement the diet, a mouse was fed to the bird after 5 days of testing and testing was resumed 2 days later. The bird was weighed daily before and after testing; the average weight was 100 g before and 110 g after a session. Weight proved to be a sensitive index of motivation as well as a sensitive indicator of general health.

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9. It should be noted that any estimate of bird acuity given in cycles per degree of visual angle must be conservative, since the smaller eye of the bird will focus a smaller retinal image. Data should be related to retinal images expressed in cycles per millimeter of retina, but this requires information about optical characteristics of the eye, such as focal length. This information is not available for the kestrel, and in general there is a paucity of data about the optical characteristics of the eyes of Falconiformes. We thank T. Yates for an informative discussion about the problems involved in measuring the optical properties of animal eyes.
10. The thresholds for the two observers were obtained by the method of limits; monocular viewing was used for comparison with the thresholds obtained by S. Shlaer. Binocular viewing would likely have produced a significant reduction in threshold, on the basis of prior work on binocular summation; see, for example, the review by R. Blake and R. Fox, *Percept. Psychophys.* **14**, 161 (1973).
11. We thank J. Enoch for informative discussions concerning the data required to determine the energy absorption properties of cones.
12. We thank R. Bush for his assistance in data collection, and the Tennessee Wildlife Resources Agency and the U.S. Fish and Wildlife Service for the excellent cooperation extended to us. The work was authorized by state scientific collectors permit No. 204 and federal scientific collectors permit PRT 7-01-C-Z-NV. Support was provided by NIH grant EY00931.

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Flavor Aversion Studies

We applaud Bitterman's general position on comparative research (*1*), but consider his criticisms of our flavor-aversion research and theory to be unwarranted. We point to a literature so voluminous that space permits citation of only a small portion.

Bitterman says, in effect, that the evidence for associative predispositions is based on experiments where testing conditions were confounded with modality, that is, visual stimuli antedated the criterion response (eating) and gustatory stimuli followed it. It has been demonstrated in many laboratories in experiments with drinkometers where both an audiovisual signal (AV) and saccharin flavor (F) are contingent upon the criterion response (licking) that rats punished with shock become conditioned to AV not to F. Conversely, rats punished with illness become conditioned to F not to AV. Furthermore, illness can be delayed for hours without disrupting conditioning to F. By increasing saccharin concentration *and its odor*, shock-avoidance responses have been conditioned to F, but here again, when the shock is delayed 210 seconds, conditioning to AV is disrupted whereas conditioning to F is reported to be enhanced. While differing in their theoretical formulations, the authors agree that AV and F are probably handled differently by central (memory) processes and interact differently with pain and illness (*2*).

Bitterman also speculates that regurgitation or some more subtle reverse transport system returns flavor to the mouth to stimulate the taste and smell receptors at the time of illness; therefore, he says, it has not been demonstrated that flavor aversion is acquired when there is a long interval between stimulus and illness. Rats acquire aversions to harmless mouthwashes followed by toxicosis even without ingestion (*3*). Rats do not acquire aversions to untasted substances tubed directly into their stomachs before illness (*4*). Rats acquire aversions to ephemeral substances that are completely altered by digestive process long before illness is induced (*5*). Aversive effects are obtained with chronic diet deficiencies and positive effects with recuperation from dietary deficiencies where regurgitation is unlikely (*6*).

According to Bitterman this new, ethologically oriented comparative psychology leads only rarely to the comparison of different animals. The conditioning of flavor aversions by illness has been studied in man, monkey, rat, mouse, cat, wolf, coyote, ferret, cougar, blue jay, quail, hawk, turtle, fish, slug, and other species (*7*).

In addition, he argues that there is a lack of interest in functional analysis, in evolutionary history, and in relating behavior to anatomical structure. This puzzling criticism follows his reference to a paper in which Garcia, McGowan, and Green (*8*) point out, as is also done elsewhere (*9*), that natural selection favors the predisposition to associate flavor with illness and that both taste receptors and internal monitors send their fibers to the same anatomical site in the brainstem. In any case, relevant neuroanatomical research has emanated from a number of laboratories (*10*).

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